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

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ABSTRACT

This chapter reviews the physical and ecological impacts of climate change relevant to marine and inland capture fisheries and aquaculture. It is noted that the oceans are warming but that this warming is not geographically homogeneous. The combined effect of temperature and salinity changes due to climate warming are expected to reduce the density of the surface ocean, increase vertical stratification and change surface mixing. There is evidence that inland waters are also warming, with differential impacts on river run off. 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 increasing primary production. While there is some evidence of increased coastal upwelling intensity in recent decades, global circulation models do not show clear pattern of upwelling response to global warming at the global scale. However, current climate models are not yet sufficiently developed to resolve coastal upwelling and so the impacts of climate change on upwelling processes require further work. There is also evidence that upwelling seasonality may be affected by climate change. Sea level has been rising globally at an increasing rate, risking particularly the Atlantic and Gulf of Mexico coasts

of the Americas, the Mediterranean, the Baltic, small-island regions, Asian megadeltas and other low-lying coastal urban areas. Ocean acidification has decreased seawater pH by 0.1 units in the last 200 years and models predict a further reduction of 0.3-0.5 pH units over the next 100 years. The impacts of ocean acidification will be particularly severe for shell-borne organisms, tropical coral reefs and cold water corals. Climate change effects marine and inland ecosystems are in addition to changes in land-use, including changes in sediment loads, water flows and physical-chemical consequences (hypoxia, stratification, salinity changes). The consequences of these processes are complex and will impact community composition, production and seasonality processes in plankton and fish populations. This will put additional pressure on inland fish and land-based, water intensive, food production systems, particularly in developing countries.

Many effects of climate change on ecosystem and fish production processes have been observed. While a slight reduction in global ocean primary production has been observed in recent decades, a small increase in global primary production is expected over this century, but with very large regional differences. Changes in the dominant phytoplankton group appear possible. In general terms, high-latitude/altitude lakes will experience 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 will experience reduced algal abundance and declines in productivity, likely due to reduced resupply of nutrients. The intensification of hydrological cycles is expected to influence substantially limnological processes, with increased runoff, discharge rates, flooding area and dry season water level boosting productivity at all levels (plankton to fish). 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. The most rapid changes in fish communities will occur with pelagic species, and include vertical movements to counteract surface warming. Timing of many animal migrations has followed decadal trends in ocean temperature, being later in cool decades and up to 1–2 months earlier in warm years. Populations at the poleward extents of their ranges will increase in abundance with warmer temperatures, whereas populations in more equatorward parts of their range will decline in abundance as temperatures warm. 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, and these were systematically and predominantly in the direction expected from regional changes in the climate. Differential responses between plankton components (some responding to temperature change and others to light intensity) suggest that marine and freshwater trophodynamics may be altered by ocean warming through predator-prey mismatch. 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. The paper summarises the consequences of climate change along temporal scales. At "rapid" time scales (a few years) there is high confidence that increasing temperatures will have negative impacts on the physiology of fish, causing significant limitations for aquaculture, changes in species distributions, and likely changes in abundance as recruitment processes are impacted. Changes in the timing of life history events are expected, particularly affecting short lived species, such as plankton, squid, and small pelagic fishes. 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, particularly at the extremes of species' ranges, and for shorter-lived species. 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, for which information is lacking. Considerable uncertainties and research gaps remain, in particular the effects of synergistic interactions among stressors (e.g. fishing, pollution), the occurrences 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. The chapter concludes with specific anticipated responses of regional marine ecosystems (Arctic, North Atlantic, North Pacific, coastal upwelling, tropical and subtropical regions, coral reefs, freshwater systems and aquaculture systems) to climate change.

CONTENTS

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 1 000 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, Antonov and Boyer, 2005; Domingues *et al.,* 2008, Figure 1)*. S*tudies 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 m of the global ocean, but has penetrated deeper in the Atlantic Ocean (up to 3 000 m) than in the Pacific, Indian and Southern Oceans, because of the deep overturning circulation that occurs in the North Atlantic (Levitus, Antonov and Boyer, 2005). 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).

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, Dunne and Vecchia, 2005); shifts in the form of precipitation

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, Antonov and Boyer (2005); 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, Antonov and Boyer (2005) and Willis, Roemmrich and Cornuelle (2004)

Source: Bindoff *et al.*, 2007.

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.

FIGURE 2
Time series of global annual ocean heat content (1022 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

Source: modified from Domingues *et al.*, 2008.

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 Southeast 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 Southeast Asia. Precipitation in summer is likely to increase in northern Asia, East Asia, South Asia and most of Southeast 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, Southeast 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

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

Source: NASA Goddard Space Flight Centre, www.gsfc.nasa/gov.)

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, Dunne and Vecchia, 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, Lins and McCabe, 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).

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

FIGURE 4

Linear trends (1955–1998) of zonally averaged salinity (psu) in the upper 500 m of the World Oceans. 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

Source: Boyer *et al.,* 2005.

is freshening (Antonov, Levitus and Boyer, 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).

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, Allan and Ansell, 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, Velinga 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, Longworth and Cunningham, 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.

Source: 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, Miller and Di Lorenzo (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, Mix and Heusser, 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, Overpeck and Gupta, 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, Chai and Hampton, 2003; Roemmich and 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, Snyder and Sloan (2004) showed that biophysical land-cover–atmosphere feedbacks induced by CO_2 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, Southward and Genner, 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 CO_2 released by human activities between 1800 and 1994 is stored in the ocean (Sabine *et al.*, 2004), and about 30 percent of modern CO_2 emissions are taken up by oceans today (Feely *et al.*, 2004). Continued uptake of atmospheric CO_2 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 CO_2 emission scenario used (Caldeira and 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).

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 erythrogamma*, 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, Langenbuch and Michaelidis, 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 coccolitophores (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 CO_2 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 O_2 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 O_2 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

FIGURE 6

The global ocean aragonite saturation state in the year 2100 as indicated by Δ[CO²⁻₃]ₐ. The Δ[CO²⁻₃]ₐ is the *in situ* [CO²⁻₃] 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 Δ[CO²⁻₃]ₐ indicates supersaturation; negative Δ[CO²⁻₃]ₐ indicates undersaturation

Source: Orr *et al.*, 2005.

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.*, 2004) 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, CO_2 uptake by the oceans amounted to 2.2±0.5 GtCy⁻¹ (out of 7.2 GtCy⁻¹ fossil CO_2 emissions). These values are at least double the terrestrial

biosphere intake (Denman *et al.*, 2007). Increasing CO_2 levels in the atmosphere have been postulated to deplete the ozone layer (Austin, Butchart and Shine, 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 channelization 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, Friedrich and Burns, 2001; Flöder 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, Rabalais and Turner, 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, Rabalais and Turner, 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, Halls and Barr (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, Halls and Barr, 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, Pomerance and Thomas, 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, Day and Muller, 1990) fish (Mysak, 1986; Sharp and McLain, 1993), marine mammals (Testa *et al.,* 1991; Vergani, Stanganelli and Bilenca, 2004), seabirds (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, Richardson and Robinson, 2005), and changes to behaviour (Lusseau *et al.*, 2004), sex ratio (Vergani *et al.*, 2004) and feeding and diet (Piatkowski, Vergani and Stanganelli, 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, 2005; 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 Niño 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, McFarlane and King, 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; Gillet, Graf and Osborn, 2003; Taylor, 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 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 (McFarlane, King and Beamish, 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, Mitchum and Evans, 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).

FIGURE 7

A model illustrating potential pathways by which climate change effects can be mechanistically transmitted to marine biota. 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

Source: Francis *et al.*, 1998.

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).

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 change 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. Magnuson, Crowder and Medvick, (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 viviparus*) that temperature-specific growth rates and fecundity declined at higher latitudes. Takasuka, Oozeki and Aoki, (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, McDonald and Wood (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 suboptimal) 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, Orr and Anderson, 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 Schindler (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 (*Daphnia* spp.) populations. Mackas, Batten and Trudel (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

Source: 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 (Gargett, 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 Northeast Atlantic (Brunel and Boucher, 2006).

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

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

Source: Drinkwater, 2005, modified from Planque and Frédou, 1999.

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, Barber and Smetacek, 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 Northeast 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 multinutrient and multiplankton 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).

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

FIGURE 10
Zonally integrated response of the global ocean's primary production (PgC 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)

CSIRO
GFDL
Hadley
IPSL
MPI
NCAR

CSIRO: Commonwealth Scientific & Industrial Research Organization, Canberra, Australia

GFDL: Geophysical Fluid Dynamics Lab., Princeton University, United States of America

HADLEY: Hadley Centre for Climate Prediction and Research, University of East Anglia, United Kingdom

IPSL: Institut Pierre-Simon Laplace, Gif-sur-Yvette, France

MPI: Max-Planck-Institut für Meteorologie, Hamburg, Germany

NCAR: National Center for Atmospheric Research, Boulder, United States of America

Source: modified from Sarmiento *et al.,* 2004.

discussed in section 1.3.2. Should climate change significantly impact coastal upwelling processes, plankton production predictions would have to be revised.

Vazquez-Dominguez, Vaque and Gasol (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 CO_2 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).

FIGURE 11

Time series of (a) atmospheric CO₂ (ppm) which increases at a rate of 1 percent y⁻¹, (b) global oceanic primary productivity (full line) in PgC y⁻¹ (left axis) and global ocean particulate export production at 100 m (dotted line) in PgC y⁻¹ (right axis), (c) global mean contribution of diatoms to total ocean chlorophyll and (d) climate change cumulative effect on oceanic carbon uptake (PgC)

Source: Bopp *et al.,* 2005.

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.*, 2004; 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, Ho and Trees, 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

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

	Indian Ocean			Pacific Ocean			Atlantic Ocean			Global		
	Control	Chg	% Chg	Control	Chg	% Chg	Control	Chg	% Chg	Control	Chg	% Chg
Northern Hemisphere												
Marginal sea ice				3.8	-1.7	-45.3	3.2	-1.2	-37.5	7.0	-2.9	-41.7
Subpolar				8.5	1.2	13.9	5.5	1.1	19.7	14.0	2.3	16.2
Subtropical seasonal				4.9	-0.7	-13.4	8.8	-0.8	-9.4	13.6	-1.5	-10.9
Subtropical permanent	3.3	0.1	2.3	35.4	1.0	2.9	12.5	0.9	7.4	51.2	2.0	4.0
Low latitude upwelling	2.1	-0.1	-6.8	10.9	0.2	1.6	4.4	0.0	0.8	17.3	0.1	0.4
5 °S to 5 °N												
Upwelling	4.5	0.5	10.1	14.6	0.2	1.3	4.6	0.1	2.4	23.7	0.7	3.2
Downwelling	2.3	-0.5	-19.5	4.4	-0.2	-4.3	1.3	-0.1	-10.9	7.7	-0.8	-9.7
Southern Hemisphere												
Low latitude upwelling	7.9	-0.1	-0.7	8.7	-0.6	-7.3	3.8	0.2	4.8	20.4	-0.5	2.5
Subtropical permanent	15.0	1.1	7.3	37.4	3.6	9.7	13.9	1.5	10.8	66.3	6.2	9.4
Subtropical seasonal	13.8	-0.5	-3.3	12.1	-1.8	-14.7	6.4	-1.2	-18.4	32.3	-3.4	-10.6
Subpolar	8.2	1.5	18.7	12.5	0.4	3.3	7.1	0.2	3.4	27.8	2.2	7.9
Marginal sea ice	8.8	-2.1	-23.7	8.8	-1.5	-16.9	7.8	-0.8	-10.3	25.3	-4.4	-17.2
TOTAL	65.8			161.9			79.3			306.7		

FIGURE 12
(A) Meta-analysis of the relation between marine phytoplankton abundance and sea surface temperature, showing no overall relation. Weighted mean correlations (circles) are shown with 99 percent confidence limits (bars) calculated using the random-effects model B for the entire study area (r_{All}) and a subset of nine non contiguous regions ($\bar{r}_{Subset}$). 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

Source: Richardson and Schoeman, 2004.

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, Feldman and Hooker, 2004; Sarmiento *et al*., 2004; Polovina, Howell and Abecassis, 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 Northeast 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 Northeast Atlantic to hydroclimatic forcing, as expressed by the NAO (Edwards *et al.,* 2006). 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).

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, Chai and Hampton, 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, Pomerance and Thomas, 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, Pisaric and Smol, 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, 2004b; 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, Jonsson and Jansson, 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, Hecky and Kling, 2003; Hecky, Bootsma and Odada, 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

FIGURE 13
Lake Tanganyika, Africa. Carbon isotope records in sediment cores indicating a post- 1950s trend towards more negative $\delta^{13}C$ values (lower phytoplankton productivity) in both relatively undisturbed (filled symbols), as well as developed (open symbols) watersheds

Source: O'Reilly *et al.,* 2003.
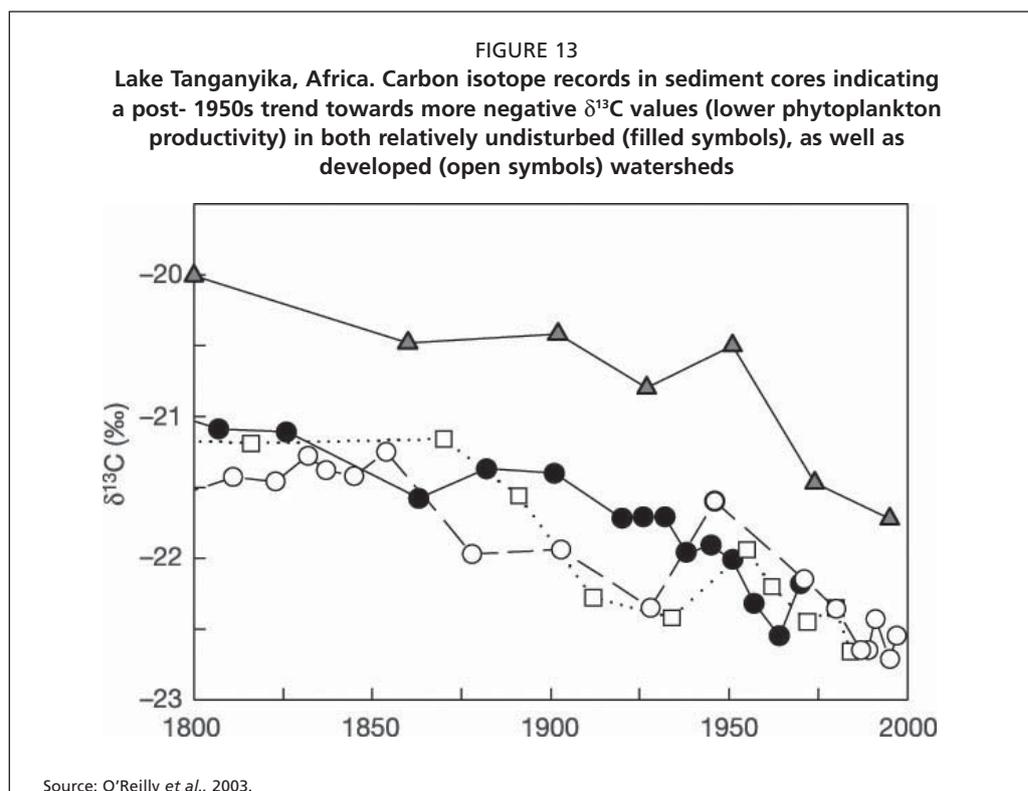
60 years in Lake Malawi, as well as measured reduced ventilation of the deep waters since 1980 (Vollmer, Weiss and Bootsma, 2002), leading to reduced nutrient loading and, presumably, reduced productivity.

Enhanced UV-B radiation and increased summer precipitation will significantly increase dissolved organic carbon (DOC) concentrations, altering major biogeochemical cycles (Zepp, Callaghan and Erickson, 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, Odate and Fukuchi, 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 and 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, Thompson and Galbraith (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 pseudooceanic 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*

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 (cm³ 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 (10⁶ m³ s⁻¹), calculated between stations 80.55 and 80.90 for each cruise, and (f) monthly upwelling index anomalies (m³ 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
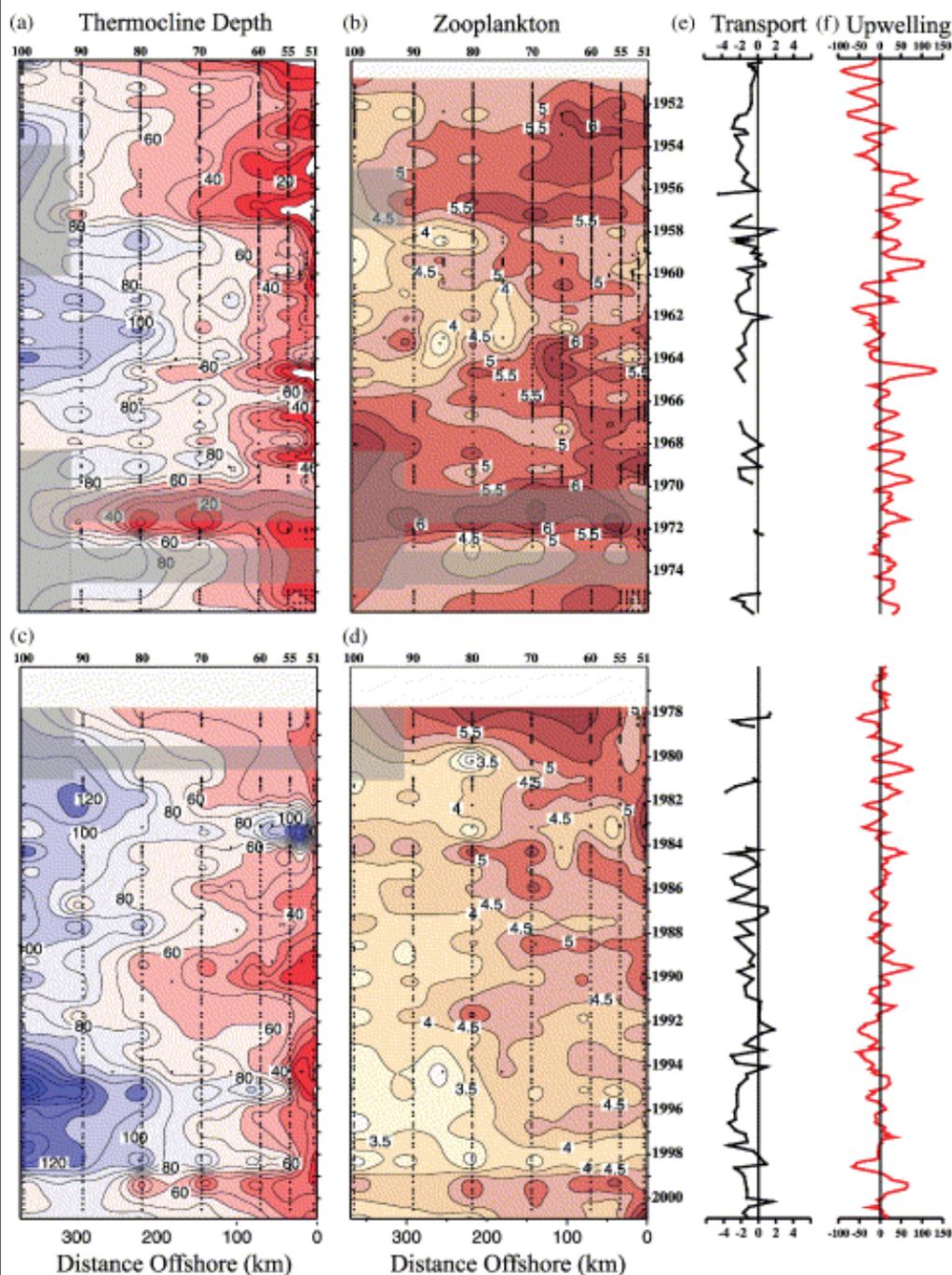
(Beaugrand *et al.*, 2002). Transport processes from their deep overwintering basins to shelf regions determines *C. finmarchicus* distribution and abundance (Speirs *et al.*, 2005) and high abundances are generally associated with increased presence of higher nutrient Atlantic waters, either through increased levels of primary production, direct transport or a combination (Astthorsson and Gislason, 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).

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 (Möllmann, *et al.*, 2005). Under laboratory conditions, Isla, Lengfellner and Sommer (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, Hawkins and Burrows (1995), which demonstrated many changes in the abundance of Northeast 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, Richardson and Robinson, 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, Richardson and Robinson, 2005; Richardson and Schoeman, 2004). Some copepod communities have shifted as much as 1 000 km northward. Beaugrand *et al.* (2002) documented a major large-scale reorganization 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, Hawkins and Burrows, 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, Schmitt and Stephens, 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 aequoreus*), 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, Hawkins and Burrows, 1995; Southward *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, Schmitt and Stephens (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