FISHERIES SOCIETY OF THE BRITISH ISLES
CLIMATE CHANGE AND THE FISHES OF BRITAIN AND IRELAND: BRIEFING PAPER 4[1, 2]

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1 EXECUTIVE SUMMARY

- The aim of this fourth FSBI briefing paper is to provide an objective account of the current understanding of climate change and its likely consequences for the fishes of Britain, Ireland and the surrounding seas.

- There is a wide scientific consensus that human activities have modified the composition of the atmosphere, and that this will result in significant future climatic change (*e.g.* increased air temperature in Britain of 2-3.5°C over the next 80 years). Environmental change is a characteristic feature of life on earth, and has played a major role in the evolution and global distribution of biodiversity. However, the predicted rate of climatic change, especially in temperature, is such that it 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 anthropogenic stress (*e.g.* overfished seas).

- Humans rely heavily on aquatic systems for many goods and services, and climate change is likely to have widespread implications for Britain and Ireland. Governments are obliged to maintain, protect and conserve biodiversity, but to do this they require reliable information on the effects of climate change. Ecologists therefore face a fundamental challenge to provide data and advice regarding the response of natural systems to environmental conditions that have no parallel in recent time.

- Climatic variation has a major influence on the ecology and distribution of fishes, for instance most fishes are thermal conformers, and body temperatures reflect that of the surrounding water. Temperature is an important controlling factor for biotic and abiotic processes at all levels of biological organisation: cellular, individual, population, community and ecosystem, and influences many aspects of the physiology and ecology of fishes. Aquatic taxa by definition require water - any modifications in the quality and quantity of water following climate change will have consequences for fish and their habitats. Due to their close association with temperature, and aquatic health, we can consider fish as excellent indicators of the expected changes from global climate change. However, responses to climate change are likely to be complex and difficult to predict.

- In order to understand why climate change has important consequences for the fishes of Britain and Ireland, we describe how the climate of Britain and Ireland has changed in recent decades and describe future climate predictions using the UKCIP02 United Kingdom Climate Impacts Programme report. UKCIP02 predicts significant changes in the climate of Britain and Ireland over the next 80 years, which will undoubtedly lead to significant abiotic and biotic changes in aquatic ecosystems and shifts in freshwater, marine and brackish water fish communities:

  - Average annual air temperatures will rise by 2-3.5°C, with warming most apparent in the southeast of Britain
  - Precipitation patterns will change, *e.g.*, annual precipitation may decrease by between 0-15% by the 2080s
  - By the 2050s, typical spring temperatures will occur 1-3 weeks earlier than at present
  - Cloud cover will decrease, especially in the south of Britain, and summer sunshine and solar radiation will increase correspondingly
  - The seas around Britain and Ireland will warm, with some areas (southern North Sea and English Channel) increasing by 2-4°C
  - Summers will become drier and hotter, with an increased frequency of droughts – by 2080, half of all summers will be similar to the hot and very dry summer of 1995
  - Winters will become shorter, warmer and wetter, extreme winter precipitation will become more frequent, and very cold winters will become increasingly rare
  - Sea levels will rise between 9-69 cm by the 2080s, but due to changes in relative sea level this will lead to significant local differences in sea level change

- We review the current understanding of the role of climatic variation as a factor in the ecology of aquatic systems and fishes, and present a series of case studies detailing the likely response of several marine, inshore and freshwater fishes to climate change.

- Changes in water temperature and the quality and quantity of water inputs will modify the suitability of aquatic habitats for fishes. Increased temperatures are likely to result in increased overall production due to improved growth rates in many fishes. However, the ability to adapt to the predicted changes in climate will vary between species, 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 cod and herring from some areas around Britain and Ireland, and the establishment of some new, warm-adapted species. However, changes in food web dynamics and physiological adaptation, for example due to climate change, may obscure or alter predicted responses.

- Evidently freshwater fishes found in Britain and Ireland currently exist within their thermal limits, but increased temperatures are likely to favour cool (*e.g.* perch, *Perca fluviatilis*) and warm-adapted fishes (*e.g.* roach *Rutilus rutilus* and other cyprinids) rather than cold-adapted species (*e.g.* salmonids). The distribution and reproductive success of these species may currently be constrained by temperature, and in future their geographical range will potentially increase. Increased water temperatures and longer growing seasons will increase the potential for growth and production of cold-adapted freshwater species in northern and upland populations. However, southern or lowland populations may face unsuitable temperatures and loss of habitat following climatic change and their potential ranges will shrink. Conservationally important populations (*e.g.* Arctic charr and *Coregonus* spp.) may be lost.

- Routine monitoring has played a vital role in revealing the controlling role of climatic variation on aquatic ecosystems and fish population/community dynamics. Although modelling and simulation studies are important, only by collecting relevant data through routine monitoring can ecologists record and understand the effects of climatic change and better parameterise models with non-linear dynamics. Funding for such basic science needs to be available if the UK and Irish Governments are going to fulfil their national and international obligations to conserve and protect aquatic biodiversity.

- Our predictions of the consequences of climate change on the ecology, exploitation and management of fishes are based on information available in the published literature. This information is based on field and laboratory studies, the results of which often contrast. A reliance on unrepresentative laboratory studies to estimate environmental optima or tolerances of wild fish is a valid criticism that can be levelled at many studies (including this one). In future, it is likely that such data will be increasingly determined from wild fish through modern techniques such as electronic tags that record or transmit environmental or physiological data (*e.g.* temperature) from free-ranging individuals. Our predictions include a level of uncertainty that is difficult to quantify and make it difficult to ascribe certainty to our conclusions, but reflect a best attempt to provide guidance on the likely of the consequences of climate change for fish, their ecology, management and exploitation.

- Climate change will lead to changes in human behaviour. Recreational patterns will shift, and demand for water will increase. Those involved in fisheries and aquaculture will face challenges as some long-exploited and economically important species move or are lost from increasingly warm waters. However, potential changes also present opportunities to exploit new species. Climate change will increase the probability that invasive species and new parasites and pathogens become established in Britain and Ireland. Those groups involved in the import and movement of fish (*e.g.* aquaculturists, aquarists, recreational fishery managers), and those regulating and managing these activities need to appreciate the risks.

- Initiatives have been launched by UK and Irish Governments to limit the use of fossil fuels and to restrict emissions of the gases associated with climate change. 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, we can expect major changes in fish communities over the next 50 years.

2 INTRODUCTION

2.1 *AIMS & INTENDED AUDIENCE*

The aim of this briefing paper, fourth in an ongoing series (FSBI, 2001, 2002, 2004), is to provide an objective account of the current understanding of climate change and its effects on the fishes of Britain and Ireland and their surrounding seas. This paper will examine the potential future climate of Britain and Ireland following the most recent and detailed predictions (Hulme *et al.*, 2002). Using representative species, we examine the likely effects of changing climate regimes on the fishes of Britain and Ireland at an individual, population, community and ecosystem level. We will also consider some ecological and socio-economic consequences of these predicted changes. This document is aimed at an anticipated wide audience, and we hope that it will be of interest to all who are interested in the consequences of climate change on the fishes of Britain and Ireland.

2.2 *CLIMATE CHANGE*

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; Vitousek, 1994). Although the causes and likely impacts are subject to debate (Sharp, 2003; Veizer, 2005), the scientific consensus is that climate change is real (Houghton *et al.*, 2001; Karl & Trenberth, 2003; King, 2004; Walther *et al.*, 2005), and will impact both the UK (Hulme *et al.*, 2002) and the Republic of Ireland (Sweeney *et al.*, 2003). Average global temperatures have increased by ~0.6°C over the past century (See Fig.1; 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; Tonn, 1990).

A large proportion of the recent increase in global temperature has been associated with increased inputs of several atmospheric gases *e.g.* carbon dioxide (CO_2), methane (CH_4) and water vapour (H_2O) following human activities *e.g.* industrial/agricultural activities, deforestation and the burning of fossil fuels (Houghton *et al.*, 2001; Hulme *et al.*, 2002; Raper *et al.*, 1997). These so-called greenhouse gases are naturally present in the atmosphere, and are important for life on earth: without them temperatures on earth would be *ca.* 30°C colder than they are today (Raper *et al.*, 1997; Ruddiman, 2001). The greenhouse gases allow short-wave radiation from the sun to pass through the atmosphere and heat the earth, and also to retain some of the radiation that is subsequently emitted from the warmed surface of the earth (Kiehl & Trenberth, 1997). However, anthropogenic emissions have increased the concentrations of these gases to levels greater than at any time in the preceding 650 000 years (Siegenthaler *et al.*, 2005; Spahni *et al.*, 2005). This has led to an increased retention of energy (an enhanced greenhouse effect), warming of the planet, and an increase in global temperature (Karl & Trenberth, 2003; Raper *et al.*, 1997; Ruddiman, 2001). Emissions of greenhouse gases continue to rise, and although it is unclear exactly how global climate will change in the future, considerable international effort is being directed into predicting future climatic conditions (Houghton *et al.*, 2001; Hulme *et al.*, 2002), the consequences for humans (Karl & Trenberth, 2003; McCarthy *et al.*, 2001), and the ecosystems and species on which they rely (Kappelle *et al.*, 1999; Levitus *et al.*, 2000; McCarthy *et al.*, 2001; Sweeney *et al.*, 2003). Without climate mitigation policies, Wigley & Raper (2001) suggest the 90% probability interval for 1990 to 2100 warming is 1.7° to 4.9°C globally. There are marked regional differences in the predicted levels of warming, but northern latitudes are predicted to be the most affected (Houghton *et al.*, 2001).

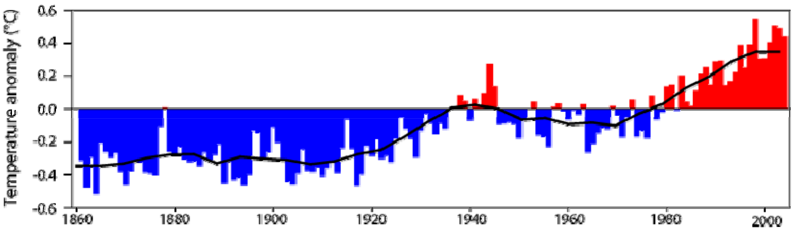

Figure 1: Variation in global-average (land and sea) surface temperatures (1860-2004) fitted with a 30-year running-mean smoother. Individual bars show annual mean values as deviations (anomalies) from the 1961-1990 mean. Data includes components of the OA series: -1869 HadCRUT2OA & 1870-2004 HadCRUT2vOA. Data Source: UK Met office (www.metoffice.com/research/hadleycentre/CR_data/Annual/land+sst_web.txt)

The effects of climate change on the phenology, abundance and distribution of terrestrial taxa has been well documented (Parmesan, 2006; Parmesan & Yohe, 2003; Root *et al.*, 2003; Walther *et al.*, 2002). In a meta-analysis, Parmesan & Yohe (2003) calculated that spring events (*e.g.* bird-nesting, and frog-breeding) had advanced, on average by 2.3 days per decade and that diverse taxa had undergone significant range shifts towards the poles, averaging 6.1 km per decade. Myneni *et al.* (1997) associated recent increases in the length of the terrestrial plant growing season at higher latitudes with increased air temperatures.

Thomas *et al.* (2004) predicted that between 15 and 37% of the *ca.* 1 100 terrestrial animal and plant species they analysed across a vast range of global terrestrial ecosystems will be committed to extinction by 2050 under a mid-range climate-warming scenario, although phenotypic and genetic adaptation to climate at the population level were not considered in their analysis (Harte *et al.*, 2004). Soto (2002) detailed several fundamental differences between terrestrial and aquatic ecosystems, differences that extend beyond the physical and chemical properties of air and water (*e.g.* specific heat capacity), for instance the increased dispersal ability of many aquatic species relative to those from terrestrial habitats. She suggested that these differences were very likely to lead to contrasting responses by terrestrial and aquatic taxa to climate change (Soto, 2002).

2.3 FISH AND CLIMATE

Fish are thermal conformers (Jobling, 1997) and in most species body temperature is effectively that of the surrounding water, *i.e.* they are ectotherms. Some fishes however are endothermic *e.g.* scombroids (Block & Finnerty, 1994), and some elasmobranchs (Lowe & Goldman, 2001), with body temperatures elevated above ambient. Temperature has long been recognised as a major influence on the ecology and the physiology of fish (Brett, 1956; Ferguson, 1958; Fry, 1947, 1971; Magnuson *et al.*, 1979). Enzymatic rates are strongly temperature-dependent in fish; hence temperature is a key determinant of an individual's physiological and biochemical (vital) rates (Clarke, 1993; Coutant, 1987b; Fry, 1971; Regier *et al.*, 1990), and influences behaviour (Kramer *et al.*, 1997; Sims *et al.*, 2006). Temperature variation influences almost all aspects of a fishes' ecology: *e.g.* hatching and development time of eggs and larvae (Fonds, 1979; Guma'a, 1978; Pauly & Pullin, 1988; Rombough, 1997), activity (Koch & Wieser, 1983; Nyman, 1972), oxygen demand (Clarke & Johnston, 1999), swimming performance (DiMichele & Powers, 1982), distribution (Coutant, 1987b; Kramer *et al.*, 1997; Sundby, 2000), 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 (Brett, 1956; Fry, 1947, 1971; Griffiths & Harrod, 2007; Pauly, 1980; Petersen & Kitchell, 2001).

Understandably, temperature is considered as a fundamental component of the niche of fishes (Magnuson *et al.*, 1979; Magnuson & Destasio, 1997; Tracey & Christian, 1986). Some fishes are capable of detecting and responding to extremely small temperature variations, with estimates as low as 0.001 (Brown, 2003) and 0.03°C (Bull, 1957; Murray, 1971), and fish tend to select thermal habitats that maximise 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 (*e.g.* Mills & Mann, 1985) and community levels (*e.g.* Persson, 1986; Southward *et al.*, 1988). Predicting the effects of temperature change on fish is difficult due to the huge variation in possible responses that individuals can exhibit, and the potentially confounding influence of many other physiological or environmental factors (Burton, 1979; Fry, 1971).

The thermal niche of a fish species can be defined by lethal, controlling, and directive criteria (Fry, 1947, 1971). For example, extreme temperatures may be lethal if certain limits are exceeded (Jobling, 1981), but temperature also directs behaviour (Reynolds, 1977) and controls individual physiology (Regier *et al.*, 1990). The lethal criterion has relatively wide limits (*e.g.* fish can survive within an upper and lower temperature limit). Conversely, the optimal range, within which performance factors will be greatest (*e.g.* growth rate, swimming speed, foraging efficiency), is constricted (Magnuson *et al.*, 1979). If fish encounter habitats with unsuitable thermal regimes, they respond behaviourally and attempt to move into areas closer to their preferred temperature, as they lack the physiological ability to regulate their body temperature (Jobling, 1997; Sims *et al.*, 2006). A species preferred temperature is not fixed, but can vary according to individual genotype (Petersen & Steffensen, 2003), life stage (Beitinger & Fitzpatrick, 1979; Brett, 1956; Ferguson, 1958; Hokanson, 1977; Magnuson & Destasio, 1997) or thermal history (Beitinger *et al.*, 2000; Fry, 1947). Preferred temperatures change with patterns of consumption (Despatie *et al.*, 2001; Mac, 1985), and fish fed on lower rations typically select lower temperatures. Preferred temperatures are generally considered to reflect situations where different physiological processes, *e.g.* growth and gonadal development, are optimised (Brett & Groves, 1979; Kelsch & Neill, 1990).

Fishes have distinct thermal niches where they are able to optimise physiological, ecological, and reproductive performance (Coutant, 1987b). Magnuson *et al.* (1979) called for fish biologists to recognise that the thermal niche may be as important as more commonly regarded descriptors of resource use such as food. Lehtonen (1996) suggested that fishes demonstrate adaptations to local conditions, *e.g.* to climate (but see Larsson *et al.*, 2005), and that extreme temperatures at the northern and southern boundaries of their distribution would increase mortality rates and recruitment fluctuations relative to those at optimal temperatures (Fromentin *et al.*, 1998; Planque & Frédou, 1999; Shuter & Post, 1990).

Species that are restricted to narrow ranges of temperatures are referred to as stenothermic, and are typically found in environments with predictable thermal regimes. Conversely, fishes with wider temperature tolerances are referred to as eurythermic. Within a species, individual populations or life-stages may differ in their tolerance to temperature fluctuations (Hubbs, 1964). Different fish species (Brandt *et al.*, 1980; Magnuson *et al.*, 1979), and even life-stages within a species, (Coutant, 1985; Otto *et al.*, 1976), may partition habitats according to temperature (Attrill & Power, 2004; Magnuson *et al.*, 1979). The literature suggests that partioning of habitats according to temperature may be more typical of freshwater than marine or estuarine habitats, presumably as freshwaters may be more heterogeneous over shorter temporal and spatial scales (Attrill & Power, 2004; but see Hernández *et al.*, 2002; Pulgar *et al.*, 2005; Thiel *et al.*, 2003). Using field and laboratory data, some authors have categorised temperate freshwater fishes into different thermal guilds according to their preferred temperatures: *e.g.* stenothermal, mesothermal and eurythermal (Hokanson, 1977); or coldwater, coolwater and warmwater (Magnuson *et al.*, 1979; Magnuson *et al.*, 1990).

Due to their close association with temperature and other aspects of climate (Lehodey *et al.*, 2006), and the level of human interest and scientific understanding, fish potentially represent excellent indicators of the expected changes from global climate change (Sharp, 2003; Wood & McDonald, 1997). However, although increased water temperature is likely to be the principal ecological impact, climate change will influence many environmental factors with the potential to affect fish: *e.g.* cloud cover, ultraviolet radiation, sea and lake levels, storm surges, hydrographic regimes in estuaries, precipitation, runoff, wind intensity and patterns, evaporation, river and stream discharge. Changes in temperature and other abiotic factors are likely to result in changes in interspecific interactions (*e.g.* predation, competition, 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.

Both historically (Hoffmann, 2005), and at present, human societies depend on aquatic systems for many essential goods and services (Costanza *et al.*, 1997; McCarthy *et al.*, 2001; Wilson & Carpenter, 1999). For instance, the biota of the oceans has immense global socio-economic value, estimated by Costanza *et al.* (1997) at *ca.* US$21 trillion y^{-1} globally, through food production, recreation, nutrient recycling and gas regulation. Impacts of climate change on aquatic systems, their function and their inhabitants (*e.g.* fishes) are therefore likely to have widespread implications for human societies.

The role of climatic fluctuations in long-term variation in fish population dynamics and changes in community structure has been long recognised (Lehodey *et al.*, 2006; Sharp, 2003). However, the scale of predicted climate change (McCarthy *et al.*, 2001) is such that it has no parallel in recent geological history (Crowley, 1983), and ecologists face a fundamental challenge in predicting how natural systems will respond to climatic change. However, ecologists have a considerable suite of tools at their disposal (Shuter & Meisner, 1992). Long-term monitoring studies provide a basic understanding of the ecology, distribution and natural variation in abundance of different taxa (Genner *et al.*, 2004; Perry *et al.*, 2005; Southward *et al.*, 2004), and essential baseline data that allow change to be quantified (Elliott, 1990; Visser & Both, 2005). Such studies, if conducted over suitably long periods, have often demonstrated a strong controlling influence of climatic cycles on many aspects of the ecology of organisms, which can help ecologists understand potential mechanisms, and hence better predict the effects of climate change (George *et al.*, 2004; Ottersen *et al.*, 2001; Stenseth *et al.*, 2002). Controlled empirical studies have detailed the environmental tolerances of different taxa in the laboratory (Alabaster & Lloyd, 1980), which provide essential data for use in models where scientists can simulate conditions under climate change and predict the ecological consequences for individuals, populations or communities (Fang *et al.*, 2004a, b, c; Lappalainen & Lehtonen, 1997; Magnuson *et al.*, 1990; Magnuson *et al.*, 1997). Ecologists can examine how aquatic organisms may respond to environmental change under situations that may be analogous to the predicted changes in climate, such as extreme climatic events, *e.g.* floods (Brown *et al.*, 2001) or droughts (Elliott *et al.*, 1997). Waters that receive thermal effluents from power stations can be seen as large scale experiments of many of the predicted consequences of climate change: *e.g.* prolonged autumns, warm winters and early springs (Luksiene *et al.*, 2000). Finally, scientists have begun to design and implement manipulative studies in the laboratory and field that mimic predicted climatic conditions and examine the effects on the ecology of different species and communities (Hogg & Williams, 1996; Pörtner & Knust, 2007), and the function of aquatic ecosystems (Moss *et al.*, 2003).

Throughout our examination of the literature there was a clear contrast in the intensity of relevant European or British/Irish research directed at detailing and understanding the role of climate in the ecology of marine fishes, and the relatively understudied freshwater fishes. Although this probably reflects their relative economic importance in Britain and Ireland, it has also influenced this briefing paper. For instance, the detailed long-term studies that have proved essential in describing the significant shifts in marine fish assemblages in the seas around Britain and Ireland (Genner *et al.*, 2004; Perry *et al.*, 2005; Southward *et al.*, 2004) are simply not available for freshwater species. For example, a detailed literature search revealed a single peer-reviewed citation that focussed on the consequences of global warming on freshwater fishes in Britain or Ireland (Weatherley *et al.*, 1991). In our examination of the likely consequences of climate change on freshwater fishes, out of necessity, we have combined laboratory studies with field or modelling studies conducted in areas that for climatic or biogeographical reasons may not be fully relevant to Britain and Ireland (*e.g.* North America and Scandinavia). We have supplemented this approach by including aquaculture studies, or those that have examined modified freshwater systems *e.g.* waters that have received thermal effluents from power stations.

Fishes play important functional and ecological roles in ecosystems, but they are not found in isolation. Scientists need to not only consider the effects of climate change on abiotic factors, but also how climate change affects biota at different levels of taxonomic organisation. Other key taxa found in aquatic ecosystems include viruses, bacteria, fungi, algae, bryophytes, macrophytes, invertebrates, amphibians, and other aquatic or semi-aquatic vertebrates such as birds or marine mammals, all with the potential to undergo complex responses to climate change (Edwards & Richardson, 2004; Frederiksen *et al.*, 2004; Hogg & Williams, 1996; Hogg *et al.*, 1995; Magnuson *et al.*, 1997; Mooij *et al.*, 2005; Moss *et al.*, 2003). As individual taxa will respond differently to climate change, there is clear scope for shifts in community level interactions following climate change (*e.g.* predator-prey relationships, competition and parasitism) to influence the ecology of fishes and other taxa (Harley *et al.*, 2006).

Climate change has the potential to affect fishes at several levels: *i.e.*, cellular, individual, life-stage, population, species, community and ecosystem. Changes in temperature will affect the chemistry of aquatic systems (Arnell, 1998; Harley *et al.*, 2006): chemical reactions are more rapid at high temperatures, oxygen is less soluble in warm water (Weiss, 1970) and the mobility of contaminants may increase following climate change (Moore *et al.*, 1997). Clearly, this leaves considerable scope for the fishes of Britain and Ireland to respond to the predicted changes in climate, and fish can be considered excellent sentinels of climate change.

2.4 STUDY AREA

This briefing paper examines the consequences of global climate change on the fishes of Great Britain (consisting of the England, Scotland and Wales), Ireland (Northern Ireland and the Republic of Ireland), and surrounding seas (Fig. 2). For the sake of simplicity, we refer to these islands as Britain and Ireland in this briefing paper. The islands are located off the Northwest coast of continental Europe, and extend through 13° of longitude and 11° of latitude (Hayward & Ryland, 1995). Britain and Ireland are delimited by the Atlantic Ocean to the west and are separated by the Irish Sea. Britain is separated from mainland Europe to the East by the North Sea, and to the south, by the English Channel (Fig. 2). Britain and Ireland have a temperate marine climate, which due to 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).

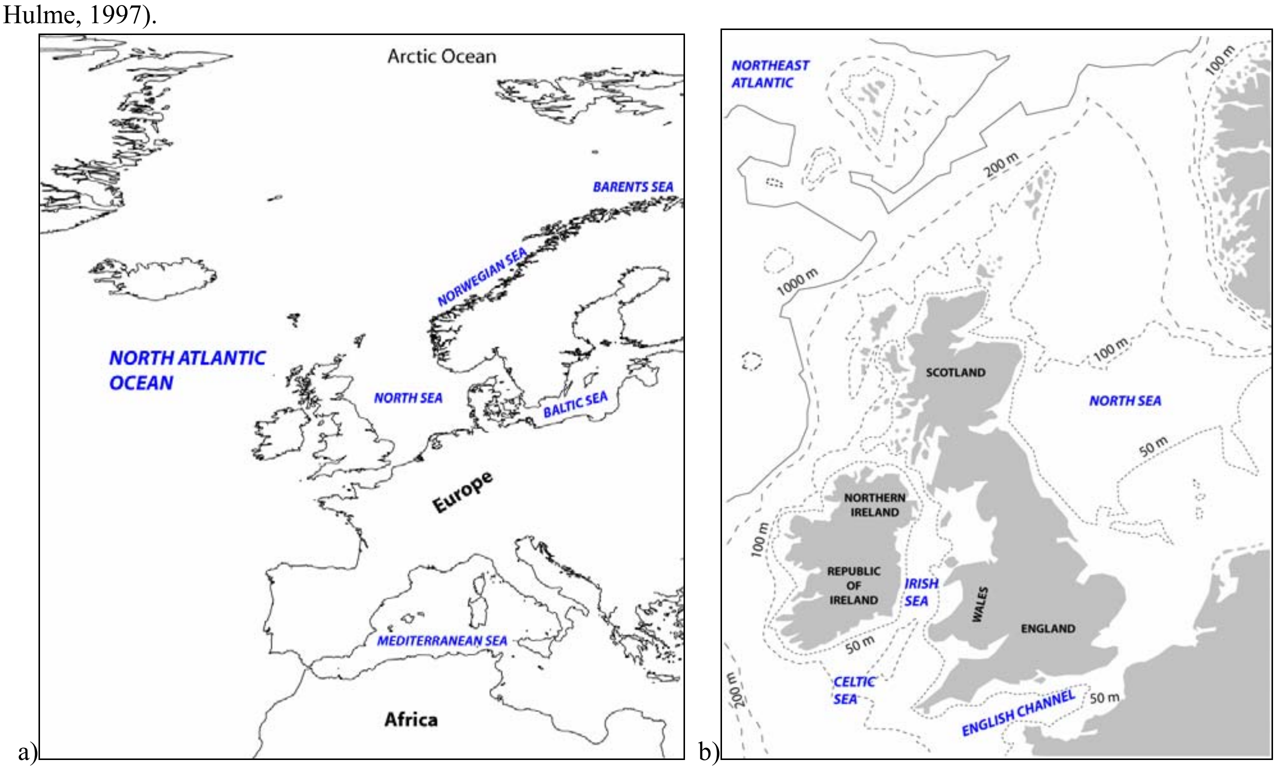

Figure 2: a) Location of Britain and Ireland and b) showing surrounding seas and simplified bathymetry (After Lee & Ramster, 1981).

The marine, freshwater and estuarine ecosystems of Britain and Ireland vary considerably with regard to physical form (*e.g.* size, depth), chemistry (*e.g.* trophic status) and biology (*e.g.* fish community structure) (Hughes *et al.*, 2004; Hughes *et al.*, 2001; Ladle & Westlake, 1995; Macan, 1984; Reynolds, 1998). The seas surrounding Britain and Ireland are diverse in terms of bathymetry (Fig. 2b: Lee & Ramster, 1981): *e.g.* maximum depths are only *ca.* 50 m in the southern North Sea (Zijlstra, 1988), but 300 m to the southwest of England and more than 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). A recent series of reviews provide useful summaries of oceanographic, biological and environmental conditions in the Irish Sea (Hartnoll, 2000), North Sea (Ducrotoy *et al.*, 2000) and English Channel (Southward *et al.*, 2004; Tappin & Reid, 2000).

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; Macan, 1984; Reynolds, 1998). Terrestrial landscapes include some fragmented areas of natural, and semi-natural habitats, and many urbanised areas, but the greater part has been modified by human activities to form agricultural landscapes (Gardiner & Matthews, 2000; Mitchell, 1986). Many freshwater and brackish systems have undergone human modification and have been degraded from natural conditions including hydrological alterations: *e.g.* abstraction, channelisation, construction of weirs, modifying drainage regimes (Ladle & Westlake, 1995; Raven *et al*., 1994); and pollution due to agricultural or industrial use of land and water (Haygarth & Jarvis, 2002; Mason, 1991). Following a typical pattern shown globally (Wetzel, 1990), most lentic (stillwater) waters in Britain (Hughes *et al*., 2004) and Ireland (Smith *et al*., 1993) are relatively small (*e.g.* < 1 ha: Fig. 3), but most support fish communities. There are significant numbers of medium sized and larger lakes with areas varying up to 383 km^2. Lotic (flowing) habitats in Britain (total length *ca.* >100 000 km) and Ireland (ca. 28 000 km: Reynolds, 1998) are extremely varied in form (Ladle & Westlake, 1995). Upland systems are typically oligotrophic, fast flowing and well oxygenated, whilst lowland systems are slower flowing, less well-oxygenated, and often nutrient enriched (Arnell, 1998), but most support fishes. Fish communities vary within and between river systems, following patterns of physical zonation (Cowx, 1988), geology (Berrie, 1992), land use (Ladle & Westlake, 1995) and geography (Maitland, 2004). Human activities have left their mark on many rivers in Britain and Ireland and their fish communities often reflect this (Maitland & Campbell, 1992). In both Britain and Ireland, numerous freshwater habitats have been constructed by humans, *e.g.* for navigation and transportation of goods (canals), to store water for human or agricultural usage (reservoirs), and for land drainage.

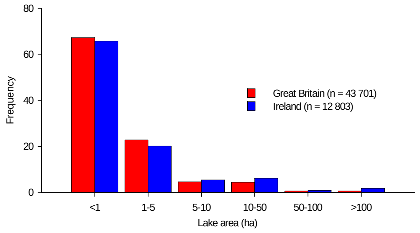

Figure 3: The frequency distribution of lake surface area in Britain and Ireland (Source: Britain - Hughes *et al.*, 2004; Ireland - Dr. Ian Donohue, Trinity College, Dublin Pers. Com.; Smith *et al.*, 1993).

The seas around Britain and Ireland have also been subject to human disturbances, including overfishing (Cushing, 2003; Hutchings, 2000; Russell, 1931) and significant inputs of anthropogenic pollutants, including nutrients (Allen *et al*., 1998; Stapleton *et al*., 2000) and other contaminants (Leah *et al*., 1997; Matthiessen & Law, 2002; McCartney *et al*., 1994; Stapleton *et al*., 2000). Although there is considerable evidence that fish and other marine biota were impacted by anthropogenic pollution (Stapleton *et al*., 2000), recent studies indicate that conditions in the seas around Britain and Ireland are improving following changes in industrial activity (Matthiessen & Law, 2002).

The freshwater/diadromous ichthyofauna of Britain and Ireland is depauparate relative to mainland Europe (Griffiths, 2006; Hughes *et al*., 2001; Maitland, 2004; Maitland & Campbell, 1992) due to the region's recent glacial history (Svendsen *et al*., 2004; Fig. 4; Wilson, 1986). Following glacial retreat, fish were able to colonise newly available habitats via three main colonisation routes: 1, euryhaline or diadromous fishes that invaded from marine habitats; 2, stenohaline fishes that colonised Great Britain from NW Europe via rivers in the landbridge that formed in the area that is now the North Sea (See Fig. 4); and 3, fishes that have been accidentally or intentionally introduced by humans (Maitland & Campbell, 1992; Went, 1946, 1950; Wheeler, 1969). Within Great Britain, there is a general trend of

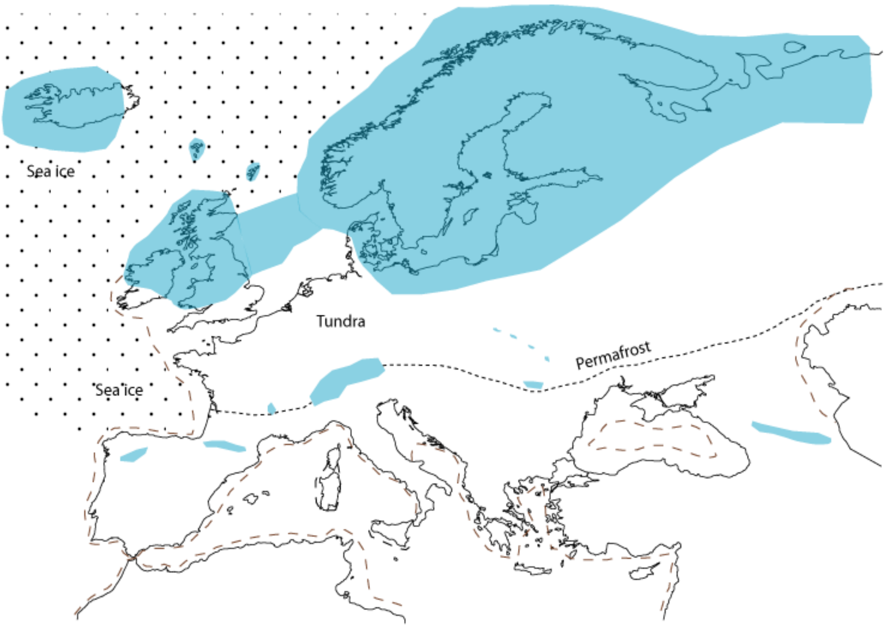

Figure 4: Europe at the end of the last ice age (ca. 18 000 yBP), showing estimated extent of ice cover (filled area), sea ice (stippled area), and permafrost (small broken line). A reduction in sea level (larger broken line) meant that during this period both Britain and Ireland were connected to mainland Europe (after Hewitt, 1999).

reduced diversity in fish community structure with increased distance north or west from the south-east of England (Hughes *et al.*, 2001; Wheeler, 1969), and the stenohaline freshwater fishes may originally have been indigenous only to the river catchments bordering the eastern English Channel and southern North Sea. Ireland, which never had a direct freshwater connection with mainland Europe, has a much reduced native freshwater fish fauna of only 14 native species, although human introductions have augmented this total to 25 species (Griffiths, 1997).

Describing the biogeography of marine fishes is more difficult than for freshwater species (Gill & Mooi, 2002). During relative recent geological time, fishes would have been excluded from many marine areas surrounding Britain and Ireland due to sea level change and glaciation (Hewitt, 1999; Fig. 4). Today, Britain and Ireland sit at a biogeographical boundary between the coldwater, Atlantic/Boreal and the warmwater, southern Lusitanean regions (Ekman, 1953; Fig.5; Hayden *et al.*, 1984). The warm North Atlantic Drift (NAD) runs northwards along the western coasts of Britain and Ireland, and enables some southerly species to extend their distribution northwards (Hayward & Ryland, 1995). Rogers (1991) notes that *ca.* 70% of the regional marine fish fauna comprises species which are widely distributed and do not originate exclusively from either a northern or southern fauna.

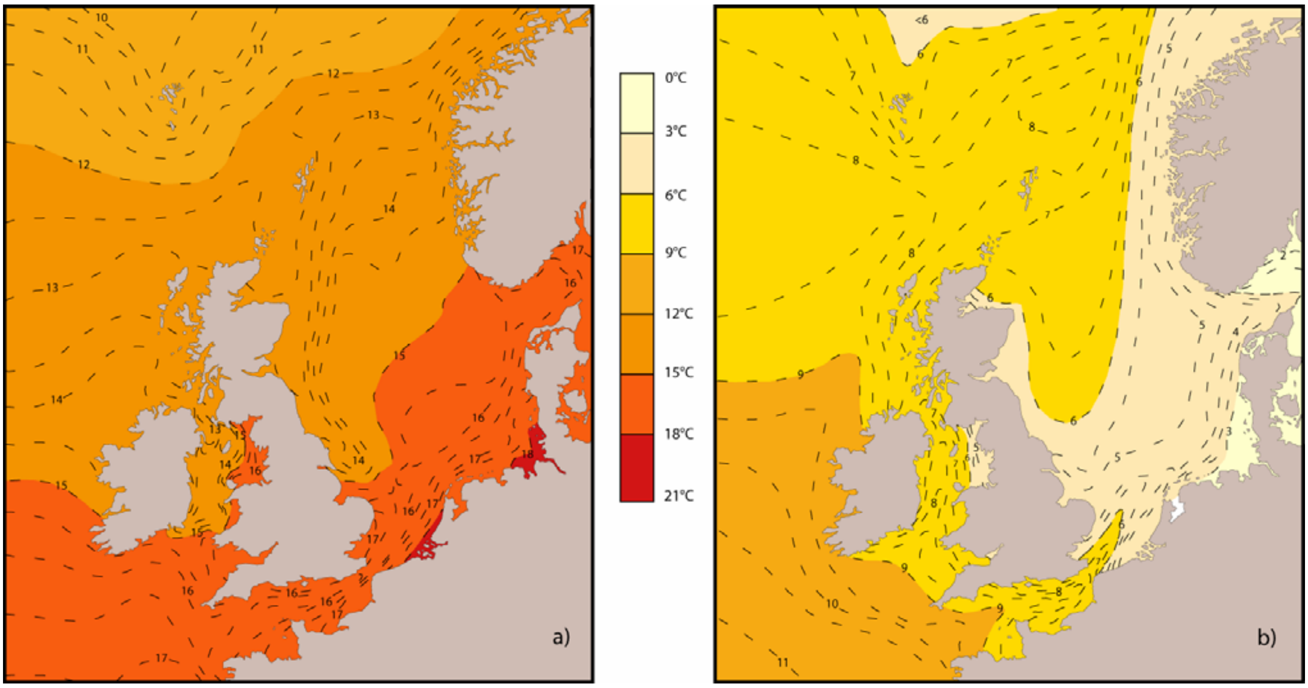

Figure 5: Mean summer sea surface temperature (SST) in °C (left), and (right) mean winter SST in the seas around Britain and Ireland (After Lee & Ramster, 1981). Note that over the last 70-100 years, annual mean SSTs in the seas around Britain and Ireland have increased by *ca.* 0.6°C (Hulme *et al.*, 2002).

The seas surrounding Britain and Ireland include some of the most productive, heavily-exploited and studied fisheries in the world (Anon, 2005b; Heath, 2005; Rogers & Ellis, 2000). These fisheries have often existed for centuries (Cushing, 2003; Hoffmann, 2005), and have been associated with marked declines in the abundance of large-bodied fishes, and shifts in community structure and ecosystem function (Anon, 2005b; Greenstreet *et al.*, 1999; Pinnegar *et al.*, 2002).

Due to their location at the western margin of Europe, Britain and Ireland represent the western extreme of the distribution of several freshwater and diadromous fishes. Many of these geographically disjunct stocks (Lesica & Allendorf, 1995) may have been isolated from mainland Europe since the end of the last ice age (Maitland & Campbell, 1992), with subsequent limitations on gene flow. Populations located on the periphery of their geographical range may encounter environmental conditions beyond their optimal range (Frank, 1991; Lawton, 1993; Philippart *et al.*, 1998; Planque *et al.*, 2003). This may explain why some environment-recruitment correlations tend to be stronger for such populations compared to those found closer to the centre of their distributions (Miller *et al.*, 1991; Myers, 1998; but see Philippart *et al.*, 1998). Although there is debate about the importance of peripheral populations to conservation and evolution (Garner *et al.*, 2004; Sagarin *et al.*, 2006), it is possible that reduced genetic diversity could limit their ability to adapt to environmental extremes following climatic change (Lesica & Allendorf, 1995).

Global climate change represents a further stress on fish that are already subject to a plethora of natural and anthropogenic stressors (Allan & Flecker, 1993; Jackson *et al.*, 2001): species introductions (Bøhn & Amundsen, 2004; 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 (Bøhn & Amundsen, 2004; Heath, 2005; Vander Zanden *et al.*, 1999), intensive aquaculture (Gross, 1998), overfishing (Hutchings, 2000; Rose, 2004), river obstacles such as dams and weirs (Baxter, 1977; Crisp, 1993), pollution, (Alabaster & Lloyd, 1980; Hesthagen *et al.*, 1999; Winfield, 1992), riparian deforestation (Jones *et al.*, 1999), 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 (Hulme *et al.*, 2002) will likely further compound the adverse effects from anthropogenic sources on fish populations (Schindler, 2001), regardless of how well they and their environments have been managed to date.

3 CLIMATE CHANGE

As the basis for predicted changes in the climate of Britain and Ireland, we use UKCIP02: Climate Change Scenarios for the United Kingdom (Hulme *et al.*, 2002: http://www.ukcip.org.uk). The climate change scenarios reported by Hulme *et al.* (2002) were generated by the HadCM3 climate model, which generates results at a regional scale of 50 km, which compares favourably with spatial resolution of 250-500 km of other global models. This results in an improved spatial resolution and more credible representations of changes in extreme weather than in previous models (Hulme *et al.*, 2002). It is important to note that although HadCM3 shows models for the Republic of Ireland, it does not incorporate any analysis involving observed data from this area, as they were not available (Hulme *et al.*, 2002). We strongly recommend that readers refer to the UKCIP02 report for further details.

3.1 WHAT IS CLIMATE CHANGE?

Climate can be defined as the meteorological conditions, including temperature, precipitation, solar radiation and wind that characteristically prevail in a particular region. Climate varies for reasons that are natural, such as volcanic eruptions, changes in solar output and natural changes in the orbital characteristics of the Earth, which are known to have profound impacts on global change (Hulme & Barrow, 1997). However, there is now convincing evidence for a growing human influence on global climate. Our industrial economy, through its reliance on carbon-based fuels, has and continues to alter the properties of the Earths atmosphere. In less than two hundred years, humans have managed to increase the atmospheric concentrations of greenhouse gases by *ca*. 50% relative to pre-industrial levels (see Introduction). Given the inertia in our energy systems and the long memory exhibited by the climate system, this human-induced climate change will become increasingly important relative to natural climate variability during the century to come (Hulme *et al.*, 2002).

3.2 HOW HAS CLIMATE CHANGED?

3.2.1 Temperature

Many aspects of the world’s climate are changing, but the increase in global average surface temperature is the dimension that is changing most clearly (see Fig.1). Of the 16 warmest years in Central England since 1659, no fewer than 8 have occurred since 1989, and central England and the Scottish Isles are warmer now than any time since records began (Hulme *et al.*, 2002). This warming over 20th Century Britain has resulted in a lengthening of the thermal growing season (*i.e.* the period when plants are able to grow) which is now longer than any time since records began in 1772. For example in 2000, the growing season extended for 328 days in Central England, the longest on record (Hulme *et al.*, 2002). This warming of the UK climate has been accompanied by an increase in the number of heat waves, particularly during May and July. Extremes of weather often have their greatest impact when they are sustained over a few days. The increased frequency of heat waves has been accompanied by a decrease in cold waves, particularly during March and November. In Central England, the 1990s were exceptionally warm by historical standards and about 0.5°C warmer than the 1961-1990 average (Hulme *et al.*, 2002).

3.2.2 Long-term trends in precipitation

Contrary to annual temperature, there are no long-term trends in the amount of annual precipitation received by the UK. There is however, considerable variation in the annual precipitation amount between individual years and decades (indicating large scale changes in circulation, such as the North Atlantic Oscillation (NAO: see below)) and there is a trend in seasonality of precipitation, with winters becoming wetter and summers drier (Hulme *et al.*, 2002). Importantly, the intensity of short-duration precipitation has changed, with the proportion of winter precipitation that falls over short periods of time increasing and the opposite occurring in summer. In spring and autumn, there are less consistent and generally smaller trends in precipitation intensity. Although there has been an increase in winter precipitation over high ground, this has not resulted in an increase in snow cover due to an increase in temperature and there has only been three winters since 1987/88 in Scotland with above-average snow cover (Hulme *et al.*, 2002).

3.2.3 Long-term trends in circulation patterns and gales

Many aspects of UK winter climate are strongly influenced by the NAO (Hulme *et al.*, 2002) as it is the dominant mode of atmospheric behaviour in the North Atlantic (Hurrell, 1995; Hurrell & Dickson, 2004) and is considered a proxy for a variety of climatic processes (Brander & Mohn, 2004; Hallett *et al.*, 2004; Ottersen *et al.*, 2001). 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). A high or positive NAO is characterised by an intense low in the Azores and a strong Icelandic high (Ottersen *et al.*, 1998). 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 (Hulme & Barrow, 1997; Hurrell, 1995). Understandably, variation in the NAO is linked to variation in many biological systems (See below).

3.2.4 Long-term trends in marine climate and sea level

Sea temperatures in the coastal waters surrounding Britain and Ireland are affected by interactions between the atmosphere and the ocean, and by freshwater run-off - particularly in the shallower water regions such as the North Sea and Irish Sea (Fig. 2). Records show an increase of 0.6°C in annually averaged temperature over the last 70 to 100 years, consistent with the observed warming over the land. A substantial proportion of this increase occurred over the last 20 years. The few long-term records for salinity in UK waters do not show any significant long-term trend (Hulme *et al.*, 2002).

Global average sea levels rose by 1.5 mm per year during the 20th Century, believed to be due mainly to the thermal expansion of the warming oceans and the melting of glaciers. However, the rise in relative sea level is partly due to land movements and, after adjustment for this natural phenomenon, the average rate of sea level rise around Britain and Ireland is 1 mm per year (Hulme *et al.*, 2002). Wave height is dependent on wind strengths over the ocean and hence related to the behaviour of the NAO. There is large temporal and spatial variability in wave height around Britain and Ireland, but in general terms the wave climate roughened between the 1960s and 1990s. However, there are no century time-scale changes in UK storm-surge statistics (Hulme *et al.*, 2002).

3.3 PREDICTED CLIMATE UNDER UKCIP02

Climate change is predicted based on four different scenarios of greenhouse gas emissions (Low, Medium-Low, Medium High and High Emissions) based on the path and nature of future world development (Hulme *et al.*, 2002). The authors of the UKCIP02 report assign no probabilities to any of the four scenarios. However, they assign relative levels of confidence (high, medium or low confidence) to a selective set of largely qualitative statements made about future change in UK climate. It is important to note that differences between emission scenarios have relatively little effect on the climate we will experience over the next 30-40 years since climate change over this period has already been determined by past and current emissions (Hulme *et al.*, 2002). In this briefing paper, we will, for simplicity's sake, show examples of how climate is predicted to change under two of the four UKCIP02 emissions scenarios: Low and Medium High (Hulme *et al.*, 2002).

3.3.1 Future changes in air temperature

In all seasons and for all scenarios, there is a north-west to south-east gradient in the magnitude of the average climate warming across Britain and Ireland (Fig. 6: H[*]) and temperature increase will be greater in the summer and autumn than in winter (L) and spring respectively (L). Temperature in the southeast of Britain will rise in excess of 4°C by the 2080s (H) (Hulme *et al.*, 2002).

3.3.2 Future changes in precipitation

Predictions indicate little change or a slight drying in average total annual precipitation, but there are likely to be significant seasonal shifts in precipitation patterns (Fig. 7). Winter precipitation is anticipated to increase by 5 to 30 % (H), depending on scenario and region. However, this increase in winter precipitation will be accompanied by reduced summer precipitation, with drier summers (up to 50%) (M), and therefore the contrast between the two seasons will increase (H). There is a southeast to northwest gradient in the magnitude of this average precipitation change. Snowfall will decline in all regions under all model scenarios, with the greatest proportional reduction increasing on a north to south gradient (H) (Hulme *et al.*, 2002).

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

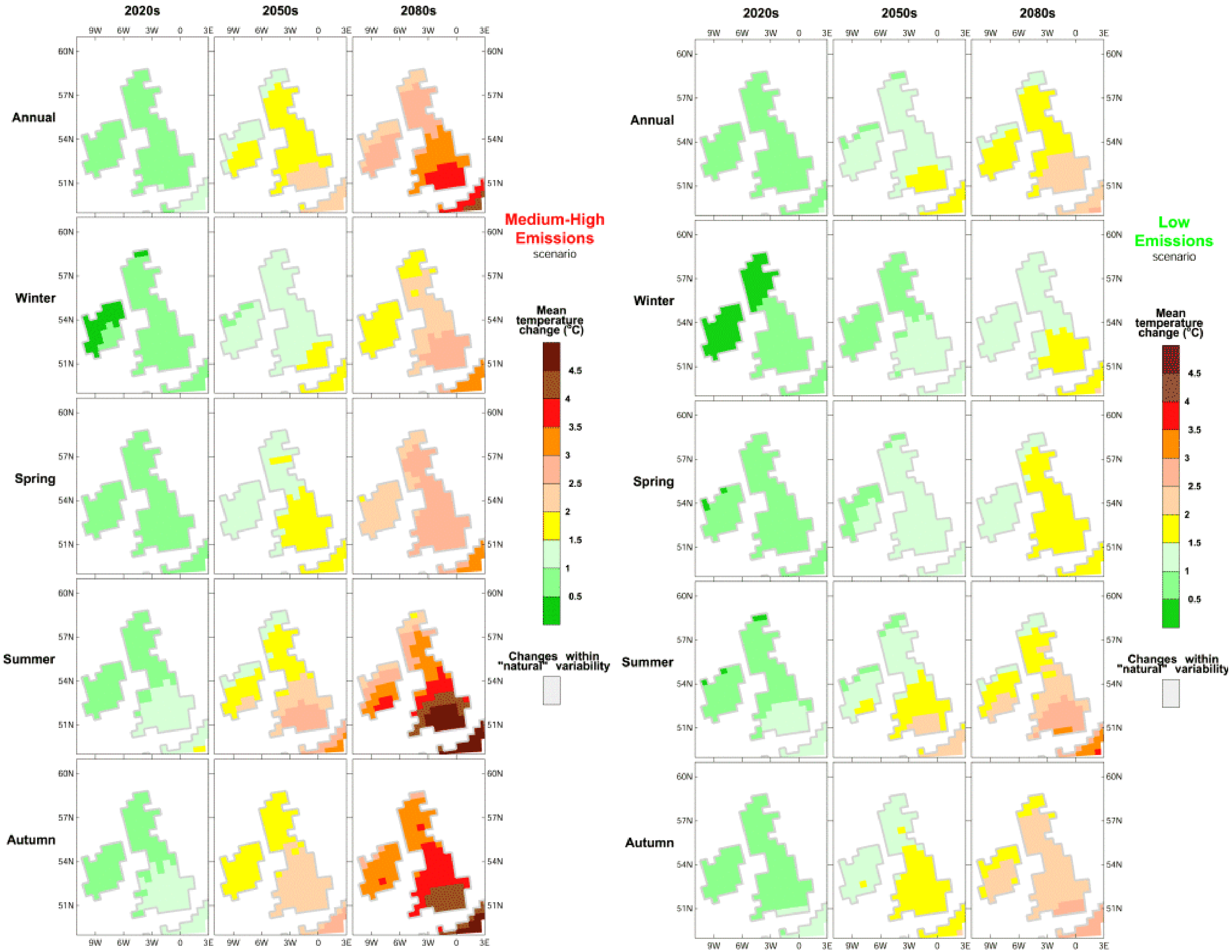

Figure 6: Predicted changes in seasonal and annual mean air temperature for Britain and Ireland under the two UKCIP emissions scenarios considered here: left, Medium-High, and right, Low emissions (Source: Hulme *et al.*, 2002). See Hulme *et al.* (*op cit.*) for full details and predicted changes under other scenarios.

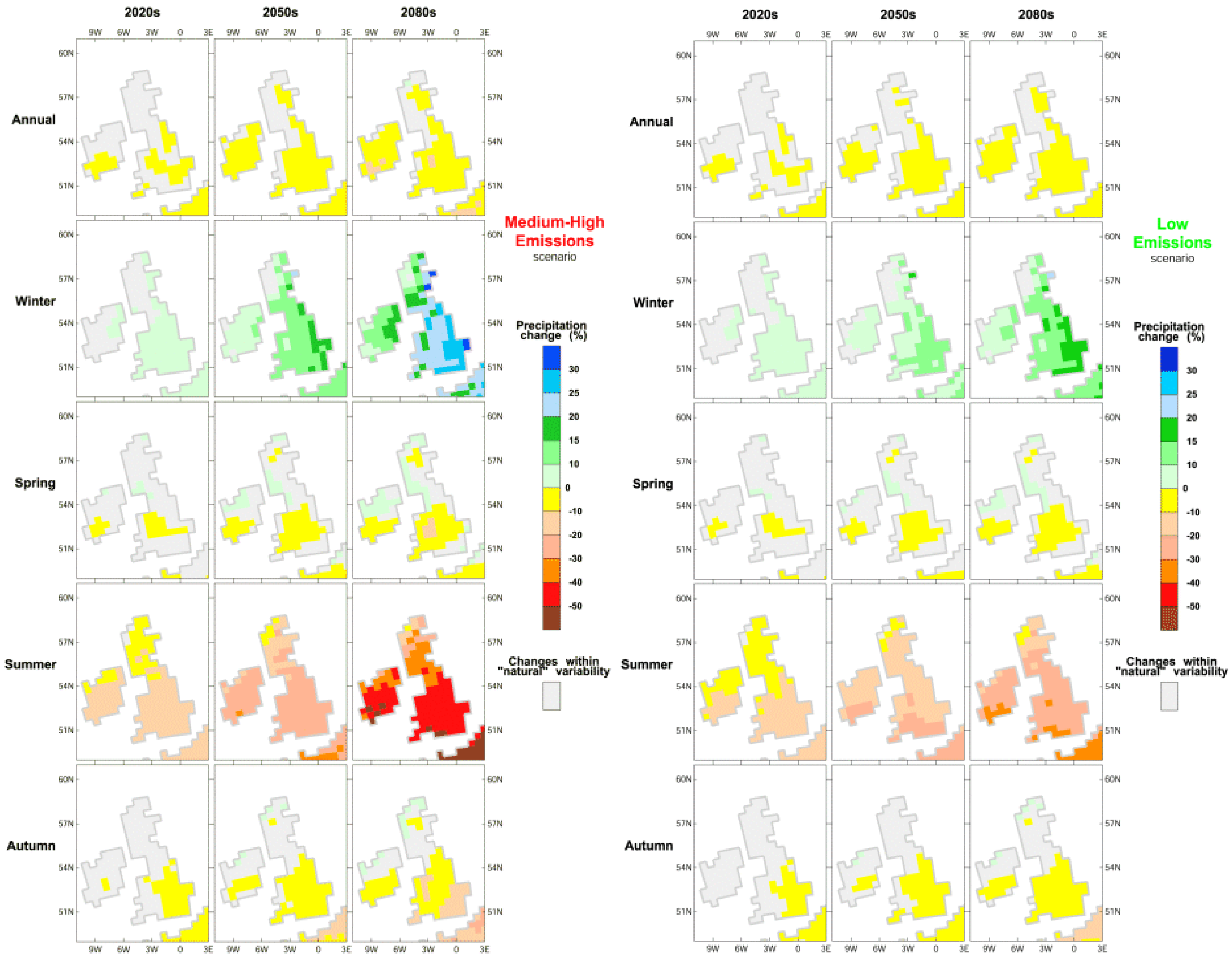

Figure 7: Predicted changes in seasonal and annual mean precipitation rates for Britain and Ireland under the two UKCIP emissions scenarios considered here: left, Medium-High, and right, Low emissions (Source: Hulme *et al.*, 2002). See Hulme *et al.* (*op cit.*) for full details and predicted changes under other scenarios.

3.3.3 Future changes in inter-annual variability and daily climate

Winter and spring temperatures over most of Britain and Ireland become less variable, especially in the north. Conversely, summer and autumn temperatures become more variable (L), especially in the west. This inter-annual variation of summer temperatures is predicted to increase by 25% or more. Almost the whole of Britain and Ireland is predicted to experience an increase in winter and spring precipitation variability (L), and in summer there will be mostly decreases in precipitation variability, with the exception of Scotland, where it will increase. Summers will become much hotter (H) and drier (M) and winters milder and wetter (H). Drought (M) and flooding events will increase, due mainly to the prediction of increasing intense precipitation frequency throughout the region in winter (H), with roughly a doubling of intense precipitation frequency (daily climate) in both southwest Scotland and Wales by the 2080s in the Medium-High emission scenario (from 1.0-1.5 to 2.5-3 events annually). It is predicted that the opposite will occur in summer, with a decrease in intense rainfall throughout the region. Drought, leading to water shortages and reduced crop yield is predicted in the future through a reduction in precipitation, an increase in summer temperatures and an increase in the number of extremely hot days. The number of very hot days is predicted to increase by more than 200% over most of the region in summer and autumn (H). In spring and winter, the frequency of warm days will increase substantially, particularly in the southern coast of England in winter (H) (Hulme *et al.*, 2002).

Daily wind speed is predicted to change, with a slight increase in winter, a more substantial decrease in summer, and very little change in spring and autumn. However, the results are tentative, and Hulme *et al.* (2002) did not feel able to assign any confidence level to this prediction. The shifts in temperature and precipitation are unlikely to occur at a constant pace and may even include periods of cooling.

Other important aspects of future climate change

Diurnal temperature, which is closely associated with cloud cover, will decrease in winter as the climate becomes wetter and cloudier (L). However, the opposite will happen in summer, as the drier climate will have less cloud cover (L). As a result of these predicted changes in cloud cover, short-range radiation will show increases and decreases consistent with the pattern of precipitation and diurnal temperature range discussed above (L) (Hulme *et al.*, 2002). Relative humidity will decrease throughout the year for all scenarios (H) and more so in summer (M) than in winter and especially in the south of the region (Hulme *et al.*, 2002).

Little change is anticipated in the average wind speeds from today in spring, and small decreases are predicted for autumn. In winter, winds are predicted to strengthen in southern and central Britain but conditions in Scotland and Ireland are not expected to change from those encountered at present. Summer winds are predicted to increase in the southeast of Britain, but the models predict a substantial decrease in wind speed in northern and eastern parts of Ireland (Hulme *et al.*, 2002). Storms, caused by depression tracks, will change little in spring and autumn but will increase and decrease in frequency in winter and summer respectively but not change in severity (L). In the medium-high scenario, the NAO index (see above) is predicted to become more positive (L) although the year-to-year variability is large. 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 southeast to northwest gradient and it is likely that occasional years with year-round terrestrial thermal growing seasons will occur before the 2080s (Hulme *et al.*, 2002).

3.3.4 Future changes in marine climate

Future changes in sea level

Hulme *et al.* (2002) predict that sea levels will continue to rise for several centuries (H), mostly due to thermal expansion of the oceans and the melting of land ice in mountain glaciers. The positive melting of the Greenland ice-sheet on global sea level rise will most likely be offset by the negative effect of Antarctica ice-sheet, which will expand slightly due to increased precipitation (H). The rate at which sea level will rise in each of the four scenarios, as calculated by the Hadley Centre models, is shown in Table 1 along with IPCC (International Panel on Climate Change) estimates given in their Third Assessment Report (Houghton *et al.*, 2001). The differences in these values were generated using the same emission scenarios but using different models with representations for the atmosphere and ocean and for the mass balance of land ice such as the Greenland and Antarctic ice-sheets. It is important to note that the large range of sea rise estimates results from a combination of scientific as well as emission uncertainty, whereas the different climate change predictions estimated above resulted only from emission uncertainty (Hulme *et al.*, 2002).

However, the change in the average level of the sea relative to the land will not be uniform across Britain and regional differences will be experienced due to natural land movements and regional variations in the rate of climate-induced sea-level rise (H) (*e.g.* due to differences in temperature around the coast resulting in non-uniformity of sea water expansion). The London area is envisaged to experience the greatest sea level rise (+26 and +86 cm in the low and high emission scenarios respectively by the 2080s), whilst the lowest level is forecast for south-west Scotland (-2 and +58 cm for the low and high emission scenarios respectively).

Table 1: Global average sea level change (cm) relative to the 1961-1990 average as generated by the Hadley centre models for each of the UKCIP02 emission scenarios (From Hulme *et al.*, 2002). Figures in brackets are ranges of predictions from the model used by the IPCC (Houghton *et al.*, 2001), with data generated from the same emission scenarios but using different models.

UKCIP02 Scenario	2020s	2050s	2080s
Low Emissions	6 (4-14)	14 (7-30)	23 (9-48)
Medium-Low Emissions	7 (4-14)	15 (7-32)	26 (11-54)
Medium-High Emissions	6 (4-14)	15 (8-32)	30 (13-59)
High Emissions	7 (4-14)	18 (9-36)	36 (16-69)

Future changes in extreme sea levels, coastal flooding and wave height

Although the century-scale rise in average sea level may threaten some low lying areas, it is the predicted combination of sea level rise, storm surges and large waves that will cause most damage (Hulme *et al.*, 2002). A separate, high-resolution (30 km) model from the Proudman Oceanographic Laboratory was driven by atmospheric winds and pressure from the regional (HadRM3) Hadley Centre model in order to predict storm surges. This model suggests that storm surge heights will increase around Britain and Ireland for every scenario (Hulme *et al.*, 2002), and that the greatest increases will be off southeast England (L), ≥ 1.2 m by the 2080s, under the Medium-High emissions scenario. The changes in offshore wave climate and wind direction are not well quantified and no quantitative estimates are presented in the UKCIP02 report. The few models that have been designed to quantify wave heights have not been conclusive and vary widely from model to model (Hulme *et al.*, 2002).

Future changes in surface marine temperatures

All areas show an increase in the temperature of coastal waters (Fig. 8), with the shallowest areas such as the North Sea and English Channel warming the most, by up to 3°C by the 2080s for the Medium-High emissions scenario (H). This relates to an equivalent of a *ca*. three-month increase in the duration when sea temperatures reach, or exceed the present August-September average of 16°C. Therefore, by the 2080s, average sea surface temperatures in these regions would exceed the current mid-August to mid-September maximum for a five-month period from mid-June to mid-November (Hulme *et al.*, 2002).

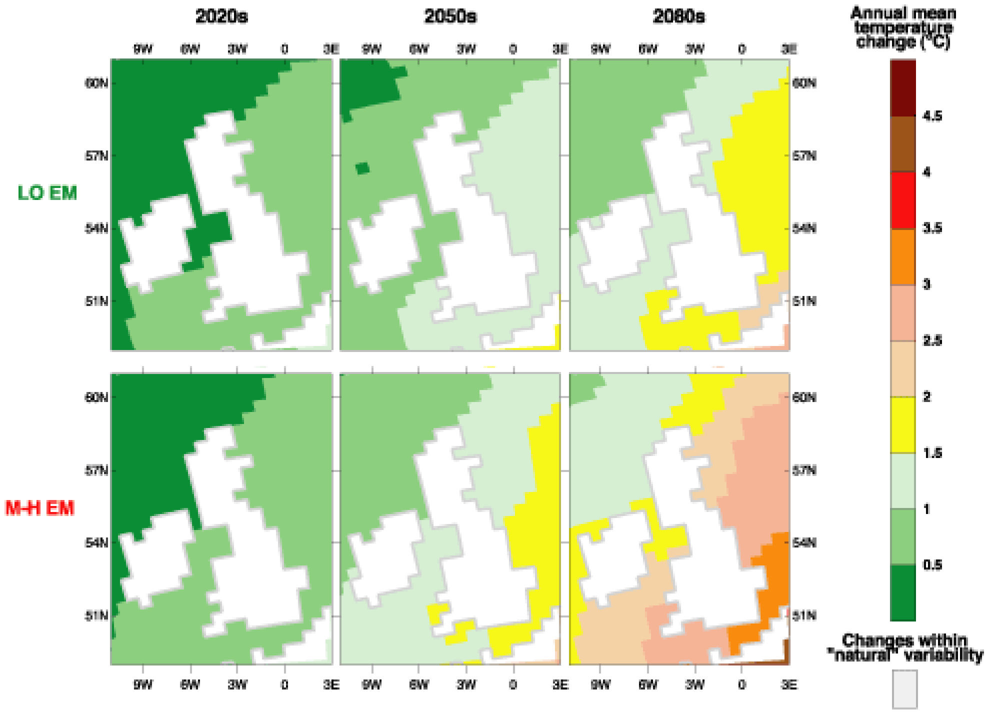

Figure 8: Predicted changes in mean sea surface temperatures (SST) around Britain and Ireland under the Low and Medium-High UKCIP02 scenarios (Source: Hulme *et al.*, 2002).

Future changes in daily average wind speed

Areas off the south and east coasts of England will experience the greatest wind speed increases in winter and spring, (2-8 %, depending on scenario). In summer and autumn, wind speed is predicted to decrease as temperatures increases especially in the Irish Sea and Atlantic coast of Ireland. Wind speeds are predicted to increase in some parts of the North Sea (Hulme *et al.*, 2002).

Possible changes to the North Atlantic Drift/Gulf Stream

The warm NAD (see Section 2.4) is driven partly by surface wind patterns and partially by differences in density caused by spatial variations in temperature and salinity (Hansen *et al.*, 2004). The density driven component is part of a larger ocean circulation, known as the thermohaline circulation (THC). Cold water from the Arctic sinks and moves towards the equator (deepwater formation), creating a compensating draw of water from the Gulf of Mexico across the North Atlantic that forms the NAD (Hansen *et al.*, 2004). It has been postulated that a reduction in the formation of the THC, *e.g.* caused by reduced salinity following a large input of freshwater, could result in a reduction and even shutdown of the THC and NAD (Bryden *et al.*, 2005; Curry *et al.*, 2003; Hansen *et al.*, 2004). The Greenland ice sheet is currently relatively stable and unlikely to melt in the short-to-medium term. However, circulation patterns have changed in recent years, leading some researchers to warn that the overall Atlantic circulation system may be weakening (Bryden *et al.*, 2005; Curry *et al.*, 2003; Hansen *et al.*, 2004). One third of the water that forms this current flows through the Faeroe Banks Channel: this outflow has warmed and become less saline over time, whilst volume has estimated to have decreased by as much as 20% since 1950 (Hansen *et al.*, 2001). If there is no compensation by increased flow through the Denmark Strait, and none has been detected to date, the consequences must be a weakening of the global thermohaline circulation (Hansen *et al.*, 2004; Hansen *et al.*, 2001). The Hadley Centre's climate models predict that without anthropogenic influences, the THC exhibits no long term trend but when the concentrations of greenhouse gases are increased, the THC steadily reduces by 25% under all four UKCIP02 scenarios. A shut-down of the THC is not predicted over the next century, but the NAD may weaken (Bryden *et al.*, 2005). However, this is unlikely to lead to cooling of the climate of Britain and Ireland as increased greenhouse gas heating greatly exceeds this cooling effect (M-H). All of the above previous predictions include the effect of the weakening THC (Hulme *et al.*, 2002).

4 THE ECOLOGICAL EFFECTS OF CLIMATE CHANGE

Fishes, either as individuals, or as populations, experience climate through temperature, winds, currents and precipitation (Ottersen *et al.*, 2004; Ottersen *et al.*, 2001). The present ichthyofauna of Britain and Ireland and the surrounding seas reflect the effects of climate change experienced in the past (Wheeler, 1969; 1977; see study area above). Understanding how climate change will affect the planet is a key issue worldwide (Hays *et al.*, 2005; Houghton *et al.*, 2001; Karl & Trenberth, 2003; McCarthy *et al.*, 2001). Although species have encountered and responded to climatic changes throughout their evolutionary history (Cox & Moore, 1993; Crowley, 1983), a primary concern for wild species and their ecosystems is the rapidity of climate change (Root *et al.*, 2003) with the rate of temperature increase predicted for the future to exceed any seen in the last 10,000 years (Houghton *et al.*, 2001). During previous periods of climatic change, fish and other aquatic taxa dispersed into thermal refugia (Bernatchez & Wilson, 1998). Marine fishes can still disperse relatively freely and may therefore be able to move to more suitable habitats if climatic conditions become unsuitable, but freshwater ecosystems have become fragmented following human disturbances, which may prevent freshwater fishes migrating to suitable areas under similar conditions (Allan & Flecker, 1993).

Climate profoundly influences ecological processes in a number of direct, indirect and complex ways (Friedland *et al.*, 2000; Ottersen *et al.*, 2004; Ottersen *et al.*, 2001). A number of complementary processes may be acting on a fish population or aquatic ecosystem (Ottersen *et al.*, 2004; Ottersen & Loeng, 2000; Rothschild, 1998) *e.g.* exploitation and climate change (Beaugrand *et al.*, 2003; Blanchard *et al.*, 2005; Heath, 2005; Rose, 2004). Furthermore, climate-induced changes may act on several aspects of the ecology of a fish (Clark *et al.*, 2003; Friedland *et al.*, 2000; O'Brien *et al.*, 2000), and its interactions with its biotic and abiotic environment. Predicting the outcomes of environmental change on fish populations is clearly complicated (Planque & Frédou, 1999; Rothschild, 1998). Understandably, as interest has grown in the potential for climate change to influence fish and fisheries, the number of publications in the scientific literature referring to climate change has rapidly increased (Fig. 9).

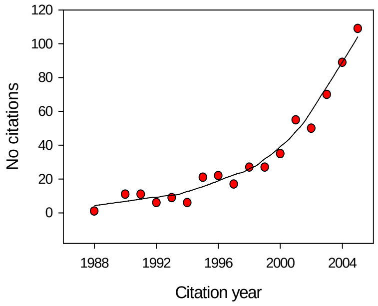

Figure 9: Rapid increase in the number of articles referring to 'Climate change' and 'fish/fishes/fisheries' in recent years (ISI Web of Science 1988-2005).

Aquatic ecosystems are influenced by a complex range of abiotic and biotic processes that interact to determine the availability and suitability of habitats for fish and other organisms (Barnes & Mann, 1991), and this may alter following climatic change. For instance, as the temperature of the troposphere warms, it will also lead to increased temperatures in the hydrosphere and lithosphere (Meisner *et al.*, 1987). Responses to climate change by aquatic ecosystems are likely to be complex and difficult to predict (Fig. 10), will vary greatly according to system type, and responses may be non-linear (Harley *et al.*, 2006; Mohseni *et al.*, 2003). For instance, temperatures in shallow waters are typically closely related to that of the air, whilst in larger and deeper aquatic systems, the influence of hydrological, climatic, geographical and oceanographic factors, and the thermal inertia of water, leads to increased lags (both positive and negative) between air and water temperatures (Arai, 1981; Caissie, 2006; Cayan, 1980; McCloy & Dolan, 1973; Wetzel, 2001).

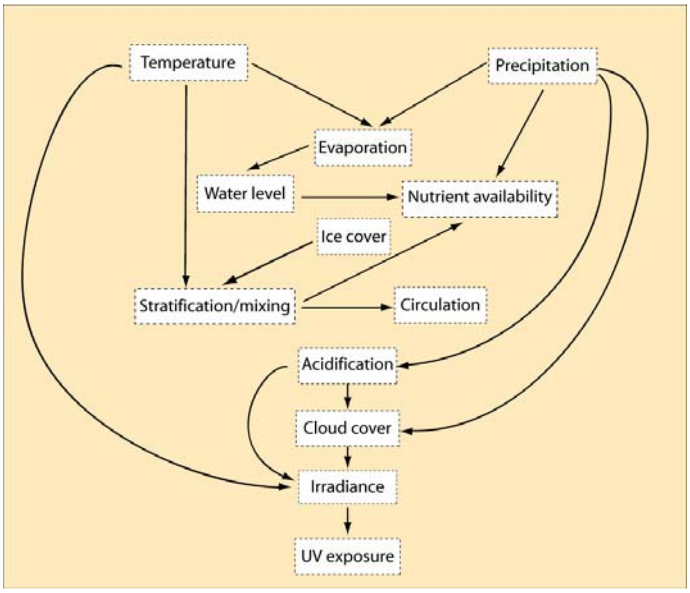

Figure 10: Conceptual diagram detailing the range of environmental factors likely to affect aquatic systems predicted from climate change scenarios (Modified with permission from Marcogliese, 2001).

Climate change will affect aquatic taxa at the cellular, individual, population, species, community and ecosystem level. The response of fishes, and of other aquatic taxa will vary according to their individual tolerances and life stage (Fig. 11) and are therefore likely to be complex and difficult to predict. 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 (Hallett *et al.*, 2004; Harvell *et al.*, 2002; Marcogliese, 2001; Ottersen *et al.*, 2001; Taniguchi *et al.*, 1998). Harley *et al.* (2006) outlined probable proximate and emergent ecological responses by aquatic taxa to climate change (Fig. 11). Proximate responses to climate change include changes in the performance of individual fish at different stages in their life cycle due to shifts in behaviour or physiology. Changes in the performance of individual fish will be reflected at the population level, *e.g.* changes in abundance or age structure, but these changes will be mediated by the response of interacting taxa, leading to community-level responses to climate change. The combined effects 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.

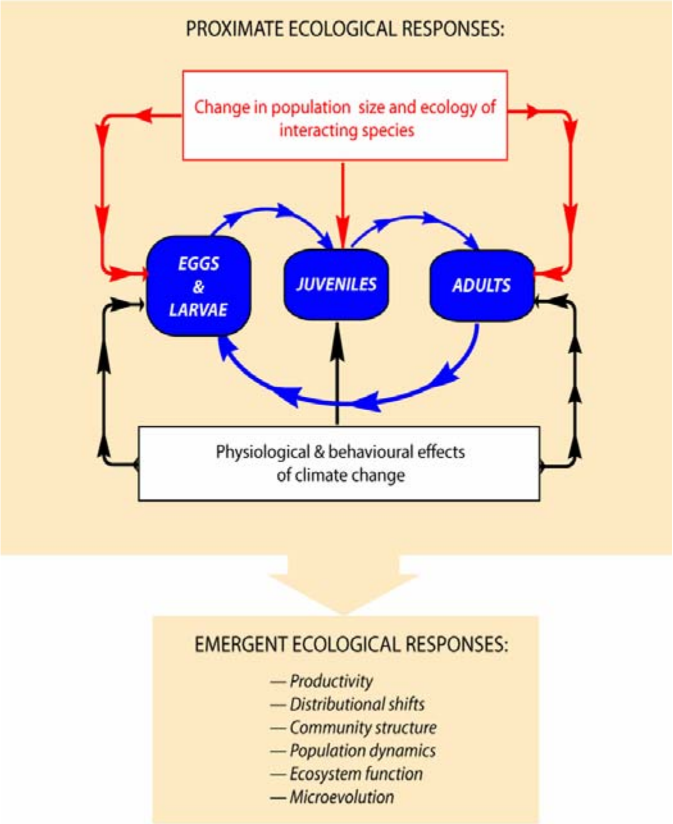

Figure 11: Conceptual diagram detailing potential ecological responses to climate change of a typical fish. Abiotic changes will lead to physiological and behavioural shifts in individual fish, which will influence their performance in community and population level interactions. Hence climate change 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 (After Harley *et al.*, 2006).

Temperature directly controls metabolic processes and, besides food availability, is the single most important factor that determines growth rates in fish (Brett, 1979; Elliott, 1994; Fry, 1971). As temperature decreases, metabolic processes slow 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 utilise 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 due to reduced metabolic costs (Elliott, 1994; Swain *et al.*, 2003). 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 (Bergman, 1987; Persson, 1986). Fishes have evolved to fit distinct thermal niches where they are able to optimise physiological, ecological, and reproductive performance (Coutant, 1987b; Crawshaw & O'Connor, 1997; Magnuson & Destasio, 1997).

Temperature stress may leave individual fish open to additional stresses due to parasitism (Marcogliese, 2001), competition (Persson, 1986; Taniguchi *et al.*, 1998), predation (Elliott & Leggett, 1996), dissolved oxygen (Alabaster & Lloyd, 1980) and invasive species (Dukes & Mooney, 1999). Climate change may also affect the chemistry of aquatic environments indirectly: increased water temperatures are likely to result in the increased mobilisation and availability of xenobiotic contaminants to aquatic food chains (Moore *et al.*, 1997; Schindler, 2001). Reductions in cloud cover during summer may expose fishes in shallow or clear-water habitats to increased risk of ultraviolet radiation damage (Walters & Ward, 1998; Williamson *et al.*, 1997; Zagarese & Williamson, 2001).

In association with other environmental factors (*e.g.* photoperiod), temperature plays an extremely important role in the reproduction of temperate fishes (Potts & Wootton, 1984; Wootton, 1990). For example the reproductive cycle in perch is closely linked to water temperature (Hokanson, 1977; Thorpe, 1977): typically oocytes begin to develop in August, and vitellogenesis extends from September to April/May, when females are ripe and ready to spawn (See Sandström *et al.*, 1997 for a review). In the closely related yellow perch (*Perca flavescens*), an extended exposure to low temperatures is required for successful vitellogenesis (*e.g.* ≤ 6°C for *ca.* 6 months). Elevated water temperatures can accelerate egg development and thus shorten hatching periods (Crisp, 1981; Guma'a, 1978; Pauly & Pullin, 1988). In their simulations of the effects of climate warming on the development and growth of juvenile brown trout (*Salmo trutta*), Weatherly *et al.* (1991) suggested that an increase in winter water temperature of 3°C resulted in fry emerging from redds 7 weeks earlier relative to baseline conditions. Increases in the length of the growing season (Hulme *et al.*, 2002) are likely to affect fish populations by increasing the potential for growth (Weatherley *et al.*, 1991). This is likely to be particularly important for young-of-the-year of those species where individual size is closely associated with the risk of mortality during the winter period (Griffiths & Kirkwood, 1995; Lappalainen *et al.*, 2000).

An obvious aim of climate change researchers is to predict how individuals, populations and communities will respond to climate change. They have developed two primary approaches to examine how populations and communities will respond to climate change (Genner *et al.*, 2004). One, the climate (or bioclimatic) envelope hypothesis relates the current distribution and abundance of species to their physiological tolerances in order to predict the abundance and distribution under alternative climates (Pearson & Dawson, 2003). This approach is appealingly simple, but extremely controversial as the current distribution of species is also a function of interactions with other species, including predators, parasites and competitors (Davis *et al.*, 1998; Hampe, 2004). Other researchers have shown that distribution of individuals and the often-complex interactions between species are also influenced by climate change (Davis *et al.*, 1998; Kiesecker *et al.*, 2001; Mark *et al.*, 1999), and suggest that these factors must be included in any predictions of biotic responses under future climates. The biogeographical location of Britain and Ireland 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 to 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 being extirpated or impacted 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 (Gozlan *et al.*, 2005; Marcogliese, 2001), which may be more harmful to fishes stressed following environmental change (Lafferty & Kuris, 1999; Snieszko, 1974).

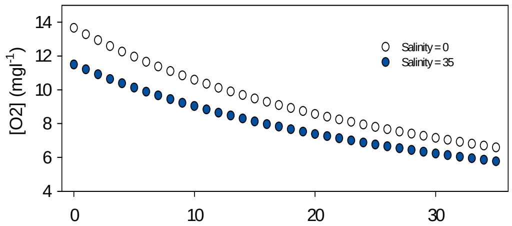

Figure 12: Changes in the solubility of oxygen in water with increased temperature: note that salinity reduces the solubility of oxygen in water (Weiss, 1970).

Although the bulk of research on the likely effects of climate change on fish has rightly concentrated on the role of temperature, it must be remembered that 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; see Fig. 12), 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, 1987b; Kramer, 1987), reproductive success (Coutant, 1987a), capacity for growth (Brett, 1979; Pauly, 1981), activity (Domenici *et al.*, 2000) and predation risk (Headrick & Carline, 1992). Recently Pörtner & Knust (2007) showed a strong negative correlation between summer temperature and estimated eelpout (*Zoarces viviparous*) population size in the Wadden Sea. They provided good evidence that physiological factors (thermal constraints on oxygen transport) were responsible for this relationship. Genetic variation within or between populations may modify the response of individual fish to different dissolved oxygen conditions depending on their genotype (Petersen & Steffensen, 2003; Sick, 1961).

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, household supplies) as well as natural ecosystems (Arnell, 1998; Hughes & Morley, 2000). Climate change predictions for Britain and Ireland 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 freshwater and habitats receiving freshwater discharge, *e.g.* estuaries (Struyf *et al.*, 2004). Other predicted changes in climate (*e.g.* temperature) may also lead to reduced quality of freshwater inputs, with further detrimental impacts (Arnell, 1998; Struyf *et al.*, 2004). The influence of these changes on the ecology of fishes will depend on the sensitivity of different habitats to modifications in flow or water quality. 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 due to increased water temperatures, decreased dilution of pollutants 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 (Natsumeda, 2003; Poff, 2002; Schlosser, 1991).

4.1 CLIMATE CHANGE AND AQUATIC ECOSYSTEMS

4.1.1 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, 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 2% could lead to an increase in fisheries yield of *ca.* 25%. An increase 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 utilised 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*) (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; George *et al.*, 2004; Magnuson *et al.*, 1997; Meisner *et al.*, 1987; Mooij *et al.*, 2005; Stefan *et al.*, 2001; Straile *et al.*, 2003).

4.1.2 Running waters

Apart from increases in water temperature, climate change is likely to impact riverine systems following shifts in precipitation patterns (*e.g.* increases in winter, reductions in summer: Arnell, 1998; Hulme *et al.*, 2002), including an increased probability of extreme events (Christensen & Christensen, 2003). Residence times, import and export of organic matter, dilution of pollutants, primary production and dissolved oxygen concentrations are all likely to be altered (Arnell, 1998; Carpenter *et al.*, 1992; Conlan *et al.*, 2005; 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; Hulme *et al.*, 2002). Migratory species have evolved to utilise predictable floods for migrations (Crisp, 1996; Vøllestad *et al.*, 1986), and changes in the frequency or intensity of floods may impact 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 (Jager *et al.*, 1999; Jowett & Richardson, 1989; Mann, 1996; 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 (Masters *et al.*, 2002; Ross & Baker, 1983). 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 impacts on habitat availability for fish, and their production and diversity (Robinson *et al.*, 2002). Reductions in streamflow during warm periods may lead to increased stream temperatures, decreased concentrations of dissolved oxygen and reduced dilution of pollutants (Mohseni *et al.*, 2003). A series of studies detail the likely ecological and hydrological effects of climate change on riverine habitats (Arnell, 1998; Carpenter *et al.*, 1992; Daufresne *et al.*, 2003; Eaton & Scheller, 1996; Mohseni *et al.*, 2003).

4.1.3 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 will potentially 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 (Kennedy, 1990; Roessig *et al.*, 2004). Predicted increases in sea levels (Hulme *et al.*, 2002) will also lead to shifts in salinity profiles, which are likely to result in changes in estuarine fish community structure towards salinity-tolerant estuarine fishes, or those typical of fully marine habitats. 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. Predicted increases in winter precipitation will result in greater run-off to surface waters, including estuarine waters (Arnell, 1998; Hulme *et al.*, 2002). Increased freshwater discharge during winter will result in an overall decrease in salinity and shifts in estuarine salinity gradients. Residence time will fall, and nutrients, contaminants, and organic material will be transferred to coastal waters more rapidly (Struyf *et al.*, 2004), potentially reducing the productivity of estuarine habitats. Several authors have reviewed the likely effects of climate change on estuarine fishes (Kennedy, 1990; Roessig *et al.*, 2004; Scavia *et al.*, 2002).

4.1.4 Marine and coastal habitats

The seas around Britain and Ireland are predicted to continue to warm following climate change (Hulme *et al.*, 2002). However, the likely impacts of climate change on marine ecosystems extend beyond increased water temperature (Harley *et al.*, 2006; Scavia *et al.*, 2002) 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, circulation) environments of marine fishes are significant, it is likely that interactions between individuals and species will be modified, impacting 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).

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 which has led to significant acidification of seawaters (Royal Society, 2005). If global emissions of CO_2 continue, it is feared that the average *p*H of the oceans could fall by 0.5 *p*H units (equivalent to a threefold increase in H^+ ions) by 2100 (Royal Society, 2005). Although the impact of such acidification is likely to be less extreme in the seas around Britain and Ireland than in tropical or southern seas, it has clear potential to impact 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 impact the physiology and reproductive success of water breathing organisms including larger invertebrates and fishes (Ishimatsu *et al.*, 2004; Pörtner *et al.*, 2004). Increases in sea level around Britain and Ireland due to thermal expansion of seawater (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). Climate change predictions for Britain and Ireland (Hulme *et al.*, 2002) suggest that the intensity and frequency of storm events and surges will increase in some areas (*e.g.* south east England). 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 (Brander & Mohn, 2004; Edwards *et al.*, 2002; George *et al.*, 2004; Harley *et al.*, 2006; Hays *et al.*, 2005; Hurrell & Dickson, 2004; Ottersen *et al.*, 2004; Scavia *et al.*, 2002; Sharp, 2003; Soto, 2002; Stenseth *et al.*, 2002; Stenseth *et al.*, 2004).

5 CLIMATE CHANGE AND THE FISHES OF BRITAIN & 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. In this briefing paper we have focused on well-studied species, including examples of typical cold, cool and warmwater fishes (Hokanson, 1977; Magnuson *et al.*, 1979), and species that are important for ecological, trophic and socio-economic reasons.

The Atlantic cod (*Gadus morhua*) is a predatory, demersal, cold-water species and a typical inhabitant of the continental shelf. It is of high economic importance, well known to the public and has been the subject to more intensive study than any other marine fish. First, we discuss the effects of climate change on cod in detail, and in doing so introduce several key features of the ecology of fish that are likely to be influenced by climatic change. The migratory Atlantic herring (*Clupea harengus*) is an abundant and trophically important cold-water pelagic predator, which is highly fecund and short-lived. It matures at a young age and supports significant fisheries around Britain and Ireland. Many distinct stocks of this fish are found in the North East Atlantic and different stocks spawns at different times of the year. We compare the role of climatic variation on the distribution and ecology of the herring with that of the pilchard (*Sardina pilchardus*). Sandeels, and in particular, the lesser sandeel (*Ammodytes marinus*) support the largest fishery in the North Sea. This abundant and important component of the marine food web represents a key forage fish for a diverse assortment of commercial and non-commercial fish species and several seabird and mammal species. Britain and Ireland represent the southern limit of the distribution of this fish as well as the herring and cod. The elasmobranch fishes (rays, skates and sharks) are relatively understudied with regard to climate change, and we use the basking shark (*Cetorhinus maximus*) as an indicator species.

In the estuarine/brackish/inshore environment we review the effects of climate change on three species: 1. flounder, (*Platichthys flesus*), which can tolerate a wide salinity range (0->30[†]) and is a characteristic inhabitant of estuaries. Britain and Ireland are located approximately at the centre of the flounder's range; 2. sole, (*Solea solea*), is a commercially important flatfish that uses estuarine environments as nursery habitats before migrating to deeper waters later in life. The northern distribution of this fish is found in the North Sea; and 3. The eelpout - this abundant, non-migratory inhabitant of the coastal zone has its southern distributional limit located around the Thames Estuary. In the marine environment, we discuss the potential effects of changing climate, and in particular rising temperatures, on the distribution of fish around Britain and Ireland and how this will change regarding global warming and also the effect of climate change on fish assemblages in inshore/estuarine environment.

We discuss the potential consequences of climate change on an important anadromous fish, the Atlantic salmon (*Salmo salar*). This extensively studied salmonid fish undertakes lengthy migrations, and encounters a variety of habitats throughout its life cycle (Armstrong *et al.*, 2003; Crisp, 2000; Klemetsen *et al.*, 2003). Consequentially, the salmon faces changing climate of a number of different habitats, all of which have the potential to greatly affect the biology of this extraordinary fish (Boisclair, 2004; Davidson & Hazlewood, 2005). Although listed in the EU Habitats Directive (EU, 1992) as a species of conservation concern, the salmon continues to be a species of considerable economic interest, particularly regarding its exploitation by recreational fisheries and in aquaculture.

Britain and Ireland have a depauparate freshwater ichthyofauna relative to mainland Europe (Griffiths, 2006; Maitland, 2004). In order to consider the likely consequences of climate change for freshwater fishes we selected a set of species that in laboratory studies exhibit a gradient of temperature preference and tolerance (Fry, 1947, 1971), and can be considered representative of the larger freshwater fish community of Britain and Ireland: 1, a stenothermal coldwater specialist, the Arctic charr (*Salvelinus alpinus*) (Larsson *et al.*, 2005); 2, the perch (*Perca fluviatilis*), a mesothermal generalist (Hokanson, 1977); and 3, the roach (*Rutilus rutilus*), a eurythermal generalist (Lehtonen, 1996).

5.1 CLIMATE CHANGE: MARINE FISHES

5.1.1 Atlantic cod

The Atlantic cod 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 extending from the 1960s (Heath, 2005). Cod have a boreal distribution and are a typical inhabitant of the continental shelf (Pörtner *et al.*, 2001). Cod stocks are found around the North Atlantic margin from North Carolina (USA) to west of Greenland (Ottersen *et al.*, 2004) and from the Celtic Sea to the Barents Sea in the eastern North Atlantic (Ottersen *et al.*, 2004; Planque & Frédou, 1999). The species range encompasses average water temperatures from 2 to 11°C (Brander, 1995).

[†] Until recently salinity was reported as part per thousand (‰ or ppt). As salinity relates to the ratio of mass of dissolved substances to the mass of seawater, it is dimensionless and therefore does not require units.

Cod in waters around Britain and Ireland are assessed and managed as four separate stocks (*i.e.* west of Scotland, Irish Sea, Celtic Sea and North Sea) that vary in their spawning-stock biomass and landings (Brander, 2005). These stocks are independent, having different spawning areas and migration patterns, and according to tagging and genetic studies have low exchange rates (Brander, 2005; ICES, 2005a; Pogson *et al.*, 1995). Molecular (Hutchinson *et al.*, 2001), length at age and mark-recapture (reviewed in: Metcalfe *et al.*, 2005) data provide good evidence for further population sub-structuring within the North Sea cod stock. The following substocks stocks are currently recognised: Flamborough Head, German Bight, Southern Bight, Moray Forth, Shetland, Viking and Skagerrak.

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).

Cod abundance has changed markedly around Britain and Ireland over the last century, particularly in the North Sea (Clark *et al.*, 2003; ICES, 2001). Until the 1960s, the North Sea cod stock was estimated at *ca.* 100 000 t (ICES, 2001). However, between the early 1960s to the mid-1980s, during what is known as the gadoid outburst (Brander & Mohn, 2004; ICES, 2001), the stock increased four-fold, following greatly increased recruitment (Beaugrand *et al.*, 2003; ICES, 2001). This resulted in increased stock size, fishing effort and catches (Clark *et al.*, 2003; ICES, 2001). However, following over-exploitation (Beaugrand *et al.*, 2003), the SSB of these stocks are now at an historic low (Brander, 2005) and today, North East Atlantic cod stocks are considered at risk of total collapse (Cook *et al.*, 1997; Schiermeier, 2002).

Cod and climatic variation

Brander (1995) studied 17 stocks of cod 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 to 0.6 kg at 2°C (Labrador, Canada) (Brander, 1995). Cod stocks from the relatively warm waters of Britain and Ireland are more than four times as productive than 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). Swain *et al.* (2003) showed that cod in the Gulf of St. Lawrence grow faster at higher temperatures and Pörtner *et al.* (2001) reported reduced growth and fecundity of cod at the more northern latitudes of the species' range. Growth performance of cod was optimised 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 cod fed to satiation ranged between 16 and 7°C for 2 g and 2000 g cod 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), but Neat & Righton (2007) have recently demonstrated that some North Sea cod utilise habitats with water temperatures above those considered optimal for growth. The situation is further complicated by a haemoglobin polymorphism in cod (Sick, 1961) that is expressed differently across the geographical distribution of cod (Jamieson & Birley, 1989). The haemoglobin polymorphism is correlated with mean annual sea temperatures in the wild (Sick, 1961), and is reflected by different temperature preferences in the laboratory (Petersen & Steffensen, 2003). Wild fish may select temperatures that are sub- or super-optimal relative to estimates from laboratory studies as a result of interactions with other species, including potential prey, predators and competitors (Ottersen *et al.*, 2004), and it is possible that laboratory studies describing the thermal ecology of cod (and other species) are not fully representative of wild fish.

The spatial distribution (*e.g.* depth) of cod has been associated with temperature variation in a series of studies. Comparison of the spatial distribution of mature Icelandic cod with several environmental parameters, including temperature, indicated they migrated between depths to actively maintain optimum temperatures (Begg & Martinesdottir, 2002). North East Atlantic cod migrate into the Barents Sea during warm years, but cod migrate in cold years only as a result of high densities (Ottersen *et al.*, 1998). Castonguay *et al.* (1999) found that cod 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. Data gathered at the level of individual fish using electronic data storage tags (DST) has revealed that cod can show high variability in migratory behaviour, both between stocks and individuals. Pálsson and Thorsteinsson (2003) demonstrated that the depth and temperature conditions encountered by cod 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 cod followed that of the seasonal trend in the shelf region (highest in summer and autumn, and coolest in the winter months), but deep-water cod were found in deeper and cooler waters during summer months, and encountered warmer water in winter months. Gødo and Micalsen (2000) described a similar situation in the Barents Sea. They suggested that cod were resident in the colder northern and eastern parts of the Barents Sea in summer and autumn, and then migrated to warmer regions in the south and west during winter and spring. Pálsson and Thorsteinsson

(2003) suggested that the use of deeper and colder waters in the summer and autumn permitted large-bodied cod to minimise maintenance costs under conditions of reduced food availability. Using a similar DST approach in the shallower waters of the North and Irish Seas, Righton and co-workers (Righton *et al.*, 2001; Righton & Metcalfe, 2002) revealed marked differences in behaviour between North Sea and Irish Sea cod. They showed that fish from the Irish Sea were active year round, with no obvious diurnal or seasonal pattern, whilst North Sea fish displayed complicated seasonal activity patterns. North Sea cod were active during April and May, relatively inactive during June and July, with activity at night increasing in August and September, and finally become fully active in October and November (Righton *et al.*, 2001). The temperatures encountered by cod in the North Sea were on average higher (range 5-18°C) than those of their conspecifics from the Irish Sea (range 7-12°C) (Righton & Metcalfe, 2002). Further DST work by Neat & Righton (2007) demonstrated that in the southern North Sea at least, cod were found in areas with super-optimal temperatures for growth, even though suitable cold-water habitats were available. What DST studies clearly demonstrate is that the temperature regime encountered by individual fish can be extremely complex. They also highlight the difficulties in producing reliable estimates of ambient temperatures for free ranging fish, even though these data may be crucial for many predictive models used by fishery biologists (Gødo & Michalsen, 2000).

Temperature affects the developmental rate of fish eggs, with higher temperatures resulting in faster development and hatching (Crisp, 2000; Nissling, 2004; Pauly & Pullin, 1988). Laboratory experiments have demonstrated that the development rate of cod eggs is positively correlated with temperature, and that egg survival is unaffected at temperatures between 3-9°C (Nissling, 2004), 2-10°C (Laurence & Rogers, 1976) and up to 10°C (Iversen & Danielsen, 1984 cited by Nissling, 2004). However, above these temperatures, egg survival was significantly reduced. Laboratory studies show that the growth of larval cod 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.

Cod 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). Recruitment depends on reproductive output, *i.e.* viable eggs produced by the stock and the survival of the eggs, larvae and juveniles (Cushing, 1996). 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). Therefore, reproductive output and survival of young fish and hence, recruitment, is sensitive to environmental influences (Myers, 1998; Paxton *et al.*, 2004). Early life stages are considered to be the principal determinants of year-class strength (YCS) and recruitment success (Cushing, 1990; 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 cod was 8.5-8.8°C (Steinarsson & Björnsson, 1999). Interannual variability of temperature affects the survival and recruitment of cod, 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). Irish Sea cod are situated towards their southern distributional limit and display a strong negative connection between the 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 cod, whereas in the north-east Arctic, Ottersen *et al.* (1998) reported a positive relationship between temperature and recruitment. When Planque and co-workers (2003) incorporated sea surface temperature into a North Sea cod stock recruitment model it accounted for 46% of the variance in past recruitment compared to 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.* NAO as it does not have local values and can be considered a proxy for temperature, wind and precipitation (Brander & Mohn, 2004; Ottersen *et al.*, 2001). The NAO has significant effects on the recruitment of cod throughout the North Atlantic: Brander & Mohn (2004) demonstrated that recruitment was independent of spawning stock biomass and negatively correlated with the NAO in some areas (*e.g.* Irish Sea, North Sea, Baltic Sea, Western Scotland,) and positively correlated in others (*e.g.* Iceland, Northeast Arctic, Faroes). These findings show recruitment to be positively correlated with the NAO in colder, northerly regions and negatively correlated in the southern, warmer range of Atlantic cod, and are consistent with the effects of temperature on growth of cod discussed above. However, it should be noted that temperature is not the only process acting in each area (Brander & Mohn, 2004). Further analysis on cod stocks demonstrating negative correlations between recruitment and the NAO by Brander (2005), suggested that the NAO only significantly affects recruitment when spawning biomass is low. 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 (Brander, 2005; Ottersen *et al.*, 2001), and is predicted to continue this pattern. The NAO probably affects all cod 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 interannual variability in cod recruitment along the Norwegian Skagerrak coast. They hypothesised that this was due to this population being located close to the centre of the latitudinal distribution of Atlantic cod, and that climate variability was more likely to affects species at the edge of their range than in the centre, 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 impact of sea temperature on cod recruitment appears to be a robust statistical observation (Planque *et al.*, 2003).

Clark *et al.* (2003) modelled the likely future effects of climate change on North Sea cod 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. It accelerated the decline in SSB and recruitment, and led to a predicted collapse of the stock (Clark *et al.*, 2003). Laboratory studies indicate that when fed to satiation, the optimal temperature for growth in Icelandic cod is *ca.* 8.5°C (Björnsson *et al.*, 2001). Assuming that optimal temperatures are similar for wild cod (Blanchard *et al.*, 2005), increases in environmental temperature above current levels (*e.g.* 1998-2000 = 8.67°C) would not result in increased growth, with no compensatory effect on recruitment or SSB (Clark *et al.*, 2003). It should be noted wild fish might be food limited and therefore exhibit different temperature preferences to that of well-fed laboratory fish (Brett, 1979). North Sea and Irish Sea cod may also have a higher optimal temperature for growth, as the larger size at age for southern stocks cannot be explained on the basis of increased availability of food alone (Brander, 1995). The utility of models based on optimal temperatures estimated from laboratory-studies of cold-adapted northern cod may therefore be reduced. Clark *et al.*'s (2003) model indicated that changes in temperature would affect population dynamics through recruitment rather than adult growth. The February-June period appears to be critical, as SST is most strongly correlated to recruitment during this time (O'Brien *et al.*, 2000; Planque & Frédou, 1999). The southern limit of adult cod corresponds to the 10°C surface isotherm during April (Brander, 1997). Clark *et al*'s (2003) model suggests that in the North Sea, April temperatures will not reach 10°C, even by 2100, and it seems unlikely that adult cod will be totally forced out of the North Sea over the next century. However, if adult cod are required to return to specific spawning locations to maximise transportation of juveniles to nursery grounds (Begg & Martinesdottir, 2002), changes in temperature are likely to have considerable implications for North Sea cod stocks. In a follow-up study to Clark *et al.* (2003), Kell *et al.* (2005) indicated that a 50% reduction of fishing mortality from current levels allowed the recovery and persistence of North Sea cod even under climate scenarios similar to those used by Clark *et al.*

Critical periods, match/mismatch theory & trophic cascades: cod 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), and cannot actively feed until they have functional mouth and digestive systems. They must however 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 this point of no return 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 in order to minimise 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 cod in the seas around Britain and Ireland has been below safe biological limits for some time (Brander, 2005; Cook *et al.*, 1997). This may further limit the likelihood of the formation of a strong year class (Garrod, 1983; Myers & Barrowman, 1996).

Food availability for rapidly growing cod larvae affects their survival in many, if not all areas (Brander & Mohn, 2004) and food quantity and quality are both essential (Munk, 1997). The survival of larval cod depends on four key biological parameters of prey: mean size, seasonal availability, food quality and abundance. These aspects 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 cod (Beaugrand *et al.*, 2003). Detailed analysis of zooplankton data has revealed that the gadoid outburst that occurred between the late 1960s and early 80s (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, whilst the abundance of certain important species increased at the time of year when juvenile cod were developing, and this is believed to have increased gadoid recruitment (Beaugrand *et al.*, 2003). Unfavourable shifts in the plankton ecosystem occurred in the years following the gadoid outburst, and these were associated with poor recruitment of cod (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 eat a sufficient quantity of suitable prey in order to avoid starvation and grow (Brander *et al.*, 2001). *Calanus* (from eggs to adults) are an important source of food for larval and juvenile cod until July-August (Munk, 1997) and the progressive substitution of *C. finmarchicus* by *C. helgolandicus* (Hays *et al.*, 2005; see Fig. 13) has delayed the timing of occurrence of *Calanus* prey in the North Sea from spring to late summer, when juvenile cod feed more on euphausiids and other fish larvae (Beaugrand *et al.*, 2003). Euphausiids are a very important, high-energy source of food for juvenile cod and a long-term decrease in euphausiids is significantly related to these plankton anomalies. Such plankton anomalies are more significantly correlated to SST than cod recruitment changes in the North Sea (Beaugrand *et al.*, 2003). This implies a multiple negative impact of increasing temperature on cod recruitment: increasing temperatures increase cod metabolism and energy costs (Otterlei *et al.*, 1999) which subsequently hasten exhaustion of yolk sac energy reserves, and if food availability is reduced (Beaugrand *et al.*, 2003), the optimal temperature for growth decreases, further compounding the effects of increased temperatures (Fiogbé & Kestemont, 2003; Michalsen *et al.*, 1998; Swain *et al.*, 2003).

In some regions, *e.g.* towards the northern distributional limit of cod, the largest early juveniles are typically found in areas where the larvae experience the highest temperatures (Suthers & Sundby, 1993), and increased growth probably results from a combination of increased temperature and greater food concentrations. On the Faroe Shelf, the spawning stock biomass of cod fluctuated between *ca.* 60 000 and 160 000 tonnes until 1990-1994 when the biomass of cod and other major demersal species declined (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 (Steingrund & Gaard, 2005) following strong recruitment in 1992 and 1993, due to an increased scope for growth (the energy available for growth once other metabolic costs have been met (Brett, 1979)) 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 cod stocks was closely linked to phytoplankton production. In this area, annual phytoplankton production can vary by a factor of five, and years of low phytoplankton production result in low cod recruitment through limitation of food for both larval (zooplankton prey) and post-settlement cod (sandeel prey) (Steingrund & Gaard, 2005). Sandeels represent an important prey, and when abundant they form the principal food item of cod on the Faroe Plateau, and are associated with high abundance and growth of cod (Steingrund & Gaard, 2005). Brander *et al.* (2001) also speculated about possible connections between local meteorological forcing, timing of phytoplankton spring blooms and recruitment of cod in Iceland and the Irish Sea through prey match/mismatch.

Effects of climate change on primary and secondary production – Phenology

Sea surface warming in the Northeast Atlantic has been associated with increased and decreased phytoplankton abundance in cooler and warmer regions, respectively (Richardson & Schoeman, 2004). Through bottom-up effects, this impact can propagate up foodwebs through herbivorous and carnivorous zooplankton. That this will have an effect on higher trophic levels seems inevitable, and it is likely that fish and other top predators will have to adapt to changing spatial distribution of primary and secondary production within marine pelagic ecosystems following climate change (Richardson & Schoeman, 2004). Results from Continuous Plankton Recorder surveys have shown that south of 59° North in the Northeast 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 timing (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 synchronisation 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 (Hays *et al.*, 2005; Reid *et al.*, 1998) leading to trophic mismatch (Beaugrand *et al.*, 2003; Edwards & Richardson, 2004).

The copepod *C. finmarchicus* is of key trophic importance in the Northeast Atlantic, but is in pronounced decline. It is being gradually replaced by its warm-temperate congener *C. helgolandicus* with some negative impacts on fish recruitment in species including cod (Beare *et al.*, 2002; Beare *et al.*, 1998; Beaugrand *et al.*, 2003). In the North Sea (Fig. 13), *C. finmarchicus* has shown a rapid, and almost complete collapse (Hays *et al.*, 2005), with a twenty-fold decrease recorded in the northern North Sea between 1958 and 1998 (Beare *et al.*, 1998) and an increasing overall prevalence of temperate Atlantic and neritic (shallow-water) 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 (Heath *et al.*, 1999; Planque & Taylor, 1998). 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 over-wintering areas (*e.g.* the Faroe-Shetland Channel) (Heath & Jonasdottir, 1999).

The decline of *C. finmarchicus* and its progressive substitution by *C. helgolandicus* (Beaugrand *et al.*, 2003) has been associated with the influence of an increasingly positive NAO on oceanic currents around Britain and Ireland (Beare *et al.*, 2002; Fromentin & Planque, 1996; Planque & Reid, 1998; Planque & Taylor, 1998) and temperatures in the North Sea (Beare *et al.*, 2002; Planque & Taylor, 1998), 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 of inflow through the English Channel of presumably temperate Atlantic species is thought to be the driving mechanism for its decline. Rising temperatures would result in increased winter survival of temperate and neritic species in the North Sea. However, two ecological features clearly differentiate these two species of calanoid copepod: their temperature preferences and over wintering strategy (Planque & Taylor, 1998).

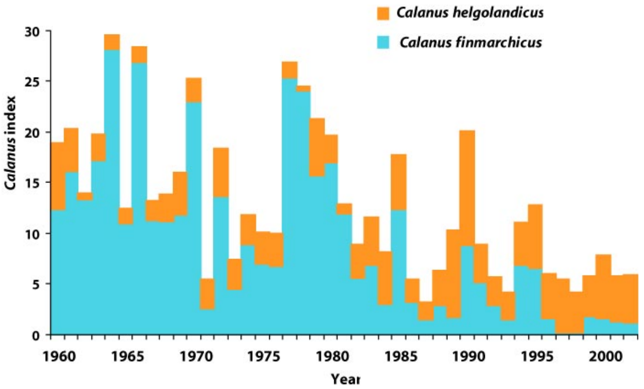

Figure 13: Population fluctuation and community change in *Calanus* spp. in the North Sea over recent decades. The relative contribution of *Calanus finmarchicus* and *Calanus helgolandicus* is shown in relation to overall Calanus abundance (after Hays *et al.*, 2005).

Future predictions for cod

Pörtner *et al.* (2001) modelled the likely effects of future climate (*e.g.* temperature) on cod populations and predicted a northerly distribution shift. Their predictions also included increased growth rates and fecundity of cod in northern stocks consistent with some observations (*e.g.* Laurence, 1978; Swain *et al.*, 2003; 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 the cod's distribution might increase recruitment in these areas and decrease recruitment in what becomes the new southern distribution of cod (O'Brien *et al.*, 2000; Planque & Frédou, 1999). However, it should be noted these observations reflect estimates of optimal temperatures from laboratory studies (which may not be directly applicable to natural conditions or different stocks *e.g.* Neat & Righton 2007) 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 northward shift in the distribution of cod across its southern distribution (but see: Perry *et al.*, 2005).

The long adult life span of cod buffers occasional recruitment failures, but overfishing has truncated the age structure of cod stocks. Unfortunately, this has enhanced the vulnerability of this keystone species to the adverse effects of prolonged climate warming (Planque & Frédou, 1999). It is clear that exploitation of cod will compound the effects of climate change and phenology/mismatch on the recruitment success of cod. A diverse stock composed of multiple age classes, distributed over a large geographic area, will spawn in regions providing progeny with optimal survival conditions and recruitment success (Begg & Martinesdottir, 2002) due to dispersal of the mortality risk of the early life stages by increasing the spatial and temporal range over which progeny develop (Martinesdottir *et al.*, 2000). 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; Ware, 1975). At the onset of spawning, larger, older cod spawn earlier than smaller, younger cod (Begg & Martinesdottir, 2002). The spatial distribution of spawning cod also varies according to age and size, with larger cod 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 cod eggs hatch later. Furthermore, the intensity and the extent of spawning covary with the size of individual cod (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 spawning stock biomass.

Cod are well studied both in the field and in the laboratory (Brander, 1997), and the proceeding sections have clearly highlighted the importance of climatic variation on their ecology, and the difficulties in predicting what the future holds for cod. The survival of larval cod (Steinarsson & Björnsson, 1999), their subsequent recruitment (Brander & Mohn, 2004; Planque & Frédou, 1999), food (Brander *et al.*, 2001), subsequent growth (Björnsson *et al.*, 2001; Brander, 1995), fecundity (Kraus *et al.*, 2000; Pörtner *et al.*, 2001) and spawning date (Wieland *et al.*, 2000) at the individual, inter-annual or inter-stock level have been associated with certain aspects of climate, especially temperature. Recently, it has become apparent that although individual cod are highly mobile, their populations can be spatially and genetically structured (Hutchinson *et al.*, 2001; Metcalfe, 2006; Metcalfe *et al.*, 2005; Pampoulie *et al.*, 2006; Wright *et al.*, 2006). There is a pressing need to examine whether differences exist in the ecology or physiology of different sub-stocks (*e.g.* Mork *et al.*, 1983; Petersen & Steffensen, 2003; Sick, 1961) due to its potential to influence the response of cod to climatic change.

Although sea temperatures around Britain and Ireland have warmed in recent years, and some authors suggest that the geographical distribution of cod 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 cod (Neat & Righton, 2007), assuming they are not removed through fishing (Blanchard *et al.*, 2005). However, sea temperatures are predicted to continue to warm (Clark *et al.*, 2003; Hulme *et al.*, 2002), and it is likely that this heavily exploited fish faces an uncertain future in the seas around Britain and Ireland.

5.1.2 Herring & Pilchard

There are a number of separate herring stocks in the Northeast Atlantic, stretching from the Bay of Biscay to the Barents Sea (McQuinn, 1997). Atlanto-Scandinavian herring can be divided into three stocks: the Norwegian spring, Icelandic spring and the Icelandic summer-spawners. The Norwegian spring-spawning stock is the largest of the three and represents the largest herring stock in the world (Alheit & Hagen, 1997; Englehard & Heino, 2004). Routine sampling of this stock has been conducted since 1907 (Alheit & Hagen, 1997). These spring-spawning herring undertake long-distance migrations during their life cycle (Toresen & Østvedt, 2000). Around Britain and Ireland there are several stocks of herring 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). The North Sea stock is complex and is managed as one stock (Nash & Dickey-Collas, 2005) (with the exception of the Western Baltic Spring spawning herring). Within the North Sea, there are four main spawning stocks, with a number of minor spawning stocks (Heath *et al.*, 1997; Roel *et al.*, 2004). Exploitation of herring 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 herring fishing from 1977 to 1983. Since then exploitation has been subject to a total allowable catch (TAC) regulation for the international fleet, which has resulted in biomass rising to an estimated 1.5 million tonnes in the early 1990s (Heath *et al.*, 1997). The ability of herring 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 minimise bycatch.

Herring are highly mobile, rely on short, plankton-based food chains, are highly fecund and show plasticity in growth, survival and other life-history traits. These biological characteristics make them sensitive to environmental forcing and highly variable in their abundance (Alheit & Hagen, 1997). Naturally short-lived fishes like herring are extremely sensitive to recruitment fluctuations (Axenrot & Hansson, 2003). Nash & Dickey-Collas (2005) reported a positive relationship between abundance of herring 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 herring 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 herring, 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 (Sætre *et al.*, 2002; Toresen & Østvedt, 2000). 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 and Loeng (2000) suggest that these higher than average temperatures allow juvenile herring 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 herring feeding earlier and attaining maximal lipid concentrations by June-July as opposed to August-September when the water is cooler and plankton growth slower.

Axenrot & Hansson (2003) attempted to relate herring recruitment with the density of young-of-the-year (YOY) fish, spawning stock biomass and climate (NAO). All factors were positively (if weakly) correlated with year class strength (YCS), but when combined, there was a strong positive relationship with YCS (adjusted $R^2 = 0.93$), and the authors stressed the significance of climate change to recruitment in this stock.

Figure 14: Comparison of the geographical ranges of two pelagic clupeid fishes, herring and pilchard. For the latter, the normal breeding range is shown in darker shading and the lighter shading represents extreme limits during warm spells. (After Southward *et al.*, 1995).

The English Channel represents the approximate geographical boundary between the distribution of the cold-water herring and the warm water pilchard (also known as sardine) (Southward *et al.*, 1988; Southward *et al.*, 1995; Fig. 14). Both species have been captured in the sea off South 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 pilchard 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, herring even dominated in areas off the south coast of England, and pilchard retreated (Russell *et al.*, 1971; Southward *et al.*, 1988; Southward *et al.*, 1995). Southward *et al.*(1995) reported that during warmer periods, the density of pilchard eggs increased (by up to a factor of three) and the plankton community structure shifted. During cooler periods, plankton were characterised by an abundance of large diatoms in spring, a profusion of *Calanus* in the summer and the presence of intermediate trophic levels such as euphausiids. The warm water plankton community consisted of smaller diatoms and flagellates in spring, whilst dinoflagellates dominated the summer plankton.

In the North Sea during the summers of 1988-1990, the northern extent of herring was greater and some of the stock may have left the North Sea and migrated to the Faroe Plateau, a move that appears to reflect a response to short-term climatic variation (Corten, 2001). The period was characterised by a combination of high winter temperatures and a 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 herring in 1988-1990 could become the normal pattern in future years (Corten, 2001). Recently, pilchards, and another typical warm-water pelagic species, the anchovy *Engraulis encrasicholus*, 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 region.

From their analyses of historical catch records of pilchards and herring, 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, herring fisheries off the west coast of Sweden (Bohuslän) and Southern England showed abundant fish and high catches. In contrast, the Norwegian spring spawning herring and pilchard fishery off the South coast of England was negatively impacted. 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). Sinclair & Tremblay (1984) noted that although different herring stocks spawn throughout the year across the North Atlantic, larval metamorphosis is restricted to a five-month period (April to August). The authors hypothesised 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 exposed to high predation for a prolonged period (Sinclair & Tremblay, 1984).

5.1.3 Sandeels

Sandeels represent an abundant and important component of food webs in the North Atlantic (Lewy *et al.*, 2004), playing a central role in the North Sea ecosystem (Frederiksen *et al.*, 2006) as a prey for several commercially significant fish species (Greenstreet, 1995; Pedersen, 1999) as well as for seabirds (Wanless *et al.*, 1998; Wright, 1996) and marine mammals (Harwood & Croxall, 1988). Although five species of sandeels are found around Britain and Ireland (Macer, 1966; Wheeler, 1969), the lesser sandeel *Ammodytes marinus*, is the most abundant, comprising over 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 lesser sandeel's range (Reay, 1970). Sandeels form large aggregations and support the largest single-species fishery in the North Sea, and annual landings in the last decade have varied between 0.5 and 1 million tonnes (Poloczanska *et al.*, 2004). It is estimated that 0.36 million tonnes were landed in 2004 (ICES, 2005b). Recently, the abundance of North Sea sandeels has decreased, and the status of the stock and associated fishery is uncertain (ICES, 2005b).

Sandeels spawn in winter in the sandy, shallow water habitats they inhabit as adults (Proctor *et al.*, 1998), and lay demersal eggs. Sandeel larvae are planktonic and in the early phase of life can be subject to varying transport rates according to variation in oceanic currents (Proctor *et al.*, 1998). At a size of *ca.* 30-40 mm, sandeels become demersal and settle in offshore banks where they burrow into sandy sediments, a behaviour associated with predator avoidance and energy conservation (Reay, 1970). Once settled, sandeels follow a marked diurnal cycle of activity, emerging from sediments during daylight hours to feed and in a series of tank studies, Winslade demonstrated the importance of light (1974b), food availability (1974a), and temperature (1974c) on the activity of the lesser sandeel, (*Ammodytes marinus*).

Field and laboratory studies have demonstrated that post-settled sandeels have distinct habitat preferences (Holland *et al.*, 2005; Macer, 1966; Reay, 1970; Wright *et al.*, 2000) leading to a typically patchy distribution in the wild (Macer, 1966). In a combined field and laboratory study, Wright *et al.* (2000) demonstrated that sandeels from the seas around the Shetland Islands preferred to bury themselves in medium to coarse sands (median particle size 0.25-2 mm), and actively avoided silt rich (>10% silt) sediments. Wright et al (2000) also provided evidence sandeels preferred depths between depths 30-70 m, and that larger sandeels preferred coarser sands. Holland *et al.*(2005) confirmed many of Wright *et al.*'s (2000) predictions in a larger scale study in the north-western North Sea, and suggested that sandeels actually avoided habitats where silt content was >4%. When buried in the sediments, sandeels do not maintain permanent burrow opening, and depend on interstitial waters for dissolved oxygen. It has been suggested (Holland *et al.*, 2005; Wright *et al.*, 2000) that silt-rich sediments were unsuitable for resting sandeels either due to the risk of gills becoming clogged with fine sediments, or due to reduced concentrations of dissolved oxygen compared to sandy sediments (Lohse *et al.*, 1996). The restrictive habitat preferences of sandeels suggest that studies that have inferred sandeel distributions based on the availability of sandy habitats (*e.g.* Wanless *et al.*, 1997) may have overestimated the availability of suitable sandeel habitats (Wright *et al.*, 2000).

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 recent evidence suggests that several distinct aggregations exist with limited movements taking place between them (Munk *et al.*, 2002; Pedersen *et al.*, 1999; Proctor *et al.*, 1998). One such aggregation, on the Wee Bankie, Marr Banks and associated banks off the entrance to the Firth of Forth, southeast Scotland, has supported an industrial fishery since 1990 (Wanless *et al.*, 2004). This aggregation, like others found off Shetland and Norway, includes fish that are relatively slow growing, are around half the mean weight-at-age of other North Sea populations and tend to mature at a greater age and smaller size (Bergstad *et al.*, 2002; Wright & Bailey, 1996).

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-yr 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.* (2004) 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. Conversely, late hatching results in rapid growth, but over a reduced growing period, limiting first year growth (Wanless *et al.*, 2004). The start of the recorded decrease in the average size of the Wee Bankie sandeel coincides with a major ocean anomaly in the North Sea in the 1980s, characterised by reduced salinities and temperature (Dickson *et al.*, 1988; Turrell *et al.*, 1992) which was followed by a reverse trend in the late 1980s and early 1990s. Both trends were associated with profound changes in the biomass, community structure, and phenology of plankton in the North Sea (Edwards *et al.*, 2002).

The observed decline in mean size at age of Wee Bankie sandeels could potentially increase the risk of stock collapse due to 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 (Wanless *et al.*, 2004).

The SSB of North Sea sandeel is, by itself, a poor indicator of recruitment (ICES, 2005b; Pedersen *et al.*, 1999), possibly due to the marked population sub-structuring exhibited by sandeels (Pedersen *et al.*, 1999; Proctor *et al.*, 1998). 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 with the abundance of 1+ sandeels, which typically comprises between 40-80% 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 juveniles hatch. Arnott & Ruxton (2002) suggest that the density dependent effects imposed by 1+ sandeels are largely responsible for recruitment fluctuations. 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 sandeel recruitment in the North Sea, and suggest that this is due to temperature effects operating pre-dominantly upon the egg and/or larval stages. 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. Arnott & Ruxton (2002) suggest that long-term increases in SST are likely to shift the distribution of the lesser sandeel northwards, assuming of course that suitable habitats are available to the north (Holland *et al.*, 2005; Reay, 1970; Wright *et al.*, 2000). 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.

5.1.4 Basking shark

The effects of climate change on elasmobranch fishes (rays, skates and sharks) are poorly understood, and contrast with what is known about many important teleost fishes. Some elasmobranch fishes are extremely sensitive to temperature variation (*i.e.* as low as 0.001°C: Brown, 2003). Although it is currently unclear how important this sensitivity to temperature is to their ecology, many elasmobranchs demonstrate complex behavioural trade-offs that are often associated with temperature (Sims, 2003).

The planktivorous basking shark, *Cetorhinus maximus*, 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 west 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 basking shark fishery thrived in some European temperate waters (*e.g.* Norway, Soay in Scotland and Achill Island, Ireland). Between 1946 and 1986, these fisheries captured ca. 77 000 basking sharks (Sims & Reid, 2002). The success of the fisheries varied enormously from year to year due to large variation in the abundance of basking sharks (Kunzlik, 1988). The Achill Island fishery captured a total of 12 360 sharks between 1947-1975: catches peaked in the 1950s and then fell sharply as the abundance of sharks declined (Kunzlik, 1988). The decline was originally attributed to over-fishing (Parker & Scott, 1965), but in a detailed analysis Sims & Reid (2002) concluded that the decline was probably due to a distributional shift of sharks to more productive areas rather than overfishing of a local stock.

Cotton *et al.* (2005) showed recently that a major component of the interannual variation in relative abundance of basking sharks 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 basking shark abundance. At a local scale (0.01–10 km), basking shark distribution is determined largely by the abundance of adult *C. helgolandicus* (Sims, 1999; Sims & Merrett, 1997; Sims & Quayle, 1998), with SST being less important at these small scales (Sims *et al.*, 2003a). However, at greater scales (10–1 000 km) SST correlated significantly with basking shark 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 distribution patterns, long-term behavioural choices by these ectothermic planktivores may relate more closely to occupation of an optimal thermal habitat that acts to reduce metabolic costs and enhance net energy gain (Crawshaw & O'Connor, 1997; Sims *et al.*, 2003b).

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

There have been numerous historical accounts of apparent distribution shifts of fish in response to climate change, of which the herring/pilchard shift is a particularly clear illustration (see above & Fig. 11). For example, Jensen & Hansen (1931) and Hansen (1949, cited by Ottersen *et al.*, 2004) reviewed the response to the warming of West Greenland waters in the 1920s. This included the occurrence of new species, extension northwards of warmer water species together with over wintering by some species in northerly regions. For a review of these changes in distribution of fish in response to climate change see Ottersen *et al.* (2004).

It appears that the recent warming of the North Atlantic is responsible for a shift in distribution of some species. Counts of novel immigrant or vagrant species have been positively correlated to the increased water temperatures in the North Atlantic 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. Two major studies have recently described long-term distributional shifts in marine fishes from areas around Britain and Ireland (Genner *et al.*, 2004; Perry *et al.*, 2005). Genner et al. (2004) described and compared changes in the English (1913-2002) and Bristol (1981-2001) Channels, and Perry *et al.* (2005) described changes in the North Sea (1977-2001). Although it is difficult to know how much influence spatial variation in fishing mortality has had on the shifts reported by both sets of 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 (see Section 5.2.4).

Table 2: The response of North Sea fishes to increasing temperature (adapted from Perry *et al*., 2005): mean latitude distribution (↑= northerly and ↓= southerly shift) and mean depth of fish species in the North Sea (✓ = shift in depth). For those species with a boundary of distribution in the North Sea (marked * for northern and ** for southern species) ↑ = northerly shift in the boundary. All values marked with an arrow symbol are significant.

Common Name	**Species**	**Latitude**	**Depth**	**Boundary**
Pogge**	*Agonus cataphractus*			
Atlantic wolfish*	*Anarhichus lupus*			
Argentines	*Argentina* spp.			
Scaldfish**	*Arnoglossus laterna*	↑	✓	↑
Solenette**	*Buglossidium luteum*		✓	
Dragonet	*Callionymus lyra*	↑	✓	
Lesser weever**	*Echiichthys vipera*	↑	✓	↑
Grey gurnard	*Eutrigla gurnardus*	↑	✓	
Silvery pout*	*Gadiculus argenteus*			
Atlantic cod	*Gadus morhua*	↑	✓	
Witch*	*Glyptocephalus cynoglossus*			↑
Long rough dab*	*Hippoglossoides platessoides*	↑	✓	↑
Four spot megrim*	*Lepidorhombus boscii*			
Cuckoo ray*	*Leucoraja naevus*		✓	
Dab	*Limanda limanda*	↑	✓	
Angler fish	*Lophius piscatorius*	↑	✓	
Snake blenny	*Lumpenus lampretaeformis*	↑	✓	
Haddock*	*Melanogrammus aeglefinus*		✓	↑
Whiting	*Merlangius merlangus*	↑		↑
Hake	*Merluccius merluccius*			
Blue whiting*	*Micromesistius poutassou*		✓	
Lemon sole	*Microstomus kitt*			
Ling*	*Molva molva*			↑
Hagfish	*Myxine glutinosa*			
Plaice	*Pleuronectes platessa*		✓	
Saithe*	*Pollachius virens*			↑
Turbot**	*Psetta maxima*			
Four-bearded rockling	*Rhinonemus cimbrius*	↑	✓	
Small-spotted cat shark	*Scyliorhinus canicula*			
Redfish*	*Sebastes* spp.		✓	↑
Common sole**	*Solea solea*	↓		
Spurdog	*Squalus acanthias*			
Tub gurnard**	*Trigla lucerna*			
Norway pout	*Trisopterus esmarkii*	↓	✓	
Bib**	*Trisopterus luscus*	↑		↑
Poor cod	*Trisopterus minutus*	↑	✓	

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 (Table 2). However, both Norway pout and sole shifted their centre of distribution southwards. Perry *et al.* speculate that the shift in sole may be a response to improvements in water quality in the Thames Estuary. The southern distributional shift by Norway pout may be a response to localised warming in some northern areas of the North Sea (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, whose southern limit moved northwards *ca*. 820 km in only 25 years (Table 2: Perry *et al*., 2005). Perry *et al.* (2005) speculated that if temperatures continue to increase in the North Sea, blue whiting and redfishes will probably be lost from the North Sea, and bib 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 was those species that responded most strongly to climate change. Amongst the fish reported by Perry *et al.* (2005) to have shifted their distribution northwards is the cod. Neat & Righton (2007) examined the thermal ecology of individual cod at large in the North Sea and found no evidence that current temperatures constrained the distribution of adult cod and questioned whether cod were being forced northwards due to rising sea temperatures.

5.2 CLIMATE CHANGE: ESTUARINE & 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 systems 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 (Elliott & Hemingway, 2002; Horn *et al*., 1999). Inshore and estuarine areas are extremely important habitats for fish production, and many fish spend critical juvenile stages in estuarine nursery grounds (Blaber & Blaber, 1980; 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; but see Sims *et al.*, 2004).

5.2.1 Flounder

Flounder are flatfish that inhabit shallow inshore areas, including brackish and freshwater environments such as estuaries and the lower reaches of rivers for much of their life (Maitland, 2004; Wheeler, 1969). Their distribution ranges from southern Norway and the Baltic Sea to Morocco, and includes the Mediterranean Sea (Sims *et al.*, 2004). Flounder have a wide tolerance for salinity and temperature, and are the only species of flatfish to be found in freshwater in Europe (Wheeler, 1969). Although flounder 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-July and settle in the inshore environment (Grioche *et al.*, 1997).

Sims and co-workers (2004) studied how variation in the spawning migrations of flounder in the western English Channel varied with water temperature over a 13 year period. They demonstrated that flounder migrated from colder estuarine habitats to warmer offshore spawning grounds up to two months earlier in years when sea temperatures were lower than average by 2°C. They also noted that during colder years, flounder 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 spawning ground was greatest, the day of peak abundance of flounder on the spawning grounds was significantly earlier. The authors suggested that the earlier migration to the warmer offshore waters in colder years was a response by flounder 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 flounder 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 flounder abundance (negative correlation) and average size (positive correlation) in the Thames Estuary. Genner *et al.* (2004) reported that in the Bristol Channel the abundance of flounder 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.

5.2.2 Sole

Sole are an abundant and commercially important flatfish found around Britain and Ireland (Henderson & Seaby, 2005) with a northern distributional limit in the North Sea (Fonds, 1979; Rijnsdorp *et al.*, 1992). Sole typically use inshore waters and estuaries as nursery grounds (Henderson & Seaby, 2005). Recruitment of sole is determined during the 0+ stage, and water temperature plays an important role in recruitment success (Henderson & Holmes, 1991; Henderson & Seaby, 1994, 2005; Rijnsdorp *et al.*, 1992; Wegner *et al.*, 2003). High survival and normal hatching of sole eggs has been recorded at temperatures between 10–16°C and salinities between 20–40, and the growth of sole larvae increases with increasing temperature to a maximum of 22°C (Fonds, 1979). However, relations between water temperature and sole recruitment differ between populations. In the Bristol Channel, Henderson and colleagues (Henderson & Holmes, 1991; Henderson & Seaby, 1994, 2005) demonstrated a positive correlation between YCS and spring temperatures, but in the southern North Sea, Rijnsdorp and co-workers (1992) found a negative correlation between the abundance of 0+ sole with March water temperatures. These populations are both situated around the northern extreme of the range of the sole. The stock examined by Rijnsdorp *et al.*(1992) is located further north in a region that is considered more temperature-limited, and therefore it would be anticipated to respond more positively to an increase in temperature (Henderson & Seaby, 2005).

Using a 24-year time series of monthly sampling (in contrast to the virtual population analysis and pre-recruit surveys used by Rijnsdorf *et al.* (1992)), Henderson & Seaby (2005) confirmed the high positive correlation between spring temperature and sole abundance in the Bristol Channel, and demonstrated a ten fold increase in the abundance of juvenile sole since 1987. They also noted that while size was only weakly positively correlated with temperature, juvenile size was strongly and positively correlated with the NAO, a result supported by work in the Thames Estuary (Attrill & Power, 2002). The size (Henderson & Seaby, 2005) and number (Genner *et al.*, 2004; Henderson & Seaby, 2005) of adult sole also appear to be increasing in the Bristol Channel. These observations prompted Henderson & Seaby (2005) to conclude that increased primary and secondary production, associated with the increasingly positive trend in the NAO led to enhanced growth and abundance of sole through increased food availability and higher temperatures in the Bristol Channel and that this trend probably extended over the entire south-western region of Britain.

5.2.3 Eelpout

The eelpout 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 eelpout develops its eggs within the body cavity of the female, and gives birth to several fully formed young (Rogers *et al.*, 1998). The thermal tolerance of eelpout is closely correlated with the southern limits of its range (Pörtner *et al.*, 2001; van Dijk *et al.*, 1999) with an upper critical temperature limit between 21 and 24°C (van Dijk *et al.*, 1999). Pörtner *et al.*(2001) examined variation in eelpout abundance over four decades and demonstrated a distinct relationship between hot summer events and low abundance in the following year, suggesting that eelpout are sensitive to elevated temperatures. Recently Pörtner & Knust (2007) provided further evidence that variation in eelpout abundance was associated with sea temperatures. Using both field and laboratory data they developed a model that suggests that mortality increases above threshold temperatures due to physiological constraints on oxygen transport.

The distribution of eelpout is likely to shift northward as a response to global warming, with increased growth performance and fecundity at more northern latitudes as water temperatures rise (Pörtner *et al.*, 2001; van Dijk *et al.*, 1999), 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 a recent study (Greenwood *et al.*, 2002) showed a marked decrease in eelpout abundance from the most abundant (1981-1987) to the seventh most abundant species in 2001. The shift in abundance was negatively correlated with January bottom water temperatures in the area (Greenwood *et al.*, 2002). Hiscock *et al.* (2001) noted that eelpout could be the only commonly occurring marine fish in the Forth Estuary that could potentially disappear from Scotland. Catches of eelpout 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* is a species akin to eelpout 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 eelpout (Wheeler, 1969). Greenwood *et al.'s* (2002) long-term study of fish community structure of the Firth estuary showed increases in the abundance of shorthorn sculpin that were positively correlated with temperature. They speculated that the increase might reflect sculpin populations shifting into northern regions as a result of climate warming, or that sculpin were expanding into the niche being vacated by the declining eelpout.

5.2.4 Climate change effects on inshore fish communities

Genner *et al.* (2004) reported that climate change has a dramatic effect on community composition with significant community level responses to sea surface temperature. However, species within communities did not demonstrate consistent trends between sites, possibly due to additional local environmental determinants, interspecific ecological interactions and dispersal capabilities. In their two study areas, the English Channel (representing inshore marine habitats) and the Bristol Channel (representing estuarine habitats), only core species (those representing >99.4 % of the catch in terms of frequency) were analysed. Genner *et al.* (2004) identified 33 core species in the English Channel and 44 core species in the Bristol Channel. In the English Channel, nine species responded positively to warmer temperatures by increasing abundance: butterfly blenny (*Blennius ocellaris*), dragonet, topknots (*Phrynorhombus* sp.), solenette, poor cod, lesser-spotted dogfish (*Scyliorhinus canicula*), greater pipefish (*Syngnathus acus*), thickback sole (*Microchirus variegates*), and red bandfish (*Cepola macropthalma*). In the Bristol Channel assemblage, nine species responded strongly to temperature, again through increased abundance: sprat (*Sprattus sprattus*), whiting, five-bearded rockling (*Ciliata mustela*), cod, sand goby (*Pomatoschistus minutus*), bass (*Dicentrarchus labrax*), Dover sole, plaice and flounder. A tenth, the sea snail (*Liparis liparis*), responded negatively. It is worth noting that not one species is common to both lists detailed by Genner *et al.* (2004). This emphasises how the effects of sea temperature warming can act differently on species in adjacent sea areas. Regional differences such as those shown by Genner *et al.* (2004) highlight the sometimes complex interactions between species and their environments, and again question the relevance of the climate-envelope approach for predicting the response of fishes to climate change (Davis *et al.*, 1998; Mark *et al.*, 1999; Pearson & Dawson, 2003).

The Thames estuary fish assemblage is composed largely of juvenile individuals of marine species that use the estuary as a nursery habitat (Attrill & Power, 2002). Attrill & Power (*op. cit.*) demonstrated that the NAO influenced variation in the structure of the assemblage (54% of variation), the growth of many juvenile residents (76% of variation) and the abundance of many of the dominant species (69% of variation). Growth was positively correlated with the NAO, which explained higher proportions of the variation in growth than either estuarine water temperatures or North Sea temperatures alone. Nine of the fifteen fish species examined by Attrill & Power (2002) showed a significant relationship between variation in population abundance and the NAO. Flatfish and 'northern' species (*e.g.* herring: Wheeler, 1969) showed a negative relationship between abundance and the NAO, whilst those species considered 'southern' (*e.g.* bass, sprat: Wheeler, 1969) showed a positive relationship. The abundance of gadoid fishes, sole and estuarine species such as smelt, pipefish and pogge was not related to variation in the NAO (Attrill & Power, 2002).

The authors suggest that their data provide strong evidence for facultative use of estuarine environments by marine fishes in response to climate-induced temperature shifts.

5.3 CLIMATE CHANGE: DIADROMOUS FISHES

5.3.1 Atlantic salmon

A distinctive and recognisable fish, the Atlantic salmon has long been important for human populations in Britain and Ireland (Green *et al.*, 1993). Salmon are anadromous, and adult fish return from marine habitats to spawn in freshwater. After hatching, juvenile salmon reside and grow in freshwater. Following a metamorphosis that allows them to tolerate saline waters, they are known as smolts and migrate via estuaries or sea lochs to the sea. Salmon grow rapidly at sea, and after one year, some individuals known as grilse, return to their natal streams to spawn. Other individuals spend more than one year at sea and are referred to as multi-sea winter (MSW) fish.

Historically, the salmon was 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 effects, particularly man-made barriers such as dams and deterioration of water quality due to urban expansion and changes in agricultural practises (Crisp, 2000; NASCO, 2005). The distribution, ecology, habitat requirements and behaviour of salmon are extremely well studied (Armstrong *et al.*, 2003; Crisp, 2000; Hendry & Cragg-Hine, 2003; Klemetsen *et al.*, 2003). The current distribution of the Atlantic salmon extends from Russia, North America, Iceland, Greenland, and the Baltic Sea to Iberia (Crisp, 2000; Klemetsen *et al.*, 2003).

The Atlantic salmon is still widespread in some parts of Britain and Ireland, occurring in suitable water river systems not affected by poor water quality or barriers to migration. In England and Wales, salmon are found in rivers all around the coast with the noticeable exception of the east and southeast coasts stretching from south of the Yorkshire Esk to east of the River Itchen in Hampshire (Maitland, 2004). Many of the most productive salmon rivers are in the very North of England (Anon, 2005a). Salmon from rivers in England and Wales have recently undergone a marked decline (Anon, 2005a; Hendry & Cragg-Hine, 2003), with a *ca.* 50% reduction in the number of adults returning to freshwater since the 1970s. MSW fish are thought to contribute most (65%) of this decline (Anon, 2005a). Scotland is also famous for its salmon, and in 2003 alone, over 52 000 salmon were captured by rod and line, (*ca.* 60% of these fish were subsequently released alive). A further 33 000 fish were captured by the commercial fishery. 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, 2004a). 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 *ca.* 250 000 fish in 2001 to less than 145 000 in 2004 (Anon, 2004b).

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 Atlantic salmon 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; Magee *et al.*, 2003), riparian deforestation (Stefansson *et al.*, 2003) and over-extraction of water (Parrish *et al.*, 1998). Most of these factors act in concert to affect salmon stocks (Parrish *et al.*, 1998). Now, accelerating climate change (Hulme *et al.*, 2002) will likely further compound the adverse effects from anthropogenic sources on all salmon 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 Atlantic salmon (Ottersen *et al.*, 2004), whose oceanic migrations rival those of the large pelagic species such as tuna (Ottersen *et al.*, 2004). The consequences of global climate change may be more profound for migratory species such as the Atlantic salmon that depend on the timing of seasonal events and that use environmental variables as migratory cues (Friedland *et al.*, 2003). The anadromous life history strategy of many salmonid fishes has proved to be very successful, largely as this life history allows exploitation of resources in both freshwater and marine environments (Gross *et al.*, 1988). However, new and multiple challenges face salmon as they are dependent on the health and environmental state of both marine and freshwater ecosystems for their survival. In order to understand the relationship between salmon and climate variation, it is important to consider each of the key life history stages of this fish: eggs and juveniles in freshwater, smoltification, migration of smolts to the sea, post-smolts and maturing adults in the marine environment, and migration 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 Atlantic salmon (Crisp, 1996; Elliott, 1991). For example, acclimatised juvenile Atlantic salmon (parr) can survive at high temperatures with an incipient mean (± SE) lethal level (survival over seven 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

Atlantic salmon yolk-sac larvae (alevins) have upper temperature tolerance only slightly lower than that of the parr used by Elliot (1991).

Juvenile Atlantic salmon begin feeding in spring at water temperatures between 6-7°C, with preferred temperatures between 9-19°C and optimal growth is exhibited between 16 and 19°C (Elliott, 1991; Elliott & Hurley, 1997; Gibson, 1978; Javaid & Anderson, 1967). However, salmon become stressed at temperatures between 22-24°C and respond behaviourally by seeking refugia (Cunjak *et al.*, 1993). Lund and co-workers (2002) noted that parr from the Miramichi River, 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 about 30 days every summer (Lund *et al.*, 2002).

UKCIP02 predicts reduced summer precipitation for most of Britain and Ireland (the only exception is for Northern Scotland under the Medium-High and High scenarios), especially in the southeast of England (Hulme *et al.*, 2002). Rivers and their tributaries are therefore likely to become shallower, and may be less turbid due to reduced runoff. Ghent & Hanna (1999) speculated that this could increase the risk of avian predation of salmon 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. Salmon, 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.

Atlantic salmon 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 timeframe will not smoltify in the following spring (Evans *et al.*, 1984; Metcalfe, 1998). If parr attain a length of *ca.* 100-130 mm in autumn, they typically undergo smoltification in the following spring and migrate to the sea (Elson, 1957). Metcalfe (1998) suggests that the decision to smoltify is made in the previous summer and is triggered once the parr is on course to reach a certain size. The probability of smoltification therefore depends both on size and the rate of growth. Over the geographical range of Atlantic salmon, 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).

Atlantic salmon 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 due to climate change and temperature thresholds not only occur earlier in the year but 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 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 salmon parr grew faster and smolted earlier as a result of river water temperature increasing by 1-3°C due to distillery cooling effluent entering a Scottish river.

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, the 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 impacts during the short time that salmon 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 Atlantic salmon (McCormick *et al.*, 1999; Zydlewski *et al.*, 2005). In the spring, when parr smoltify, the temperature experienced by the young salmon determines the rate and timing of smoltification, and cumulative degree-days (rather than an absolute temperature threshold) provide a better indicator of the smoltification process and subsequent downstream movement (Zydlewski *et al.*, 2005). Zydlewski and co-workers 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 timeframe 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 findings are supported by several field studies.

Whalen *et al.* (1999) reported that peak migration of salmon 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 smolt migratory period of steelhead trout (*Oncorhynchus mykiss*) was extended and when the reverse occurred, the migratory period was shortened. Also, annual variation in the timing of peak migration of Atlantic salmon is related to variation in annual temperatures (McCormick *et al.*, 1999). 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 freshwater at high temperatures (Duston *et al.*, 1991; 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.*, 1999). 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 seawater.

At sea, Atlantic salmon mortality is highest during the first few months (Friedland *et al.*, 2003; Salminen *et al.*, 1995). This has been shown to exert a more profound effect on the numbers of spawning fish than mortality in freshwater (Chadwick, 1987; Friedland *et al.*, 1993). Most fish are believed to be lost to predation during the first weeks in the ocean (Friedland, 1998; Friedland *et al.*, 2000; 2003). In this phase, young salmon are sensitive to variable environmental factors such as water temperature, the NAO and to food availability (Davidson & Hazlewood, 2005; Friedland *et al.*, 2000; Friedland *et al.*, 1993; Friedland *et al.*, 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 Atlantic salmon 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 Atlantic salmon (Friedland *et al.*, 2003). Friedland *et al.* (1998) observed that thermal regimes during the first two 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). Further elucidation of this observation by 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. Post-smolt survival of Atlantic salmon appears to be influenced by the same mechanisms hypothesised for many fishes, *e.g.* better growth during a critical period is associated with reduced predation risk, and increased survival (Anderson, 1988; Pepin, 1991, 1993; Sogard, 1997).

Reddin & Friedland (1993) described a positive correlation between a winter temperature index and Atlantic salmon stock size in North America. Davidson and Hazlewood (2005) demonstrated positive relationships between post-smolt growth and the NAO winter index in four salmon 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 Atlantic salmon. Friedland and co-workers (2003) identified a negative effect of marine water temperature on post-smolt survival in spring of North American stocks, whereas in European stocks of Atlantic salmon, 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.

Low water flow in rivers can have a deleterious effect on upstream migration of salmon returning from the sea to spawn (Solomon & Sambrook, 2004; Solomon *et al.*, 1999). Studying radio-tagged salmon in four south western rivers in England, Solomon & Sambrook (2004) noted that when water flows were relatively high, the majority of migrating adult salmon 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 freshwater 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 salmon 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). Variations in return timing are generally considered to be phenotypic responses to changes or localised differences in local flow and temperature regimes (Hodgson & Quinn, 2002; Juanes *et al.*, 2004; Lilja & Romakkaniemi, 2003; Webb & McLay, 1996).

The predicted decrease in rainfall in the south of England in summer (Hulme *et al.*, 2002) could result in earlier and later runs of salmon (spring and autumn) becoming more prevalent in rivers such as the Fowey and Camel in Cornwall and Plym 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, USA, 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 migrations.

Increasing marine temperature affects growth of salmon at sea and can thus affect maturation and the relative contribution of grilse and MSW salmon returning to natal streams to spawn (Jonsson & Jonsson, 2004; Martin & Mitchell, 1985; Scarnecchia, 1983). Martin & Mitchell (1985) associated increasing marine temperature with larger numbers of fish returning as multi-sea-winter salmon and fewer as grilse in a Scottish system, with the average weight of grilse increasing with an increasing proportion of grilse. However, these results are in contrast to those of Saunders *et al.* (1983) and Scarnecchia (1983). Saunders *et al.* (1983) showed that cold winters inhibited maturation of cage-reared salmon and significantly reduced the grilse to salmon ratio. Scarnecchia (1983) showed a similar effect of smolts migrating from north Icelandic rivers into the subarctic compared to southern Icelandic stocks migrating into the warmer North Atlantic. He concluded that warmer temperatures resulted in better growth and earlier maturation (Scarnecchia, 1983). However, Martin & Mitchell (1985) concluded that the difference between the two sets of contrasting results is that cultured and Icelandic salmon, either by circumstance or design, were forced to endure cold sea temperatures while the Scottish fish could avoid such conditions.

The proportion of salmon returning as grilse to a Norwegian river was positively correlated with the NAO of the winter after smoltification (warmer marine conditions during positive NAO), as was the total number of returning fish (Jonsson & Jonsson, 2004). The weight increment of these grilse also positively correlated to 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 salmon returning as grilse (Jonsson & Jonsson, 2004).

There are concerns that Atlantic salmon 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 due to 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 Atlantic salmon habitat (Minns *et al.*, 1995), a view supported by the work of Lund and co-workers (2002), who suggested that any further increases in water temperature could have a profound effect for the salmon in Canada. In Britain, Davidson and Hazlewood (2005) predicted that freshwater growth of salmon 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 salmon in rivers in the south east of England are likely to decline, and that this will have adverse consequences for survival and abundance.

5.4 CLIMATE CHANGE: FRESHWATER FISHES

An extensive literature search (Fig. 9) demonstrated a distinct lack of detailed studies examining the effects of climate change of freshwater fishes in Britain and Ireland (*e.g.* Maitland, 1991; Weatherley *et al.*, 1991), which contrasts greatly with the situation in the marine environment. Such studies have been conducted elsewhere in Europe (Lappalainen & Lehtonen, 1997; Lehtonen, 1996, 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 (*e.g.* Fang *et al.*, 2004a, b, c; Magnuson *et al.*, 1997; Meisner *et al.*, 1987; Mohseni *et al.*, 2003; Tonn, 1990). It is probable that many of the predictions made for the effects of climate change on freshwaters in the continental USA 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 (*e.g.* perch: Shuter & Post, 1990) and these can be used to aid our understanding of the likely effects of climate change on our freshwater fishes. However, in contrast to the situation in the marine environment, our 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.

5.4.1 Arctic charr

The Arctic charr is a Holarctic salmonid, and its distribution is the most northerly of any freshwater fish (Klemetsen *et al.*, 2003; Maitland, 1995). 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 the species is non-anadromous (Klemetsen *et al.*, 2003), and typically inhabits oligo- or ultraoligotrophic lakes, where some populations migrate into running water for spawning (Maitland, 1995). Britain and Ireland support *ca.* 250 populations of charr (Maitland, 2004), all of which are lacustrine and non-anadromous. These populations may include charr 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 *et al.*, 2003; McCarthy *et al.*, 2004). It is currently unknown whether different morphs would exhibit differential responses to climate change.

Our understanding of the ecology of charr in Britain and Ireland ranges from some well-studied populations (*e.g.* Lake Windermere: 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 charr in a certain lake system (Igoe *et al.*, 2003). In his study of Lake Windermere charr, Swift (1964) provided evidence that suggested that charr populations inhabiting Britain and Ireland may have become adapted to warmer conditions than more northern populations.

Charr 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 (ca. 12°C: Larsson, 2005), even compared to other salmonids. Recent studies suggests an optimal temperature for growth (under conditions of unlimited food) of 15-16°C (Larsson & Berglund, 1998). Comparison of growth potential of Arctic charr, collected along a north-south gradient to examine potential adaptation to local temperatures (Larsson *et al.*, 2005), showed little evidence of interpopulation thermal adaptation in charr, and suggested that in European populations, growth is possible between 1-3°C, reaches a maximum between 15 and 17°C, and stops at *ca.* 21-22°C. Studies of upper lethal temperatures of juvenile charr from northern (*e.g.* Scandinavia: Elliott & Klemetsen, 2002; Lyytikainen *et al.*, 1997; Thyrel *et al.*, 1999) and southern (Lake Windermere: Baroudy & Elliott, 1994) areas of the species' European distribution show very similar results, and indicate that lethal temperatures for juvenile charr are in the region of 23°C.

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

Maitland & Lyle (1991) and Igoe *et al.* (2003) described a series of threats to the long-term conservation of Arctic charr 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 charr 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, charr should still be able to utilise 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 charr populations.

Mild increases in water temperature may lead to improved individual growth and production by charr in the short term (as already reported from some populations from Greenland: Kristensen *et al.*, 2006). However, it seems likely that due to the limited thermal tolerance of the species, the charr 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 charr 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 charr populations, future biologists may simply be limited to reporting the loss of charr from Britain and Ireland (Igoe *et al.*, 2001).

5.4.2 Perch

The perch 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, 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, 1946, 1950). As in Britain, perch represent an important resource for anglers in Ireland (Maitland, 2004).

Information on the effects of climate on perch mostly relate to temperature. For instance, the relationship between temperature and the ecology of the Eurasian perch (*Perca fluviatilis*) and its close relation, and ecological equivalent, the North American yellow perch (Craig, 2000; Thorpe, 1977), are well studied (Craig, 1980; Hokanson, 1977; Magnuson *et al.*, 1979). The optimal temperature for growth of perch in aquaculture settings is reportedly 23°C (Fiogbé & Kestemont, 2003), whilst Willemsen (1978) suggested a slightly 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 Eurasian and yellow perch ranged between 29.2 and 34°C. Weatherly (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 (Netherlands) perch congregated in waters heated to 31°C, and estimated a critical thermal maximum for perch 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).

In Britain and Ireland, perch spawn between April and June, in shallow water in structurally complex areas, *e.g.* among vegetation or sunken trees (Maitland, 2004). Eggs are laid in long strings, and hatch after 15-20 days, depending on water temperature (Guma'a, 1978). The development of perch eggs is strongly temperature dependent. Saat and Veersalu (1996) reported that embryonic development was successful between 8-18°C and optimal at 13°C. In an aquaculture setting Wang & Eckmann (1994) demonstrated that the mortality, development and hatching success of perch eggs were most efficient at temperatures between 12-20°C, but they presented evidence that there may be adaptation at the population level. For instance, Guma'a (1978) suggested that in Windermere, perch egg mortality was least between 6 and 10°C.

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 perch and other littoral spawners. Yellow perch eggs were shown by Williamson *et al.* (1997) to be extremely sensitive to ultraviolet 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. Although Mooij *et al.* (2005) predict that climate change will reduce transparency in shallow lakes, perch spawning success in shallow, clear-water lakes may decrease under future climates.

In northern Europe, the perch reproductive cycle is closely associated with seasonal changes in climate. Oocyte development starts in August (Le Cren, 1951; Treasurer & Holliday, 1981), and vitellogenesis typically extends from September to April–June when the fish are ripe for spawning (Guma'a, 1978; Treasurer & Holliday, 1981). Low winter temperatures are essential for successful vitellogenesis, and Hokansson (1977) suggested that in the case of the closely related yellow perch, exposure to temperatures below 6°C for a period of six months was optimal for gonad maturation. Studies examining the reproductive cycle of perch in waters receiving heated effluents have demonstrated that female perch are extremely sensitive to temperature during oogenesis, and elevated temperatures may lead to gonad malfunctions (Luksiene *et al.*, 2000; Sandström *et al.*, 1997). The spread of perch in Australia may have been restricted due to temperature-related disruptions to gonadogenesis, as winter temperatures often remain above 10°C (Hokanson, 1977).

Although food availability plays an important role (Persson, 1983), temperature is probably the strongest influence on the growth potential of perch (Craig, 1980; Goldspink & Goodwin, 1979; Hokanson, 1977; Karås & Neuman, 1981; Le Cren, 1958; Mooij *et al.*, 1994; Sandström *et al.*, 1995; Wang & Eckmann, 1994). Juvenile size is linked to the probability of survival in perch (Shuter & Post, 1990) as in many fishes (Sogard, 1997), and many authors have demonstrated an association between year class strength and warmer temperatures (Bohling *et al.*, 1991; Craig, 1980; Craig & Kipling, 1983; Goldspink & Goodwin, 1979; Lehtonen & Lappalainen, 1995; Paxton *et al.*, 2004; Tolonen *et al.*, 2003). In a detailed analysis, using multiple regression to examine the relationship between recruitment of perch and predator abundance, food availability, parent stock size as well as temperature, Paxton *et al.* (2004) showed that relationships between perch recruitment and temperature could be complex.

Perch are carnivorous, and undergo a well-described dietary shift from zooplankton, macroinvertebrates to piscivory as they grow (Allen, 1935). In a laboratory study, perch 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 perch and other species (Bergman, 1987, 1988; Persson, 1986). The well-recognised competitive-interaction between perch and roach (Persson, 1986, 1990b) is temperature dependent, and in laboratory experiments roach outperformed perch at temperatures above 18°C (Persson, 1986).

In order to examine the possible consequences of climate change on cool-water fishes, a number of authors have used perch or yellow perch as a model species (De Stasio *et al.*, 1996; Eaton & Scheller, 1996; Fang *et al.*, 2004a; Jansen & Hesslein, 2004; Lappalainen & Lehtonen, 1997; Magnuson *et al.*, 1990; Shuter & Post, 1990). Under climate warming these studies typically predict an expansion in the distribution of perch, due to increased scope for growth and reduced overwintering mortality (Shuter & Post, 1990), and it is likely that perch 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, perch 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 perch 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 it may be that in some waters, winter temperatures rise above optimal levels for perch oogenesis (Hokanson, 1977).

5.4.3 Roach

The roach 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 (Maitland, 2004). Roach are a popular species with anglers, both as bait for piscivorous fishes and as a target for angling in their own right. This characteristic has led to their translocation, both intentional and accidental (*e.g.* Winfield & Durie, 2004) and subsequent range expansion across Britain and Ireland into regions where for biogeographical reasons they were naturally absent (Wheeler, 1977). Today, roach are found in much of Great Britain, but are still absent from some areas of Scotland *e.g.* north of the Great Glen (Davies *et al.*, 2004; Maitland, 2004). After their accidental introduction into Ireland during the 19th Century, roach rapidly dispersed (Fitzmaurice, 1981), and today many Irish freshwaters are dominated by roach, a occurrence that has lead to concern on conservation and fisheries-management grounds (*e.g.* Lough Neagh: Harrod *et al.*, 2002).

Roach are omnivorous (Michel & Oberdoff, 1995), commonly feeding on zooplankton and macroinvertebrates, and are one of the few freshwater fishes of Britain and Ireland that can consume and assimilate plant and detrital materials. The generalist feeding habits of roach, combined with their potential to reach extremely high densities means that they can directly and indirectly impact other species within a system (Brabrand *et al.*, 1986; Persson, 1991), and even the function of the ecosystem itself. Roach are potentially strong competitors and under certain conditions have been shown to be capable of depressing populations of other fishes in lake systems *e.g.* perch (Persson, 1990a, b). Roach have also been associated with declines in *Coregonus* spp. in Britain and Ireland (Harrod *et al.*, 2002) and elsewhere in Europe (Langeland & Nøst, 1994; Raitaniemi *et al.*, 1999), especially following cultural eutrophication. Roach are effective zooplanktivores, 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; Cryer *et al.*, 1986). Removal of zooplankton not only impacts other fishes (see above), but can also lead to reduced grazing of phytoplankton (Brabrand *et al.*, 1986) which, combined with internal loading and recycling of nutrients by excretion and bioturbation (Horppila *et al.*, 1998) can impact water quality (Brabrand *et al.*, 1986).

Roach are 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 and van Dijk (2003) suggested this is due to reduced activities of digestive enzymes at low temperature. Experimental studies (Cocking, 1959a, b; Horoszewicz, 1971) suggest that lethal temperatures for juvenile roach 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 roach of 27°C, a temperature higher than that reached in many European lakes and rivers inhabited by roach (Staaks, 1996). Experimental studies by Hardewig and van Dijk (2003) indicate that in juvenile roach growth is maximised between 20-27°C. Forstner and Wieser (1990) examined the effect of water temperature on roach activity and metabolic requirements, whilst Holker (2003) examined how individual size and temperature interacted in terms of standard and routine metabolic rates. Feeding activity in the wild is positively correlated with water temperature (Hellawell, 1972), and Persson (1986) showed that the foraging ability of juvenile roach improved significantly at temperatures between 17–19°C, due to increased swimming speeds, reduced handling time and increased capture rates.

As might be expected, temperature not only affects the physiology of individual roach, 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 inter-annual variation in temperature plays a large role in the recruitment of roach. Reproduction is controlled both by photoperiod and temperature in roach (Jafri, 1989, 1990). Published accounts of roach 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 roach 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 due to an abrupt weather change. Roach held in the laboratory spawned at temperatures between 18 and 20°C (Jafri, 1990).

Future warming may lead to roach spawning earlier in the year, and hence an increased growing season for young of the year fish. A series of studies examining the effects of thermal effluent on reproductive biology of roach implies that a small (+2-3°C) increase in temperature over ambient conditions simply resulted in an advanced spawning date (Mattheeuws *et al.*, 1981) whilst 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 of roach reproductive biology in Lake Geneva, Gillet & Quétin (2006) describe a 15-day advancement in the date on roach spawning was initiated, a shift associated with a 2°C increase in mean May water temperature over the same period. In a similar study in the Narva River (Estonia), Nõges and Järvet (2005) reported that the temperature at the onset of roach spawning increased by 3°C due to warming of average water temperature between 1951-1990, but they found no evidence that roach advanced the date of spawning over the same period.

Currently, water temperatures in some parts of Britain and Ireland may be such that small roach 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 roach 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.

As a eurythermal generalist, it can be expected that roach 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 other limiting factors do not come into play (*e.g.* food, predation, disease or parasitism). Roach are likely to spawn earlier in the year (Gillet & Quetin, 2006), and YOY fish will forage with greater efficiency (Persson, 1986) over an extended growing season. If roach 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 roach do respond to climate warming in this way, there is considerable scope for predation on zooplankton to intensify, with subsequent community (*e.g.* roach-perch 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 roach populations (Linfield, 1980). Adult roach may respond to increased temperatures by increasing growth, with associated increases in fecundity in female fish (Vøllestad & L'Abee-Lund, 1990). Roach can withstand low dissolved oxygen concentrations (~1 mgl^{-1}: Doudoroff & Shumway, 1970) for short periods, even if water temperatures reach ~30°C (Cocking, 1959a). Although clearly at risk if water levels fall significantly or if small rivers, shallow lakes and ponds dry out, compared to many other fishes, roach should be relatively resistant to drought conditions. Riverine roach 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; Nunn *et al.*, 2003). Extreme precipitation events are predicted to increase in frequency (Arnell, 1998; Hulme *et al.*, 2002), which may lead to the loss of juvenile roach if suitable refugia are not available (Mann, 1996; Mann & Bass, 1997). However, on a larger scale, climate change represents an opportunity for roach in Britain and Ireland: warmer waters will result in increased recruitment due to earlier spawning, improved growth and survival of juvenile roach, and it is extremely likely that roach will expand their distribution, and intensify their influence on those habitats where they are found (Brabrand *et al.*, 1986).

5.4.4 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.* perch, roach, bream (*Abramis brama*) and carp (*Cyprinus carpio*), (Goldspink, 1978, 1981; Lappalainen & Lehtonen, 1997; Lehtonen & Lappalainen, 1995; Tolonen *et al.*, 2003). Following climate change, some lake-dwelling coldwater stenothermal fishes may be exposed to conditions beyond their thermal limits *e.g.* Arctic charr 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 (Harrod *et al.*, 2001; Maitland & Lyle, 1991; Winfield *et al.*, 1996). The response of other, more widely distributed stenothermal freshwater fishes, *e.g.* brown trout, 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), whilst southern or lowland populations may face conditions that restrict growth due to elevated temperatures, reduced dissolved oxygen concentrations or loss of habitat.

6 CONCLUSIONS

6.1 THREATS, REQUIREMENTS AND POSSIBILITIES

There is a growing scientific consensus that human activities have modified the composition of the atmosphere, and that these changes have, and will continue to, cause significant shifts in the climate of Britain and Ireland, including changes in air and water temperatures, precipitation, solar radiation and wind speed (Hulme *et al.*, 2002; Sweeney *et al.*, 2003). Many studies discussed in this briefing paper have demonstrated the often strong influence climate can have on the ecology and distribution of fishes (*e.g.* Attrill & Power, 2002; Brander & Mohn, 2004; Heath, 2005; Planque & Taylor, 1998; Stenseth *et al.*, 2004; Taylor, 1995). As might be expected, human-forced climate change has, and will continue to affect the fishes of Britain and Ireland (Genner *et al.*, 2004; Hiscock *et al.*, 2004; Perry *et al.*, 2005; Stebbing *et al.*, 2002). Humans rely heavily on aquatic systems for many goods and services, *e.g.* food production, recreation, nutrient recycling and gas regulation. Impacts 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.

Existing international agreements and legislation, *e.g.* the Ramsar convention (UNESCO, 1971), various European directives (EU, 1979, 1992, 2000), and the International Convention on Biological Diversity (UNCED, 1992) provide a clear obligation for Governments and managers to respond to this challenge. 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. Harley *et al*. (2006) noted that ecologists face immense challenges if they are to predict how natural systems will respond to environmental conditions that have no parallel in recent time. Ecologists have a variety of tools at their disposal (Harrington *et al.*, 1999; Shuter & Meisner, 1992), including the results of long-term monitoring studies (Genner *et al.*, 2004; Perry *et al.*, 2005), which provide baselines against which change can be quantified (Elliott, 1990; Visser & Both, 2005). Although Clarke (1993) notes that short-term laboratory experiments are of limited value to ecologists attempting to understand how organisms adapt to climate change, controlled laboratory and field studies have been essential sources of tolerance data of individual fishes (Alabaster & Lloyd, 1980). These data are essential for modelling responses to climate change at the individual, population or community level (Fang *et al.*, 2004a, b, c; Lappalainen & Lehtonen, 1997; Magnuson *et al.*, 1990; Magnuson *et al.*, 1997). However, to date, little work has examined how interspecific interactions might influence the response of fishes or other aquatic taxa to climate change (cf. Davis *et al.*, 1998) and there is a pressing need for such studies.

Much of our understanding of the likely consequences of climate change on aquatic ecosystems and fishes has resulted from routine monitoring of environmental and ecological data (Barrow & Hulme, 1997; Edwards & Richardson, 2004; Elliott, 1990, 1994; Genner *et al.*, 2004; George *et al.*, 2004; Hawkins *et al.*, 2003; Hays *et al.*, 2005; Paxton *et al.*, 2004; Planque & Taylor, 1998; Straile *et al.*, 2003; Winfield *et al.*, 1998). 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. If UK 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 (EU, 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).

If future climates follow the predictions detailed in UKCIP02 (Hulme *et al.*, 2002), fishes will continue to respond to climate change (Attrill & Power, 2002; Genner *et al.*, 2004; Heath, 2005; Perry *et al.*, 2005). Climatic change is likely to lead to considerable changes in the distribution of fishes as some species face increased, and others reduced, opportunities (Meisner *et al.*, 1987). Species that are currently at the southern limits of their temperature tolerances will encounter unsuitable conditions, and should, at least theoretically, shift their distribution. Future climates will favour mesothermal and eurythermal fishes and they are likely to extend their distribution, and their growth and production will increase, assuming other limiting factors *e.g.* availability of food, do not come into play (Hill & Magnuson, 1990). In freshwater, fish communities will be increasingly dominated by warm-adapted cyprinid and percid fishes, and cold-adapted salmonid fishes will face temperature stress. In extreme circumstances, some populations of extreme cold-adapted salmonid fishes may become extirpated *e.g.* Arctic charr and *Coregonus* spp. In marine fish communities, it is likely that the shift to warm-adapted fishes will be continued, and some cold-adapted fishes lost from our waters (Perry *et al.*, 2005), if existing environmental heterogeneity and organismal plasticity are insufficient to allow their continued existence. Diadromous species face particular uncertainties due to their utilisation 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. Holt (1990) observed that it is unlikely that we know enough relevant ecology, physiology and genetics to predict the evolutionary response of any fish species to climate change.

Climate warming may increase the probability that non-native taxa become successfully established in Britain, Ireland and surrounding waters (Brönmark & Hansson, 2002; Dukes & Mooney, 1999; Hickley & Chare, 2004; Sweeney *et al.*, 2003). The ecological implications of invasive species are complex (Chapin *et al.*, 2000), and can include competitive or predation effects on native taxa (Vander Zanden *et al.*, 1999), changes in ecosystem function (Crooks, 2002) or the introduction of novel parasites and pathogens that challenge the immunological capacity of native fishes (Gozlan *et al.*, 2005; Marcogliese, 2001).

As noted by Carpenter *et al.* (1992) and Magnuson (1991), the fisheries and aquatic ecology literature has 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 provide detailed models that are focussed on a relevant scale (Brander, 2005; Kapetsky, 2000; Wilby *et al.*, 1998). For example, Elliott *et al.* (2005) utilised 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 (EU, 2000).

Managers, scientists and other stakeholders (*e.g.* anglers) would benefit from simulation exercises designed to make detailed predictions of the likely changes in the ecology of particular fishes or water bodies under climate change following studies conducted in North America and elsewhere in Europe (Conlan *et al.*, 2005; Eaton & Scheller, 1996; Fang & Stefan, 1999; Fang *et al.*, 2004a, b, c; Lappalainen & Lehtonen, 1997; Mohseni *et al.*, 2003). A series of studies and projects that aim to investigate the effects of climate change on aquatic systems and taxa in Britain and Ireland are currently ongoing. The MarClim project aims to detail how intertidal species (including some fishes) across Britain and Ireland have responded to the rapid climate change that has occurred during the last century (http://www.mba.ac.uk/marclim). The EU-funded EUROLIMPACS project (www.eurolimpacs.ucl.ac.uk) includes partners from 36 different institutions and focuses on the key drivers of aquatic ecosystem change (land-use, nutrients, acid deposition and toxic substances) and examines their interactions with global change. Within England and Wales, the PRINCE project (Conlan *et al.*, 2005) examines the potential for climate change to impact freshwaters, from the perspective of physico-chemical drivers of ecosystem function and the process-based ecosystem interactions that could influence habitat, assemblage and/or species functioning and dynamic evolution. Several groups have developed databases containing information on physical and chemical features of many of the standing waters of Britain and Ireland (Hughes *et al.*, 2004; Smith *et al.*, 1993; Dr Ian Donohue, Trinity College, Dublin, pers. comm.). These data, combined with information on fish community and local predictions of future climate change would allow an assessment of waters most at risk from climate change (*e.g.* those that include sensitive species). These approaches would compliment the ongoing MONARCH study (Berry *et al.*, 2002; Cook & Harrison, 2001; Pearson & Dawson, 2003) that aims to predict the future climate envelopes of 120 UK BAP non-fish species.

6.2 EXPLOITATION & MANAGEMENT OF FISH STOCKS

The exploitation of fishes, via both wild-capture and aquaculture, is likely to be impacted by climate change, and adaptation strategies should be developed (*e.g.* targeting or culturing new species) in order to enhance the sustainable use of marine resources (McCarthy *et al.*, 2001; Troadec, 2000). Historically, humans have responded to climate-driven shifts in the abundance of exploited species by either transferring attention to other species or by fishing in other, often distant areas for similar resources (Sharp, 2003). Today, marine ecosystems are heavily exploited across the globe (Pauly *et al.*, 2002) and there is little scope for commercial fisheries to move to new areas. It is likely that commercial fisheries in Britain and Ireland will respond rapidly to shifts in the distribution of fishes following climate change (Attrill & Power, 2002; Genner *et al.*, 2004; Heath, 2005; Perry *et al.*, 2005).

During the assessment of exploited stocks, increased attention should be paid to quantifying the effects of climatic factors (*e.g.* temperature) on the growth of exploited species, as they may have significant influence on stock assessment, catch forecasting and evaluation of the consequences of climate change. In order to investigate the effect for individual stocks, data on temperature and fish distribution need to be analysed jointly (Brander, 1995). Further work is needed on stock recruitment relationships in order to ensure that climatic influences (such as the temperature or the NAO) are modelled in an appropriate manner (Axenrot & Hansson, 2003; Brander, 2005; Clark *et al.*, 2003; Planque *et al.*, 2003). Failure to include environmental factors can result in over-estimates of stock biomass, potentially leading to overly high quotas being set (Brander, 2005; Brander & Mohn, 2004) especially in areas where stocks occur at the edge of the species distribution (Planque *et al.*, 2003; Planque & Frédou, 1999). The development of such models will become increasingly important as the effects of climate change on marine ecosystems become more pronounced (Clark *et al.*, 2003).

Between the 1950s and the early 2000s, total annual aquaculture production in Britain and Ireland increased from less than 1000 to more than 240 000 t (FAO, 2005). Aquaculture currently provides employment and income to *ca.* 10 000 people in Britain and Ireland, often in areas where there are few other options for employment. Some aspects of climate warming will be beneficial for aquaculture, for instance the scope for growth will increase in many species, and productivity will increase. Currently in Britain and Ireland, the bulk of aquaculture production is of Atlantic salmon, but warming following climate change is likely to allow diversification to novel species or increased production from cultured species that are currently temperature limited (McCarthy *et al.*, 2001; Troadec, 2000). UKCIP02 predicts significant reductions in summer precipitation in some parts of Britain and Ireland (Hulme *et al.*, 2002), indicating that aquaculture facilities and hatcheries may face restricted water supplies, and changes in groundwater following warming could further impact inland aquaculture systems (Arnell, 1998). Salmonid hatcheries may have to invest in equipment to oxygenate water during future summers (Lehtonen, 1996). Clearly, those responsible for the regulation and development of aquaculture in Britain and Ireland need to consider the implications of climate change.

It is not only cultured fishes that will respond to climatic change: currently, temperatures restrict the range of fish pests and parasites, and warmer waters are likely to lead to an increase in the incidence of outbreaks of unwelcome infections (Högland & Thulin, 1990; Lafferty & Kuris, 1999; Marcogliese, 2001), especially as many parasites of temperate fishes have temperature thresholds below which transmission is limited (Chubb, 1976). Temperature variations of a range of only a few degrees could have indirect implications for aquaculture facilities: *e.g.* increased temperatures may lead to an increased incidence of harmful algal blooms that release toxins into the water and generate fish kills (Shumway, 1990; Smayda, 2006). Caged fish will be particularly susceptible to such occurrences, unlike wild fishes that may have the opportunity to avoid contaminated waters (Kent & Poppe, 1998).

6.3 ANGLING AND CLIMATE CHANGE

A considerable proportion of the funding for management and protection of freshwater resources in some parts of Britain and Ireland (*e.g.* England and Wales) comes from recreational fishing (Arnell, 1998). Although the numbers of participants are falling, angling is still an extremely popular participation activity (Hughes & Morley, 2000) and forms an important source of employment and income to many in Britain and Ireland. Some freshwater anglers are likely to benefit from climate change as meso and eurythermal species respond positively to increased temperatures through increased consumption rates, growth, production and reproductive success (see above). However, is difficult to predict how fish communities will respond, *e.g.* invasive and other non-target species may benefit more from climate change than the species preferred by anglers. Warmer summers may lead to considerable problems in highly stocked lake fisheries including deoxygenation and disease. North (2002) reported extreme stocking densities in some commercial coarse fisheries (range: 250 - 14 000 kg ha^{-1}). Under future precipitation patterns, availability of water may be restricted (Arnell, 1998) which, combined with increased water temperature suggests that fisheries managers will have to limit stocking densities, and possibly oxygenate stocked lakes (Lehtonen, 1996). Fisheries for salmonid fishes face marked threats, especially in southern regions, both for wild stocks (see above) and for stocks managed for recreational angling, such as the put and take rainbow trout fisheries that are common in Britain and Ireland (Maitland, 2004).

Like other human activities, anglers follow fashions, and for several years some anglers in Britain have followed a preference for exotic, non-native species that are stocked legally and illegally into fisheries (Hickley & Chare, 2004). Currently, the spread of these non-native fishes is controlled through legislation and sometimes ecologically, as reproduction and growth can be temperature limited under present climatic conditions. However, in a warming climate there is a risk that these species will be more successful in invading new water bodies (Dukes & Mooney, 1999). These invasive species can actively predate on native species (Wysujack & Mehner, 2005), compete for resources (Hickley & Chare, 2004) or introduce new diseases or parasites (Gozlan *et al.*, 2005). Improved education of anglers and fisheries managers, combined with stricter legislation and enforcement may be required.

6.4 RESOURCE USE, POWER GENERATION AND EMISSION CONTROL

Recent droughts have highlighted the vulnerability of water supplies in Britain and Ireland (Hughes & Morley, 2000), and climate predictions indicate that the availability of water will be reduced for aquatic systems in some areas of Britain and Ireland in the future (Hulme *et al.*, 2002; Sweeney *et al.*, 2003). Bodies responsible for the management of water resources will undoubtedly face increased demands for water supplies as climate changes (*e.g.* for agricultural, industrial and household usage). Although there is increased promotion of sustainable water use (Hughes & Morley, 2000) large volumes are lost from piped supplies (*e.g.* in the year 2005-6, an estimated 3 576 x10^{6} litres were lost *per day* by companies supplying water in England and Wales (OFWAT, 2006)). In future, it is essential that water resources be managed to ensure supplies of water in sufficient volume and quality to sustain aquatic ecosystems (Arnell, 1998).

Although controls have been proposed on atmospheric emissions (United Nations, 1997), these have not been effective, and emissions continue to rise worldwide. There is continued debate regarding how human societies should react to climate change, including changes in the ways that energy is generated (*e.g.* shifts from fossil-fuels). Although current means of energy generation affect fish (Carter & Reader, 2000), proposed changes may lead to further impacts. Renewed interest in the potential for nuclear power clearly has implications for fishes, *e.g.* radiation (McCartney *et al.*, 1994), thermal effluent (Sandström *et al.*, 1995), and impingement of eggs, larvae and small fishes (Turnpenny, 1988). There are also potential ecological impacts from the renewable sources of energy *e.g.* wind, tidal or hydroelectric power (Davies, 1988; Gill, 2005; Mathers *et al.*, 2002). For instance, noise produced by windfarms may interfere with acoustic communication between fishes, or trigger fright responses (see Wahlberg & Westerberg, 2005 for a review), whilst electromagnetic fields emanating from buried cables have the potential at least to interfere with electrolocation by elasmobranch fishes (Kalmijn, 1971).

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 (United Nations, 1997), including initiatives by the UK and Irish Governments (DEFRA, 2006; DEHLG, 2000) to limit emissions of the gases associated with climate change. However, the residual inertia in climate systems (Hulme *et al.*, 2002) is such that even a total cessation of emissions tomorrow would leave fishes exposed to continued climate change for *ca.* 50 years. Hence, regardless of the success or failure of programmes aimed at curbing climate change, we can expect major changes in fish communities.

7 ACRONYMS USED

BAP	Biodiversity Action Pan
CITES	The Convention on International Trade in Endangered Species of Wild Fauna and Flora
DST	Data Storage Tags
FSBI	Fisheries Society of the British Isles
HadCM3	The HadCM3 (Hadley Centre Coupled Model, version 3) is a coupled atmosphere-ocean general circulation model developed at the Hadley Centre, UK
ICES	International Council for the Exploration of the Sea
IPCC	Intergovernmental Panel on Climate Change
IUCN	The World Conservation Union (known as the International Union for the Conservation of Nature and Natural Resources prior to 1990)
MSW	Multi-sea winter salmon (salmon that spend more than one year at sea)
NAD	North Atlantic Drift
NAO	North Atlantic Oscillation
SSB	Spawning Stock Biomass
SST	Sea Surface Temperature
THC	Thermohaline Circulation
UKCIP02	United Kingdom Climate Impacts Programme 2002 report
UV	Ultra Violet radiation
YCS	Year Class Strength
YOY	Young of the year fish

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