



UvA-DARE (Digital Academic Repository)

Out of balance: implications of climate change for the ecological stoichiometry of harmful cyanobacteria

van de Waal, D.B.

Publication date
2010

[Link to publication](#)

Citation for published version (APA):

van de Waal, D. B. (2010). *Out of balance: implications of climate change for the ecological stoichiometry of harmful cyanobacteria*. [Thesis, fully internal, Universiteit van Amsterdam].

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, P.O. Box 19185, 1000 GD Amsterdam, The Netherlands. You will be contacted as soon as possible.

Chapter 2

Climate-driven changes in the ecological stoichiometry of aquatic ecosystems

ABSTRACT - Advances in ecological stoichiometry, a rapidly expanding research field investigating the elemental composition of organisms and their environment, shed new light on the impacts of climate change on freshwater and marine ecosystems. Current changes in the Earth's climate alter the availability of carbon and nutrients in lakes and oceans. In particular, CO₂ concentrations will rise to unprecedented levels by the end of this century, while global warming will enhance stratification of aquatic ecosystems and may thereby diminish the supply of nutrients into the surface layer. These processes enrich phytoplankton with carbon, but suppress nutrient availability. Phytoplankton with a high carbon:nutrient content provide poor food quality for most zooplankton species, which may shift the species composition of zooplankton and higher trophic levels to less nutrient-demanding species. As a consequence, climate-driven changes in plankton stoichiometry may alter the structure and functioning of entire aquatic food webs.

*This chapter is based on the paper: Dedmer B Van de Waal, Antonie M Verschoor, Jolanda MH Verspagen, Ellen Van Donk, and Jef Huisman. 2010. Climate-driven changes in the ecological stoichiometry of aquatic ecosystems. *Frontiers in Ecology and the Environment* 8: 145-152*

2.1 Out of balance

In 1934, Alfred C Redfield reported that the ratios between the elements carbon, nitrogen, and phosphorus (C, N, and P, respectively) in marine phytoplankton were remarkably constant (Redfield 1934). His famous C:N:P ratio of 106:16:1 (by atom) has become known as the “Redfield ratio” (Falkowski and Davis 2004). Redfield further noted that the N:P ratios of phytoplankton resembled the nitrate:phosphate ratio found in the deep waters of the oceans (Redfield 1934). Thus, the elemental composition of marine plankton reflected that of their environment, and vice versa. However, even the seemingly constant pelagic environment is currently affected by changes in the Earth’s atmosphere. The 1934 atmosphere contained ~300 parts per million (ppm) of carbon dioxide (CO₂), which has risen to the present-day value of 385 ppm, a level that by far exceeds that of the natural range of the past 650 000 years. Atmospheric CO₂ levels are expected to rise further, to ~750 ppm by the year 2100 (Solomon *et al.* 2007). The rapid increase in atmospheric CO₂ and other greenhouse gases is accompanied by global warming. Average global temperatures have risen by 0.6 °C since 1934, and an additional 3 °C increase is expected to occur over the course of the 21st century (Solomon *et al.* 2007). These changes in global climate will affect many chemical and physical processes in aquatic ecosystems, with possible implications for the elemental composition of plankton communities.

Ecological stoichiometry is a rapidly expanding research field investigating how the elemental composition of organisms affects ecological processes (Sterner and Elser 2002). Inspired by Redfield and the recent advances in ecological stoichiometry, this review explores the potential impacts of climate change on the carbon and nutrient availability in aquatic ecosystems, its consequences for the C:N:P stoichiometry of plankton communities, and its implications for the structure of aquatic food webs.

2.2 Rising CO₂ and ocean acidification

The current rise in atmospheric CO₂ levels is having a major impact on the carbon chemistry of the oceans (Doney *et al.* 2009). In fact, it is estimated that almost 50% of the anthropogenic CO₂ input into the atmosphere since the Industrial Revolution has been absorbed by the oceans (Sabine *et al.* 2004). Compared to the large pool of bicarbonate (HCO₃⁻), dissolved CO₂ constitutes only a minor fraction of the total concentration of dissolved inorganic carbon (DIC) in the oceans. Yet, rising concentrations of atmospheric CO₂ increase the concentration of dissolved CO₂ in ocean surface waters. Dissolved CO₂ reacts with water to form carbonic acid (H₂CO₃), which rapidly dissociates into HCO₃⁻, releasing a proton and thereby reducing pH levels. This phenomenon has become known as “ocean acidification” (Caldeira and Wickett 2003; Doney *et al.* 2009). Since the industrial

revolution, ocean acidification has decreased the pH of ocean surface waters by ~ 0.1 units, to an average surface pH of 8.1 (Orr *et al.* 2005). At atmospheric CO_2 levels of 750 ppm – expected by the year 2100 – the pH of surface seawater will have dropped by an additional 0.3 units, to a pH of ~ 7.8 (Orr *et al.* 2005). This is equivalent to a doubling of the proton concentration. The projected concentration of dissolved CO_2 at that point will be outside the natural range of the past 20 million years (Solomon *et al.* 2007).

Ocean acidification causes a decrease in the concentration of carbonate ions (Caldeira and Wickett 2003; Solomon *et al.* 2007). This increases the solubility of calcium carbonate (CaCO_3) in the oceans. Cold waters are less saturated with respect to CaCO_3 than are warmer waters; high-latitude ecosystems are therefore likely to be the first to suffer from ocean acidification. Model simulations project that Southern Ocean surface waters will begin to become undersaturated with respect to aragonite, a metastable form of CaCO_3 , by about the year 2050 (Orr *et al.* 2005; Doney *et al.* 2009). By 2100, this undersaturation could extend throughout the entire Southern Ocean and into the subarctic Pacific Ocean. When water becomes undersaturated with aragonite, key marine organisms, such as corals, foraminifers, and coccolithophores, have difficulty in forming their CaCO_3 skeletons (Orr *et al.* 2005; Hoegh-Guldberg *et al.* 2008). Laboratory experiments with coccolithophores exposed to elevated CO_2 yielded malformed and smaller coccoliths (Riebesell *et al.* 2000), although effects varied depending on the strain and growth conditions (Iglesias-Rodriguez *et al.* 2008). Many other calcifying organisms, including pteropods, mollusks, crustaceans, and sea urchins, will also be negatively affected by ocean acidification (Orr *et al.* 2005; Doney *et al.* 2009).

2.3 Carbon supersaturation in freshwater ecosystems

In contrast to open ocean waters, many freshwater ecosystems, estuaries, and some coastal environments receive substantial amounts of carbon from terrestrial ecosystems (Sobek *et al.* 2005). This occurs mainly in the form of dissolved organic carbon (DOC). Bacterial activity mineralizes the available DOC into CO_2 . As a result, the CO_2 concentration of lakes is usually not in equilibrium with the atmosphere, but is related to the concentration of DOC (Fig. 2.1). In fact, CO_2 concentrations of 1000-3000 ppm are quite common in lakes. On a global basis, inland waters receive up to 1.9 petagram carbon year⁻¹ (equal to 1.9×10^{15} g C year⁻¹) from the surrounding watershed, of which about half is ultimately flushed into the oceans (Cole *et al.* 2007). A fraction of the carbon received by inland waters is buried in sediments, whereas an estimated 0.8 petagram carbon year⁻¹ is processed by aquatic biota, where it is finally respired to CO_2 (Cole *et al.* 2007; although the exact values are still under debate; LJ Tranvik pers. comm.). Accordingly, most inland waters are supersaturated with CO_2 , and thus serve as net sources of CO_2 to the atmosphere (Sobek *et al.* 2005; Cole *et al.* 2007).

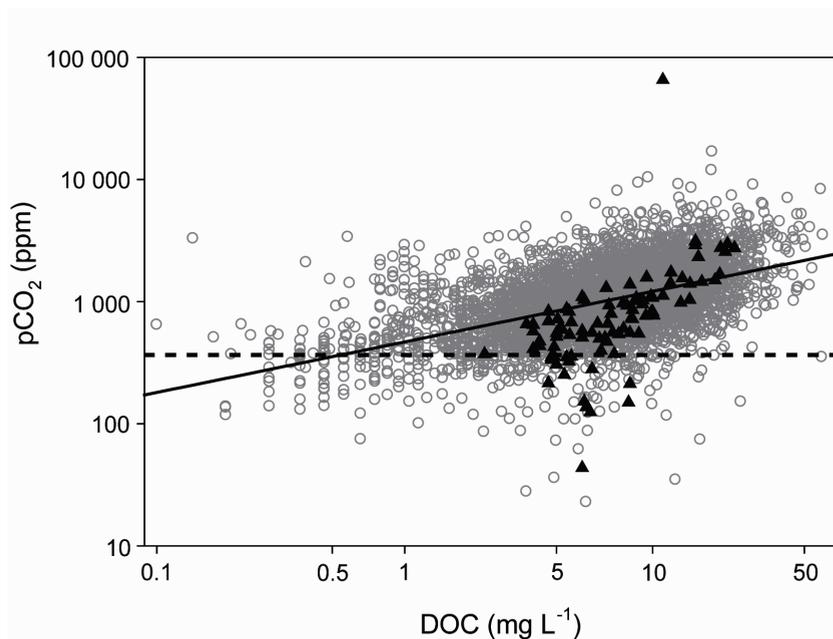


Figure 2.1. Carbon dioxide concentration ($p\text{CO}_2$) against the concentration of dissolved organic carbon (DOC) in 4555 globally distributed lakes. Each point represents one individual lake. Circles denote lakes with a single measurement. Triangles represent mean values for lakes with multiple measurements. The solid line shows linear regression for all data points ($\log[p\text{CO}_2] = 2.67 + 0.414 \times \log[\text{DOC}]$; $r^2 = 0.26$; $n = 4555$; $P < 0.0001$). The horizontal dashed line indicates the present atmospheric CO_2 level of 385 ppm. (From Sobek *et al.* 2005. Reproduced with permission from the American Geophysical Union. © 2005 American Geophysical Union).

Global warming and rising atmospheric CO_2 levels may alter the input of DOC into freshwater ecosystems, although the magnitude and direction of these changes will vary regionally. At high latitudes, rising temperatures will thaw large areas covered by permafrost in Siberia, Canada, and Alaska, releasing massive amounts of trapped organic carbon that may flow into ponds and lakes (Zimov *et al.* 2006). Climate scenarios also predict more extreme rainfall events and more frequent storms in many parts of the world (Solomon *et al.* 2007), which may result in increased runoff of DOC from terrestrial ecosystems into lakes (Hinton *et al.* 1997). Conversely, DOC concentrations in the Experimental Lakes Area in Canada decreased by 15-25% during two decades of climatic warming, as a result of reduced streamflow caused by drought (Schindler *et al.* 1997). Rising atmospheric CO_2 concentrations lead to increased stomatal closure of terrestrial vegetation. This reduces plant transpiration, and has been estimated to increase global runoff by 6% (Betts *et al.* 2007). In peatlands, elevated CO_2 induces shifts in plant species composition, which could amplify DOC export from peatland catchments (Fenner *et al.* 2007). Other processes also affect the DOC input into freshwater ecosystems, however. For

instance, increased DOC concentrations in lakes in Europe and North America have been explained by a reduction in atmospheric acid deposition (Monteith *et al.* 2007). All in all, the effects of climate change on DOC concentrations in lakes will greatly depend on the local setting (e.g. local meteorology, catchment hydrology, land use, vegetation, and water retention times). Yet, the processes described above suggest that DOC concentrations may increase in many lakes.

2.4 Global warming and stratification

Rising temperatures influence the physical structure of aquatic ecosystems. In particular, warming of the upper layers of lakes and oceans enhances the density difference between the surface mixed layer and the deeper waters beneath. All else being equal, this increased density difference will strengthen the vertical stratification of both lakes (Jöhnk *et al.* 2008; Peeters *et al.* 2008) and oceans (Sarmiento *et al.* 2004; Doney 2006). Stratification suppresses vertical mixing across the density gradient, with contrasting effects on nutrient and light availability for phytoplankton growth. On the one hand, stratification reduces the nutrient influx from deep, nutrient-rich waters into the surface mixed layer, thus limiting the availability of nutrients for phytoplankton growth (Behrenfeld *et al.* 2006; Huisman *et al.* 2006). On the other hand, stratification keeps phytoplankton populations in the surface mixed layer, thereby improving light conditions for phytoplankton growth (Huisman *et al.* 1999; Berger *et al.* 2007).

Many waters in the tropics and subtropics are permanently stratified. Nutrient concentrations in the surface mixed layer of these waters are strongly depleted (Karl *et al.* 1997; Huisman *et al.* 2006). As a result of severe nutrient limitation, permanently stratified oceans in the tropics and subtropics are characterized by extremely low primary production (Fig. 2.2a, b). Climate-ocean models predict that, by the year 2050, the ocean area covered by permanent stratification will have expanded by 4.0% and 9.4% in the Northern and Southern hemispheres, respectively (Sarmiento *et al.* 2004), thereby reducing overall ocean productivity (Behrenfeld *et al.* 2006). These predictions are surpassed by recent observations, which indicate a much faster expansion of the ocean's least productive waters over the past 9 years (Fig. 2.2c–e; Polovina *et al.* 2008).

In the temperate zone and at high latitudes, waters are not permanently stratified, and deep mixing during winter and/or spring provides nutrients into the surface layer. In these regions, phytoplankton growth is often light-limited in winter, due to short day lengths as well as deep vertical mixing. Climate warming causes an earlier onset of stratification in spring, which brings the phytoplankton cells in the well-lit surface layer while nutrients are not yet depleted, and thereby favors their growth. This leads to an earlier spring bloom and a substantially longer growing season in the temperate zone (Winder and Schindler 2004; Peeters *et al.* 2008).

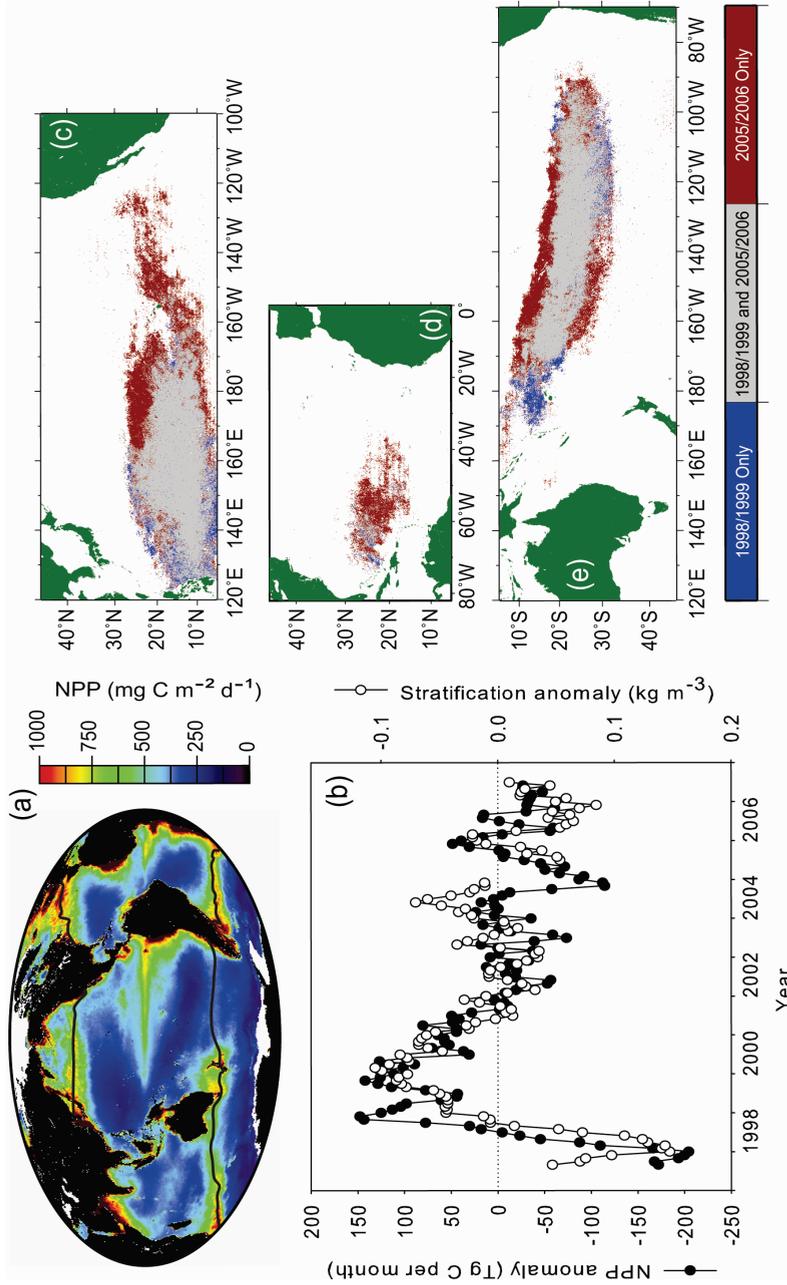


Figure 2.2. Relationships between stratification and primary production. (a) Global distribution of annual net primary production (NPP), with low values (blue) in permanently stratified waters of subtropical and tropical oceans. (b) Changes in ocean stratification (open symbols) are well correlated with NPP anomalies (closed symbols) in the subtropical and tropical oceans (Pearson product-moment correlation: $r^2 = 0.73$; $n = 112$; $P < 0.001$). Expansion of waters with very low net primary production during the past decade, for (c) North Pacific Ocean, (d) North Atlantic Ocean, and (e) South Pacific Ocean. Grey areas had very low chlorophyll concentrations in both 1998/1999 and 2005/2006, blue areas only in 1998/1999, and red areas only in 2005/2006. [(a) and (b) from Behrenfeld *et al.*, 2006; adapted with permission from Macmillan Publishers Ltd: Nature, © 2006. [(c-e) from Polovina *et al.*, 2008; reproduced with permission from the American Geophysical Union. Published 2008 American Geophysical Union].

2.5 Changes in phytoplankton stoichiometry

The elemental composition of phytoplankton can vary widely, and often reflects the resource availability in their environment (Sterner and Elser 2002). Climate-driven changes in carbon, light, and nutrient availability are therefore likely to affect phytoplankton stoichiometry. In dense phytoplankton blooms, the photosynthetic demand for inorganic carbon can be very high, and this can deplete inorganic carbon to limiting concentrations (Ibelings and Maberly 1998). Rising CO₂ levels may alleviate these dense blooms from carbon limitation, especially in low-alkalinity freshwater ecosystems. In marine ecosystems, however, DIC is dominated by vast amounts of HCO₃⁻.

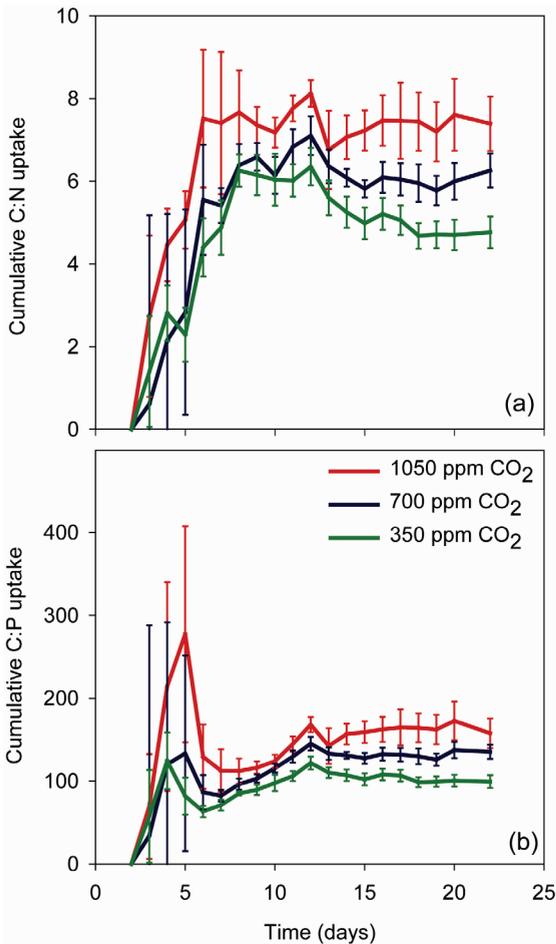


Figure 2.3. Carbon:nutrient uptake ratios during a marine CO₂ enrichment study. The graphs illustrate (a) C uptake relative to N uptake (C:N), and (b) C uptake relative to P uptake (C:P), both integrated over the duration of the experiment from day 2 onwards. The treatments consisted of 350, 700, and 1050 ppm CO₂, represented by green, blue, and red lines, respectively. Error bars indicate one standard deviation. (From Bellerby *et al.* 2007).

Many phytoplankton species can take up both dissolved CO_2 and HCO_3^- (Kaplan and Reinhold 1999; Martin and Tortell 2008). Inorganic carbon is therefore rarely a limiting resource in marine ecosystems. However, large, species-specific differences exist in the relative uptake rates of HCO_3^- versus CO_2 (Martin and Tortell 2008). This interspecific variability will likely have important implications for the phytoplankton species composition in response to rising CO_2 concentrations.

In a recent, large-scale mesocosm experiment in a Norwegian fjord, an increase of the CO_2 partial pressure to 1050 ppm resulted in 39% more uptake of inorganic carbon by the natural plankton community (Bellerby *et al.* 2007; Riebesell *et al.* 2007). Since nutrient uptake remained largely unaffected in this experiment, this resulted in enhanced uptake of carbon relative to nitrogen and phosphorus (Fig. 2.3). Furthermore, recent laboratory experiments have shown that increased concentrations of CO_2 stimulated both nitrogen and carbon fixation in a marine nitrogen-fixing cyanobacterium (Hutchins *et al.* 2007; Levitan *et al.* 2007). For these nitrogen-fixing organisms, C:N ratios did not change with increasing CO_2 availability, because their cellular nitrogen and carbon contents increased in parallel. However, phosphorus uptake was not stimulated, so that their C:P and N:P ratios increased markedly at higher CO_2 levels (Hutchins *et al.* 2007; Levitan *et al.* 2007).

Changes in stratification patterns are likely to affect phytoplankton stoichiometry in two ways. First, a stronger stratification reduces the nutrient supply from deep waters below. Second, a stronger stratification keeps the phytoplankton in the well-lit surface layer. Phytoplankton exposed to these nutrient-limited but light-saturated conditions typically show increased cellular carbon:nutrient ratios (Sterner and Elser 2002). Moreover, a reduced nitrogen supply and increased light availability promote the competitive success of nitrogen-fixing cyanobacteria (Agawin *et al.* 2007). The proliferation of these organisms may force phosphorus concentrations in surface waters to limiting values. This mechanism seems to apply to the subtropical Pacific Ocean, where the presence of nitrogen-fixing organisms yields an overall increase in cellular N:P ratios, and shifts the entire ecosystem towards phosphorus limitation (Karl *et al.* 1997). This suggests that, with climate-driven warming and the expansion of ocean stratification, cellular carbon:nutrient ratios – and in particular C:P ratios – are likely to increase in substantial parts of the world's oceans.

Thus, both rising atmospheric CO_2 levels and enhanced stratification by global warming may shift phytoplankton stoichiometry in a similar direction, causing an increased carbon:nutrient ratio of the phytoplankton community and associated changes in phytoplankton species composition toward species that can proliferate under high CO_2 /low nutrient conditions.

2.6 Implications for zooplankton and higher trophic levels

The elemental composition of phytoplankton communities affects the cellular concentrations of proteins, fatty acids, and various other phytoplankton constituents important for zooplankton growth (Sterner and Elser 2002; Jensen and Verschoor 2004). The carbon:nutrient ratio of phytoplankton is therefore a major determinant of their quality as food for zooplankton (see also Chapter 1 in this thesis). Zooplankton can become nutrient limited if the nutrient content of their food is low compared to their nutrient demands. Several zooplankton species are capable of compensating for the reduced nutrient content of their food through compensatory feeding (i.e. by increasing their feeding rates). Nevertheless, the costs of compensatory feeding and processing of surplus carbon restricts this strategy to a limited range of carbon:nutrient ratios. Indeed, laboratory experiments have shown that growth rates of herbivorous zooplankton species, such as the cladoceran *Daphnia* and the rotifer *Brachionus*, are reduced when feeding on phytoplankton with high C:P ratios (Sterner and Elser 2002; Urabe *et al.* 2003; Jensen and Verschoor 2004).

As an example, laboratory experiments performed by Urabe *et al.* (2003) showed that elevation of the CO₂ concentration from 360 to 1500 ppm resulted not only in an increased phytoplankton biomass (Fig. 2.4a), but also in an increased C:P ratio (Fig. 2.4b). This reduction in food quality suppressed the growth rate of the cladoceran *Daphnia* at elevated CO₂ (Fig. 2.4c). Similar results were obtained by Urabe and Waki (2009), although the latter study also shows that this adverse effect of rising CO₂ on *Daphnia* growth can be mitigated by mixed algal diets. Other zooplankton species with lower phosphorus requirements, like copepods, may be able to sustain their growth when feeding on phytoplankton with high C:P ratios. Accordingly, if growth rates of high phosphorus-demanding species, such as cladocerans, are reduced, low phosphorus-demanding species, such as copepods, might gain a competitive advantage. This may cause shifts in zooplankton species composition in response to climate-driven changes in phytoplankton stoichiometry.

An elemental imbalance between phytoplankton and zooplankton may also affect the recycling efficiency of different elements (Sterner and Elser 2002). For instance, zooplankton feeding on phytoplankton with a high N:P ratio show an increased release of nitrogen as compared to phosphorus (Elser and Urabe 1999). Similar relationships apply for carbon:nutrient ratios, as zooplankton excrete the excess carbon obtained in their food (Hessen and Anderson 2008). Consequently, a climate-driven increase in phytoplankton carbon:nutrient ratios may enhance carbon release by zooplankton, whereas nutrients are retained. This positive feedback will further increase DOC concentrations and, subsequently, the CO₂ availability for phytoplankton. Since nutrient limitation continues or is enhanced, due to reduced nutrient recycling by herbivores, this leads to even higher carbon:nutrient ratios in the phytoplankton.

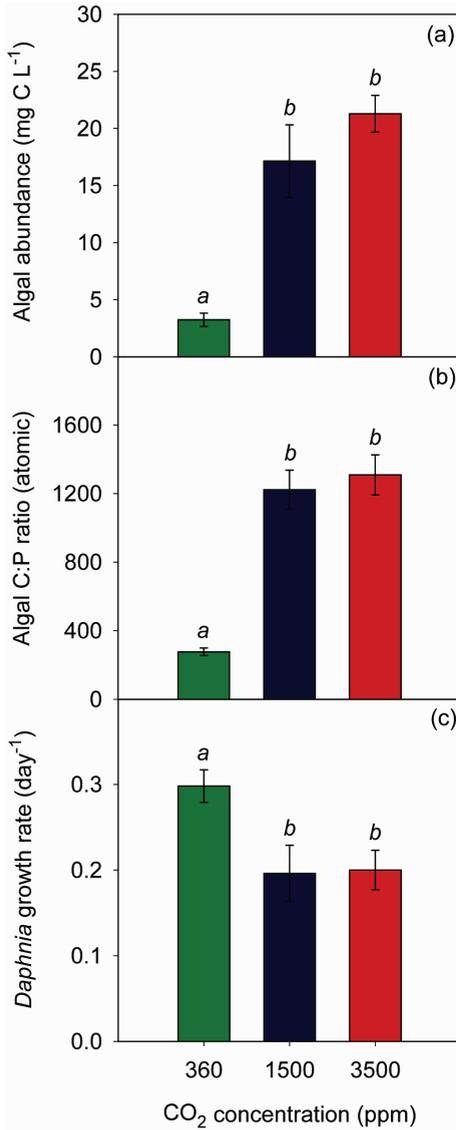


Figure 2.4. Effects of CO₂ enrichment in a laboratory experiment. (a) Biomass of the green alga *Scenedesmus*, (b) the corresponding algal C:P stoichiometry, and (c) specific growth rates of *Daphnia* when fed with these green algae. The treatments consisted of 360, 1500, and 3500 ppm CO₂, represented by green, blue, and red bars, respectively. Error bars indicate the standard error of the mean. Bars with different letters were significantly different ($P < 0.05$, Tukey's pairwise comparison). (From Urabe *et al.* 2003; adapted with permission from Blackwell Publishing Ltd: Global Change Biology).

The potential increase in carbon:nutrient ratios of phytoplankton and the subsequent shift in zooplankton species composition may cascade up through higher trophic levels. During the past decades, shifts in large zooplankton and fish communities have been observed in many seas and oceans. For instance, recent studies indicate that krill in the Southern Ocean is gradually being replaced by salp species (Atkinson *et al.* 2004), and jellyfish numbers seem to be on the rise worldwide (Purcell 2005). Furthermore, fish size distributions are shifting towards smaller fish in various marine ecosystems (Pauly *et al.* 2005). Although these changes are primarily attributed to fisheries, climate change may also be playing a role (Pauly *et al.* 2005; Purcell 2005). Interestingly, salp seems to have a low body phosphorus demand compared to copepods and krill, whereas jellyfish and small fish have a lower body phosphorus demand than larger fish (Ikeda and Mitchell 1982; Malej *et al.* 1993; Sterner and Elser 2002). Furthermore, there are indications that the growth rates of some phosphorus-rich fish species, particularly of herbivorous fish growing on high C:P food, can become phosphorus limited (Hood *et al.* 2005). A climate-driven decrease in the phosphorus content of plankton may therefore exacerbate the impacts that fisheries have on the species composition of higher trophic levels in marine pelagic food webs.

2.7 Caveats and conclusions

Climate change can have many impacts on aquatic ecosystems. It may favor the development of harmful algal blooms (Paerl and Huisman 2008), cause ocean acidification (Caldeira and Wickett 2003), and affect the biogeographical distribution of many species (Hays *et al.* 2005). Current knowledge about the impacts of climate change on plankton stoichiometry is still limited. Although we have argued that climate change is likely to increase the carbon:nutrient stoichiometry of plankton communities, several processes may impede or completely reverse this pattern. For instance, as a result of global warming, air temperatures are increasing to a greater extent than ocean water temperatures, causing more frequent storms (Solomon *et al.* 2007). Storms can prevent or suppress stratification, and the resultant vertical mixing of the water column may enhance the flux of nutrients from deeper waters into surface layers. Furthermore, stoichiometric effects of climate change may be mitigated or even counteracted by eutrophication, through anthropogenic nitrogen and phosphorus loading. These processes provide more nutrients for phytoplankton growth, especially near the more densely human populated regions of our planet, and may thereby lead to local or regional trends in plankton stoichiometry that deviate from our expected pattern.

Moreover, the response of species, communities, and ecosystems to changing environmental conditions can be highly complex, with many non-linear interactions and surprising feedbacks (Scheffer *et al.* 2001; Benincà *et al.* 2008). Many planktonic organisms are also quite flexible in their stoichiometry, and have considerable potential for

physiological acclimation and evolutionary adaptation to changing carbon and nutrient conditions (Sterner and Elser 2002). It may therefore be difficult to predict long-term changes in the ecological stoichiometry of aquatic ecosystems, based on only a few climatic drivers.

Nevertheless, by and large, the current state of knowledge indicates that rising atmospheric CO₂ levels will increase CO₂ availability for biological production, while global warming will tend to strengthen vertical stratification of aquatic ecosystems, thus reducing nutrient availability in the surface mixed layer. It seems plausible that the combination of rising CO₂ availability and reduced nutrient levels will result in higher phytoplankton carbon:nutrient ratios. These alterations in phytoplankton stoichiometry are likely to suppress zooplankton growth, shift zooplankton species composition to less nutrient-demanding species, and thereby affect the entire aquatic food web. If we were to follow in the footsteps of Redfield (1934) and measure plankton stoichiometry at the end of the 21st century, we might discover a different Redfield ratio, one reflecting a carbon-rich world.

Acknowledgements - This review was inspired by a scientific symposium supported by the Royal Netherlands Academy of Arts and Sciences (KNAW). We thank MJ Behrenfeld, RGJ Bellerby, JJ Polovina, S Sobek, and J Urabe for kind provision of data and figures, and DO Hessen, RW Sterner, and J Urabe for helpful comments on the manuscript. The research of DBvdW, AMV, and JMHV was supported by the Earth and Life Sciences Foundation (ALW), which is subsidized by the Netherlands Organization for Scientific Research (NWO).