

In addition, visual predators are generally less abundant in extremes of low temperature. The appropriate combination of conditions is rarely found in shelf sea waters, and the majority of the overwintering stock resides at depths of 600-2000m in the open ocean, especially in the Norwegian Sea and, it is assumed, in the Labrador/Irminger Sea in the northwest Atlantic. In the Norwegian Sea, these depths correspond to temperatures less than 1°C. Modelling and field observations have shown that most of the productive populations in shelf seas are sustained by annual recolonisation from these oceanic overwintering stocks. This explains why the long-term trends in abundance in, for example, the North Sea appear to be driven by the changes occurring over the wider northeast Atlantic (Figure 3).

So, the issue resolves to what is driving the basin scale changes in *C. finmarchicus* abundance in the ocean? One theory is that changes in the deep circulation of the North Atlantic and the availability of overwintering

habitat in deep water masses are playing a large role. Data from the Faroe-Shetland Channel, which lies between the Faroe Islands and the Shetland Islands off northern Scotland, show that between October and March, dense concentrations of overwintering *C. finmarchicus* are found in the deep (>600m) cold overflow of Norwegian Sea Deep Water into the Atlantic. This overflow is part of the thermohaline circulation system which ventilates the global oceans. Norwegian Sea Deep Water is generated by deep convection in the Greenland Sea, and as this process has slowed down in concert with the rise in the NAO since the 1960s, so the volume of Deep Water in the Faroe-Shetland Channel has decreased. In consequence, the abundance of overwintering stock available to colonise the North Sea each spring has also declined, thus providing a possible explanation for the Continuous Plankton recorder observation in the North Sea. Are similar relationships responsible for the long-term dynamics in the North Atlantic as a whole? A

detailed modelling and observation programme in the North Atlantic basin scale will be getting underway in late 2001 to address this question. The work will be a collaboration between the UK-GLOBEC programme and GLOBEC research programmes in Canada, Iceland, Norway and USA.

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Effects of increasing atmospheric CO₂ on phytoplankton communities and the biological carbon pump

by U. Riebesell, I. Zondervan, B. Rost, and R.E. Zeebe

In global assessments of potential anthropogenic CO₂ sources and sinks, the oceanic biosphere has commonly been considered to remain constant over time scales relevant to 'global change'. The 'constant oceanic biosphere' concept is based on the assumption that anthropogenic perturbations of environmental conditions determining ocean productivity are insignificant on a global scale. However, large-scale changes in surface ocean chemical equilibria and elemental cycling have occurred in the framework of 'global change' and are expected to continue and intensify in the future. One of the most prominent anthropogenic perturbations, the progressive increase in atmospheric CO₂, affects the marine biota in various ways: indirectly through rising mean global temperatures causing increased surface ocean stratification, and directly through changes in surface ocean carbonate chemistry.

A climate-induced increase in surface ocean stratification has two opposing effects on phytoplankton productivity: it reduces nutrient supply from deeper layers and increases light availability due to shoaling of the upper mixed layer. These changes are likely to cause an overall decrease and – due to a longer growing season at high latitudes – a poleward shift in oceanic primary production. Recent model calculations in fact indicate large regional differences in the effects of climate change on the marine biota, predicting a 20% decrease in export production in low latitudes and a 30% increase in high latitudes for a 2 × CO₂ scenario [3]. Changes in the amount and distribution of primary production will affect higher trophic

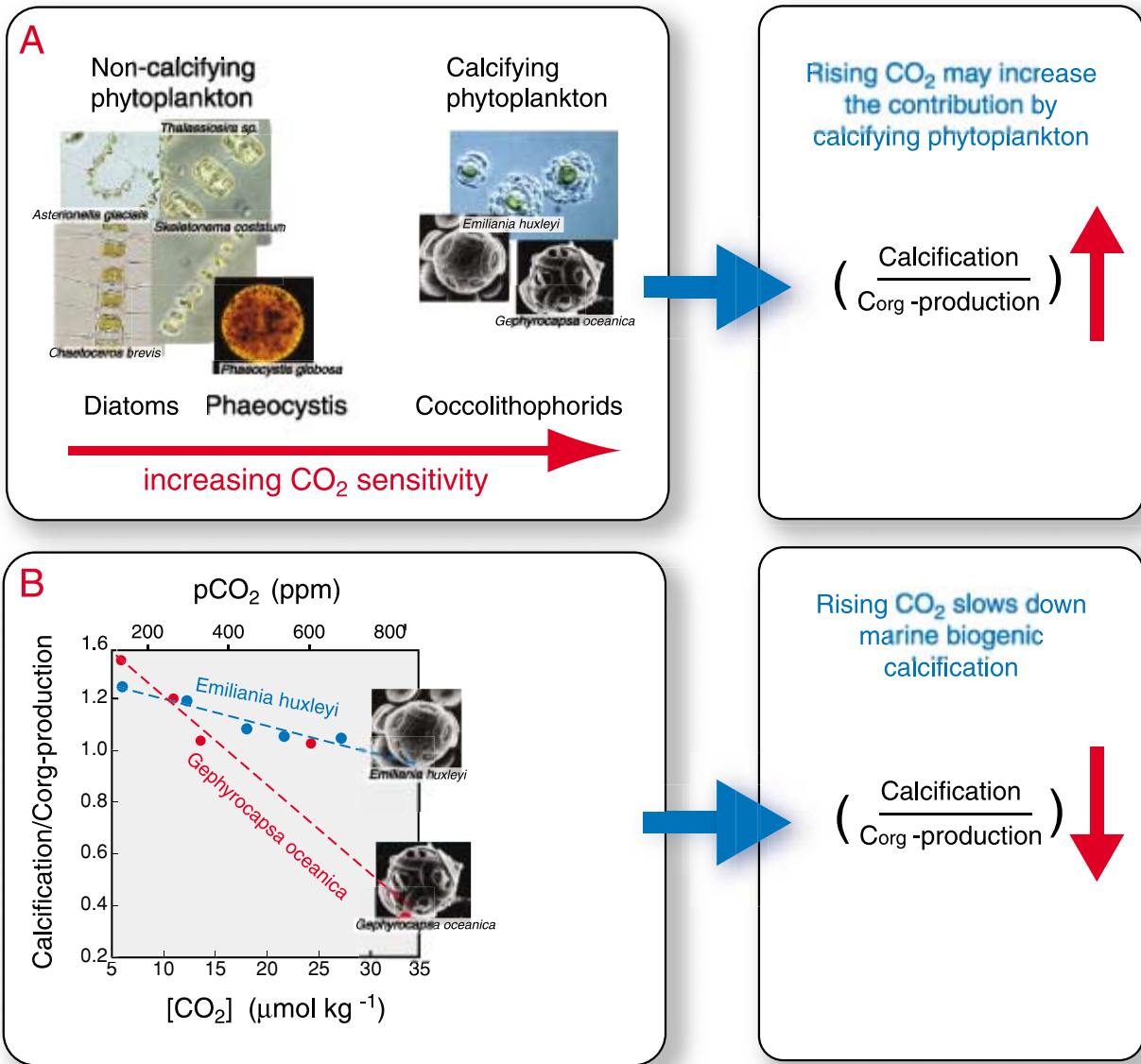


Figure 1. Potential effects of rising CO₂ on phytoplankton: A. Due to differences in CO₂ sensitivity between phytoplankton taxonomic groups, rising CO₂ is likely to influence phytoplankton composition and succession. One possible consequence could be shift in the contribution of calcifying phytoplankton on to total primary production. B. Rising CO₂ decreases the ratio of calcification to organic carbon production in two coccolithophore species (Riebesell et al 2000: Nature 2000).

Note that the decrease in this ratio is caused by both reduced calcification and enhanced C_{org}-production. A and B have opposing effects on the ratio of calcification to organic matter production.

levels, with likely consequences for key economic fisheries.

Aside from its indirect effect on climate, the present rise in atmospheric CO₂ concentration directly impacts the marine biota by changing the surface ocean carbonate chemistry. By the end of the next century, the expected increase in atmospheric CO₂ will give rise to an almost three-fold increase in surface water CO₂ concentrations

relative to pre-industrial values (assuming IPCC's 'business as usual' scenario IS 92a). This will cause CO₃²⁻ concentrations and seawater pH to drop by ca. 50% and 0.35 units, respectively. These changes in seawater carbonate chemistry are likely to affect phytoplankton taxonomic groups differently. For instance, large differences between major phytoplankton groups exist with

respect to the CO₂ specificity of the predominant carboxylating enzyme ribulose biphosphate carboxylase/oxygenase (Rubisco). Rubisco specificity - the enzyme's affinity to CO₂ relative to its affinity to O₂ - decreases with increasing evolutionary age of the phytoplankton [9]. Highest Rubisco specificities are found in the most recently evolved group of phytoplankton,

the diatoms. Progressively lower values occur in coccolithophorids, green algae, dinoflagellates, and the most ancient phytoplankton, the cyanobacteria.

Recent studies further indicate that dominant phytoplankton species differ in their CO₂ requirement. Whereas some species preferably use CO₂ as a carbon source, others mainly draw their inorganic carbon from the large pool of HCO₃⁻ (e.g. [6]). Also, group-specific differences in CO₂ sensitivity exist with respect to carbon metabolism. Most notably, the photosynthetic carbon fixation rates of all diatom species tested thus far, as well as of the prymnesiophyte *Phaeocystis globosa*, are at or close to CO₂-saturation at present day CO₂ levels [4, 5; Rost et al. unpubl.]. In contrast, the coccolithophorids *Emiliania huxleyi* and *Gephyrocapsa oceanica* are well below saturation at these levels [Rost et al. unpubl.; 8]. These findings suggest large differences in CO₂-sensitivity between major phytoplankton taxonomic groups. CO₂-sensitive taxa, such as the calcifying

coccolithophorids, would be expected to benefit more from the present increase in atmospheric CO₂ compared to the non-calcifying diatoms and

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Phaeocystis. Rising CO₂ levels might therefore increase the contribution of the calcifying phytoplankton to overall primary production, which would consequently increase the ratio of calcification to organic carbon production in the ocean (Fig. 1A). Since coccolithophorid blooms predominantly occur in well-stratified waters, projected climate-induced changes in the marine environment may prove even more advantageous for this group of phytoplankton.

A shift in phytoplankton species composition and succession is likely to impact both

ecosystem regulation and biogeochemical cycling. Diatoms, *Phaeocystis*, and coccolithophorids each serve a specific role in the marine

ecosystem and have distinct effects on elemental cycling. This is reflected in the ‘functional groups concept’, in which phytoplankton taxa are grouped according to their role in ecological and biogeochemical processes. One of the most prominent examples of this is the impact calcifying and non-calcifying

phytoplankton have on CO₂ air-sea exchange. While the latter drive the organic carbon pump, which causes a draw-down of CO₂ in the surface ocean, the former also contribute to the calcium carbonate pump, which releases CO₂ into the environment (Fig. 2). An increase in the ratio of calcium carbonate to organic carbon in the vertical flux of biogenic material (the so-called ‘rain ratio’), as could result from an increased contribution of coccolithophorids to total primary production, would enhance the relative strength of the carbonate pump. This would in turn lower biologically-mediated

CO₂ uptake from the atmosphere. A basin-wide shift in the composition of sedimenting particles - seen in a decrease of the opal:carbonate ratio - has in fact been observed across the entire North Atlantic and is suggested to be related to large-scale changes in climatic forcing [1].

Rising atmospheric CO₂ may impact the marine biota in yet another form. CO₂-related changes in seawater carbonate chemistry were recently shown to affect marine biogenic calcification. A doubling in present-day atmospheric CO₂ concentrations is predicted to cause a 20-40% reduction in biogenic calcification of the pre

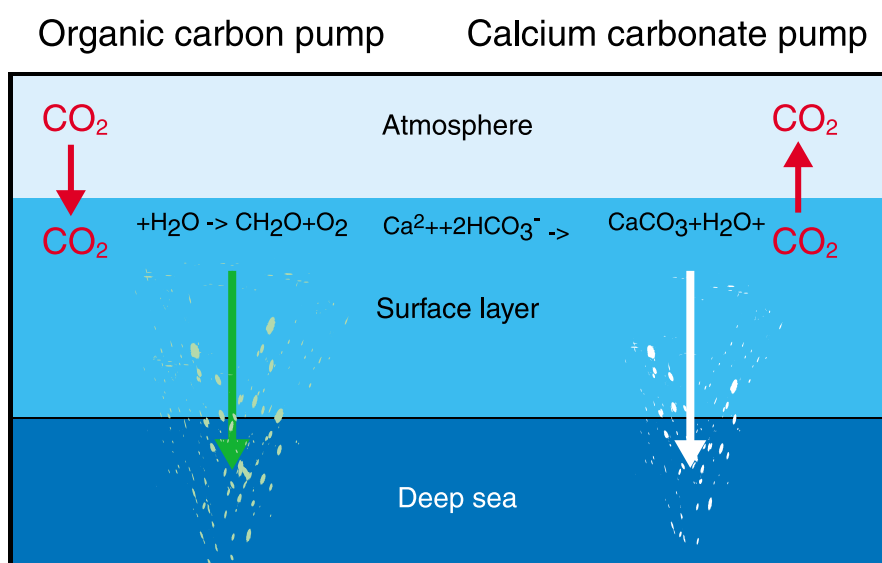


Figure 2. The biological carbon pumps: Photosynthetic carbon fixation in the surface layer of the flux of organic matter to depth, termed organic carbon pump, generates a CO₂ sink in the ocean. In contrast, calcium carbonate production and its transport to depth, referred to as the calcium carbonate pump, releases CO₂ in the surface layer. The relative strengths of these two processes largely determine the biologically-mediated ocean atmosphere CO₂ exchange.

dominant calcifying organisms - the corals, foraminifera, and coccolithophorids [2, 7, 8]. A CO₂-related reduction in calcification decreases the ratio of calcification to organic matter production (Fig. 1B). With ca. 80% of global CaCO₃ production contributed by planktonic organisms, reduced calcification decreases the strength of the calcium carbonate pump and thereby increases the biologically-driven uptake of CO₂ into the surface ocean [10].

As illustrated above, a climate-induced increase in the contribution of coccolithophorids to total primary production,

hypothetical at present, and a CO₂-related decrease in biogenic calcification would have opposing effects on the marine carbon cycle. Their net effect on carbon cycling will depend on their relative importance and sensitivity to global change. Changes in marine production and phytoplankton species composition and succession will also impact other biogeochemical cycles, such as the nitrogen, opal, and sulfur cycles, which in turn is bound to feedback on the climate. Despite the potential importance of global change-induced biogeochemical feedback, our understanding of these

processes is still in its infancy. It is now becoming increasingly clear, however, that the assumption of a constant oceanic biosphere in assessments of future global change is no longer viable.

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