

Microalgae under Global Environmental Change: Implications for Growth and Productivity, Populations and Trophic Flow

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ABSTRACT: The world is currently going through a period of rapid change in global environment associated with increases in atmospheric CO₂, rises in temperature and elevated UVBR fluxes at high and mid latitudes. In this review, we analyse the consequences of such alterations in environmental factors for the microalgae that form the basis of many aquatic food chains. We show that the effects of these changes can be species specific, and so lead to shifts in community composition as well as biomass. These environmental factors also lead to changes in elemental and biochemical composition of microalgae and this can have consequences for the flow of energy and materials to higher trophic levels.

KEYWORDS: Microalgae; global climate change; environmental change.

INTRODUCTION

The global environment is going through a period of rapid change, the pace of which is unprecedented in our geological history. While CO₂ levels, global temperatures and exposure to ultraviolet radiation have all been higher, sometimes much higher, in the geological past than they are at present, it is the current rate of change that will pose problems for biota.

The biota of the ocean has huge socioeconomic value, estimated at ~US\$21-trillion y⁻¹ globally, through food production, recreation, nutrient recycling and greenhouse gas regulation¹. Therefore the impact of global environmental changes on the ocean biota might have widespread economic implications. Since algae are at the base of most aquatic food chains, impacts on these organisms have enormous implications for the higher trophic levels.

The microalgae that comprise the phytoplankton can be a good proxy for climate change for several reasons - since phytoplankton in nature are not exploited commercially, it is possible to draw possible links between long-term changes in population size and structure and climate change (assuming no direct human impacts via top-down consumers such as fish). Also, most species are short-lived so population size is less influenced by the persistence of individuals from previous years, which leads to tight coupling between environmental change and plankton dynamics. Recent evidence suggests that plankton are more sensitive indicators of changes than are even the environmental variables themselves, because the nonlinear responses of biological communities can amplify subtle environmental perturbations^{2,3}.

Elevated CO₂ will have both direct effects on algae through photosynthesis, but also indirect effects on aquatic biota through acidification and alterations to elemental composition. Changing atmospheric and surface sea temperatures will potentially alter ocean currents and atmospheric circulation, and thus will not only affect the distribution of algae but will also have indirect effects related to other changing climatic conditions including patterns of aeolian dust distribution and its consequences for nutrient supply. Furthermore, the anthropogenic release of compounds such as chlorofluorocarbons (CFCs) into the atmosphere results in the destruction of ozone in the stratosphere, especially (but not exclusively) at high latitudes, and a consequent increase in UV radiation (UVBR) reaching the Earth's surface. Such ozone destruction is, in turn, affected by warming of the troposphere. Although the implementation of the Montreal Protocol has done much to stabilise the effects of CFCs, the Antarctic and Arctic ozone holes and elevated UVBR levels at high and mid latitudes are expected to persist until at least 2050⁴, and probably later unless illegal use of CFCs is stopped. These changes in global environment are likely to have profound effects on aquatic biota.

Microalgae in the world's oceans and freshwaters account for around 50% of the net amount of 111–117 Pg C assimilated annually (1 Pg = 10¹⁵ g) by photoautotrophs^{5,6}. The oceans have acted as a sink for approximately 30% of all anthropogenic C emissions since the onset of the Industrial Revolution and the biological activity of microalgae in these environments accounts for around 50% of the 3.8 Pg C yr⁻¹ released into the atmosphere by human activities^{5,6}.

Understanding how future changes in global climate will impact upon microalgal populations, which themselves are an important component of the global C cycle, is thus of great significance. Recently we have examined the potential consequences of global environmental change for algae from a physiological viewpoint, and attempted to provide insights into how environmental change might impact on algal performance^{6,7}. In the current review, we have taken a broader outlook and extended this approach to an assessment of the consequences of environmental change for algal population biomass and community composition as well as for trophic flow. In so doing, we have not attempted to be inclusive of all literature on the topic, but to provide a broad overview of the sorts of changes that microalgal populations might experience as the global environment continues to change over the next century.

Our Changing Global Environment

Atmospheric CO₂ concentrations in the geological past have been very much higher than at present. For example, in the Cretaceous, CO₂ levels were 3–12 × higher than they are currently⁶. In a sense then, algae in the present day are living in a low CO₂ environment. However, over the last 200 years or so, the atmospheric CO₂ pool has risen and is currently increasing by ~3.8 Pg C yr⁻¹⁸. CO₂ concentrations in the atmosphere have thus increased from around 280 ppm (28 Pa at sea level) in 1800 to 380 ppm (38 Pa) at present, with most of this increase occurring over the last 100 years^{9,10}. Although forecasts vary, depending on the inputs for growth in CO₂ emissions used, the most likely scenario is for a two- to threefold increase in atmospheric CO₂ concentration over the next century, attaining values between 750 and 1000 ppm (75 – 100 Pa) by 2100^{6,7}.

The inevitable consequences of atmospheric CO₂ increases on dissolved inorganic carbon and its components have been discussed previously^{6,7,9,10}. The chemistry of inorganic carbon in water dictates that an increase in gaseous CO₂ from 38 to 100 Pa will lead to a proportional increase in dissolved CO₂ in completely air-equilibrated (cf. ref. 11) seawater at 15°C, from 14.7 to 38.6 μM. However, increased CO₂ in solution will lead to a decrease in the pH, and the equilibria among the dissolved inorganic carbon (DIC) species will therefore shift, so that overall there will be a decrease (~50%) in carbonate concentrations but only minor changes in bicarbonate and total DIC (~10% increase)⁶. Similar results are obtained for freshwater systems, though the absolute values of pH and the components of the DIC system attained will depend on the alkalinity and buffering capacity of the waters, as well as on inputs from groundwater that can lead to freshwater systems often being at greater than

atmospheric equilibrium levels of CO₂. These changes in CO₂ concentration, but not HCO₃⁻ concentration, may have important repercussions for the ability of aquatic plants to acquire inorganic carbon under elevated global CO₂.

As for CO₂ levels, estimates of palaeoclimate suggest that global temperatures have been higher than at present. For instance seawater temperatures in the Cretaceous, at least in higher latitudes, were considerably higher than they are now¹². However, although average global temperatures were remarkably constant for the 1000 years or so before the onset of the Industrial Revolution, since the late 18th Century we have seen a significant increase in temperatures, particularly in the last 100 years^{9,10}. The increase in atmospheric CO₂ predicted over the next 100 years is expected to lead to an average further rise in global sea temperature of 2–3 °C, though the actual rise will not be homogenous and some parts of the world will see far larger shifts in temperature than this¹³.

UVBR and UVCR levels were much higher ~2500 to 2000 Mya than they are today. At this time however, oxygen levels in the atmosphere began to rise due mainly to the evolution of oxygenic photosynthesis¹⁴. The rise in O₂ levels resulted in the formation of an ozone layer of sufficient density and depth to significantly attenuate UVBR (and UVCR), and by 1000 Mya UVR levels were reduced to approximately present-day fluxes⁶. Although UVR fluxes were essentially constant from ~1000 Mya onwards, periodic natural phenomena such as bolide impacts, cosmic events such as supernovae, and volcanic eruptions could have all impacted on ozone levels and caused periodic rises in UVR levels¹⁴. Ferrous ion is UVBR-absorbing, but as oxygen levels increased, iron would have been stripped out of the oceans^{14,15}, leading to greater UVBR penetration.

Since the 1970s, the solar flux of UVBR at the Earth's surface has been increasing at particular locations¹⁶, because of decreasing stratospheric ozone concentrations associated with release of chlorofluorocarbons (CFCs) into the atmosphere¹⁷. While increases in UVBR fluxes to the Earth's surface are most marked in the Antarctic¹⁸, and are also observed in the Arctic¹⁹, over the last decade significant increases in UVBR have been observed as far south as France and northern Italy and this has extended over parts of the North Atlantic^{20, 21}. Present-day UVR penetration into water bodies is extremely varied. The depths to which UVBR will be attenuated to 10% of surface fluxes range from 0.4 m in the Baltic Sea to > 16 m in waters off the Canary Islands (Table 1 in ref. 22). Ecologically significant effects of UVR have been reported in waters as deep as 30 m²³ or even down to

60–70 m²⁴.

Although our planet has thus, in the past, been exposed to much higher CO₂ concentrations and UVBR fluxes and, in some latitudes at least, higher temperatures, it is the rapidity of the present global climate change that is of concern and unprecedented in geological history. Given the importance of algal photosynthesis in the global carbon budget, it is thus crucial to understand how algae will react to the changes in global environment predicted to take place over the next century and beyond.

Elevated Carbon Dioxide

The effects of elevated carbon dioxide on the relative rates of photosynthesis and growth performance of microalgal species has been dealt with in some detail by Beardall and Raven⁶. Suffice it to say here that different species have differing requirements for inorganic carbon due to the activity of CO₂ concentrating mechanisms in their cells²⁵. Species relying on diffusive uptake of CO₂²⁶ are far more likely to show stimulation of photosynthesis and growth than species using HCO₃⁻ or taking up CO₂ actively via a CCM.

Cells lacking CCMs and acquiring CO₂ by diffusive uptake are potentially inorganic carbon-limited under present-day CO₂ levels and might be expected to show some stimulation of growth as atmospheric CO₂ levels increase over the next 100 years^{6,26}. One of the most striking examples of this influence of CO₂ levels on species lacking CCM activity comes from work by Lucy Ball²⁷ on Lake Windermere and on cultures of species of freshwater chrysophytes and synurophytes, which appear to be the major exception to the rule that most microalgae possess some form of CCM activity²⁶. It is clear from historical records that chrysophytes and synurophytes only appear in significant numbers in Lake Windemere when dissolved CO₂ levels are at greater than air-equilibrium values (S. Maberly, Centre for Ecology & Hydrology, Lancaster Environment Centre, pers. comm.). Elevated atmospheric CO₂ might then be expected to stimulate growth of these species more than that of other components of the phytoplankton, though there is no direct experimental evidence for this at present.

However, even in species that have a CCM, differences in CCM activity result in differing affinities for CO₂ and slightly different responses to CO₂ levels, which could lead to shifts in species composition. For instance, in phytoplankton of the Equatorial Pacific there was no overall difference in total biomass between samples exposed to high CO₂ (750 ppm) or low CO₂ (150 ppm) treatments for 8–10 days. However, high CO₂ favoured the haptophyte *Phaeocystis* sp. at the expense of diatoms whereas at low CO₂ diatom growth was stimulated²⁸.

Increases in CO₂ bring about changes in cellular composition as well as in photosynthetic and growth rates. Riebesell's group^{29,30} have examined elemental ratios in a range of microalgae grown at different CO₂ levels and found a decrease in C:N and an increase in C:P and N:P at higher CO₂ concentrations, though such changes were very species dependent and less marked above present-day CO₂ levels. Riebesell's group has also investigated changes in lipid and fatty acid composition in the coccolithophorid *Emiliania huxleyi* in relation to CO₂ levels³¹. Total fatty acids were strongly dependent on CO₂ concentrations below 14.5 μM, but stayed at approximately 1100 fg/cell at elevated CO₂. Similarly, increasing CO₂ concentration for growth from 1.1 to 14.5 μM resulted in an increase in 14:0, 18:1 and 18:2 fatty acids, with a strong decline in the percentage content of more unsaturated fatty acids (18:5 and 22:6). However, the effects of CO₂ above present-day levels (c. 14 μM) were less obvious. Although elevated CO₂ levels in the experiments of Riebesell et al.³¹ do not accurately mimic the effects of climate change as the growth conditions were achieved by increasing the total dissolved inorganic carbon (increasing the alkalinity and keeping the pH more or less constant), rather than by adjusting inorganic carbon and pH, the possibility of changes in macromolecular content under elevated CO₂ is quite important, not only for microalgal growth and function, but also for flow of materials to higher trophic levels. There are few examples in which the effects of elevated CO₂ on trophic flow have been examined, though Urabe et al.³² has grown freshwater *Daphnia* on alga [*Scenedesmus dimorphus* (Turpin) Kützing (= *S. acutus*)] cultured at a range of CO₂ concentrations. Under elevated CO₂ *Scenedesmus* had higher C:P ratios and it was found that this P-depauperate algal source, rather than a direct effect of CO₂ on *Daphnia*, led to poorer *Daphnia* growth.

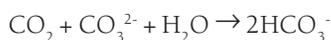
Changing patterns of macromolecular synthesis can also be observed in the production of extracellular polysaccharides. Engel et al.³³ have shown that *Emiliania huxleyi* blooms produce large amounts of transparent exopolymer particles (TEPs), which increased with cell number and were produced at the expense of dissolved polysaccharide (PCHO). TEPs are known to promote cell aggregation and could thus promote sinking of cells as marine snow. In an earlier work, Engel³⁴ showed that TEP production by natural phytoplankton populations in the Baltic Sea was enhanced by elevated CO₂ concentrations up to 30 μM. These observations combined suggest that elevated CO₂ could increase phytoplankton aggregation and transport out of the surface mixed layer as marine snow, thereby decreasing the recycling of carbon and (other nutrients) through the microbial loop. Such a phenomenon could have significant effects on nutrient cycling and ecosystem

function in the surface mixed layer of the oceans.

In addition to changes associated with elevated CO_2 *per se*, the lower pH of seawater in a “high CO_2 environment” will affect calcification processes. Growth of coralline algae and corals will potentially be inhibited under elevated CO_2 . Calcification in corals and some macroalgae is based on the formation of calcium carbonate in the form of the mineral aragonite. The saturation of seawater with respect to aragonite is given by

$$\Omega_{\text{arag}} = \frac{[\text{Ca}^{2+}][\text{CO}_3^{2-}]}{K'_{\text{sp}}}$$

where K'_{sp} is the stoichiometric solubility product of the aragonite form of CaCO_3 . Since Ca^{2+} is essentially constant in seawater, aragonite formation is determined by $[\text{CO}_3^{2-}]$ and is thus strongly affected by the partial pressure of CO_2 in solution



Elevated CO_2 thus leads to decreased $[\text{CO}_3^{2-}]$ and hence decreased calcification. In corals, decreased pH as a consequence of elevated CO_2 will lead to inhibition of calcification, though this is quite species dependent³⁵. The other form of calcium carbonate deposited by aquatic organisms, calcite (found in some macroalgae and most coccolithophores), is less affected by lowered pH than aragonite. Nonetheless, it has been shown that elevated CO_2 can still have a significant effect on coccolithophores. In work by Riebesell's group, cell size (measured as POC production) by two species of coccolithophorid was increased under elevated CO_2 , though *Gephyrocapsa oceanica* showed a greater response than *Emiliania huxleyi*. Calcification by the two species was significantly decreased by elevated CO_2 , though again, *Gephyrocapsa oceanica* showed a greater response than *Emiliania huxleyi*. Both species showed significant malformations of coccoliths under elevated CO_2 ³⁶.

Increased Temperature

As a consequence of increased atmospheric CO_2 concentration, average global sea surface temperatures are expected to increase by 1.7-1.9 °C over the next century³⁷. However, as mentioned above, shifts in temperature will be varied, with some areas of the world's aquatic ecosystems experiencing much greater shifts than the average 2 °C or so.

Temperature can exert effects directly on the biology of microalgae, but can also influence populations indirectly. Thus one likely linkage between climate change and phytoplankton is the impact of changes in global temperatures on weather and thereby on the intensity of ocean mixing (and its reverse, ocean stratification). This intensity, in turn, affects light levels,

surface temperature and the magnitude of nutrient recycling from deep layers, thereby influencing phytoplankton growth and thus driving bottom-up processes throughout the pelagic food chain³.

Differences in species response to temperature have been documented in laboratory cultures, with some species having preferences for cooler waters, and others for warmer waters. For instance Clegg et al.³⁸ showed *Euglena gracilis* was an example of the former while others (including *Ceratium hirundinella*, *C. furcoides*, *Chlamydomonas* sp) preferred higher temperatures. Temperature ranges for growth are also dependent on algal species, with some having a wide range of temperature for growth, while the others have very narrow range (e.g. 5-25 °C for *Asterionella formosa*, 5-10 °C in *Chaetoceros* sp.)³⁹.

Such differences in temperature preferences (as occurs in nature, for instance with seasonal change) are, together with the availability of nutrients in the water, responsible for shifts in species composition. Even though this is a natural occurring process, there is data that supports the idea that we are currently seeing shifts in species composition of phytoplankton in oceans and lakes, not previously known for those bodies, caused by global climate change.

These changes in species composition and dominance may affect the structure and functioning of the pelagic system, for example, by their nutrient uptake characteristics, edibility, repression of indigenous species, and release of toxins or other properties⁴⁰. The geographical distribution of organisms could be a sensitive indicator of climate change – for instance, the genus *Ceratium* is widely distributed in tropical and temperate waters. However, one species (*C. trichoceros*) previously recorded as occurring only south of the UK has extended its geographical range to the west coast of Scotland and northern North Sea^{3, 41}. The presence of other species outside their previously documented geographical ranges has also been recorded in the North Sea, with 16 non-indigenous phytoplankton species becoming permanently established, of these 13 have colonized the German Bight, which corresponds to an increase of 1% in the total number of phytoplankton species found in this area⁴⁰. The establishment of 10 non-indigenous “thermophilic” phytoplankton species in the North Sea during recent years coincides with a period of slightly increased sea surface temperature anomalies in the northern oceans⁴⁰, although it should be recognised that, apart from increased temperature, other components e.g. an increased influx of Atlantic water through the English Channel in 1989-1991 could have contributed to such changes.

Some of “new comers” are potentially toxic bloom-forming species, such as *Gymnodinium catenatum* and

Alexandrium minutum, which presents a possible risk of new blooms forming in this area. Sediment analyses of these waters have shown that cysts of *G. catenatum* were found from a period between ~ 6000-300 BP, which suggests that inflow of warmer waters in prehistoric times contributed to the occurrence of fossil blooms, which then disappeared during the "Little Ice Age" (~ 300 BP) ⁴².

Field and laboratory data over the past 20 years have indicated that blooms of *Alexandrium* and *Gonyaulax* species are triggered by warm sea surface temperatures, high runoff and storm driven re-suspension of their resting cysts ⁴³. Sediment data showing peaks in numbers of *Gymnodinium catenatum*-like cysts were shown to correspond to intervals of climate warming during the past 2000 years ⁴⁴.

However, some data have shown that increased temperature might not always have the same effect. When investigating shallow lake microcosms, Moss et al. ⁴⁵ observed that warming had considerably smaller effects on the phytoplankton community than did nutrients, with minor effects on chl *a* and total phytoplankton biovolume. However, it did significantly decrease the biovolumes of Cryptophyceae and Dinophyceae. The effect on the cyanobacteria was not as expected, since warming did not increase their abundance.

Long term changes in phytoplankton have also been observed in other systems, but in these cases the effect of temperature has been indirect, being exerted via the stability of the water column. Thus, in the Baltic Sea, the intensity of the winter cooling controls the onset of thermal stratification in spring, while salinity has only a minor effect on density stratification above the halocline. The shift in winter surface temperatures appears to have brought about pronounced changes in the Baltic Sea – the spring diatom bloom biomass dropped dramatically from 1988 to 1989 and stayed low at this level, whereas dinoflagellate biomass showed a steady increase from 1989 onwards ⁴⁶. The long term decrease of diatom biomass and the increase of dinoflagellate biomass together with the reduction of total phytoplankton biomass, coincided with an increase in surface temperature in the central Baltic Sea since the late 1980s, while the spring phytoplankton bloom seems to have shifted to an earlier start ⁴⁶.

Similar effects have been observed in the Mediterranean. Thus, under favourable conditions, diatoms were the major constituents of phytoplankton peaks in the high salinity water of the Bay of Calvi (NW Mediterranean) until 1986 ⁴⁷. However, between 1986-1997 there was a major decline in phytoplankton populations during the bloom period. This could be explained by increasing stratification brought about by elevated sea surface temperatures, which led initially

to a reduction in diatom abundance through Si limitation, and the replacement of diatoms with nanoflagellates. In later years, decreasing nitrate availability led to nitrate limitation, which further caused progressive reduction in non-siliceous phytoplankton biomass ⁴⁷.

Due in part at least to extended periods of negative Southern Oscillation Index (SOI) since the late 1970s, the North Pacific Subtropical gyre (NPSG) has also experienced long-term changes in phytoplankton community composition. *Prochlorococcus* has become more abundant over the past few decades, associated with increased stratification and nutrient limitation, phenomena which would favour strong selection for small cells with enhanced nutrient uptake and light absorption capabilities, as well as photosynthetic diazotrophs. The prolonged "endless summer" in the NPSG provides the selection pressure necessary for a several decade-long succession of *Prochlorococcus* to have taken place under generally stratified, nutrient-depleted conditions ⁴⁸. This has seen a shift in phytoplankton composition, also favouring larger N₂ fixing species of cyanobacteria such as *Trichodesmium* ⁴⁹. How the larger diazotrophic cells cope with the ensuing potential limitation in P supply is not certain, though recent data suggests they can utilise pools of dissolved phosphonates found in oligotrophic oceans ⁵⁰.

Shifts in phytoplankton species composition, as a response to climate change, have been shown not only in oceans, but also in some lakes. Palaeolimnological records from lakes in the circumpolar Arctic showed widespread species changes and ecological reorganizations in algae and invertebrates since approximately the 1850s ⁵¹. Changes in these distributions were mainly driven by climate warming, through a lengthening of the summer growing season and related limnological changes. Big community shifts in the last 150 years had occurred in 67% of investigated lakes, expressed in terms of both algal and invertebrate assemblages. Changes were especially pronounced in areas that have warmed the most (Canadian High Arctic) ⁵¹.

Temperature can have an effect on phytoplankton not only directly, but indirectly as well. Thus, simulation studies have predicted that doubling CO₂ would increase water temperatures in lakes and shorten the period of ice cover, affecting in particular, primary production ⁵². Climate change effects on lake ecosystems are expected to be pronounced at high latitudes since predicted global warming is dramatic in polar regions, and because the unproductive lakes of the northern areas are highly sensitive to even small environmental changes ⁵³. These authors found an association between elevated temperature and high productivity in high altitude lakes, brought about by an increase in the time of ice-free periods.

However, higher temperatures do not always cause an increase in phytoplankton biomass. Keller et al.⁵⁴, using mesocosms set up to mimic either present day conditions or the 2 °C rise in oceanic temperature expected over the next 100 years, found that phytoplankton biomass and cell counts were elevated in the cooler treatments relative to the warmer. They showed that this could be ascribed to the importance of zooplankton in controlling bloom dynamics via grazing – increasing temperature effectively enhances the match between the peak abundance of phytoplankton and zooplankton, resulting in a reduced bloom biomass and the funnelling of carbon to the pelagic rather than the benthic system⁵⁴. The overall impact of grazing would be expected to increase as a result of the greater abundance of zooplankton in warm years, affecting the phytoplankton standing stock in warmer waters⁵⁵.

One final influence of rising temperatures on phytoplankton growth that should be considered is the effect of higher temperature on large scale climatic phenomena such as the North Atlantic Oscillation (NAO) and El Niño Southern Oscillation (ENSO, associated with the Pacific Ocean). For instance, El Niño events are recognized as responsible for changes in the phytoplankton of the Santa Barbara Basin, where coccolithophore species, adapted to warm surface waters and fertilization by iron and NO₃⁻, were correlated with higher temperatures in the upper water column (~3 °C during El Niño with respect to La Niña periods)⁵⁶. There is some evidence that El Niño events are becoming more frequent (see e.g. data in ref 57), though the evidence for a link with climate change is not strong at present.

The NAO has profound effects on weather and water characteristics, especially temperature, in the North Atlantic Ocean⁵⁸. A high NAO is related to increased westerly winds and milder temperatures over northern Europe, and a low NAO causes cooler temperatures from decreased westerly winds⁴⁶. Besides the associated wind forcing, the impact of the NAO on the marine ecosystems is mainly through the heat flux between the atmosphere and the ocean, which controls the temperature of the upper mixed layer⁴⁶. It has been shown that surface air temperature and surface sea temperature across wide regions of the North Atlantic Ocean, North America, the Arctic, Eurasia and the Mediterranean are significantly correlated with the NAO variability⁵⁸. A substantial part (31%) of the recent warming in the Northern Hemisphere (~ 0.15 °C per decade) is linked to the behaviour of the NAO, in particular a trend in its index from large amplitude anomalies of one phase in the 1960s (negative index values) to large amplitude anomalies of the opposite phase since the early 1980s (positive index values)^{59,58}.

The NAO has been shown to affect the length of the growing season for phytoplankton in the North Sea, which has increased in parallel with the warming of SST associated with the NAO⁶⁰. Barton et al.⁶¹ have demonstrated a strong link between the development of spring phytoplankton in British coastal waters and the NAO, mediated not only through direct temperature effects but a range of subtle biological and physical interactions. However, changes in species blooms are complex and have been shown to depend on the functional groups – phytoplankton blooms in the North Sea have generally advanced more in response to warming than their zooplankton grazers⁶².

Clearly, the effects of temperature are complex and varied. Much more work is needed on the consequences of global warming on phytoplankton, at a number of scales, before we fully understand the impacts of global climate change.

Increased Ultraviolet B Radiation (UVBR)

UVR is known to have deleterious effects on marine primary producers. The effects of UVBR include inhibition of photosynthesis (due to damage to Rubisco and to D1 and D2 proteins in PSII) and damage to DNA (due to formation of pyrimidine dimers (=‘cyclobutane-type dimers’ or ‘CTDs’), photohydrates and (6-4) pyrimidones [=‘(6-4) photoproduct’]). In diatoms, it has been demonstrated that UVBR causes arrested cell division in the G2 phase of the cell cycle and consequent inhibition of growth⁶³. UVBR will also lead to production of reactive oxygen species and the production of lipid peroxides. Such effects are reviewed in detail by, *inter alia*, Vincent and Neale⁶⁴.

The effects of UVR on phytoplankton growth rates are species specific, thus elevated UVR could induce changes in community composition. For example, UVR exposure has been shown to cause an increase in diatom numbers at the expense of flagellates⁶⁵. In contrast, Watkins et al.⁶⁶ reported a decrease in epilithic diatom populations in the littoral zone of a boreal lake exposed to UVBR and Peletier et al.⁶⁷ and Roux et al.⁶⁸ found no effect of UVBR on species composition of the diatom-dominated microphytobenthos of tidal flats. Interpretation of such changes is, however, not always straightforward and is associated with interactions between microalgae and higher trophic levels (herbivores). For instance the components of a plankton community in the St. Lawrence Estuary changed after 7 days of UVBR treatments. In the presence of enhanced UVBR, there was a marked inhibition of growth of ciliates and large phytoplankton (mostly diatoms) compared to that under normal UVBR. At the same time the numbers of heterotrophic bacteria and autotrophic flagellates increased in the high UVR treatment. These observations could be ascribed to a

major effect of UVBR on the ciliate population, which are major predators on the smaller organisms and thus normally keep flagellate populations in check. Under UVBR, ciliate populations are kept low and hence flagellate populations could increase. Clearly then, UVBR levels can have profound effects on the structure and dynamics of aquatic ecosystems and trophic flow.

In other cases, differential responses of components of microalgal communities can be associated with the ability of the organisms to protect themselves with UV screening compounds. Principally these protective agents are mycosporine-like amino acids (MAAs), though other compounds such as scytonemin are important in cyanobacteria. Since different species of microalgae have differing capacities to produce UV screening compounds^{18,69,70,71}, increased UVBR levels could potentially result in changing species dominance in phytoplankton communities. For instance, the bloom-forming species *Phaeocystis pouchetii* (Hariot) Lagerheim, which is common in polar waters, produces high concentrations of UV-screening compounds⁷². Increases in UVBR could thus lead to increased dominance and frequency of blooms of this organism. This is important to the ecology of polar waters as *Phaeocystis* can form mucilaginous colonies, which are not readily consumed and passed on to higher trophic levels. Jeffrey et al.⁶⁹ examined a range of microalgae for the constitutive ability to produce UV screening compounds. Many species that produce high concentrations of UV-screening compounds are responsible for dense surface blooms and some of them, like *Gymnodinium catenatum*, are toxic, leading to the possibility that enhanced UVBR levels may increase the incidence of toxic surface blooms. More recently, Mengelt and Prezelin⁷³ have shown that the domoic acid-producing diatom *Pseudo-nitzschia* has a strong resilience under UV radiation (due in part to its ability to use UVAR to enhance C fixation), possibly explaining its capacity to produce large blooms in shallow, surface waters.

The differential ability of some species to screen out UVR is associated in part with cell size⁶. For a given concentration of MAAs, for example, a larger cell will offer a longer path length for UVR absorption. As a consequence, enhanced UVR should lead to increased dominance of larger celled species. This has been shown for benthic diatom communities^{74,75} and is also true for freshwater phytoplankton⁷⁶.

Recently it has been observed that the effects of UVBR are modulated by other environmental factors such as P-starvation^{77,78,75,79} and N-limitation⁸⁰. We have pointed out earlier in this review that increased thermal stratification that is caused by increased temperatures of surface waters, will lead to increased incidence of nutrient limitation/starvation in

phytoplankton. The effect of nutrient depletion on UVBR sensitivity thus provides an additional, synergistic, stress on these organisms.

CONCLUSION

It is clear from the discussion above that the various components of global environmental change (climate change), namely elevated CO₂, temperature and UVR, can potentially have profound effects on microalgae and that these effects can have consequences for higher trophic levels. It is also becoming apparent that these individual components can interact with other environmental factors such as nutrient availability. The extent to which the increasing levels of CO₂, UVBR and temperature interact between one another is an area that has little attention so far but has far reaching implications to our understanding of the effects of global change on aquatic ecosystems. This is a problem that is currently engaging the authors' research efforts!

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