Physical and ecological impacts of climate change relevant to marine and inland capture fisheries and aquaculture

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1. Climate change: the physical basis in marine and freshwater systems

In recent years numerous long-term changes in physical forcing have been observed at global, regional and basin scales as a result of climate and other anthropogenic changes. Impacts of these on biological processes supporting fish and fisheries production in marine and freshwater ecosystems have already been observed and may be used as proxies to estimate further global climate change impacts. These physical factors include atmospheric circulation, intensity and variability patterns, ocean currents and mixing, stratification, hydrological cycles and seasonal patterns.

1.1. HEAT CONTENT AND TEMPERATURE

1.1.1. Ocean ecosystems

The ocean plays an important role in regulating the climate. Its heat capacity (and thus net heat uptake) is about 1000 times larger than that of the atmosphere. Biological activity interacts substantially with physical processes, creating several feedback loops. For example, heat absorption by phytoplankton influences both the mean and transient state of the equatorial climate (e.g. Murtugudde et al., 2002; Timmermann and Jin, 2002; Miller et al., 2003), and the global mean sea surface temperature field (Frouin and Lacobellis, 2002).

There is significant consensus to conclude that the world ocean has warmed substantially since 1955 and that the warming accounts for over 80 percent of changes in the energy content of the Earth’s climate system during this period (Levitus et al., 2005a; Domingues et al., 2008, Figure 1). Studies have attributed anthropogenic contributions to these changes (Bindoff et al., 2007), and it has been suggested that climate change models underestimate the amount of ocean heat uptake in the last 40 years (Domingues et al., 2008). While the global trend is one of warming, significant decadal variations have been observed in the global time series (Figure 2), and there are large regions where the oceans are cooling (Bindoff et al., 2007). For example, Harrison and Carson (2007) observed large spatial variability of 51-year trends in the upper ocean, with some regions showing cooling in excess of 3 °C, and others warming of similar magnitude. They concluded that additional attention should be given to uncertainty estimates for basin average and World Ocean average thermal trends.

Observations indicate that warming is widespread over the upper 700 metres of the global ocean, but has penetrated deeper in the Atlantic Ocean (up to 3000 m) than in the Pacific, Indian and Southern Oceans, because of the deep overturning circulation that occurs in the North Atlantic (Levitus et al., 2005a). At least two seas at subtropical latitudes (Mediterranean and Japan/East China Sea) are also warming.

It is predicted that even if all radiative forcing agents were held constant at year 2000 levels, atmospheric warming would continue at a rate of about 0.1 °C per decade due to the slow response of the oceans. Geographical patterns of projected atmospheric warming show greatest temperature increases over land (roughly twice the global average temperature increase) and at high northern latitudes, and less warming over the southern oceans and North Atlantic (Meehl et al., 2007).
FIGURE 1.
Energy content changes in different components of the Earth system for two periods (1961–2003, blue, and 1993–2003, burgundy). The ocean heat content change is from Levitus et al. (2005c); continental heat content from Beltrami et al. (2002); atmospheric energy content based on Trenberth et al. (2001); and arctic sea ice release from Hilmer and Lemke (2000); rest from IPCC (2007). Positive energy content change means an increase in stored energy. All error estimates are 90 percent confidence intervals. No estimate of confidence is available for the continental heat gain. Some of the results have been scaled from published results for the two respective periods. Ocean heat content change for the period 1961 to 2003 is for the 0 to 3,000 m layer. The period 1993 to 2003 is for the 0 to 700 m (or 750 m) layer and is computed as an average of the trends from Ishii et al. (2006), Levitus et al. (2005a) and Willis et al. (2004). From Bindoff et al. (2007).

FIGURE 2
Time series of global annual ocean heat content (10^22 J for the 0-700 m layer (black) and 0-100 m layer (thick red line; thin red lines indicate estimates of one standard deviation error), and equivalent sea surface temperature (blue; right-hand scale). All time series were smoothed with a three-year running average and are relative to 1961 (modified from Domingues et al. 2008).
1.1.2. Inland waters

The International Panel on Climate Change (IPCC) has examined the implications of projected climate change for freshwater systems. Overall, it concludes that freshwater resources are vulnerable to, and have the potential to be strongly impacted by, climate change (Bates et al., 2008). Expected changes include (Kundzewicz et al., 2008): decreases of between 10 and 30 percent of average river runoff at mid-latitudes and in the dry tropics by mid-century, but increases of 10 - 40 percent at high latitudes and in the wet tropics (Milly et al., 2005); shifts in the form of precipitation from snow to rain and a consequent change in the timing of peak river flows; and changes in flood and drought frequency and intensity. The IPCC assessment also concluded that the impacts of climate change and effective adaptations will depend on local conditions, including socio-economic conditions and other pressures on water resources (Kundzewicz et al., 2008). Patterns of temperature change for inland waters are expected to follow the changes over land areas which are warming at greater than global atmospheric annual means because there is less water available for evaporative cooling and a smaller thermal inertia as compared to the oceans (Christensen et al., 2007).

Since the 1960s, surface water temperatures have warmed by 0.2 °C to 2 °C in lakes and rivers in Europe, North America and Asia (Rosenzweig et al., 2007). Increased water temperature and longer ice free seasons influence thermal stratification. In several lakes in Europe and North America, the stratified period has advanced by up to 20 days and lengthened by two to three weeks as a result of increased thermal stability (Rosenzweig et al., 2007; O’Reilly et al., 2003). Ninety percent of inland fisheries occur in Africa and Asia (FAO, 2006). Therefore, a brief summary of likely physical impacts of climate change in these regions follows. Warming in Africa is very likely to be larger than the global annual mean warming throughout the continent and in all seasons, with drier subtropical regions warming more than the wetter tropics. Annual rainfall is likely to decrease in much of Mediterranean Africa and the northern Sahara, with a greater likelihood of decreasing rainfall as the Mediterranean coast is approached. Rainfall in southern Africa is likely to decrease in much of the winter rainfall region and western margins. There is likely to be an increase in annual mean rainfall in East Africa. It is unclear how rainfall in the Sahel, the Guinea Coast and the southern Sahara will evolve (Christensen et al., 2007).

Warming is likely to be well above the global mean in central Asia, the Tibetan Plateau and northern Asia, above the global mean in eastern Asia and South Asia, and similar to the global mean in South East Asia. Precipitation in boreal winter is very likely to increase in northern Asia and the Tibetan Plateau, and likely to increase in eastern Asia and the southern parts of South East Asia. Precipitation in summer is likely to increase in northern Asia, East Asia, South Asia and most of South East Asia, but is likely to decrease in central Asia. It is very likely that heat waves/hot spells in summer will be of longer duration, more intense and more frequent in East Asia. Fewer very cold days are very likely in East Asia and South Asia. There is very likely to be an increase in the frequency of intense precipitation events in parts of South Asia, and in East Asia. Extreme rainfall and winds associated with tropical cyclones are likely to increase in East Asia, South East Asia and South Asia. There is a tendency for monsoonal circulations to result in increased precipitation because of enhanced moisture convergence, in spite of a tendency towards weakening of the monsoonal flows themselves. However, many aspects of tropical climatic responses remain uncertain (Christensen et al., 2007).

Inland water temperatures are strongly linked to the dynamics of the hydrological cycle. Overall, there were many studies on trends in river flows and lake levels during the twentieth century at scales ranging from catchment to global. Some of these studies detected significant trends, such as rising levels in response to increased snow and ice melt, or declines because of the combined effects of drought, warming and human activities (Rosenzweig et al., 2007). Overall, no globally homogeneous trend has been reported (Rosenzweig et al., 2007). Variation in river flows from year to year is very strongly influenced in some regions by large
scale atmospheric circulation patterns associated with El Niño Southern Oscillation (ENSO) North Atlantic Oscillation (NAO) and other decadal variability systems. On a global scale, there is evidence of a broadly coherent pattern of change in annual runoff, with some regions experiencing an increase at higher latitudes and a decrease in parts of West Africa, southern Europe and southern Latin America (Milly et al., 2005). Labat et al., 2004) claimed a 4 percent increase in global total runoff per 1 °C rise in temperature during the twentieth century, with regional variation around this trend, but this has been challenged (Legates et al., 2005) because of the effects of non climatic drivers on runoff and bias due to the small number of data points.

Worldwide a number of lakes have decreased in size during the last decades, mainly because of human water use. For some, declining precipitation was also a significant cause; e.g. Lake Chad (Coe and Foley, 2001; Figure 3). In general, atmospheric warming is contributing to a reduction of rainfall in the subtropics and an increase at higher latitudes and in parts of the tropics. However, human water use and drainage is the main reason for inland water shrinkages (Christensen et al., 2007).

FIGURE 3
Comparison of the area and volume of Lake Chad in 1973 and 1987. Lake Chad, which supplies water to Chad, Cameroon, Niger and Nigeria, was once one of the largest lakes in Africa. Extensive irrigation projects, encroaching desert and an increasingly dry climate have caused it to shrink to 5 percent its former size (from NASA Goddard Space Flight Centre, www.gsfc.nasa.gov)

Predictions suggest that significant negative impacts will be felt across 25 percent of Africa’s inland aquatic ecosystems by 2100 (SRES B1 emissions scenario, de Wit and Stankiewicz, 2006) with both water quality and ecosystem goods and services deteriorating. Because it is generally difficult and costly to control hydrological regimes, the interdependence between catchments across national borders often leaves little scope for adaptation.

1.2. OCEAN SALINITY, DENSITY AND STRATIFICATION
Ocean salinity changes are an indirect but potentially sensitive indicator of a number of climate change processes such as precipitation, evaporation, river runoff and ice melt, although data are much more limited than those for temperature. Figure 4 shows linear trends of zonally averaged salinity in the upper 500 m of the World Ocean for five-year periods from 1955 to 1998 (Boyer et al., 2005). In summary, changes in ocean salinity at gyre and basin scales in the past half century have been observed, with near surface waters in the more evaporative regions increasing in salinity in almost all ocean basins, and high latitudes showing a decreasing trend due to greater precipitation, higher runoff, ice melting and advection. Overall indications are that the global ocean is freshening (Antonov et al., 2002),
but with large regional differences. Salinity is increasing in the surface of the subtropical North Atlantic Ocean (15-42 °N), while further north there is a freshening trend. In the Southern Ocean there is a weak freshening signal. Freshening also occurs in the Pacific, except in the upper 300 m and in the subtropical gyre, where salinity is increasing. The Indian Ocean is generally increasing its salinity in the upper layers (Bindoff et al., 2007). Although the low volume of available data precludes us from reaching stronger conclusions, the apparent freshening of the World Ocean seems to be due to an enhanced hydrological cycle (Bindoff et al., 2007).

**FIGURE 4**
Linear trends (1955–1998) of zonally averaged salinity (psu) in the upper 500 m of the World Oceans (from Boyer et al. 2005). The contour interval is 0.01 psu per decade and dashed contours are ±0.005 psu per decade. The dark solid line is the zero contour. Red shading indicates values equal to or greater than 0.005 psu per decade and blue shading indicates values equal to or less than –0.005 psu per decade.

Predictions of salinity patterns in a warmer ocean are consistent with observations. Sarmiento et al. (2004) expected salinity changes as a result of an enhancement of the hydrologic cycle that occurs due to the increased moisture bearing capacity of warmer air. The combined effect of the temperature and salinity changes would be an overall reduction of the surface density, resulting in an expected increase in vertical stratification and changes in surface mixing (Sarmiento et al., 2004). In most of the Pacific Ocean, surface warming and freshening act in the same direction and contribute to reduced mixing, which is consistent with regional observations (Freeland et al., 1997; Watanabe et al., 2005). In the Atlantic and Indian Oceans, temperature and salinity trends generally act in opposite directions, but changes in mixing have not been adequately quantified.

Sea ice changes are one of the major factors involved in the above mentioned salinity patterns in a warmer ocean. Sea ice is projected to shrink in both the Arctic and Antarctic over the twenty-first century, under all emission scenarios, but with a large range of model responses (Meehl et al., 2007). In some projections, arctic late summer sea ice disappears by 2030 (Stroeve et al., 2007).

Large salinity changes have been historically observed in the North Atlantic in association with sporadic changes in fresh water inputs and the NAO. These Great Salinity Anomalies (Dickson et al., 1988) result from strengthening of the subpolar gyre during positive NAO phases, and cause lower surface salinity in the central subpolar region. Three such anomalies have been documented in 1968 to 1978, the 1980s and 1990s (Houghton and Visbeck, 2002).

### 1.3. OCEAN CIRCULATION AND COASTAL UPWELLING

Observed and predicted changes in the ocean’s heat content and salinity are and will continue to affect circulation patterns. A full description of existing and potential impacts is beyond the scope of this review, and readers are directed to the relevant IPCC 4AR for details (Bindoff et al., 2007). We will however, discuss two specific circulation issues: possible changes in the North Atlantic Meridional Overturning Circulation (MOC), as impacts could be extreme; and
long-term patterns in coastal upwelling, because of its implication to biological production in eastern boundary currents. In addition, it is worth noting that there is evidence that mid-latitude westerly winds have strengthened in both hemispheres since the 1960s (Gillett et al., 2005) and this is predicted to be enhanced under global warming conditions, with concomitant ocean circulation changes.

1.3.1. Meridional Overturning Circulation (MOC)
The Atlantic MOC carries warm upper waters into far-northern latitudes. In the process it cools, sinks and returns southwards at depth. Changes in the hydrological cycle (including sea ice dynamics, as freezing water releases salt) have the potential to influence the strength of the MOC. The heat transport of the MOC makes a substantial contribution to the climate of continental Europe and any slowdown would have important atmospheric climate consequences (up to 4 °C lower than present for a total shutdown, Vellinga and Wood, 2002). Observations and model predictions indicate increased freshwater input in the Arctic and sub Arctic (both through precipitation reduced sea ice, Schrank, 2007; Figure 5), potentially increasing stratification, with increased stability of the surface mixed layer, reduction in salt flux, reduced ocean convection, and less deepwater formation (e.g. Stenevik and Sundby, 2007), which could lead to a prolonged reduction in thermohaline circulation and ocean ventilation in the Atlantic. A reduction of about 30 percent in the MOC has already been observed between 1957 and 2004 (Bryden et al., 2005). Model simulations indicate that the MOC will slow further during the twenty-first century (up to a further 25 percent by 2100 for SRES emission scenario A1B, Meehl et al., 2007). Whereas a positive NAO trend might delay this response by a few decades, it will not prevent it (Delworth and Dixon, 2000). Currently, none of the available climate models predict a complete shutdown of the MOC, but such an event cannot be excluded if the amount of warming and its rate exceed certain thresholds (Stocker and Schmittner, 1997). Schmittner (2005) suggested that a disruption of the thermohaline circulation (THC) would collapse North Atlantic zooplankton stocks to less than half of their original biomass. Kuhlbrodt et al. (2005), conducted an in-depth study of the physical, biological and economic consequences of a THC change for northern Europe. They concluded that a major THC change might increase sea level by more than 50 cm. They further suggested strong impacts on the whole marine food web in the northern North Atlantic, from algae to plankton, shrimp and fish. In one specific study, Vikebo et al. (2005) investigated the consequences of a 35 percent reduction in the THC on Norwegian seas. The main results were a drop in sea surface temperature (SST) in the Barents Sea of up to 3 °C, because of reduced inflow of Atlantic Water to the Barents and an increased flow west of Svalbard. Simulations of the transport of larvae and juvenile cod under the new scenario indicate a possible southward and westward shift in the distribution of cod year classes from the Barents Sea onto the narrow shelves of Norway and Svalbard and reduced individual growth of the pelagic juveniles with subsequent poorer year classes (probably <10 percent of the strong year classes of today). An increasing number of larvae and juveniles would be advected towards the western parts of Svalbard and possibly further into the Arctic Ocean where they would be unable to survive (under present conditions).

FIGURE 5
Sea ice extent anomalies (computed relative to the mean of the entire period) for (a) the Northern Hemisphere and (b) the Southern Hemisphere, based on passive microwave satellite data. Symbols indicate annual mean values while the smooth blue curves show decadal variations. Linear trend lines are indicated for each hemisphere. For the Arctic, the trend is equivalent to approximately −2.7 percent per decade, whereas the Antarctic results show a small positive trend. The negative trend in the NH is significant at the 90 percent confidence level whereas the small positive trend in the SH is not significant (from Lemke et al 2007).
1.3.2. Coastal upwelling

Wind driven Ekman pumping drives the four major eastern boundary upwelling systems of the world: the Humboldt, Benguela, California and Canary currents, supplemented by a region off North East Africa in the Arabian Sea that is driven by monsoonal wind forcing. There is contradicting evidence and differing predictions with regard to impacts of climate change on upwelling processes. Bakun (1990) predicted that differential warming between oceans and land masses would, by intensifying the alongshore wind stress on the ocean surface, lead to acceleration of coastal upwelling. He suggested that this effect was already evident in the Iberian margin, California and Humboldt currents. This hypothesis was later supported by Snyder et al. (2003) who observed a 30-year trend in increased wind driven upwelling off California, corroborated by regional climate forced modelling outputs. In support of the above, Auad et al. (2006) concluded that increased stratification of warmed waters was overcome by increased upwelling caused by the intensification of alongshore wind stress off California. Positive correlations between upwelling and atmospheric temperature in paleo records in the California Current have also been observed (Pisias et al., 2001). SST records obtained from sediment cores off Morocco indicate anomalous and unprecedented cooling during the twentieth century, which would be consistent with increased climate change driven upwelling (McGregor et al., 2007). Increased twentieth century Arabian Sea upwelling, attributed to global warming-related heating of the Eurasian landmass, has also been observed (Goes et al., 2005). The conclusion was arrived at through
paleo records linking declining winter and spring snow cover over Eurasia with stronger southwest (summer) monsoon winds, and thus coastal upwelling (Anderson et al., 2002), suggesting that further increases in southwest monsoon and upwelling strength during the coming century are possible as a result of greenhouse gas concentrations.

In contrast to the above observations, Vecchi et al. (2006) suggest that because the poles will warm more dramatically than the tropics, the trade wind system which also drives upwelling favourable winds should weaken. Simulations conducted by Hsieh and Boer (1992) indicated that the mid-latitude continents do not all follow Bakun’s (1990) scenario in developing anomalous low pressure in summer and enhancing coastal winds favourable to upwelling. In the open ocean the equatorial and subpolar zonal upwelling bands and the subtropical downwelling bands would weaken as winds diminish because of the weakening of the equator-to-pole temperature gradient in the lower troposphere under global warming. With a weakening of open ocean upwelling and an absence of enhanced coastal upwelling, the overall effect of global warming could be to decrease global biological productivity. In fact, most recent contributions agree that global warming would strengthen thermal stratification and cause a deepening of the thermocline, both reducing upwelling and decreasing nutrient supply into the sunlit regions of oceans, thus reducing productivity (Cox et al., 2000; Loukos et al., 2003; Lehodey et al., 2003; Roemmich & McGowan, 1995; Bopp et al., 2005).

On the basis of global circulation model (GCM) studies, Sarmiento et al. (2004) conclude that there is no clear pattern of upwelling response to global warming at the global scale, except within a couple of degrees of the equator, where all but one atmosphere-ocean general circulation models show a reduction (Sarmiento et al., 2004). Overall, the equatorial and coastal upwelling within 15 ° of the equator drops by 6 percent. However, it must be noted that current climate models are not yet sufficiently developed to resolve coastal upwelling (Mote and Mantua 2002) and so the results of large scale GCM simulations have to be treated with caution. The consequences of generic increases or decreases in coastal upwelling as a result of climate change can be dramatic and not limited to biological production. Bakun and Weeks (2004) suggested that, should upwelling intensify in coming decades, it could lead to switches to undesirable states dominated by unchecked phytoplankton growth by rapidly exported herbivorous zooplankton, sea floor biomass depositions and eruption of noxious greenhouse gases.

Overall, the response of coastal upwelling to climate warming is likely to be more complex than a simple increase or decrease. Focusing on the California Current, Diffenbaugh et al. (2004) showed that biophysical land-cover–atmosphere feedbacks induced by CO₂ radiative forcing enhance the land–sea thermal contrast, resulting in changes in total seasonal upwelling and upwelling seasonality. Specifically, land-cover–atmosphere feedbacks lead to a stronger increase in peak- and late-season near-shore upwelling in the northern limb of the California Current and a stronger decrease in peak- and late-season near-shore upwelling in the southern limb. Barth et al. (2007) show how a one month delay in the 2005 spring transition to upwelling-favourable wind stress off northern California resulted in numerous anomalies: near-shore surface waters averaged 2 °C warmer than normal, surf-zone chlorophyll-a and nutrients were 50 percent and 30 percent less than normal – respectively – and densities of recruits of mussels and barnacles were reduced by 83 percent and 66 percent respectively. The delay was associated with 20-to-40-day wind oscillations accompanying a southward shift of the jet stream resulting in the lowest cumulative upwelling-favourable wind stress for 20 years. They concluded that delayed early-season upwelling and stronger late-season upwelling are consistent with predictions of the influence of global warming on coastal upwelling regions. Because upwelling is of fundamental importance in coastal marine systems, further elucidation of the relationship between climate and upwelling is a high research priority.

1.4. SEA LEVEL RISE
Global average sea level has been rising at an average rate of 1.8 mm per year since 1961 (Douglas, 2001; Miller and Douglas, 2004; Church et al., 2004), threatening many low
altitude regions. The rate has accelerated since 1993 to about 3.1 mm per year as a result of declines in mountain glaciers and snow cover in both hemispheres and losses from the ice sheets of Greenland and Antarctica (Bindoff et al., 2007; Figure 5). Ice loss from Greenland has been aggravated by melting having exceeded accumulation due to snowfall. Sea ice extent in the Antarctic however, shows no statistically significant average trends, consistent with the lack of warming reflected in atmospheric temperatures (Lemke et al., 2007; Figure 5).

There is evidence of increased variability in sea level in recent decades, which may be consistent with the trend towards more frequent, persistent and intense El Niños (Folland et al., 2001). Model-based projections of global average sea level rise at the end of the twenty-first century (2090 to 2099) relative to 1980 to 1999 range between 0.18 m (minimum under B1 scenario, world convergent to global sustainability principles) and 0.59 m (maximum under A1F1 scenario, very rapid, fossil-intensive world economic growth, Meehl et al., 2007), although empirical projections of up to 1.4 m have been estimated (Rahmstorf, 2007). IPCC models used to date do not include uncertainties in climate-carbon cycle feedback nor do they include the full effects of changes in ice sheet flow, because a basis in published literature is lacking. In particular, contraction of the Greenland ice sheet is projected to continue to contribute to sea level rise after 2100. Revised estimates of upper ocean heat content (Domingues et al., 2008) imply a significant ocean thermal expansion contribution to sea level rise of 0.5 to 0.8 mm per year in water below 700 m depth. Since the start of the IPCC projections in 1990, sea level has actually risen at near the upper end of the third (and equivalent to the upper end of the fourth) assessment report, including an estimated additional allowance of 20 cm rise for potential ice sheet contributions. It is important to note that sea level change is not geographically uniform because it is controlled by regional ocean circulation processes.

All coastal ecosystems are vulnerable to sea level rise and more direct anthropogenic impacts, especially coral reefs and coastal wetlands (including salt marshes and mangroves). Long-term ecological studies of rocky shore communities indicate adjustments apparently coinciding with climatic trends (Hawkins et al., 2003). Global losses of 33 percent in coastal wetland areas are projected given a 36 cm rise in sea level from 2000 to 2080. The largest losses are likely to be on the Atlantic and Gulf of Mexico coasts of the Americas, the Mediterranean, the Baltic, and small island regions (Nicholls et al., 2007). Sea level rise may reduce intertidal habitat area in ecologically important North American bays by 20 to 70 percent over the next hundred years, where steep topography and anthropogenic structures (e.g. sea walls) prevent the inland migration of mudflats and sandy beaches (Galbraith et al., 2002).

Key human vulnerabilities to climate change and sea-level rise exist where the stresses on natural low-lying coastal systems coincide with low human adaptive capacity and/or high exposure and include: deltas, especially Asian megadeltas (e.g. the Ganges-Brahmaputra in Bangladesh and West Bengal); low-lying coastal urban areas, especially areas prone to natural or human-induced subsidence and tropical storm landfall (e.g. New Orleans, Shanghai); small islands, especially low-lying atolls (e.g. the Maldives) (Nicholls et al., 2007).

1.5. ACIDIFICATION AND OTHER CHEMICAL PROPERTIES

Roughly half the CO₂ released by human activities between 1800 and 1994 is stored in the ocean (Sabine et al., 2004), and about 30 percent of modern CO₂ emissions are taken up by oceans today (Feely et al., 2004). Continued uptake of atmospheric CO₂ has decreased the pH of surface seawater by 0.1 units in the last two hundred years. Model estimates of further pH reduction in the surface ocean range from 0.3 to 0.5 units over the next hundred years and from 0.3 to 1.4 units over the next three hundred years, depending on the CO₂ emission scenario used (Caldeira & Wickett, 2005). The impacts of these changes will be greater for some regions and ecosystems and will be most severe for shell-borne organisms, tropical coral reefs and cold water corals in the Southern Ocean (Orr et al., 2005, Figure 6). Recent modelling results of Feely et al. (2008) suggest that by the end of the century the entire water column in some regions of the subarctic North Pacific will become undersaturated with respect to aragonite. Warmer tropical and sub tropical waters will likely remain
supersaturated over the range of IPCC-projected atmospheric CO$_2$ concentration increases (Feely et al., 2008).

**FIGURE 6**
The global ocean aragonite saturation state in the year 2100 as indicated by $\Delta[\text{CO}_3^{2-}]_A$. The $\Delta[\text{CO}_3^{2-}]_A$ is the in situ $[\text{CO}_3^{2-}]$ minus that for aragonite-equilibrated sea water at the same salinity, temperature and pressure. Shown are modelled median concentrations in the year 2100 under scenario IS92a: a, surface map; b, Atlantic; and c, Pacific zonal averages. Thick lines indicate the aragonite saturation horizon in 1765 (Preind.; white dashed line), 1994 (white solid line) and 2100 (black solid line for S650; black dashed line for IS92a). Positive $\Delta[\text{CO}_3^{2-}]_A$ indicates supersaturation; negative $\Delta[\text{CO}_3^{2-}]_A$ indicates undersaturation (from Orr et al. 2005).

Impacts on other marine organisms and ecosystems are much less certain than the physical changes because the mechanisms shaping sensitivity to long-term moderate CO$_2$ exposures are insufficiently understood. It is expected that pH reduction will change the depth below which calcium carbonate dissolves, increasing the volume of ocean that is undersaturated with respect to aragonite and calcite, which are used by marine organisms to build their shells (Kleypas et al., 1999; Feely et al., 2004). Changes in pH may affect marine species in ways other than through calcification. Havenhand et al. (2008) report that expected near-future levels of ocean acidification reduce sperm motility and fertilization success of the sea urchin *Heliocidaris erythrogramma*, and suggest that other broadcast spawning marine species may be at similar risk. Impacts on oxygen transport and respiration systems of oceanic squid make them particularly at risk of reduced pH (Pörtner et al., 2005). However, the degree of species adaptability and the rate of change of seawater pH relative to its natural variability are
unknown. Aragonite undersaturation is expected to affect corals and pteropods (Hughes et al., 2003; Orr et al., 2005), as well as other organisms such as coccolithophores (Riebesell et al., 2000; Zondervan et al., 2001). In contrast to experiments where no adaptation is possible, Pelejero et al. (2005) observed that ~three hundred-year-old massive Porites corals from the southwestern Pacific had adapted to ~fifty-year cycles of large variations in pH, covarying with the Pacific Decadal Oscillation. This would suggest that adaptation to long-term pH change may be possible in coral reef ecosystems. Research into the impacts of high concentrations of CO₂ in the oceans is in its infancy and needs to be developed rapidly.

Other chemical properties subject to climate change driven trends include oxygen and inorganic nutrients. The oxygen concentration of the ventilated thermocline (about 100 to 1000 m) has been decreasing in most ocean basins since 1970 (Emerson et al., 2004), ranging from 0.1 to 6 µmol kg⁻¹ yr⁻¹, superposed on decadal variations of ±2 µmol kg⁻¹ yr⁻¹ (Ono et al., 2001; Andreev and Watanabe, 2002). The observed O₂ decrease appears to be driven primarily by a reduced rate of renewal of intermediate waters (Bindoff et al., 2007), and less by changes in the rate of O₂ demand from downward settling of organic matter. As mentioned above, global warming is likely to strengthen thermal stratification, deepen the thermocline, and as a result decrease nutrient supply to surface waters. Only a few studies have reported decadal changes in inorganic nutrient concentrations. In the North Pacific, the concentration of nitrate plus nitrite (N) and phosphate decreased at the surface (Freeland et al., 1997; Watanabe et al., 2005) and increased below the surface (Emerson et al., 2001) in the past two decades. There are no clear patterns in nutrient changes in the deep ocean (Bindoff et al., 2007).

1.6. ATMOSPHERE-OCEAN AND LAND-OCEAN EXCHANGES

In the period 2000-2005, CO₂ uptake by the oceans amounted to 2.2±0.5 GtCy⁻¹ (out of 7.2 GtCy⁻¹ fossil CO₂ emissions). These values are at least double the terrestrial biosphere intake (Denman et al., 2007). Increasing CO₂ levels in the atmosphere have been postulated to deplete the ozone layer (Austin et al., 1992), potentially leading to enhanced levels of ultraviolet radiation at the earth’s surface, with possible indirect effects on ocean processes (see Section 2.7).

Land-use change, particularly deforestation and hydrological modifications, has had downstream impacts, particularly erosion in catchment areas. Suspended sediment loads in the Huanghe (Yellow) River, for example, have increased two to ten times over the past two thousand years (Jiongxin, 2003). In contrast, damming and channelisation have greatly reduced the supply of sediments to the coast from other rivers through retention of sediment by dams (Syvitski et al., 2005). Changes in fresh water flows will affect coastal wetlands by altering salinity, sediment inputs and nutrient loadings (Schallenberg et al., 2001; Floder and Burns, 2004). Changed fresh water inflows into the ocean will lead to changes in turbidity, salinity, stratification, and nutrient availability, all of which affect estuarine and coastal ecosystems (Justic et al., 2005), but consequences may vary locally. For example, increased river discharge of the Mississippi would increase the frequency of hypoxia events in the Gulf of Mexico, while increased river discharge into the Hudson Bay would lead to the opposite (Justic et al., 2005). Halls and Welcomme (2004) conducted simulation studies to develop criteria for the management of hydrological regimes for fish and fisheries in large floodplain–river systems. They concluded that, in general, fish production was maximized by minimizing the rate of drawdown and maximizing the flood duration and flood and dry season areas or volumes.

Little attention has been paid to trade offs between land use and inland capture production, such as dry season trade off between rice and inland fish production on the floodplains of Bangladesh. Shankar et al. (2004) noted that floodplain land and water in Bangladesh are coming under ever-increasing pressure during the dry winter months, which are critical to the survival and propagation of the floodplain resident fish. River floodplain systems, particularly in the developing world, need to consider the trade offs between fish and rice production in the context of climate change effects on hydrological systems (Shankar et al., 2004).
Mangroves are adapted for coastal areas with waterlogged and often anoxic soils but their tolerance of salinity stress varies among species. Freshwater influx not only reduces the salinity of coastal waters but also enhances the stratification of the water column, thereby decreasing nutrient resupply from below. Flood events are associated with an increase in productivity as nutrients are washed into the sea (McKinnon et al., 2008). While diatoms seem to be negatively affected by increases in river discharge, dinoflagellates have been observed to profit from the increase in stratification and availability of humic substances associated with riverine freshwater input (Carlsson et al., 1995; Edwards et al., 2006). Regardless of the direction of change, modifications in rain water runoff and accompanying changes in salinity and resource supply should therefore affect the composition and, potentially, the productivity of the phytoplankton community in coastal waters.

1.7. LOW FREQUENCY CLIMATE VARIABILITY PATTERNS

Atmospheric circulation patterns arise primarily as a consequence of heating contrasts between the poles and the equator, modulated by seasonality, and because land and water absorb and release heat at different rates. The result is a patchwork of warmer and cooler regions characterized by a number of patterns of atmospheric circulation with different persistence. The extent to which preferred patterns of variability can be considered true modes of the climate system is debatable, but certainly these patterns are used to explain physical and biological variability in the ocean, particularly at decadal scale (e.g. Lehodey et al., 2006). Because of the long time scales of some natural climate patterns, it is difficult to discern if observed decadal oceanic variability is natural or a climate change signal, and have to be treated separately from the gradual, linear, long-term warming expected as a result of greenhouse gas emissions. Furthermore, there may be impacts of gradual climate change on the intensity, duration and frequency of these climate patterns and on their teleconnections.

Overland et al. (2008) concluded that most climate variability in the Atlantic and Pacific Oceans is accounted for by the combination of intermittent one to two-year duration events (e.g. ENSO), plus broad-band “red noise” (large signals are only visible when a number of otherwise random contributions add together in the same phase) and intrinsic variability operating at decadal and longer timescales. ENSO predictability has had some degree of success. However, although heat storage and ocean time lags provide some multi-year memory to the climate system, basic understanding of the mechanisms resulting in observed large decadal variability is lacking. Decadal events with rapid shifts and major departures from climatic means will occur, but their timing cannot yet be forecast (Overland et al., 2008). In this section we describe the main patterns of climate variability relevant to fish production and their observed impacts on biological processes. Impacts at the ecosystem level, which often take the form of regime shifts, are discussed in more detail in Section 2.9 (Regime shifts).

The most obvious driver of interannual variability is the El Niño Southern Oscillation (ENSO). Climate scientists have arbitrarily chosen definitions for what is and what is not an “ENSO event” (Trenberth, 1997), and today, warm phases of ENSO are called “El Niño” and cool phases “La Niña”. ENSO is an irregular oscillation of three to seven years involving a warm and a cold state that evolves under the influence of the dynamic interaction between atmosphere and ocean. Although ENSO effects are felt globally (Glynn 1988; Bakun 1996), the major signal occurs in the equatorial Pacific with an intensity that can vary considerably from one event to another. El Niño events are associated with many atmospheric and oceanic patterns, including abnormal patterns of rainfall over the tropics, Australia, southern Africa and India and parts of the Americas, easterly winds across the entire tropical Pacific, air pressure patterns throughout the tropics and sea surface temperatures (Nicholls 1991; Reaser et al., 2000; Kirov and Georgieva, 2002). Coincident ecological changes are both vast and global and include influences over plankton (MacLean 1989), macrophytes (Murray and Horn 1989), crustaceans (Childers et al., 1990) fish (Mysak, 1986; Sharp and McLain, 1993), marine mammals (Testa et al., 1991; Vergani et al., 2004), sea birds (Anderson, 1989; Cruz and Cruz, 1990; Testa et al., 1991) and marine reptiles (Molles and Dahm, 1990).
El Niño events have three major impacts in coastal upwelling systems: they increase coastal temperatures, reduce plankton production by lowering the thermocline (which inhibits upwelling of nutrients) and change trophodynamic relationships (Lehodey et al., 2006). In non-upwelling areas they change the vertical structure of the water column, increasing and decreasing available habitats (Lehodey, 2004). The warm-water phase of ENSO is associated with large-scale changes in plankton abundance and associated impacts on food webs (Hays et al., 2005), and changes to behaviour (Lusseau et al., 2004), sex ratio (Vergani et al., 2004) and feeding and diet (Piatkowski et al., 2002) of marine mammals. The strong 1997 ENSO caused bleaching in every ocean (up to 95 percent of corals in the Indian Ocean), ultimately resulting in 16 percent of corals destroyed globally (Hoegh-Guldberg, 1999, 2005b; Wilkinson, 2000). Evidence for genetic variation in temperature thresholds among the obligate algal symbionts suggests that some evolutionary response to higher water temperatures may be possible (Baker, 2001; Rowan, 2004). However, other studies indicate that many entire reefs are already at their thermal tolerance limits (Hoegh-Guldberg, 1999).

Some studies expect stronger and more frequent El Niños as a result of global warming (e.g. Timmerman et al., 1999; Hansen et al., 2006). Others suggest that the evidence is still inconclusive (Cane, 2005) because ENSO is not well enough simulated in climate models to have full confidence in these projected changes (Overland et al., 2008). ENSO events are connected to weather changes outside the Pacific Ocean that are linked by remote atmospheric associations or teleconnections (Mann and Lazier, 1996). This means that changes in the position and intensity of atmospheric convection in one area will result in adjustments in pressure cells in adjacent areas and can lead to altered wind and ocean current patterns on a global scale. Teleconnected shifts could occur if they are linked to the Earth nutation (wobbling motion of the earth’s axis, Yndestad, 1999) or changes in the Earth’s rotational speed (Beamish et al., 2000).

The most prominent teleconnections over the Northern Hemisphere are the North Atlantic Oscillation (NAO) and the Pacific-North American (PNA) patterns (Barnston and Livezey, 1987). Both patterns are of largest amplitude during the winter months. The NAO is an index that captures north-south differences in pressure between temperate and high latitudes over the Atlantic sector (Hurrell et al., 2003). Thus, swings in the NAO index from positive to negative (and vice versa) correspond to large changes in the mean wind speed and direction over the Atlantic, the heat and moisture transport between the Atlantic and the neighbouring continents and the intensity and number of Atlantic storms, their paths and their weather. It appears that the NAO does not owe its existence primarily to coupled ocean-atmosphere-land interactions: it arises from processes internal to the atmosphere, in which various scales of motion interact with one another to produce random and thus largely unpredictable variations with a fundamental time scale of ten days and longer (Overland et al., 2008).

Changes in the NAO index have occurred concurrently with changes in biological communities evident at multiple trophic levels, e.g. zooplankton community structure (Planque and Fromentin, 1996), timing of squid peak abundance (Sims et al., 2001), gadoid recruitment and biomass (Hislop 1996; Beaugrand et al., 2003) and herring (Clupea harengus, Clupeidae) and sardine populations (Southward et al., 1988), and occasionally in the form of regime shifts (see Section 2.9). Observation and model predictions using General Circulation Models (GCMs) both seem to indicate that the NAO has been high (positive) over recent decades (Cohen and Barlow, 2005) and despite fluctuations is likely to remain high during the twenty-first century because of climate change effects (Palmer, 1999; Gillett et al., 2003; Taylor et al., 2005). There is some indication as well, that some of the upward trend in the NAO index over the last half of the twentieth century arose from tropical SST forcing or/and freshening at high latitudes and increased evaporation at subtropical latitudes. It is not unreasonable to claim that part of the North Atlantic climate change, forced by the imposed slow warming of tropical SSTs, constitutes an anthropogenic signal that has just begun to emerge (Overland et al., 2008). Moreover, as both ENSO and the NAO are key determinants of regional climate, our ability to detect and distinguish between natural and anthropogenic regional climate change is limited.
The PNA teleconnection pattern relates to four centres of high and low pressure in a roughly great circle route from the central Pacific, through the Gulf of Alaska and western Canada to the southeastern United States. Over the North Pacific Ocean pressures near the Aleutian Islands vary out-of-phase with those to the south, forming a seesaw pivoted along the mean position of the Pacific subtropical jet stream, the centre of the main westerly (coming from the west) winds in the atmosphere. Over North America, variations over western Canada and the northwestern United States are negatively correlated with those over the southeastern United States but are positively correlated with the subtropical Pacific centre. At the surface, the signature of the PNA is mostly confined to the Pacific. Like the NAO, the PNA is an internal mode of atmospheric variability. The PNA is closely related to an index consisting of variability in North Pacific sea surface temperatures (SST), called the Pacific Decadal Oscillation (PDO). The NAO and PNA explain about 35 percent of the climate variability during the twentieth century (Quadrelli and Wallace, 2004).

Changes in climate variability patterns in the North Pacific are often referred to as regime changes (see Section 2.9). The index generally used to identify the shifts is based on the Pacific Decadal Oscillation (PDO), which is defined as the first empirical orthogonal function of sea surface temperature in the North Pacific (Mantua et al., 1997). The 1977 regime change led to changes in surface wind stress (Trenberth, 1991), cooling of the central Pacific, warming along the west coast of North America and decreases in Bering Sea sea ice cover (Miller et al., 1994; Manak and Misak, 1987). There are indications of other shifts in 1925, 1947 (Mantua et al., 1997) and 1989 (Beamish et al., 1999) and possibly 1998 (MacFarlane et al., 2000). Around the time of the 1977 regime shift, total chlorophyll a nearly doubled in the central North Pacific owing to a deepening of the mixed layer (Venrick, 1994), while the mixed layer in the Gulf of Alaska was shallower (but also more productive, Polovina et al., 1995). These changes resulted in a dramatic decrease in zooplankton biomass off California caused by increased stratification and reduced upwelling of nutrient-rich water (Roemmich and McGowan, 1995). However, zooplankton responses were far from linear, and have been largely attributed to salps and doliolids (Rebstock, 2001).

There is evidence that the existence of these climate patterns can lead to larger-amplitude regional responses to forcing than would otherwise be expected. It is therefore important to test the ability of climate models to simulate them and to consider the extent to which observed changes related to these patterns are linked to internal variability or to anthropogenic climate change. In general, a primary response in the IPCC climate models to climate patterns is a rather spatially uniform warming trend throughout the ocean basins combined with the continued presence of decadal variability similar to that of the twentieth century, NAO, PDO, etc. (Overland and Wang, 2007). Climate variables such as temperature and wind can have strong teleconnections (large spatial covariability) within individual ocean basins, but between-basin teleconnections, and potential climate-driven biological synchrony over several decades, are usually much weaker (Overland et al., 2008).

2. Observed effects of climate variability and change on ecosystem and fish production processes

Direct effects of climate change impact the performance of individual organisms at various stages in their life history via changes in physiology, morphology and behaviour. Climate impacts also occur at the population level via changes in transport processes that influence dispersal and recruitment. Community-level effects are mediated by interacting species (e.g. predators, competitors, etc.), and include climate-driven changes in both the abundance and the strength of interactions among these species. The combination of these proximate impacts results in emergent ecological responses, which include alterations in species distributions, biodiversity, productivity and microevolutionary processes (Harley et al., 2006).
In general, there is limited observational information on climate change impacts on marine ecosystems. For example, only 0.1 percent of the time series examined in the IPCC reports were marine (Richardson and Poloczanska, 2008). Generalizations are thus difficult to make, compounded by the fact that impacts are likely to manifest differently in different parts of the world’s oceans. For example, observed patterns of sea surface variability in the Pacific and Indian oceans exceed those in the Atlantic Ocean (Enfield and Mestas-Nunez, 2000), mostly because the western Pacific and eastern Indian Oceans have the largest area of warm surface water in the world. The effects that this warm-water pool exerts on interannual and multi-decadal time scales can result in significant variations in primary production, fish abundance and ecosystem structure at basin scales (Chavez et al., 2003).

In spite of this scarcity of data, there is now significant evidence of observed changes in physical and biological systems in every continent, including Antarctica, as well as from most oceans in response to climate change, although the majority of studies come from mid and high latitudes in the Northern Hemisphere. Documentation of observed changes in tropical regions and the Southern Hemisphere is particularly sparse (Parry et al., 2007).

FIGURE 7
A model illustrating potential pathways by which climate change effects can be mechanistically transmitted to marine biota (from Francis et al. 1998). a/s, atmosphere/sea; MLD, mixed layer depth; MLT, mixed layer temperature; Store boxes in the trophic ladder inserted between levels indicate that the effects of climate variation may be felt differently by the actual production process and by storage and dispersal of accumulated biomass.
Marine and freshwater systems respond to the combined and synergistic effects of physical and chemical changes acting directly and indirectly on all biological processes (see Figure 7). We begin with a brief summary of the physiological, spawning, and recruitment processes by which marine and freshwater populations respond to environmental and climate variability. These are also the processes and responses that individuals and populations must use to adjust to climate change. We then provide examples of how marine and freshwater populations, communities, and ecosystems have responded to observed climate variability as proxies for their potential responses to climate change.

2.1. SUMMARY OF PHYSIOLOGICAL, SPAWNING, AND RECRUITMENT PROCESSES SENSITIVE TO CLIMATE VARIABILITY

2.1.1. Physiological effects of climate changes on fish
Most marine and aquatic animals are cold-blooded (poikilotherms) and therefore their metabolic rates are strongly affected by external environmental conditions, in particular temperature. The thermal tolerances of fish have been described by Fry (1971) as consisting of lethal, controlling, and directive responses, which indicate that fish will respond to temperature long before it reaches their lethal limits. Magnusson et al. (1979) proposed the concept of a thermal niche similar to niches for other resources such as food or space. For North American freshwater fishes they found that fish spent all of their time within ± 5 °C of their preferred temperature, and that three thermal guilds could be recognised: cold, cool, and warm water-adapted species. Moderate temperature increases may increase growth rates and food conversion efficiency, up to the tolerance limits of each species.

Marine species are also strongly affected by temperature and have thermal tolerances of often similar ranges to those of freshwater fishes (e.g. Rose, 2005, lists distributional temperature limits for 145 fish species in the subarctic North Atlantic). Thermal tolerance of marine organisms is non-linear, with optimum conditions at mid-range and poorer growth at temperatures which are too high or too low. Pörtner et al. (2001) found, for both Atlantic cod (Gadus morhua) and common eelpout (Zoarces viviparous) that temperature-specific growth rates and fecundity declined at higher latitudes. Takasuka et al. (2007) suggested that differences in optimal temperatures for growth during the early life stages of Japanese anchovy (Engraulis japonicus; 22 °C) and Japanese sardine (Sardinops melanostictus; 16.2 °C) could explain the shifts between the warm “anchovy” regimes and cool “sardine” regimes in the western North Pacific Ocean.

Many macrophysiological studies have found that organisms transferred into conditions different from those to which they have been adapted, function poorly compared with related organisms previously adapted to these new conditions (Osovitz and Hofmann, 2007). Pörtner (2002) describes an interaction of thermal preference and oxygen supply, such that the capacity to deliver oxygen to the cells is just sufficient to meet the maximum oxygen demand of the animal between the high and low environmental temperatures to be expected. When fish are exposed to conditions warmer than those to which they have been adapted their physiologies are incapable of supplying the increased tissue demand for oxygen over extended periods. This restricts the exposure of whole-animal tolerances to temperature extremes (Pörtner and Knust, 2007). According to Pörtner and Knust (2007), it is the lack of oxygen supply to tissues as conditions warm and metabolic demands increase that lead to altered distributions or extinction of fish from cooler conditions. Larger individuals may be at greater risk of this effect as they may reach their thermal aerobic limits sooner than smaller individuals (Pörtner and Knust, 2007).

In many cases, such changes in thermal conditions are also accompanied by changes in other characteristics, such as changes in sea levels (and therefore exposure regimes, e.g. Harley et al., 2006) and lake levels (e.g. Schindler, 2001); changes in the composition and amount of food; and changes in acidity and other chemical characteristics. In a study of the effects of temperature changes on rainbow trout (Oncorhynchus mykiss) in the presence of low pH and high nitrogen, Morgan et al. (2001) found improved growth during winter with a
2 °C temperature increase but decreased growth in summer when the 2 °C increase was added to the already high temperatures. Therefore, seasonal influences and instances when such changes occur may be equally (or more) important than changes expressed on an annual basis. The term “bioclimate envelope” has been used to define the interacting effects and limits of temperature, salinity, oxygen, etc. on the performance and survival of species (e.g. Pearson and Dawson, 2003). Such bioclimate envelopes could be used to model changes in species’ distributions and abundance patterns as a result of climate change. The increasing experimentation in culture operations for a wide variety of marine and freshwater vertebrate and invertebrate species should provide opportunities to learn more about their responses to environmental conditions and which conditions lead to optimal (and sub-optimal) growth.

2.1.2. Spawning
The characteristics of spawning and successful reproduction of marine and freshwater organisms are largely under evolutionary control; organisms adapt to the prevailing conditions, and possibly the variability of these conditions, so that they can complete their life cycle and reproduce. In this context, the influences of climate variability and change on the characteristics of spawning and reproduction are also closely related to their influences on growth and successful recruitment to the mature population. Spawning times and locations have evolved to match prevailing physical (such as temperature, salinity, currents) and biological (such as food) conditions that maximize the chances for a larva to survive to become a reproducing adult; or at the very least to minimize potential disruptions caused by unpredictable climate events. Whereas evolution is responsible for the type of spawning, environmental features such as temperature have significant influences on specific characteristics of spawning. These include its timing (e.g. Atlantic cod; Hutchings and Myers, 1994), and the size of eggs and consequent size of larvae at hatch (e.g. Atlantic cod; Pepin et al., 1997). Crozier et al. (2008) concluded that climate change is likely to induce strong selection on the date of spawning of Pacific salmon in the Columbia River system. Temperature has also been demonstrated to influence the age of sexual maturity, e.g. Atlantic salmon (Salmo salar; Jonsson and Jonsson, 2004) and Atlantic cod (Brander, 1994). For these cold water species, warmer conditions lead to earlier (younger) age-at-maturity.

2.1.3. Fish recruitment processes and climate change
The issue of recruitment variability and its causes and consequences to commercial fish populations, in particular, has been the single most important problem in fisheries science over the past hundred years. Great advances have been achieved, but it is still rare for quantitative recruitment forecasts to be used to provide fisheries management advice. Such forecasts, often based on relationships with environmental variables, tend to be used for species with short life spans (e.g. California sardine, Jacobson et al., 2005; squid, Rodhouse, 2001) because the abundances of species with long life spans can usually be assessed more accurately using directed surveys of the later age classes.

Many theories and processes have been proposed to explain the huge reduction in the numbers of most marine and aquatic species as they develop from egg to larva to juvenile and finally the adult (e.g. see Ottersen et al., 2008, for a recent synthesis). These hypotheses can be grouped into three general categories: starvation and predation, physical dispersal and synthesis processes.

One of the principal hypotheses proposed to relate the impact of starvation on recruitment, which has clear connections with climate variability and change is the match-mismatch hypothesis of Cushing (1969; 1990; see also Durant et al., 2007). It recognises that fish, particularly in the early stages, need food to survive and grow. It also recognises that periods of strong food production in the ocean can be variable and are often under climate control (strength of winds, frequency of storms, amount of heating or fresh water supplied to the surface layers). The hypothesis proposes, therefore, that the timing match or mismatch between when food is available and when and where fish (particularly in the early stages) are able to encounter and consume this food (Figure 8), is a principle determinant of recruitment and the subsequent abundance of marine and freshwater species. Winder and Schindeler (2004a) have shown how increasingly warmer springs in a temperate lake have advanced
thermal stratification and the spring diatom bloom, thereby disrupting trophic linkages and causing a decline in a keystone predator (*Daphne* spp.) populations. Mackas *et al.* (2007) observed similar responses of earlier zooplankton blooms and their consequences for the growth and survival of pelagic fish as a result of warming in the North East Pacific. Predation is an alternative to starvation as a source of mortality, and the two may be related in that slower growing larvae are more susceptible to predators. The vulnerability to predation of larval fish depends on the encounter rate of predators and prey (a function of abundances, sizes and their relative swimming speeds and turbulent environments) and the susceptibility to capture (Houde, 2001).

**FIGURE 8**
Cushing’s (1969, 1990) match-mismatch hypothesis for recruitment variations of marine species. Left panel represents a match between zooplankton prey and larval fish abundance, resulting in good recruitment. The right panel represents a mismatch between predator and prey, resulting in poor fish recruitment. The separation time between peaks of prey and predators is represented by $t_0$. Modified from Cushing (1990).

Physical dispersal is largely concerned with the effects of physical processes, in particular the circulation, on the distributions of marine and aquatic species, and their abilities to grow, survive, and spawn to successfully close the life cycle. Since physical processes play a direct role in these processes, they are likely to be susceptible to climate variability and change. Three hypotheses relate climate effects directly to the recruitment and abundance of marine fish populations. These are the optimal environmental window hypothesis of Cury and Roy (1989), the Triad hypothesis of Bakun (1996), and the oscillating control hypothesis of Hunt *et al.* (2002).

Cury and Roy’s (1989) optimal environmental window hypothesis assumes that species are adapted to the typical (“optimal”) conditions within their preferred habitats. This implies that better recruitment success should be expected with “mean” rather than with “extreme”, either high or low, conditions, i.e. a non-linear relationship. The concept of an optimal environmental window for recruitment success has subsequently been proposed for a variety of species including Pacific salmon (Garrett, 1997). The concept can also be applied in a spatial context, such that stocks living at the edges of the adapted range should be expected to experience more marginal conditions and greater environmental influences on recruitment success than stocks in the middle of their range (Figure 9). This has been verified for 62 marine fish populations of 17 species in the North East Atlantic (Brunel and Boucher, 2006).
FIGURE 9
The relationship between the log$_2$ recruitment anomaly and sea surface temperature anomaly (in °C) for various cod stocks in the North Atlantic. The large axis in the bottom centre of the diagram shows the axis legends for all of the plots. The numerical value at the bottom of each plot represents the mean annual bottom temperatures for the stocks. For the cold-water stocks, the SST-recruitment relationship is generally positive whereas for the warm-water stocks it is negative. There is no relationship in the mid-temperature range. From Drinkwater (2005), modified from Planque and Fredou (1999).

Bakun’s (1996) Triad hypothesis posits that optimal conditions of enrichment processes (upwelling, mixing, etc.) concentration processes (convergences, fronts, water column stability) and retention within appropriate habitats is necessary for good recruitment. Locations in which these three elements exist to support favourable fish habitats are called “ocean triads”. Since the processes of enrichment, concentration and retention are in opposition, the Triad hypothesis also requires non-linear dynamics, with optimal conditions for each component located at some mid-point of the potential range. Bakun (1996) proposed the Triad hypothesis for Atlantic bluefin tuna (Thunnus thynnus), Japanese sardine (Sardinops melanostictus), albacore tuna (Thunnus alalunga) and various groundfish species in the North Pacific, and anchovy (Engraulis spp.) in the Southwest Atlantic. It has subsequently been described for anchovy (Engraulis ringens) in the Humboldt upwelling system off Peru (Lett et al., 2007), sardine (Sardinops sagax) in the southern Benguela ecosystem (Miller et al., 2006), and anchovy in the Mediterranean Sea (Agostini and Bakun, 2002). Since such systems are based on optimal conditions across these otherwise opposing processes, they are likely to be sensitive to disruptions or systematic alterations in these processes that may occur with climate change.

The oscillating control hypothesis (Hunt et al., 2002) was developed for the southern Bering Sea. It posits that the pelagic ecosystem is driven by plankton production processes in cold years but predominately by predation in warm periods. During cold years, production of
walleye pollock (*Theragra chalcogramma*) is limited by cold temperatures and low food reserves. Early in the warm period, strong plankton production promotes good fish recruitment but as the abundance of adult pollock increases, their recruitment is reduced by cannibalism and other predators. A comparable impact of climate on oscillating trophic control has also been found for Pacific cod (*Gadus macrocephalus*) and five prey species in the North Pacific (Litzow and Ciannelli, 2007).

**2.2. PRIMARY PRODUCTION**

**2.2.1. Global ocean**

In general, observations and model outputs suggest that climate change is likely to lead to increased vertical stratification and water column stability in oceans and lakes, reducing nutrient availability to the euphotic zone and thus reducing primary (Falkowski *et al.*, 1998; Behrenfeld *et al.*, 2006) and secondary (Roemmich and McGowan, 1995) production. The climate–plankton link in the ocean is found most strongly in the tropics and mid latitudes, where there is limited vertical mixing because the water column is stabilized by thermal stratification (that is, when light, warm waters overlie dense, cold waters). In these areas, the typically low levels of surface nutrients limit phytoplankton growth. Climate warming further inhibits mixing, reducing the upward nutrient supply and lowering productivity (Doney 2006). However, in certain regions (e.g. high latitudes) a compensation mechanism has been proposed through which the residence time of particles in the euphotic zone will increase, assuming the nutrient supply remains the same (Doney 2006).

Observations in support of the above include a 6 percent reduction in global oceanic primary production between the early 1980s and the late 1990s, based on the comparison of chlorophyll data from two satellites (Gregg *et al.*, 2003). Extrapolating the satellite observations into the future suggests that marine biological productivity in the tropics and mid latitudes will decline substantially. Observations in higher latitudes may reflect the compensation mechanism mentioned above, as chlorophyll in the North East Atlantic for example, has increased since the mid-1980s (Raitsos *et al.*, 2005; Reid *et al.*, 1998; Richardson and Schoeman, 2004).

Predicting climate change impacts on primary and secondary production is subject to uncertainties in the parameterization of biogeochemical models. In a major comparative study Sarmiento *et al.* (2004) simulated the effect of greenhouse gas emissions using six Atmosphere-Ocean General Circulation Models (AOGCMs), comparing emission scenarios for the period from pre-industrial to 2050 and 2090 with a control in which emissions remained at pre-industrial levels. The models assessed chlorophyll and primary production distribution changes using temperature, salinity and density at the sea surface, upwelling, stratification and sea ice cover. Predicted climate-induced alterations in nutrient supply and production are predominantly negative, due to reduced vertical mixing. However, in high latitude regions the resultant increased stability of the water column and increased growing season will have a positive effect on production (Figure 10). Primary production was estimated for a set of seven biomes, further subdivided into biogeographical provinces. Global estimates predicted a small global increase in primary production of between 0.7 percent and 8.1 percent, with very large regional differences (Table 1). For example, decreases in the North Pacific and the area adjacent to the Antarctic continent are slightly more than offset by increases in the North Atlantic and the open Southern Ocean.

Bopp *et al.* (2005) used a multi-nutrient and multi-plankton community model to predict a 15 percent decrease of global primary production at 4xCO$_2$ levels, balanced between an increase in high latitudes due to a longer growing season and a decrease in lower latitudes due to a decrease in nutrient supply. Their model results suggest that climate change leads to more nutrient-depleted conditions in the surface ocean, favouring small phytoplankton at the expense of diatoms, whose relative abundance is reduced by more than 10 percent at the global scale and by up to 60 percent in the North Atlantic and in the sub Antarctic Pacific (Figure 11). It is worth noting that this simulated change in the ecosystem structure impacts oceanic carbon uptake by reducing the efficiency of the biological pump, thus contributing to the positive feedback between climate change and the ocean carbon cycle. Similarly, Boyd
and Doney (2002) used a complex ecosystem model incorporating multi-nutrient limitation (N, P, Si, Fe) and a community structure with planktonic geochemical functional groups, i.e. diatoms (export flux and ballast), diazotrophs (nitrogen fixation) and calcifiers (alkalinity and ballast), to predict a 5.5 percent decrease of the global primary production and an 8 percent decrease of the global new production due to enhanced stratification and slowed thermohaline overturning. They conclude that regional floristic shifts can be as important as changes in bulk productivity (see also Leterme et al., 2005).

FIGURE 10
Zonally integrated response of the global ocean’s primary production (Pg-C deg⁻¹ yr⁻¹, in response to the combined effect of the chlorophyll change and temperature increase) shown as the difference between the warming and the control simulation for each of the six atmosphere-ocean GCMs averaged over the period 2040 to 2060 (except for MPI, which is for the period 2040 to 2049). Modified from Sarmiento et al. 2004.

It must be noted, however, that the above global predictions are based on large scale simulation work at resolutions that do not to resolve coastal upwelling processes, as discussed in section 1.3.2. Should climate change significantly impact coastal upwelling processes, plankton production predictions would have to be revised. Vazquez-Dominguez et al. (2007) determined experimentally the effects of a 2.5 °C sea temperature increase on bacterial production and respiration throughout a seasonal cycle in a coastal Mediterranean site. These results indicate an increase of nearly 20 percent in the total carbon demand of coastal microbial plankton without any effect on their growth efficiency, which could generate a positive feedback between coastal warming and CO₂ production.
Another recent study which combines modelling with empirical evidence looks at the consequences for global primary productivity of disruption of the Atlantic Meridional Overturning (AMO) circulation and concludes that a 50 percent reduction in North Atlantic primary production and a 20 percent reduction in global carbon export production is possible and was a feature of previous ice ages (Schmittner, 2005). Although the conclusions from these two studies appear to be very different, the results are probably compatible with each other when differences in time scales and processes are taken into account. In the Schmittner model, the spindown in AMO is relatively slow, occurring over a period of 500 years, but there is evidence that changes can be more rapid (Cubash et al., 2001) and that reduction in meridional overturning may have begun in both the North Atlantic (Curry and Mauritzen, 2005) and the North Pacific (McPhaden and Zhang, 2002). Since even partial shutdown of the AMO may result in substantial reduction of productivity, it is evident that the causes, likelihood and consequences merit close scrutiny (Kuhlbrodt et al., 2005).
TABLE 1.  
Average response of biogeographical province areas to global warming averaged over the period 2040 to 2060 (from Sarmiento et al. 2004). Areas are in 1012 m2. “Chg” is the difference between the model average warming minus the control; “%Chg” is the percent change.

<table>
<thead>
<tr>
<th></th>
<th>Indian Ocean</th>
<th>Pacific Ocean</th>
<th>Atlantic Ocean</th>
<th>Global</th>
</tr>
</thead>
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<tr>
<td></td>
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<td>Chg</td>
<td>% Chg</td>
<td>Control</td>
</tr>
<tr>
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<tr>
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<td>2.3</td>
<td>35.4</td>
</tr>
<tr>
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<tr>
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<tr>
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</tr>
<tr>
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<td>161.9</td>
<td>79.3</td>
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</table>
2.2.2. Regional impacts
Projections of ocean biological response to climate warming by 2050 show contraction of the highly productive marginal sea ice biome by 42 percent and 17 percent in Northern and Southern Hemispheres (Sarmiento et al., 2004b; see also Meehl et al., 2007; Christensen et al., 2007). The sea ice biome accounts for a large proportion of primary production in polar waters and supports a substantial food web. As timing of the spring phytoplankton bloom is linked to the sea ice edge, loss of sea ice (Walsh and Timlin, 2003) and large reductions of the total primary production in the marginal sea ice biome in the Northern Hemisphere (Behrenfeld and Falkowski, 1997; Marra et al., 2003) would have strong effects, for example, on the productivity of the Bering Sea (Stabeno et al., 2001). Climate warming would also lead to an expansion of the low productivity permanently stratified subtropical gyre biome by 4.0 percent in the Northern Hemisphere and 9.4 percent in the Southern Hemisphere. In between these, the subpolar gyre biome expands by 16 percent in the Northern Hemisphere and 7 percent in the Southern Hemisphere, and the seasonally stratified subtropical gyre contracts by 11 percent in both hemispheres. The expansion of the subtropical gyre biomes has already been observed in the North Pacific and Atlantic (McClain et al., 2004; Sarmiento et al., 2004b; Polovina et al., 2008).

At smaller scales warming may either increase or decrease productivity based on what specific atmospheric-ocean processes dominate. For example, global warming is increasing the intensity of monsoon winds and, through increased upwelling, has resulted in over 350 percent increase in average summertime phytoplankton biomass along the Arabian Sea coast and 300 percent offshore (Goes et al. 2005). It is therefore likely that warming may make the Arabian Sea more productive.

Hashioka and Yamanaka (2007) modelled the Northwest Pacific region under a global warming scenario and predicted increases in vertical stratification and decreases in nutrient and chlorophyll-a concentrations in the surface water by the end of the twenty-first century. Significantly with global warming, the onset of the diatom spring bloom is predicted to take place one half-month earlier than in the present-day simulation, because of stronger stratification. The maximum biomass in the spring bloom is also predicted to decrease significantly compared to present conditions. In contrast, the biomass maximum of the other small phytoplankton at the end of the diatom spring bloom is the same as the present, because of their ability to adapt to low nutrient conditions (as a result of their small half-saturation constant). Therefore a change in the dominant phytoplankton group appears noticeably at the end of spring bloom. Hashioka and Yamanaka (2007) find that changes, due to warming are not predicted to occur uniformly in all seasons, but that they may occur most noticeably at the end of the spring and in the fall bloom.

A study based on over 100 000 plankton samples collected between 1958 and 2002 with the Continuous Plankton Recorder (CPR) (Richardson and Schoeman, 2004) showed an increase in phytoplankton abundance in the cooler regions of the North East Atlantic (north of 55 °N) and a decrease in warmer regions (south of 50 °N; Figure 12). The likely explanation for this apparently contradictory result is that although both areas have undergone warming over this period, with consequent reduction of vertical mixing the nutrient supply in the cooler, more turbulent regions remains sufficient and plankton metabolic rates benefit from the increased temperature. Another study based on the CPR data attributed the observed decadal variability in phytoplankton biomass in the North East Atlantic to hydroclimatic forcing, as expressed by the NAO (Edwards et al., 2001). In the North Sea this resulted in a shift in seasonal timing of the peak in phytoplankton colour from April to June which may have been accompanied by a taxonomic shift from diatoms to dinoflagellates (Leterme et al., 2005).
model B for the entire study area ($r_{all}$) and a subset of nine noncontiguous regions ($r_{subset}$). Bars not overlapping zero are significant. (B) The inverse relation between marine phytoplankton abundance–SST correlations and mean SST (°C) in each region. Points represent individual regions (from Richardson and Schoeman, 2004).

In the tropical Pacific, models have been developed to understand the links between climate, primary and secondary production, forage fish and, ultimately, skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tuna. Key to these models is the definition of suitable tuna habitat which is linked to varying regimes of the principal climate indices El Niño-La Niña Southern Oscillation Index (SOI), and the related Pacific Decadal Oscillation (PDO). Both statistical and coupled biogeochemical models (Lehodey, 2001; Lehodey et al., 2003) capture the slowdown of Pacific meridional overturning circulation and decrease of equatorial upwelling, which has caused primary production and biomass to decrease by about 10 percent since 1976 to 1977 (McPhaden and Zhang, 2002).

In the southeastern Bering Sea, the spring bloom is affected by the timing of the ice retreat (Hunt et al., 2002). During warm years when sea ice retreats early there is insufficient light to support a phytoplankton bloom and there is little stratification due to strong winter winds. The bloom is thus delayed until light and stratification increase. In contrast, when the ice retreat is late, there tends to be ice-melt induced stratification and sufficient light to support a bloom.

Coral reefs provide habitat for a highly diverse ecosystem and short-term extreme water temperatures can cause the symbiotic algae in corals to leave, resulting in coral “bleaching”.
When bleached corals do not recover, algae may grow over the corals resulting in an algal-dominated ecosystem. Bleaching usually occurs when temperatures exceed a “threshold” of about 0.8 to 1 °C above mean summer maximum levels for at least four weeks (Hoegh-Guldberg, 1999). Many reef-building corals live very close to their upper thermal tolerances and are thus extremely vulnerable to warming (Hughes et al., 2003; McWilliams et al., 2005). Numerous reports of coral bleaching due to recent warming have been reported (e.g. Hoegh-Guldberg, 1999; Sheppard, 2003; Reaser et al., 2000). Coral destruction can lead to declines in reef community biodiversity and the abundance of a significant number of individual species (Jones et al., 2004). In addition, one of the most obvious expected consequences of sea level rise will be a poleward shift in species distributions. However, contrary to most other species, many corals are not expected to be able to keep pace with predicted rates of sea level rise (see Knowlton, 2001).

2.2.3. Inland waters
As in oceanic environments, the impacts of global warming on biological production in inland waters depends strongly on the combination of contrasting processes such as ice cover, water flows, stratification and nitrification, with the additional impact of human water and land use.

In high-latitude or high-altitude lakes, atmospheric warming has already led to reduced ice cover, warmer water temperatures, longer growing seasons and, as a consequence, increased algal abundance and productivity (e.g. Battarbee et al., 2002; Korhola et al., 2002; Karst-Riddoch et al., 2005). There have been similar increases in the abundance of zooplankton, correlated with warmer water temperatures and longer growing seasons (e.g. Battarbee et al., 2002; Gerten and Adrian, 2002; Carvalho and Kirika, 2003; Winder and Schindler, 2004; Hampton, 2005; Schindler et al., 2005). For upper trophic levels, rapid increases in water temperature after ice break-up have enhanced fish recruitment in oligotrophic lakes (Nyberg et al., 2001). Studies along an altitudinal gradient in Sweden show that net primary productivity (NPP) can increase by an order of magnitude for a 6 °C air temperature increase (Karlsson et al., 2005).

In contrast, some lakes, such as deep tropical lakes, are experiencing reduced algal abundance and declines in productivity because stronger stratification reduces upwelling of nutrient-rich deep water (Verburg et al., 2003; Hecky et al., 2006). Primary productivity in Lake Tanganyika may have decreased by up to 20 percent over the past two hundred years (O’Reilly et al., 2003, Figure 13). Vollmer et al. (2005) have also documented rising temperatures over the last 60 years in Lake Malawi, as well as measured reduced ventilation of the deep waters since 1980 (Vollmer et al., 2002), leading to reduced nutrient loading and, presumably, reduced productivity.

FIGURE 13
Lake Tanganyika, Africa. Carbon isotope records in sediment cores indicating a post-1950s trend towards more negative δ¹³C values (lower phytoplankton productivity) in both relatively undisturbed (filled symbols), as well as developed (open symbols) watersheds. (from O’Reilly et al. 2003).
Enhanced UV-B radiation and increased summer precipitation will significantly increase dissolved organic carbon (DOC) concentrations, altering major biogeochemical cycles (Zepp et al., 2003; Phoenix and Lee, 2004; Frey and Smith, 2005).

2.3. SECONDARY PRODUCTION
There is currently no global assessment of secondary productivity impacts of climate change, although Richardson (2008) provides a general review of the potential climate warming impacts to zooplankton. Demographic characteristics of marine zooplankton should make them good candidates for assessing the rapid impacts of climate change because of their lifespan (often annual) and the fact that they are rarely fished commercially, facilitating comparative analyses to separate "environment" from fishing' impacts (Mackas and Beaugrand, 2008). Some patterns can be deduced from recent observations at regional scales. Shifts and trends in plankton biomass have been observed in the North Atlantic (Beaugrand and Reid, 2003), the North Pacific (Karl, 1999; Chavez et al., 2003) and in the southern Indian Ocean (Hirawake et al., 2005), among others, but the spatial and temporal coverage of these is limited. One of the complications in estimating warming effects on secondary producers is that different ontogenetic stages are differentially susceptible to environmental stress (Pechenik, 1989). Surprisingly, the more eurythermal and specifically heat-tolerant, mid- to high-intertidal species might actually be more vulnerable to climate change than less heat-tolerant species, because they may live closer to their physiological limits (Harley et al., 2006). This pattern may also hold at the latitudinal scale as low-latitude species may live nearer to their thermal limits than higher-latitude species (Tomanek & Somero, 1999; Stillman, 2002).

McGowan et al. (2003) show that significant ecosystem changes have taken place in the California Current system including a large, decadal decline in zooplankton biomass, along with a rise in upper-ocean temperature (Figure 14). Specifically, they note the abrupt temperature change that occurred around 1976 to 1977, concurrent with other Pacific basin-wide changes associated with an intensification of the Aleutian low pressure system. McGowan et al.’s (2003) results are consistent with the “optimal stability window” hypothesis (Gargett, 1997), wherein increased water column stability along the eastern boundary of the North Pacific would reduce (enhance) biological production at southern (northern) latitudes, where productivity is nutrient (light) limited. Trends in total biological production may however mask complex impacts of climate change. Investigating 15-year anomalies in zooplankton abundances in British Columbia, Mackas et al. (2001) noted that species-specific biomass anomalies are much larger than anomalies in total annual biomass, recognizing that there was more variability in the structure of the zooplankton community than would be implied by trends in its total biomass.

One of the better studied impacts of climate variability and change on marine zooplankton is the North Atlantic copepod community, which contributes up to 90 percent of the zooplankton biomass in the region. This community is dominated by the congeneric calanoid copepod species Calanus finmarchicus and C. helgolandicus. C. finmarchicus is mainly located north of the Oceanic Polar Front (Beaugrand and Ibanez, 2004) while the psuedoocceanic species C. helgolandicus occurs in more temperate waters south of the Oceanic Polar Front, mostly between 40 and 60 °N (Beaugrand and Ibanez, 2004; Bonnet et al., 2005). In regions where they occur together (e.g. the North Sea), the two species generally have different seasonal timing (Beaugrand 2003). C. finmarchicus abundance has declined throughout most of the North Atlantic since the 1950s and has collapse in the North Sea to the benefit of C. helgolandicus (Beaugrand et al., 2002). Transport processes from their deep overwintering basins to shelf regions determines C. finmarchicus distribution and abundance (Spiers et al., 2005) and high abundances are generally associated with increased presence of higher nutrient Atlantic waters, either through increased levels of primary production, direct transport or a combination (Astthorsson and Gislaason, 1995). Recently, Helaouet and Beaugrad (2007) proposed that temperature change alone could be sufficient to have affected the ecological niche of both species (C. finmarchicus reflecting the fate of Atlantic Polar biome and C. helgolandicus that of the Atlantic westerly winds biome), suggesting that
impacts of climate change at the biome level are responsible for the fate of these species. These changes in species dominance have also resulted in substantial changes in phenology, which affect trophic interactions, foodweb structure and ecosystem functioning (Edwards and Richardson, 2004).

FIGURE 14
Time-distance plots of depth of the 12°C isotherm (m; a proxy for thermocline depth and nutricline depth) off California (~34°N) for (a) 1950–75 and (c) 1976–2000, and log$_{e}$ of macrozooplankton volume (cm$^3$ 1000 m$^{-3}$) for (b) 1950–75 and (d) 1976–2000. Regions requiring significant interpolation or extrapolation are shaded gray, and nearshore areas in white are where the 12°C isotherm outcrops. Stations are marked by a dot and their labels are given on the top axis of each plot. Time series of (e) alongshore volume transport (10$^6$ m$^3$ s$^{-1}$), calculated between stations 80.55 and 80.90 for each cruise, and (f) monthly upwelling index anomalies (m$^3$ s$^{-1}$ 1000 m$^{-1}$; base period 1946–1997), which are estimates of offshore Ekman transport driven by the alongshore geostrophic wind stress at 34°N, 120°W, are shown to the right of the time-distance plots (from McGowan et al. 2003).
Antarctic krill (Euphausia superba), one of the most abundant animal species on earth, have declined (from 38 percent to 75 percent per decade) since 1976 in the high latitude southwest Atlantic sector, probably due to reduction in winter sea ice around the western Antarctic Peninsula (Atkinson et al., 2004). Krill are dependent on the highly productive summer phytoplankton blooms in the area east of the Antarctic Peninsula and south of the Polar Front. Salps, by contrast, which occupy the extensive lower-productivity regions of the Southern Ocean and tolerate warmer water than krill, have increased in abundance. This change has significant implications for the Southern Ocean food web because krill, not salps, are the primary food for penguins, seals, and whales in this system.

It is particularly important to ascertain impacts in regions where secondary producers are directly linked to fisheries production. For example, a decline in the relative importance of Pseudocalanus sp. in the Baltic Sea, driven by warming effects on the hydrographic conditions (MacKenzie and Schiedek, 2007), has been linked to fish stock size and condition (Mollmann et al., 2005). Under laboratory conditions, Isla et al. (2008) investigated the physiological response of Pseudocalanus sp. under different degrees of warming above decadal averages of the western Baltic Sea, and detected an increase in instantaneous mortality rates and a reduction in the net growth efficiency with temperature. They anticipate that temperature rise will negatively affect Pseudocalanus sp. and, as a result, fish stocks in the Baltic Sea.

Perhaps the most comprehensive study on the impacts of climate variability on marine ecosystem production, from zooplankton to fish and from intertidal to open waters, is that of Southward et al. (1995), which demonstrated many changes in the abundance of North East Atlantic taxa. Finally, Schmittner (2005) estimated that a disruption of the Atlantic meridional overturning circulation would lead to a collapse of the plankton stocks to less than half of their current biomass (see section 1.3.1).

2.4. DISTRIBUTION CHANGES
Climate change plays a major role in defining the habitat and distribution of marine and aquatic fishes through its influences on the physical properties of marine and aquatic environments. These include temperature, salinity, vertical mixing rates and thermohaline and wind-driven circulations. The environmental tolerances (bio-climate envelopes) to which populations have evolved (e.g. see Section 2.1.1), then interact with these climate-controlled environmental conditions to determine the preferred or suitable habitats and distributions of marine and aquatic organisms.

Decades of ecological and physiological research document that climatic variables are primary drivers of distributions and dynamics of marine plankton and fish (Hays et al., 2005; Roessig et al., 2004). Globally distributed planktonic records show strong shifts of phytoplankton and zooplankton communities in concert with regional oceanic climate regime shifts, as well as expected poleward range shifts and changes in timing of peak biomass (Beaugrand et al., 2002; deYoung et al., 2004; Hays et al., 2005; Richardson & Schoeman, 2004). Some copepod communities have shifted as much as 1 000 km northward. Beaugrand et al. (2002) documented a major large-scale reorganisation of the plankton communities, especially the calanoid copepod crustaceans, in the eastern North Atlantic Ocean and European shelf seas. A northward extension of more than 10° in latitude occurred for warm-water species over the last four decades associated with a decrease in the number of colder water species and were related to both the increasing trend in Northern Hemisphere temperature and the North Atlantic Oscillation. Beaugrand et al. (2003) showed that, in addition to the effects of overfishing, these fluctuations in plankton abundance have resulted in long-term changes in cod recruitment in the North Sea through three bottom-up control processes (changes in mean size of prey, seasonal timing and abundance).

Climate change is expected to drive most terrestrial and marine species ranges toward the poles (Southward et al., 1995; Parmesan and Yohe, 2003), as was the case in the Pleistocene–Holocene transition (reviewed in Fields et al., 1993) although the amplitude might be different. Shifts in marine fish and invertebrate communities have been particularly well documented off the coasts of western North America and the United Kingdom. These two
systems make an interesting contrast (see below) because the west coast of North America has experienced a 60-year period of significant warming in nearshore sea temperatures, whereas much of the United Kingdom coast experienced substantial cooling in the 1950s and 1960s, with warming only beginning in the 1970s (Holbrook et al., 1997; Sagarin et al., 1999; Southward et al., 2005). Species with greater mobility and migratory characteristics, such as smaller pelagic species with habitat requirements defined primarily by hydrographic characteristics such as temperature and salinity, are predicted to respond most quickly to such climate-driven interannual variability in habitat and distributions (Perry et al., 2005; Figure 15). Much of the data from the North Atlantic, North Sea, and coastal United Kingdom have exceptionally high resolution and long time series, so they provide detailed information on annual variability and long-term trends. Over 90 years, the timing of animal migration (e.g. veined squid, Loligo forbesi, and flounder Platichthys flesus) followed decadal trends in ocean temperature, being later in cool decades and up to one to two months earlier in warm years (Southward et al., 2005). Pilchard (Sardina pilchardus) increased egg abundances by two to three orders of magnitude during recent warming. In the North Sea, warm-adapted species (e.g. anchovy Engraulis encrasicolus and pilchard) have increased in abundance since 1925 (Beare et al., 2004), and seven out of eight species have shifted their ranges northward (e.g. bib, Trisopterus luscus) by as much as 100 km per decade (Perry et al. 2005). Some of these shifts are extremely fast, averaging over 2 km.y⁻¹ (Perry et al., 2005). The snake pipefish (Entelurus aequreus), for example, moved its upper latitude from southern England in 2003 to the Spitzbergen in 2007 (Harris et al., 2007). In the pelagic environment, shifts are not only horizontal but also vertical, with species responding to warming trends by moving towards deeper cooler waters (Perry et al., 2005; Dulvy et al., 2008). Records dating back to 1934 for intertidal invertebrates show equivalent shifts between warm- and cold-adapted species (e.g. the barnacles Semibalanus balanoides and Chthamalus spp., respectively), mirroring decadal shifts in coastal temperatures (Southward et al., 1995, 2005).

FIGURE 15
Examples of North Sea fish distributions that have shifted north with climatic warming. Relationships between mean latitude and 5-year running mean winter bottom temperature for (A) cod, (B) anglerfish, and (C) snake blenny are shown (from Perry et al. 2005).
Sagarin et al. (1999) related a 2 °C rise of SST in Monterey Bay, California, between 1931 and 1996 to a significant increase in southern-ranged species and decrease of northern-ranged species. Holbrook et al. (1997) found similar shifts over the past 25 years in fish communities in kelp habitat off California. There are also many examples of changes in distributions resulting from inter-annual climate variability, in particular relating to ENSO events. Off California, anchovy spawning expands northwards during El Niño events (Checkley et al., in press). Likewise, the northern limit of California sardines in Canadian waters is broadly related to sea surface temperature, expanding north during the months of June through August and returning south when sea temperatures begin to cool (McFarlane et al., 2005). Rodríguez-Sánchez et al. (2002) have described how Pacific sardine (Sardinops caerulens) in the California Current System changed its core habitat locations from the central to the southern and then back to the central parts of its full distributional range over the period 1931 to 1997 as the prevailing climate regimes shifted. Cross-shelf habitat is also affected by productivity conditions. California sardine shows significant interannual variation in the geographic extent of spawning, extending further offshore during La Niña and being compressed shoreward during El Niño (e.g. Lynn, 2003).

In the California Current upwelling system, the extent of the northwards migrations by Pacific hake (Merluccius productus) is positively correlated with increasing water temperatures (Ware and McFarlane, 1995). Philips et al. (2007) have also observed a northward expansion of the spawning areas for Pacific hake in the California Current system. Distributions of other species in the southern parts of the California Current System in relation to ENSO variations are provided by Lluch-Belda et al. (2005). Variations in Peruvian anchoveta have been explained by changes in carrying capacity (Cisrke et al., 1996), based on habitat productivity regimes (Chavez et al., 2003). Skipjack tuna (Katsuwonus pelamis) in the western Pacific alter their distribution to follow the convergence zone between the tropical Pacific warm pool and the eastern Pacific cold tongue as it moves in response to ENSO cycles (Lehodey et al., 1997).

Marked shifts have been observed in Arctic ecosystems. Diatom and invertebrate assemblages in Arctic lakes have shown huge species’ turnover, shifting away from benthic species toward more planktonic and warm-water-associated communities (Smol et al. 2005). Sea ice decline in the Arctic has been more evenly distributed than in the Antarctic. Polar bears (Ursus maritimus) have suffered significant population declines at both of their geographic boundaries. At their southern range boundary, polar bears are declining both in numbers and in mean body weight (Stirling et al. 1999). It is likely that climate change will extirpate polar bears from many areas in which they are presently common and will fragment the total population into a few isolated populations (Wüg et al., 2008). Penguins and other seabirds in Antarctica have shown dramatic responses to changes in sea ice extent over the past century (Ainley et al., 2003; Croxall et al., 2002; Smith et al., 1999), particularly those sea ice dependent species like the Adelie and emperor penguins (Pygoscelis adeliae and Aptenodytes forsteri, respectively) (Gross, 2005; Barbraud & Weimerskirch, 2001; Emslie et al., 1998; Fraser et al., 1992). In the long-term, sea ice-dependent birds will suffer a general reduction of habitat as ice shelves contract or collapse. In contrast, open-ocean feeding penguins — the chinstrap and gentoo — invaded southward along the Antarctic Peninsula between 20 and 50 years ago, with paleological evidence that gentoo had been absent from the Palmer region for 800 years previously (Emslie et al., 1998; Fraser et al., 1992).

If changes in climate conditions persist, then demersal species will also alter their distributions and migration patterns. However, because habitat for demersal species often includes particular bottom features (such as kelp forests or coral reefs) and sediment types (rock or sand), they are likely to alter their distribution patterns more slowly than pelagic species. This suggests that changes in the distributions of such demersal species might be used as an index of persistent longer-term changes in habitat conditions. Such large-scale changes, persisting for at least a few decades, have occurred in the past. The effects of the warming event in the North Atlantic from the 1920s to 1940s and later, are particularly well-documented (Cushing, 1982; Brander et al., 2003; Rose, 2005; Drinkwater, 2006), Tåning (1948) and Fridriksson (1948) described how Atlantic cod (Gadus morhua), haddock
Melanogrammus aeglefinus), redfish (Sebastes spp.) and Greenland halibut (Reinhardtius hippoglossoides) all expanded northwards, with cod spreading 1 200 km farther north along West Greenland that its previous distribution (Jensen, 1939, cited in Drinkwater, 2006). Such shifts involved benthic invertebrates as well as demersal finfish (Drinkwater, 2006). In general, species adapted to warmer waters expanded their distributions northwards, whereas species adapted to colder waters retracted their distributions northwards. More recently, major range extensions northwards of tropical and warm water marine species have been observed in the eastern North Atlantic (Quero et al., 1998; Brander et al., 2003) and in the North Sea (Brander et al., 2003; Perry et al., 2005; Clemmensen et al., 2007; Dulvy et al. 2008).

It has been suggested (Harley et al., 2006) that a warming-associated weakening of alongshore advection (Pisias et al., 2001) could actually break down certain marine biogeographical barriers that currently prevent range expansions. For example, two particularly cold-sensitive coral species (staghorn coral, Acropora cervicornis, and elkhorn coral, Acropora palmata) have recently expanded their ranges into the northern Gulf of Mexico (first observation in 1998), concurrent with rising SST (Precht & Aronson, 2004). Although continued poleward shift will be limited by light availability at some point (Hoegh-Guldberg, 1999), small range shifts may aid in developing new refugia against extreme SST events in future.

Long-term monitoring of the occurrence and distribution of a series of intertidal and shallow water organisms in the southwest of the United Kingdom has shown several patterns of change, particularly in the case of barnacles, which correlate broadly with changes in temperature over the several decades of record (Hawkins et al., 2003; Mieszkowska et al., 2006). It is clear that responses of intertidal and shallow marine organisms to climate change are more complex than simple latitudinal shifts related to temperature increase, with complex biotic interactions superimposed on the abiotic (Harley et al., 2006; Helmuth et al., 2006). Examples include the northward range extension of a marine snail in California (Zacherl et al., 2003) and the reappearance of the blue mussel in Svalbard (Berge et al., 2005).

2.5. ABUNDANCE CHANGES

Change in the abundance and biomass of marine populations are due to changes in their recruitment and growth rates, and ultimately to the productive capacity of the region in which they live. For example, changes in temperature can have direct impacts on fish abundance and biomass by stressing the physiological systems of individuals (as described in Section 2.1), causing them to change their locations or ultimately die. Temperature can also have indirect effects on fish abundance through its influences on growth and recruitment. Populations at the poleward extent of their ranges, such as Atlantic cod in the Barents Sea, increase in abundance with warmer temperatures, whereas populations in more equatorward parts of their range, such as cod in the North Sea, tend to decline in abundance as temperatures warm (Ottersen and Stenseth, 2001; Sirabella et al., 2001; Fig. 9).

Higher individual growth rates translate to greater productivity for the entire population, with the most productive stocks associated with higher bottom temperature and salinity conditions (Dutil and Brander, 2003), although Pörtner et al. (2001) found the growth performance of cod was optimal at 10 °C regardless of the latitudinal population investigated. This relatively simple picture becomes more complicated when food availability is also considered. Since increasing temperatures increase the metabolic demands of fish, it is possible that increased food supplies along with increasing temperatures may lead to faster growth and improved recruitment success for populations at equatorward locations in their range. Beaugrand et al. (2003) found that an index of plankton prey explained 48 percent of the variability of North Sea cod recruitment, with periods of good recruitment coinciding with higher abundances of its preferred prey. Cod populations living in the Irish Sea and on Georges Bank, therefore, have individuals whose sizes are substantially larger than those living off Labrador or in the Barents Sea (Brander, 1995). These findings lead to the hypothesis that, for cod in the North Atlantic, increasing temperatures improve recruitment for stocks in cold water, but decrease recruitment for stocks in warmer water (Planque and Fredou, 1999, Figure 9). When food supply is good, however, stocks in southern areas may be
able to overcome this increased metabolism due to the warmer temperatures, and capitalise on their increased food resources to increase growth rates. These relationships can be countered if the warmer temperatures also cause changes in the species composition of the plankton, such that its energetic quality as food is decreased. For example, Omori (1969) found low carbon to nitrogen ratios in zooplankton from the warmer tropical Pacific compared with those from the colder sub Arctic Pacific.

Taylor and Wolff (2007) have suggested that differences in plankton quality may be a key factor explaining the exceptional production of anchovy in the Peru upwelling system. In summary, warmer temperatures increase metabolic rates, but for populations at the equatorward parts of their ranges, if food is either insufficient or is of poor quality then both growth rates and recruitment will decline. Studies in freshwater systems show similar results, such that cold- and cool-water species like lake trout (*Oncorhynchus mykiss*), whitefish (*Coregonus commersonii*), and perch (*Perca* spp.) increase their growth rates in response to increased temperatures only when food supply is adequate to these increased demands (Ficke et al., 2007).

In Section 1.3 we noted that global warming is increasing the intensity of monsoon winds and, through increased upwelling, has resulted in increases in average summertime phytoplankton biomass in the Arabian Sea (Goes et al., 2005). The intensification of the hydrological cycles in this region is expected to influence limnological processes as well. Snow and glacier melt in the Eurasian mountains may result in changes in the flows of the Indus, Brahmaputra, Ganga and Mekong rivers, which sustain major river and floodplain fisheries and supply nutrients to coastal seas. Predictions for consequences of flow regimes are uncertain but increased run-off and discharge rates may boost fish yield through more extensive and prolonged inundation of floodplains. In Bangladesh, a 20 to 40 percent increase in flooded areas could raise total annual yields by 60 000 to 130 000 tonnes. These potential gains may be counter balanced by greater dry season losses due to lower dry season flows and greater demands on dry season water resources for irrigation, threatening fish survival and making the fish more susceptible to capture. Damming for hydropower, irrigation and flood control may also offset any potential fishery gains (Mirza et al., 2003). Recent declines in fish abundance in the East African Rift Valley lakes have been linked with climate impacts on lake ecosystems (O’Reilly et al., 2003). Lake Tanganyika, in particular, has historically supported one of the world’s most productive pelagic fisheries. A 30 to 50 percent decline in clupeid catch since the late 1970s has been attributed partially to environmental factors, because the lake had sustained high yields under similar fishing pressure for the previous fifteen to twenty years, although contrasting views have been expressed (Sarvala et al., 2006). The decline in catch was accompanied by breakdown of the previously strong seasonal patterns in catch, suggesting decoupling from ecosystem processes driven by the weakening of hydrodynamic patterns. These changes in the pelagic fishery are consistent with a lake-wide shift in ecosystem functioning (O’Reilly et al., 2003).

In freshwater ecosystems one of the most significant impacts of global warming would be a reduction in suitable habitat. In a simulation based on a doubling of the atmospheric CO$_2$ Mohseni et al. (2003) estimated a reduction of 36 percent and 15 percent of the suitable thermal habitat for cold and cool water species, respectively, while the habitat for warm water species would increase by 31 percent. This study was based on the maximum and minimum temperature tolerances for 57 species in 764 stream stations in the United States.

### 2.6. PhenoLOGICAL CHANGES

Parmesan & Yohe (2003) estimated that more than half (59 percent) of 1 598 terrestrial, freshwater or marine species exhibited measurable changes in their phenologies and/or distributions over the past 20 to 140 years. They were systematically and predominantly in the direction expected from regional changes in climate (Parmesan & Yohe, 2003; Root et al., 2003). A surprising result is the high proportion of species that responded to recent, relatively mild climate change (global average warming of 0.6 °C). The proportion of wild species impacted by climate change was estimated at 41 percent of all species investigated (655 of 1598; Parmesan & Yohe, 2003).
2.6.1. Ocean environments
Shifts in the timing of blooms of primary or secondary producers can cause a mismatch with their predators (the match-mismatch hypothesis proposed by Cushing (1969), section 2.1.3). Efficient transfer of marine primary and secondary production to higher trophic levels such as commercially important fish species is largely dependent on temporal synchrony between successive trophic production peaks in temperate systems. For example, the demographic timing of zooplankton in both the North East Pacific (Mackas et al., 2007) and the North East Atlantic (Greve et al., 2004, 2005) is strongly correlated with the temperature that the juvenile zooplankton encounter during early spring. There is concern that marine trophodynamics may have already been radically altered by ocean warming through predator-prey mismatch (Stenseth and Mysterud, 2002; Abraham and Sydeman, 2004; Edwards and Richardson, 2004; Visser and Both, 2005). In the North Sea, for example, dinoflagellates have advanced their seasonal peak by nearly one month, while diatoms have shown no consistent pattern of change (Edwards and Richardson, 2004; Figure 16) because their reproduction is triggered principally by increases in light intensity. Responses of copepods have been more variable but some species have their seasonal maximum earlier in the year (Edwards and Richardson, 2004). Beaugrand et al. (2003) and Reid et al. (2003) showed that fluctuations in plankton abundance in the North Sea due to climate change affected larval cod survival because of a mismatch between the size of prey (calanoid copepods) and cod larger than 30 mm after the mid-1980s. The timing of Macoma balthica spawning in NorthWestern Europe is also temperature dependent. Recent warming trends have led to earlier spawning but not earlier spring phytoplankton blooms, resulting in a temporal mismatch between larval production and food supply (Philippart et al., 2003). A further complication regarding match-mismatch is the need to consider the amplitude of the peak and possibly a threshold effect (Stenseth and Mysterud, 2002; Durant et al., 2005). Durant et al. (2005), for example, demonstrated that in the case of the herring/puffin match-mismatch the abundance of herring was structuring the match between predator and prey.

FIGURE 16

Mackas et al. (2007) review copepod abundance and phenology time series from net tow and Continuous Plankton Recorder surveys in the sub Arctic North East Pacific over recent decades. The two strongest responses observed are latitudinal shifts in centres of abundance of many species (poleward under warm conditions), and changes in the life cycle timing of Neocalanus plumchrus (earlier by several weeks in warm years and at warmer locations). Observations of zooplankton and high trophic level indices (fish, birds) in the North Pacific showed consistent patterns that are strongly correlated with large scale year-to-year and decade-to-decade ocean climate fluctuations, as reflected by spring season temperature anomalies in the surface mixed layer. The change in zooplankton developmental timing
cannot be explained solely by physiological acceleration, and thus differential mortality rates between cohorts are hypothesised (Mackas et al., 1998). Mackas et al. (2007) conclude that, in strongly seasonal environments, anomalously high temperature may provide misleading environmental cues that contribute to timing mismatch between life history events and the more-nearly-fixed seasonality of insolation, stratification and food supply. There are indications that such changes in timing may be coherent among different ocean basins (Figure 17; Perry et al., 2004). Edwards & Richardson (2004) also noted that water temperature affects the timing of ontogenetic transitions, which would decouple changes in the larval environment from the cues used by the adult population.

2.6.2. Inland waters
With the earlier ice break-up and warmer water temperatures, many lakes are responding with phenological adaptations. The spring algal bloom now occurs about four weeks earlier in several large European lakes (Gerten and Adrian, 2000; Straile and Adrian, 2000). In many cases where the spring phytoplankton bloom has advanced, zooplankton have not responded similarly, and populations are declining because their emergence no longer corresponds with high algal abundance (Gerten and Adrian, 2000). For example, in a lake in the Northwestern United States, the phytoplankton bloom has advanced by 19 days from 1962 to 2002 whereas
the zooplankton peak is more varied, with some species showing advance and others remaining stable (Winder & Schindler, 2004 a,b). Phenological shifts have also been demonstrated for some wild and farmed fish species (Ahas, 1999; Elliott et al., 2000). Because not all organisms respond similarly, differences in the magnitude of phenological responses among species has affected food-web interactions (Winder and Schindler, 2004a).

2.7. SPECIES INVASIONS AND DISEASES

On a global scale, outbreaks of disease have increased over the last three decades in many marine groups including corals, echinoderms, mammals, molluscs and turtles (Ward & Lafferty, 2004). Causes for increases in diseases of many groups remain uncertain, although temperature is one factor that has been implicated (Harvell et al., 2002). Previously unseen diseases have also emerged in new areas through shifts in distribution of hosts or pathogens, many of which are in response to climate change (Harvell et al., 1999).

The ecology of some of the human pathogenic microorganisms associated with the aquatic environment has also been linked to temperature change. *Vibrio parahaemolyticus* is a pathogen often involved in gastroenteritis associated with consumption of raw oysters and though the organism has worldwide distribution, it is rarely isolated when water temperatures are less than 15 °C (ICMSF, 1996). The outbreak of gastroenteritis associated with Alaskan oysters in 2004 extended by 1 000 km the northernmost documented source of oysters that caused illness due to this organism (McLaughlin et al., 2005). It has been reported that since 1997, mean water temperatures during July and August at the implicated region increased by 0.21 °C per year. This suggests that increases in sea surface temperatures might lead to microbial hazards in areas where they were never considered before (e.g. the outbreak of *V. parahaemolyticus* diarrhea in Puerto Montt, Chile, in 2004, 2005 and 2006 ; Gonzalez-Escalona et al., 2005; Fuenzalida et al., 2007). *Vibrio cholerae* has a symbiotic association with zooplankton and extreme events related to climate change may lead to increased hazards as a result of this pathogen being transmitted through water and fish (Lipp et al., 2002). Events associated with climate change such as storms and flash floods might lead to the transport of pathogens like viruses (noroviruses, hepatitis A virus) from waste water sources to shellfish growing areas. Bivalves being filter feeders can bioconcentrate viruses to much higher levels compared to water (Richards, 2001). Therefore, fish safety management programmes need to consider these hazards for risk assessment.

There are also latitudinal shifts of diseases in terrestrial and marine environments, due either to direct response of the pathogen or to the response of its vector. Climate warming can increase pathogen development and survival rates, disease transmission and host vulnerability, although a subset of pathogens might decrease with warming, releasing hosts from disease (Harvell et al., 2002). Relatively little evidence exists in marine ecosystems except for marine mammals, marine invertebrates such as oysters, and eelgrass (although the mechanisms for pathogenesis are unknown for these last two groups) and most of all the growth rates of marine bacteria and fungi in coral ecosystems which could be positively correlated with temperature (Harvell et al., 1999). An exception is the northward spread of two protozoan parasites (*Perkinsus marinus* and *Haplosporidium nelsoni*) from the Gulf of Mexico to Delaware Bay and further north, where they have caused mass mortalities of Eastern oysters (*Crassostrea virginica*). Winter temperatures consistently lower than 3 °C limit the development of the Multinucleated Spore Unknown (MSX) disease caused by the protozoan pathogen, *Haplosporidium nelsoni* (Hofmann et al., 2001) and the poleward spread of this and other pathogens can be expected to continue as such winter temperatures become rarer. This example also illustrates the relevance of seasonal information when considering the effects of climate change, since in this case it is winter temperature which controls the spread of the pathogen.

Some massive mortalities of pelagic fish have been proved to be caused by diseases, as in the case of sardine off Australia which was caused by a virus (Gaughan, 2002), but are related to human introduction of the pathogen agent rather than to climate change. Other massive mortalities, such as observed in the Moroccan sardine in 1997, seem more related to abrupt environmental changes. In a single year (1991), the oyster parasite *Perkinsus marinus*...
extended its range northward from Chesapeake Bay to Maine, a 500 km shift. Censuses from 1949 to 1990 showed a stable distribution of the parasite from the Gulf of Mexico to its northern boundary at Chesapeake Bay. The rapid expansion in 1991 has been linked to above-average winter temperatures rather than human-driven introduction or genetic change (Ford 1996).

Marcogliese (2001) recognized that parasites of freshwater and marine organisms will be affected directly by climate change, but also indirectly through the effects of climate change on their hosts. Climate change may also influence the selection of different modes of transmission and virulence (Marcogliese, 2001).

In addition to allowing natural range expansions, warming temperatures can facilitate the establishment and spread of deliberately or accidentally introduced species (Carlton, 2000; Stachowicz et al., 2002b).

Some authors have suggested that harmful algal blooms (HABs) are increasing globally due to anthropogenic influences (Smayda, 1990; Hallegraeff, 1993), while others have stressed that climate variability (apart from increased monitoring and awareness) are equally important (Sellner et al., 2003). Edwards et al. (2006) showed that HABs are indeed increasing in some areas of the North East Atlantic, although the increase is not spatially homogenous and is restricted to specific habitat types. It is evident that increase in the ratio of dinoflagellates versus diatoms has been observed in the southern North Sea (Hickel, 1998) and the Baltic Sea (Wasmund et al., 1998), and predicted in many climate change models (see section 2.2.2). The dominance of dinoflagellates was related to milder winter temperatures. In the context of HABs, if these climatic changes persist, they may lead to the emergence of a new successional regime in phytoplankton (Edwards et al., 2006). Although not classed as an HAB, satellite-detected coccolithophore activity (Smyth et al., 2004) is strongly correlated with warm-temperature and low salinity events off the northern coast of Norway and the Barents Sea. For example, on the other side of the Atlantic in the Grand Banks region, changes in the diatom/dinoflagellate ratio have been observed, with an increasing abundance of dinoflagellate species (notably Ceratium arcticum) (Johns et al., 2003). These changes, since the early 1990s, have been linked to hydroclimatic variations, specifically increased stratification and stability in the region and indicate a progressive freshening of this region likely caused by regional climate warming.

According to geological records taken from Atlantic and Pacific Canada when summer SST was much warmer during the late glacial–early Holocene (up to 58 °C), there was a period of sustained high production of red-tide blooms (Mudie et al., 2002). This led the authors to suggest that global warming is strongly implicated in the historical increase in the frequency of red tides and other HABs (see also Dale, 2001).

A final impact, yet to be evaluated properly, involves the depletion of the ozone layer in response to the increase of CO₂ concentrations (Austin et al., 1992). This process will result in an increase in ultraviolet radiation at the ocean surface, which is likely to affect biological processes. The response of a given species to UV exposure might depend on the presence of other species (Harley et al., 2006). For example, marine phytoplankton were protected from UVB damage when co-cultured with marine viruses (Jacquet & Bratbak, 2003).

2.8. FOOD WEB IMPACTS FROM PLANKTON TO FISH

Climatically driven changes in species composition and abundance will alter species diversity, with implications for ecosystem functions such as productivity (Duffy, 2003) and resistance to species invasions (Stachowicz et al., 2002a; Duffy, 2003). Understanding links between species diversity and ecosystem function is a general research gap in marine ecology and is wide open to investigations in the context of climate change.

Climate change is likely to affect ecosystems and their species both directly and indirectly through food web processes, which at the same time differentially interact (Figure 7). Whether direct or indirect processes predominate is likely to vary between systems, often depending on whether they are structured from the top down, from the bottom up or from the middle (Cury et al., 2000). For example, increases in the frequency of blooms of gelatinous zooplankton have been observed (in the Bering Sea: Brodeur et al., 2002) and predicted to
increase with global warming (in the North Sea: Attrill et al., 2007). In the tropical Pacific, it appears that direct effects on the dominant pelagic fish species predominate, whereas food web processes are more significant in the western Gulf of Alaska and even more so in the Barents Sea (Ciannelli et al., 2005; Ottersen et al., 2008). Frank et al. (2007) showed that the type of trophic forcing is strongly correlated with species richness and temperature. They suggest that very cold and species-poor areas might readily succumb to top-down control and recover slowly (if ever); warmer areas with more species might oscillate between top-down and bottom-up control, depending on exploitation rates and possibly, changing temperature regimes.

The connectivity of the food web also plays a role. While traditional food webs have a number of predators feeding on different prey in a balanced way, there are many examples where one species dominates as food, thus playing a significant control role: capelin (Mallotus villosus) in boreal seas of the North Atlantic, pollock (Theragra chalcogramma) in the Bering Sea, small pelagics in upwelling regions (Cury et al., 2000), etc. Even when there are several species of fish that serve as prey, there is often one species of invertebrate dominating the next level down (often a copepod, Ware and Thomson, 1992) whose decadal fluctuations are often accompanied by synchronous dynamics in their main fish larval and juvenile stages (e.g. Beaugrand et al., 2003; Beaugrand, 2004; Heath and Lough, 2007). In general, however, the presence of a single species as the primary channel for energy from lower to higher trophic levels makes it extremely difficult to relate the dynamics of any single upper trophic level to a single lower trophic level (Pimm et al., 1991; Rice, 1995). For this reason, models that analyse climate impacts on food webs have low predictive capacity. The following example details this complexity. The dynamics of the Barents Sea cod (Gadus morhua), capelin (Mallotus villosus) and herring (Clupea harengus) interact strongly and are all influenced by differential harvesting. Harvesting and predation of capelin by herring are capable of causing the population to collapse, whereas predation by cod (Gadus morhua) delays capelin recovery after a collapse (Hjermann et al., 2004a). Temperature and the NAO index are positively correlated with cod growth for ages up to four years old, but not for older fish, which are more affected by the ratio between cod and capelin (Hjermann et al., 2004b). The link between pairs of species can also vary between areas. For example, the time lag structure of the Barents Sea system indicates that the indirect effect of herring on cod is more important than the direct effect (Hjermann et al., 2004a,b), while the opposite is true for the Baltic Sea (Koester et al., 2001). Thus, the effect of herring on cod depends on the size of the cod stock in the Barents Sea but less so in the Baltic Sea (Hjermann et al., 2007). This is the way lags between climate and biological effect are likely to develop, and trophic position alone is not a precise indicator of whether populations respond directly or are lagged to climate (e.g. Ottersen et al., 2004; Post, 2004).

Most common is to observe synchronized changes in several trophic levels, without a clear cause-effect relationship. In the North Sea, changes to planktonic and benthic community composition and productivity have been observed since 1955 (Clark and Frid, 2001), and since the mid-1980s may have reduced the survival of young cod (Beaugrand et al., 2003). Large shifts in pelagic biodiversity (Beaugrand et al., 2002) and in fish community composition have been detected (Genner et al., 2004; Perry et al., 2005). Changes in seasonality or recurrence of hydrographic events or productive periods could be affected by trophic links (Stenseth et al., 2002, 2003; Platt et al., 2003; Llope et al., 2006). Elevated temperatures have increased mortality of winter flounder eggs and larvae (Keller and Klein-Macphee, 2000) and have led to later spawning migrations (Sims et al., 2004). A 2 °C rise in SST would result in removal of Antarctic bivalves and limpets from the Southern Ocean (Peck et al., 2004). Tuna populations may spread towards presently temperate regions, based on predicted warming of surface water and increasing primary production at mid and high latitudes (Loukos et al., 2003).

The direct effect of temperature on cod recruitment in different areas of the North Atlantic has been reinterpreted by Sundby (2000) who suggests that, in addition to its direct effect, temperature was likely to be a proxy for zooplankton abundance, which in turn has a major effect on cod larvae survival. Sundby (2000) argues that, at least in the Barents Sea,
zooplankton changes are caused by the advection of warm and zooplankton-rich Atlantic water from the Norwegian Sea. In the Norwegian Sea itself, temperature could directly control the growth of copepods, especially Calanus finmarchicus. Additionally, Sundby (2000) suggests that the abundance of the zooplankton population also depends on the abundance of its prey, phytoplankton. In the end, the optimal temperature window observed for cod abundance by Planque and Frédou (1999, Figure 9) could result from the combination and interaction of a direct effect of temperature on cod but also through indirect effects of temperature on the foodweb modulated by advective processes that, depending on the flux direction, will associate prey abundance for cod with cool or warm temperature. Sundby’s finding is likely to apply to these species in the North Sea and elsewhere because copepods are also a main prey of small pelagic fish such as herring and capelin..

2.9. REGIME SHIFTS AND OTHER EXTREME ECOSYSTEM EVENTS
A recently accepted mechanism through which climate variability and change interact in affecting ecosystem dynamics is based on the concept of “regime shifts”. A common definition of this term usually involves the notion of multiple stable states in a physical or ecological system, a rapid transition from one semi-permanent state to another and a link to climate forcing (deYoung et al., 2004). Although they have been observed in terrestrial, freshwater and marine ecosystems (Scheffer et al., 2004; deYoung et al., 2004) the underlying dynamics remain contentious (deYoung et al., 2008). In an ecological context, regime shifts propagate through several trophic levels (Cury and Shannon, 2004; Scheffer et al., 2001; Carpenter, 2003) and are thus ecosystem-wide processes with a single forcing mechanism. Whilst regime shifts in marine ecosystems are generally attributed to climate forcing, they can also result from overfishing, pollution or a combination (Hare and Mantua, 2000; Jackson et al., 2001; Beaugrand et al., 2002; Daskalov, 2002; Frank et al., 2005; Greene and Pershing, 2007). Equally, regime shifts in lakes have been found to be both climate-driven (Carpenter, 2003; Smol et al., 2005) as well as mediated by overfishing and pollution (Carpenter, 2003; Scheffer and Van Ness, 2004). In comparing the dynamics of freshwater and marine regime shifts, Scheffer and Van Nes (2004) concluded that similar mechanisms may be involved in causing alternative attractors (and thus occasional regime shifts) in both systems. However, they hypothesized that benthic regime shifts might happen easily but be relatively local, while open ocean shifts might not arise so easily but would be larger in magnitude and scale.

An important consideration highlighted by Hsieh et al. (2005) is that biological responses to shifting climatic conditions can be non-linear (e.g. a change in regime), even though the underlying abiotic changes may be linear and stochastic. This sensitivity of ecosystems to amplify climatic signals (Taylor et al., 2002) suggests that gradual changes in future climate may provoke sudden and perhaps unpredictable biological responses as ecosystems shift from one state to another (e.g. Smol et al., 2005). For this reason the pattern of the biological shift can vary from a smooth, quasi-linear relationship between the forcing and the biological response (Collie et al., 2004), to an abrupt, non-linear relationship between the forcing and the response variables (Scheffer et al., 2004; Collie et al., 2004). Such patterns may include discontinuous relationships which exhibit a hysteresis response in which the forcing variable exceeds a critical threshold causing the response variable to pass through unstable conditions while transiting from one equilibrium state to another (Scheffer et al., 2001; Collie et al., 2004). The difference between the three responses emerges when the forcing variable is reversed. For a discontinuous regime shift to be reversed, the forcing variable must exceed a second critical threshold, which is lower than the first, thus exhibiting hysteresis (Collie et al., 2004).

Large scale regime shifts are particularly significant considering their potential consequences. At basin scales, regime shifts have been identified in the North Atlantic in the early 1960s and late 1980s (Reid et al., 2001; Beaugrand, 2004; Genner et al., 2004; Clark and Frid, 2005 Figure 18), and in the North Pacific in 1925, 1945, 1977, 1989 and 1998 (Hare and Mantua, 2000; Benson and Trites, 2002; King, 2005).
A high biomass and large mean size of calanoid copepods and a high abundance of *Calanus finmarchicus* characterized the North East Atlantic during a negative NAO phase in the 1960s (Beaugrand et al., 2003). Changes in North Atlantic planktonic community structure were observed coincident with the climatic regime shift that occurred in the mid-1980s, with a decrease in mean size of calanoid copepods, delayed timing in the occurrence of *Calanus* from spring to late summer, decrease in the total biomass of copepods and a decrease in the abundance of Euphausiids (Beaugrand et al., 2003, Figure 18). The shift in zooplankton biomass coincided with changes in climate, commercial fish recruitment and in spawning stock biomass (SSB; Parsons and Lear, 2001). The signal of change in the zooplankton biomass occurred two years later than the signal evident in the NAO index (Lees et al., 2006). During the 1960s (negative North Atlantic oscillation phase), recruitment of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and saithe (*Pollachius virens*) in the North Sea rose to record levels, in a period called “the gadoid
outburst” (Hislop, 1996; Beaugrand et al., 2003). No strong year classes in saithe, cod or whiting have been observed following the late 1980s, shortly after the North Atlantic climatic regime shift and the shift in zooplankton biomass. This may be attributable to high fishing mortality, climate change or a combination of both (Beaugrand et al., 2003; Lees et al., 2006). North Sea saithe, cod and whiting recruitment appeared to change from relatively high mean recruitment to relatively low mean recruitment around the late 1980s and were positively correlated with zooplankton biomass with time lags of two, five and six years, respectively (Lees et al., 2006). Cod spawning stock biomass appeared to shift from a high to low quasi-stable state in the late 1980s. Saithe and whiting SSB show evidence of a low quasi-stable state from the late 1970s and mid-1980s, respectively (Lees et al., 2006).

Climatic regime shifts evident in the Pacific Decadal Oscillation (PDO) in 1977, 1989 and 1998 have each been associated with large-scale ecological changes (Hare and Mantua, 2000; Benson and Trites, 2002; King, 2005). Total North Pacific zooplankton biomass was in its most persistent and positive phase on record between 1965 and 1970, reaching its most positive value in 1968. It decreased to the lowest on record in 1989 and remained persistently low between 1990 and 1997 (Lees et al., 2006). This shift occurred coincident with the proposed 1989 climatic regime shift. However, no shift in North Pacific zooplankton biomass was observed following the 1977 climatic regime shift. Coincident with the climate shift, Bering Sea Greenland halibut (Reinhardtius hippoglossoides) recruitment decreased from a high to low phase between 1978 and 1982. In the Gulf of Alaska, sablefish (Anoplopoma fimbria) recruitment declined from a high to low phase between 1980 and 1981. Pacific halibut (Hippoglossus stenolepis), shortspine thornyhead (Sebastolobus alascanus) and arrowtooth flounder (Atheresthes stomias) recruitment increased from low to high phases in the late 1970s. Clark and Hare (2002) incorporated this concept of high and low ocean productivity regimes into a generalised stock-recruitment model for Pacific halibut, based on their finding that recruitment was higher during warm regimes. They concluded that Pacific halibut recruitment could double for the same spawning stock size depending on the productivity regime. More recently, a number of large-scale ecological changes are reported to have occurred coincident with the proposed 1998 North Pacific climatic regime shift. King (2005) reported a decreased productivity throughout the central North Pacific food web, increased productivity in the California Current system and increased productivity in some areas of the Gulf of Alaska and the western North Pacific, but no apparent response in the Bering Sea and the Aleutian Islands.

Chavez et al. (2003) noted that several characteristics of the entire North and South Pacific Ocean changed in the early 1950s and late 1970s (Figure 19). In the subtropical regions of both ocean basins, warmer conditions favoured sardine populations whereas cooler conditions favoured anchovy, although several other changes in nutrient supply, rockfish, salmon, tuna and seabirds also coincided with these warm and cool conditions. Chavez et al. (2003) attributed these changes to large spatial and long temporal scale alterations in the slope of the sea level, and therefore the proximity of the thermocline to the sea surface and subsequent supply of nutrients to the upper ocean layers.

Several authors have noted an apparent synchrony in fluctuations (or regimes) based on abundances of fish stocks from different parts of the same ocean basin, and even across ocean basins. This has been most apparent for small pelagic species (e.g. Kawasaki, 1992) although not exclusively (e.g. Bakun, 1996; Klyashtorin, 2001; Chavez et al., 2003; Weijerman et al., 2005). The implication would be that planetary-scale changes in atmospheric circulation patterns can induce seemingly related fluctuations in widely separated fish populations. These analyses have been criticized, however, based on statistical and mechanistic issues (Freon et al., 2003; Stenseth et al., 2003). Overland et al. (2008) concluded that while climate variables can have strong teleconnections within individual ocean basins, between-basin teleconnections and potential climate-driven biological synchrony over several decades are usually much weaker. Overland et al. (2008) also noted the cumulative effects of monthly weather anomalies, El Niño-type events, plus broad-band “red noise” variability at multi-decadal time scales. When transferring this variability to biological systems, the various time lag and feedback effects plus non-linearities, cause them to respond to climate changes with a
mix of slow fluctuations, prolonged trends, and step-like changes that may be difficult to predict, and yet that cannot be avoided. Added to these natural system influences on possible large-scale synchrony of fish populations are human influences, such as the movement of fishing boats and expertise from California to South America following the collapse of the California sardine fishery in the 1940 and 1950s (Ueber and MacCall, 1992) and common trends in herring catches between Iceland and British Columbia, Canada, as a result of the development of similar technologies and markets (Hamilton et al., 2006).

FIGURE 19
Representation of changes in several climate and Pacific biological indices, relating to global air temperature (A), the Pacific Decadal Oscillation (PDO; B), atmospheric circulation index (a measure of the ‘waviness’ of the zonal atmospheric circulation, C), atmospheric CO₂ concentration (D), basin-wide index of sardine and anchovy catches (E), an index of seabird abundances and sardine and anchovy landings in the South East Pacific (F), seabird abundance and sardine and anchovy landings in Peru (G). From Chavez et al. (2003).
De Young et al. (2008) present a conceptual framework to enhance the ability to detect, predict and manage regime shifts in the ocean and conclude that the ability to adapt to, or manage regime shifts, depends upon their uniqueness, our understanding of their causes and linkages between ecosystem components and our observational capabilities. Because the likelihood of climate-driven regime shifts increases when humans reduce ecosystem resilience (understood as the disturbance an ecosystem can tolerate before it shifts into a different state, e.g. Scheffer et al., 2001; Cropp and Gabrica, 2002; Folke et al., 2004), for example by removing key functional species, age groups, trophic levels, or adding waste and pollutants (Folke et al., 2004), a primary issue remains whether ecosystem resilience will be sufficient to tolerate future anthropogenic climate change.

Of interest in the context of global climate change, are a separate set of non-linear biological events that can be generated not by linear climate influences but by greater storminess. Two studies raise this point. Trenberth et al. (2007) recently reported a 75 percent increase (since 1970) in tropical storms in the North Atlantic and western North Pacific, and Saunders and Lea (2008) demonstrated a high correlation between sea surface temperature and hurricane frequency and activity in the Atlantic Ocean. Greater storminess can alter disturbance regimes in coastal ecosystems and lead to changes in diversity and hence ecosystem functioning. Salt marshes, mangroves and coral reefs are likely to be particularly vulnerable (e.g. Bertness and Ewanchuk, 2002; Hughes et al., 2003). Coral reefs are also well known to be susceptible to fresh water as well as the effects of turbidity and sedimentation that vary with coastal weather patterns. Numerous examples of coral communities being killed off or adversely affected purely as a result of extreme rainfall events have already been reported (e.g. Alongi & McKinnon, 2005; Fabricius, 2005).

3. Scenarios of climate change impacts on fish production and ecosystems

3.1. GENERAL IMPACTS
Climate change represents several factors associated with increasing atmospheric concentrations of greenhouse gases. These are detailed in Section 1 of this report and include increasing sea temperatures, increasing acidification of the oceans, increasing sea level and related factors such as changes in winds, strengths of storms, precipitation patterns, etc..To these must be added non-climate stresses on marine environments such as harvesting, contaminants, non-native species introductions, habitat and coastal zone modifications and changes in nutrient additions and freshwater runoff patterns, which vary in the spatial pattern of their impacts (Halpern et al., 2008). Non-climate related stresses to freshwater systems include over-exploitation, flow obstructions such as dams, habitat change, non-native species introductions, and contaminants and nutrient additions (Schindler, 2001). These will interact to make sweeping generalised conclusions of the impacts of global climate change on marine and aquatic systems difficult, but should improve the predictions for local areas if the correct sets of global, regional and local stressors can be identified. For example, whereas the oceans are warming in general, they are not warming at the same rate everywhere, and some locations are cooling (Section 1.1). Similarly, the global ocean is decreasing in salinity, but with large regional variations (Section 1.2).

General impacts on marine and aquatic systems as a result of large-scale changes related to temperature, winds and acidification can be predicted however, in some cases with a high degree of confidence. These impacts will occur on a variety of time scales from rapid (a few years) to slow (multiple decades). They generally can be grouped into changes in: distributions and abundance, phenology (timing), species community composition and community structure and dynamics, including productivity (Hennessy et al., 2007).
3.1.1. Rapid time scales
There is high confidence that increasing temperatures will have negative impacts on the physiology of fish because of limited oxygen transport to tissues at higher temperatures. Specifically, at some temperature the evolved circulatory system will be unable to deliver sufficient oxygen to meet tissue metabolic demands (Pörtner and Knust, 2007). This process forms the physiological basis for the observed and predicted changes in distributions and recruitment (abundance). It may be more significant for high-latitude and polar species, many of which have low tolerances for temperature changes (stenothermic). Many fish species in polar regions have reduced numbers of red blood cells and therefore are less efficient at carrying oxygen when temperature-related metabolic demands increase (Roessig et al., 2004). This physiological constraint is likely to cause significant limitations for aquaculture. In the short term, higher temperatures may produce increased food conversion efficiencies and increased growth rates, but as temperatures continue to increase and because cultured species cannot move, their productivity is likely to decline (medium confidence). Optimal locations for aquaculture species are expected to move polewards (Stenevik and Sundby, 2007).

These constraints on physiology will result in changes in distributions of both freshwater and marine species and likely cause changes in abundance as recruitment processes are impacted by changing temperatures and circulation patterns (Section 2.5). Strongest and most rapid changes will be to those stocks at the edges of their species’ ranges, such that stocks at both the equatorward and poleward limits will move poleward (high confidence). These responses will be most rapid for highly mobile pelagic species (Harley et al., 2006) as has already been demonstrated by tuna in the tropical Pacific in response to ENSO variability (Lehodey et al., 1997), zooplankton and pelagic fish in the Northeast Pacific (Ware and McFarlane, 1995; McFarlane and Beamish, 2002, Mackas et al., 2007), small pelagics in the English Channel (Hawkins et al., 2003) and Norwegian herring in the North East Atlantic (Sissener and Bjørndal, 2005). Less mobile, often demersal, species have also been observed to move poleward (Perry et al., 2005; Drinkwater, 2006) or to deeper depths and cold upwelling centres (Clark, 2006).

Changes in the timing of life history events (phenology, Section 2.6) are expected with climate change (high confidence). Short life span rapid turnover species, for example plankton, squid and small pelagic fishes, are those most likely to experience such changes. This will lead to earlier spring plankton blooms (Mackas et al., 1998; Edwards and Richardson, 2004) for some species but not for others (Greve et al., 2005; Hays et al., 2005). It will also lead to changes in species composition as the development times for different components of marine communities are altered. This will result in mismatches between early life stages of fish and their prey, with recruitment failures and declines in abundance as consequences (e.g. Platt et al., 2003; Section 2.1.3).

3.1.2. Intermediate time scales
At intermediate time scales of a few years to a decade, temperature-mediated physiological stresses and phenology changes will impact the recruitment success and therefore the abundances of many marine and aquatic populations (high confidence). The earliest impacted species are again likely to be those with shorter life-spans and faster turnover rates, since biomass of species with longer life-spans tends to be less dependent on annual recruitment. These impacts are also likely to be most acute at the extremes of species’ ranges, and may manifest themselves as changes in fish distributions (e.g. loss of more southerly populations and stocks). Changes in abundance will alter the composition of marine and aquatic communities, with possible consequences to the structure and productivity of these marine ecosystems (Worm and Duffy, 2003) in particular if keystone or “high leverage” species are affected (Harley et al., 2006). Since these processes involve many unknowns, predicting impacts and directions for any specific case can only be done with low confidence. Predicting net community impacts such as total biomass or productivity may be done with intermediate confidence, however, because of compensatory dynamics among the members within the various functional groups that make up that community (Mackas et al., 2001; Jennings and Brander, 2008).
Increasing vertical stratification is predicted for many marine areas (e.g. Houghton et al., 2001) and lakes (Ficke et al., 2007). It is expected to reduce vertical mixing and therefore reduce nutrient supply to the productive photic layers, thereby decreasing productivity (intermediate confidence). In addition, increasing stratification is predicted to alter the balance between pelagic and benthic recycling of nutrients, favouring the pelagic pathway and pelagic fishes at the expense of the benthos (Frank et al., 1990). This will drive changes in species composition (e.g. in the Baltic, Mackenzie et al., 2007) and affect the timing of life cycle processes (e.g. in the Pacific, Mackas et al., 2007, and Atlantic, Greve et al., 2005). Evidence of such increasing vertical stratification is available for the North Pacific Ocean (Freeland et al., 1997) and the North Atlantic (Curry and Mauritzen, 2005; see also Section 1.2); its impacts on lower trophic levels of the Northwest Pacific (Chiba et al., 2004) and fish productivity in East African lakes (O’Reilly et al., 2003) have also been demonstrated.

3.1.3. Long time scales
Predicted impacts to marine systems at long (decadal) time scales are dependent upon predicted changes in net primary production in the oceans and its transfer to higher trophic levels, about which there is still low (Brander, 2007) but increasingly promising (Jennings et al., 2008; Cheung et al., 2008) confidence. Section 2.2 describes several studies which have modelled the global responses of ocean primary production to climate change. There are significant differences between models. Regional predictions may have improved confidence because of better knowledge of the specific processes involved, e.g. as for the Arabian Sea, Goes et al. (2005). Future net primary production may increase in some high latitude regions because of warming and reduced ice cover, but decrease in low latitude regions because of reduced vertical mixing and replenishment of nutrients (Sarmiento et al., 2004) and changes in circulation and direct human impacts (Cruz et al., 2007). The result is that primary production may increase in some areas but decrease in others, with the net global impact unknown (Brander, 2007). Modelling and paleo oceanographic studies suggest a 50 percent decline in the plankton biomass in the North Atlantic during periods when the Meridional Overturning Circulation is weak (Schmittner, 2005). In contrast, coupled bio-physical models suggest global increases in net marine primary production of 0.7 percent to 8.1 percent but with large regional differences (Sarmiento et al., 2004). Most simulation studies, however, conclude that – in general – global net marine primary production will decrease with climate change, although there is large regional variation. Empirical observations of changes in net primary production over the past few decades have actually shown a decrease, but also with large regional variability (Gregg et al., 2003). Other simulation studies have shown that changes in phytoplankton composition are likely towards smaller forms (Bopp et al., 2005) and with changes in seasonality (Hashioka and Yamanaka, 2007). Such changes in regional production and species composition will impact all other trophic levels, including marine mammals, in particular those whose ranges are already restricted with little opportunity for expansion (Learmonth et al., 2006).

A new approach to estimating climate change impacts on global fish production based on ecosystem properties has been recently proposed by Jennings et al. (2008). They observed that marine ecosystems have remarkably constant and simple relationships between body size, energy acquisition and transfer and suggested that this approach could be used to assess the role of changing climatic temperature and primary production on production at higher trophic levels and to set baselines for assessing the impacts of fisheries (Jennings and Blanchard, 2004). This work is still in progress (see http://web.pml.ac.uk/quest-fish/default.htm). Cheung et al. (2008), using a somewhat different approach based on observed current geographic ranges, trophic levels, primary production and fish catch, found a significant relationship between primary production and fisheries catch, with a high probability of shifts in locations of maximum catches. However, many impacts of global change on marine ecosystems are likely to be non-linear, in which small changes in the forcing can result in large responses. For example, Beaugrand et al. (2008) identified a critical thermal boundary in the North Atlantic at which abrupt shifts have been reported.
3.2. CASE STUDIES

A case studies approach illustrates the general and particular responses of specific marine and freshwater ecosystems to climate change. We focus on Arctic, North Atlantic, North Pacific, upwelling, South West Pacific, coral reef and freshwater systems, and aquaculture systems.

3.2.1. Arctic

The Arctic Climate Impact Assessment (ACIA), (Symon, 2005; see also Schrank, 2007) provides an assessment and predictions of climate change impacts to Arctic ecosystems. Climate change scenarios for Arctic marine systems are very uncertain because most models have focused on atmospheric effects (Schrank, 2007). Predicted physical changes by 2050 include increases in air temperature of 5°C, a 6 percent increase in precipitation, a 15 cm rise in sea level, a 5 percent increase in cloud cover, a 20 day reduction in sea ice duration and 20 percent reduction in winter ice with substantial ice-free areas in summer (Schrank, 2007). The ecological consequences of these physical changes are expected (high confidence) to be (Table 2; Loeng, 2005; Schrank, 2007):

- decreased sea ice may allow primary production to increase two to five times over present conditions, although consequences of these changes for match or mismatch of this production with zooplankton and the rest of the food web are unclear;
- increased temperatures are very likely to shrink the ranges of cold water fish and benthic species but expand the ranges of Atlantic and Pacific species northwards. Long-lived Arctic species with narrow temperature tolerances and with late reproduction are likely to be first to disappear from more southerly habitats;
- changes to migration timing are likely, as are increases in growth rates;
- non-native species are likely to increase in Arctic waters but the assessment considers the extinction of any present Arctic fish species unlikely.

Endemic marine mammals (seals and whales) are expected to face severe habitat changes, most significant of which is the reduction of sea ice. Thinner ice and substantial ice-free areas will impact ice-associated mammals such as seals and may lead to extinction of some populations within decades, and possibly species extinctions at longer time scales (Kovacz and Lydersen, 2008).

3.2.2. North Atlantic

Large areas of the North Atlantic Ocean have already been impacted by climate warming-related changes, including phytoplankton (Edwards and Richardson, 2004), zooplankton (Beaugrand et al., 2002) and fish (Quero et al., 1998; Perry et al., 2005; Dulvy et al., 2008). Climate conditions in the North Atlantic are strongly modulated by the atmospheric pressure shifts that are indexed by the North Atlantic Oscillation. Details of future climate change impacts in the North Atlantic are therefore likely to continue to vary with the state of the NAO. If the warming trend with a high NAO index continues, then sea temperatures in the North Sea, Nordic seas and Barents Sea are likely to increase by 1 to 3°C over the next 50 years, with the largest changes occurring in the northernmost regions (Stenevik and Sundby, 2007). In addition, increased wind-induced fluxes of warm Atlantic waters into these regions can be expected, which will increase the vertical stratification (Stenevik and Sundby, 2007) and reduce ice cover (Ellingsen et al., 2008). Simulations suggest that primary production is likely to increase in the Barents Sea, although zooplankton production is likely to decrease as production by Arctic zooplankton declines (Ellingsen et al., 2008). These will cause northward shifts of the distributions of all species, increase biomass production of species in Arcto-boreal regions, but introduce southern invaders into the southern North Sea (Stenevik and Sundby, 2007). Spawning areas for capelin in the Barents Sea are predicted to shift eastwards and spawning is predicted to occur earlier because of warmer temperatures (Huse and Ellingsen, 2008). A significant change in the meridional overturning circulation would have substantial impact on the Barents Sea (see Section 1.3). The North Sea is likely to become dominated by pelagic species such as herring and mackerel in the north and sardine and anchovy in the south, although the total system productivity may not be too different than today (Stenevik and Sundby, 2007). The Baltic Sea is predicted to become warmer and
fresher, with significant increases in its vertical stratification (Mackenzie et al., 2007). The biodiversity of the Baltic is particularly sensitive to salinity changes; decreased salinity is predicted to exclude many marine-tolerant species and to favour those more tolerant of low salinities (Mackenzie et al., 2007). Non-native species may enter the Baltic, but few are expected to be able to colonise because of the salinity stress (Mackenzie et al., 2007).

**TABLE 2**

**Potential (‘very likely to happen’) long-term ecological changes in Arctic marine systems as a result of climate warming. From Loeng et al., 2005.**

<table>
<thead>
<tr>
<th></th>
<th>Phytoplankton</th>
<th>Zooplankton</th>
<th>Benthos</th>
<th>Fish</th>
<th>Marine mammals and seabirds</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Production</strong></td>
<td>Increased production in Arctic Ocean, Barents and Bering Sea shelves.</td>
<td>Difficult to predict; depends on timing of phytoplankton blooms and water temperature.</td>
<td>Difficult to predict; depends on timing of plankton blooms and water temperature. Crab and shrimp production may decline.</td>
<td>Depends on timing of plankton blooms and drift patterns of eggs and larvae.</td>
<td>Declines in ice-associated species and increases by temperate species; seabird production dependent on changes in food availability.</td>
</tr>
<tr>
<td><strong>Species composition and diversity</strong></td>
<td>Depends on mixing depth: deep mixing favours flagellates.</td>
<td>Adaptable Arctic copepods favoured.</td>
<td>Cold water species decline in abundance; warm water species increase.</td>
<td>Cod, herring, pollock, some flatfish likely to move north and become more abundant; capelin, polar cod, Greenland halibut will have restricted range and decrease in abundance.</td>
<td>Declines of polar bears, ringed, harp, hooded, spotted, ribbon and possibly bearded seals. Increases of harbour and grey seals. Possible declines of several whale species. Ivory gulls, small auk species likely to decline.</td>
</tr>
</tbody>
</table>
North West Atlantic, capelin (*Mallotus villosus*) are important prey of cod, but spawning times for capelin are susceptible to delays due to cold water from melting glaciers (Vasseur and Cato, 2008). In the North East Atlantic, climate model simulations of North Sea temperatures suggest that increasing temperatures will lead to declines in North Sea cod populations compared to simulations which exclude climate change effects (Clark *et al*., 2003).

### 3.2.3. North Pacific

Overland and Wang (2007) have examined the implications for the North Pacific Ocean of the results from ten models of atmospheric climate change. They conclude that anthropogenic impacts on the future North Pacific climate will be as large in 30 to 50 years as natural climate variability is today. This suggests that climate-ecosystem-fisheries relationships developed during the latter half of the twentieth century may not be robust in the twenty-first century. The implication is that relationships between fish production and indices of atmospheric state such as the Pacific Decadal Oscillation (PDO) may not be valid as the climate changes. As with the North Atlantic, the North Pacific is strongly influenced by variations in the strengths and positions of atmospheric pressures centres, which are indexed by east-west and north-south variations in sea surface temperature as captured in the PDO. Overland and Wang (2007) conclude that this pattern of decadal variability will continue into the twenty-first century, but it will occur on top of a persistent upward trend in sea surface temperature (Figure 20). Pierce (2004) modelled the impacts of increasing greenhouse gases to the plankton of the North Pacific and found the subpolar system changed from one with strong variability and winter lows to one with much more constant annual values and decreased yearly-averaged primary productivity. The productivity increased in other regions of the North Pacific as warmer temperatures enabled higher growth rates. Pierce (2004) found that his results were largely driven by changes in mixed layer depths (shoaling) and temperature (increasing). In contrast, the simulations by Hashioka and Yamanaka (2007) found that warmer conditions led to changes in the seasonal patterns of primary production in the North West Pacific. On the west coast of North America, northward shifts of fish populations are predicted (Overland and Wang, 2007) and have been observed (e.g. Okey *et al*., 2007). Welch *et al*., (1998) predicted the restriction of suitable thermal habitat for sockeye salmon (*Oncorhynchus nerka*) in the North Pacific under a 2xCO$_2$ scenario to be reduced to the Bering Sea. The Bering Sea itself is predicted to be significantly impacted by climate change, including large-scale retreats of sea ice, losses of cold-water species and increasing abundances of species from the North Pacific (Overland and Stabeno, 2004). As noted above (Section 1.5), the sub Arctic North Pacific is particularly sensitive to the effects of increasing acidification and by the the end of this century, some regions will become under-saturated in the aragonite form from surface to bottom (Feely *et al*., 2008a). Upwelling of aragonite undersaturated waters onto the continental shelf of western North America has already been reported (Feely *et al*., 2008b). Various vertebrate and invertebrate species have been shown to be negatively impacted by these low pH concentrations, including pteropods (common prey for many open ocean fish) and squid (Fabry *et al*., 2008).
FIGURE 20
Projected winter sea surface temperature anomalies (SSTA, °C) relative to a 1980–1999 base period for the central North Pacific Ocean, showing a steady upward trend to 2050. Grey and thin coloured lines represent projected temperatures from 10 climate models; the bold blue line represents the trend of the all-model mean SSTA. From Overland and Wang (2007).

3.2.4. Wind-driven coastal upwelling systems
Major coastal wind-driven upwelling systems tend to occur on the eastern boundaries of the world’s oceans. The interaction of the wind-driven circulation with the bathymetry produces highly productive ecosystems, largely of pelagic species but which may also include demersal species. Predictions of the responses of coastal wind-driven upwelling systems are contradictory, however, partially because higher model resolution is required to resolve coastal upwelling at the global scale (see Section 1.3). Bakun (1990) proposed that with global warming the land-sea air pressure gradient would increase, thereby intensifying the alongshore wind stress and increasing coastal upwelling. This would have the effect of offsetting in these regions the global trend of increasing water temperatures and increasing vertical stratification, since such upwelled waters are cold and rich in nutrients. Snyder et al. (2003) modelled wind-driven upwelling along the coast of California with increasing atmospheric CO$_2$ concentrations and found an intensified upwelling season with some change in seasonality. They concluded this effect should enhance the productivity of the system and possibly offset the local effects of increasing temperatures. McGregor et al. (2007) found that the upwelling system off North West Africa intensified during the twentieth century, and suggested it will continue to intensify with global warming. This should enable the system to retain its high productivity as the climate changes, although the composition of the predominant pelagic species may change (e.g. Zeeberg et al., 2008). Predicted impacts of climate change to parts of the Benguela upwelling system are different, however. This system is very productive, often with phytoplankton settling on the sea floor where it decomposes, consuming oxygen and producing hydrogen sulphide. When these oxygen-depleted waters are upwelled towards the surface, significant species displacements and mortalities can result (Bakun and Weeks, 2004). With climate change, intensified Benguela upwelling may therefore further increase nutrient inputs, primary production and low-oxygen events (Clark, 2006). The emergence of increasing areas of hypoxia and anoxia in the California Current upwelling system (Chan et al., 2008) suggests that similar events may also occur in this system with climate change. Therefore, even with consistent predictions of increasing winds and coastal upwelling, each system may respond differently because of its unique characteristics of background productivity, consumer populations, etc. As outlined in Section
1.3. however, different predictions have been made of the physical responses to climate change, with some studies predicting weakening winds (Vecchi et al., 2006). The primary production model of Sarmiento et al. (2004) also showed no consistent global response of upwelling regions to climate change.

3.2.5. Tropical and subtropical seas
Tropical and subtropical marine regions have a wide variety of diverse habitats, each with highly diverse and distinct fauna (Roessig et al., 2004). There have been fewer studies of the potential tropical ocean responses to climate change than have been reported for temperate latitudes. A particularly important question, not yet resolved, is whether the tropical Pacific will take on a more ‘El Niño-like’ character, in which the east-west gradient in time-mean SST is reduced, or will assume a more ‘La Niña-like’ character with an increased east-west SST gradient (Vecchi et al., 2008). Simulations of the response of primary production in the tropical Pacific predict a decline because of increased stratification and decreased nutrient supply (Bopp et al., 2005). The combined effects of changes in circulation, temperature, nutrients and primary production cascade up the food web to influence prey availability and habitat conditions for tuna (Loukos et al., 2003). Tuna habitat conditions east of the date line could improve, similar to El Niño-related warming events (Loukos et al., 2003; see also Section 2.2.2). A similar result was found by Watters et al. (2003) using a different modelling approach applied to the eastern tropical Pacific, in which a warming trend resulted in a persistent decline in abundances at all trophic levels as the region became more stratified and nutrient limited. Hennessy et al. (2007) concluded, for the waters about Australia and New Zealand, greatest impacts as a result of climate change would occur to coastal species and subtidal nursery areas, temperate endemic species rather than tropicaals and coastal and demersal species rather than pelagic and deep-sea species. Hobday et al. (2006) and Poloczanska et al. (2007) provide a review of predicted climate change impacts to the marine ecosystems surrounding Australia. Models predict physical changes similar to other regions: ocean warming, increased vertical stratification, strengthening of poleward coastal currents, increasing ocean acidification, sea level rise and altered storm and rainfall regimes (Poloczanska et al., 2007). The analyses of Hobday et al. (2006) concluded that warming and increasing stratification will alter plankton community composition, alter their distributions polewards, and change the timing of their bloom dynamics so that transfers to higher trophic levels may be impaired. Benthic and demersal fishes will shift their distributions southward and may decline in abundance. Pelagic species will also shift their distributions southwards and some species may benefit from increased local wind-driven upwelling (e.g. anchovy). Hobday et al. (2006) concluded that the eastern-central and southeast marine regions of Australia were the most vulnerable to the impacts of climate and other stressors.

3.2.6. Coral reef systems
Coral reef ecosystems occur in warm and cold-water regions of the global ocean and are among the world’s most iconic places. They provide habitat for one-quarter of all marine species and are important sources of protein and income for many developing countries (Parry et al., 2007). They are at risk from climate change impacts related to increasing temperatures, acidity, storm intensity and sea levels (see Section 2.2.2), and non-climate factors such as over-exploitation, non-native species introductions and increasing nutrient and sediment loads. The risks to coral reefs are not distributed equally, with increasing temperatures a significant issue for warm-water systems, increasing acidity and decalcification a significant issue for both warm- and cold-water systems (e.g. Feely et al., 2008a), and direct human impacts a significant issue in more populous regions. Graham et al. (2006), however, suggested that even isolated and remote reef systems may be severely at risk from climate-related impacts alone.

Three different time scales can be identified for climate change-related impacts to coral reef systems:
- years: increased temperature effects on coral bleaching, which have become more frequent with recent ENSO events and may lead to steady degradation of reefs;
• a few decades: increasing acidification and dissolution of carbonate structures of reefs;
• multi-decades: weakening of structural integrity of reefs and increasing susceptibility to storms and erosion events as a result of increased temperatures and acidification, leading to large-scale composition shifts.

Coral reef ecosystems are usually able to recover from weak chronic environmental stresses, such as temperature increases or reduced calcification, as long as acute stresses such as temperature spikes associated with ENSO events, disease, or severe storms are not too strong or too frequent (Buddemeier et al., 2004). Combination of chronic plus acute stress can lead to regime shifts with replacement of coral by algae-dominated systems (Hughes et al., 2003). In the Indo-Pacific, frequent ENSO-related bleaching events are believed to be inhibiting corals by not allowing enough time for recovery between successive events (Buddemeier et al., 2004). Such bleaching events occur when sea temperatures are greater than 1 °C above mean summer temperatures for more than four weeks (Hough-Guildberg, 1999). Climate change models predict these thresholds will be exceeded more often and therefore bleaching events are likely to occur more frequently than corals can recover (Donner et al., 2005). If this same bleaching threshold remains, then more frequent bleaching events and increased coral mortality is likely for a majority of reefs by 2030 to 2050 (Parry et al., 2007).

Increasing acidity (decreasing pH) of the world’s oceans is a significant and pervasive longer-term threat to coral reefs. Although the in situ response of coral growth to increasing acidity is unknown (Parry et al., 2007), laboratory studies indicate that decreased aragonite saturation at reduced pH can disrupt coral calcification (Orr et al., 2005). This impact may be especially severe for deep cold-water corals such as occur along the continental slopes of the North East Pacific, where aragonite saturation levels are already shoaling at 90 to 150 m (Feely et al., 2008a). In warm waters, increasing acidity will lead to declining calcification and weakening of the coral skeleton, such that reduced coral cover and greater erosion of coral reefs is predicted by 2070 (Parry et al., 2007).

The potential for coral reef systems to adapt to these environmental stresses is uncertain. A change of symbiotic zooxanthellae to species more tolerant of high temperatures could reduce bleaching events and delay the demise of reefs from 2050 to 2100 (Parry et al., 2007). Migration of corals to higher latitudes is considered unlikely because of a lack of suitable substrates and decreasing aragonite concentrations at higher latitudes (Parry et al., 2007). Buddemeier et al. (2004) calculated that a 2 °C warming of the oceans would expand the thermal range of corals (which are presently limited by the 18 °C isotherm) by only a small amount. Declines in corals have had negative impacts on reef fish biodiversity in at least one study in Papua New Guinea (Jones et al., 2004). To date, however, there has been little evidence for a link between climate warming and bleaching events with impacts on coastal fisheries (e.g. Grandcourt and Cesar, 2003). However it is also clear that large-scale weakening and erosion of coral reefs over the longerterm will undoubtedly severely impact the animals which depend on these reefs for their food and habitat.

3.2.7. Freshwater systems

Freshwater lakes and their ecosystems are highly vulnerable to climate change. At very long time scales (greater than centennial) paleo records show that lakes have altered their shapes and distributions and have disappeared entirely, with the processes related to climate change as a result of the shifting dynamics among precipitation, evaporation and runoff (Poff et al., 2002). In general and at longer time scales (multiple decades) in North America, the anticipated response is for cold-water species to be negatively affected, warm-water species to be positively affected, and cool-water species to be positively affected in the northern but negatively affected in the southern parts of their range (Mohseni et al. 2003; Field et al., 2007). A general shift of cool- and warm-water species northward is expected in North America and likely the rest of the Northern Hemisphere. However, the responses of particular lake ecosystems to climate change will depend strongly on the size, depth, and trophic status of the lake. In a modelling study of climate warming (2xCO₂) effects on lakes in central North
America, Stefen et al. (1995) concluded that cold-water fish would be most affected because of losses of optimal habitats in shallow, eutrophic lakes. Growth conditions for cool- and warm-water fishes should improve in well-mixed lakes, small lakes and those with oligotrophic nutrient conditions. Since the production rates of invertebrate prey in lakes increases logarithmically with temperature (rates increase two to four times for each 10 °C increase in temperature; Watson et al., 1997) this should lead to long-term increases in fish production, although changes in prey species composition may offset this effect (Watson et al., 1997). In the short-term, however, lags between fish predators and their zooplankton prey may initially decrease fish production due to timing mismatches (Watson et al., 1997).

Similar issues regarding productivity and timing mismatches have been proposed as likely in shallow lakes in the Netherlands (Mooij et al., 2005). The rates of change of freshwater systems to climate will depend on the ability of freshwater species to “move across the landscape”, i.e. will depend on the existence of dispersal corridors; these can be strongly altered by human activities (Poff et al., 2002). Most affected are likely to be fish in lowland areas that lack northward dispersal corridors and cold-water species generally (Poff et al., 2002).

Freshwater ecosystems are also highly bio-diverse, supporting some 40 percent of all fish species despite accounting for only a small proportion (0.01 percent by volume) of aquatic habitats (Arthington et al., 2003). Accurate data are difficult to collect but approximately 20 percent of freshwater species are threatened, endangered or extinct in areas studied (Revenga et al., 2000). The protection of freshwater biodiversity is increasingly recognized as a major conservation priority (Abell et al., 2002).

3.2.8. Aquaculture systems
Handisyde et al. (2006) and de Silva and Soto (2008) noted that climate change impacts on aquaculture have both direct (e.g. through physical and physiological processes) and indirect (e.g. through variations in fish meal supplies and trade issues) impacts. Here we discuss only the direct issues. Handisyde et al. (2006) noted that the physical changes related to climate change, i.e. in temperature, solar radiation, current and wave actions, sea level rise, water stress, and the frequency of extreme events, will impact physiological, ecological and operational (e.g. species and site selection, containment technologies, etc.) processes. The Third Assessment Report of the IPCC (McLean and Tsyban, 2001) identified the impacts of climate change on aquaculture; these were reiterated in the Fourth Assessment Report (Easterling et al., 2007). Negative impacts include:

- stress due to increased temperature and oxygen demands;
- uncertain supplies of freshwater;
- extreme weather events;
- sea level rise;
- increased frequency of diseases and toxic events;
- uncertain supplies of fishmeal from capture fisheries.

Positive impacts of climate change on aquaculture include increased food conversion efficiencies and growth rates in warmer waters, increased length of the growing season, and range expansions polewards due to decreases in ice (Easterling et al., 2007).

If primary production was to increase in aquaculture areas, it would provide more food for filter-feeding invertebrates (Alcamo et al., 2007). There may also be additional problems with non-native species invasions, declining oxygen concentrations and possibly increased blooms of harmful algae (Alcamo et al., 2007), although these latter are also strongly influenced by non-climate related factors. Local conditions in traditional rearing areas may become unsuitable for many traditional species, which may then need to be moved polewards (Stenevik and Sundby, 2007) or to cooler offshore water, or replaced with other species (Clemmensen et al., 2007).

De Silva and Soto (2008) provide a review of potential impacts of climate change on aquaculture. They note that the greatest proportion (50 to 70 percent) of aquaculture activities occurs in the tropical and subtropical regions, particularly in Asia. The taxonomic group with the highest production is finfish. It takes place predominantly in freshwater, whereas the
culture of crustaceans is greatest in brackish waters and that of molluscs is in marine waters. De Silva and Soto (2008) concluded that the impacts of climate change (e.g. sections 1.1.2, 2.2.3, and 3.2.7) on freshwater aquaculture in tropical and subtropical regions is difficult to predict. Increasing temperatures and increasing plankton growth as a result of eutrophication may increase the growth rates and productivity of cultured species. Changes in water availability, extreme weather events, vertical stratification and nutrient supply may have negative effects on freshwater aquaculture production, depending on local conditions. Aquaculture activities in brackish waters may be affected by changes in salinity (increasing or decreasing), again depending on local conditions of runoff, marine circulation, etc. Aquaculture in temperate regions may be adversely impacted by increased prevalence of pathogens as temperatures warm at a greater rate than low latitude regions (e.g. Handisyde et al., 2006), in addition to cultured species suffering from physiological stress. Table 3 summarizes potential impacts of climate change on aquaculture.

**TABLE 3**
Potential impacts of climate change on aquaculture systems (modified from Handisyde et al., 2006).

<table>
<thead>
<tr>
<th>Drivers of change</th>
<th>Impacts on culture systems</th>
<th>Operational impacts</th>
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<tbody>
<tr>
<td>Sea surface temperature changes</td>
<td>Increase in harmful algal blooms</td>
<td>Changes in infrastructure and operation costs</td>
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<tr>
<td></td>
<td>Decreased dissolved O₂</td>
<td>Increased fouling, pests, nuisance species and predators</td>
</tr>
<tr>
<td></td>
<td>Increased disease and parasites</td>
<td>Expanded geographic ranges for species</td>
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<td></td>
<td>Longer growing seasons</td>
<td>Changes in production levels</td>
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<td></td>
<td>Changes in locations and ranges of suitable species</td>
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<td></td>
<td>Reduced winter natural mortality</td>
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<tr>
<td></td>
<td>Enhanced growth and food conversion rates</td>
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<tr>
<td></td>
<td>Competition, parasitism and predation from altered local ecosystems, competitors, and exotic species</td>
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<tr>
<td>Changes in other oceanographic variables</td>
<td>Decreased flushing rates and food availability to shellfish</td>
<td>Accumulation of wastes under nets</td>
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<td></td>
<td>Changes in abundance of species used for food and fish meal</td>
<td>Increased operating costs</td>
</tr>
<tr>
<td>Sea level rise</td>
<td>Loss of areas for aquaculture</td>
<td>Infrastructure damage</td>
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<td></td>
<td>Loss of areas providing physical protection</td>
<td>Change in aquaculture zoning</td>
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<td></td>
<td>Greater flooding risks</td>
<td>Increased insurance costs</td>
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<td></td>
<td>Salt intrusions into groundwater</td>
<td>Reduced freshwater availability</td>
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<tr>
<td>Increased storm activity</td>
<td>Larger waves</td>
<td>Loss of stock</td>
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<td></td>
<td>Higher storm surges</td>
<td>Facility damage</td>
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<td></td>
<td>Flooding from precipitation</td>
<td>Higher costs for designing new facilities</td>
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<td></td>
<td>Salinity changes</td>
<td>Increased insurance costs</td>
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<td></td>
<td>Structure damage</td>
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<tr>
<td>Drought and water stress</td>
<td>Salinity changes</td>
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<td></td>
<td>Reduced water quality</td>
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<td></td>
<td>Increased diseases</td>
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<td></td>
<td>Uncertain water supplies</td>
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</table>

3.3. UNCERTAINTIES AND RESEARCH GAPS
Predicting the impacts of climate change on marine and aquatic ecosystems has many uncertainties and needs for research. Some predictions, such as impacts and distributional changes to populations at the northern and southern limits of their ranges, can be made with
high confidence, at least in general. Predicting impacts on any specific region or local area will have lower confidence because local factors may increase in importance. If those local factors can be identified and understood however, then it may be possible for local predictions of climate change impacts to be made with high confidence. This illustrates that one of the biggest uncertainties in predicting impacts are the synergistic effects to marine and freshwater populations of multiple climate and non-climate stressors. These are likely to manifest themselves with significant non-linear dynamics and interactions (e.g. Scheffer et al., 2001). Perhaps foremost among these are the interactions of increasing temperatures (Section 1.1), decreasing oxygen (both in absolute concentrations, Section 1.5, and in the ability to meet metabolic tissue demands, Section 2.1.1), decreasing salinity (Section 1.2), increasing acidification (Section 1.5), and the effects of fishing (e.g. Planque et al., 2008; Perry et al., 2008). In freshwater systems, the impacts of changing water flows and water use demands can be added to this list (Sections 1.1 and 1.6). The information learnt during aquaculture activities should be systematised to help establish bioclimate envelopes for species’ tolerances. Research is needed to identify and determine the functional roles of keystone or “high leverage” species, which may have significant effects on system characteristics and function. Hsieh et al. (2006) suggest that at the ecosystem level, reduced complexity by elimination of species due to overexploitation could lead to reduced resilience to climate change perturbations. The consequences of climate change for net primary production is highly uncertain at both global and regional scales, as is how this production may respond to significant variations in the thermohaline circulation (Section 1.3).

Significant uncertainties remain as to the direction of effect (increasing, decreasing) that climate change will have on upwelling systems, in particular coastal wind-driven systems. This is an important research issue since these are highly productive regions supporting valuable fisheries.

Several research issues remain regarding the state of simulation models. These include model resolution (physical, biogeochemical and ecological), their integration across scales, levels of certainty of the projections and the lack of sufficient data to force and validate the models (e.g. Werner et al., 2007). General Ocean Circulation Models (GCMs) used to make projections of future marine ecosystem states, in response to climate, are presently run at spatial resolutions of one degree (i.e. grids of 100x100 km; e.g. Sarmiento et al., 2004). However, physical processes determining biogeochemical and biological responses require resolutions on the order of kilometres in the open ocean and finer in coastal regions. The use of regional climate models and methods for downscaling to regional models, e.g. through nesting (Hermann et al., 2002; Snyder et al., 2003; Clark, 2006; Penven et al., 2006; Vikebø et al., 2007) are yielding new insights. Methodological approaches linking basin-scale models to coastal domains (e.g. Chassignet et al., 2006) and advances in adaptive and unstructured grid refinements appear to be promising (e.g. Pain et al., 2005; Fang et al., 2006). Development of Atmosphere-Ocean GCMs should include the specific kinds of information and output needed to evaluate climate change impacts on marine systems. The relationship between expected long-term changes and decadal (and shorter) variability is extremely important in considering climate impacts on fisheries. Downscaling and regional modelling of ocean climate change is also critical in making realistic regional forecasts of impacts. Present models of change in global marine primary production are very sensitive to the effect of temperature, which should therefore be a prominent topic for further field study and theoretical work.

Marine and aquatic systems have experienced warm conditions in the past, and have responded with significant changes of distributions and reorganisations of species community composition (e.g. Finney et al., 2002; Drinkwater, 2006). What marine systems have not experienced, at least as estimated from pre-industrial times, are acidification conditions as high as at present (Orr et al., 2005) and predicted to increase further. The large-scale impacts on marine systems of this interaction between increasing temperatures and increasing acidification are unknown. In contrast to experiments where no adaptation is possible, Pelejero et al. (2005) observed that 300-year-old massive Porites corals from the south western Pacific had adapted to 50-year cycles of large variations in pH, covarying with the
Pacific Decadal Oscillation. This would suggest that adaptation to long-term pH change may be possible in some coral reef ecosystems. Research into the impacts of high concentrations of CO$_2$ in the oceans is in its infancy and needs to be developed rapidly.

The impacts of fishing on the detailed abilities of marine populations and ecosystems to respond to climate change are also unknown, but general features can be described (Planque et al., 2008; Perry et al., 2008). Fishing makes marine populations more sensitive to climate variability and change by removing older age classes and spatial subunits, and by changing lifehistory traits such as reducing the age-at-first spawning (Perry et al., 2008). Fishing also decreases the mean size and trophic level and increases the turnover rates of the fish component of marine communities, and causes marine ecosystems to change towards stronger bottom-up control (Perry et al., 2008). Hsieh et al. (2006) analysed the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton data and showed that interannual variability is higher in exploited species than in unexploited ones, including pelagic species. The major process seems to be the decrease in the number of fish of older ageclasses caused by exploitation. Older fish are more fecund than younger ones, produce eggs of higher quality, perform more extended migrations and buffer the interannual variability in recruitment (Beamish et al., 2006). The net result is that marine systems become less resilient and more susceptible to the stresses caused by climate variability and change.

Significant uncertainties in the responses of marine and aquatic individual animals, populations, communities, and ecosystems to climate change relate to the roles of feedbacks, critical thresholds and transition points to different stable states. Such thresholds clearly provide lethal tolerance limits, e.g. temperatures above which an organism will die of heat shock, but also occur at (initially) sublethal levels which over-stress the physiological system (Pörtner and Knust, 2007) or disrupt commensal arrangements (coral bleaching). Significant shifts in the states of marine systems have already been observed (Scheffer et al., 2001; de Young et al., 2008). The points at which such thresholds exist will differ for different species, systems and stressors, most of which are as yet unknown. When these thresholds are passed and significant changes occur, they are often called “surprises”.

The ability for marine organisms to adapt and evolve to climate change, on the relevant time scales is also generally unknown. There is some evidence that genetic differences in fish do occur between cohorts from warm and cold years (Smith, 1979). Rapid adaptation and evolution, at least to fishing-induced stresses, can occur on relatively rapid time scales of a few decades (de Roos et al., 2006; Law, 2007). Berteaux et al. (2004), addressing the potential for evolutionary change in response to climate change in Arctic terrestrial animals, also concluded that evolutionary changes due to natural selection could occur on a time scale of a few decades, although they noted that all species may not have equal capacities for such changes. Species with longer generation times and clonal species (because of their low effective population size) may take longer to show an evolutionary response (Harley et al., 2006). Species with complex life histories, such as salmonids, may experience conflicting selection pressures due to the impacts of climate change on the various life stages (Crozier et al., 2008). As noted by Stockwell et al. (2003), evolutionary responses will be influenced by the strength of selection, population size, genetic variation and gene flow, making most species relatively unique.

Detecting the impact of climate change requires increased and more sophisticated monitoring of ocean biology and environmental change, both from space and with instruments in the water. Ideally, measures are needed not only of parameters such as chlorophyll concentration and productivity, but also of plankton taxonomy (what is there?) and physiology (how healthy are they?). New remote sensing technologies may help meet these challenges.
4. Summary of findings

4.1. CLIMATE CHANGE: THE PHYSICAL BASIS IN MARINE AND FRESHWATER SYSTEMS

4.1.1. Heat content and temperature
- The oceans are warming, but with some geographical differences and showing some decadal variability.
- Warming is not exclusive to surface waters, with the Atlantic showing particularly clear signs of deep warming.
- Freshwater resources are vulnerable to, and have the potential to be strongly impacted by, climate change. Many lakes have experienced moderate to strong warming since the 1960s.
- Lake water levels (which affect temperature impacts) have been decreasing in many areas, mostly as a result of human use, but precipitation patterns are also important.
- River run off is expected to increase at higher latitudes and decrease in parts of West Africa, southern Europe and southern Latin America.
- There are concerns over future warming in African lakes, as atmospheric temperature predictions for the continent are larger than the global average and rainfall is projected to decrease in parts.

4.1.2. Salinity and stratification
- In general, salinity is increasing in surface ocean waters of the more evaporative regions, while there is a decreasing trend in high latitudes.
- The combined effect of the temperature and salinity changes due to climate warming would reduce the density of the surface ocean, increase vertical stratification and change surface mixing, but with some geographical differences.
- Large salinity anomalies have been observed in the past with important ecosystem responses.

4.1.3. Ocean circulation and coastal upwelling
- A reduction of about 30 percent in the meridional overturning circulation was observed in the second half of the twentieth century. Further reductions are expected as a result of increased freshwater input in the Arctic and subArctic, increased stability of the surface mixed layer, reduction in salt flux, reduced ocean convection and less deepwater formation. This would have important consequences on the physical and biological components of the North Atlantic ecosystem.
- There is some evidence of increased upwelling intensity in recent decades in several areas (California, North West Africa and Arabian Sea), consistent with the hypothesis that global warming would lead to increased upwelling activity through intensification of alongshore wind stress. However, an alternative hypothesis suggests that different pole-equator warming and increased stratification would counteract this effect. Low-resolution ecosystem simulations indicate that there is no clearly discernable pattern of upwelling response to warming at the global scale, except within a couple of degrees of the equator, where a small reduction is expected.
- There are indications that upwelling seasonality may be affected by climate change, with important food web consequences.

4.1.4. Sea level rise
- Global average sea level has been rising at an average rate of 1.8 mm per year since 1961. The rate has accelerated since 1993 to about 3.1 mm per year. Higher rates in coming decades are likely. Sea level change is not geographically uniform, however, because it is controlled by regional ocean circulation processes.
• The largest losses expected from sea level rise are likely to be on the Atlantic and Gulf of Mexico coasts of the Americas, the Mediterranean, the Baltic and small-island regions.
• Intertidal and coastal wetland habitats may be substantially reduced in the future as a result of sea level rise.

4.1.5. Acidification and other chemical properties
• Surface seawater pH has decreased by 0.1 units in the last 200 years. Model estimates predict further reduction of 0.3 to 0.5 pH units over the next 100 years.
• Biological impacts of ocean acidification are uncertain because sensitivities at individual and population level are unknown. However, they are expected to be severe for shell-borne organisms, tropical coral reefs and cold water corals in the Southern Ocean.
• The oxygen concentration of the ventilated 100 to 1 000 m of the world’s ocean has been decreasing since 1970, driven by a reduced rate of renewal of intermediate waters.
• Global warming is likely to decrease nutrient supply to surface waters due to increased stratification.

4.1.6. Atmosphere-ocean and land-oceans exchanges
• Land-use change has significant hydrological impacts with consequences for ecosystem production, including changes in sediment loads, water flows (through damming) and physico-chemical consequences (hypoxia, stratification and salinity changes). The consequences of these processes cannot be generalised. However, they are known to impact community composition, production and seasonality processes in plankton and fish populations.
• The above will put additional pressure on inland fish and land-based, water intensive, food production systems (e.g. rice), particularly in developing countries.

4.1.7. Low frequency climate variability patterns
• Some studies indicate an increase in the intensity and frequency of particular atmospheric patterns (e.g. NAO, ENSO), but in general climate models predict a rather spatially uniform warming trend throughout the ocean basins combined with the continued presence of decadal variability similar to that of the twentieth century.
• Atmospheric patterns can have strong teleconnections within individual ocean basins, but between-basin teleconnections and potential climate-driven biological synchrony over several decades, are usually much weaker.

4.2. OBSERVED EFFECTS OF CLIMATE VARIABILITY AND CHANGE ON ECOSYSTEM AND FISH PRODUCTION PROCESSES

4.2.1. Summary of physiological, spawning and recruitment processes sensitive to climate variability
• Organisms have specific ranges of environmental conditions to which they are adapted and within which they perform optimally. Physiological performance, often related to tissue metabolic oxygen demands, may degrade and cause stress at conditions (e.g. temperatures) which may be considerably below lethal limits.

4.2.2. Primary production
• Satellite observations suggest a 6 percent reduction in global oceanic primary production between the early 1980s and the late 1990s, but with substantial regional differences. For example, chlorophyll in higher latitudes has increased in the last 20 years, followed by a change in the relative dominance of diatoms over small phytoplankton.
• Increased vertical stratification and water column stability in oceans and lakes is likely to reduce nutrient availability to the euphotic zone and thus primary and secondary production in a warmed world. However, in high latitudes the residence time of particles in the euphotic zone will increase, extending the growing season and thus may increase primary production. Overall, a small global increase in primary production will be expected, with very large regional differences.
• Climate warming should lead to a contraction of the highly productive marginal sea ice biome and the seasonally stratified subtropical gyre, and an expansion of the low productivity permanently stratified subtropical gyre biome and the subpolar gyre biome.
• Simulations suggest that under global warming, the onset of the diatom spring bloom could be delayed and its peak biomass reduced. Changes in the dominant phytoplankton group appear possible.
• In general terms, in high-latitude or high-altitude lakes, atmospheric warming leads to reduced ice cover, warmer water temperatures, a longer growing season and, as a consequence, increased algal abundance and productivity. In contrast, some deep tropical lakes are experiencing reduced algal abundance and declines in productivity, likely as a result of reduced resupply of nutrients.
• The intensification of hydrological cycles is expected to influence substantially limnological processes. In general, increased run-off, discharge rates, flooding area and dry season water level may boost productivity at all levels (plankton to fish). Changes in the timing of floods may trigger production at the wrong time and flush biological production out of its habitat.

4.2.3. Secondary production
• There are no global assessments of the potential impacts of climate change on oceanic secondary production. Results tend to be dominated by local or regional conditions, although this is an area of active research (e.g. Mackas and Beaugrand, 2008).
• However, regional results suggest that climate change effects may be more evident in the structure of zooplankton communities than in its total biomass.

4.2.4. Distributional changes
• Climate change is expected to drive most terrestrial and marine species ranges toward the poles, expanding the range of warmer-water species and contracting that of colder-water species.
• Observations of distributional changes consistent with the above have been recorded in, among others, the North Sea, the North Atlantic and the North American east and west coasts for copepods, demersal invertebrates, intertidal organisms and fish species. The most rapid changes in fish communities occur with pelagic species, and include vertical movements to counteract surface warming.
• The timing of many animal migrations has followed decadal trends in ocean temperature, being later in cool decades and up to one to two months earlier in warm years.

4.2.5. Abundance changes
• Populations at the poleward extents of their ranges tend to increase in abundance with warmer temperatures, whereas populations in more equatorward parts of their range tend to decline in abundance as temperatures warm.
• Increased growth rates in response to increased temperatures are only achieved when food supply is adequate to these increased demands.

4.2.6. Phenological changes
• More than half of all terrestrial, freshwater or marine species studied have exhibited measurable changes in their phenologies over the past 20 to 140 years. These were systematically and predominantly in the direction expected from regional changes in the climate.
• Observations in the North Sea indicate that plankton community structure is changing: dinoflagellates have advanced their seasonal peak in response to warming, while diatoms have shown no consistent pattern of change because their reproduction is triggered principally by increases in light intensity.
• Observations in many European and North American lakes suggest that the spring phytoplankton bloom has advanced due to warming but that zooplankton has not responded similarly, and their populations are declining because their emergence no longer corresponds with high algal abundance. There is concern that marine and freshwater trophodynamics may have already been radically altered by ocean warming through predator-prey mismatch.

4.2.7. Species invasions and diseases
• There is little evidence in support of an increase in outbreaks of disease linked to global warming, although spread of pathogens to higher latitudes has been observed.
• Harmful algal blooms seem to be more common, but whether this is caused by climate change is unclear. The expected change in the ratio of diatoms to dinoflagellates in a warming ocean may also play a role.
• Extinction risks due to climate change are possible, but there are no known examples yet. Evolutionary adaptations will occur, although on time scales and with characteristics that may be species-dependent.

4.2.8. Food web impacts from zooplankton to fish
• Climate change is likely to affect ecosystems and their species both directly and indirectly through food web processes. Whether direct or indirect processes predominate is likely to depend on whether they are structured from the top down, from the bottom up or from the middle. It is suggested that ecosystem control is correlated with species richness and temperature.

4.2.9. Regime shifts and other extreme ecosystem events
• It is increasingly appreciated that one of the mechanisms through which climate variability and change interact in affecting ecosystem dynamics is through non-linear “regime shifts”. The sensitivity of ecosystems to amplify climatic signals suggests that gradual (or even stochastic) changes in climate can provoke sudden and perhaps unpredictable biological responses as ecosystems shift from one state to another.
• Regime shifts have been observed in the North Atlantic and North Pacific oceans, among others, affecting productivity and species dominance in the pelagic and demersal domains.

4.3. SCENARIOS OF CLIMATE CHANGE IMPACTS ON FISH PRODUCTION AND ECOSYSTEMS
• General impacts on marine and aquatic systems as a result of large-scale changes related to temperature, winds and acidification can be predicted, in some cases with a high degree of confidence.
• At “rapid” time scales (a few years) there is high confidence that increasing temperatures will have negative impacts on the physiology of fish because of limited oxygen transport to tissues at higher temperatures. This physiological constraint is likely to cause significant limitations for aquaculture. These constraints on physiology will result in changes in distributions of both freshwater and marine species, and likely cause changes in abundance as recruitment processes are impacted. Changes in the timing of life history events are expected with climate change (high confidence). Short life span, rapid turnover species, for example plankton, squid and small pelagic fishes, are those most likely to experience such changes.
• At intermediate time scales (a few years to a decade), temperature-mediated physiological stresses and phenology changes will impact the recruitment success and therefore the abundances of many marine and aquatic populations (high confidence). These impacts are also likely to be most acute at the extremes of species’ ranges and for
shorter-lived species. Changes in abundance will alter the composition of marine and aquatic communities, with possible consequences for the structure and productivity of these marine ecosystems. Predicting net community impacts (e.g. total biomass or productivity) has intermediate confidence because of compensatory dynamics within functional groups. Increasing vertical stratification is predicted for many areas, and is expected to reduce vertical mixing and decrease productivity (intermediate confidence). It will drive changes in species composition.

- At long time scales (multi-decadal), predicted impacts depend upon changes in net primary production in the oceans and its transfer to higher trophic levels. Models show high variability in their outcomes so any predictions have low confidence. Regional predictions may have improved confidence because of better knowledge of the specific processes involved. Most models show decreasing primary production with changes of phytoplankton composition to smaller forms, although with high regional variability.

- Considerable uncertainties and research gaps remain, in particular the effects of synergistic interactions among stressors, extrapolating beyond historical conditions, reduced ecosystem resilience to climate variability as a result of changes caused by fishing, the locations and roles of critical thresholds and the abilities of marine and aquatic organisms to adapt and evolve to the changes.

- Regarding freshwater systems, there are specific concerns over changes in timing, intensity and duration of floods, to which many fish species are adapted in terms of migration, spawning and transport of spawning products as a result of climate change. It is important to develop management systems capable of addressing the needs for fresh water by fish and land-based food production systems (e.g. rice) in the context of climate change, particularly in developing countries.

Anticipated responses of regional ecosystems to climate change are expected to include:

**Arctic**

Physical changes:
- 5 °C increase in air temperature;
- 6 percent increase in precipitation;
- 15 cm rise in sea level;
- 5 percent increase in cloud cover;
- 20 day reduction in sea ice duration;
- 20 percent reduction in winter ice with substantial ice-free areas in summer.

Ecological consequences:
- primary production increased two to five times over present conditions;
- reduced ranges of cold water fish and benthic species, but expanded ranges of Atlantic and Pacific species northwards;
- long-lived Arctic species with narrow temperature tolerances and late reproduction are likely to disappear from southerly habitats;
- changes to migration timing and increases in growth rates;
- non-native species are likely to increase in Arctic waters;
- extinction of any present Arctic fish species unlikely.

**North Atlantic**

North East Atlantic

Physical changes:
- future climate change impacts in the North Atlantic are likely to continue to vary with the state of the North Atlantic Oscillation;
- sea temperatures in the North Sea, Nordic seas and Barents Sea are likely to increase by 1 to 3 °C over the next 50 years, with largest changes in the northernmost regions;
• increased wind-induced fluxes of warm Atlantic waters into these northern regions;
• increased vertical stratification;
• reduced ice cover.

Ecological changes:
• primary production likely to increase in the Barents Sea;
• zooplankton production likely to decrease as production by Arctic zooplankton declines;
• northward shifts in the distributions of all species;
• increased biomass production of species in Arcto-boreal regions;
• fish species from south of the North Sea likely to appear in the North Sea;
• spawning areas for capelin in the Barents Sea likely to shift eastwards;
• North Sea dominated by pelagic species such as herring and mackerel in the north, and sardine and anchovy in the south, although the total system productivity may not be too different than today;
• Baltic Sea is predicted to become warmer and fresher, with significant increases in its vertical stratification;
• in the Baltic, exclusion of marine-tolerant species in favour of species more tolerant of low salinities;
• non-native species may enter the Baltic, but few are expected to be able to colonise because of the salinity stress.

North West Atlantic
• predictions of distributions and migration changes similar to North East Atlantic;
• populations at their range limits will be most affected;
• in some locations and at some times, decreased temperatures may occur as a result of increased glacial melting in Greenland. This may provide refuges for some cold water species, or may provide lethal cold shocks to other species such as Atlantic cod;
• species adapted to cool and narrow temperature conditions, such as Atlantic salmon, may be extirpated from their present habitats.

Atlantic cod:
• cod survival in simulations of Gulf of Maine declined with increasing temperatures which offset their increases in growth;
• in middle range in the North West Atlantic, capelin (Mallotus villosus) are important prey of cod, but spawning times for capelin are susceptible to delays due to cold water from melting glaciers;
• in North East Atlantic, model simulations suggest increasing temperatures in North Sea will cause declines in cod populations.

North Pacific
• anthropogenic warming in 30 to50 years likely to be as large as natural climate variability today;
• climate-ecosystem-fisheries relationships developed during the latter half of the twentieth century may not be resilient to the new conditions in the twenty-first century;
• Pacific Decadal Oscillation pattern of decadal variability will continue into the twenty-first century, but will occur on top of persistent upward trend in sea surface temperature;
• changes in mixed layer depths (shoaling) and temperature (increasing);
• subpolar planktonic system change from strong variability and winter lows to more constant annual values and decreased yearly-averaged primary productivity;
• other areas (e.g. coastal) may experience higher growth rates as temperatures warm;
• in the North West Pacific, expect warmer conditions to cause changes in seasonal patterns of primary production;
• northward shifts of fish populations are predicted for west coast of North America;
• Pacific sockeye salmon may be restricted to Bering Sea;
• Bering Sea: extensive retreat of sea ice, losses of cold-water species and increasing abundances of species from the North Pacific;
• North Pacific is sensitive to the effects of increasing acidification, and likely to become under-saturated in aragonite from the surface to bottom;
• various species are negatively impacted by low pH concentrations.

Wind-driven coastal upwelling systems
• responses to global warming of coastal wind systems that drive upwelling ecosystem are contradictory;
• if alongshore wind stress increases coastal upwelling, this would offset in these regions the global trend of increasing water temperatures and increasing vertical stratification;
• other model studies predict decreasing upwelling-favourable winds;
• global models of primary production responses to warmer conditions are contradictory. In the Pacific, the model of Sarmiento et al. (2004) showed no consistent global response of upwelling regions to climate change;
• intensified Benguela upwelling may increase nutrient inputs, primary production and low-oxygen events. Such may also occur in other upwelling systems;
• there is considerable local variability among systems which makes generalizations difficult.

Tropical and subtropical seas
• highly diverse habitats and biology; poorly studied;
• not resolved whether tropical Pacific will become more “El Niño-like” (east-west gradient in SST is reduced), or more “La Niña-like” character (increased east-west SST gradient);
• primary production in the tropical Pacific expected to decline because of increased stratification and decreased nutrient supply;
• combined effects of changes in circulation, temperature, nutrients, primary production cascade up the food web to influence prey availability and habitat conditions for tuna;
• tuna habitat conditions east of the date line could improve, similar to El Niño-events;
• for waters of Australia and New Zealand, greatest impacts likely on coastal species and subtidal nursery areas, temperate endemic species rather than tropicaals and coastal and demersal species rather than pelagic and deep-sea species;
• models for Australia predict physical changes similar to other regions: ocean warming, increased vertical stratification, strengthening of poleward coastal currents, increasing ocean acidification, sea level rise and altered storm and rainfall regimes;
• warming and increasing stratification will alter plankton community composition, alter their distributions polewards and change the timing of their bloom dynamics so that transfers to higher trophic levels may be impaired;
• benthic and demersal fishes will shift their distributions southward and may decline in abundance. Pelagic species will also shift their distributions southwards and some species may benefit from increased local wind-driven upwelling (e.g. anchovies).

Coral reef systems
• at risk from climate change impacts related to increasing temperatures, acidity, storm intensity and sea levels and non-climate factors such as over-exploitation, non-native species introductions and increasing nutrient and sediment loads;
• risks to coral reefs not distributed equally: increasing temperatures significant issue for warm-water systems; increasing acidity and decalcification a significant issue for both warm- and cold-water systems; direct human impacts a significant issue in more populous regions;
• three different time scales can be identified for climate change-related impacts to coral reef systems:
  – years: increased temperature effects on coral bleaching;
  – decades: increasing acidification and dissolution of carbonate structures of reefs;
  – multi-decades: weakening of structural integrity of reefs and increasing susceptibility to storms and erosion events.
• increasing acidity (decreasing pH) is a significant and pervasive longer-term threat to coral reefs. Potential for coral reef systems to adapt to these environmental stresses is uncertain: symbiotic zooxanthellae may adapt to be more tolerant of high temperatures. Migrations of corals to higher latitudes is unlikely;
• declines in corals had negative impacts on reef fish biodiversity in at least one study, however, to date there is little evidence for a link between climate warming and bleaching events with impacts on coastal fisheries.

**Freshwater systems**
• freshwater lakes and their ecosystems are highly vulnerable to climate change;
• paleo records show the shapes and distributions of lakes can change and they can disappear entirely with shifting dynamics among precipitation, evaporation and runoff;
• anticipated response is for cold-water species to be negatively affected, warm-water species to be positively affected and cool-water species to be positively affected in the northern, but negatively affected in the southern parts of their range;
• general shift of cool- and warm-water species northward is expected in North America and likely the rest of the Northern Hemisphere;
• responses of particular lake ecosystems to climate change depend on size, depth and trophic status of the lake;
• modelling studies concluded cold-water fish would be most affected because of losses of optimal habitats in shallow, eutrophic lakes;
• growth conditions for cool- and warm-water fishes should improve in well-mixed lakes, small lakes and those with oligotrophic nutrient conditions;
• rates of change of freshwater systems to climate will depend on ability of freshwater species to “move across the landscape”, i.e. use of dispersal corridors;
• most affected are likely to be fish in lowland areas that lack northward dispersal corridors, and cold-water species generally;
• river ecosystems are particularly sensitive to changes in the quantity and timing of water flows, which are likely to change with climate change;
• changes in river flows may be exacerbated by human efforts to retain water in reservoirs and irrigation channels;
• abundance and species diversity of riverine fishes are particularly sensitive to these disturbances, since lower dry season water levels reduce the number of individuals able to spawn successfully and many fish species are adapted to spawn in synchrony with the flood pulse to enable their eggs and larvae to be transported to nursery areas on flood plains.

**Aquaculture systems**
• direct impacts include changes in the availability of freshwater, changes in temperature, changes in sea level, and increased frequencies of extreme events (such as flooding and storm surges);
• indirect effects include economic impacts, e.g. costs and availability of feed;
• negative impacts include (Table 4):
  – stress due to increased temperature and oxygen demands;
  – uncertain supplies of freshwater;
  – extreme weather events;
  – sea level rise;
  – increased frequency of diseases and toxic events;
  – uncertain supplies of fishmeal from capture fisheries.
• positive impacts of climate change on aquaculture include increased food conversion efficiencies and growth rates in warmer waters, increased length of the growing season, and range expansions polewards due to decreases in ice;
• increased primary production would provide more food for filter-feeding invertebrates;
• may be problems with non-native species invasions, declining oxygen concentrations, and possibly increased blooms of harmful algae;
• local conditions in traditional rearing areas may become unsuitable for many traditional species;
• temperature stress will affect physiological processes such as oxygen demands and food requirements;
• increased food supplies are needed for aquaculture activities to realise benefits from increased temperatures;
• freshwater aquaculture activities will compete with changes in availability of freshwater due to agricultural, industrial, domestic and riverine requirements, as well as changes in precipitation regimes;
• increases in precipitation could also cause problems such as flooding;
• sea level rise also has the potential to flood coastal land areas, mangrove and sea grass regions which may supply seed stock for aquaculture species.
References


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