Marine manipulations

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The effect of increasing levels of atmospheric carbon dioxide on carbon uptake in and export from the upper ocean is one of the big questions in environmental science. But it can be tackled experimentally.

Marine phytoplankton are major players in the carbon cycle, accounting for about 50% of the global biological uptake of carbon dioxide[1]. Near the ocean surface, these single-celled organisms use light energy to convert CO_2 into organic molecules for building cellular structures and driving their metabolism. Some of this organic carbon eventually sinks into the deep ocean, where most of it is either converted back to CO_2 or sequestered in sediments. This 'biological pump' effectively removes CO_2, a greenhouse gas, from the atmosphere for hundreds to millions of years.

In a recent issue of *Nature*, Riebesell *et al.*[2] describe evidence that the biological pump may become stronger at elevated concentrations of CO_2 in the atmosphere, and thus provide a negative feedback on increasing atmospheric CO_2. According to their calculations, that feedback has accounted for about 10% of the extra CO_2 pumped into the atmosphere since pre-industrial times (the past 200 years or so).

Since industrialization, atmospheric CO_2 has risen from about 280 parts per million (p.p.m.) to more than 385 p.p.m., increasing by some 2 p.p.m. per year during the past decade. Each year, approximately 25–30% of anthropogenic CO_2 enters the surface ocean, where it increases both the concentration of dissolved inorganic carbon (DIC) and acidity. The latter has potentially adverse consequences for phytoplankton that require calcium carbonate to build their shells. Although the oceans are Earth's largest reservoir for DIC, only about 1% is in the form of CO_2, the molecule required by the photo-synthetic enzyme rubisco. At the low CO_2 concentrations typical of sea water, rubisco operates at rather low efficiency[3]. So increasing ambient concentrations of CO_2 in sea water could boost photosynthetic efficiency and increase biological uptake of anthropogenic CO_2, just as some marine phytoplankton use intracellular carbon-concentrating mechanisms to increase their photosynthetic capacity.

This is the context for Riebesell and colleagues' research[2] into how phytoplankton might respond to increasing CO_2 concentrations. They conducted CO_2 manipulations in large cylindrical enclosures called mesocosms that were placed in a fjord in southern Norway and extended from the surface to a depth of approximately 9–10 metres. Although this approach is complex and logistically difficult, the advantage is that mesocosms are exposed to the same environmental influences as the surrounding waters, making them reasonable analogues for natural systems. And they can be manipulated experimentally. In Riebesell and colleagues' study, phytoplankton were grown in different mesocosms with the partial pressure of CO_2 adjusted to simulate the present (350 µatm) or projected future (2 × present CO_2, 700 µatm, and 3 × present CO_2, 1,050 µatm) atmosphere.

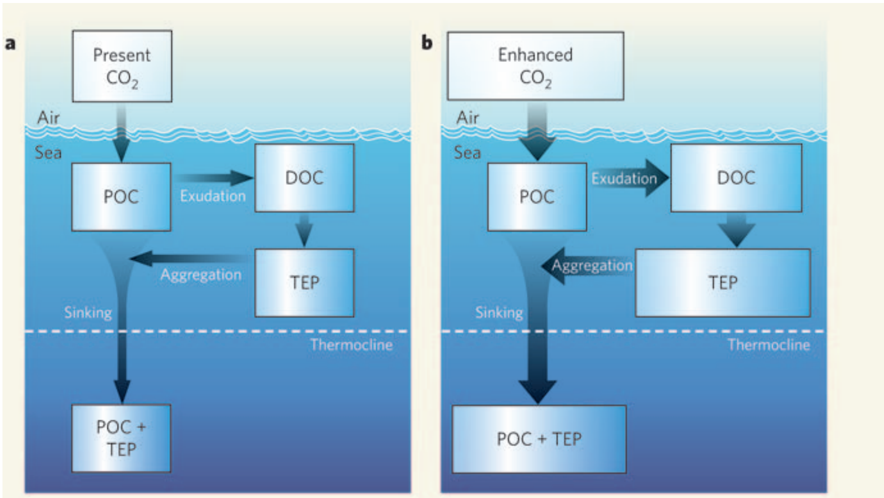

Figure 1 Carbon dioxide in the atmosphere, and organic carbon in the ocean. **a**, The size, relative to part b, of the different pools and fluxes of organic carbon under present levels of atmospheric CO_2 (POC, particulate organic carbon; DOC, dissolved organic carbon; TEP, transparent exopolymeric particles). The thermocline is an abrupt temperature discontinuity that acts as a barrier between the upper mixed ocean and deeper waters. **b**, According to the results of Riebesell *et al.*[2], uptake of CO_2 by phytoplankton increases at enhanced CO_2 concentrations (thicker arrow). Exudation of DOC from the pool of POC (primarily phytoplankton) also increases, although the POC pool itself remains unchanged. This extra DOC coalesces to form a larger pool of TEP that facilitates increased POC aggregation and enhances sinking fluxes. Thus, the flux of carbon from the atmosphere to the deep ocean is increased at higher atmospheric concentrations of CO_2.

What the authors found was intriguing. Uptake of CO_2 by phytoplankton (mainly bloom-forming diatoms and coccolithophores) in the 2 × CO_2 and 3 × CO_2 treatments was 27% and 39% higher, respectively, than in the present-day CO_2 treatment. But the additional CO_2 removed from surface waters at elevated CO_2 was not balanced by increases in particulate organic carbon (POC) in the surface layer. Furthermore, the loss of nitrate from the surface waters was the same in all three CO_2 treatments, indicating that the ratio of carbon to nitrogen uptake increased at higher CO_2 concentrations whereas the cellular carbon/nitrogen ratio of the phytoplankton remained unchanged.

This result suggests that, although higher ambient CO_2 concentrations increased CO_2 uptake by phytoplankton, the additional carbon incorporated into cells was rapidly lost as dissolved organic carbon (DOC). However, although DOC concentrations in the mesocosms increased, these were insufficient to balance the measured CO_2

deficits. In nature, organic molecules excreted from phytoplankton (for example, as DOC), or otherwise lost as these organisms die or are grazed, can coalesce to form semi-solid structures called transparent exopolymer particles (TEPs). These structures are sticky and facilitate the aggregation and increased sinking speeds of other particulate matter. In the mesocosms, TEP concentrations increased fourfold during the experiment (the carbon content of these TEPs is not presented by Riebesell *et al.*).

The authors propose that accumulations of TEPs in the elevated-CO_2 treatments facilitated aggregate formation, increasing the flux of particulate matter from the mesocosm surface. Coupled with higher DOC production, this may explain why POC did not increase in the elevated CO_2 treatments. Thus, it seems that increased CO_2 uptake fuelled by higher CO_2 concentrations was rapidly converted to DOC and TEPs, and any additional carbon incorporated into POC was lost from the surface of the mesocosm owing to increased particle aggregation and sinking (Fig. 1). Assuming that their results are representative of the larger ocean, increased atmospheric CO_2 may lead indirectly to increased particle fluxes from the surface ocean to depth, providing a negative feedback to increasing atmospheric CO_2 concentrations. Unfortunately, the authors did not measure POC sinking fluxes in their mesocosms to confirm this link.

Nevertheless, there are some notable conclusions to be drawn from this study. First, although CO_2 uptake by phytoplankton may be stimulated in a high-CO_2 world, this negative feedback will only partly offset expected increases in atmospheric CO_2. In fact, Riebesell *et al.* perform some clever calculations to show that the CO_2-enhancement effect they identified has probably reduced the rise in atmospheric CO_2 by only 11 μatm (about 10%) since the dawn of the industrial revolution.

More importantly, their study provides a vivid example of the fact that ocean biology is not in steady-state and that fundamental biological and biogeochemical processes are likely to respond to climate change, resulting in either positive or negative feedbacks that are difficult to predict. One positive feedback between biology and climate has already been identified, whereby future increases in stratification of the Southern Ocean could favour types of phytoplankton that have a reduced capacity to take up CO_2 (ref. 4). Conversely, increased CO_2 has been shown to enhance fixation of free nitrogen, thereby relaxing nutrient limitation by nitrogen availability and increasing CO_2 uptake[5]. Riebesell and colleagues document another negative feedback whereby CO_2 use by the dominant bloom-forming groups of phytoplankton could increase as atmospheric levels of CO_2 rise. Neither these, nor other possible non-steady-state biological feedbacks, are currently accounted for in models of global climate — a potentially serious omission, given that the biological pump is responsible for much of the vertical CO_2 gradient in the ocean.

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Published online: 21 November 2007
doi:10.1038/450491a

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Article originally published in *Nature* (491–492, Vol 450, 22 November 2007). Please refer to this for citation purposes.