## Chapter 12

# Sea Life (Pelagic and Planktonic Ecosystems) as an Indicator of Climate and Global Change

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## 1. PELAGIC AND PLANKTONIC ECOSYSTEMS

The marine pelagic realm is the largest ecological system on the planet occupying 71% of the planetary surface and a major part of the Earth's overall biosphere. As a consequence of this, pelagic ecosystems play a fundamental role in modulating the global environment via its regulatory effects on the Earth's climate and its role in biogeochemical cycling. Changes caused by increased warming on marine pelagic communities are likely to have important consequences on ecological structure and function thereby leading to significant feedbacks on the Earth's climate system.

This chapter will mainly concentrate on the epipelagic zone where biological production, biogeochemical cycles and marine food-webs are maintained by the inhabiting planktonic organisms. Apart from discussing the effects of climate on higher trophic organisms, particularly pelagic fish, the overall emphasis of this chapter is focused on the planktonic community. More specifically, the chapter will concentrate on observational evidence from contemporary plankton indicators over the past multidecadal period rather than palaeo planktonic indicators. The free floating photosynthesising life of the oceans (algal phytoplankton, bacteria and other photosynthesising protists), at the base of the marine food-web, provides food for the animal plankton (zooplankton) which, in turn, provide food for many other marine organisms ranging from the microscopic to whales. The carrying capacity of pelagic ecosystems in terms of the size of fish resources and recruitment to individual stocks as well as the abundance of marine wildlife (e.g., seabirds and marine mammals) is highly dependent on variations in the abundance, seasonal timing and composition of the plankton.

Phytoplankton also comprise approximately half of the total global primary production and play a crucial role in climate change through biogeochemical cycling and the export of the greenhouse gas to the deep ocean by carbon sequestration in what is known as the 'biological pump'. Phytoplankton have thus already helped to mitigate some of the climate effects of elevated $CO_2$ observed over the last 200 a with the oceans taking up ~40% of anthropogenic $CO_2$ [1]. In terms of feedback mechanisms on Earth's climate, it is speculated that these biological pumps will be less efficient in a warmer world due to changes in the phytoplankton composition favouring small flagellates [2] and less overall nutrient mixing due to increased stratification (see Section 1.1). It is also predicted that warmer temperatures would shift the metabolic balance between production and respiration in the world's oceans towards an increase in respiration thus reducing the capacity of the oceans to capture $CO_2$ [3]. Apart from playing a fundamental role in the Earth's climate system and in marine food-webs, plankton are also highly sensitive contemporary and palaeo indicators of environmental change and provide rapid information on the 'ecological health' of our oceans. There is some evidence that suggest that plankton are more sensitive indicators than environmental variables themselves and can amplify weak environmental signals due to their nonlinear responses [4]. A plankton species, defined by its abiotic envelope, in affect has the capacity to simultaneously represent an integrated ecological, chemical and physical variable.

## 1.1. Sensitivity of Pelagic and Planktonic Ecosystems to Climate and Global Change

Temperature is a key driver of marine ecosystems and, in particular, its effects on pelagic populations are manifested very rapidly [5–7]. This is hardly surprising when more than 99% of pelagic and planktonic organisms are ectothermal making them highly sensitive to fluctuations in temperature [8]. The rapidity of the planktonic response is predominantly due to their short life-cycles and its passive response to advective changes. For example, phytoplankton fix as much $CO_2$ per year as all terrestrial plants but due to being unicellular they represent at any one time only 1% of the Earth's biomass. This means the rate of turnover in the world's oceans is huge and on average the global phytoplankton population is consumed in days to weeks [9]. This all makes plankton tightly coupled to fluctuations in the marine environment and highly sensitive indicators of environmental change such as nutrient availability, ocean current changes and climate variability.

In the marine environment the effect of short-term climate variability and inter-annual variability on populations of higher trophic levels such as seabirds and whales can to a degree be somewhat buffered due to their longer life-cycles. In the long-term, their ability to undergo large geographical migrations may also help them to mitigate some of the effects of global change; however, this hypothesis has not been investigated. In both cases, this is not applicable to planktonic organisms. Biologically speaking, changes in temperature have direct consequences on many physiological processes (e.g., oxygen metabolism, adult mortality, reproduction, respiration, reproductive development, etc.) and control virtually all life-processes from the molecular to the cellular to whole regional ecosystem level and biogeographical provinces. Ecologically speaking, temperature also modulates both directly and indirectly species interactions (e.g., competition, prey–predator interactions and food-web structures), ultimately, changes in temperatures can lead to impacts on the biodiversity, size structure and functioning of the whole pelagic ecosystem [10,11].

While, temperature has direct consequences on many biological and ecological traits, it also modifies the marine environment by influencing oceanic circulation and by enhancing the stability of the water-column and hence nutrient availability. The amount of nutrients available in surface waters directly dictates phytoplankton growth and is the key determinant of the plankton size, community and food-web structure. In terms of nutrient availability, warming of the surface layers increases water column stability, enhancing stratification and requiring more energy to mix deep, nutrient-rich waters into surface layers. Particularly warm winters will also limit the degree of deep convective mixing and thereby limit nutrient replenishment necessary for the following spring phytoplankton bloom. In summary, climatic warming of surface waters will increase the density contrast between the surface layer and the underlying nutrient-rich waters. The availability of one of the principle nutrients (nitrate) that limits phytoplankton growth has therefore been found to be negatively related to temperatures globally [12,13]. Similarly, a global analysis of satellite derived chlorophyll data shows a strong inverse relationship between Sea Surface Temperatures (SST) and chlorophyll concentration [9]. Furthermore, other abiotic variables like oxygen concentration (important to organism size and metabolism [14]), nitrate metabolism [15] and the viscosity of seawater (important for the maintenance of buoyancy for plankton) are also directly linked to temperature. So unlike terrestrial environments, where precipitation plays a key role, the chemical and upper-ocean temperature regime in open oceans and its consequent biological composition are inexorably entwined.

## 1.2. Marine and Terrestrial Biological Responses to Climate and Global Change

Many planktonic organisms live in narrow temperature ranges (stenothermal) and often undergo a much more rapidly observed change due to temperature, be it biogeographically or phenologically [10,11], in comparison to their terrestrial counterparts [16]. Apart from this and the fact that planktonic organisms having shorter life-cycles, already mentioned above, there are a number of distinct reasons why the speed of the response to climate and global change of pelagic organisms differs from those of terrestrial organisms. Some of the primary reasons are, firstly, due to the high specific heat of water in open ocean systems many planktonic organisms are largely buffered against extremes in daily and seasonal temperature fluctuations. Daily and seasonal variations in temperature are therefore less variable in comparison to the terrestrial domain allowing marine species to become firmly embedded in their optimum thermal envelope. Secondly, unlike terrestrial environments, many planktonic organisms can quickly track evolving bioclimatic envelopes by being largely free of geographical barriers hindering their dispersal range and do not need a large amount of energy expenditure to do so, being primarily passively advected. Ocean currents, therefore, provide an ideal mechanism for dispersal over large distances and this is seemingly why a vast many of marine organisms have evolved at least a portion of their life-cycles as planktonic entities. Thirdly, many terrestrial organisms are geographically and ecologically bound by their habitat type mainly dictated by the vegetative composition. In terrestrial systems, the development of these vegetative types can be particularly slow moving (e.g., forest ecosystems) and hence organisms that rely on this habitat will be restricted in terms of their geographical spread. This is not the case for phytoplankton that have extremely short life-cycles in comparison allowing rapid temporal and spatial spread of planktonic herbivores and associated communities. Furthermore, the presence of inimitably terrestrial anthropogenic pressures such as habitat fragmentation and habitat loss, which clearly limits the geographical spread of organisms in the terrestrial environment, is seemingly absent from open ocean systems [17].

### 1.3. Ocean Acidification and other Anthropogenic Influences on Pelagic and Planktonic Ecosystems

While temperature, light and nutrients are probably the most important physical variables structuring marine ecosystems, the pelagic realm will also have to contend with, apart from global climate change, with the impact of anthropogenic $CO_2$ directly influencing the pH of the oceans [18]. Evidence collected and modelled to date indicates that rising $CO_2$ has led to chemical changes in the ocean which has led to the oceans becoming more acidic. Ocean acidification has the potential to affect the process of calcification and therefore certain planktonic organisms (e.g., coccolithophores, foraminifera, pelagic molluscs) may be particularly vulnerable to future $CO_2$ emissions. Apart from climate warming, potential chemical changes to the oceans and its affect on the biology of the oceans could further reduce the ocean's ability to absorb additional $CO_2$ from the atmosphere which, in turn, could affect the rate and scale of global warming (see Chapter 21). Other anthropogenic driving forces of change that are operative in pelagic ecosystems are predominantly overfishing and its effect on modifying marine pelagic food-webs [19], (see Chapter 14) and in coastal regions nutrient input from terrestrial sources leading in some cases to enhanced biological production and Harmful Algal Blooms (HABs) and other general chemical and inorganic contaminants. The impacts of atmospheric derived anthropogenic nitrogen on the open ocean have only been recently investigated but may also play a significant role on annual new marine biological production [20].

## 2. OBSERVED IMPACTS ON PELAGIC AND PLANKTONIC ECOSYSTEMS

There is a large body of observed evidence to suggest that many pelagic ecosystems, both physically and biologically are responding to changes in regional climate caused predominately due to the warming of air and SST and to a lesser extent by the modification of precipitation regimes and wind patterns. The biological manifestations of rising SST have variously taken the form of biogeographical, phenological, biodiversity, physiological, species abundance changes and whole ecological regime shifts. Any observational change in the marine environment associated with climate change, however, should be considered against the background of natural variation on a variety of spatial and temporal scales. Recently, long-term decadal observational studies have focused on known natural modes of climatic oscillations at similar temporal scales such as the El Nino-Southern Oscillation (ENSO) in the

Pacific and the North Atlantic Oscillation (NAO) in the North Atlantic in relation to pelagic ecosystem changes (see reviews [21,22]). Many of the biological responses observed have been associated with rising temperatures. However, approximating the effects of climate change embedded in natural modes of variability, particularly multidecadal oscillations like the Atlantic Multidecadal Oscillation (AMO) [23], is extremely difficult and therefore observed evidence of planktonic changes directly attributable to anthropogenic climate and global change must be treated with a degree of scientific caution.

Evidence for observed pelagic changes is also biased towards regions, particularly seas around Europe and North America, which have had some form of biological monitoring in place over a consistently long period. Apart from a number of important long-term coastal research stations sampling plankton (e.g., Helgoland Roads time-series in the southern North Sea [24]) there are only a few long-term biological surveys that sample the open ocean. For this reason some of the strongest evidence detected for observed changes in open ocean ecosystems comes from the North Atlantic where an extensive spatial and long-term biological survey exists in the form of the Continuous Plankton Recorder (CPR) survey. The CPR survey has been in operation in the North Sea and North Atlantic since 1931 and has systematically sampled up to 500 planktonic taxa from the major regions of the North Atlantic at a monthly resolution [25]. Important multidecadal evidence from the Pacific is mainly derived from the Californian Cooperative Oceanic Fisheries Investigations (CalCOFI) survey operating off the coast of Californian since 1949.

## 2.1. Biogeographical Changes and Northward Shifts

Some of the strongest evidence of large-scale biogeographical changes observed in our oceans comes from the CPR survey. In a study geographically encompassing the whole NE Atlantic over a 50 year period, Beaugrand et al. [10] showed rapid northerly movements of the biodiversity of a key zooplankton group (calanoid copepods). During the last 50 years there has been a northerly movement of warmer water plankton by 10° latitude in the northeast Atlantic and a similar retreat of colder water plankton to the north (a mean poleward movement of between 200 and 250 km per decade) (Fig. 1). This geographical movement is much more pronounced than any documented terrestrial study, mainly due to advective processes and in particular the shelf-edge current running north along the northern European continental shelf. The rapid movement of plankton northward is only seen along the continental shelf, where deeper water is warming much more rapidly. Further along the shelf, plankton are upwelled from this deeper water to make an appearance in the surface plankton community. Hence the plankton have moved 10° latitude northward via mainly deep water advective processes not seen in the movement of surface isotherms. In other areas in the North

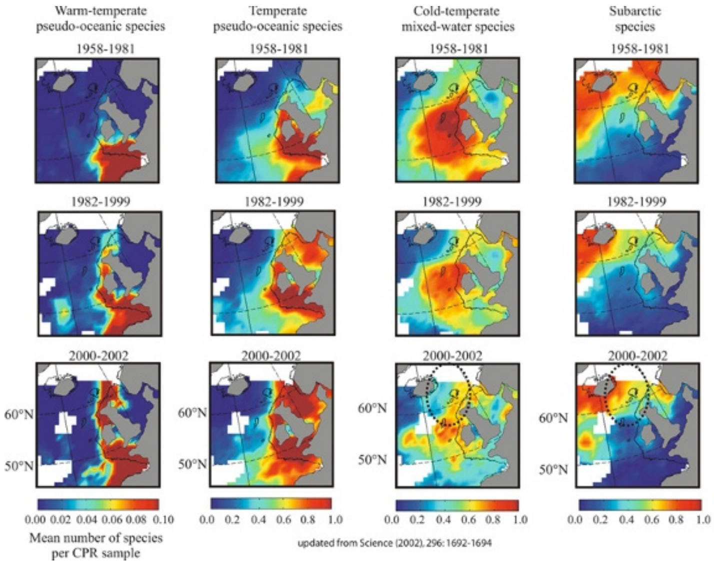

**FIGURE 1** Changes in the geographical distribution of four different plankton assemblages over a multidecadal period. There has been a rapid northerly movement of warm-temperate species and a subsequent decline in sub-arctic species over 40 years. Particularly rapid movement is observed along the European Continental Shelf. Data derived from the Continuous Plankton Recorder survey. Updated from Ref. [76].

East Atlantic the plankton shifts were more moderate and varied between 90 and 200 km per decade, still faster than any other documented terrestrial study which has a meta-analytic average of 6 km per decade [16]. Similar to the North Atlantic, in the north-east Pacific there has been a general increase in the frequency of southern species moving northward [26]. Interestingly, in the North West Atlantic, pelagic organisms have been moving southward [27]. This initially seems to contradict general thinking of homogenous global climate warming throughout the world's oceans. However, this movement has been linked to the strengthening of the Labrador Current which has spread colder water southward over the last decade carrying pelagic organisms with cold-water affinities as far south as Georges Bank.

These large-scale biogeographical shifts observed in the plankton have also seen paralleled latitudinal movements of fish species distribution [28–30]. Northerly geographical range extensions or changes in the geographical distribution of fish populations have been recently documented for European Continental shelf seas and along the European Continental shelf edge [31–33]. Similar to the plankton, the largest movements of fish species towards north have also been observed along the European Continental shelf. These geographical movements have been related with regional climate warming and are predominantly associated with the northerly geographical movement of fish species with more southern biogeographical affinities. These include the movement of pelagic fish species such as sardines and anchovies northward in the North Sea and red mullet and bass extending their ranges northward to western Norway [31,32]. New records were also observed over the last decade for a number of Mediterranean and north-west African species on the south coast of Portugal [32]. The cooling and the freshening of the north-west Atlantic over the last decade has had an opposite effect similar to the plankton patterns, with some groundfish species moving further south in their geographical distribution [34]. Northerly range extensions of pelagic fish species have also been reported for the Northern Bering Sea region related to regional climate warming [35]. Climate variability and regional climate warming have also been associated with variations in the geographic range of marine diseases [36]. New diseases typically have emerged through host or range shifts of known pathogens. For example, over the past few decades pathogens detrimental to oysters have spread from the mid-Atlantic states into New England [36]. In comparison to terrestrial systems, epidemics of marine pathogens can spread at extremely rapid rates [37].

Again it is noteworthy that fish with northern distributional boundaries in the North Sea have shifted northward at rates of up to three times faster than terrestrial species [16,30]. One of the largest biogeographical shifts ever observed for fish species is the dramatic increase and subsequent geographical spread northward of the Snake Pipefish (*Entelurus aequreus*). Once confined mainly to the south and west of the British Isles before 2003, it can now be found as far north as the Barents Sea and Spitzbergen [38]. While this present discussion has described surface geographical changes in epipelagic organisms it is worth remembering the three-dimensional nature of the pelagic environment. Recent research has observed not just changes in fish biogeography but also changes in fish species depth (towards deeper waters) in response to climate warming [39]. This change can be seen as analogous with the upward altitudinal movement of terrestrial organisms in alpine environments. All these studies highlight the consistency of pelagic organisms undergoing large-scale distributional changes in response to hydro-climatic variability.

## 2.2. Life-Cycle Events and Pelagic Phenology

Phenology, or repeated seasonal life-cycle events such as annual migrations or spawning, is highly a sensitive indicator of climate warming. This is because many terrestrial and marine organisms, apart from photoperiod, are dependant on temperature as a trigger for seasonal behaviour. In the terrestrial realm, phenology events such as bird migrations, egg-laying, butterfly emergence and flowering of certain plants are all getting earlier in response to milder spring weather [16]. In terms of the pelagic phenological response to climate warming, many plankton taxa have also been found moving forward in their seasonal cycles [11]. In some cases, a shift in seasonal cycles of over 6 weeks was detected, again a far larger shift than observed for terrestrial based observations. Summarising a terrestrial study of phenology using over 172 species of plants, birds, insects and amphibians, Parmesan & Yorke [16] calculated a mean phenological change of 2.3 d. It is thought that temperate pelagic environments are particularly vulnerable to phenological changes caused by climatic warming because the recruitment success of higher trophic levels is highly dependant on synchronisation with pulsed planktonic production [11]. Furthermore in the marine environment, and just as important, was the response to regional climate warming varied between different functional groups and trophic levels, leading to mismatch in timing between trophic levels (Fig. 2). For example, while the spring bloom has remained relatively stable in seasonal timing over five decades (mainly due to light limitation and photoperiod rather than temperature dictating seasonality [11,40]) many zooplankton organisms as well as fish larvae have moved rapidly forward in their seasonal cycles.

These changes, seen in the North Sea, have the potential to be of detriment to commercial fish stocks via trophic mismatch. For example, regional climate warming in the North Sea has affected cod recruitment via changes at the base of the food-web [41]. Cod, like many other fish species, are highly dependent on the availability of planktonic food during their pelagic larval stages. Key changes in the planktonic assemblage and phenology, significantly correlated with the warming of the North Sea over the last few decades, have resulted in a poor food environment for cod larvae and hence an eventual decline in overall recruitment success. The rapid changes in plankton communities observed over the last few decades in the North Atlantic and European regional seas, related to regional climate changes, have enormous consequences for other trophic levels and biogeochemical processes. Similarly, other pelagic phenology changes have been observed in the North Sea [24], the Mediterranean [42] and the Pacific [43,44].

## 2.3. Plankton Abundance and Pelagic Productivity

Contemporary observations of satellite-*in situ* blended ocean chlorophyll records indicate that global ocean net primary production has declined over the last decade [9]. Although this time-series is only 10 years in length it does show a strong negative relationship between primary production and SST and is evidence of the closely coupled relationship between ocean productivity and climate variability at a global scale. In the North Atlantic and over multidecadal periods, both changes in phytoplankton and zooplankton species and communities have been associated with Northern Hemisphere Temperature (NHT) trends and variations in the NAO index. These have included changes in species distributions and abundance, the occurrence of sub-tropical species

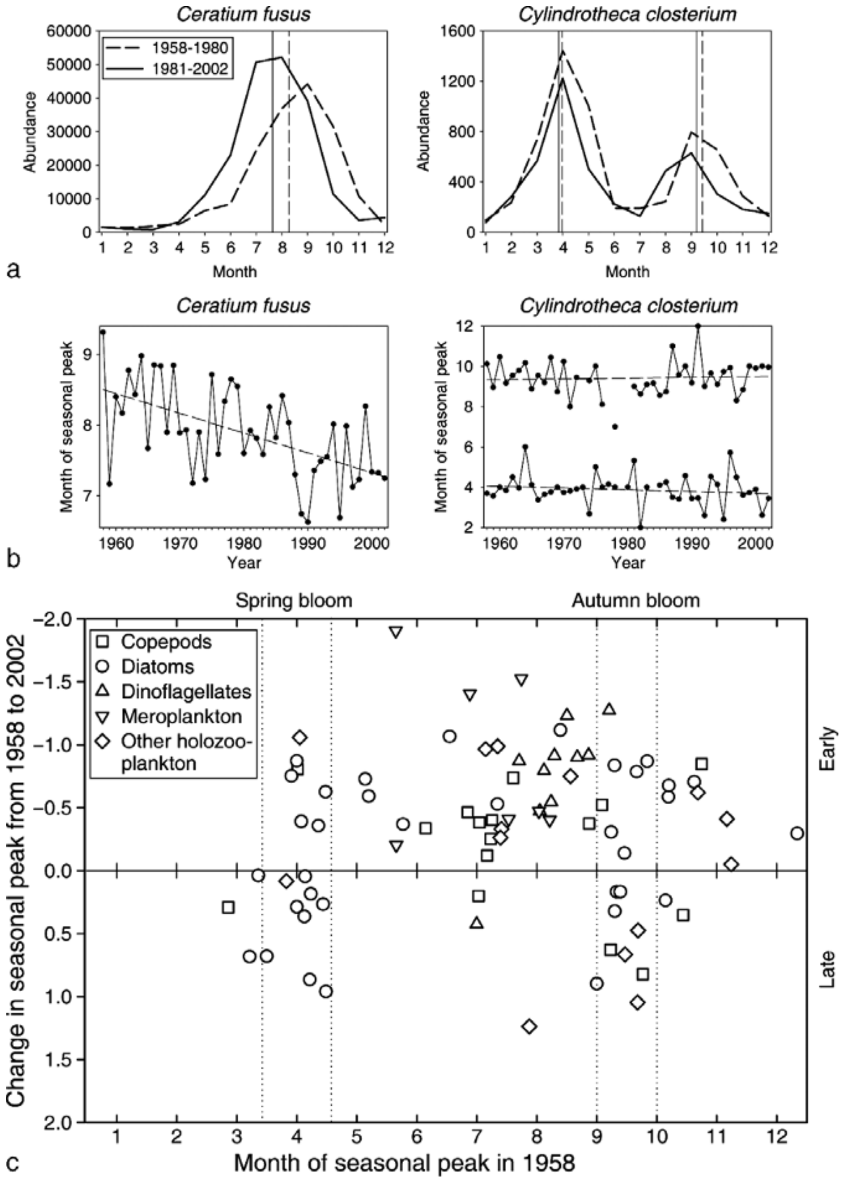

**FIGURE 2** (a) Seasonal cycles for two phytoplankton for the periods 1958–1980 and 1981–2002: the dinoflagellate *Ceratium fusus* and the diatom *Cylindrotheca closterium*. (b) Inter-annual variability of the seasonal peak for the above two species from 1958 to 2002. (c) The change in the timing of the seasonal peaks (in months) for the 66 taxa over the 45 a (year) period from 1958 to 2002 plotted against the timing of their seasonal peak in 1958. For each taxon, the linear regression in (b) was used to estimate the difference between the seasonal peak in 1958 and 2002. A negative difference between 1958 and 2002 indicates seasonal cycles are becoming earlier. Standard linear regression was considered appropriate because there was minimal autocorrelation (determined by the Durbin–Watson statistic) in the phenology time series. From Ref. [11].

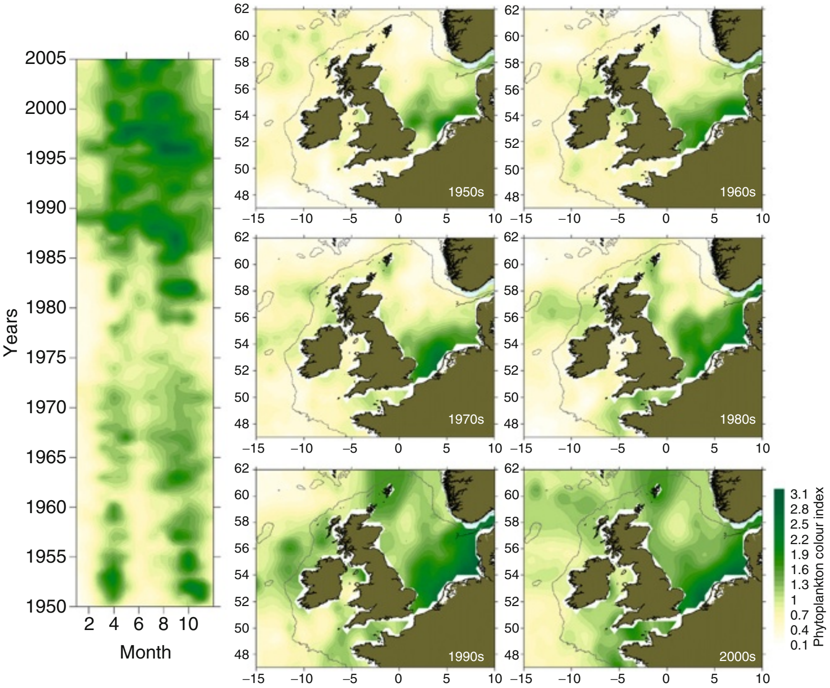

**FIGURE 3** Spatial-temporal maps of the changes in the abundance of phytoplankton colour (an index of total phytoplankton biomass) for the NE Atlantic averaged per decade from the 1950s to the present. The contour plot shows monthly mean values from 1950 to 2005 of phytoplankton colour averaged for the North Sea. Large increases in phytoplankton colour are observed towards the end of the 1980s and have continued since. The increase in colour has been associated with a regime shift in the North Sea. Updated from Ref. [47].

in temperate waters, changes in overall phytoplankton biomass and seasonal length (Fig. 3), changes in the ecosystem functioning and productivity of the North Atlantic [10,11,45–52]. The increase in overall phytoplankton biomass in the North Sea has been associated with an increase in smaller flagellates which favour more warmer and stratified conditions [46,47]. Over the whole NE Atlantic there has been an increase in phytoplankton biomass with increasing temperatures in cooler regions but a decrease in phytoplankton biomass in warmer regions [53]. Presumably, this is a trade-off between increased phytoplankton metabolic rates caused by temperature in cooler regions but a decrease in nutrient supply in warmer regions. Regional climate warming in the North Sea has also been associated with an increase in certain HABs in some areas of the North Sea [54]. A recent link has been established between the changes in the plankton in the North Sea to sandeels and eventual seabird breeding success (encompassing four trophic levels) [55]. In the North

Sea, the population of the previously dominant and ecologically important zooplankton species (the cold water species *Calanus finmarchicus*) has declined in biomass by 70% since the 1960s [56]. Species with warmer-water affinities are moving northward to replace this species but these species are not as numerically abundant or nutritionally beneficial to higher trophic levels. This has had inevitably important ramifications for the overall carrying capacity of the North Sea ecosystem.

The ecological changes that have occurred in the North Sea since the late 1980s (predominately driven by change in temperature regime and more warmer winters) have also been documented for the Baltic Sea for zooplankton and fish stocks [57,58]. The related changes that have taken place in these Northern European waters are sufficiently abrupt and persistent to be termed as ‘regime shifts’ [59]. Similarly in the Mediterranean, zooplankton communities have also been linked to regional warming and the NAO index [60]. All these observed changes appear to be closely correlated to climate-driven sea temperature fluctuations. Indirectly, the progressive freshening of the Labrador Sea region, attributed to climate warming and the increase in freshwater input to the ocean from melting ice, has resulted in the increasing abundance, blooms and shifts in seasonal cycles of dinoflagellates due to the increased stability of the water-column [61]. Similarly, increases in coccolithophore blooms in the Barents Sea and HABs in the North Sea are associated with negative salinity anomalies and warmer temperatures leading to increased stratification [54,62].

In the Benguela upwelling system in the South Atlantic, long-term trends in the abundance and community structure of coastal zooplankton have been related to large-scale climatic influences [63]. Similarly, changes in mesozooplankton abundance have also been related to large-scale climate influences in the Californian upwelling system [64]. The progressive warming in the Southern Ocean has been associated with a decline in krill [65] and an associated decline in the population sizes of many seabirds and seals monitored on several breeding sites [66,67]. In the Southern Ocean the long-term decline in krill stock has been linked to changes in winter ice extent which in turn has been related to warming temperatures [65]. Changes in the abundance of krill have profound implications for the Southern Ocean food-web. The progressive warming of the Southern Ocean has also been associated with the decline in the population sizes of many seabirds and seals monitored on several breeding sites [67]. Recent investigations of planktonic foraminifera from sediment cores encompassing the last 1400 a has revealed anomalous changes in the community structure over the last few decades. The study suggests that ocean warming as already exceeded the range of natural variability [68]. A recent major ecosystem shift in the northern Bering Sea has been attributed to regional climate warming and trends in the Arctic Oscillation [35]. Decadal changes in zooplankton related to climatic variability in the west sub arctic North Pacific have also been observed [69] and in the Japan/East Sea [70].

Many changes in abundance of marine commercial fish stocks have been observed over the last few decades in the Atlantic and Pacific Oceans but it is extremely difficult to separate, in terms of changes in population densities and recruitment, regional climate effects from direct anthropogenic influences like fishing. Geographical range extensions mentioned earlier or changes in the geographical distribution of fish populations, however, can be more confidently linked to hydro-climatic variation and regional climate warming. Similar to the observed changes in marine planktonic systems many long-term changes in pelagic fish populations have been associated with known natural modes of climatic oscillations such as ENSO and the Pacific Decadal Oscillation (PDO) in the Pacific and the NAO in the North Atlantic (see reviews: [5,21,22,26]). For example, variations in SST driven by NAO fluctuations have been linked to fluctuations in cod recruitment both off Labrador and Newfoundland and in the Barents Sea [71]. Populations of herring, sardine, salmon and tuna have also been related to fluctuations in the NAO index [5,45]. Warm events related to El Nino episodes and climate induced ecological regime shifts in the Pacific have been related to the disruption of many commercial fisheries [21,26,72]. These changes highlight the sensitivity of fish populations to environmental change. Direct evidence of biological impacts of anthropogenic climate change is, however, difficult to discern due to the background of natural variation on a variety of spatial and temporal scales and in particular natural oscillations in climate. A recent study based on a 50 a larval fish time-series from CalCOFI showed that exploited fish species were more vulnerable to the impacts of climate change than non-exploited species. The authors suggest that the enhanced response to environmental change of exploited species was due to a reduced spatial heterogeneity caused by fishery-induced age truncation and a restriction of geographic distribution that had accompanied fishing pressure [73].

## 2.4. Pelagic Biodiversity and Invasive Species

At the ocean basin scale studies on the pelagic biodiversity of zooplankton copepods are related to temperature and an increase in warming over the last few decades has been followed by an increase in diversity [74–76]. In particular, increases in diversity are seen when a previously low diversity system like Arctic and cold-boreal provinces undergo prolonged warming events. The overall diversity patterns of pelagic organisms, peaking between 20° and 30° north or south, follow temperature gradients in the world's oceans [77]. Similarly, phytoplankton show a relationship between temperature and diversity which is linked to the phytoplankton community having a higher diversity but an overall smaller size-fraction and a more complex food-web structure (i.e., microbial-based versus diatom based production) in warmer more stratified environments. Climate warming will therefore increase planktonic diversity throughout the cooler regions of the world's oceans as temperature isotherms shift poleward. However, the relationship between temperature and pelagic fish diversity is far more complex due to other anthropogenic pressures such as over fishing apparently playing a significant role in diversity patterns [19] (see Chapter 14).

Climate warming will open up new thermally defined habitats for previously denied non-indigenous species (e.g., sub-tropical species in the North Sea) and invasive species allowing them to establish viable populations in areas that were once environmentally unsuitable. Apart from these thermal boundaries limits moving progressively poleward and in some cases expanding, the rapid climate change observed the Arctic may have even larger consequences for the establishment of invasive species and the biodiversity of the North Atlantic. The thickness and areal coverage of summer ice in the Arctic have been melting at an increasingly rapid rate over the last two decades; to reach the lowest ever recorded extent in September 2007. In the spring following the unusually large ice free period in 1998 large numbers of a Pacific diatom *Neodenticula seminae* were found in samples taken by the CPR survey in the Labrador Sea in the North Atlantic. *N. seminae* is an abundant member of the phytoplankton in the subpolar North Pacific and has a well defined palaeo history based on deep sea cores. According to the palaeo evidence and modern surface sampling in the North Atlantic since 1948 this was the first record of this species in the North Atlantic for at least 800 000 a. The reappearance of *N. seminae* in the North Atlantic, and its subsequent spread southwards and eastwards to other areas in the North Atlantic, after such a long gap, could be an indicator of the scale and speed of changes that are taking place in the Arctic and North Atlantic oceans as a consequence of climate warming [78]. The diatom species may itself could be the first evidence of a trans-Arctic migration in modern times and be a harbinger of a potential inundation of new organisms into the North Atlantic. The consequences of such a change to the function, climatic feedbacks and biodiversity of Arctic systems are at present unknown.

## 3. CONCLUSION AND SUMMARY OF KEY INDICATORS

The case-studies highlighted in this review collectively indicate that there is substantial observational evidence that many pelagic ecosystems, both physically and biologically are responding to changes in regional climate caused predominately by the warming of SST, ocean current changes and to a lesser extent by the modification of precipitation regimes and wind patterns. The biological manifestations of climatic variability have rapidly taken the form of biogeographical, phenological, biodiversity, physiological, species abundance changes, community structural shifts and whole ecological regime shifts. Some of the most convincing evidence for the biological response to regional climate variability comes from the bottom of the marine pelagic food-web especially from phytoplankton and zooplankton communities. Many other responses associated with climate warming on higher trophic levels are also indirectly associated with changes in the plankton and imply bottom-up control of the marine pelagic environment. It is therefore assumed that one of the ways in which populations respond to climate is in part the determined by changes in the food-web structure where the population is embedded, with synchrony between predator and prey (match–mismatch) playing an important role.

At the species level, some of the first consequences of climate warming and global change are often seen in a species phenology (i.e., timing of annual occurring life-cycle events) and in species geographical distribution responses. This is mainly because temperature continually impacts the life cycle of the species and naturally the population will respond over time, providing it is not biotically restrained or spatially restricted, to its optimum position within its bioclimatic envelope. Whether this is within a temporal niche as in seasonal succession (observed as a phenological response) or in its overall biogeographical distribution (observed as a geographical movement in a population). These biological changes as well as those changes observed in biodiversity and planktonic abundance and productivity are perhaps the key indicators signifying the large scale changes occurring in our world's oceans as a consequence of climate and global change.

Summarising the observed case-studies, what particularly stands out in this review is the rapidity of the pelagic and planktonic response, be it biogeographically or phenologically, to climate warming and global change compared to their terrestrial counterparts. For example, plankton shifts of up to 200 km per decade [10] have been observed in the North East Atlantic compared with a meta-analytic terrestrial average of 6 km per decade [16]. Similarly, changes in phenology of up to 6 weeks have been observed in pelagic ecosystems [11] compared with a mean phenological change of 2.3 collectively observed for 172 species of plants, birds, insects and amphibians [16]. Of the myriad differences between the terrestrial and marine realm (see section 1.2 the rapidity of the planktonic response is predominantly due to their short life-cycles and in their mainly passive response to advective changes. These changes highlighted in this review are set to continue into the future following current climate warming projections. It is therefore thought that the currently observed and future warming have and are likely to continue altering the geographical distribution of primary and secondary planktonic production [53], affecting marine ecosystem services such as oxygen production, carbon sequestration and biogeochemical cycling and placing additional stress on already depleted fish and mammal populations.

In terms of feedback mechanisms on Earth's climate, it is thought that these biological pumps will be less efficient in a warmer world due to changes in the phytoplankton composition (floristic shifts) and less overall nutrient mixing (reduced bulk properties) due to increased stratification of the world's oceans. In particular, this will affect large areas of the tropical oceans that are permanently stratified [9]. There also exists a strong negative relationship between ocean productivity and SST (linked through nutrient availability) at a global scale [9,12,13]. Although climate change and its spatially heterogeneous effect on surface wind-patterns, wind strength, upwelling and deep-water mixing makes many regional predictions beset with uncertainty. It is also worth noting that potential habitat expansion for pelagic organisms in the Northern Hemisphere due to the melting of Arctic ice will be severely restricted by light limitations dictating seasonal phytoplankton production. However, many of these scenarios are still at their infancy stage and while it is relatively simpler to predict changing ocean physics under climate forcing, understanding the biological response due to the underlying complexity of biological communities and their quite often nonlinear responses to environmental change makes predicting floristic changes fraught with uncertainty. Investigating the importance of biological nitrogen fixation and the production of dimethylsulfide (DMS) by certain phytoplankton is currently needed to understand the biological consequences of increased stratification on nitrogen cycles [79,80] and biological feedbacks [81,82].

Ecologically speaking and on a planetary scale, plankton and pelagic ecosystems as a metaphorical collective entity, are perhaps some of the most sensitive organisms to environmental change and one of the most important biological communities on the planet. They are responsible for the overwhelming majority of marine biological production that fuel marine food-webs and nutrient cycling as well as contributing to approximately half of the world's oxygen production and carbon sequestration. Virtually, all the biological observations highlighted in this review result from financially fragile multidecadal monitoring programmes. Future biological monitoring of these ecosystems, through an integrated and sustained observational approach, will be essential in understanding the continuing impacts of climate and global change on our planetary system. This in turn may allow us through international collaboration to mitigate and adaptively manage some of their more detrimental impacts.

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