In hot water: zooplankton and climate change

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An overview is provided of the observed and potential future responses of zooplankton communities to global warming. I begin by describing the importance of zooplankton in ocean ecosystems and the attributes that make them sensitive beacons of climate change. Global warming may have even greater repercussions for marine ecosystems than for terrestrial ecosystems, because temperature influences water column stability, nutrient enrichment, and the degree of new production, and thus the abundance, size composition, diversity, and trophic efficiency of zooplankton. Pertinent descriptions of physical changes in the ocean in response to climate change are given as a prelude to a detailed discussion of observed impacts of global warming on zooplankton. These manifest as changes in the distribution of individual species and assemblages, in the timing of important life-cycle events, and in abundance and community structure. The most illustrative case studies, where climate has had an obvious, tangible impact on zooplankton and substantial ecosystem consequences, are presented. Changes in the distribution and phenology of zooplankton are faster and greater than those observed for terrestrial groups. Relevant projected changes in ocean conditions are then presented, followed by an exploration of potential future changes in zooplankton communities from the perspective of different modelling approaches. Researchers have used a range of modelling approaches on individual species and functional groups forced by output from climate models under future greenhouse gas emission scenarios. I conclude by suggesting some potential future directions in climate change research for zooplankton, viz. the use of richer zooplankton functional groups in ecosystem models; greater research effort in tropical systems; investigating climate change in conjunction with other human impacts; and a global zooplankton observing system.

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Introduction

In this review, I examine the observed and potential future response of zooplankton communities to climate change. This review is not meant to be exhaustive but to highlight case studies where climate has had a clear impact on zooplankton communities and has had or is likely to have substantial ecosystem consequences. Such a case-study approach is useful for the insight it provides, but it also demonstrates that climate-impact research on zooplankton is at an earlier developmental stage than many terrestrial groups, such as birds, butterflies, or flowering plants. The focus is on global warming, with its heating effect on the ocean's upper layers, and impacts on stratification and nutrient enrichment processes. The literature on zooplankton is dominated by work on copepods because of their cosmopolitan nature, their importance in marine foodwebs, their robust nature in the laboratory, and because of sampling and preservation bias. Wherever possible, however, I draw on examples from other important groups including euphausiids, foraminifera, ichthyoplankton, jellyfish, and fresh-water phyto- and zooplankton. This review deliberately does not discuss microzooplankton (see Calbet, 2008) or ocean acidification (see Fabry et al., 2008).

I also leave it to other workers to synthesize the findings from laboratory and molecular work on physiological and genetic mechanisms through which temperature operates at the organism level.

Global importance of zooplankton

Zooplankton are critical to the functioning of ocean foodwebs because of their sheer abundance and vital ecosystem roles. The most prominent zooplankton, the copepods, are the most abundant multicellular animals on Earth, even outnumbering insects by possibly three orders of magnitude (Schminke, 2007). Zooplankton communities are highly diverse and thus perform a variety of ecosystem functions. Arguably, the most important role of zooplankton is as the major grazers in ocean foodwebs, providing the principal pathway for energy from primary producers to consumers at higher trophic levels, such as fish, marine mammals, and turtles. Interestingly, the largest animals in the ocean, such as baleen whales, feed solely on zooplankton. This is in stark contrast with terrestrial ecosystems, where the largest animals, such as ungulates, are herbivores. There are no similar large herbivores in the ocean, presumably because the size of marine primary producers is too small for efficient grazing.

Zooplankton not only support the large, highly visible, and charismatic components of the ocean foodweb, but also the microbial community. Regeneration of nitrogen through excretion by zooplankton helps support bacterial and phytoplankton production. Microbes colonize zooplankton faecal pellets and carcasses, making them rich sources of organic carbon for detrital feeders. These zooplankton products slowly yet consistently rain down on the dark seabed, sustaining diverse benthic communities of sponges, echinoderms, anemones, crabs, and fish (Ruhl and Smith, 2004).

Zooplankton also play an important role in shaping the extent and pace of climate change. The ocean's ability to act as a sink for CO_2 relies partially on the biological pump. Zooplankton play a role in the biological pump because much of the CO_2 that is fixed by phytoplankton, then eaten by zooplankton, eventually sinks to the seabed. Much of this carbon can be locked up in sediments and removed from the carbon cycle. Zooplankton also facilitate this process by moving large quantities of carbon from the ocean's surface to deeper layers when they dive each day into the ocean depths to avoid near-surface predatory fish.

Without the diverse roles performed by zooplankton, our oceans would be devoid of the large fish, mammals, and turtles that are of such immense aesthetic, social, and financial value to society. In fact, much of the economic value of the oceans, estimated at US$21 trillion per annum and similar to the global gross national product (Costanza et al., 1997), stems from critical ecosystem services, such as fishery production, nutrient cycling, and climate regulation provided by zooplankton.

Beacons of climate change

Zooplankton are beacons of climate change for a host of reasons. First, zooplankton are poikilothermic, so their physiological processes, such as ingestion, respiration, and reproductive development, are highly sensitive to temperature, with rates doubling or tripling with a $10°C$ temperature rise (Mauchline, 1998). Second, most zooplankton species are short-lived (<1 year), so there can be tight coupling of climate and population dynamics (Hays et al., 2005). In fact, some evidence suggests that plankton are more sensitive indicators of change than even environmental variables themselves, because the non-linear responses of plankton communities can amplify subtle environmental signals (Taylor et al., 2002). Third, unlike other marine groups, such as fish and many intertidal organisms, zooplankton are generally not commercially exploited (exceptions include krill and some jellyfish species), so studies of long-term trends in response to environmental change are generally not confounded with trends in exploitation. Fourth, the distribution of zooplankton can accurately reflect temperature and ocean currents because plankton are free floating, and most remain so for their entire life. In contrast, terrestrial organisms are either rooted to their substratum or need to spend considerable energy to migrate or move. Further, reproductive products of zooplankton are distributed by currents and not by vectors, making changes in zooplankton distribution with climate change easier to understand than the more complex responses of terrestrial species. Last, because ocean currents provide an ideal mechanism for dispersal over large distances, almost all marine animals have a planktonic stage in their life cycles; therefore, alterations in the distribution of many marine groups are at least partially determined while floating in the zooplankton. As we will see, recent evidence suggests that many of the meroplanktonic life stages are even more sensitive to climate change than their holozooplanktonic neighbours living permanently in the plankton. All of these attributes combine to make zooplankton sensitive beacons of climate change.

Fundamental importance of temperature

Temperature is probably the single most important physical variable structuring marine ecosystems. There is growing appreciation that the composition, abundance, and trophic efficiency of plankton communities are tightly linked to water temperature, beyond their direct physiological responses. It is this critical influence of temperature that makes marine systems acutely vulnerable to global warming.

The size structure and taxonomic composition of plankton communities are regulated by their physical and chemical environment (Bouman et al., 2003; Badosa et al., 2007; McKinnon et al., 2007). The plankton community can be envisaged as existing somewhere within a continuum of states between two extremes, with nutrient enrichment the key determinant. Under cold, well-mixed, and turbulent conditions, surface waters are replete with nutrients, the phytoplankton community is dominated by centric diatoms, and the ratio of new production to total community production is high. These conditions result in the zooplankton being dominated by crustaceans, such as large copepods. This short, efficient foodweb is nutritionally rich, supporting large numbers of planktivorous and piscivorous fish, seabirds, and marine mammals. In contrast, under warm, stratified, and stable conditions, surface waters are depleted in nutrients, the phytoplankton community is dominated by picoplankton and flagellates, and trophodynamics depend on recycled nitrogen. These conditions often result in the zooplankton being dominated by gelatinous zooplankton (salps, doliolids, ctenophores) and small crustaceans. This long, inefficient foodweb is of poor nutritional quality, supporting a far smaller biomass of higher trophic levels. The degree of nutrient enrichment is thus the key determinant of the type of foodweb present.

Surface temperature is a good proxy for nutrient enrichment in the ocean. Warming of surface waters makes the water column more stable, enhancing stratification and requiring more energy to mix deep, nutrient-rich water into surface layers. This results in nitrate, the principal nutrient that limits phytoplankton growth in the ocean, being negatively related to temperature globally (Kamykowski and Zentara, 1986). Further, nutrient limitation is greatest when warmer-than-normal conditions prevail in a region (Kamykowski and Zentara, 2005). Temperature is therefore a powerful proxy for describing the structure and functioning of marine systems. This is fundamentally different from terrestrial systems, where there is no such direct link between temperature, nutrient availability, and ecosystem attributes; instead, rainfall is much more important.

Observed warming

Changes in atmospheric concentrations of greenhouse gases alter the energy balance of the climate system (IPCC, 2007a). Carbon dioxide is the principal anthropogenic greenhouse gas; its atmospheric concentration has increased dramatically since 1750 through the burning of fossil fuels and changes in land use (Figure 1). The rate of increase has accelerated over the past 50 years. The atmospheric concentration of carbon dioxide in 2005 far exceeded the natural range over the past 650 000 years (180 to 300 ppm).
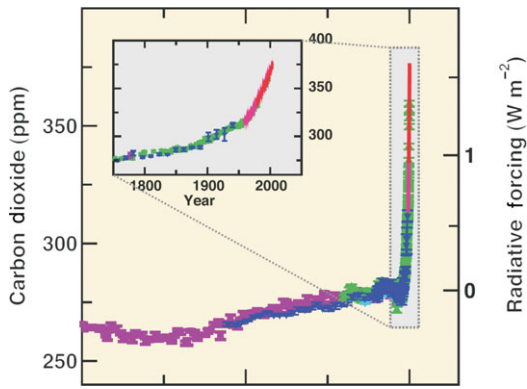
Figure 1. Atmospheric concentration of carbon dioxide over the past 10 000 years (large panel) and since 1750 (inset panel). Measurements are shown from ice cores (symbols with different colours for different studies) and atmospheric samples (red lines). The corresponding radiative forcing is shown on the right axes of the large panel (from IPCC, 2007a, with permission).

Increases in greenhouse gases have led to rapid warming of the atmosphere and oceans, evident in the surface temperature anomalies for 2001–2005, relative to those for 1951–1980 (Figure 2). Oceans have warmed less than the land because of the greater thermal heat capacity of water, and high latitudes have warmed more than tropical regions. The 100-year linear trend (1906–2005) is 0.74°C, but the slope is steeper since 1960 (Bindoff *et al.*, 2007). Eleven of the 12 hottest years since instrumental recording began in 1850 have occurred since 1995 (Hansen *et al.*, 2006). The Earth's rapid warming has pushed temperatures to their highest level in nearly 12 000 years and within ∼1°C of the maximum estimated temperature of the past million years. There has been an increase of 0.31°C since the 1950s in the top 300 m of the oceans (Levitus *et al.*, 2000), with most warming confined to the top 700 m, although it has penetrated to a depth of at least 3000 m (Barnett *et al.*, 2005).
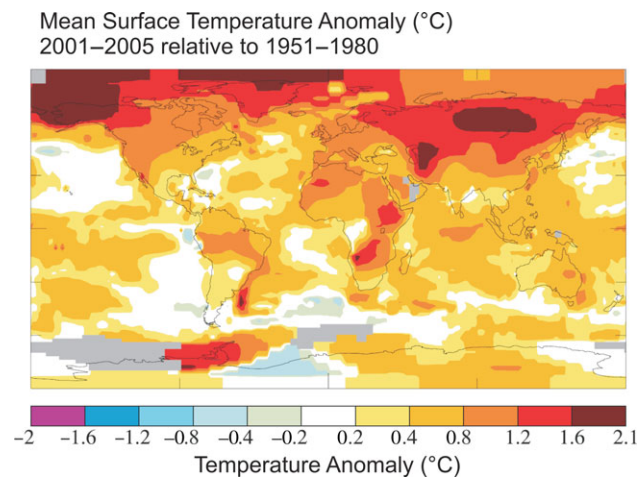

Figure 2. Mean surface temperature anomalies for 2001–2005 relative to 1951–1980 from surface air measurements at meteorological stations and ship and satellite sea surface temperature measurements (from Hansen *et al.*, 2006; National Academy of Sciences, USA).

Global warming has many effects on ocean climate. Warming has caused snow and ice to melt; satellite data since 1978 demonstrate that the extent of summer Arctic sea-ice has shrunk by 7.4% per decade (IPCC, 2007a). Changes in precipitation and evaporation over the oceans have led to a freshening of mid- and high-latitude waters but to increased salinity in low-latitude waters. Human influence also extends to wind patterns, with mid-latitude westerly winds strengthening in both hemispheres since the 1960s. Such changes in water properties could alter large-scale ocean circulation, although as yet there is no clear evidence for such changes: over the past 50 years, there is no coherent evidence of a decline in the strength of the meridional overturning circulation (Bindoff *et al.*, 2007).

The clearest evidence of attribution for global warming comes from atmosphere–ocean general circulation models (GCMs) that simulate the dynamics of the ocean–atmosphere system (IPCC, 2007a). The warming trend over land and in the oceans since the early 1900s cannot be reconstructed by these models when they are driven by changes in natural forcing (solar activity and volcanism) alone. Observed spatial and temporal patterns of warming can only be simulated by including anthropogenic greenhouse gas forcing.

Observed impacts on zooplankton

Impacts of global warming on zooplankton are manifest as poleward movements in the distribution of individual species and assemblages, earlier timing of important life cycle events or phenology, and changes in abundance and community structure. A summary of the impacts of global warming on marine zooplankton is shown in Table 1, and specific examples will be highlighted in the following section.

Distribution

Although few zooplankton datasets cover much of the spatial range of any species for an extended period, available data indicate that zooplankton exhibit range shifts in response to global warming that are among the fastest and largest of any marine or terrestrial group. The general trend, as on land, is for animals to expand their ranges polewards as temperatures warm. The most striking examples are from the Northeast Atlantic where the Continuous Plankton Recorder survey has been operating since 1931 (Richardson *et al.*, 2006). Members of the warm-water copepod assemblages (the southern shelf edge assemblage and pseudo-oceanic assemblage) have moved more than 1100 km polewards over the past 50 years (Figure 3; Beaugrand *et al.*, 2002). The distribution of two individual copepod species in the Northeast Atlantic have also been studied in relation to ocean warming (Lindley and Daykin, 2005). *Centropages chierchiae* and *Temora stylifera* both moved north from the vicinity of the Iberian Peninsula in the 1970s and 1980s to the English Channel in the 1990s (∼6° of latitude). Concurrent with the expansion polewards of warm-water copepods, the Arctic assemblage has retracted to higher latitudes (Beaugrand *et al.*, 2002). Although these translocations have been associated with regional warming of up to 1°C, they may also be partially explained by stronger north-flowing currents on the European shelf edge. These shifts in distribution have had dramatic impacts on the foodweb of the North Sea (Beaugrand *et al.*, 2003). In particular, the cool-water copepod assemblage has high biomass and is dominated by relatively large species, especially *Calanus finmarchicus*. Because this assemblage has retracted north as waters have

Table 1. A summary of the impacts of climate change on marine zooplankton.

Observation	Taxa	Region	Period	Observation (change/ decade or change/ degree)	Potential cause	Reference/s
Distribution	Southern shelf edge assemblage (nine species); pseudo-oceanic assemblage (five species)	NE Atlantic	1958–1999	Northward extension by 10° of latitude (1100 km) = 260 km per decade	Warming/ hydrography	Beaugrand et al. (2002)
	Centropages chierchiae and Temora stylifera	NE Atlantic	1959–2000, although consistent distribution data from 1978 only	Northward movement of the centre of distribution from off the Iberian Peninsula to the Bay of Biscay (~6° of latitude) = 157 km per decade	Warming	Lindley and Daykin (2005)
	Arctic assemblage (three species); Subarctic assemblage (four species)	NW Atlantic	1958–1999	Southward movement of communities as cool water penetrates south	Cooling/ hydrography	Beaugrand et al. (2002). Online Supplementary Material (www. sciencemag.org/cgi/ content/full/sci;296/ 5573/1692/DC1)
	Calanus hyperboreus	NW Atlantic	1962–1999	Southward movement as cool water penetrates south	Cooling/ hydrography	Johns et al. (2001)
Phenology	*Neocalanus plumchrus*	Subarctic Pacific (Ocean Station P)	1956–1997	Earlier timing of zooplankton biomass peak (60 days) =14 days per decade =73 days per °C (given site warmed by 1.96°C per century)	Warming	Mackas et al. (1998)
	Neocalanus plumchrus	Strait of Georgia	1956–1997	Earlier timing of zooplankton biomass peak (25–30 days) =9.1 days per decade (no temperature change for area given)	Warming	Bornhold et al. (1998)
	Decapod larvae	Central North Sea	1958–2004	Peaks 4–5 weeks earlier in summer =7 days per decade	Warming	Edwards et al. (2006)
	Meroplankton (seven taxa)	Central North Sea	1958–2002	Peaks 27 days earlier in summer =6 days per decade (=4.9 days per decade, excluding decapod and echinoderm larvae reported separately) =30 days per °C	Warming	Edwards and Richardson (2004)
	Echinoderm larvae	Central North Sea	1958–2002	Peaks 47 days earlier in summer =10.4 days per decade =52.2 days per °C	Warming	Edwards and Richardson (2004)
	Copepods (12 taxa)	Central North Sea	1958–2002	Peaks 10 days earlier in summer =2.2 days per decade =11.1 days per °C	Warming	Edwards and Richardson (2004)
	Other holozooplankton (11 taxa)	Central North Sea	1958–2002	Peaks 10 days earlier in summer =2.2 days per decade =11.1 days per °C	Warming	Edwards and Richardson (2004)

Table 1. *Continued*

Observation	Taxa	Region	Period	Observation (change/decade or change/degree)	Potential cause	Reference/s
	Evadne spp.	Helgoland	1975–1999	Peaks 36.8 days earlier (estimated from Figure 5 in Greve *et al.,* 2004) =14.7 days per decade =60.2 days per °C	Warming	Greve *et al.* (2004)
	Mnemiopsis leidyi	Narragansett Bay	1951–2003	Advanced by 59 days =11.1 days per decade =49.2 days per °C	Warming	Costello *et al.* (2006)
	Acartia tonsa	Narragansett Bay	1951–2003	No significant change in *A. tonsa* phenology	Warming	Costello *et al.* (2006)

warmed, *C. finmarchicus* has been replaced in the North Sea by *Calanus helgolandicus*, a dominant member of the warm-water assemblage. This assemblage typically has lower biomass and contains smaller species. Despite these *Calanus* congeners being almost indistinguishable, the two species have contrasting seasonal

Figure 3. The northerly shift of the warm temperate copepod assemblage (containing *Calanus helgolandicus*) into the North Sea and the retraction of the Arctic copepod assemblages (containing *Calanus finmarchicus*) to higher latitudes. Scale is the mean number of species per assemblage, which provides an index of abundance. Reprinted by permission of Gregory Beaugrand.

cycles: *C. finmarchicus* abundance peaks in spring, whereas *C. helgolandicus* abundance peaks in autumn (Bonnet *et al.,* 2005). This is critical because Atlantic cod, traditionally a major fishery of the North Sea, spawn in spring, and cod larvae require a diet of large copepods then, or mortality is high and recruitment is poor. Since the late 1980s, *C. finmarchicus* has been virtually absent, there is very low copepod biomass in the North Sea during spring and summer, and cod recruitment has plummeted (Beaugrand *et al.,* 2003).

The studies above report movement rates of 260 km per decade for the copepod assemblages in the Northeast Atlantic and 157 km per decade for *C. chierchiae* and *T. stylifera* (Lindley and Daykin, 2005), giving a mean translocation of ∼200 km per decade. By comparison, a global meta-analysis of range shifts across 99 species of birds, butterflies, and alpine herbs found that they moved polewards (or upwards) by an average of only 6.1 km per decade (Parmesan and Yohe, 2003). If the range shifts highlighted here for zooplankton are anywhere near typical of those experienced more broadly in the plankton, they would dwarf the distribution shifts reported from terrestrial systems.

It is interesting that there have also been substantial changes in zooplankton distribution in the Northwest Atlantic, but in the opposite direction (towards the equator) to what would be predicted from simple assumptions of uniform global warming. The same Arctic and Subarctic copepod assemblages that have moved north in the Northeast Atlantic are moving south in the Northwest Atlantic (see supplementary information in Beaugrand *et al.,* 2002). Although no quantitative rates of change have been derived, these assemblages exhibit substantial southward penetration over the last 30 years of the 20th century. In a separate analysis, Johns *et al.* (2001) report that one of the species in the Arctic copepod assemblage, *Calanus hyperboreus*, had spread so far south that in 1998 it was recorded off the Georges Bank shelf edge at 39°N, its southernmost position in 50 years of sampling. Rather than casting doubt on the hypothesized impact of global warming, these findings provide support for the tenet that plankton communities are extremely sensitive and respond quickly to environmental changes. Ocean climate in the Northwest Atlantic is driven by thermohaline mechanisms, and these influence the south-flowing Labrador Current. The Labrador–Newfoundland area experienced abnormally cold temperatures during the late 1980s and early 1990s (Prinsenberg *et al.,* 1997), which increased the production of Labrador seawater and thus the strength of the Labrador Current (Dickson, 1997). This cold water has spread farther south, bringing colder
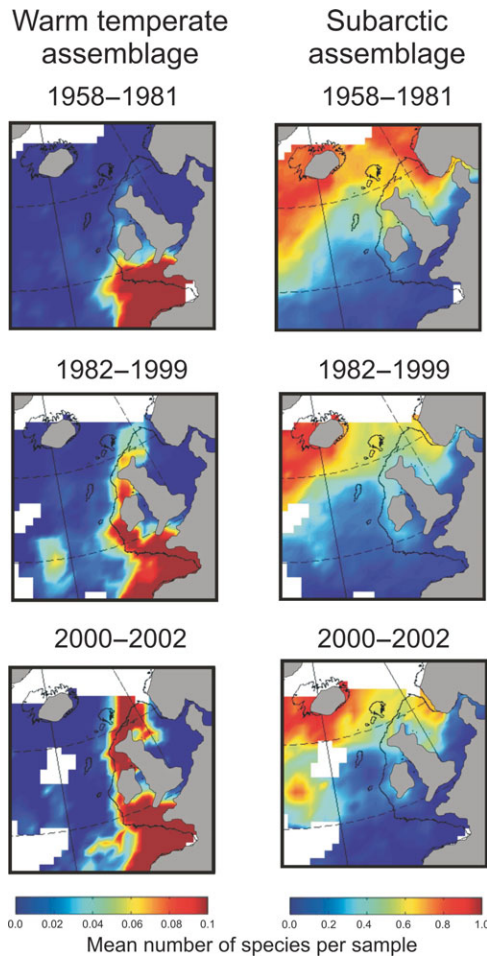
conditions to an area formerly unfavourable for *C. hyperboreus* (Johns *et al.*, 2001). A similar southward penetration is evident for the Arctic dinoflagellate *Ceratium arcticum* (Johns *et al.*, 2003).

These studies highlight the complex interactions between hydroclimate and zooplankton species distribution. They are consistent, however, with the principle that zooplankton undergo large-scale changes in distribution in response to warming (or regional cooling) and hydrography.

Phenology

Phenology, or the timing of repeated seasonal activities such as migrations or reproduction, is highly sensitive to global warming. On land, events in spring, including the arrival of swallows in the UK, the emergence of butterflies in the US, or the blossoming of cherry trees in Japan, are all happening earlier in the year as the temperature rises. Although there have been far fewer studies of the phenology of zooplankton than terrestrial plants, insects, or birds, a synthesis of available data suggests that corresponding changes in zooplankton are significantly greater than those for terrestrial groups.

The most striking example of ecosystem repercussions of climate-driven changes in phenology is evident in the Subarctic North Pacific Ocean. Here, a single copepod species, *Neocalanus plumchrus*, dominates the zooplankton biomass (Mackas *et al.*, 1998). Its vertical distribution and development are strongly seasonal, with young copepodites emerging from deep water and arriving near the surface in late winter; they develop into CVs over spring and summer, before descending again in autumn (Miller *et al.*, 1984). This life-history strategy results in a strong but ephemeral (lasting no longer than 2 months) annual peak in upper ocean zooplankton biomass in spring and early summer. Because *N. plumchrus* constitutes so much of the biomass, changes in its peak timing (when half of the copepodites are CVs) are evident in changes in the total zooplankton biomass. The timing of this annual maximum has shifted dramatically over the past 50 years, with peak biomass 60 days earlier in warm than in cold years (Mackas *et al.*, 1998). The change in developmental timing is probably a consequence of both increased survivorship of early cohorts in warm years and physiological acceleration. Other populations of *N. plumchrus* exhibit similar temperature responses: those in the Strait of Georgia shifted earlier by 25–30 days over the last three decades of the 20th century (Mackas *et al.*, 1998), and those along the British Columbia continental margin now leave the surface layer and enter diapause as early as mid-May (Goldblatt *et al.*, 1999).

The timing of the zooplankton biomass peak is likely to be ecologically significant because it influences the availability of large copepodites to upper-ocean predators such as salmon, herring, hake, and seabirds. Individuals from the world's largest colony of the planktivorous seabird, Cassin's auklet, off British Columbia prey heavily on *Neocalanus* (Bertram *et al.*, 2001). When conditions are warm, spring is early, and the duration of overlap of seabird breeding and *Neocalanus* availability in surface waters is short; a mismatch between prey and predator populations arises, resulting in reduced growth of chicks. During cold years, there is tighter synchrony between food availability and the timing of breeding. In this way, the reproductive performance of Cassin's auklet is compromised in warmer years relative to that in colder years. If this species does not adapt to the changing food conditions, global warming could diminish its long-term survival chances.

Substantial phenological changes in plankton communities have also been observed in the central North Sea (Edwards and Richardson, 2004). The timing of meroplankton seasonal cycles seems particularly sensitive to climate change. As a group, meroplankton (including larvae of cirripedes, cyphonautes, decapods, echinoderms, fish, and lamellibranchs) have advanced their appearance in the plankton by 27 days over the past 45 years. However, some groups have reacted more strongly than others. For example, larvae of benthic echinoderms in the North Sea are now appearing in the plankton 47 days earlier than they did 50 years ago, when waters were on average 1°C cooler (Edwards and Richardson, 2004). Temperature stimulates physiological development and larval release in echinoderms (Kirby *et al.*, 2007). Similarly, observations off Helgoland in the southern North Sea for 1990–1999 reveal that fish larvae are extremely sensitive to temperature changes, so much so that more than one-third of the species studied exhibit significant correlations between the middle of their seasonal peak in abundance and mean temperature (Greve *et al.*, 2005).

One aspect of phenological change considered in relation to the temperate North Sea is whether the timing of the spring or autumn bloom altered with warming. This is important because the most obvious and widespread timing changes on land have been in spring. In the North Sea, there has been no general advancement (or delay) in the timing of spring or autumn over the past 45 years (Figure 4; Edwards and Richardson, 2004). In contrast, 34 out of 37 taxa that peak with low-turbulence conditions during summer have advanced in their seasonality, with the plankton functional groups on average 10–27 days earlier. Although the timing of the spring bloom is often thought to be determined by the onset of stratification, this is not a prerequisite (Townsend *et al.*, 1992) and, in many areas, may instead be more tightly coupled with the regulation of diatom spore germination by photoperiod (Eilertsen *et al.*, 1995; Eilertsen and Wyatt, 2000), which is invariant to global warming.

Intriguingly, the timing of various plankton functional groups seems not to respond to ocean warming synchronously, resulting in predator–prey mismatches that could resonate to higher trophic levels (Edwards and Richardson, 2004). Over the past 45 years, dinoflagellates in the North Sea are peaking earlier by 23 days, diatoms by 22 days, copepods by 10 days, and other holozooplankton by 10 days. This differential response of phytoplankton and zooplankton may lead to a mismatch between successive trophic levels and a change in the synchrony between primary, secondary, and tertiary production. Efficient transfer of marine primary and secondary production to higher trophic levels, such as those occupied by commercial fish species, depends largely on the temporal synchrony between successive trophic production peaks, especially in temperate marine systems. Here, successful fish recruitment is highly dependent on synchronization with pulsed planktonic production (Hjort, 1914; Cushing, 1990; Beaugrand *et al.*, 2003).

This type of mismatch, where warming has disturbed the temporal synchrony between the dynamics of herbivores and their food, has also been noted in fresh-water, estuarine, and terrestrial ecosystems. For example, in Lake Washington (USA), the timing of the phytoplankton spring peak has advanced by 19 days from 1962 to 2002, as winters have warmed and led to an earlier onset of stratification, but this has not been matched by the zooplankton (Winder and Schindler, 2004). In fact, zooplankton blooms have lagged behind, with the timing of peak spring abundance in the
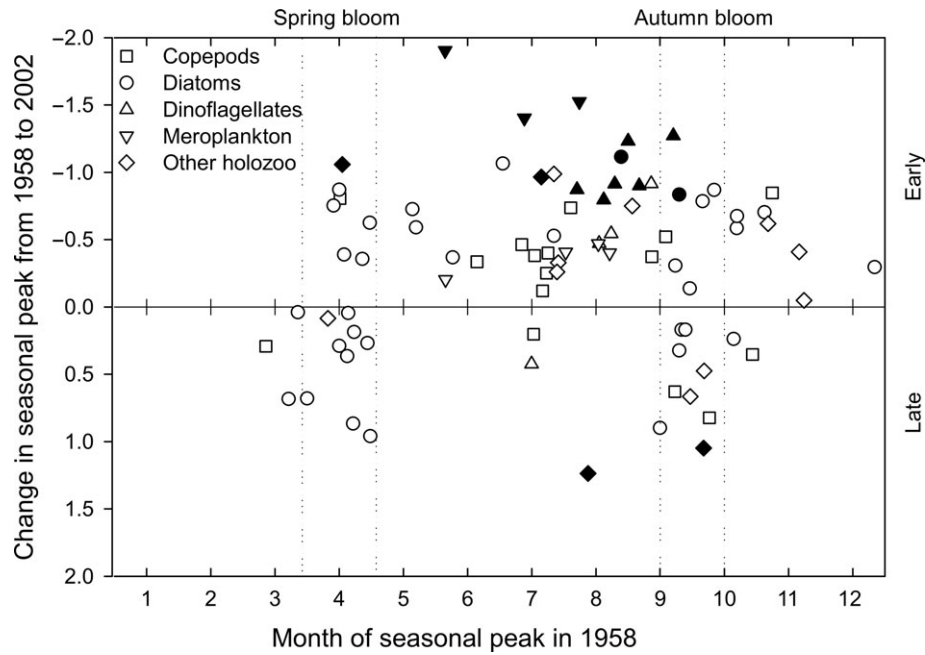
Figure 4. Changes in phenology in the central North Sea from 1958 to 2002. The change in timing of the seasonal peaks (in months) for the 66 taxa over the 45-year period (1958–2002), plotted against the timing of their seasonal peak in 1958. A negative difference between 1958 and 2002 indicates seasonal cycles are occurring earlier (Edwards and Richardson, 2004). Reprinted by permission of Macmillan Publishers Ltd.
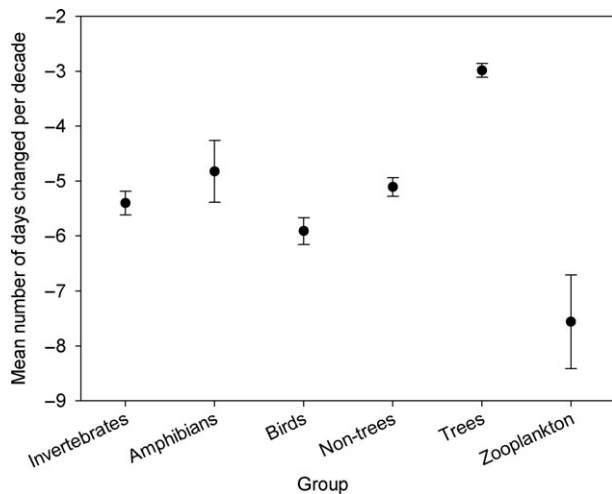

Figure 5. Changes in phenology from different studies (mean ± s.e.). Data for zooplankton from this study and other groups from Root *et al.* (2003).

rotifer *Keratella* 15 days earlier, that of the copepod *Leptodiaptomus* only 9 days earlier, and that of the cladoceran *Daphnia* showing no movement. These changes have led to a mismatch between the spring phytoplankton peak and some members of the zooplankton, particularly *Daphnia*. Members of the plankton in Lake Müggelsee (Germany) have also displayed disparate responses to warming, and these have been attributed to the different pace of life cycles of individual species (Adrian *et al.*, 2006). Plankton, such as diatoms and *Daphnia*, which grow rapidly in spring, showed synchronous advances of about 1 month in

response to earlier ice break-up and warmer spring water temperature from 1979 to 2003. However, there was no such synchrony for slow-growing summer zooplankton, such as copepods and the larvae of the mussel *Dreissena polymorpha*, which have longer and more complex life cycles. In particular, the summer zooplankton exhibited species-specific responses to warming that depended strongly on whether the timing of warming matched their individual thermal requirements at important life stages, such as emergence from diapause for copepods or spawning for *Dreissena*.

Mismatch has also been documented in the estuarine environment of Narragansett Bay (USA). Here, the timing of the first appearance of the top predator *Mnemiopsis leidyi* has advanced by 59 days between 1951 and 2003 (see Figure 1 in Purcell, 2005), whereas the timing of one of its major prey items, *Acartia tonsa*, has remained unchanged over this time (Costello *et al.*, 2006). In this case, species-specific responses are thought to be a consequence of the differential warming of their individual winter refugia: there is substantial warming in shallow regions of the Bay that has severely affected overwintering *Mnemiopsis*, but relatively small temperature changes in deeper regions of the Bay that have had little influence on seasonal excystment of over-wintering *A. tonsa* eggs. In terrestrial systems, global warming has led to trophic mismatches between great tits and caterpillars, flycatchers and caterpillars, winter moth and oak bud burst, and the red admiral butterfly and stinging nettles (Visser and Both, 2005). In each case, mismatches in timing compromise the survival of the herbivore that depends on its particular prey source.

Several striking results emerge from the phenological studies summarized here. The first is that observed changes in zooplankton are significantly greater than those observed for taxonomic groups on land. In a phenological study of 172 species of herbs,

shrubs, trees, birds, butterflies, and amphibians, Parmesan and Yohe (2003) noted a mean phenological change of 2.3 days per decade. Root *et al*. (2003) calculated the phenological shift for invertebrates, amphibians, birds, and trees, and found mean phenological changes of 3–6 days. In contrast, the mean phenological change observed for zooplankton is dramatically and significantly greater at 7.6 days per decade (Figure 5; Table 1). Second, the spring bloom has been stationary in the temperate North Sea, which is in stark contrast with terrestrial systems where most documented changes have taken place in spring (Parmesan and Yohe, 2003; Root *et al*., 2003). Third, the phenology of phytoplankton appears to be more sensitive than zooplankton, consistent with terrestrial plants and grazers. Undoubtedly, over historical time, these predator–prey systems have undergone substantial temperature changes and remained viable, so a critical question is how long will it take these phenological relationships to adapt to the warmer temperatures and resynchronize, especially with other concomitant anthropogenic stressors (see the section on synergistic effects and bolstering ecosystem resilience). Finally, responses to global warming are species-specific and may be determined by whether the exact timing of warming coincides with critical life cycle stages or events. This suggests that an intimate knowledge of the life history of an organism may be needed for an adequate explanation of population impacts and prediction of ecosystem responses.

Abundance

Changes in abundance are more difficult to attribute to global warming than are shifts in distribution or phenology, although they may have greater ecosystem ramifications. One of the most striking examples of changes in abundance in response to long-term warming is from foraminifera in the California Current (Field *et al*., 2006). Foraminifera are ideal for long-term climate change studies because their populations are controlled more by changes in climate and primary productivity than by changes in predation, and they are also well preserved in sediments. As a result, their temporal dynamics can be linked to changes in climate over long time-scales. Throughout the 20th century, the number of tropical/subtropical species has been increasing, reflecting a warming trend; this phenomenon is most dramatic after the 1960s (Figure 6). This change towards tropical foraminifera echoes similar increases in abundance of many other subtropical and tropical taxa and decreases in temperate algae, zooplankton, fish, and seabirds in the California Current over the past few decades.

An illustration from the Northeast Atlantic highlights the effect that global warming can have on stratification and plankton abundances, and emphasizes the region-specific consequences (Richardson and Schoeman, 2004). Here, phytoplankton become more abundant with warming of cool, windy, and well-mixed regions, probably because warmer temperatures boost metabolic rates and enhance stratification, thereby increasing the amount of time phytoplankton cells spend in the euphotic zone. However, phytoplankton become less abundant when already warm regions get even warmer, probably because warmer surface water blocks further nutrient-rich deep water from rising to the euphotic layer. This regional phytoplankton response is transmitted up the plankton foodweb to herbivorous copepods and carnivorous zooplankton. Therefore, over long time- and broad space scales, plankton foodwebs are controlled from the "bottom up" by primary producers, rather than from the "top down"
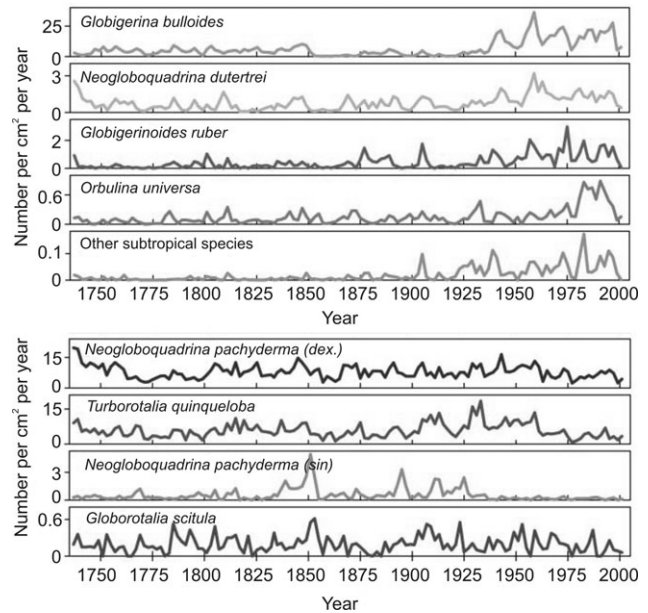

Figure 6. Fluxes of planktonic foraminifera in Santa Barbara Basin sediments. Top panel shows increased abundances of tropical–subtropical foraminifera in the 20th century. Bottom panel shows no temporal trend in temperate-polar foraminifera in the 20th century. Reprinted from Field *et al*. (2006), by permission of AAAS.

by predators. Because the amount of phytoplankton and zooplankton in a region is likely to influence the carrying capacity of fish (Ware and Thompson, 2005), the response to climate change of lower trophic levels suggests that the abundance and distribution of fish will change in the future, having regional impacts on fisheries.

Most evidence of climate impacts on zooplankton is from the northern hemisphere because this is where most (plankton) science is concentrated, but nevertheless, there have been dramatic changes documented from waters elsewhere. Since the 1970s, there has been a decline in krill (*Euphausia superba*) biomass in the Southern Ocean and a concomitant increase in salps, which occupy less productive and warmer regions (Atkinson *et al*., 2004). It is likely that these changes are a consequence of global warming. Strong summer phytoplankton blooms and winters of extensive sea ice, with plentiful food from ice algae, enhance survival of krill larvae as well as recruitment to adult stocks. As waters have warmed, the extent of winter sea ice and its duration have declined, which is likely to have impaired larval krill survival and explains the observed decline in krill density. Warmer waters also provide more favourable habitat for salps. The declining population abundance of krill could be deleterious to the populations of baleen whales, fish, penguins, seabirds, and seals that depend on krill as their primary food source.

Probably the zooplankton that people are most familiar with in their daily lives are jellyfish. Jellyfish outbreaks have a host of societal consequences: loss of tourist revenue through beach closures and even death of bathers; blockage of coastal power plant cooling intakes, forcing electricity shutdowns; damage to fish nets and contamination of catches; interference with acoustic fish assessments; mortalities among farmed fish; and reduced commercial fish abundance through competition and predation. Although dense jellyfish aggregations are a natural feature of

healthy pelagic ecosystems, evidence is accumulating that the severity and frequency of outbreaks is increasing in many areas, including the Bering Sea, northeastern US shelf, Gulf of Maine, Gulf of Mexico, Azov Sea, Black Sea, Caspian Sea, Northern Benguela upwelling ecosystem, East China and Yellow seas, Sea of Japan, and Seto Inland Sea [see reviews by Mills (2001), Purcell *et al.* (2007), and references therein]. For example, in the Northern Benguela upwelling ecosystem off Namibia, jellyfish now outweigh fish in terms of total biomass (Lynam *et al.*, 2006). However, there is no general agreement on the causes underlying the observed increases, and a suite of human activities, including climate change, as well as overfishing, eutrophication, translocation, and habitat modification, are likely to be responsible (Purcell *et al.*, 2007).

Global warming could lead to jellyfish increases because of their physiological response and its effect on plankton foodwebs. In an analysis of 15 long-term jellyfish and ctenophore time-series, Purcell (2005) found that 11 species increased in abundance with warming. She concluded that temperate species may benefit from global warming, but tropical jellyfish could decline in abundance because many species may have a thermal maximum around 34–35°C. Further, experimental evidence suggests that jellyfish exhibit faster rates of both asexual and sexual reproduction at warmer temperatures (Purcell, 2005). Global warming also enhances stratification, causing flagellates to outcompete diatoms in the nutrient-poor surface waters. Many jellyfish have broad diets and can feed satisfactorily on flagellates. However, flagellates are a poor food source for fish, so jellyfish may do better than their fish competitors and predators under warmer conditions (Parsons and Lalli, 2002).

Climate variability

Much of the impact of climate change on zooplankton is likely to act through existing modes of variability in the Earth's climate system. Such climate modes are expressed as differences in synoptic atmospheric pressure fields. These pressure fields alter regional windfields, current strengths, nutrient dynamics, and water temperatures (Ottersen *et al.*, 2001; Peterson and Schwing, 2003). The dominant mode of variability in the tropical Pacific is a strong multi-annual frequency, the El Niño Southern Oscillation (ENSO). Studies in the Pacific have demonstrated that ENSO influences the abundance of copepods (White *et al.*, 1995; Lavaniegos *et al.*, 2002; Mackas *et al.*, 2006) and jellyfish (Dawson *et al.*, 2001; Raskoff, 2001). At higher latitudes in the North Pacific, the dominant pressure field is the Pacific Decadal Oscillation (PDO), which can be considered a long-lived ENSO signal with a multidecadal fingerprint (Hare and Mantua, 2000). This index has been related to abundances of copepods (Peterson and Schwing, 2003; Chiba *et al.*, 2006), euphausiids (Brinton and Townsend, 2003), and jellyfish (Anderson and Piatt, 1999). The North Atlantic Oscillation (NAO) is the dominant mode of climate variability in the North Atlantic. There, it regulates the abundance and community structure of copepods (Fromentin and Planque, 1996; Bleckner and Hillebrand, 2002; Piontkovski *et al.*, 2006; Fernández de Puelles and Molinero, 2007) and jellyfish (Lynam *et al.*, 2004; Purcell and Decker, 2005).

At times, abrupt and dramatic changes in ecosystems occur in response to often subtle climate or physical oceanic forcing. Such abrupt reorganization, known as a regime shift, can transform systems from one stable state to another (Hare and Mantua, 2000). Once in a new state, it is difficult for the system to return

to its original configuration (Scheffer and Carpenter, 2003). As ecological systems can exhibit non-linear behaviour, subtle changes in climate phenomena can be amplified by responses of lower trophic levels, and these amplified signals can then be transmitted farther up the foodweb. The message here is that even subtle changes in climate can lead to large-scale reorganization of biological systems.

There is clear evidence that regime shifts are relatively common in the ocean, and there is even some evidence suggesting that they may be synchronous between ocean basins. A robust method of identifying regime shifts is to assemble a suite of physical and biological variables, perform a principal components analysis to identify the major pattern of variation in the multivariate physical and biological time-series, then use a sliding window analysis to determine rapid transitions in the series impartially. In a comprehensive analysis of 31 physical (ocean and atmosphere) and 69 biological time-series (from plankton to fish) in the North Pacific, Hare and Mantua (2000) identified two stepwise regime shifts, the first in 1977 and the second in 1989. More recent evidence suggests another regime shift in 1998 (Peterson and Schwing, 2003; Batten and Welch, 2004). These regime shifts exhibit dramatic, synchronous changes in atmospheric, oceanic, and biological variables. Applying a similar analytical approach to that of Hare and Mantua (2000), Weijerman *et al.* (2005) assembled 28 physical and 50 biological time-series from the North Atlantic. This analysis revealed remarkably similar timing of regime shifts there and in the North Pacific, viz. 1979 and 1988, and perhaps 1998. Taken together, these studies suggest shifts in climate–ocean interactions in close synchrony across the entire temperate zone of the northern hemisphere (Weijerman *et al.*, 2005).

The clearest example of the regulation of zooplankton by climate and a subsequent regime shift is for the PDO in the North Pacific. When the PDO is negative, upwelling winds strengthen over the California Current, there are cool ocean conditions in the Northeast Pacific, copepod biomass in the region is high and is dominated by large, cool-water species, and fish stocks such as coho salmon are abundant (Figure 7; Peterson and Schwing, 2003). In contrast, when the PDO is positive, upwelling in the region diminishes and warm conditions prevail, tropical species expand their range northwards, the copepod biomass declines and is dominated by small, less nutritious species, and the abundance of coho salmon plunges.

Such relationships between plankton composition or abundance and integrative climate indices provide a window of insight into how climate change may affect the world's oceans in the future, as climate models predict changes in many important climate indices. A pressing goal, therefore, is to improve our understanding of how zooplankton respond to climate indices. This is a key aim of the current SCOR (Scientific Committee on Oceanic Research) Working Group 125 Global Comparisons of Zooplankton Time Series, which is comparing plankton dataseries from around the world with relevant integrative climate indices. Complicating future predictions will be the possibility that, if climate change exceeds some critical threshold, some marine systems will switch to a new state that might not only be less favourable than the present one, but also prove impossible to reverse.

Projected ocean warming

Because of the considerable time-lag between the release of CO_2 into the atmosphere and the consequent warming of the
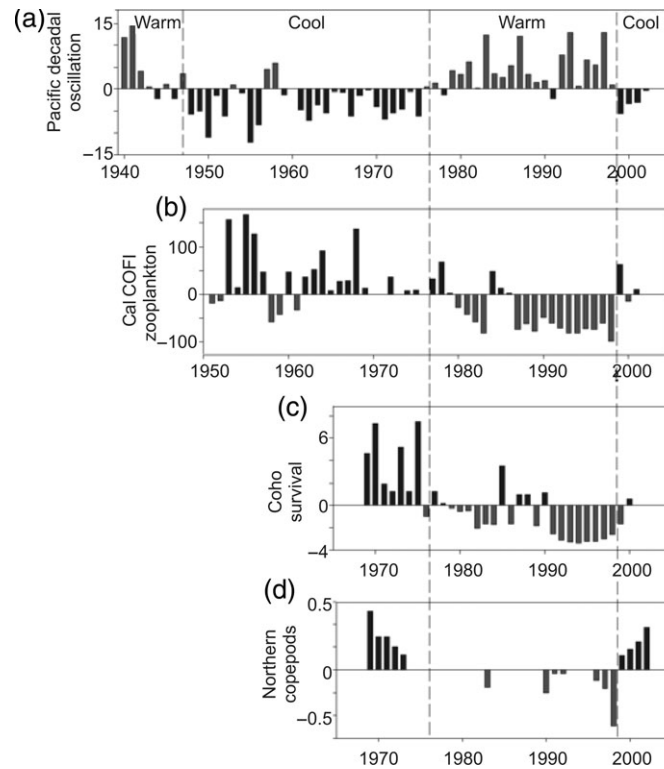
Figure 7. Time-series of (a) the PDO index summed annually over May–September; (b) annual anomalies of CalCOFI zooplankton volumes from the California Current region; (c) coho salmon survival; and (d) biomass anomalies of cold-water copepod species. Positive (negative) PDO index indicates warmer (cooler) than normal temperatures in coastal waters off North America (from Peterson and Schwing, 2003, with permission from AAAS).

atmosphere and ocean, there is little expected difference in the amount of warming anticipated under a range of emission scenarios by 2020–2029 (Figure 8; Bindoff *et al.*, 2007; IPCC, 2007a). However, by the 2090s, there are major differences among scenarios. By 2090–2099, mean global temperatures are projected to rise by ∼2°C under B1, a relatively low-emissions scenario, 2.75°C under A1B, a future of intermediate emissions, and 3.5°C under A2, a high-emissions scenario. Under the A2 scenario, climate models predict that most of the world's oceans will have warmed by 2–3.5°C by the end of this century, with the Arctic approaching 8°C warmer, and extremely warm temperatures penetrating south into Canada, Russia, and Scandinavia. Common to both periods presented is that the greatest warming is likely to occur over land and at northern latitudes, and least warming over the Southern Ocean and parts of the North Atlantic. This reduced warming in the North Atlantic is a consequence of the predicted slowing of the meridional overturning circulation during the 21st century; multimodel comparisons suggest a 25% reduction by 2100 under the A1B emission scenario. However, it is considered very unlikely that the meridional overturning circulation will undergo an abrupt transition during the 21st century.

Drivers of ocean productivity other than temperature will also be transformed by climate change. Ocean warming is likely to fuel more intense tropical cyclones that have faster maximum windspeeds and heavier rain events. Storms in mid- to high-latitudes are likely to move polewards, leading to changes in wind, precipitation, and temperature. Although it is impossible to know with certainty which emission scenario will most closely reflect future

emissions, what we do know is that we are currently tracking the very high end of emission scenarios, and thus the high end of projected warming from IPCC reports (Rahmstorf *et al.*, 2006). Irrespective of future emissions, some global warming is likely to continue for centuries to come, even if emissions are stabilized, because of time-lags in the system and the long time-scales required to remove CO_2 from the atmosphere (IPCC, 2007a).

Potential future impacts on zooplankton

Here, I briefly illustrate some of the approaches that are being used to probe the consequences of climate change on zooplankton, from the species to the ecosystem level. For brevity, I select two types of approach: a simple empirical approach and a more complex, mechanistic one. Other types of model are also useful for predicting future impacts; one of some interest is species distribution modelling (climate envelope modelling), which operates on the premise that an organism can only survive within a niche characterized by physical and chemical environmental factors. This approach has rarely been applied in marine systems, but is commonly used in terrestrial systems (e.g. Araújo and Rahbek, 2006). This modelling approach also allows one to investigate the effect of climate change on thousands of species, without requiring sophisticated and time-consuming mechanistic models that depend heavily on detailed knowledge of processes for each species, which are likely to be lacking for all but a few species. Another promising approach in marine systems is to force existing coupled population–physical models with output from climate models. Many population models that have been coupled to hydrodynamic models describe the life history, demography, and
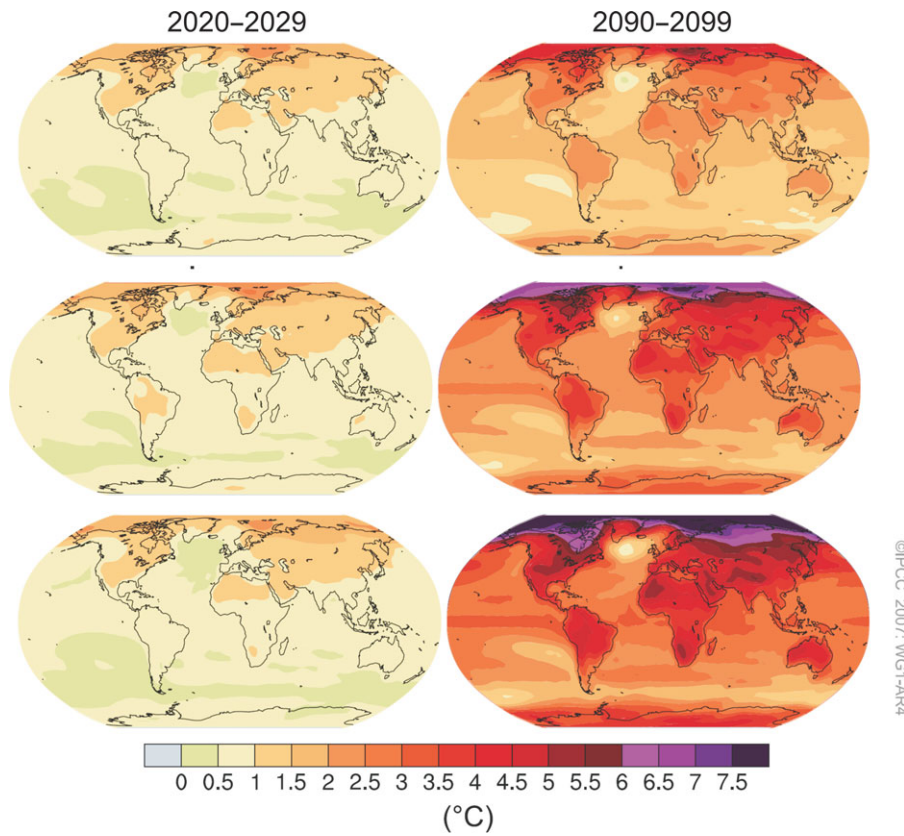
Figure 8. Projected surface temperature changes for decades early (2020–2029, left) and late (2090–2099, right) in the 21st century relative to 1980–1999. Panels show the GCM multimodel average projections for the B1 (top), A1B (middle), and A2 (bottom) emission scenarios. The three scenarios range from a relatively low emissions scenario (B1), through an intermediate scenario (A1B), to a high-emissions future (A2; from IPCC, 2007a, with permission).

survival of key members of the zooplankton (e.g. the spatio-temporal demographic model for *C. finmarchicus* in the Northeast Atlantic; Spiers *et al.*, 2005). Such models could be used relatively easily to investigate the impact of climate change on critical life-history processes.

Empirical correlative approaches

The simplest and usually initial approach to assessing the potential biotic responses to climate change is to use correlative relationships between zooplankton populations and an oceanic or atmospheric variable. Based on projections from GCMs, the relationship identified can then be used to assess future consequences. For example, Attrill *et al.* (2007) report a positive relationship between an index of jellyfish abundance from 1958 to 2000 and the positive phase of the NAO. This relationship was then used predictively by obtaining the projected future trajectory of the NAO over the 21st century under different climate scenarios (Figure 9). As GCMs are generally forecasting an increased prevalence of the positive NAO phase, Attrill *et al.* (2007) predict jellyfish blooms will increase substantially in the future. Such correlative environmental relationships are a favoured tool of marine ecologists, although caution is needed when identifying and interpreting the relationships (Myers, 1998). This type of empirical modelling is open to criticism for extrapolating beyond the range of the data when there is no mechanistic underpinning and has the implicit assumption that populations will be

regulated in the future similarly to the way they are now. This is clearly not always true; one of the best examples is the extremely tight inverse relationship from 1962 to 1992 ($r = -0.76$, $p < 0.01$, $n = 31$) between *C. finmarchicus* abundance in the Northeast Atlantic and the NAO, a consequence of the influence
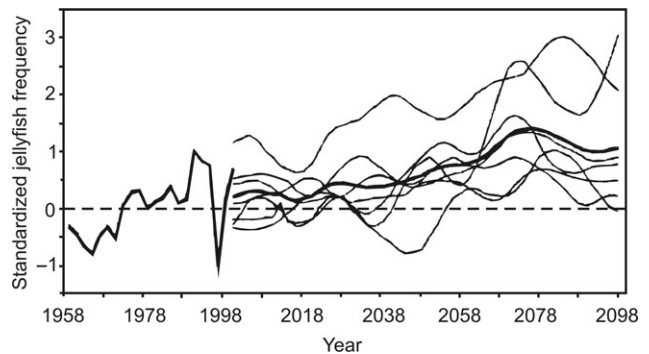

Figure 9. Predicted exploratory trends in jellyfish frequency in the west-central North Sea until 2100. Regression model between jellyfish and the NAO (initial solid line for existing data) coupled with outputs from NAO predictions under seven future climate change scenarios (Osborn, 2004; thin lines). The thick black line represents the mean for the seven scenarios (from Attrill *et al.*, 2007). Reprinted by permission of the American Society of Limnology and Oceanography, Inc.
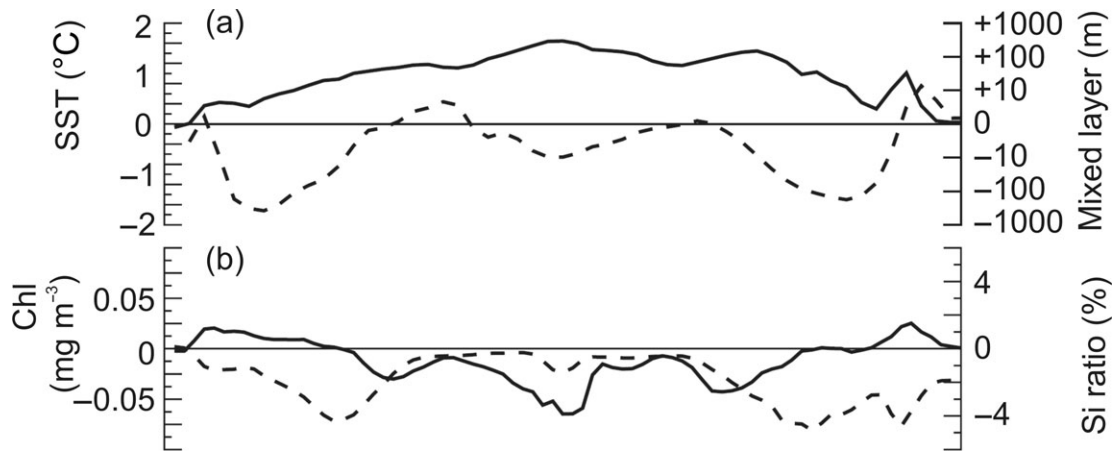
Figure 10. Zonally averaged change (global warming minus control) of (a) sea-surface temperature (solid line, °C) and mixed layer depth (broken line, m, log-scale); (b) surface chlorophyll (solid line, mg m^{-3}) and relative abundance of siliceous phytoplankton species (Si ratio, broken line, %; from Bopp et al., 2004).

of this climate index on westerly winds and temperature (Fromentin and Planque, 1996). This relationship broke down from 1996 on (Reid et al., 2003), presumably because conditions and circumstances underpinning the relationship changed. Temperatures in the region have warmed, resulting in a progressive northerly shift in distribution of C. finmarchicus in the Northeast Atlantic over the past 45 years in response to regional warming (Bonnet et al., 2005), and this is likely to have been especially strong over the very warm years of the past decade. As the NAO has different regional impacts on local hydroclimate (Ottersen et al., 2001), it is not surprising that a relationship linking the NAO to the abundance of C. finmarchicus may not be stable through time when the distribution of a species changes. Having said this, correlative approaches give testable predictions (albeit on a long time-scale) and provide a valuable starting point for building more mechanistic models that better capture underlying processes and may therefore provide better predictions.

Nutrient – phytoplankton – zooplankton modelling

As plankton occur in vast numbers, exhibit relatively simple behaviour, and are amenable to experimental manipulation and automated measurements, their dynamics are far more easily elucidated, modelled, and verified than higher trophic levels. This makes it easier to investigate potential impacts of climate change on plankton communities in a mechanistic way compared with higher trophic levels.

Dynamics of plankton communities at a first approximation are captured by nutrient–phytoplankton–zooplankton (NPZ) models. The basic biological units in such models are based on a functional group (guild) representation of plankton communities, where species with similar ecological function are grouped in guilds. NPZ models can be coupled to GCMs of the Earth's climate system, allowing investigation of the potential future states of plankton communities under alternative projections of climate.

Results from the NPZ model of Bopp et al. (2004, 2005) suggest that under doubling of pre-industrial CO_2 levels, global primary productivity may decline by 5–10%. This trend is not uniform, but indicates productivity increases of 20–30% in high latitudes and marked declines in the stratified tropical oceans (Figure 10).

This and other models generally suggest that warmer, more stratified conditions in the tropics will reduce nutrient concentrations in surface waters, which will lead to smaller phytoplankton cells dominating over larger diatoms, thereby lowering zooplankton biomass. A decrease in export production is also projected, reducing the oceanic uptake of CO_2 by lowering the efficiency of the biological pump. This could contribute to a positive feedback between climate change and the ocean carbon cycle, leading to rapid and potentially unstable climate shifts (Denman and Peña, 2002).

There is already observational evidence supporting some of these model projections. Decreased nitrate availability was apparent in the 20th century during warm periods in both hemispheres, and a decreasing trend is clearly evident globally since the 1970s (Kamykowski and Zentara, 2005). Ocean colour satellite data based on CZCS (1979–1986) and SeaWiFS (1997–2000) show that global ocean phytoplankton chlorophyll decreased 8% from the early 1980s to the late 1990s (Gregg and Conkright, 2002). Behrenfeld et al. (2006) demonstrate that global, depth-integrated chlorophyll biomass since 1999 has dropped by an average of 0.01 Tg year^{-1}. This decline was driven by El Niño-like climatic conditions that enhanced stratification in the expansive stratified low-latitude oceans and consequently reduced nutrient availability for phytoplankton. As some climate models predict more permanent El Niño conditions in a warmer system state, this study suggests that the abundance and productivity of plankton communities in the tropical oceans could decline in the future. There is also some evidence that global time-series of zooplankton abundance are declining in the tropical North Atlantic (Piontkovski and Castellani, 2007). Any future reductions in primary and secondary productivity and export production will not only reduce the food available for higher trophic levels in pelagic ecosystems, but will also impact deep ocean communities (Ruhl and Smith, 2004).

Potential future directions
Richer zooplankton functional groups

To achieve the breakthroughs needed to answer the many questions concerning the impact of climate change on zooplankton,

we need a better description of zooplankton functional groups, their habitat preferences, and ecosystem roles. Within NPZ models, phytoplankton components are being expanded and refined to include different functional groups such as centric and pennate diatoms, picoautotrophs, dinoflagellates, nanoflagellates, coccolithophores, and nitrogen-fixers (e.g. Le Quéré *et al.*, 2005), but there has been less progress to date on incorporating zooplankton functional groups. An example of more detailed, refined phytoplankton functional types is found in Smayda and Reynolds (2001), who describe dinoflagellate functional types for harmful algal blooms and their habitat preferences. Of course, for phytoplankton, automated discrimination techniques and satellite oceanography can often separate functional groups providing model validation; this is not as easy for zooplankton. Zooplankton researchers want answers to basic questions associated with climate change, such as whether jellyfish or ctenophores may increase, whether large crustaceans will be replaced by smaller ones, and whether we are likely to see ecosystems dominated by meroplankton of benthic species. Therefore, we need to develop more complete and meaningful zooplankton functional groups and implement these in appropriate models. Incorporating extra zooplankton complexity is laden with difficulties related to poorly understood ecology, scarcity of data, and the best way to aggregate diversity within functional groups. Zooplankton researchers could take a leaf out of the phytoplankton ecologists' book and progress towards richer zooplankton functional groups in global NPZ models.

A valuable step in this direction is the recent paper investigating the role of biogeochemical fluxes through mesozooplankton using an NPZ model (Buitenhuis *et al.*, 2006). Global NPZ models typically lump micro- and mesozooplankton into a single functional group, despite their different trophic roles, habitat preferences, and contributions to vertical carbon flux. Buitenhuis *et al.* (2006) parameterized the mesozooplankton separately from the microzooplankton and validated the model against biomass estimates. They found that food selection by mesozooplankton was currently not sufficiently quantified in the model. Salps are another important zooplankton group that must be included in NPZ models, because these gelatinous grazers have faecal pellets that sink rapidly and are thus an important source of carbon export from surface layers and provide a mechanism of pelagic–benthic coupling. Many other important zooplankton groups, such as jellyfish, that may be increasing in our oceans need to be included in ecosystem models. We must synthesize our knowledge of the identity, abundance, and key parameters needed for incorporating zooplankton functional groups into NPZ models. This is starting to happen. Le Quéré *et al.* (2005) have recently described a prototype "dynamic green ocean model" by identifying key zooplankton functional types, the key processes controlling their dynamics, and the sources of information necessary to parameterize these processes. Working with ecosystem modellers to incorporate additional zooplankton complexity will not only help answer our questions concerning the impacts of climate change on zooplankton, but it will also provide a better understanding of the feedback mechanism between marine ecosystems and climate.

Enhanced effort in tropical systems
Currently, we have far less understanding of how the phenology, distribution, community composition, and abundance of tropical pelagic systems will respond to climate change compared with their temperate counterparts. Most zooplankton research has been in northern hemisphere temperate systems, where environmental conditions and populations undergo marked seasonality. For example, the latest IPCC report indicates that, of the 28 586 biological dataseries globally in terrestrial systems that have revealed a significant change consistent with global warming, only 39 come from areas outside Europe and North America (IPCC, 2007b), highlighting the dearth of knowledge from tropical and southern hemispheric systems. Although observed and projected warming is greatest towards the poles (IPCC, 2007a), there will still be substantial warming in equatorial regions (Figure 8). In terms of zooplankton, only 4 of the 28 time-series (≥ 10 consecutive years) listed in Perry *et al.* (2004) are from tropical systems, and all of these are from upwelling areas. This situation is being redressed by amalgamating sampling programmes to form conglomerate time-series (Piontkovski and Castellani, 2007), and some existing programmes such as HOTS and BATS are now ~ 10 years long.

In a study of potential impacts of climate change on the tropical plankton community of the Great Barrier Reef, McKinnon *et al.* (2007) concluded that the effects of changes in nutrient enrichment processes in that region will outweigh changes in distribution and phenology. Certainly, phenology is likely to change less in relatively aseasonal tropical areas, where light is almost never limiting, compared with highly seasonal temperate and polar regions, where light is limiting in winter. In warm oligotrophic regions that dominate much of the world's oceans, small changes in nutrient enrichment will have profound implications for phyto- and zooplankton communities.

Investigating ecosystem resilience
Research on climate change impacts should not be performed in isolation but must be linked with research into impacts of other anthropogenic stressors on marine ecosystems. Marine systems that have already been highly modified by a host of anthropogenic stresses, such as fishing, eutrophication, pollution, and exotic pests, are less resilient to climate change (Jackson *et al.*, 2001; Hughes *et al.*, 2003; Pandolfi *et al.*, 2005; Poloczanska *et al.*, 2007). Marine systems already exhibit signs of heavy fishing pressure, with most fish species overexploited (Hilborn *et al.*, 2003), individual species shrinking in mean size (Ward and Myers, 2005), fishers harvesting smaller species (Essington *et al.*, 2006), and fishers needing to harvest from deeper waters (Watson *et al.*, 2004). Eutrophication is a major problem for coastal areas and can lead to jellyfish blooms (Mills, 2001). Introduced species can also have severe consequences for marine ecosystems (e.g. exotic ctenophores introductions in the Black Sea; Purcell, 2005). All these anthropogenic stresses decrease the resilience of marine ecosystems to climate change.

Some of the current leading conceptual thinkers in marine ecology have warned (e.g. Jackson *et al.*, 2001; Parsons and Lalli, 2002; Pandolfi *et al.*, 2005; Bakun and Weeks, 2006) that marine systems are undergoing abrupt shifts to unwanted stable states dominated by microbes, flagellates, bacterial mats, and jellyfish. These opportunistic species are capitalizing on ecosystems stressed by overfishing, eutrophication, pollution, and climate change.

If we are to minimize the impact of climate change on marine ecosystems, we cannot concentrate on climate change in isolation but must address the issue of the impact of human activities holistically. Our science must develop innovative ways to bolster ecosystem resilience to climate change. For example, zooplankton

communities will be more resilient to climate change if we develop new ways of minimizing ballast-water introductions, reducing nutrient inputs through improved farming practices, reducing pollution sources, and improving fishery management and compliance to reduce overexploitation of marine resources. These non-climate stressors can be managed faster than climate change by altering policy and management practices on national and regional scales (Poloczanska *et al.*, 2007). Applied integrated research that assesses management options for addressing synergistic effects of climate change, together with other human stressors, is urgently required.

A species-level zooplankton observing system

Although adopting a functional group approach is useful in modelling studies to simplify large and complex problems, species-specific information is essential in many circumstances. A common theme throughout this review has been the importance of particular species for interpreting climate change impacts. The clearest example of this need has been the replacement of *C. finmarchicus* by *C. helgolandicus*, as water has warmed in the North Sea, and the resulting mismatch between the spawning of cod in spring and the availability of a suitable food environment (see the section on distribution changes). This is despite these *Calanus* congeners being almost indistinguishable to all but the trained eye. Only with such a species-specific analysis could the causal link between food abundance and successful cod recruitment be made (Beaugrand *et al.*, 2003). Currently we must rely on skilled para-taxonomists for identification of samples collected at sea.

Almost all case studies highlighted in this review are the result of multidecadal monitoring programmes. Continuation of these time-series in the past has been extremely difficult at times. During the 1980s, 40% of the marine time-series that were initiated after World War II were discontinued because monitoring was viewed as poor science by administrators and many scientists (Duarte *et al.*, 1992). Monitoring programmes have experienced a renaissance since the 1990s, because it has been realized that long-term datasets are key to documenting and understanding impacts of climate change. This has markedly improved the support for many monitoring programmes (Hays *et al.*, 2005). We are fortunate to have the long-term zooplankton time-series that we do, the result of the persistence and vision of individual scientists decades ago. We must be aware when interpreting the impacts of climate change that almost all zooplankton time-series are no longer than 50 years in duration, and do not span the 1930s–1940s warm event (Hobson *et al.*, 2008).

Closer alliances with international initiatives, such as the Global Ocean Observing Systems (GOOS), may strengthen the long-term prospects of zooplankton time-series. A truly integrated marine observing system needs to have a strong biological component, otherwise it will run the risk of being able to detail future physical and chemical changes but be unaware of biological consequences. Monitoring the biological environment is part of GOOS, but it has often been overshadowed by the easier process of physical and chemical monitoring. Linking zooplankton time-series regionally and globally into a zooplankton observing system as a major component within GOOS may help mobilize long-term financial support from funding agencies.

I hope that this review helps to reinforce the compelling scientific case for the continued financial support for zooplankton observing systems.

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