

Ocean ecosystem responses to future global change scenarios: a way forward

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10.1 Introduction

The overall aim of GLOBEC was ‘To advance our understanding of the structure and functioning of the global ocean ecosystem, its major subsystems, and its response to physical forcing so that a capability can be developed to forecast the responses of the marine ecosystem to global change’. GLOBEC specified four objectives, and objective 3 was ‘To determine the impacts of global change on stock dynamics using coupled physical, biological, and chemical models linked to appropriate observation systems and to develop the capability to project future impacts’. During the GLOBEC era, earth observational networks were developed such as the Global Climate Observing System (GCOS), which includes the Global Ocean Observing System (GOOS). Although imperfect, this global observational network is providing an unprecedented view of climate change in the earth system, and has increased our understanding tremendously over the past several decades. An increasing number of independent observations of the atmosphere, land, cryosphere, and ocean are providing a consistent picture of a warming world. Such multiple lines of evidence, the physical consistency among them, and the consistency of findings among multiple, independent analyses, form the basis for the iconic phrase of the observations chapter in the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC-AR4, IPCC 2007a)

that the ‘warming of the climate system is unequivocal’. Moreover, the evidence is strong that, especially in recent decades, human activities have contributed to the global warming. The IPCC-AR4 additionally cautioned that further warming and changes in the global climate system will very likely emerge over the next century.

The climate changes anticipated during the twenty-first century have the potential to greatly affect marine ecosystems. A major challenge facing the scientific community is to develop modelling and data analysis approaches for determining how climate change will affect the structure and functioning of marine ecosystems. During the GLOBEC era, our understanding of ecosystem structure and dynamics has improved greatly (deYoung *et al.*, Chapter 5; Moloney *et al.*, Chapter 7, both this volume), and new ecosystem modelling approaches have been developed and existing methods improved (see deYoung *et al.*, Chapter 5, this volume). As we look forward, the next step is to use the knowledge gained from GLOBEC as a foundation, as we continue to develop data collection and modelling tools that can make sufficiently confident projections of marine ecosystem responses to future global climate change.

In this chapter, we summarize the available evidence for recent changes in climate effects in the oceans, and the status of our ability to project ecosystem responses to likely future global change.

We first present the evidence for changes in the physical and chemical properties of the oceans, including changes in water temperature, nutrient supply, mixing and circulation, micronutrient supply, transport of plankton, acidification, and sea-level rise. We then discuss the evidence for consequent responses of the marine ecosystem to the documented changes in the oceans, organized by trophic level (primary production, zooplankton, and higher trophic levels). Whenever possible, for each trophic level, we include the results of published examples of future projections of ecosystem

responses. With this information as the basis, we conclude with a discussion of our vision of the next steps that are needed to develop models capable of projecting ecosystem responses to global change.

To develop future climate projections, assumptions must be made on the levels of population increase and the rates of development (emission scenarios) that, in turn, determine the rate of CO₂ build-up in the atmosphere. Many examples of future projections cited in this chapter used emission scenarios taken from the IPCC (IPCC 2000), which are briefly described in Fig. 10.1. One exception is an

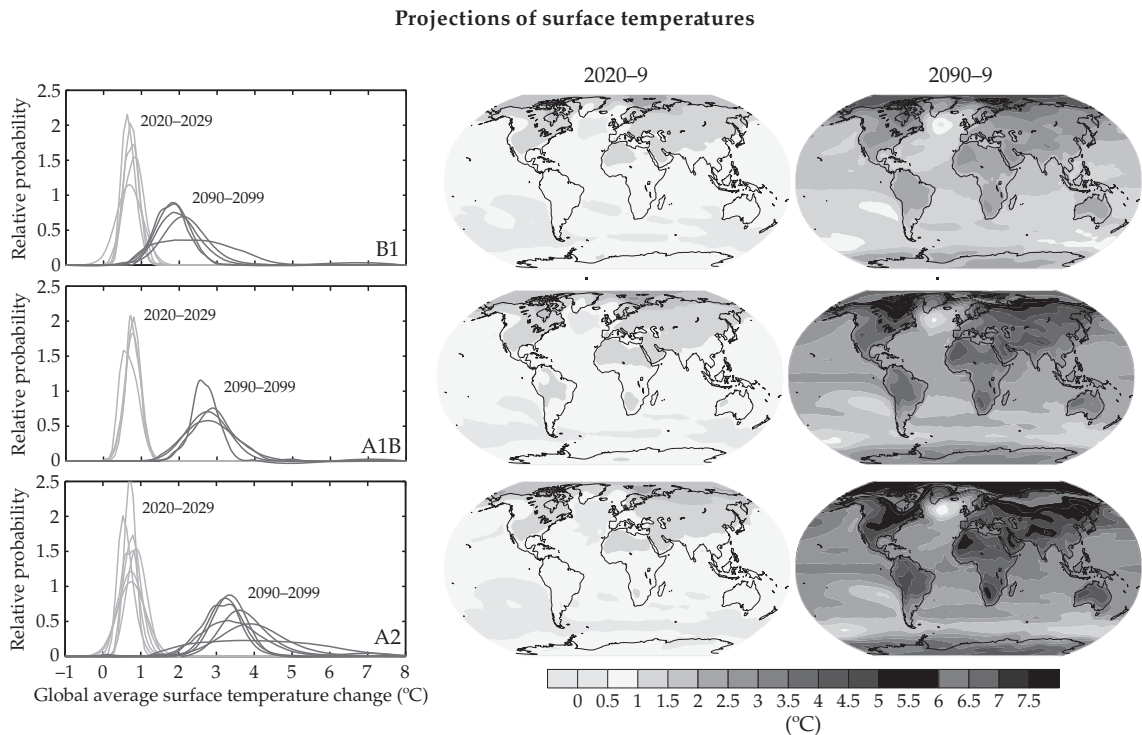


Figure 10.1 Projected surface temperature changes for the early and late twenty-first century relative to the period 1980–99. The central and right panels show the atmosphere-ocean coupled general circulation model (AOGCM) multi-model average projections for B1 (*top*), A1B (*middle*) and A2 (*bottom*) IPCC Special Report on Emissions Scenarios (SRES) scenarios averaged over the decades 2020–9 (*centre*) and 2090–9 (*right*). IPCC has assumed four storylines that encompass a marked portion of the underlying uncertainties in the main driving forces (demographic change, economic development, and technological change). Four qualitative storylines describe four sets of scenarios called families: A1 (world market), A2 (provincial enterprise), B1 (global sustainability), and B2 (local stewardship). The A1 family was divided into three groups characterizing alternative developments of energy technologies: A1FI (fossil fuel intensive), A1B (balanced), and A1T (predominantly non-fossil fuel). The scenario used historical data for atmospheric CO₂ between 1860 and 2000, and then assumed atmospheric CO₂ concentrations will reach 850 ppm (A2), 720 ppm (A1B), 500 ppm (B1) in the year 2100, respectively. The left panels show the corresponding uncertainties as the relative probabilities of estimated global average warming from several different AOGCM and Earth System Model of Intermediate Complexity studies for the same periods. (From IPCC 2007a). (See Plate 22).

earlier IPCC emission scenario, IS92, which was used by several cited studies. IS92a begins in 1990 and assumes an effective CO₂ concentration increase of 1% per year. IS92a differs from the IPCC Special Report on Emissions Scenarios (SRES) scenarios (Fig. 10.1) because it starts from 1990 and the many economic and political issues during the 1990s are not incorporated. IS92a can be roughly thought of as resulting in CO₂ concentrations in 2100 similar to those of A1B, although the emission scenario is very different and intermediate between the SRES B2 and A2 scenarios (IPCC 2000).

We note that we use the terms global climate change and global change throughout this chapter to refer to anthropogenic-induced climate changes. In many instances, and especially with the examination of historical data, we emphasize that the changes in the properties and biota of the oceans reflect various mixtures of local, regional, and global variation and trends in climate. We cannot attribute all of the documented changes or responses to global-scale phenomena, nor can we infer the role of anthropogenic versus natural influences (e.g., see Drinkwater *et al.*, Chapter 2, this volume, for a discussion of climate-induced effects on ocean ecosystems).

10.2 Emergence of global changes in the ocean environments and projected future ocean conditions

There has been extensive analysis of the physics and chemistry of the oceans to detect and quantify global change effects on ocean properties. We briefly summarize the changes in the ocean properties that have already emerged as signals of global change and that have clear links to ecosystem responses, and how these properties are projected to further change in the future. The properties we focus on are: water temperature, nutrient supply, mixing and circulation, micronutrient supply, transport of plankton, acidification, and sea-level rise.

10.2.1 Changes in sea water temperature

The global atmospheric concentrations of carbon dioxide, methane, and nitrous oxide have increased

markedly as a result of human activities since 1750, owing mainly to combustion of fossil fuels and changes in land use. Together, the combined radiative forcing from these three greenhouse gases is a 2.3 watts per square metre (W m⁻²) increase relative to 1750, which dominates the increase in the total net anthropogenic forcing (1.6 W m⁻²) (IPCC 2007a). The total net anthropogenic forcing includes contributions from aerosols (a negative forcing) and several other sources, such as tropospheric ozone and halocarbons. Evidence for their important role is that climate model simulations, which include changes in greenhouse gases, better match the historical increase observed in water temperature than simulations without the increasing greenhouse gases (e.g. Barnett *et al.* 2005).

The increased heat is absorbed by the continents, the lower atmosphere, and the ocean, and is available to melt the glaciers, ice sheets on land, and sea ice. Since 1979, overall ocean surface water temperatures (SST) have warmed $0.133 \pm 0.047^\circ\text{C}$ (Rayner *et al.* 2006), and the warming is evident, to varying degrees, at most latitudes and in most ocean basins. A large part of the change in ocean heat content during the past 50 years has occurred in the upper 700 m of the world ocean, although warming has been detected to a depth of 3000 m (Levitus *et al.* 2005). The warming is not uniform; notable exceptions are the cooling observed in mid-latitude North Pacific and in some areas of the high-latitude North Atlantic. Current evidence indicates that the ocean is absorbing most of the heat being added to the climate system (Levitus *et al.* 2005). The global averaged surface temperature is projected to continue to increase in the future (Fig. 10.1, IPCC 2007a), although the magnitude depends on the specific emission scenario assumed.

SSTs in the oceans also show variation on the scale of years to decades related to the *El Niño*-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) for the Pacific Ocean (see Drinkwater *et al.*, Chapter 2, this volume). ENSO events are typically 2–3 years in duration that encompass the *El Niño* and *La Niña* phases. During the *La Niña* phase, the trade winds push warm water to the western equatorial Pacific. During the *El Niño* phase, the trade winds relax permitting the warm waters to propagate to the eastern Pacific.

Atmosphere-ocean coupled general circulation models (AOGCMs) project that ENSO events will continue to occur in the twenty-first century; however, general statements about how global change will affect the frequency and amplitude of ENSO events are difficult to make because the projections differ among the models.

There is also evidence for global change effects on SST variability reflected in changes in the PDO index. The PDO features an SST anomaly pattern nearly symmetric about the equator with larger amplitudes in the middle than in the low latitudes and an opposite signed anomaly along the eastern rim of the Pacific (Mantua *et al.* 1997). Overland and Wang (2007a) identified those AOGCMs that were able to capture the spatial pattern of the PDO (i.e. whose spatial correlation with the observed PDO exceeded 0.7) and compared their future SST projections. For example, the simulated spatial patterns of the first leading mode of North Pacific SST during the 2001–100 period under the A1B scenario showed a rather uniform and single-signed spatial pattern with linear trends in all of the examined models. The second leading mode of the simulated North Pacific SST during the 2001–100 (which corresponds to PDO) showed a pattern with projected amplitudes that did not change significantly. These projections also indicated that the change in the mean background SST field under anthropogenic influences will surpass the magnitude of natural variability in the North Pacific in less than 50 years (Fig. 10.2).

A sea surface height mode of variability is the North Pacific Gyre Oscillation (NPGO), which is likely to become more energetic under global warming (Di Lorenzo *et al.* 2008). The NPGO represents the second principal component of sea-level height (the breathing mode of Cummins and Freeland 2007; see also the Victoria mode of Bond *et al.* 2003). The NPGO is strongly correlated with salinity, nutrient supply, and biological variables in parts of the eastern North Pacific (Di Lorenzo *et al.* 2008). A more energetic NPGO could result in a shift in conditions in the eastern Pacific more associated with the NPGO than with the PDO.

Changes in temperature and precipitation are expected to cause a reduction in the meridional overturning circulation (MOC), with implications for general ocean circulation patterns and SST, especially in the North Atlantic (Clark *et al.* 2002). The latitudinal difference of ocean density gradients and the large-scale winds drive the MOC, together with the sinking of water in the high latitudes and broad upwelling in other regions. The MOC is connected to the Southern Ocean and the Indonesian Throughflow, yielding a global-scale pathway (Schmitz 1996), which has been called the Great Ocean Conveyor Belt (Broecker 1991). Under global warming conditions, there will be less cooling and increased precipitation at the high latitudes, which will weaken the MOC and affect broad oceanic areas. Schmittner *et al.* (2005), using 28 projections from nine different coupled global climate models under the A1B scenario, projected a gradual

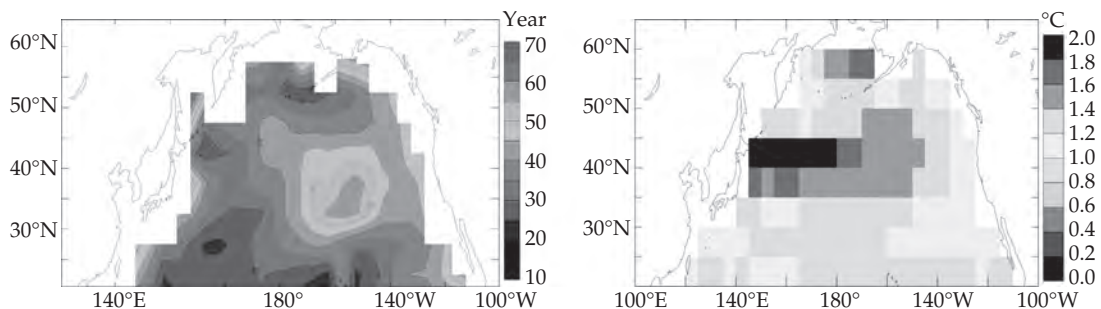


Figure 10.2 *Left:* Estimated year (+2000) when the net warming exceeds the magnitude of natural variability. This year for each location was defined by dividing twice the standard deviation of the observed sea surface temperature (SST) by the modelled temperature trend. This threshold is generally reached for the North Pacific before the middle of the twenty-first century. *Right:* Projected winter SST change for 2040–9 minus 1980–99. Changes are in the range of 1–2°C. (From Overland and Wang 2007a). (See Plate 23).

weakening of the North Atlantic MOC by 25% ($\pm 25\%$) through to 2100. The weakening of the MOC could cool the North American and European summer climate and SST in the North Atlantic (Sutton and Hodson 2005), and decrease the amplitude of a multi-decadal (~ 60 years) pattern in the SST covering the entire North Atlantic Ocean called the Atlantic Multidecadal Oscillation (AMO).

10.2.2 Changes in nutrient supply systems

Changes in mixing and circulation due to global warming will affect the nutrient supply to the euphotic zone, and can have major consequences for primary production and higher trophic levels. Warming increases stratification, thereby reducing vertical mixing by wind and tide, the timing and intensity of upwelling in coastal regions, and the strength of the MOC.

Several analyses suggest a general reduction of vertical mixing in recent decades over a wide region of the North Pacific. For example, surface layer stratification increased in intensity in the Oyashio region (subarctic north-western Pacific) from the 1960s to the 1990s (Ono *et al.* 2002). The apparent oxygen utilization (AOU) in the subsurface layer also increased during the same time period (e.g. Watanabe *et al.* 2001; Emerson *et al.* 2004), indicating reduced mixing between surface and subsurface layers. In the subtropical North Pacific, water density and nutrient concentrations decreased in the wintertime mixed layer (Watanabe *et al.* 2005).

In ocean areas associated with sea ice, melting water from sea ice could increase stratification due to the freshening of the oceanic waters and reduce nutrient supply into the surface layer. Sea-ice melting is one of the most visible results of global warming. The annual mean ice extent in the Arctic showed a significant decreasing trend in recent years, while sea-ice extent in the Antarctic showed a smaller decreasing trend (Comiso 2003; Stroeve *et al.* 2007). Arctic sea-ice extent at the end of the melt season in September has exhibited an especially sharp decline from 1953 to 2006. Although, future projections also indicate a decrease of Arctic ice cover (IPCC 2007a), the observational decline is much faster than model projections (Stroeve *et al.* 2007). Further global

warming will induce sea-ice melting and lead to surface freshening and increased stratification. A likely consequence of increased stratification is a reduction in nutrient supply to the surface layer. This effect will be especially strong in areas downstream of Antarctica and the Arctic seas.

Global warming will also affect stratification by changing the salinity of oceanic waters via changes in precipitation and the melting of water from other cryospheric (frozen water) sources besides sea ice. Changes in freshwater inputs affect salinity, which is a driver of vertical stratification. In high-latitude regions, salinity is the dominant source of vertical stratification (Carmack 2007). Salinity data in the ocean are more limited than temperature data. Boyer *et al.* (2005) attempted to calculate linear trends in salinity, averaged for 5-year periods from 1955–9 through 1994–8. Salinity decreased in the high latitudes and increased in the subtropics. Most of the Pacific is freshening with the exception of the subtropical South Pacific. Future projections under global warming scenarios by various AOGCMs suggest increased precipitation in the high latitudes and reduced precipitation in most subtropical land regions, which would tend to decrease surface salinity in high latitudes and increase surface salinity in subtropical areas (IPCC 2007a). The decrease of surface salinity in the high latitudes will increase the stratification and reduce the nutrient supply to the surface layer. Exceptions include those regions where advection carries the influence from one area to the other; for example, the Barents Sea where salinities are expected to increase due to advection of high-salinity waters from the southern regions (Bethke *et al.* 2006)

Upwelling is another important nutrient supply mechanism in coastal regions, especially in the eastern boundary of major ocean basins, such as the Benguela, Canary, Humboldt, and California Current systems. These areas support very high biological productivity and large populations of small pelagic fish, and were the focus of the Small Pelagic and Climate Change (SPACC) programme within GLOBEC (Fréon *et al.* 2009). Bakun (1990) proposed that, in eastern boundary regions, stronger warming on land compared to the sea leads to the enhancement of upwelling-favourable winds. He showed an increasing trend in upwelling in the

eastern boundary regions, which was further supported by analyses of recent data for the California, Humboldt, and Benguela Current systems (Mendelssohn and Schwing 2002; McGregor *et al.* 2007). Auad *et al.* (2006) projected how global warming would affect upwelling in the California Current system using a high-resolution model forced by atmospheric fields derived from a coarse-resolution AOGCM. Their projection showed about a 30% increase in near-surface upwelling velocities during the key month of April, which cooled the upper-ocean (<70 m depth) region. The cooling effect was partially offset by heat fluxes from an unusually warm atmosphere during the time period of simulation, so that only a net mild cooling effect was projected.

However, other analyses provide contradictory results, suggesting that global warming would reduce upwelling in coastal systems. Diffenbaugh (2005) used an ensemble approach with coupled climate models and projected wind fields, and reported that some components of the ensemble showed a potential relaxation of the strength and variability of upwelling-favourable (equatorward) wind forcing in all four of the eastern boundary regions. Vecchi *et al.* (2006) used an AOGCM and projected a weakening of the Walker Circulation in the tropical Pacific. They found that the projected slowdown of the Walker Circulation was consistent with the slowdown observed historically since the mid-nineteenth century. Their model projections suggested further slowdown of the tropical Walker Circulation under global warming, which leads to a reduction in the trade winds and a concomitant reduction in upwelling-favourable winds. Perhaps these studies can be reconciled if one considers that global warming effects on local wind systems enhance upwelling, while effects on large-scale wind systems act to decrease upwelling. Regardless of the net effect, both local- and large-scale wind effects would act to change the timing (seasonality) of the upwelling.

The expected weakening of the MOC can have major effects on the nutrient supply to the euphotic zone. The sinking water in high latitudes drives deep-water circulation, and the deep water is rich in nutrients because decomposition of organic material takes a long time. These nutrient-rich waters

then supply nutrients to the euphotic zone in broad regions by upwelling. A weakening of the circulation could lower nutrient supplies in broad areas of the ocean. Schmittner (2005) estimated that a disruption of the Atlantic MOC would lead to a halving of plankton biomass in the North Atlantic, and a reduction in primary productivity in many other regions.

Recently, the concept of nutrients fueling primary productivity has been expanded from the classical focus on nitrogen and phosphorus to include micronutrients such as iron (Behrenfeld *et al.* 1996), and it is uncertain how global warming will affect the supply of these micronutrients. For example, one of the major sources of iron to the open ocean is atmospheric transport of dust by winds, such as the mid-latitude westerlies. Mid-latitude westerly winds have strengthened in both hemispheres since the 1960s (Gillett *et al.* 2005), and these winds are projected to be enhanced under global warming conditions. How such changes in wind patterns will affect the supply of iron to the ocean is not clear. One possibility is that more iron will be transported to the oceans; however, the net effect of changes in wind-driven transport on iron fluxes to the oceans is uncertain. Similar arguments can be made for other micronutrients; the best we can say, at this point, is that their delivery rates to the oceans might change substantially under global warming.

10.2.3 Transport of plankton

The possible changes in water temperature, salinity, and atmospheric circulation (wind patterns) would have major effects on the horizontal circulation in the ocean. Changes in horizontal circulation will affect the advective transport of phytoplankton, zooplankton, and early life stages of fish. Sakamoto *et al.* (2005) calculated the linear trend of the dynamic sea surface height between 1965 and 2003 in the north-western Pacific and detected an intensification of the Kuroshio Extension. The magnitude of the intensification was relatively small, especially in the context of the large decadal-scale variability observed in the north-western Pacific. Future projections of the ocean circulation under global warming scenarios also indicate an acceleration of the Kuroshio and Kuroshio Extension, accompanied by

an enhancement of eddy activity in the Kuroshio Extension region (Fig. 10.3).

Another example of possible changes in horizontal circulation is how global change might affect circulation in the North Atlantic. The NAO (North Atlantic Oscillation) index is used to characterize the winter climate variability and is a rough meas-

ure for the intensity of the Icelandic Low, which influences the intensity of ocean circulation between the northern North Atlantic and the Arctic (Hurrell 1995). A high NAO Index (i.e. a strong Icelandic Low) increases the flux of warm Atlantic water into the Nordic Seas and simultaneously increases the flux of cold Arctic water into the Labrador causing

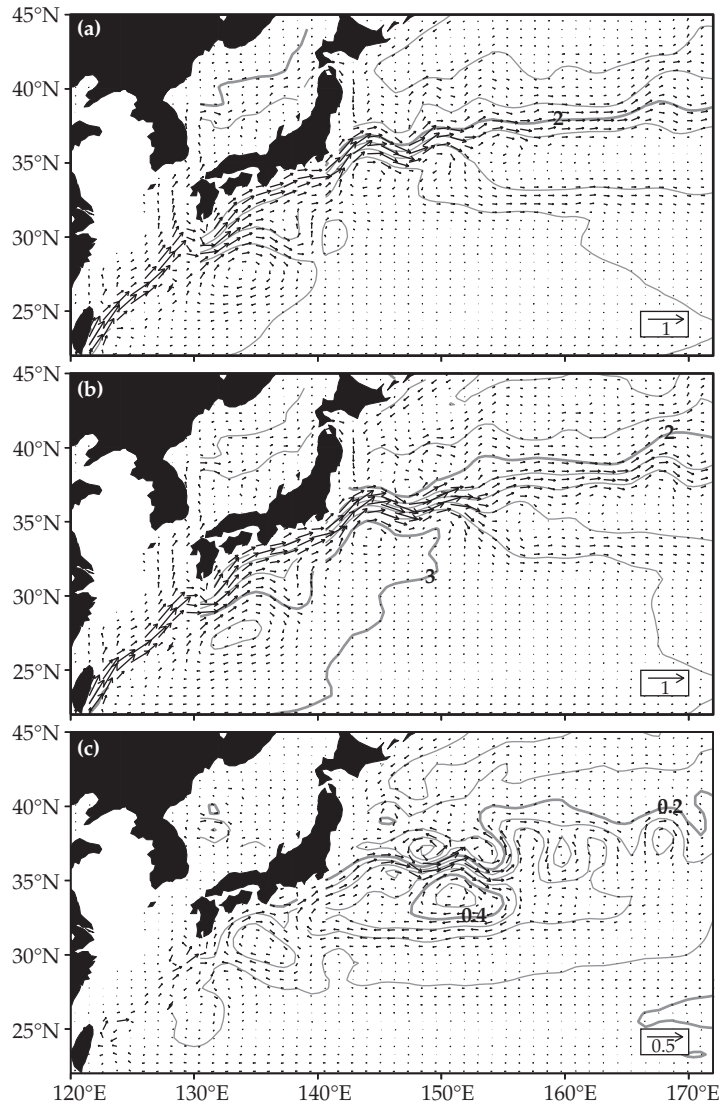


Figure 10.3 Long-term mean current velocities at 100 m depth (vectors, unit: m s^{-1}) and dynamic sea surface height (contours, unit: m) relative to 2048 m depth in (a) the simulation under pre-industrial conditions, (b) the simulation under double CO₂ conditions (1% increase of CO₂ concentration for 90 years), and (c) the difference between (b) and (a) (former minus latter). Contour intervals are 0.2 m in (a) and (b), and 0.05 m in (c). (Reprinted by permission of Macmillan Publishers Ltd: Geophysical Research Letters Sakamoto *et al.* Copyright 2005.)

opposite climate trends in the north-east Atlantic (e.g. the Nordic Seas) and the north-west Atlantic (e.g. the Labrador Sea) (Sundby and Drinkwater 2007). Historically, the NAO index has shown decadal-scale variation that creates temperature oscillations in the two North Atlantic regions with opposite phase. Miller *et al.* (2006) and Stephenson *et al.* (2006) used multiple AOGCMs to investigate how global warming would affect the NAO (or NAM: Northern Annular Mode). They found that none of the models projected a decrease in the NAO index and more than half of the models projected a positive increase in the NAO index; however, the magnitude of the increase was generally small. An increase in the NAO index potentially leads to an increase in the transport of warm Atlantic water and an associated influx of zooplankton into the Nordic Seas (Sundby 2000).

10.2.4 Acidification

The absorption of carbon in the ocean, including carbon from anthropogenic emissions, leads to increased acidification of oceanic waters. Over the period 1800 to 1994, the ocean was estimated to have absorbed 118 ± 19 petagrams (Pg) of carbon, or about 48% of the total emitted during the period (Sabine *et al.* 2004). Hydrolysis of CO_2 in water increases the hydrogen ion concentration, which can affect the ionic balance of many organisms and the ability of some organisms (e.g. corals and bivalves) to maintain their external calcium carbonate skeletons (Kurihara 2008; Vezina and Hoegh-Guldberg 2008).

Future projections using models of the ocean carbon cycle suggest that the Southern Ocean surface waters will become undersaturated with respect to aragonite, a metastable form of calcium carbonate, by the year 2050 (Orr *et al.* 2005). By 2100, this undersaturation could extend throughout the entire Southern Ocean and into the subarctic Pacific Ocean (Fig. 10.4). Ongoing studies show that the undersaturation in the Arctic Ocean may be even more severe than in the Southern Ocean.

Global-scale ocean acidification will also modify oceanic biogeochemical fluxes. Increased acidification reduces export fluxes related to CaCO_3 and hence weakens the strength of the biological carbon pump. A weakened biological pump is projected to

increase oxidization of organic matter in shallow waters and can result in the expansion of hypoxic zones (Hofmann and Shellnhuber 2009).

10.2.5 Sea-level rise

Melting water from landlocked cryospheric fields and the thermal expansion of warmed sea water will contribute to a rise in sea level. Sea-level rise will influence the habitat quality and quantity of near-shore marine ecosystems and estuaries, which are nursery grounds for many higher trophic level species. Averaged sea-level rise by the thermal expansion was estimated as $0.33 \text{ mm year}^{-1}$ during 1955 to 2003 (Antonov *et al.* 2005). The IPCC-AR4 (IPCC 2007a) suggested that global sea level will rise between 0.18 and 0.59 m during the twenty-first century. Thermal expansion is estimated to cause 70 to 75% of the rise in sea level; however, one of the major unknowns is what will happen to the Greenland ice sheet. The melting of the Greenland ice sheet would greatly increase sea-level rise. Indeed, melting at the edges of the Greenland ice sheet is presently more than compensated for by the accumulating mass in its interior regions due to increased precipitation (Rignot and Kanagaratnam 2006). Some investigators say that the Greenland ice sheet could respond to global warming on a timescale of hundreds of years, while other investigators suggest that the ice sheet could melt abruptly within this century (IPCC 2007a).

10.2.6 Feedback mechanisms

Changes in the physical or chemical properties of the oceans cause ecosystem responses that can, in turn, affect the physical or chemical changes. For example, phytoplankton can act to affect the distribution of heat within the water column by absorbing solar radiation in the surface layer. The heat absorption by phytoplankton influences both the mean and transient state of the equatorial climate (Murtugudde *et al.* 2002; Timmermann and Jin 2002), decadal variations of climate (Miller *et al.* 2003), and the global mean SST field (Frouin and Iacobellis 2002). Phytoplankton can also influence atmospheric radiation processes because they

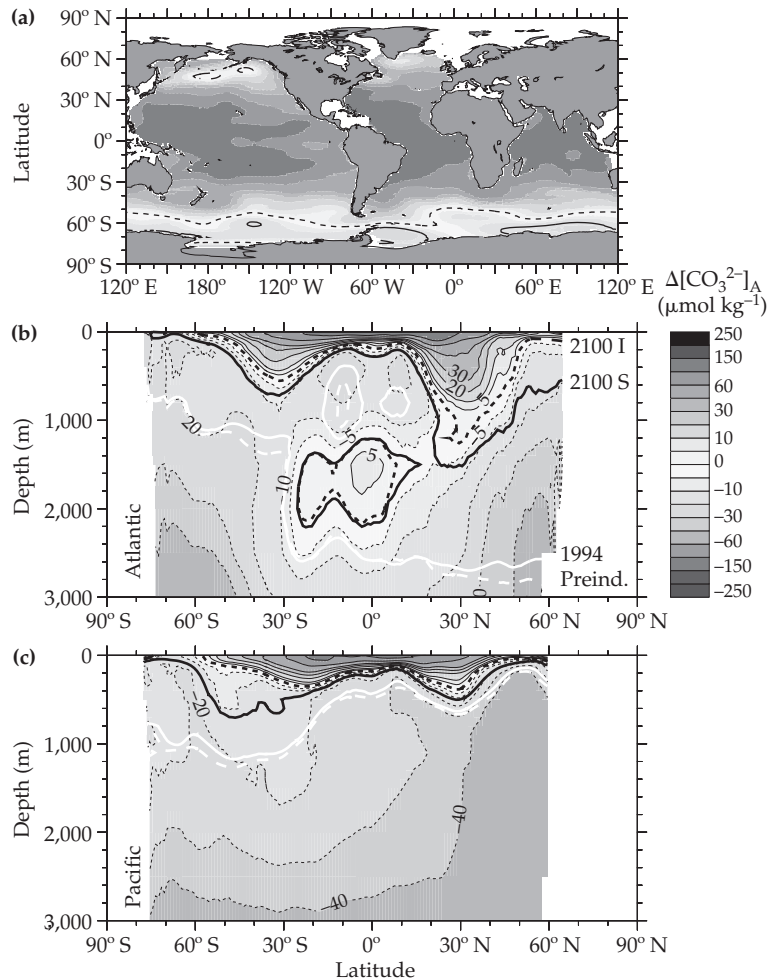


Figure 10.4 The aragonite saturation state in the year 2100 as indicated by $\Delta[\text{CO}_3^{2-}]_A$. The $\Delta[\text{CO}_3^{2-}]_A$ is the *in situ* $[\text{CO}_3^{2-}]$ minus that for aragonite-equilibrated sea water at the same salinity, temperature, and pressure. Shown are the OCMIP-2 median 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 (pre-industrial; white dashed line), 1994 (white solid line) and 2100 (black solid line for S650; black dashed line for IS92a). Positive $\Delta[\text{CO}_3^{2-}]_A$ indicates supersaturation; negative $\Delta[\text{CO}_3^{2-}]_A$ indicates undersaturation. (After Orr *et al.* 2005. Reprinted by permission of Macmillan Publishers Ltd: Nature copyright 2005). (See Plate 24).

release dimethylsulfide (DMS), one of the major sources of cloud condensation nuclei over the ocean (Charlson *et al.* 1987). Another example is that absorbed carbon in the oceans can be transported to the subsurface layer by the sinking of particulate organic materials such as dead phytoplankton and zooplankton fecal pellets (Ducklow *et al.* 2001). Projecting ecosystem response to global warming may need to consider these and other feedbacks in order to ensure sufficient accuracy in the projected physical and chemical ocean properties.

10.3 Ecosystem responses to global change

Biota can respond in a variety of ways to the changes in the physical and chemical properties of the oceans that are expected under global warming. Analyses of ecosystem responses have their own uncertainties, and often use the outputs of the physical and biogeochemical models, and thus inherit the uncertainty associated with the physical and chemical property projections as well. High uncertainty in

ecosystem responses results from the need to quantitatively represent how environmental conditions affect biota plus the ecological interactions that can substantially affect biological responses. Below, we summarize some of the available evidence for historical responses of oceanic ecosystems to variation in climate, and highlight some examples where ecosystem responses have been projected under future global change. We organize the results by trophic level (primary production, zooplankton and higher trophic levels), and to the extent possible, we relate ecosystem responses to changes in the physical and chemical properties discussed above.

10.3.1 Primary production

Primary production in the ocean will be strongly influenced by global warming through changes in the water temperature, nutrient supply, and transport. Understanding and projecting responses of primary production to global warming is critical because primary production acts as the starting point for much of the energy that is channelled into

biological pathways. Simple general statements about how primary production will respond to global warming are difficult because primary production, and the factors controlling it, vary spatially (e.g. latitude, upwelling versus mid-ocean, shelf seas versus deep-ocean). We must expect that the effects of climate change will therefore also vary spatially.

10.3.1.1 Emergence of primary production responses to global change

Several broad-scale analyses of ship-based observations have shown a decline in primary production in recent decades. Watanabe *et al.* (2005) noted a general decline in phosphate concentration in the subtropical region, and a decrease in net primary production of $0.26 \text{ gC m}^{-2} \text{ year}^{-1}$ between winter and summer from 1971 to 2000. Ono *et al.* (2002) estimated an averaged decline in primary production of $0.51 \pm 0.09 \text{ gC m}^{-2} \text{ year}^{-1}$ (corresponding to 0.9% of the primary production) in the Oyashio (subarctic) region (Fig. 10.5). Both trends were associated with a reduction of the wintertime

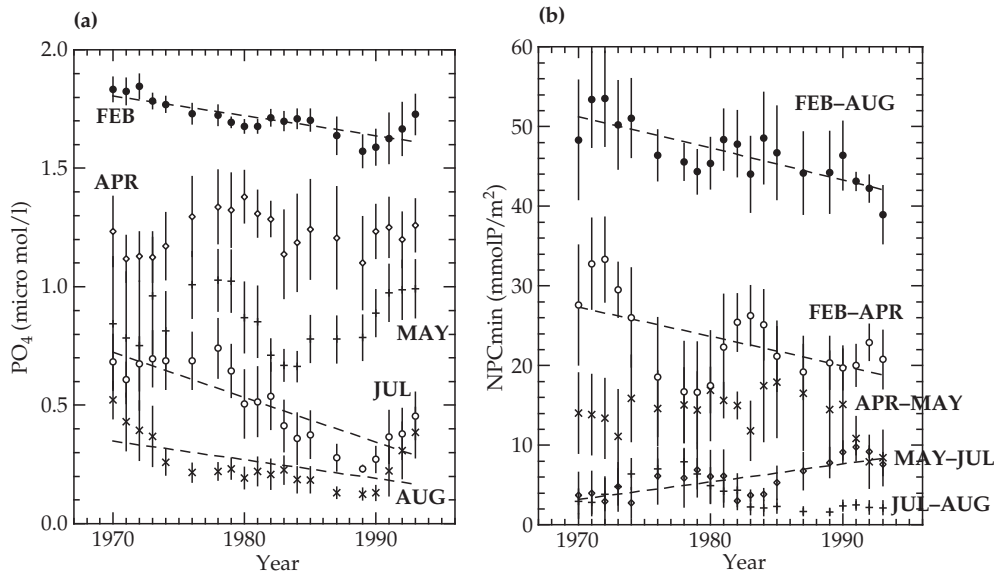


Figure 10.5 (a) Five-year running mean of monthly mean phosphate concentration within a mixed layer ($\mu\text{mol l}^{-1}$) for February, April, May, July, and August. (b) Five-year running mean of minimum net phosphate consumption within a mixed layer (mmol P m^{-2}) between the months: February to April, April to May, May to July, July to August, and the total (February to August). Regression lines are drawn only for the statistically significant case (95%). Error bars represent the 95% confidence limit of each average and are calculated from the original values rather than the 5-year running mean. (From Chiba *et al.* 2004 and redrawn from Ono *et al.* with permission of Macmillan Publishers Ltd: Geophysical Research Letters copyright 2002.)

mixed-layer depth, which was related to global change as a response to changes in the intensification of stratification (Ono *et al.* 2002; Chiba *et al.* 2004; Watanabe *et al.* 2005). Two caveats to these results are that Ono *et al.*'s analysis included phosphate only, even though nitrate and silicate are known to limit primary production in the Oyashio region, and the attribution of the changes to global warming in both analyses is tempered by the observed data being collected during certain PDO conditions that vary decadal and therefore the decrease in primary production may not purely reflect the effects of global warming.

Analyses of coastal regions using ocean colour satellite imagery suggest an increase in primary production over the past decade. Satellite imagery enables greater spatial and temporal coverage than ship-based observations; however, the imagery is for surface conditions and time series data are typically less than 10 years in duration. Gregg *et al.* (2005) used a 6 year (1998–2003) time series of Sea-viewing Wide Field-of-view Sensor (SeaWiFS) data, and detected a linear increase in ocean chlorophyll of 4.1% ($p < 0.05$), which corresponds to $0.00261 \text{ mg m}^{-3} \text{ year}^{-1}$. However, this increase has occurred mostly in coastal regions where bottom depth is shallower than 200 m, whereas chlorophyll-*a* concentrations have decreased in the subtropical open ocean regions of both the Pacific and Atlantic. Gregg *et al.* (2005) showed that the decline in chlorophyll-*a* in the subtropics was associated with an increase in SST in the North and South Pacific and the South Atlantic. Behrenfeld *et al.* (2006) used a longer 10-year (1997–2006) SeaWiFS data set and found that chlorophyll and net primary production increased during 1997–9, corresponding to an *El Niño* to *La Niña* transition, and then subsequently decreased during 1999–2005. These changes occurred mainly in the permanently stratified regions of the open ocean (i.e. tropics and subtropics). Extrapolating these changes to the stratified areas of the ocean, results in changes in annual net primary production with an increase of $1.25 \text{ gC m}^{-2} \text{ year}^{-1}$ for the 1997–9 period and a decrease of $0.94 \text{ gC m}^{-2} \text{ year}^{-1}$ for the 1999–2005 period. Behrenfeld *et al.* (2006) related their estimated values to the Multivariate ENSO Index (MEI). The MEI (Wolter and Timlin 1998) is the

first leading mode in the tropical Pacific Ocean consisting of sea-level pressure, zonal and meridional components of the surface wind, SST, surface air temperature, and total cloudiness fraction of the sky. Behrenfeld *et al.* found that net primary production decreased with an increase in the MEI (warmer conditions), and that the MEI was positively correlated with the strength of stratification as indicated by the difference in water densities between the surface and the 200 m depth. These results suggest a possible mechanism whereby surface warming enhances stratification in the subtropical and tropical oceans, which then suppresses nutrient exchange, resulting in a decrease in net primary production. Recently, Polovina *et al.* (2008b) used a 9-year (1998–2006) SeaWiFS dataset to show an increasing trend in oligotrophic regions in the North and South Pacific and Atlantic (Fig. 10.6). In contrast, annual primary production in the Arctic increased between 2006 and 2007 with 30% of this increase attributable to decreased minimum summer ice extent and 70% due to a longer phytoplankton growing season (Arrigo *et al.* 2008). Assuming these trends continue, they estimated that the additional loss of ice during the Arctic spring could boost productivity more than three-fold above 1998–2002 levels, potentially altering marine ecosystem structure and the degree of pelagic-benthic coupling.

Simultaneous with the enhanced stratification reducing nutrient supply in the North Pacific has been a freshening of the Okhotsk Sea, which could affect primary production by changing the supply of iron. The Okhotsk Sea Intermediate Water is an important source of iron for the North Pacific (Nishioka *et al.* 2007). Hill *et al.* (2003) suggested that the surface layer is freshening in the Okhotsk Sea, and Nakanowatari *et al.* (2007) reported warming of the Okhotsk Sea Intermediate Water and the consequent warming of the North Pacific Intermediate Water. These results suggest that the freshening of the Okhotsk Sea has reduced the formation of the Okhotsk Sea Intermediate Water, and hence reduced the iron supply from the Okhotsk Sea to the North Pacific. The relative contributions of reduced iron supply versus weakening of stratification to the reduction in primary production in the North Pacific are unknown.

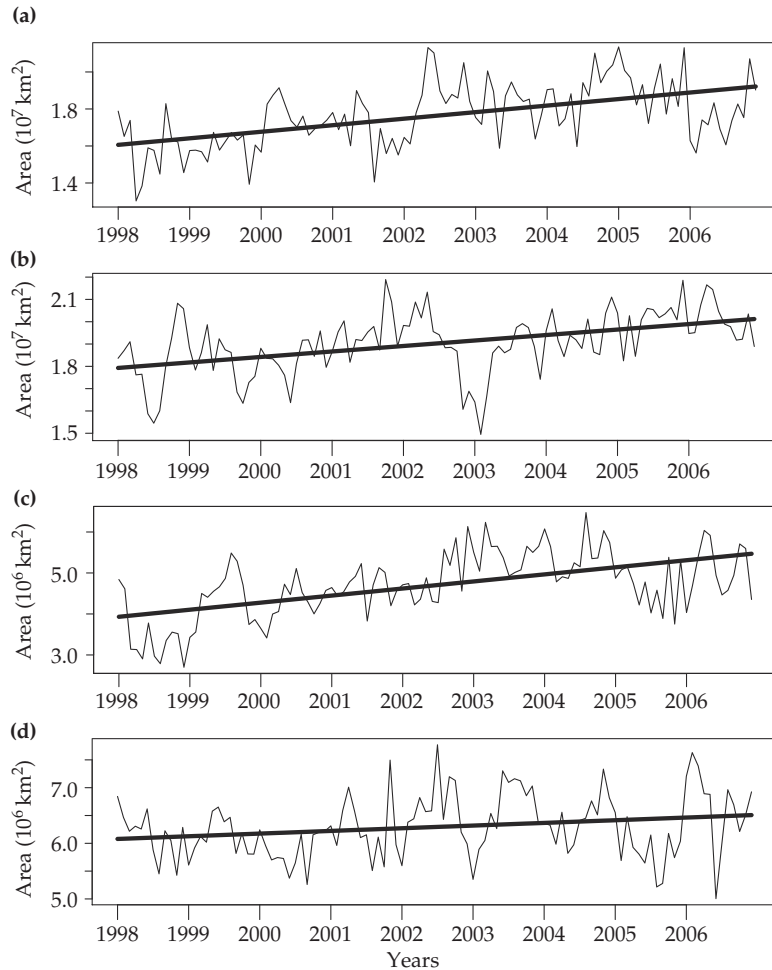


Figure 10.6 Time series of the monthly mean area (km^2) of oligotrophic regions (surface chlorophyll less than or equal to $0.07 \text{ mg chlorophyll m}^{-3}$) between $5\text{--}45^\circ\text{N/S}$ latitude with the modelled seasonal cycle removed in (a) the North Pacific, (b) the South Pacific, (c) the North Atlantic, and (d) the South Atlantic. Straight lines show the linear trend. (Reprinted by permission of Macmillan Publishers Ltd: Geophysical Research Letters, Polovina *et al.* 2008b, copyright 2008.)

10.3.1.2 Future projections of primary production

Global-scale models project moderate reductions in global primary production. Cox *et al.* (2000) used a nutrient-phytoplankton-zooplankton-detritus (NPZD) coupled to an AOGCM with an ocean resolution of $2.5^\circ \times 3.75^\circ$. They projected a global average reduction of about 5% from 2000 to 2100 under global warming with the IS92a scenario. Boyd and Doney (2002) used a more complex ecosystem model that incorporated multi-nutrient limitation (N, P, Si, and Fe) and three groups of planktonic geochemically based functional groups: diatoms

(export flux and ballast), diazotrophs (nitrogen fixation), and calcifiers (alkalinity and ballast). They used the IPCC A1 scenario, and projected an average 5.5% decline in primary production. Bopp *et al.* (2005) used a similar type of multi-nutrient (NO_3^- , NH_4^+ , PO_4^- , SiO_3 , and Fe) and plankton community model (diatoms, nano-phytoplankton, microzooplankton, and mesozooplankton), named Pelagic Interactions Scheme for Carbon and Ecosystem Studies (PISCES), and projected a 15% decline with a scenario in which CO_2 started at pre-industrial conditions and increased at a rate of $1\% \text{ year}^{-1}$

thereby reaching $4 \times \text{CO}_2$ after 140 years. All three models generated reduced primary production due to lower nutrient supply because of enhanced stratification, especially in lower latitudes, that exceeded the increased primary production projected to occur in higher latitudes due to an extended growing season.

Bopp *et al.* (2005) and Boyd and Doney (2002) also projected a shift in the phytoplankton community with a decrease in diatoms and an increase in nano-phytoplankton. The relative abundance of diatoms was projected to decline about 10% on a global scale and by up to 60% in the North Atlantic and in the subantarctic Pacific (Bopp *et al.* 2005). These shifts in diatoms showed good coincidence with the projected spatial distribution of the nutrient limitation factors (Fig. 10.7), with Fe limitation occurring south of 60°S (mainly in the South Pacific), NO_3 and Si limitation occurring between 30 and 40°S (mainly in the South Pacific and Indian Ocean), and NO_3 limitation occurring in the North Atlantic.

Cox *et al.* (2000) and Bopp *et al.* (2005) reported possible feedback effects. Cox *et al.* projected that the decrease of the ocean carbon uptake due to the reduction of primary production would be compensated for by an increase in natural CO_2 release due to reduced upwelling of CO_2 rich deep waters to the surface. Bopp *et al.* (2005) projected a 25% decrease in the export ratio, which was mainly explained by the recycling of nutrients and carbon in the surface layer by nano-phytoplankton that replaced the diatoms.

Hashioka and Yamanaka (2007) projected ecosystem responses in the western North Pacific for the end of the twenty-first century under the IS92a global warming scenario. Their analysis differed from that of Boyd and Doney (2002) and Bopp *et al.* (2005) by using a more complex food web representation (the North Pacific Ecosystem Model for Understanding Regional Oceanography or NEMURO, Kishi *et al.* 2007a) and by solving the physics with the biology rather than using off-line physics (i.e. physics is simulated first and the results are saved and read into the biology calculations). Hashioka and Yamanaka also projected that global warming would generally increase vertical stratification due to rising temperatures, decreasing nutrient and chlorophyll-*a* concentrations in the surface water,

and causing a shift in the dominant phytoplankton groups from diatoms to other smaller phytoplankton. They pointed out that these projected responses do not occur uniformly in all seasons, with the shift in phytoplankton groups occurring quite dramatically at the end of the spring, and that the onset of the diatom spring bloom was projected to occur about 2 weeks earlier (Fig. 10.8). However, the earlier onset of the diatom bloom is expected to be less at high latitudes where the Arctic summer day is exceeded by the Arctic winter night because the onset of the phytoplankton bloom would be

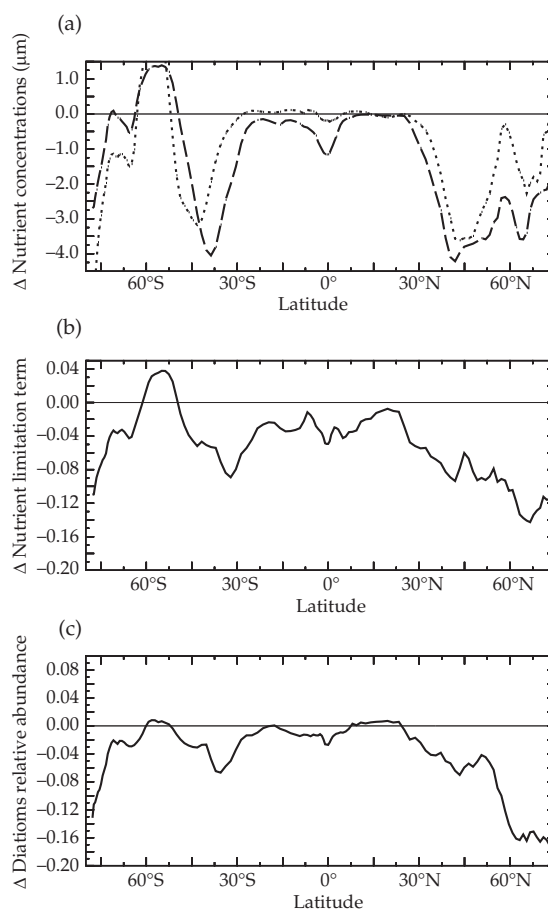


Figure 10.7 Zonal mean response to climate change ($4 \times \text{CO}_2 - 1 \times \text{CO}_2$) of (a) surface concentrations of nitrate (dashed line) and silicic acid (dotted line) in mM. (b) Nutrient limitation term of diatoms growth which is defined by four nutrient components. (c) The relative abundance of diatoms. (Reprinted by permission of Macmillan Publishers Ltd: Geophysical Research Letters, Bopp *et al.* 2005, copyright 2005.)

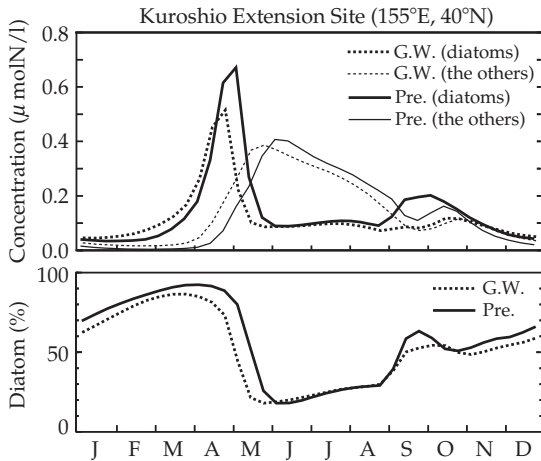


Figure 10.8 Seasonal variations of chlorophyll-*a* concentrations of diatoms (thick line) and other small phytoplankton (thin line) and biomass of diatoms as a percentage of total phytoplankton averaged over the surface 20 m at the Kuroshio Extension site (155°E, 40°N). Dotted and solid lines represent the global warming and present-day experiments, respectively. (Reprinted from Hashioka and Yamanaka 2007 with kind permission from Elsevier.)

determined by the seasonal change in light rather than a change in temperature (Eilertsen 1993).

10.3.2 Zooplankton

Zooplankton will be influenced by global warming through changes in water temperature, transport, and food availability. Shifts in the flora and timing of the bloom season can have especially important effects on the food available for zooplankton. The ship-based data available for zooplankton are more limited than for phytoplankton, and zooplankton is not monitored by satellite sensors. Furthermore, needing to know the trophodynamics between the phytoplankton and zooplankton adds considerable uncertainty to zooplankton modelling and projecting their population responses to global change. GLOBEC-related research has made progress on the understanding of phytoplankton to zooplankton trophodynamics (Moloney *et al.*, Chapter 7, this volume)

10.3.2.1 Emergence of zooplankton responses to global change

Richardson and Schoeman (2004) analysed Continuous Plankton Recorder (CPR) data for 1958 to 2002

for the north-east Atlantic and showed that zooplankton abundances were positively correlated to phytoplankton, with phytoplankton increasing during warm SST regimes in the cooler (northern) regions and decreasing in the warmer (southern) regions. The abundance of herbivorous copepods was positively related to phytoplankton, and the abundance of carnivorous zooplankton was positively related to the abundance of herbivorous copepods, but neither was directly correlated to SST. These results suggest climate-induced bottom-up forcing by which climate effects on phytoplankton propagate up the food web through herbivorous copepods to the carnivorous zooplankton. Richardson and Schoeman (2004) reported that SST during the period 1958–2002 decreased by about 0.1°C in the northern part of the study area and increased by about 0.5°C in the southern part. They also observed that plankton generally decreased in the southern area. Many AOGCMs project that SST will rise by 2–4°C in the north-eastern Atlantic by 2100, with an even higher increase in the northern area (IPCC 2007a). These results suggest that large responses of the zooplankton are possible for the north-east Atlantic, mediated through changes in their food. Additionally, CPR data from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) have shown a northward displacement of temperate species in the south and a northward displacement of boreal and arctic species in the north from the cool 1960s and 1970s to the present warm period (Beaugrand *et al.* 2002b; see Box 2.2, Fig. 1 in Drinkwater *et al.*, Chapter 2, this volume).

CPR data were also used to estimate changes in the phenology of plankton in the North Sea for 1958–90 (Edwards and Richardson 2004). The timing of species with summer peaks was earlier in the year, while the timing of species with blooms in the spring and autumn were unchanged (Fig. 10.9). The average shifts in bloom timing for the summer period were 23 days for dinoflagellates, 10 days for copepods, 10 days for non-copepod holozooplankton, and 27 days for meroplankton. SST during this same period increased by 0.9°C. The timing of the summer peaks was positively correlated with SST for all functional groups, with the highest correlations being for dinoflagellates ($r = 0.69$)

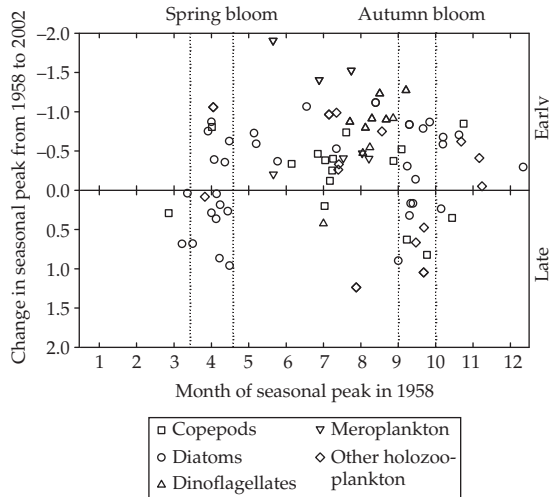


Figure 10.9 The change in the timing of the seasonal peaks (in months) for the 66 taxa over the 45-year period from 1958 to 2002 plotted against the timing of their seasonal peak in 1958. For each taxon, the linear regression was used to estimate the difference between the seasonal peak in 1958 and 2002. A negative difference between 1958 and 2002 indicates seasonal cycles are becoming earlier. (Reprinted by permission of Macmillan Publishers Ltd: Nature, Edwards and Richardson 2004. Copyright 2004.)

and meroplankton ($r = 0.70$). While the response of meroplankton can be explained by a direct species-specific effect of temperature, the response of the dinoflagellates is likely due to a mix of a direct temperature effect and indirect effects related to stratification and the responses of other taxa (Edwards and Richardson 2004).

A shift in the peak abundance of zooplankton has also been observed for the North Pacific. In the western North Pacific, Chiba *et al.* (2004) showed that the developmental timing of *Neocalanus flemingeri* has become earlier because of increased diatoms in the winter resulting from a shallower mixed layer improving light conditions. On the eastern side of the North Pacific, Mackas *et al.* (2007) reported a similar earlier shift in the peak day of *Neocalanus plumchrus* biomass since the mid-1970s that can be associated with warming (e.g. Miller *et al.* 1994), although Mackas *et al.* did not infer that the response was due to global warming. McGowan *et al.* (2003) found that the seasonal peak in bulk volumetric zooplankton biomass shifted 2 months earlier (July to May) after the mid-1970s in the southern part of the California

Current coinciding with warmer conditions and increased stratification (Kim and Miller 2007).

Wiltshire and Manly (2004) analysed a long-term data set from a single station in the North Sea for 1962 to 2002 and found the spring diatom bloom was actually delayed despite a general warming of about 1.1°C, perhaps due to responses of zooplankton to the temperature change. These data were collected three times a week (Greve *et al.* 2004). The delay in the spring bloom was hypothesized to be due to the warming trend during the autumn increasing the winter abundance of copepods, which resulted in higher grazing pressure that delayed the build-up of the diatom biomass.

In a recent review, Richardson (2008) summarized zooplankton responses to historical changes in climate. He also categorized responses of zooplankton to global warming as distributional shifts, phenology, and species composition and biomass changes. He found a general poleward movement of warm-water species and retreat of cold-water species, the opposite southward movement of cold-water species when physics pushed cooler water south (e.g. north-west Atlantic), earlier timing of life cycle events, and species abundances changes that varied in direction and mechanism by species and region.

10.3.2.2 Future projections of zooplankton

There are relatively few examples of mechanistic model projections (e.g. stage-based, NPZD) of zooplankton abundance and community composition under future climate conditions. Richardson's review (2008) cited Attrill *et al.* (2007) as an example of a correlative approach that related the NAO to jellyfish abundance and then projected jellyfish abundance under NAO conditions expected under global warming scenarios. Richardson (2008) presents some common criticisms of the empirical approach, and shows as an example how the *C. finmarchicus* abundance and NAO relationship broke down from 1996 (Reid *et al.* 2003a), likely because the mechanisms underlying the relationship had changed. The other example cited by Richardson (2008) was a version of an NPZD model (Bopp *et al.* 2004, 2005) but whose results under global warming were characterized as changes in primary production. We also were unable to locate clear examples of models being used to project zooplankton composition,

phenology, and abundances under global warming. Historically, models that included physics and zooplankton have focused on the geochemical cycling of nutrients (Le Quéré *et al.* 2005), and were not specifically designed for projecting zooplankton population dynamics. Forecasting zooplankton community and population dynamics was also not the focus of higher trophic level modelling where zooplankton was either ignored or represented very simply as food for fish. The exceptions generally involved models of larval fish feeding on a fairly detailed representation of the zooplankton (e.g. Letcher *et al.* 1996).

Ellingsen *et al.* (2008) applied a coupled model to simulate the change in the Barents Sea plankton during the period 1995–2059 (IPCC B2 scenario), and the model was validated with plankton observations for the period 1995–2004. The plankton model (Slagstad and Wassmann 1997; Slagstad *et al.* 1999; Wassmann *et al.* 2006) contained state variables for nitrate, ammonium, silicate, diatoms, flagellates, microzooplankton, dissolved organic carbon, heterotrophic flagellates, bacteria, and two groups of mesozooplankton representing Arctic and Atlantic (arcto-boreal) species. Phytoplankton production increased by 8%, and the major part of the increase happened in the eastern and northern Barents Sea (i.e. in the Arctic Water masses). The Atlantic mesozooplankton increased by 20%, but not enough to account for the 50% decrease in the Arctic zooplankton.

There are several efforts underway to use NPZD models coupled with three-dimensional physical models to project the population dynamics of key zooplankton species (e.g. *Calanus*) to global warming. These models are generally single species and use a stage-based or individual-based approach to simulating the population dynamics of the zooplankton species of interest. These efforts build upon some of the advances during the GLOBEC era in the modelling of key species of zooplankton coupled to the physics (see deYoung *et al.*, Chapter 5, this volume). For example, as part of the US GLOBEC synthesis efforts, population dynamics of key species of zooplankton will be simulated under global change using an individual-based model coupled to three-dimensional physical models of the north-west Atlantic and Arctic Ocean regions

(Cabell Davis, Woods Hole Oceanographic Institution, USA). Other models are being developed that could be used. For example, Slagstad and Tande (2007) recently developed a stage-based model of *Calanus finmarchicus* that was coupled to a nutrient, phytoplankton, and microzooplankton model and embedded into a three-dimensional hydrodynamic model for the Norwegian Sea that seems amenable to projecting zooplankton responses to global change.

10.3.3 Higher trophic levels

As we progress up the food chain, from phytoplankton to zooplankton to fish and other higher trophic level organisms, the possible interactions that can affect species responses increase, which puts enormous demands on the type and quantity of data needed. We focus on fish here but recognize that higher trophic level organisms also includes birds, marine mammals, and humans. Higher trophic level organisms such as fish are affected directly by changes in the physical and chemical properties of the ocean (temperature, salinity, and transport), but also by how these changes can directly and indirectly affect phytoplankton, zooplankton, benthos, and other fish that act as prey for piscivores. Transport and food availability during early life stages of fish are especially important because eggs and larval fish are subject to advective transport and their growth and survival are very sensitive to the timing, quantity, and quality of the available food (Lett *et al.* 2009). Mortality is high during the early life stages, and small changes become amplified when compounded over time and influence recruitment (e.g. cod in Gifford *et al.*, Chapter 4, this volume). The potential for indirect effects mediated through food web interactions to become important also presents a challenge. Our understanding of food web dynamics is limited in many situations. Higher trophic levels generally live for multiple years and can utilize a variety of habitats and prey. Thus, their monitoring is difficult but yet we need many years of data in order to be able to see their full responses at the population and community levels and to be able to isolate the responses due to global change versus other factors

that vary and can directly and indirectly affect higher trophic level organisms (Rose 2000).

10.3.3.1 Emergence of higher trophic level responses to global change

While there are examples of single-species analysis of upper trophic level responses to global change (e.g. Drinkwater 2005; Vikebø *et al.* 2007b), there are far fewer studies that involve community responses over broad spatial scales. Perry *et al.* (2005) analysed 25 years of demersal fish species data for the North Sea and found shifts in some of the species. Of the 36 species that were analysed, about half (15 species) shifted their distributional range. These species included commercially exploited and non-exploited species. The distance of the shifts ranged from 48 to 403 km, with an average of 172.3 ± 98.8 km. They found that 13 out of 15 species that shifted went northward, and that many species were able to find cooler temperatures by moving into deeper waters. Species that shifted generally had a faster life history (small-bodied, short-lived, and smaller size at maturity) than non-shifting species (Fig. 10.10). However, individual growth rates did not differ significantly between shifting and non-shifting species. Greve *et al.* (2005) used a 10-year ichthyoplankton dataset for Helgoland Roads to investigate the phenological response of fish larvae to SST change. Eleven of 27 species showed a statistically significant negative correlation (i.e. earlier in the year) to SST (Fig. 10.11) and almost all of the species showed a negative correlation.

Mueter and Litzow (2008) showed that there was a northward shift in the summer distribution of the majority of the fish species on the eastern Barents Sea shelf in response to the pool of cold bottom water ($<2^{\circ}\text{C}$) on the shelf retreating northward by over 200 km between the early 1980s and the early 2000s. This northward expansion resulted in an increase in total biomass, species richness, and average trophic level into the area formerly occupied by the cold pool. While the northward shifts were strongly related to temperature, they could not be explained by temperature alone and showed a non-linear, accelerating trend over time. Such non-linear effects suggested a reorganization of the fish community (i.e. an indirect effect) in response to a shift in average temperature. Understanding such indirect community-level responses of fish to a warming climate challenges our current state-of-knowledge (Mueter *et al.* 2009).

Intuitively, global warming effects on phytoplankton and zooplankton productivity and phenology will have large effects on higher trophic levels, although examples that document such responses are rare. We expect large responses to global change in some situations but it is difficult to find unequivocal evidence from historical analyses. Consideration of the match or mismatch between the timing of plankton blooms and the energy needs of young fish has a long history in fisheries science (Cury *et al.* 2008). Much attention has also been devoted to the mix of the species within the prey because very young fish often need certain sized

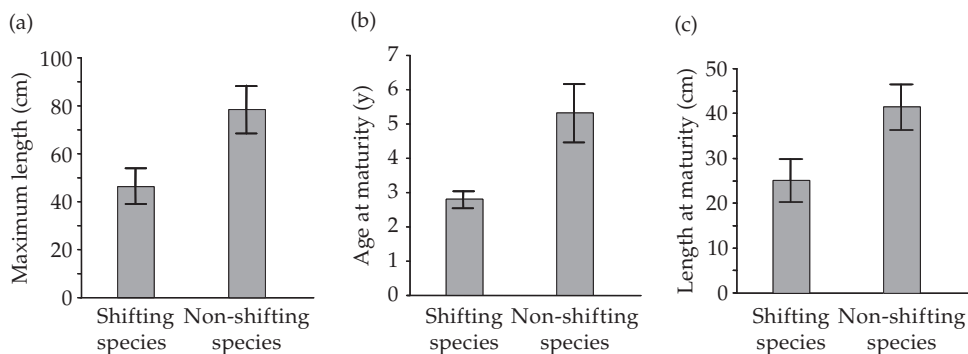


Figure 10.10 Differences in life history traits between shifting ($n = 15$) and non-shifting ($n = 21$) species with respect to centres of distribution (mean latitudes). (a) Maximum body size ($t = -2.41$, degrees of freedom (df) = 34, $P = 0.02$). (b) Age at maturity ($t = -2.86$, df = 27, $P = 0.01$). (c) Length at maturity ($t = -2.29$, df = 29, $P = 0.03$). Means are shown with standard errors. (From Perry *et al.* 2005.)

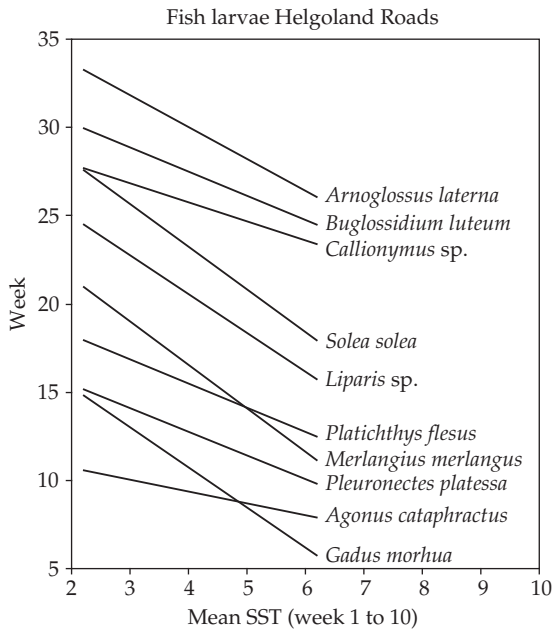


Figure 10.11 Regression lines of sea surface temperature (SST) to phenological timing of North Sea fish larvae. (From Greve *et al.* On the phenology of North Sea ichthyoplankton, ICES Journal of Marine Science, 2005, 62, 1216–23. By permission of Oxford University Press.)

prey during their first days of exogenous feeding to ensure high enough capture rates of energy-rich food (Houde and Schekter 1980; Letcher *et al.* 1996). Beaugrand *et al.* (2003a) documented how a phenological response to warming in the plankton can lead to temporal mismatches between successive trophic levels, and influence commercially important fish species production such as the cod in the North Sea. Kasai *et al.* (1992) found that the advance of the spring bloom in the north-western Pacific has the potential to influence growth and survival of larval fishes. Grebmeier *et al.* (2006) discuss how warmer air temperatures and lower winter ice cover have resulted in a contraction of the summertime cool-water bottom pool and an associated movement of the more southern community dominated by pelagic fish into waters normally characterized by a benthic-dominated (arctic) community.

10.3.3.2 Future projections of higher trophic levels

Projected shifts in spatial distributions of higher trophic levels in response to global change have generally taken a species-centric approach of

examining one or a few species in specific locations. Chavez *et al.* (2003) pointed out the existence of a periodicity of about 50 years in the landings of sardines and anchovies that coincided with variations in the productivity of coastal and open ocean ecosystems and temperature in the Pacific Ocean. They proposed a hypothesis that delineated a warm sardine regime (warm in the eastern boundary) as *El Viejo* (the old man) and a cool anchovy regime as *La Vieja* (the old woman) because of the similarity to *El Niño* and *La Niña* (Fig. 10.12). They drew attention to anthropogenic influences (e.g. global warming or overfishing) that can influence the character of regime shifts. Subsequently, Takasuka *et al.* (2007) proposed a simple hypothesis, called the optimal growth temperature hypothesis, to explain the species alternation between anchovy and sardine. The optimal growth temperature of Japanese sardine larvae is lower than that of Japanese anchovy; hence Japanese sardine will increase and anchovy will decrease during a cooler climate regime (Fig. 10.13). In contrast, the optimum temperature for California sardine is higher than that for California anchovy so that the temperature regimes have an opposite effect and cooler conditions that favour anchovy. The optimum growth temperature hypothesis is able to explain the paradox that the alternation of sardines and anchovies showed synchronicity on opposite sides of the Pacific, while the temperature anomaly showed asynchronicity. Takasuka *et al.* (2007) suggested that although fish might migrate to more favourable habitats, they cannot avoid basin-wide warming expected in the long term under global warming. Thus, historical data suggest that under global warming sardine may face collapse in the north-western Pacific while anchovy may face collapse in the north-eastern Pacific. Sardine and anchovy in upwelling systems (Peru-Humboldt, Benguela, and Canary) contribute greatly to the world's harvest (Schwartzlose *et al.* 1999). The optimal growth temperature hypothesis, developed for the Kuroshio-Oyashio and California Current, needs further evaluation, and whether the hypothesis can be applied to other upwelling regions is not known.

Vikebø *et al.* (2007b) used a temperature-dependent growth model for larval and juvenile cod coupled to a Regional Ocean Modelling System (ROMS; Shchepetkin and McWilliams 2005) circulation

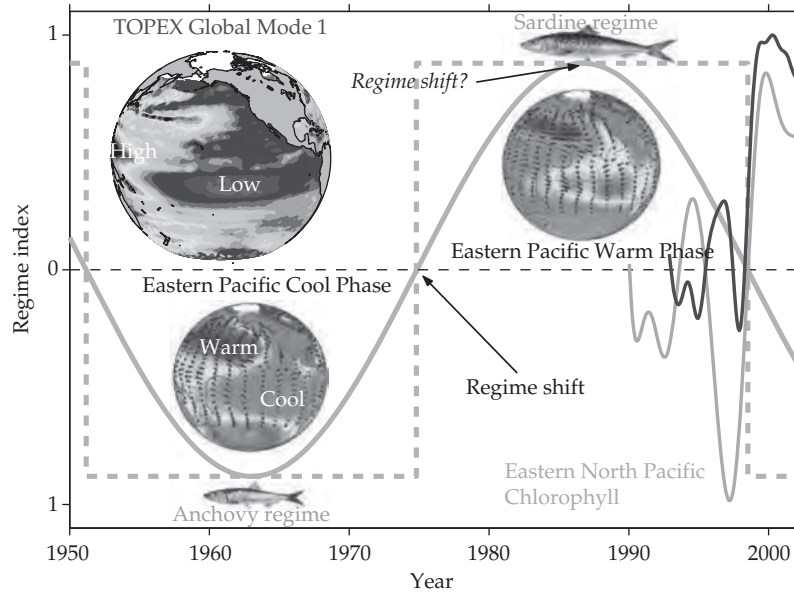


Figure 10.12 Hypothetical oscillation of a regime index with a period of 50 years. From the early 1950s to about 1975, the Pacific was cooler than average, and anchovies dominated. From about 1975 to the late 1990s, the Pacific was warmer, and sardines dominated. The spatial patterns of SST and atmospheric circulation anomalies are shown for each regime (Mantua *et al.* 1997). Some indices suggest that the shifts are rapid (dashed), whereas others suggest a more gradual shift (solid). The first empirical orthogonal function (EOF) of global TOPEX sea surface height (SSH) is shown above the cool, anchovy regime. The coefficient is shown in blue together with surface chlorophyll anomalies (green, mg m^{-3}) for the eastern margin of the California Current system from 1989 to 2001 (Pearcy 2005), also low-pass filtered. (From Chavez *et al.* 2003. Reprinted with permission from AAAS). (See Plate 25).

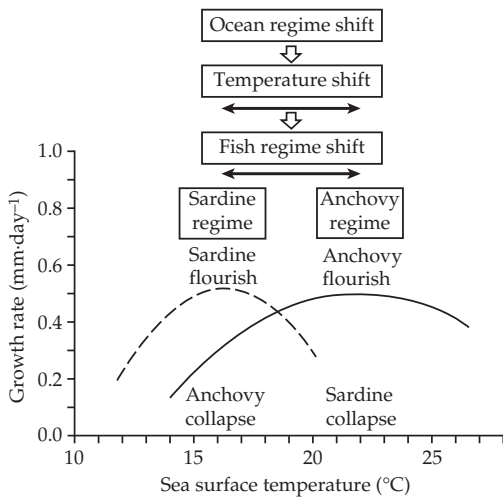


Figure 10.13 Conceptual framework of the optimal growth temperature hypothesis: a potential biological mechanism for the anchovy and sardine regime shifts under the assumption that both types of larvae experience similar temperatures during the same period. Quadratic functions for Japanese anchovy (*Engraulis japonicus*, solid curve) and Japanese sardine (*Sardinops melanostictus*, broken curve) were derived from observations. (From Takasuka *et al.* 2007 © 2008 NRC Canada or its licensors. Reproduced with permission.)

model to simulate growth and distribution of larval cod in the Nordic Seas under a climate scenario of reduced thermohaline circulation. The ROMS circulation model was forced by the Bergen Climate Model (BCM) to simulate the reduced thermohaline circulation by an increase in river run-off to the Nordic Seas and the Arctic Ocean. They found that fewer juvenile cod were transported eastwards in the Barents Sea, and those that were transported were considerably smaller in body size because of the cooler temperature. More juvenile cod were transported to the western parts of Spitsbergen, where today, and likely in the future, conditions are poorer and survival rate is lower than in the Barents Sea.

Drinkwater (2005) projected the expected responses of cod stocks throughout the North Atlantic to future temperature scenarios based upon observed responses of cod to temperature variability (Box 10.1). Population growth rates for many of the cod stocks were hypothesized to increase and lead to an overall rise in the total

Box 10.1 The response of Atlantic cod to future temperature changes

Atlantic cod are distributed throughout the continental shelves around the North Atlantic rim, which includes regions that are expected to experience some of the greatest anthropogenic climate changes. Multi-model scenarios suggest that by 2100 temperature increases of 2 to 4°C are likely in most regions of the North Atlantic occupied by cod, with a maximum increase of 6°C in the Barents Sea (IPCC 2007a). Drinkwater (2005) examined the response of cod to these modelled future warming scenarios. The responses included faster growth rates, larger weights-at-age, reduced age-of-maturity, and a northward spreading of their geographic distribution. He also suggested likely changes in recruitment based on the following two assumptions. First, if future annual mean bottom temperatures are projected to warm beyond 12°C, the cod are assumed to disappear from those regions. This is consistent with present observations that no cod stocks occupy waters with mean annual bottom temperatures exceeding approximately 12°C. Second, recruitment will increase for stocks whose bottom temperatures increase but remain below 5°C, and decrease for stocks whose bottom temperatures exceed 8.5°C. At temperatures between these two values, there would be little change in recruitment. These projected changes in temperature-dependent recruitment are consistent with observations (Planque and Frédou 1999; Drinkwater 2005).

The resulting projection showed decreased or collapsed stocks that depended on the magnitude of the temperature increase. Under a sustained 1°C

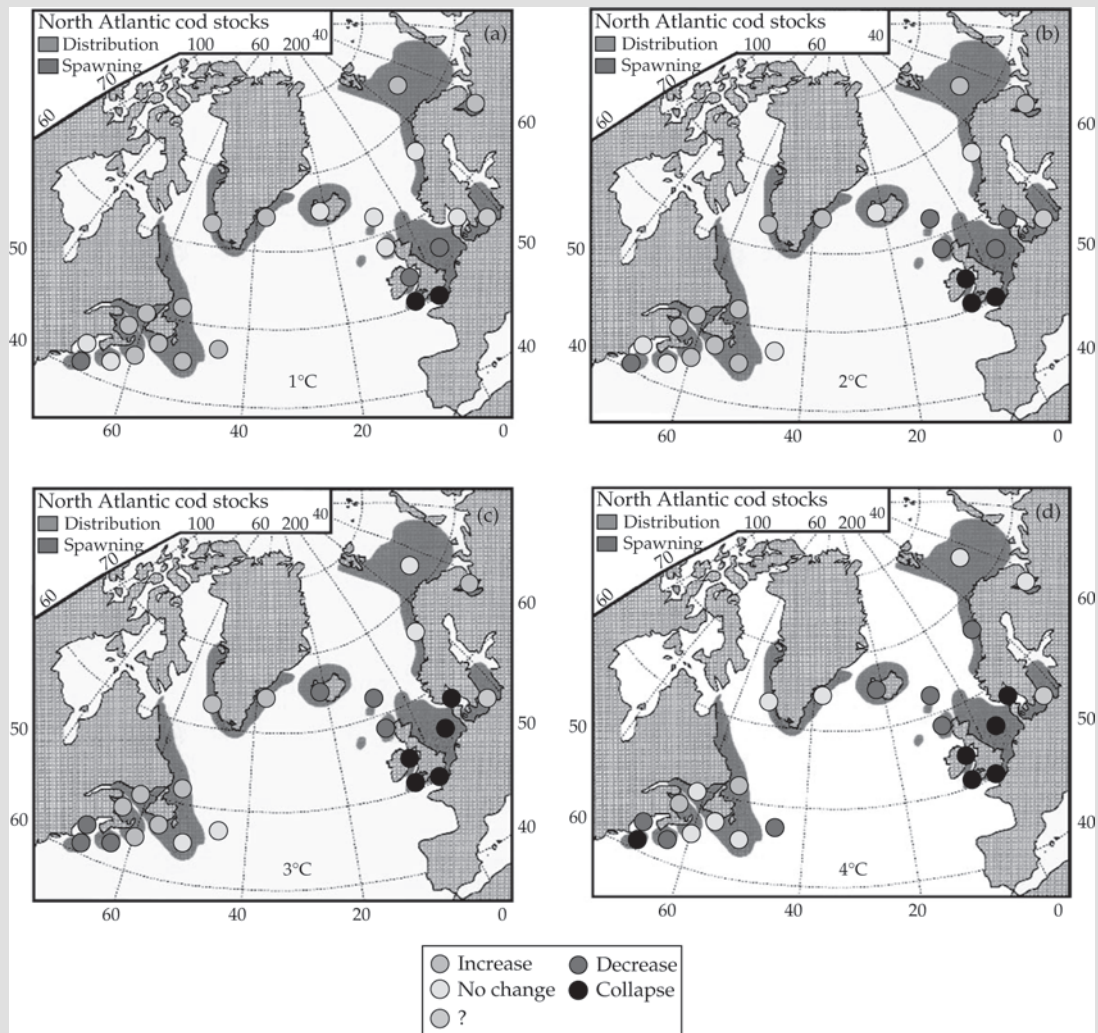
change, several southern cod stocks would decrease or collapse (Box 10.1, Fig. 1a), while cold-water stocks, such as those off eastern Canada, Greenland, and in the Barents Sea, would benefit from increased recruitment. The net result would be an increase in the total production of Atlantic cod. Under greater temperature increases (2 and 3°C), the areas of decrease and collapse were projected to expand (Box 10.1, Fig. 1b and c), especially in the eastern Atlantic, while some stocks were still projected to increase in the western Atlantic. For a 4°C temperature change, however, even the Georges Bank stock in the western Atlantic was projected to likely disappear and regions exhibiting increased stocks were very limited (Box 10.1, Fig. 1d).

While many of these projections of possible changes to the Atlantic cod under future warming are consistent with past observations, the actual response remains uncertain. Indeed, Drinkwater (2005) noted that any projection will depend upon understanding in greater detail the physiological and behavioural responses of the cod to changes in environmental conditions, future fishing intensity, and the responses of other components of the marine ecosystem. Growth rate eventually will decrease at very warm temperatures, and cod movement is the result of a complicated behavioural response of individuals to multiple cues and to gradients and variation in temperature. Cod responses can also be dependent on the changes in primary (phytoplankton) and secondary (zooplankton) production, especially to changes to specific taxa that serve as food for different life stages (*C. finmarchicus* for larval and juvenile cod; capelin for adults).

continues

production of Atlantic cod in the North Atlantic. This was based on the relationship between recruitment anomalies and bottom water temperatures. The relationship derived between temperature and recruitment was consistent with how temperature affects larval growth rates (Otterlei *et al.* 1999; Bjornasson and Steinarsson 2002; Caldarone *et al.*

2003; Buckley *et al.* 2004), and hypothesized advection patterns of *C. finmarchicus* (Sundby 2000), an important prey item for early life stage cod. Buckley *et al.* (2004) suggested that the Atlantic cod, and also haddock, on Georges Bank will decline due to global warming unless accompanied by greater prey availability.

Box 10.1 *continued*

Box 10.1, Figure 1 The expected changes in the abundance of the cod stocks with a temperature increase of (a) 1°C, (b) 2°C, (c) 3°C, and (d) 4°C. Note the changes are relative to the previous change, that is, 4°C represents the changes from those at 3°C. (From Drinkwater. The response of Atlantic cod (*Gadus Morhua*) to future climate change. ICES journal of Marine Science, 2005, **62**, 1327–37. By permission of Oxford University). (See Plate 28).

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Huse and Ellingsen (2008) used an individual-based model to simulate how the Barents Sea capelin would change its spatial distribution related to its spawning migration and selection of feeding areas. They applied the same physical and plankton models as Ellingsen *et al.* (2008) described above,

and used the surface layer values on a two-dimensional spatial grid from a simulation with the IPCC B2 scenario (Ellingsen *et al.* 2008). Movement of larvae was based on currents, while movement of adults was simulated as an evolving process using an artificial neural network with a genetic algorithm.

Multi-generational simulations used the information in the neural network from highest fitness adults to seed the neural network for next generation; movement patterns eventually stabilized. Three 300-year scenarios were simulated that repeated the 1996–2005, 2040–9, and 1996–2049 slices of output from the biophysical model. During warming, the feeding areas were projected to shift northwards as the ice edge retreated. The spawning areas were also projected to shift, from the southern border of the Barents Sea (Finnmark and Murman coasts) to the eastern border of the sea (Novaya Zemlya), and spawning was projected to occur earlier in the year. A similar analysis was also performed under the same IPCC B2 scenario that examined capelin distributions in the years 1990, 2020, 2050, and 2080 (Roderfeld *et al.* 2008).

Global change effects on temperature and horizontal circulation of zooplankton have been projected to cause a mix of effects on Norwegian fishes (Stenevik and Sundby 2007). With increased warming, the advection of *C. finmarchicus*, an important prey for many fish species, would be directed from the Norwegian Sea into the Barents Sea but would decrease in the North Sea (Sundby 2000). While *C. finmarchicus* abundance would decrease in the North Sea, the advection of southern copepod species, such as *C. helgolandicus*, from the Atlantic to the North Sea would increase. Combined effects of warmer temperature and changes in copepod composition would benefit the more southern fish species, such as sardine and anchovy, and decrease the productivity of the boreal fish species such as herring and cod. Stenevik and Sundby (2007) also projected that, under global warming (assuming warmer temperature, higher *C. finmarchicus*, and decreased sea ice), boreal fish production (e.g. cod) in the Arctic marine ecosystem of the Barents Sea would be expected to increase, with species distributions expanding northward and eastward. Fishery catches in the Russian and Norwegian sectors of the Barents Sea would therefore also likely increase.

Changes in upwelling would likely affect prey availability to fishes. Upwelling regions are areas of high fish production, and where increased upwelling and uplifted thermoclines are expected under global warming (Auad *et al.* 2006), we would expect enhanced primary production and a likely increase in

the prey available to planktivorous fishes. However, offshore transport of larvae will also be modified under global warming. Auad *et al.* (2006) projected increased offshore surface transport of fish larvae, such as Pacific sardine, in the spring in the northern part of the California Current system, while onshore transport in winter and summer in the southern part increased. Offshore waters had lower prey densities.

Ito (2007) simulated the effects of changes in temperature and local vertical mixing on Pacific saury (*Cololabis saira*) growth and survival (Box 10.2). A simple three-box model, in which local vertical mixing strength was defined by the temperature difference between the surface and subsurface layer, was coupled to a nutrient-phytoplankton-zooplankton model (NPZ)-fish bioenergetics model called NEMURO.FISH (NEMURO for Including Saury and Herring; Ito *et al.* 2004, Megrey *et al.* 2007b). Saury growth rate, body size, and survival were followed as they seasonally migrated among the three spatial boxes. Changes in temperature affected the saury directly through bioenergetics (growth) and movement, and changes in temperature and vertical mixing affected the saury indirectly via their effects on primary and zooplankton production and thus prey availability to saury. Increases in temperature expected under future anthropogenic climate change caused the saury to alter their migration patterns, during which they experienced reduced food and slower growth.

Changes in horizontal transport would clearly affect egg and larval transport under future climate change, but general statements as to their effects on fish growth and survival depend on the species and ecosystem. One can envision a variety of future scenarios, but these need to be evaluated on a case-by-case basis. For example, Sakamoto *et al.* (2005) projected an acceleration of the Kuroshio Current system. Many fish species, including sardine, saury, and predatory fish (tuna) spawn in the upstream region of the Kuroshio, and their eggs and larvae are advected to the nursery grounds by the Kuroshio. Therefore, an intensification of the Kuroshio would likely cause greater distribution of the larvae. What is uncertain is how such changes in distribution would translate into changes in growth and survival.

Multi-species approaches that attempt to include some of the interspecific interactions in their

projections of global change effects on higher trophic levels are relatively rare in marine systems. Spatial Environmental Population Dynamics Model (SEAPODYM; Lehodey *et al.* 2003) is an example of a multi-species model that simulates the population dynamics of three tuna species (skipjack, *Katsuwonus pelamis*; yellowfin, *Thunnus albacares*; and bigeye, *T. obesus*) and their forage fish species. SEAPODYM combines physical, biochemical, forage, and fish population dynamics. Lehodey *et al.* (2007) used an updated version of SEAPODYM, which includes an

enhanced definition of habitat indices, movement, and accessibility of tuna predators to different vertically migrant and non-migrant micronekton functional groups, to project the potential impact of climate change on the bigeye tuna population. The simulation was driven by physical-biogeochemical fields projected from a global earth system simulation (Bopp *et al.* 2001) with parameterizations obtained for bigeye tuna in the Pacific Ocean using optimization techniques (Senina *et al.* 2008) and the historical catch data for the last 50 years. Projections

Box 10.2 Projection of Pacific saury response

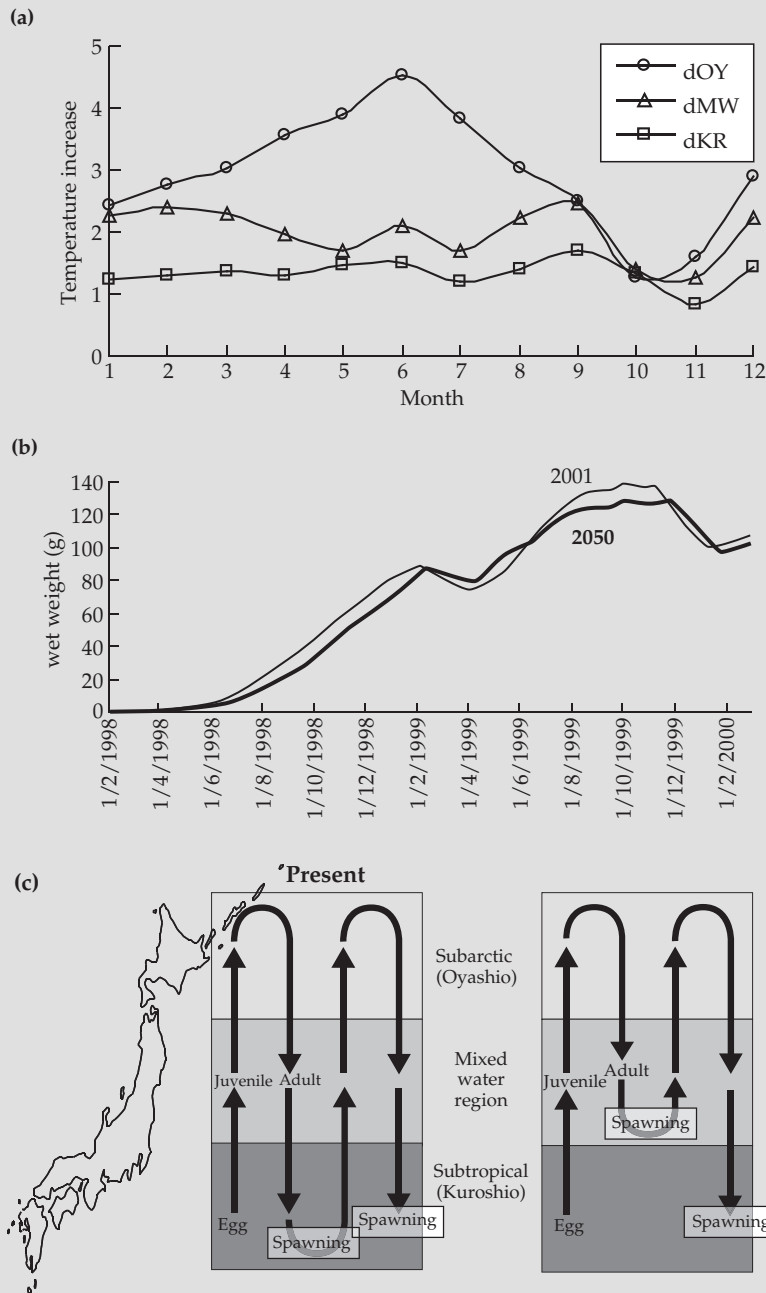
The response of Pacific saury to future climate change was explored using the NEMURO.FISH model by Ito *et al.* (2007). A simple three-box spatial model including physical, biochemical, and plankton dynamics was constructed with saury migrating among the boxes. Fish growth was calculated according to a bioenergetics equation using the simulated plankton from the lower trophic model as food. The SST input to the model was obtained from a global warming scenario (IPCC A2) simulation of an atmosphere-ocean coupled general circulation models (AOGCM; Sakamoto *et al.* 2005). The simulated SST in years 2001, 2050, and 2099 was averaged for the Oyashio (subarctic) region, the mixed water region, and the Kuroshio (subtropical) region. SST anomalies were calculated by subtracting monthly mean SSTs in 2001 from those in 2050 and in 2099 (Box 10.2, Fig. 1a). These anomalies were added to observational climatological SST and used as input to the saury version of the NEMURO.FISH model.

The model suggested that the body weight of saury will decrease with increased temperature (Box 10.2, Fig. 1b), but it was likely that there would be increased survival. Reduced body weight resulted from lowered zooplankton densities due to reduced primary production in a shallower mixed layer. The decrease in nutrient supply from

the subsurface layer to the surface due to warmer winter conditions exceeded any positive direct effect of temperature on phytoplankton production. Reduced food and higher metabolic rate resulted in slowed growth of adult saury, which triggered a change in their size-based migration patterns. Larger saury migrate to the north earlier than smaller saury because they can tolerate colder water, and the critical temperature below which saury start to migrate southward is higher for larger fish. The warmer temperatures in the mixed water region under global warming allowed smaller saury (young-of-the-year) to remain in the north and not migrate back to the south (Box 10.2, Fig. 1c). The higher prey density in the mixed water region compared to the Kuroshio region enabled faster growth and saury body sizes that were similar to baseline values by February of the first winter when saury started to spawn. Similar body size and higher food resulted in higher egg production. However, the life span of Pacific saury is 2 years and when age-1 fish repeated the northward migration in their second year, their body weight decreased by about 10 g (about 8% of final body weight) because they experienced reduced prey densities during their migration. The net effect of these changes would likely be an increase in saury abundance but with reduced individual weights.

continues

Box 10.2 continued



Box 10.2, Figure 1 (a) The temperature anomaly (°C) in 2050, relative to 2001, used as the forcing of the NEMURO model (circles for the Oyashio region, triangles for the mixed water region, squares for the Kuroshio region, respectively). (b) Wet weight (g) change of Pacific saury calculated by NEMURO.FISH (thin line for 2001 and thick line for 2050). (c) Schematic picture of simulated migration pattern of Pacific saury in the present (*left*) and in future (*right*). The saury migrate from the subtropical to the subarctic for feeding during spring-autumn and migrate back to the south during autumn-winter and spawn during autumn-winter in the mixed water region and subtropical. However, under global warming conditions, the migration pattern was modified especially in the spawning migration in the first winter. (From Ito 2007.)

of future changes in bigeye tuna population dynamics were developed based on the IPCC A2 emission scenario. The model suggests an increase in the bigeye tuna population in the eastern Pacific because increased temperatures approached the tuna's preferred temperature range, while the western bigeye tuna population would decrease (Fig. 10.14).

Salmon utilize freshwater, coastal areas, and the open ocean, and thus provide an exceptionally difficult challenge for projecting their population responses to global change (Box 10.3). In order to fully express global change effects, models that simulate the entire life cycle are needed. Representing the full life cycle (birth to death, with survivors producing the new young each year) allows for effects to accumulate through the different life stages. For example, warmer temperatures could have mixed effects on sockeye salmon during their lake phase, and positive effects in the short term but negative

effects in the long term during their migration to the ocean (Box 10.3).

We have taken a narrow view of higher trophic levels by focusing on fish, and some models consider other higher trophic organisms including humans (see Perry *et al.*, Chapter 8, this volume). In the context of modelling fish responses, we may need to take into account the economic impacts of global warming and its feedback on fisheries. Eide and Heen (2002) used a coupled fishery-economics model for northern Norway and projected how the fishery and cod and herring populations would respond to global warming scenarios. They used a biologically simple multi-species population model (focused on recruitment) coupled with a model of the multiple fishing fleets (ECONMULT); the economic factors that were simulated used an input-output approach. Warm and cold future states were simulated. The warm state was created by changing the atmospheric

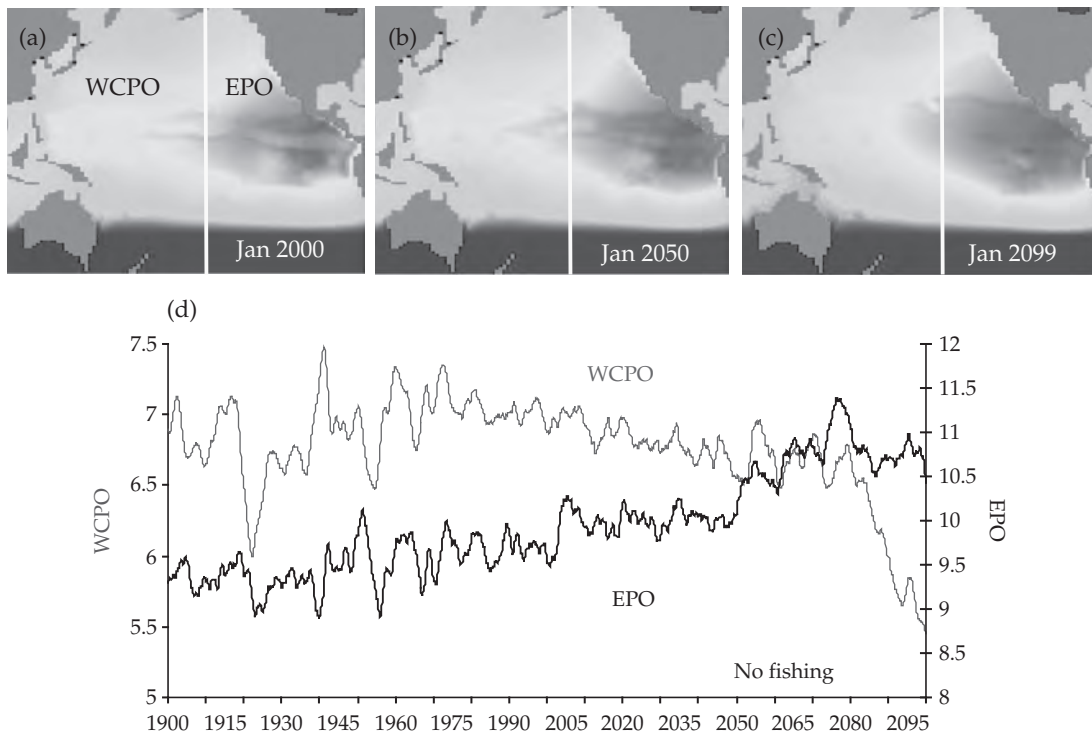


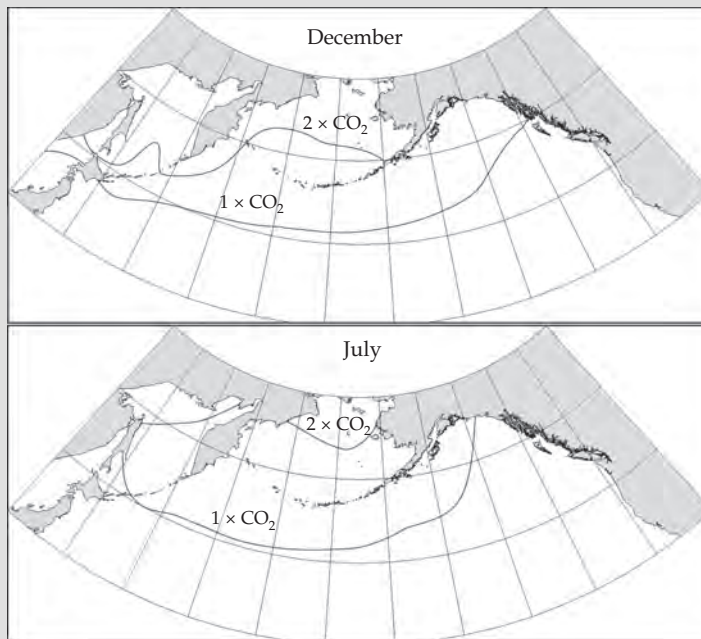
Figure 10.14 Predicted spatial distribution of bigeye tuna biomass in the Pacific Ocean (a) current, (b) in 2050 and (c) in 2099 under a global warming scenario, and (d) comparison of predicted biomass (million tons) of bigeye tuna in the western central (WCPO) and eastern (EPO) Pacific Ocean under a climate change scenario (without fishing). (From Lehodey *et al.* 2007). (See Plate 26).

Box 10.3 Salmon migration and bioenergetics

Pacific salmon *Oncorhynchus* spp. live for 1–2 years (and can live for up to 4 years) in freshwater before migrating to the ocean, where they spend the next 1–3 years. Welch *et al.* (1998) showed a sharp boundary of sockeye salmon distribution defined by temperature. They suggested that food was always limiting, and that salmon growth was very sensitive to temperature. Based on the observational results, they projected the future distribution of sockeye salmon in the North Pacific (Box 10.3, Fig. 1). Warmer temperatures in the North Pacific are expected to reduce salmon growth in the ocean. Weaker winter convection and increased glacial run-off to lakes and rivers will increase turbidity and thereby decrease prey production in freshwater lakes. These two negative effects will lead to a decline in the productivity of sockeye salmon (Melack *et al.* 1997).

Schindler *et al.* (2005) suggested that warming could have positive effects on sockeye salmon during their lake phase. They suggested that warmer conditions would bring an earlier spring ice breakup and induce a more rapid seasonal temperature rise, thereby enhancing prey for juvenile sockeye in lakes. Therefore, they projected that global warming may enhance growth conditions for juvenile salmonids in large lakes of Alaska.

Rand *et al.* (2006) focused on the energy costs of the spawning migration and applied a bioenergetics model. Their model successfully reproduced the observed energy loss of sockeye during the spawning migration from ocean to the spawning area (about 1200 km upstream). They projected that higher temperatures and higher discharge would enhance energy loss of salmon during freshets. As a result, expected future reductions in



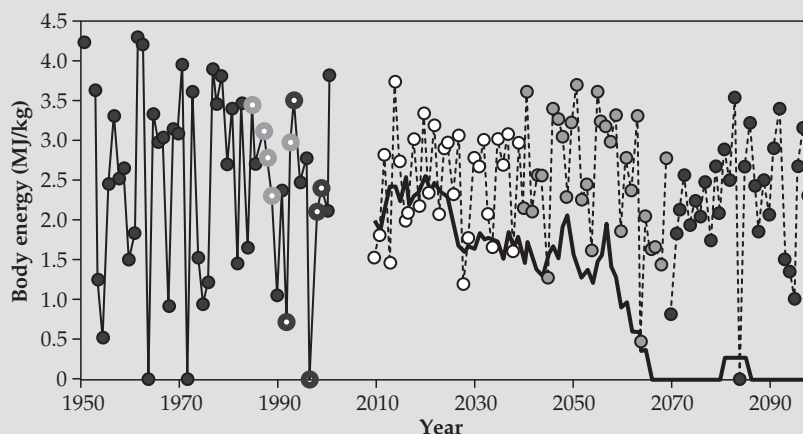
Box 10.3, Figure 1 Comparison of the predicted winter (7°C) and summer (12°C) positions of the sockeye salmon distribution under current and future climates (Albers equal area projection). Under a doubling of atmospheric CO₂ the area of acceptable thermal habitat in the North Pacific is predicted to decrease to 0 in summer and decline sharply in winter. The predictions are based on the Canadian Climate Centre's coupled ocean-atmosphere general climate model (Boer *et al.* 1992; McFarlane *et al.* 1992). (From Welch *et al.* 1998. © 2008 NRC Canada or its licensors. Reproduced with permission.)

continues

Box 10.3 continued

peak flows during freshets under global warming would reduce transit time to the spawning ground, resulting in an energy savings that compensated for the increased metabolic rates under warmer temperatures. However, if the body

mass of sockeye salmon at the beginning of the spawning migration was smaller (Welch *et al.* 1998), then their model suggests a decreased fitness during the river migration that could jeopardize their sustainability (Box 10.3, Fig. 2).



Box 10.3, Figure 2 Simulated time series of body energy for early Stuart sockeye salmon (Fraser River, British Columbia) at the spawning ground during 1950–2001 and 2010–99. With respect to the first period, note the 10 years identified with open circles, of which the five with heavy black borders represent years of high *en route* mortality and the five with heavy grey borders represent years of low *en route* mortality. Three climate stanzas are shown for the second period. Simulation results from the future scenario involving a long-term decline in the body mass of sockeye salmon at the beginning of the migration are shown with a solid black line (plotted as a 5-year running average of model output). (From Rand *et al.* 2006.)

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forcing and increasing prey production and cod, and herring growth and recruitment, while the cold state future was assumed to occur from a reduction of warm Atlantic water masses inflowing to the Barents Sea with negative effects on cod and herring growth and recruitment. Model projections showed increased stock, catch, profit (wage paying ability), and flow of profits for the warm state, and decreased values for the cold state. Without fisheries management, the increase in catch in the warm state was more than the decrease in catch in the cold state. Under some fisheries management strategies, however, the opposite was predicted: the decrease in the cold state exceeded the increase in the warm state. The range of responses was generally larger among different management

strategies than between different environmental scenarios. Thus, projections of fish population responses to global change can be affected by the fishery and by economics.

10.4 The future and challenges

The development of modelling tools capable of projecting the effects of global climate change on zooplankton and higher trophic levels has lagged behind those for nutrients (biogeochemical cycling) and physics. As documented above, the effects of global change are already being observed and thus there is a need for more and improved forecasting tools. GLOBEC and related studies have laid a

sound foundation for how to proceed to project marine ecosystem responses to likely future climate conditions. The shift from trying to understand past and current conditions to projecting ecosystem responses to previously unobserved, and somewhat uncertain, future conditions is a major challenge.

In this section, we look at the big picture issues of what is needed in the long term to develop models for the general problem of predicting ecosystem responses to future global change. We grouped the issues into the categories of mechanistic approaches, physical modelling, nutrients and phytoplankton, zooplankton and higher trophic levels, and resource management. We also focus here on fish as the higher trophic level organisms, but acknowledge that birds and marine mammals are also of great interest.

10.4.1 Mechanistic approaches

Our discussion of the next steps centres on issues related to advancing mechanistic approaches over scenario and empirical approaches (see Box 10.4). All three approaches will be required to tackle the prob-

lem of developing credible projections of ecosystem responses to global change. We envision scenario and empirical approaches as being especially useful for certain specific situations (e.g. the short-term response of a very well-studied process or species in a well-monitored location), and for broad-scale semi-quantitative analyses of processes. For example, Cheung *et al.* (2009) combined an empirical approach with simple logistic population models to project how invertebrate and fish biodiversity would change worldwide under global warming. Scenario and empirical approaches will be useful for constraining the problems that then should be investigated using mechanistic approaches; what processes and variables appear to be important and need to be included in the mechanistic models. However, as the problem requires projecting ecosystem responses on basin or similar spatial scales and for decades or longer, scenario and empirical approaches are often pushed beyond their domain of applicability, leading to the increasing reliance on mechanistic approaches that combine physical and biological simulation models. The use of mechanistic approaches has its costs. Mechanistic approaches

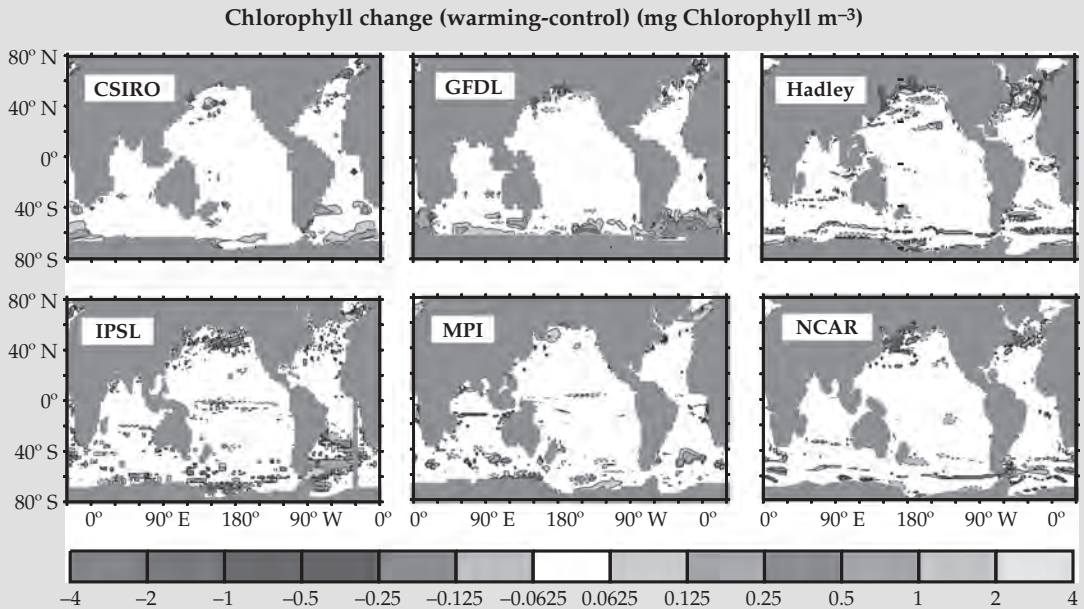
Box 10.4 Empirical modelling approaches for projecting primary production

We can categorize the approaches to projecting future marine ecosystem responses into three groups (Sarmiento *et al.* 2004): (1) mechanistic models of marine ecosystems, (2) scenario projections based on phenomena observed in the past, and (3) empirical model development based on statistical descriptions of observational data. Mechanistic models offer the best opportunity for projecting ecosystem responses under previously unobserved conditions, and these models have been improved greatly during the GLOBEC era (Chapter 5, deYoung *et al.*, this volume). The models of Boyd and Doney (2002), Bopp *et al.* (2005), and Hashioka and Yamanaka (2007) summarized in the text are examples of what we consider to be mechanistic approaches. Scenario projections are tempting because they rely on empirical observations but often generate

projections with little or unknown confidence because of the many possible differences between historical phenomena and future conditions. Here we focus on the empirical modelling approach.

Sarmiento *et al.* (2004) developed an empirical model to project chlorophyll and primary production using SST, surface salinity, surface density, upwelling, vertical density gradient at 50 m depth, mixed-layer depth, and sea-ice cover. They divided the world's ocean ecosystems into seven biomes and developed separate statistical models for each biome. Satellite-based chlorophyll data were used to estimate the parameters of the statistical models. They applied the statistical models to projected future conditions under global warming generated by atmosphere-ocean coupled general circulation models (AOGCMs). Major results were:

continues

Box 10.4 continued

Box 10.4, Figure 1 Simulations of the impact of global warming on the chlorophyll concentration in mg m⁻³. Chlorophyll is calculated for both the control and the warming simulations using the empirical model. The figure shows the difference between the warming simulation and the control simulation averaged over the period 2040 to 2060 (except for Max Planck Institut (MPI), which is for the period 2040 to 2049). Areas in white are those for which the chlorophyll change is smaller than ± 0.0625 mg m⁻³. (From Sarmiento *et al.* 2004). (See Plate 27).

- (1) Decreased chlorophyll in the North Pacific primarily due to the retreat of the marginal sea-ice biome.
- (2) Possible increased chlorophyll in the North Atlantic due to a complex combination of factors.
- (3) Increased chlorophyll in the Southern Ocean due to the retreat of the marginal sea-ice zone and to changes in its northern boundary.
- (4) Possibly decreased chlorophyll adjacent to the

Antarctic continent due to freshening within the marginal sea-ice zone (Box 10.4, Fig. 1). The net effects of these changes were that global warming was projected to increase primary production by 0.7 to 8.1%, although the uncertainty was large due to differences among the various AOGCM models in their projected future conditions.

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require extensive data, can be computationally challenging, difficult to validate, and involve trying to mesh together processes that operate on many different spatial and temporal scales.

10.4.2 Physical modelling

Physical models are continuously evolving towards a higher fidelity representation of the climate sys-

tem (Trenberth 1997). Some of the improvements stem from more accurate and efficient numerical solution schemes (e.g. time-stepping and advection; Shchepetkin and McWilliams 2005; Haidvogel *et al.* 2008), improved sub-grid-scale parameterizations (e.g. mixed-layer-depth computations, meso- and sub-mesoscale features; Gent and McWilliams 1990; Large *et al.* 1994; Fox-Kemper and Ferrari 2008), and a better understanding of the climate system feedbacks (e.g. clouds and aerosols;

Trenberth 1997). An ensemble approach is often used to quantify uncertainties in the climate projections. In the ocean, models have tended towards finer resolution grids, and the nesting of grids to allow for coverage of broad spatial areas while having finer resolution where it is needed. Highly skilled oceanographic models are now also being developed for near-shore areas (e.g. estuaries and upwelling regions) where fish productivity is high (e.g. Houde and Rutherford 1993; Cury *et al.* 2008). Even with their sometimes high degree of uncertainty, oceanographic physical models are ahead of the biological models in attempting to project responses to climate change. As summarized above, physical models are using global climate change scenarios as inputs (e.g. IPCC outputs) and projecting subsequent changes in ocean properties such as vertical and horizontal circulation patterns, stratification, temperature and salinity distributions, and sea-ice cover.

The challenge for physical models is to evolve in directions that lead not only to improvements in the representation of the physics but also to account for the needs of the biological models that rely on the outputs of the physical models. From a physical ocean point of view, this means an explicit representation of a wider range of relevant spatio-temporal scales. For example, for physical models to provide useful information for the estimation of near-shore fish production, the physical model needs to resolve the shelf and coastal morphology (bathymetry and coastline) on relatively fine temporal and spatial scales. Physical models also need to be linked to high-resolution atmospheric and hydrological models in order to resolve variation in biologically important mesoscale processes related to ocean fronts, coastal upwelling, and river run-off. Furthermore, this fine-scale variation needs to be part of decadal-long integrations. Decadal simulations are necessary in order to explore low-frequency environmental conditions and their effects on higher trophic levels. Finally, we need to anticipate the inclusion of new processes (e.g. acidification) and 'new' micronutrients (e.g. iron), and others yet to be determined.

One approach that is being used to achieve high-resolution climate-scale simulations in a given domain is the nesting of a high-resolution limited

area grid within a lower resolution large-scale numerical domain. Traditionally, for hindcast simulations, information is downscaled from the coarse-resolution region to the fine resolution region through an overlap in the domains. Downscaling works well when the forcing data are constrained by observations, such as in the reanalysis products (e.g. Curchitser *et al.* 2005; Hermann *et al.* 2009). The high-resolution nest can explicitly resolve features missing from the large-scale model, though it is still constrained through the boundaries by the large-scale circulation patterns. However, when making a future projection, the forcing functions are unconstrained by data and can be expected to respond differently to an alternative (high-resolution) ocean in the coupled model. One of the challenges, then, is to not only downscale information to the local scales, but also to understand how regional changes affect the global climate (i.e. upscaling). Furthermore, if we consider the interaction between the climate system and higher trophic levels, high-resolution nests need to be designed so as to permit large-scale spatial shifts in the distribution of biota as the climate changes.

Another challenge that needs to be addressed by global and downscaled model projections of future conditions is the estimation of uncertainties in the computations. The IPCC approach for global models is to create a super-ensemble of all the available models; that is, each individual model creates an ensemble of runs which are then assembled to a multi-model super-ensemble. Based on the super-ensemble, the assessment report assigns uncertainties to the projections (e.g. highly likely, very likely, etc.). In general, confidence limits given by ensemble modelling may be artificially narrow if the models all use similar assumptions and parameterizations, which do not reflect the full underlying uncertainty. An important question is how to use this information on uncertainty to initialize and force optimal downscaled regional projections, whose output is very relevant to biological modelling. Ådlandsvik (2008) suggested that initialization for regional studies should be derived from more than a single model. Overland and Wang (2007b) evaluated the collection of IPCC models for their suitability to force regional models of the North Pacific and the Barents Sea. They used criteria

based on each model's ability to reproduce known patterns of the current climate in a particular geographic region and on the assumption that present-day skill is indicative of future performance. They concluded that some models are considerably more skillful in the North Pacific and the Barents Sea and thus their individual ensembles should be favoured for forcing regional models. The corollary is that many of the models, when evaluated regionally, were not suitable for forcing downscaled models of specific regions.

Considerations of using models for coupled ecosystem-physical projections may also influence the choice of the large-scale models employed for downscaling. For example, in the North Pacific, some biological activity is related to the PDO, which is based on the dominant mode of variability in SST anomalies (Mantua *et al.* 1997). In other regions, variability in stratification may correlate better with biological activity than with SST, and indeed global models may show different skill levels for different variables or statistical modes. Determining which large-scale models to use for specific downscaling situations, and quantifying their associated uncertainty, will require observational networks that allow for rigorous evaluation of the models.

10.4.3 Nutrients and phytoplankton

Several issues emerge as mechanistic models of nutrients and phytoplankton dynamics are pushed towards simulating global climate change. To date, the focus has been on biogeochemical cycling of nutrients and primary production (Anderson 2005; Le Quéré *et al.* 2005). Some suggest that commonly used formulations for nutrient limitation and nutrient ratios are not always appropriate for biogeochemical cycling and predator-prey interactions (Flynn 2005). Ecological stoichiometry (Andersen *et al.* 2004) will become especially important as we push the models towards conditions (global climate change) well outside of their domain of calibration and validation. In addition, the inclusion of micronutrients, such as iron, and new biogeochemical considerations such as acidity, have stretched the available data (Hood *et al.* 2006). A long-standing issue is how to represent the effects of multiple

nutrients on primary production (Tilman *et al.* 1982; Flynn 2003; Vallina and Le Quere 2008); adding micronutrients to the possible limiting factors highlights the uncertainty on how to simulate their cycling and how to combine multiple nutrients into an overall effect on photosynthesis. For some quantities, inclusion of more detailed phytoplankton (and zooplankton) may be needed (Hood *et al.* 2006), and even inclusion of higher trophic level effects may be needed to ensure realistic simulation of biogeochemical cycling (Hood *et al.* 2006; Wilson *et al.* 2009).

For some short-lived species (e.g. phytoplankton) with rapid turnover times, adaptation via evolutionary processes can become important to accurately predict their distributions and productivity (Fussmann *et al.* 2003; Yoshida *et al.* 2003). The trade-offs among species traits as environmental conditions change affect community structure (Litchman and Klausmeier 2008). Follows *et al.* (2007) used a typical NPZD model formulation, applied globally by coupling with a three-dimensional physics model, but with key parameters of the phytoplankton species related to nutrient, light, and temperature randomly assigned within allometric constraints. They then did 10-year simulations with repeating annual environmental conditions to determine which phytoplankton types (defined by their parameter values) would comprise the phytoplankton community and contribute to primary production. Patterns of phytoplankton types were robust to different initial conditions and other variation, and roughly corresponded to the types of phytoplankton communities found in different regions. The Follows *et al.* (2007) approach allowed for self-organization among a wide range of fixed phytoplankton types, but did not allow for adaptation during the simulation. Global change will occur over long time scales relative to the generation times of phytoplankton, therefore evolutionary adaptation may need to be considered in multi-decadal projections.

Representation of the phytoplankton community with a few functional groups may need to be reconsidered as more nutrients and processes are added to the models and the models are asked to simulate a variety of systems. With broad questions that do not focus too closely on specific regions, a single

formulation of a NPZD can be used for a global analysis (e.g. Moore *et al.* 2001; Aita *et al.* 2003; Le Quéré *et al.* 2005), including very simple models that use adjustments to approximate a more complex community structure (e.g. Denman 2003). However, recent experience with the NEMURO NPZD model illustrates the fundamental trade-off we must make between generality and accuracy (*sensu* Levins 1966) when building ecological models. As the NEMURO model was applied to different areas and systems, adjustments were made to accommodate regional conditions, resulting in a dozen or more versions of the NEMURO NPZD model being in use (e.g. Yoshie *et al.* 2005; Wainwright *et al.* 2007; Werner *et al.* 2007a). Friedrichs *et al.* (2007) compared NPZD models of differing complexity for a standard water column configured for two different sites (equatorial Pacific and Arabian Sea) with all models using the same physics and concluded that simple models performed well when applied to single sites but that complex models were more portable.

We also expect the classical formulation of NPZD models to be challenged. A major overhaul of how the phytoplankton community is represented may be needed to accommodate what we anticipate to be changes in the formulation of the zooplankton. As discussed below, we envision the development of end-to-end models that combine the physics, nutrients, phytoplankton, zooplankton, fish, other higher trophic levels, and people into a single model or series of tightly coupled models. The role of zooplankton will change from primarily ensuring realistic chlorophyll to having to ensure realistic pathways of carbon transfer from the primary producers to food for fish and higher trophic levels. This will involve more detailed representation or alternative formulations of the zooplankton (e.g. more groups; size, stage, or individual-based approaches), and thus will likely require substantial changes in how the food of the zooplankton (i.e. phytoplankton) is represented.

10.4.4 Zooplankton, higher trophic levels, and end-to-end models

We expect that the mechanistic approach taken to date, and exemplified by GLOBEC, of focusing on

target species of zooplankton and fish in certain locations (deYoung *et al.* 2004a; Gifford *et al.*, Chapter 4, this volume) will continue into the future. The target species approach has been used for decades in fisheries and ecology, and has been further championed by GLOBEC. Analyses of field and long-term monitoring data, and the development of coupled biophysical models, will continue. Such approaches are needed because there will always be global change questions that are best addressed with single species and life-stage-specific models. There will be gradual improvements in the physics and a slow expansion of lower food web complexity and further inclusion of higher trophic levels, and these analyses will continue to serve a vital role in increasing our understanding of ecosystem responses to climate change.

A challenge always associated with the target species approach is how to extrapolate the methods and results to other species and to other locations. Can the results be transported or are the methods general and thus data collection and models must be replicated at each new site? The issue of extrapolation has a long history as part of how results, whether modelling or empirical, can be generalized, and we expect progress will continue in this area.

While the target species approach has been successful and extrapolation questions will continue to be addressed, this approach is better designed for examining past and current conditions rather than future conditions. Past and current conditions can be used to constrain what is needed in mechanistic models and what aspects can be reasonably treated as fixed versus dynamic. Working within the past and current conditions allows for a much more constrained problem, and for more confidence that the model structure is realistic for the new conditions in model simulations of the future. Using models to project for global change puts enormous demands on the models for a greater range of possible effects and responses. We foresee a new generation of 'end-to-end' or 'physics to fish to fishers' models (Travers *et al.* 2007) that allow for food web interactions, community composition shifts, feedbacks, and thresholds responses, all of which can be beyond the capabilities of the single-species approach.

Several things have converged making the development of end-to-end models a possibility. Ever increasing computing power is continuing to relax

computing limitations. Recent advances in physical modelling now allow for simulation of mesoscale features within broad geographic regions, while at the same time permitting multi-year simulations. We are quickly approaching the situation of being able to generate sufficient years of simulation of the high-resolution physics to allow for full life cycle models of higher trophic levels. There have also been advances in higher trophic level modelling, such as size-based and individual-based approaches that permit more realistic representation of multi-species population dynamics than the classical biomass-based approach (DeAngelis and Mooij 2005; Rose and Sable 2009). On the data side, the availability of more and more detailed data (e.g. genetics, spatially resolved measurements), especially on movement of animals (e.g. acoustic and sonic tagging) is rapidly expanding. Finally, concerns about declining fish populations, demands for ecosystem-based management, and the uncertainty of ecosystem health under global warming add a sense of urgency to the development of end-to-end models.

Understanding feedbacks and thresholds within the ecosystem is necessary for accurate projections of future ecosystem states. Short-term forecasts may avoid the necessity for inclusion of slow-reacting feedbacks, but the long-term projections needed for assessing responses to global change require that the appropriate feedbacks are included in order to ensure realistic projections. Feedbacks often become important drivers, and sometimes can dominate ecosystem responses when complex systems are integrated over long time scales. Feedbacks can be purely physical (e.g. air-water exchanges), density-dependence processes of organisms (populations hitting life cycle bottlenecks that result in non-proportional responses; deYoung *et al.*, Chapter 5, this volume), indirect responses due to changes in interspecific interactions (food web effects), coupling of pelagic and benthic pathways, evolutionary adaptations of rapid turnover biota (e.g. Follows *et al.* 2007), and treating humans as part of the ecosystem so that the environment and humans affect each other dynamically (Perry *et al.*, Chapter 8, this volume).

Density-dependent responses of growth, mortality, and reproduction are critical for projecting fish and other higher trophic level population responses because they can operate as a feedback response

and modulate the more direct effects of global change. For example, an increase in egg mortality due to warmer temperatures can be offset, or compensated for, by less crowded conditions in a later life stage leading to a decrease in mortality in that stage. Despite the importance of density-dependence for understanding and managing fish stocks and its intense study for decades, it remains a major unknown and source of controversy (Rose *et al.* 2001). Inclusion of density-dependent processes in higher trophic level organisms can also create computing issues because density-dependence requires simultaneously solving the equations of state of the food, fish, and their predators. Knowing the relative roles of bottom-up, top-down, and wasp-waist controls (Field *et al.* 2006; Bakun 2006b; Cury *et al.* 2008) is also vital for making and understanding accurate projections. The feeding interactions among a large suite of members of the food web are complex but potentially may need to be represented for long-term projections of higher trophic level responses.

We also need to include humans in the models as fully fledged members of the ecosystem (Brander *et al.*, Chapter 3; Perry *et al.*, Chapter 8, both this volume); we cannot assume a fixed fishing mortality rate or that people will maintain their identical behaviour under global change. Models are needed that can simulate density-dependent responses when they are important and allow for threshold responses in order to minimize surprises under previously unobserved future conditions. Threshold responses include abrupt changes in the ecosystem state (e.g. regime shifts), and previously rare species blooming under the new environmental conditions (e.g. jellyfish).

A major challenge will be how to represent behavioural movement of higher-level organisms (Tyler and Rose 1994). The spatial dynamics of higher trophic level organisms determine their exposure to environmental conditions, and we need to model changes in movement behaviour in response to global change in order to determine how the changes in physical and chemical properties and in the other biota will affect the growth, mortality, and reproduction of the higher trophic level organisms (Lett *et al.* 2009). The passive particle approach used for eggs and larvae is not appropriate in many situations for juveniles and adults. The modelling

approach must accommodate ontogenetic (larvae to juvenile to adult) changes in movement abilities, preferences, and tolerances. How to realistically simulate the movement-related responses of higher trophic level organisms on a mechanistic, rather than prescriptive basis, should be the focus of a concerted effort (Railsback *et al.* 1999; Humston *et al.* 2004); such algorithms are needed for realistic spatial models involving non-passive life stages of higher trophic level organisms.

Zooplankton are clearly a focal point for future model development, especially as we attempt to include food web interactions and higher trophic level organisms. GLOBEC focused on bottom-up approaches of climate forcing the physics that forces the nutrient and phytoplankton dynamics and then more vague, but still one-way upward, linkages to zooplankton and higher trophic levels (Moloney *et al.*, Chapter 7, this volume). Fisheries science, as a discipline, usually starts at the fish level and looks down to 'food' and up to predators and fishing. There are very few examples of projected zooplankton population and community responses to global change. Zooplankton have generally been included in large-scale models as biomass in order to simulate biogeochemical cycling and not included in way conducive to projecting their population and community dynamics in response to climate change (Le Quééré *et al.* 2005). Models that include key zooplankton species with structured (stage- or individual-based) approaches are presently being geared up for projecting global change effects, but there are few examples reported to date in the literature. How to include zooplankton in ecosystem models to allow for projecting their population and community responses to global change and accurate rates of energy flows up pathways appropriate to 'feed' the higher trophic level organisms, while still ensuring biogeochemical cycling, will be a major challenge. We do not think it is a simple division of the presently used functional groups into more groups, but rather a major retooling of how zooplankton should be represented for use in end-to-end models. This may require changes in how phytoplankton is represented to accommodate the new zooplankton formulations. Such restructuring of the functional groups in the mod-

els should be pursued carefully but with skepticism (Anderson 2005).

There are several approaches that show promise for end-to-end food web modelling (see review in Travers *et al.* 2007). We briefly summarize some of them here. Coupling age-structured single-species higher trophic level models to an NPZD model was used to simulate global change effects on saury growth and migration (Box 10.2), and climate regime effects on herring population dynamics (Rose *et al.* 2007). Both analyses were versions of models developed as part of the NEMURO family of models (Megrey *et al.* 2007b), and used a very simple set of spatial boxes. The NEMURO effort is continuing in this direction by converting the age-structured approach to an individual-based approach, expanding from single species to a limited multi-species food web, and by embedding the models in the ROMS physical model. Shin and Cury (2001) also used an individual-based approach but they simulated a many-species food web (called OSMOSE: Objected-oriented Simulator of Marine ecOSystems Exploitation) on a two-dimensional spatial grid of cells and coupled the higher trophic level with an NPZ-like model. The model was used to examine various aspects of fishing on the food web (e.g. Shin and Cury 2004; Travers *et al.* 2007), and a new version is being developed that is driven by the output of a three-dimensional ROMS physical model. Movement of higher trophic levels was achieved by forcing spatial distributions to match historical distributions. An alternative to representing the community at the species level is size-based models (e.g. Baird and Suthers 2007; Maury *et al.* 2007a), whereby the state variables represent a progression of size classes rather than association with any particular species. Other approaches being developed include the Integrated Generic Bay Ecosystem Model (IGBEM) and Bay Model 2 (BM2) coupled models that follow biomass for the lower trophic levels and age-structured cohort approach for fish in a coarse three-dimensional spatial grid (Fulton *et al.* 2004c), and the use of outputs from an NPZ as inputs to the Ecopath with Ecosim (EwE; Christensen and Walters 2004) modelling package (Aydin *et al.* 2005). Models being developed in parallel efforts are beneficial to the overall process of model development, and we expect eventually that

hybrid versions that combine features across these approaches will be developed as we make progress towards the goal of developing end-to-end models for projecting ecosystem responses to global change.

Two issues not yet addressed by the ongoing end-to-end modelling efforts are large-scale spatial distributional shifts and emergence of new dominants. Predicting large-scale spatial redistributions of phytoplankton, zooplankton, and fish and other predator communities, and the subsequent reorganization of the local food webs (e.g. previously rare species becoming important), have not been a focus of modelling to date. A fundamental issue is how to represent rare species that become dominants, explosions of problematic species (e.g. jellyfish—Purcell 2005, harmful algal blooms—Van Dolah 2000), and broad enough spatial areas to allow for changes in community structure and alteration of migration routes and new migration patterns to emerge.

The development of end-to-end models not only stretches our biological knowledge but also presents some practical considerations such as to how to solve coupled models that operate on different scales. Solving the zooplankton with the physics and using stored results is computationally efficient but prevents feedback between the upper trophic levels and their zooplankton food (i.e. prevents density-dependence as an emergent phenomenon). Solving the zooplankton with the fish allows for feedback between the predators and their prey but can complicate the coding, and then shifts the decision up the food chain to how to solve the zooplankton and fish with other higher trophic levels (e.g. marine mammals) and with any human components (e.g. dynamic fishing; human movement patterns). It seems clear that solving the entire modelling system simultaneously is computationally inefficient, but how to parse up the solution to allow for feasibility and computational speed while allowing for some feedbacks but ignoring others remains a challenge. Furthermore, as with any analysis that uses multiple coupled models on different scales, quantifying the uncertainty of projections is critical but difficult. One becomes limited by the number of simulations that are possible, with the challenge of specifying the uncertainty in so many variables

and parameters, and the large number of possible combinations of factors and conditions that could be analysed. Computational issues still remain with the development and exercising of comprehensive end-to-end models.

10.4.5 Resource management

Conservatively, the translation of these multi-species coupled biophysical models and end-to-end models into direct management decision making seems a long way off. These models can inform management in terms of cautionary warnings about possible changes in the population(s) of interest resulting from changed environmental conditions, and can suggest key variables to monitor. However, until these models can demonstrate that their accuracy and precision are sufficient to be defensible for management decisions, managers will continue to use their simpler population-centric approaches. Declining fish populations, increasing levels of conflict associated with multiple resource management and increasing numbers of endangered species, has made the managers less willing to change their models. Few of the currently available target species models developed during GLOBEC have been incorporated into management decision making because of their complexity, potential conflicts among stakeholders, and general unproven skill at projection (see also Barange *et al.*, Chapter 9 this volume).

Establishing the accuracy and precision of coupled physical-food web and end-to-end models will likely remain an issue into the foreseeable future. Extensive data on the physical environment, coupled with emerging methods of data assimilation, will result in ongoing improvements to the physical models. Uncertainty will remain too high with the higher trophic level components of these coupled and end-to-end models for direct management decision making. Simply, high-quality data for calibration and skill assessment data for fish population dynamics and productivity remains limited. Yet, fish are usually of greatest interest to managers. This problem of highly uncertain fish data has plagued fisheries for generations and will continue to do so, although some progress is being made.

10.5 Prognosis

We have documented how changes are already occurring in marine ecosystems, some of which are related to global climate change. While the development of climate and physical models has progressed to the point of making projections, the biological models related to zooplankton and higher trophic levels have not kept pace. There is a lack of examples of projections of zooplankton responses to global change, and the projections of higher trophic levels tend to be site-specific, species-specific, and even life-stage-specific. We anticipate a surge in mechanistic modelling that will expand the existing efforts, continuing in the GLOBEC approach, and a concerted effort for the development of end-to-end models.

Maintaining long-term monitoring, and expanding it in critical areas and dimensions, provides the empirical information for defining the questions and locations ripe for mechanistic modelling. We cannot model everything everywhere and responses detected by scenario and empirical analyses of long-term monitoring data lead to us being able to focus on specific types of ecosystems, selected species and biological communities, and certain processes in the mechanistic models. A challenge to monitoring and empirical data collection is to know to measure some variables now, which may appear unimportant under current conditions, but will become important under future conditions (e.g. acidification, iron). Development and implementation of ocean observing systems (Harris *et al.*, Chapter 6, this volume) should continue, with particular emphasis on how the observing data will mesh with quantifying changes in ocean properties directly relevant to zooplankton and higher trophic levels (i.e. fish). Further development of sophisticated data analysis methods is needed to make sense of the ever increasing amounts and types of data becoming available.

With a sound empirical foundation, we are optimistic that many of the issues surrounding the development of mechanistic end-to-end forecasting models can be solved with a concerted effort that continues and expands on the GLOBEC legacy.

GLOBEC-style analyses that focus on specific species in particular locations will continue to make significant contributions. However, when we take the long-term view, we see a need for investment in monitoring, data analysis, and model development now so that results and models that allow for broad-scale analyses and ecosystem-based analyses with end-to-end models are available in the near-future. The onus is on the oceanographic community. It is becoming a cliché to say so, but diverse groups must work together to address these issues. GLOBEC is an excellent example of such multidisciplinary, cross-cutting research. We now need to move even further from multidisciplinary to truly interdisciplinarity. We view the difference between multidisciplinary and interdisciplinarity as operational in terms of the degree of communication and feedback that occurs between the various research groups. We view multidisciplinary as different groups with specific skills working together on the same problem but exchanging information periodically at, say annual or semi-annual, team meetings. Interdisciplinary research has the groups together, ideally co-located physically near each other, with constant exchange of information and adjustments to plans in response to the needs of the other groups. Hopefully, after the next decade of effort, one of the legacies of the GLOBEC programme will be that it laid down the foundation for the development of methods for forecasting the full ecosystem responses of marine systems to global climate change.

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