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# Climate change and marine plankton

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**Understanding how climate change will affect the planet is a key issue worldwide. Questions concerning the pace and impacts of climate change are thus central to many ecological and biogeochemical studies, and addressing the consequences of climate change is now high on the list of priorities for funding agencies. Here, we review the interactions between climate change and plankton communities, focusing on systematic changes in plankton community structure, abundance, distribution and phenology over recent decades. We examine the potential socioeconomic impacts of these plankton changes, such as the effects of bottom-up forcing on commercially exploited fish stocks (i.e. plankton as food for fish). We also consider the crucial roles that plankton might have in dictating the future pace of climate change via feedback mechanisms responding to elevated atmospheric $CO_2$ levels. An important message emerges from this review: ongoing plankton monitoring programmes worldwide will act as sentinels to identify future changes in marine ecosystems.**

## The global importance of marine plankton

Oceans cover 71% of the surface of the Earth and thus we must strive to understand how a changing climate (the weather averaged over a long period of time) will affect the biota not only in terrestrial systems, but also in marine environments [1]. Oceans have a major role in the global carbon cycle and so directly impact the pace and extent of climate change [2]. Furthermore, the biota of the oceans have huge socioeconomic value, estimated at ~US$21-trillion $y^{-1}$ globally, through food production, recreation, nutrient recycling and gas regulation [3]. Climate impacts on the ocean biota might thus have widespread economic implications.

Given the importance of ocean biota, it is surprising that there are relatively few long time-series of biological measurements of marine environments. Plankton (Box 1) are particularly good indicators of climate change in the marine environment for several reasons. First, unlike other marine species, such as fish and many intertidal organisms, few species of plankton are commercially exploited; therefore, any long-term changes can be attributed to climate change. Second, most species are short lived and so population size is less influenced by the persistence of individuals from previous years. This leads to tight coupling between environmental change and plankton dynamics. Third, plankton can show dramatic changes in distribution because they are free floating and

### Box 1. What is plankton?

The word 'plankton' derives from the Greek 'planktos' meaning to 'drift' or 'wander' and is used to describe passively drifting small plants (phytoplankton) and animals (zooplankton) in aquatic systems. Although plankton can change their depth through active swimming and changes in buoyancy, they are unable to move independently of ocean currents. Plankton vary hugely in size from viruses and bacteria only a few microns in diameter up to jellyfish weighing 10s of kg.

For example, the coccolithophore *Emiliania huxleyi* (Figure Ia) is widespread in oceans worldwide. This species of phytoplankton can attain massive densities (up to 20 000 cells $ml^{-1}$) and cover 1000s of $km^2$. *Emiliania huxleyi* is thought to produce more calcium carbonate than any other organism on Earth and, as such, has a crucial role in the global carbon cycle. The external 'liths' or plates of chalk that the cells produce and then shed are highly reflective, and so their 'blooms' are readily identified by ship, aircraft and satellite [55,56], as shown in Figure Ib, a Landsat satellite image of a coccolithophore bloom off SW England in July 1999. Mesozooplankton, animals in the size range 0.2–20 mm (examples of which are shown in Figure Ic), and microzooplankton (20–200 μm) are key links in the food chain between phytoplankton and fish. Figure Id shows giant *Rhizostoma* jellyfish washed ashore in Wales. There is concern over whether climate change and overfishing will interact to cause jellyfish to replace fish in some ecosystems [10]. Scale bars = 1 μm (a), 20 km (b), 1 mm (c) and 15 cm (d). Reproduced with permission from (a) Claudia Sprengel, (b) Steve Groom and Andrew Wilson, (c) Peter Parks/imagequestmarine.com and (d) Jon Houghton.

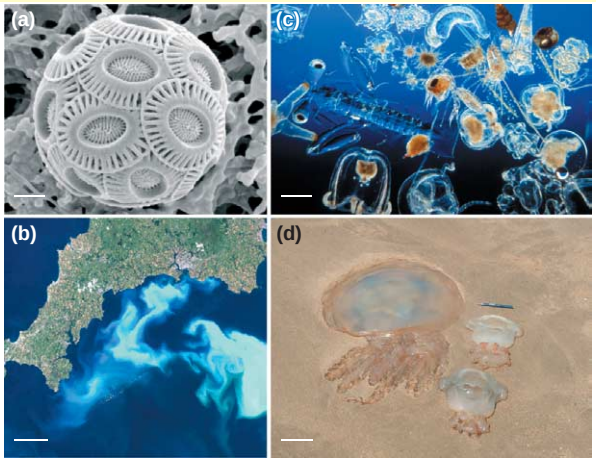


**Figure I.**

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**Box 2. History of the Continuous Plankton Recorder survey**

The typical sampling device for zooplankton is a simple ring net towed vertically, obliquely or horizontally slowly through the water. The first plankton to be sampled were crab and barnacle larvae collected by the surgeon J. Vaughan Thompson in 1828 [58]. Early work during the 19th century suggested that zooplankton were uniformly distributed throughout oceanic waters [59], with any differences observed being attributed to differences in the nets used. It was not until the invention of a new sampling device by Alister Hardy during the 1920s that this idea was finally overturned.

On the Discovery expedition of the Antarctic in 1926, Hardy collected continuous records of phyto- and zooplankton abundance that showed dramatically the patchiness of plankton [60]. He called the new sampling device the 'Continuous Plankton Recorder' (CPR) and it remains in use and little changed to this day (Figure Ia shows Hardy deploying one of the first CPR instruments). This extremely robust and durable device is towed near the surface over extended transects (up to several 1000 km), collecting plankton on a filtering silk [61]. The CPR is now the basis for the largest plankton survey in the world: the CPR survey. More than five million nautical miles have been towed in the North Atlantic (~30 times to the moon and back), resulting in the collection of 196 112 samples (Figure Ib shows the spatial coverage of the survey over the past 65 years). The abundance of ~450 phyto- and zooplankton taxa have been counted in each sample and much of our current understanding of the impacts of climate change on lower trophic levels comes from this survey.

The strength of the CPR survey lies in its unique ability to collect samples frequently over large spatial scales by using 'ships of opportunity', (i.e. any available vessel) and not just research ships. Other large-scale surveys are often conducted as part of fish stock surveys (because of cost constraints) and are thus usually collected annually, whereas samples that are collected frequently (weekly–monthly) are usually point samples taken close to the coast where they are subject to local coastal processes. The cost effective 'ship of opportunity' sampling method is now spawning new satellite surveys in the North Pacific [62] and the Southern Ocean [63], with more planned in the near future. Images reproduced with permission from the Sir Alister Hardy Foundation for Ocean Science.

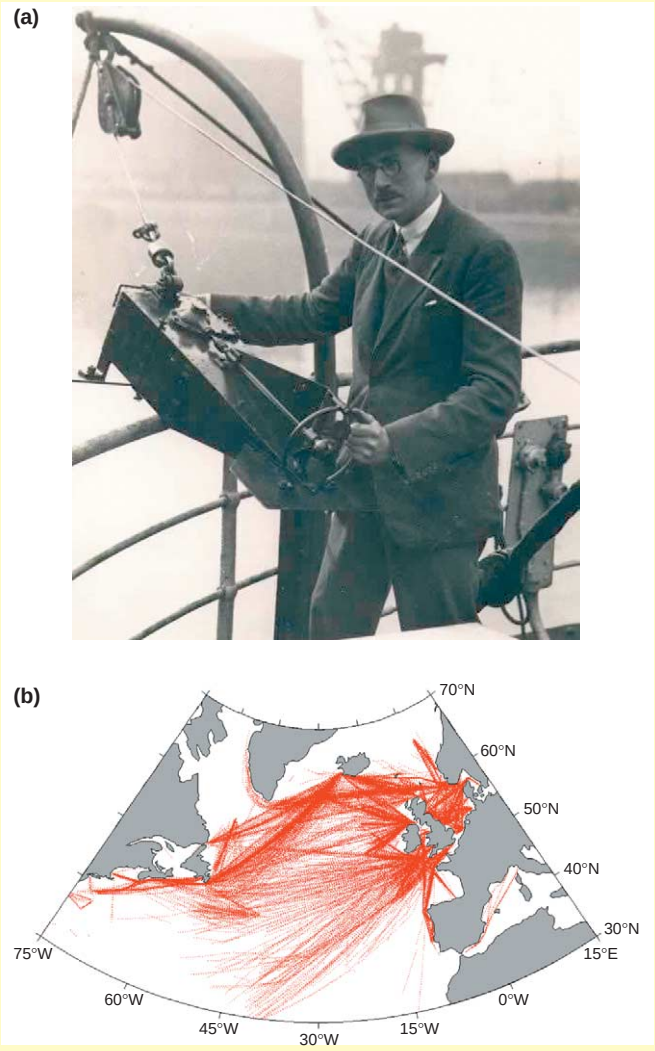


**Figure I.**

can respond easily to changes in temperature and oceanic current systems by expanding and contracting their ranges. Finally, recent evidence suggests that plankton are more sensitive indicators of change than are even environmental variables themselves, because the non-linear responses of biological communities can amplify subtle environmental perturbations [4].

Counterbalancing the potential benefits of using plankton to identify climate impacts on the ocean biota are several challenges. The first is related to sampling (Box 2) and, combined with the additional problem of funding research programmes (Box 3), means that there are relatively few long time-series of plankton abundance and distribution available (for a list of data sets mentioned here see Table 1; for a more-complete list of zooplankton time-series, see [5]; for plankton and nutrient dynamics, see [6]). Yet, those time-series (e.g. Figures 1,2) that do exist have proved invaluable for identifying some dramatic consequences of climate change.

## Links between plankton and climate

That we can make use of plankton to reveal the impact of climate is becoming increasingly evident as time-series lengthen (some have now been running for >50 years) and data-analysis techniques improve. There is strong evidence for systematic changes in plankton abundance and community structure over recent decades in many areas worldwide. Antarctic krill, which are a key component of the diet of whales and other marine mammals, have declined in abundance by more than an order of magnitude during the past 25 years [7]. This decline has been linked to reduced food availability for krill in the form of phytoplankton blooms in summer and ice algae in winter. The Humboldt Current, which is home to important commercial fisheries, is hugely impacted by the El Niño Southern Oscillation (ENSO), with phases of warm water leading to reduced plankton production (as a result of restricted nutrient upwelling) and, hence, to less food for fish [8]. Studies in the Benguela [9] and California [10]

**Box 3. The problems of maintaining long time-series**

A key problem in documenting and understanding the response of plankton to climate change has been the difficulty in maintaining long time-series. In spite of an exponential increase in the initiation of long-term physical, chemical and biological monitoring programmes in the ocean since World War II, 40% of these time-series were stopped during the 1980s because monitoring the environment was seen as poor science by science administrators [31]. This was particularly evident in the 1986–1987 funding crisis in France and the UK, which resulted in the closure or reduced spatial coverage of many surveys. For example, the Marine Biological Association (MBA; http://www.mba.ac.uk) of the UK had been sampling 30 zooplankton species from several stations off Plymouth since 1924 [64]. During 1987, all MBA plankton time-series were terminated [64] and it was not until 2001 that most were restarted. The CPR time-series was similarly affected during 1988, when it was closed down and all staff made redundant. Only a rescue package involving an international consortium of funding agencies helped save the survey. Even time-series that have remained operational expand and contract in line with funding levels. The CalCOFI programme off the coast of California began to sample mesozooplankton during 1949 using ring nets deployed at a regular grid of stations [65]. However, by the 1970s, funding cuts meant that the spatial coverage was reduced, with no sampling conducted in some years [10].

The negative perception of long-term monitoring only altered during the late 1990s, when the consequences of climate change were seen both scientifically and politically as being important. This has markedly improved the fortunes of plankton monitoring, with many new time-series starting up. In addition, work is now underway within existing sampling programmes to re-analyse archived samples in more detail: examples include the CalCOFI survey, the Benguela Current time-series, the Odate Project in Japan, and the time-series off Peru [44].

upwelling systems have shown dramatic changes in mesozooplankton (animals in the size range 0.2–20 mm, Box 1) abundance in relation to large-scale climate influences, also seen in jellyfish populations in the North Sea [11]. For example, between 1971 and 1986 in the North Sea, annual abundance of jellyfish co-varied with the North Atlantic Oscillation (NAO) index, a widely used measure of the weather each year in northern Europe. Although other factors, such as eutrophication and fishing cannot be ruled out as additional factors driving these long-term changes in jellyfish abundance, climate change is strongly implicated. Congruent long-term trends in abundance have also been observed between the freshwater zooplankton in Lake Windermere, UK, and marine mesozooplankton in the seas around the UK, providing further evidence for widespread climate effects on plankton [12].

Although the search for mechanistic links between climate and plankton continues, the impact of weather on the intensity of ocean mixing (and its reverse, ocean stratification) is likely to be central to the linkage. This intensity, in turn, affects light levels, surface temperatures and the magnitude of nutrient recycling from deep layers, thereby influencing phytoplankton growth and thus driving bottom-up processes (i.e. the role of members of one trophic level as food items for higher trophic levels) throughout the pelagic food chain [13].

### *Changes in organism distribution and event timing*

The distribution of organisms is a particularly sensitive indicator of climate change [14]. Range extensions in terrestrial systems in response to climate warming have been widely documented [15,16] and some striking examples also occur in plankton. Many members of the genus *Ceratium*, important primary producers in tropical and temperate waters, have expanded their range into warmer water [17,18]. For example, before 1970, *C. trichoceros* was only found south of the UK, but is now found off the west coast of Scotland and in the northern North Sea. Dramatic biogeographical shifts have also been documented for calanoid copepod assemblages (Figure 2 [19]). Warm-water assemblages have moved 1000 km further north in the Northeast Atlantic over the past 40 years, with a concomitant retraction in the range of cold-water assemblages.

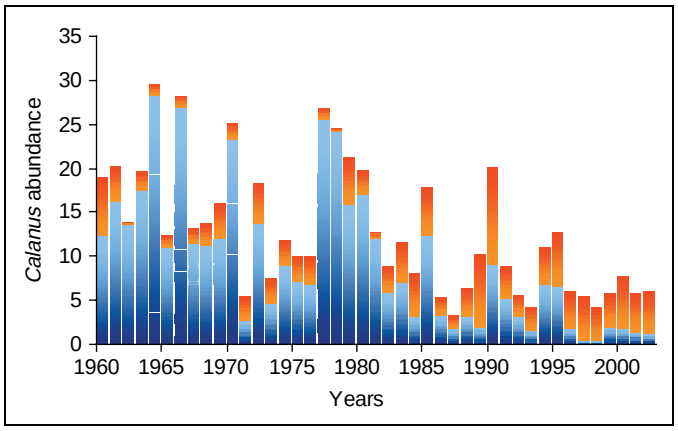


**Figure 1.** The abundance of *Calanus* populations in the North Sea from 1960 to 2002. This example serves to illustrate the type of plankton time-series now provided by long-standing projects, in this case the Continuous Plankton Recorder survey (see Box 2). The relative contribution of *Calanus finmarchicus* (blue) and *Calanus helgolandicus* (red) is shown in relation to total *Calanus* abundance. Reproduced with permission from Martin Edwards, Sir Alister Hardy Foundation for Ocean Science (http://www.sahfos.org).

Changes in the timing of important events, such as the onset of the seasons and El Niño, are also particularly responsive to climate change [14]. On land, it is clear that the on-set of spring is advancing in many areas, with earlier blooming of flowers and migration of butterflies [15]. Similar results have been noted for plants and animals at the base of the marine food web. For example, seasonal cycles of some copepods and gelatinous zooplankton in the German Bight occur earlier by up to 11 weeks during warm years [20]. Similarly, in the surface waters of the subarctic Pacific, the copepod *Neocalanus plumchrus*, which dominates the mesozooplankton biomass, has a seasonal timing of abundance that is tightly coupled with sea surface temperature, with the seasonal peak of abundance varying between early May and late July in warm and cold years, respectively [21]. Such extremes are not simply outliers owing to normal temperature and timing variation but form part of distinct trends.

Crucially, recent evidence from freshwater [22,23] and marine [24] systems suggests that a shift to earlier occurrences in response to increased water temperature is not consistent for all functional groups. For example, in the North Sea, phytoplankton blooms have generally advanced more in response to warming than have their zooplankton grazers [24]. It also appears that temporary members of the marine

**Table 1. Summary of oceanic biological, chemical and physical data sets**

| Name | Location | Description | Temporal coverage | Website |
|---|---|---|---|---|
| Atlantic Meridional Transect (AMT) | UK–South Atlantic | Physical, chemical and biological data, including bacterio-, phyto- and zooplankton | 1995–2005 (two per year) | http://www.amt-uk.org |
| Bermuda Atlantic Time-series Study (BATS) | Western Atlantic 31°40′N, 64°10′W | Physical, chemical and biological data, including bacterio-, phyto- and zooplankton | 1988–present | http://www.bbsr.edu/cintoo/bats/bats.html |
| British Atmospheric Data Centre (BADC) | Global | 103 atmospheric products | 1800s–present | http://www.badc.nerc.ac.uk |
| British Oceanographic Data Centre (BODC) | Mainly Northeast Atlantic | Physical, chemical, and biological data, including phyto- and zooplankton | Various | http://www.bodc.ac.uk |
| California Cooperative Oceanic Fisheries Investigations (CalCOFI) | Off California | Macrozooplankton biomass, physical and chemical data | 1949–present (semi-annual) | http://www-mlrg.ucsd.edu/calcofi.html |
| Continuous Plankton Recorder (CPR) Survey | North Atlantic (30–65°N) | Near-surface phyto- and zooplankton abundance data | 1931–present (monthly) | http://www.sahfos.org |
| Coastal and Oceanic Plankton Ecology, Production and Observation Database (COPEPOD) | Global | Listing of plankton data sets (currently 75) of phyto- and zooplankton abundance, biomass and composition. All data in a common format | Various | http://www.st.nmfs.gov/plankton/content/index.html |
| Hawaii Ocean Time-series program (HOT) | North Pacific Subtropical Gyre 22.75°N, 158°W | Physical, chemical and biological Data, including bacterio-, phyto- and zooplankton | 1988–present | http://hahana.soest.hawaii.edu/hot/hot_jgofs.html |
| ICES Oceanographic Database | North Atlantic | Physical, chemical, and biological data, including phyto- and zooplankton | 1800s–present | http://www.ices.dk/ocean |
| International Comprehensive Ocean-Atmosphere Data (ICOADS) | Global (1°×1°) | Monthly temperature, wind, cloudiness, sea-level and humidity measurements | 1860–2002 (monthly) | http://www.cdc.noaa.gov/coads/ |
| National Oceanographic Data Center (NODC) | Global | Physical, chemical, and phyto- and zooplankton data | 1800s–present | http://www.nodc.noaa.gov |
| Odate collection | Northwest Pacific | Zooplankton biomass | 1951–1990 (monthly-seasonally) | http://www.st.nmfs.gov/plankton/index.html |
| Pacific Decadal Oscillation (PDO) | North Pacific | Leading principal component of North Pacific monthly sea surface temperature variability poleward of 20°N | 1900–present (monthly) | http://tao.atmos.washington.edu/pdo/ |
| Southern Oscillation Index (SOI) | South Pacific | Monthly fluctuations in air pressure difference between Tahiti and Darwin | 1876–present (monthly) | http://www.cgd.ucar.edu/cas/catalog/climind/soi.html |
| Station PAPA | North Pacific (50°N, 145°W) | Zooplankton biomass, and physical and chemical data | 1956–present (monthly–seasonally) | http://www-sci.pac.dfo-mpo.gc.ca/osap/projects/linepdata/default_e.htm |
| Western English Channel (E1, L4) | English Channel 50°15′N, 04°13′W | Physical, chemical, and phyto- and zooplankton data | 1988–present (weekly–monthly) | http://www.pml.ac.uk/L4/ |
| Winter North Atlantic Oscillation (NAO) Index | North Atlantic | Difference in surface pressure anomalies between Lisbon and Reykjavik | 1864–2003 (annual) | http://www.cgd.ucar.edu/jhurrell/nao.html |

plankton ('meroplankton', e.g. species that are part of the seabed community for only part of their life cycle), such as some jellyfish and larvae of echinoderms and decapods, might be affected more by warming sea temperatures than are permanent members of the plankton ('holozooplankton'). Taken collectively, this disruption of synchrony between trophic levels in aquatic systems [25] could have severe implications for energy flow to higher trophic levels [26]. For example, over the past 45 years, the important North Atlantic copepod *Calanus finmarchicus* peaked in abundance 11 days earlier, considerably less than its potential food sources, such as the diatom *Rhizosolenia alata* (33 days earlier) and the common dinoflagellate *Ceratium tripos* (27 days earlier) [24].

### *Effects on regime shifts*

These impacts of climate change might be compounded by the tendency for aquatic systems to undergo major and abrupt reorganization in plankton and fish communities [27]. This concept of regime shifts, initially developed from mathematical models, reveals how changes in particular components of communities might lead to relatively rapid shifts between alternative steady states [28]. The term 'regime shift' is now widely used to describe pronounced and prolonged climate-linked changes in biological systems. There is evidence that such rapid shifts occurred in the northern Pacific during the mid-1970s [29] and in the North Sea during the mid-1980s [30]. In the North Sea, for example, the mid-1980s marked a shift from a predominance of cold-water to warm-water species, as the oceanic

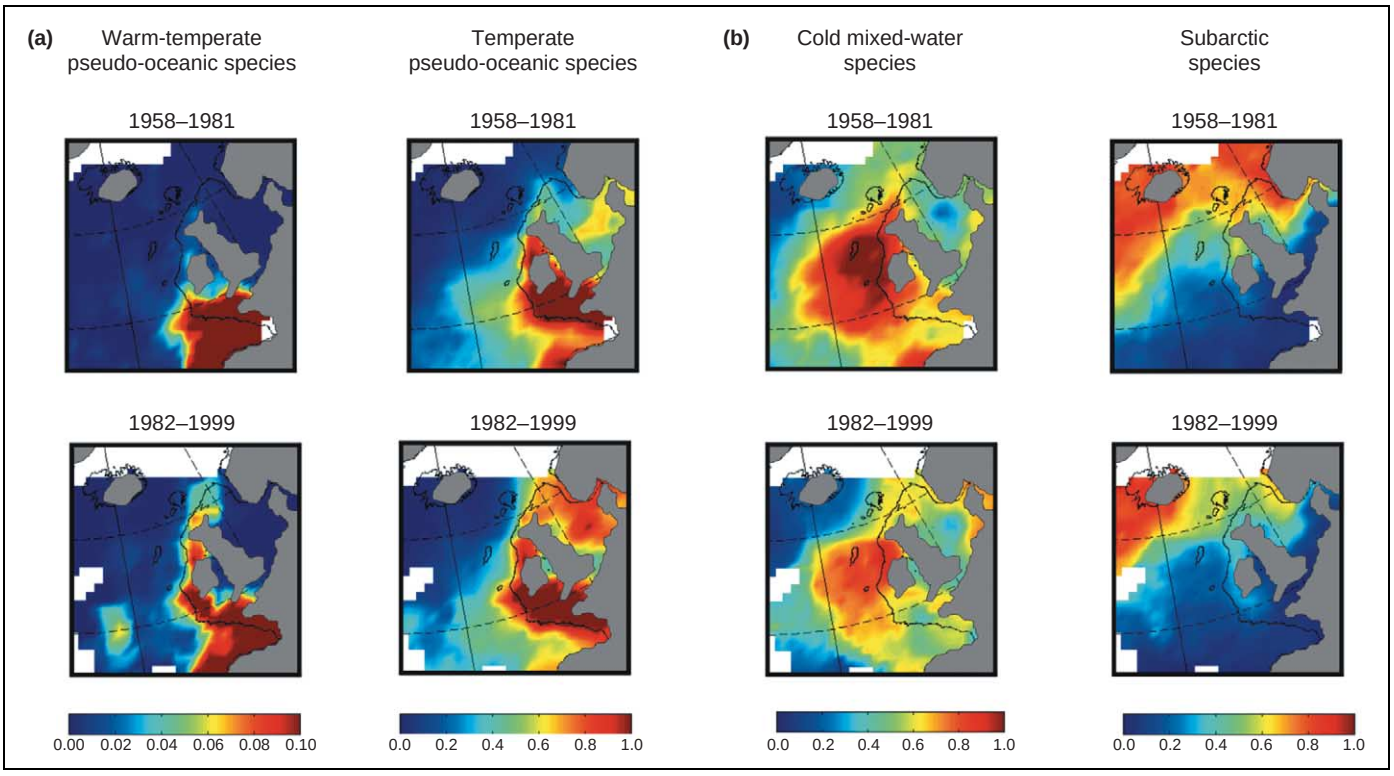


**Figure 2.** The northerly shift of mesozooplankton assemblages in the Northeast Atlantic. Analysis of assemblages based on a cluster analyses of calanoid copepod taxa from the CPR survey (see [57] for full description of these techniques) over broad spatial scales reveals (a) a northerly shift of ~1000 km for warmer-water species during the past 40 years, whereas colder-water species (b) have contracted their range. Scale is the mean number of species per assemblage, which provides an index of abundance. Pseudo-oceanic species occur maximally along shelf edges, mixed water species occur maximally at the boundary between warm and sub-arctic waters. Reproduced with permission from Gregory Beaugrand.

biogeographical boundary along the European continental shelf moved north [30,31].

In summary, there is now compelling evidence that major changes have occurred in the biota of the oceans and a range of studies have highlighted how plankton might be important harbingers of change in marine systems. These results are startling given that the pace of warming over recent decades is much slower than that predicted for the future [32].

## Plankton and ocean acidification

Most of the $CO_2$ entering the atmosphere through human activities dissolves in the oceans, increasing dissolved $CO_2$ and bicarbonate ion [$HCO_3^-$] concentration, and lowering seawater pH and carbonate ion [$CO_3^{2-}$] concentration. The increase in atmospheric $CO_2$ from a pre-industrial level of 280 μatm to the present level of 370 μatm has decreased surface ocean pH values by ~0.12 units to a pH value of 8.2. The direct effect on plankton of this increasing $CO_2$ concentration and decreasing pH is a topical issue in marine science.

Unabated, anthropogenic $CO_2$ emissions over the next few centuries are likely to produce changes in ocean pH that are greater than any over the past 300 million years [33]. These changes in pH and $CO_2$ concentration (a predicted decrease of 0.3 pH units and doubling of atmospheric $CO_2$ to 700 μatm by the end of this century) can have positive and negative effects on the growth of marine plankton [34], with a corresponding impact on their role as a net source or sink of $CO_2$ to the atmosphere.

The formation of organic matter during phytoplankton photosynthesis predominantly utilizes $CO_2$ dissolved in seawater and so provides a sink for atmospheric $CO_2$ ($CO_2 + H_2O = CH_2O + O_2$). Phytoplankton photosynthesis is stimulated (by a factor of 40 to 200%) by the increases in dissolved $CO_2$ associated with the predicted doubling of atmospheric $CO_2$ by 2100 [35]. Conversely, the production of calcium carbonate (calcification) by specialized phytoplankton, such as coccolithophores (Box 1), causes an increase in $CO_2$ and, therefore, acts as a potential source of $CO_2$ for the atmosphere. This is because the process of calcification utilizes bicarbonate, rather than dissolved $CO_2$, according to the equation $Ca^{2+} + 2HCO_3^- = CaCO_3 + CO_2 + H_2O$. $CO_2$ produced during calcification creates a negative feedback, because increasing $CO_2$ levels and the resultant decrease in pH inhibit calcification [36].

The ecological and biogeochemical interactions among calcifying plankton, non-calcifying plankton, seawater carbonate chemistry, and the resultant feedbacks to atmospheric $CO_2$ concentrations are complex [36–38]. Phytoplankton have differing sensitivities to $CO_2$ concentration and have a variety of mechanisms for carbon utilization. Thus, an increase in seawater $CO_2$ concentration will not only change the activity of individual phytoplankton species, but will also tend to favour some species over others. These shifts in phytoplankton community structure will influence the community structure of the higher trophic levels that are reliant upon phytoplankton as food and will also influence the cycling

of elements that differ between species (e.g. carbonate by calcifying organisms and silicate by non-calcifying organisms). Furthermore, the activity of bacteria (which produce $CO_2$) and the zooplankton (which consume phytoplankton) might also be affected by pH [39], resulting in changes in the structure and functioning of the marine ecosystem as a whole [40]. These ecological interactions are further complicated because seawater acidification will not occur in isolation. For example, surface temperatures are predicted to warm by 2–3°C over the next 100 years [32]. Such increases in temperature will affect the activity of the phytoplankton and the solubility of $CO_2$ in seawater. Thus, we still do not know whether plankton activity will mitigate or enhance increased atmospheric $CO_2$ caused by human activities.

### *Oceanic biogeochemical research programmes*

This unknown effect of plankton activity might be key to the overall pace of climate change and so the resolution of this uncertainty is high on the agenda of marine biogeochemists. Two recently initiated international biogeochemical programmes, the Surface Ocean Lower Atmosphere Study (SOLAS, http://www.uea.ac.uk/env/solas/) [41] and Integrated Marine Biogeochemistry Ecosystem Research (IMBER, http://www.imber.info/) [42], co-sponsored by the International Geosphere Biosphere Programme (IGBP, http://www.igbp.kva.se/) and the Scientific Committee on Oceanic Research (SCOR, http://www.jhu.edu/~scor/) aim to improve our understanding of the consequences of environmental changes, such as increasing anthropogenic $CO_2$. These programmes will incorporate large spatial- and temporal-scale monitoring of changes in surface water $CO_2$ and plankton activity, as well as experiments where large enclosures or 'mesocosms' of plankton communities are subjected to differing $CO_2$ levels [34]. In a separate initiative, the Royal Society of the UK (http://www.royalsoc.ac.uk/) has launched a review of the consequences of increased acidity levels on marine life.

## Implications for fisheries

As well as indicating climate change and affecting its pace, the reorganization of plankton communities might also have dramatic socioeconomic impacts through effects on commercial fisheries. During their larval stages, all fish consume zooplankton and some adult fish (e.g. mackerel *Scomber scombrus*) continue to be at least partly planktivorous. Synchrony between the peak in plankton abundance and the arrival of fish larvae in the plankton (the so-called 'match-mismatch hypothesis') is thought to be crucial in determining the survival of fish larval [26,43]. Consequently, the abundance and timing of mesozooplankton might affect fish recruitment (i.e. the amount of fish added to the exploitable stock each year), although the details of this linkage are only just being revealed.

For example, off the Peruvian coast (an area impacted by ENSO) bulk measures of mesozooplankton abundance (i.e. with no information about species composition) showed a long-term decline throughout the 1960s and 1970s, which has been linked to a decline in the commercial catches of anchovies [44]. However, the recovery of fish stocks in this area can only partly be explained by recent increases in the available mesozooplankton abundance measures. It might be that particular components of the mesozooplankton community have driven the recovery of fish stocks and, to explore this possibility, existing plankton samples are being reanalysed (Box 3). More-detailed plankton data are available for the North Sea, where there is huge interest in the stocks of cod *Gadus morhua* and other gadoids (members of the fish family Gadidae, which includes the cods, hakes and pollock). In spite of strong fishing pressure, gadoids increased in abundance during the 1970s, a phenomenon termed the 'gadoid outburst' [45]. Only recently has a detailed analysis of plankton data revealed that this outburst corresponded with a change in the dominant species of copepods in the North Sea [45]. During the gadoid outburst, larger copepods replaced smaller species at the time of year when cod larvae were developing. More food became available for larvae and this is believed to have increased gadoid recruitment. Recent poor recruitment of cod is thought to be explained at least partially by the recurrence of small copepods. There is also strong evidence that the return of salmon *Salmo salar* to homewaters in the Northeast Atlantic is related to the availability of plankton to juvenile salmon at sea [46]. The underlying message from such studies is clear: long-term changes in plankton can have a significant impact on commercial fish stocks.

## The way forward: synthesis of plankton time-series worldwide

Recent studies have provided tantalizing glimpses of the impacts that a changing climate might have on plankton communities. Through global comparisons of time-series, we are on the verge of making major breakthroughs in our understanding of how plankton are controlled by climate [5]. There are several reasons underlying this optimistic assessment, including the availability of long plankton time-series, accessibility of global environmental data sets, innovative synthesis techniques and new global initiatives.

As time-series lengthen, they become more valuable. Many of the long, well-established plankton time-series, such as CalCOFI (California Cooperative Oceanic Fisheries Investigations) and Station PAPA in the USA, Odate in Japan, and the Continuous Plankton Recorder (CPR) survey in the North Atlantic, now span >50 years. Some biogeochemical time-series, such as the Bermuda Atlantic Time-series Study (BATS) and Hawaii Ocean Time-series (HOT) programmes, have now been running for more than ten years [6,47,48].

There has also been an expansion in the number and type of time-series in response to the need for improved monitoring of global change (Table 1). For example, the US Volunteer-Observing-Ship (VOS) surveys now measure surface water dissolved $CO_2$ [49] and The Atlantic Meridional Transect (AMT) programme combines ecological and biogeochemical measurements on a 13 000-km biannual cruise track [50]. 'New' time-series have also been created by collating data from *ad hoc* synoptic surveys in large national and international databases

[e.g. the National Oceanographic Data Center (NODC), the ICES Oceanographic Database, the British Atmospheric Data Centre, the British Oceanographic Data Centre, and the new Coastal and Oceanic Plankton Ecology, Production and Observation Database (COPEPOD)]. More data are being added to these databases through initiatives to digitize historic data, and the stipulation by many government funding agencies to archive data collected at public expense. Although there are limits to the possibilities for this 'data archaeology', where data were simply not collected many decades ago (e.g. certain biogeochemical rate measurements), the types of global data set now available for many biotic and abiotic parameters show considerable promise.

Large-scale climate indices, along with local environmental information, are also now easily accessible. Large-scale indices capturing the variability in the climate system (based often on atmospheric pressure measurements, but sometimes on an aggregation of environmental variables), such as the North Atlantic Oscillation (NAO), the Northern Oscillation Index (NOI), the Pacific Decadal Oscillation (PDO) and the Southern Oscillation Index (SOI) are available on the Internet (Table 1). These large-scale drivers of biological variability act through local hydrology and meteorology, such as sea surface temperature, wind and ocean height, all of which have been measured remotely from satellite or recorded automatically by ocean buoys in recent times. Thus, these indices can act as proxies for local conditions that impact plankton. For environmental data stretching further back, the most complete quality-controlled data set is the International Comprehensive Ocean-Atmosphere Data (ICOADS), which has data from 1860 to 2002.

Integrating biological time-series with the amount of freely available environmental data will enable us to address more fully the global consequences of climate change for the biota of the oceans. We envisage that this comparative approach is best applied by 'replicating' tests of relationships across the globe by conducting the same analysis in different areas and combining the results in a statistically robust way. This type of meta-analysis can be used to answer questions concerning the magnitude of an effect, or whether relationships are positive or negative. Meta-analysis is a powerful method of quantitative data synthesis and has found wide applicability in ecology [15,51,52]. Researchers are starting to apply this approach more widely in studies identifying environmental forcing of trophic levels in the marine environment [13,53].

Although recent studies have shown conspicuous impacts of climate on plankton (summarized in [38]) a systematic comparison across the globe, or even across ocean basins, has yet to be achieved [5]. Lack of funding has been highlighted as one of the main impediments to such global comparisons [5]. Hopefully this situation will ameliorate from 2005 by the funding of a new SCOR Working Group on Zooplankton Time Series Analysis. This Group is tasked specifically with taking a global comparative approach to the climatic forcing of zooplankton. Such international efforts will provide the impetus for major breakthroughs in our understanding of how zooplankton will be impacted by climate change in the future.

## Conclusions

As concern over the impacts of climate change intensifies, a clear picture of major changes in plankton ecosystems over recent decades is emerging [54]. Changes in plankton abundance, community structure, timing of seasonal abundance and geographical range are now well documented, as are knock-on effects on commercial fisheries. However, it remains to be seen how the ocean biota itself might influence the pace of climate change. Ongoing plankton monitoring programmes around the world will act as sentinels to identify future changes in marine ecosystems. Crucial to identifying these future changes is the maintenance of plankton time-series and the funding of projects that continue to mine the unique data sets that these time-series provide.

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