Antarctic Marine Primary Production, Biogeochemical Carbon Cycles and Climatic Change [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1992 **338**, 289-297
doi: 10.1098/rstb.1992.0149

Antarctic marine primary production, biogeochemical carbon cycles and climatic change

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SUMMARY

In the Southern Ocean, inorganic macronutrients are very rarely depleted by phytoplankton growth. This has led to speculation on possible additional CO_2 drawdown in this region. However, the effects of climate change can only be predicted once the role of environmental and biotic factors limiting phytoplankton carbon fixation are understood. It is clear that the Southern Ocean is heterogeneous, and no single factor controls primary production overall. Ice cover and vertical mixing influence algal growth rates by modulating radiance flux. Micronutrients, especially iron, may limit growth in some areas. Primary production is also suppressed by high removal rates of algal biomass. Grazing by zooplankton is the major factor determining magnitude and quality of vertical particle flux.

Several of the physical controls on phytoplankton production are sensitive to climate change. Although it is impossible to make numerical predictions of future change on the basis of our present knowledge, qualitative assessments can be put forward on the basis of model predictions of climate change and known factors controlling primary production. Changes in water temperature and in wind-induced mixing are likely to be slight and have little effect. Model predictions of changes in sea-ice cover vary widely, making prediction of biogeochemical effects impossible.

Even if climatic change induces increased nutrient uptake, there are several reasons to suspect that carbon sequestration will be ineffective in comparison with continuing anthropogenic CO_2 emission.

1. INTRODUCTION

Current attention on likely climate change induced by anthropogenic production of radiatively active, or 'greenhouse', gases has prompted major investigations of global biogeochemical cycles. Although there is considerable uncertainty over the relative magnitude of the different sinks in the global carbon cycle, it is known that approximately half of the anthropogenic CO_2 emitted to the atmosphere enters other pools rapidly, and that much of this is taken up by the oceans (IPCC 1992). Because of this, the role of the oceans in the planet's carbon cycle has been a key area in study of global change. It is known that the oceans provide a long-term sink for atmospheric CO_2, partly through the production of particulate material in the euphotic zone and its subsequent export to the ocean interior and to the sediments: the so-called 'biological pump' (see Longhurst 1991). However, there are significant uncertainties over the fundamental mechanisms of carbon dioxide sequestration by the oceans, and prediction of future fluxes is problematic.

Hart (1934, 1942) emphasized two key features of Antarctic primary productivity, both of which are relevant to the current discussion of ocean biogeochemical cycles. First, he noted that phytoplankton production averaged over the Southern Ocean was low, although some neritic areas showed very high biomass during the short Antarctic growth season. Secondly, he confirmed that concentrations of inorganic macronutrients (N, P, Si) remained high throughout the year. The coincidence of low plant growth with high nutrient concentrations is considered atypical for oceanic primary production, and has been described as the 'Antarctic Paradox' (see Tréguer & Jacques 1992).

In contrast, production by phytoplankton in most of the ocean is nutrient-limited. It is widely believed that enhanced atmospheric CO_2 will have no direct fertilization effect on production in these areas. This assumption has been challenged for marine phytoplankton by U. Riebesell and co-workers (personal communication), but it appears likely that phytoplankton production will remain stable over much of the world ocean. Only HNLC (high-nutrient, low-chlorophyll) regions such as the Southern Ocean and the subarctic Pacific provide the potential for enhanced carbon flux to the deep ocean, because factors other than nutrient supply control annual production.

In this review, we highlight possible controls on phytoplankton production in the Southern Ocean, and speculate on the possible implications of these

Phil. Trans. R. Soc. Lond. B (1992) **338,** 289–297
Printed in Great Britain

factors on both the role and the response of the Southern Ocean in future climate change.

2. BACKGROUND TO ASSESSMENT OF THE BIOGEOCHEMICAL SIGNIFICANCE OF THE SOUTHERN OCEAN

Our aim is to assess the likely future role of the Southern Ocean in carbon cycling, and hence its effect on climate change. Before considering the present controls on primary production, we note two important problems.

(*a*) *Large-scale heterogeneity*

Partly because of the paucity of data, there has been a tendency to generalize biogeochemical processes for the Southern Ocean as a single unit. Tréguer & Jacques (1992) provide a clear account of the properties of four oceanographic régimes, whose dynamics are related primarily to the duration of sea ice cover. On the basis of this sub-system approach, it is possible to make more relevant generalizations about production and nutrient cycling.

Estimates of the mean productivity of the open waters of the Southern Ocean have changed little from those made in the late 1970s and a best estimate of the average annual production rate is 16 g C m^{-2} y^{-1} (Smith 1991). *In situ* studies, and satellite observations of chlorophyll biomass, indicate higher productivity in the receding marginal ice zone (MIZ) (Smith *et al.* 1988) and in neritic areas (Holm-Hansen & Mitchell 1991). Smith *et al.* (1988) estimated that approximately 40% of the annual production in the Southern Ocean is associated with the MIZ. Smith (1991) suggests an annual production rate for the ice edge of 38 g C m^{-2} y^{-1}, but notes that its small area means that total production is again comparatively low. Smith estimates a total annual carbon fixation over the Southern Ocean (38×10^2 m^2) of 1.23 Gtonnes per annum, compared with a global total of 27.2 Gtonnes.

(*b*) *Prediction of climate change*

Despite the rapid advances in climate modelling during the last decade (Cattle, this symposium), there remains considerable disagreement between the magnitude, and sometimes direction, of changes in environmental conditions at regional scales. Thus it is only with the inception of more complex ocean components in coupled ocean atmosphere models that a realistic oceanic heat sink has been included (Manabe *et al.* 1991). Because of this and other apparent modelling artefacts, it has been very difficult for biologists and climatologists to estimate the effects of future climate change on ecosystems and biogeochemical processes (Mellilo *et al.* 1990). As a specific example relevant to this paper, we would cite the extreme winter warming in the Southern Hemisphere indicated by the three models illustrated in the IPCC summary (Mitchell *et al.* 1990, Fig. 5.4), and contrast this with the relatively small temperature rise in the model of Manabe *et al.* (1991).

3. CONTROL OF PRIMARY PRODUCTION AND THE BIOGEOCHEMICAL CARBON CYCLE

The flux of carbon within the ocean, and between ocean and atmosphere, is determined partly by biogeochemical processes. The introduction of carbon to this cycle is largely through photosynthetic production in the euphotic zone. The particulate and dissolved organic material produced by phytoplankton growth then undergoes various transformations within the ecosystem, and only part of the fixed carbon enters long-lived pools. Clearly, climatic change can impinge upon the complete range of processes involved in the biological carbon pump. Some effects will be interconnected, and feedback to climate can also be surmised. If we are to estimate the possible impacts of climate change on oceanic primary production, and on the fate of that fixed carbon, we need first to identify the various environmental and biological controls impinging on productivity. The following sections note pertinent features only; more detailed treatment is provided in Tréguer & Jacques (1992), and in papers in Chisholm & Morel (1991) and Tréguer & Quéguiner (1991).

(*a*) *Rate-limiting factors for primary production: physical variables*

(i) *Temperature*

Consistently low environmental temperatures characterize the Southern Ocean. This has been shown to influence phytoplankton growth rates (e.g. Tilzer *et al.* 1986; Thomas *et al.* 1992), but is not the environmental factor thought to exercise overall control over production. Indeed, highest growth rates may be associated with ice (e.g. Smetacek *et al.* 1992).

(ii) *Photosynthetically available radiation*

Sakshaug & Holm-Hansen (1984) emphasize that incoming solar radiation at high latitudes is adequate for phytoplankton production, although the growth season is short. Ice- and snow-cover are important modifiers of the underwater light climate over seasonal timescales (Perovich *et al.* 1986).

Over the shorter timescales associated with phytoplankton growth rates, vertical mixing is the major physical variable influencing light availability. The critical depth concept of Sverdrup (1953) suggests that phytoplankton growth is not inhibited by vertical mixing, if phytoplankton respiration is taken as the sole loss process (Smetacek & Passow 1990; Nelson & Smith 1991). However, inclusion of other factors, especially the slow growth rates at ambient temperatures, indicates that phytoplankton blooms may only develop in very shallow mixed layers: 10–25 m (Mitchell & Holm-Hansen 1991; Sakshaug *et al.* 1991). In open water, the timescale of bloom development appears to be of the same order as that of the occurrence of storms, so that the mixed layer rarely remains shallow long enough to establish high biomass (Sakshaug *et al.* 1991).

(iii) *Ultra-violet radiation*

Chemical breakdown of stratospheric ozone results in gross increases in ultra-violet radiation flux beneath the 'ozone hole', and in smaller but significant increased global UV fluxes (Pyle, this volume). The increased flux of mid-wavelength ultraviolet radiation – UV-B – has a range of biological effects. Smith *et al.* (1992) indicate that the increased flux of UV-B could result in concomitant decrease in microalgal productivity. They compared in situ growth in the marginal ice zone beneath and outside the 'ozone hole'. Up to 12% decline in primary production occurred, although the authors acknowledge that this translates into a much smaller figure (perhaps 2%) of total Southern Ocean productivity. Although apparently a small effect, this should be included in consideration of future changes in Southern Ocean productivity, especially as UV-B flux may act as a selection pressure to alter plankton communities (El-Sayed *et al.* 1990).

(*b*) *Rate-limiting factors: chemical variables*

(i) *Macronutrients*

As already stated, macronutrients such as nitrogen, phosphorous and silicon are in plentiful supply in surface waters of the Southern Ocean. There is no evidence that limitation occurs at concentrations normally found in the Southern Ocean, although nutrient decline or, occasionally exhaustion, has been documented. Anomalous nutrient uptake kinetics (e.g. silicon half-saturation; Jacques 1983) or preference (ammonium preference; Jacques 1991; Owens *et al.* 1991; Smith & Harrison 1991) do not imply that macronutrient availability is significantly less that the water column concentration measurements imply.

(ii) *Micronutrients*

Trace elements, which are usually present in seawater at nanomolar concentrations, have key physiological roles, and have been the subject of several investigations of Antarctic marine phytoplankton (Hayes *et al.* 1984). More recently, the possibility that iron may limit phytoplankton production in both the Southern Ocean and the subarctic Pacific has led to intensive study and lively debate (Chisholm & Morel 1991). It is well-substantiated that dissolved Fe concentrations are low overall in the Southern Ocean, although there is marked spatial variability (Martin *et al.* 1990; Nolting *et al.* 1991; Westerlund & Ohman 1991). The spatial pattern of iron concentration accords with some of the gross features of phytoplankton biomass distribution. However, it is extremely problematic to make any inference based on these concentration measurements (Brand 1991; Bruland *et al.* 1991). Bioassay experiments at realistic concentrations indicate enhanced growth with iron addition (Martin *et al.* 1991). These results were confirmed by Buma *et al.* (1991), but they also note that phytoplankton nutrient uptake in control samples was sufficient to exhaust nutrients, although over a slightly longer period. Overall, it seems likely that iron effects would be most noticeable in open ocean waters (Helbling *et al.* 1991; Martin *et al.* 1990, 1991). Whatever the final outcome of this debate, it certainly seems that iron is not the sole factor determining primary production over the entire Southern Ocean.

(*c*) *Removal of standing stock: biological and physical losses*

It will be very much more difficult to consider those processes which can influence the abundance and distribution of phytoplankton biomass. Most depend critically on components of the system whose response to environmental variation on a large scale will be poorly defined. Thus it is clear that grazing by herbivorous zooplankton is an important component of biomass control, but unclear how grazing control is determined by environmental conditions and community composition.

(i) *Grazing losses*

Smetacek *et al.* (1990) point out that much of the pelagic ecosystem is dominated by a recycling community, where primary production and grazing are very tightly coupled. The members of this community are typically small and the grazers include both protists and metazoans. Superimposed upon this background are sporadic blooms of large-celled phytoplankton which form the basis for the classic Antarctic food chain. The grazing control of such events by long-lived grazers such as krill and copepods implies a complex interrelationship with the slow-growing phytoplankton. The highly patchy nature of the system, where high algal concentrations and krill swarms may be of similar physical scale (Priddle *et al.* 1990), may enable coexistence of substantial food supply with large herbivore populations.

(ii) *Sinking losses*

Loss of phytoplankton through sinking is a means of removal of biomass which is dependent on the organisms themselves and on the physical conditions in which they are growing. Motile phytoplankton can swim easily against gravity, and even nonmotile diatoms maintain suspension by means of an energy-consuming mechanism (Waite *et al.* 1992). It seems likely that, under optimal growth conditions, sinking out of cells will be negligible. Evidence from sediment trap measurements from various parts of the Southern Ocean does not implicate direct sedimentation of phytoplankton, in contrast to highly productive areas elsewhere in which mass sedimentation of diatoms is an important and recurring feature of the annual cycle (Smetacek 1985). Such events are commonly triggered by environmental conditions: nitrogen exhaustion will provoke sedimentation of diatoms (Smetacek *et al.* 1992), but is a rare event in Antarctic waters.

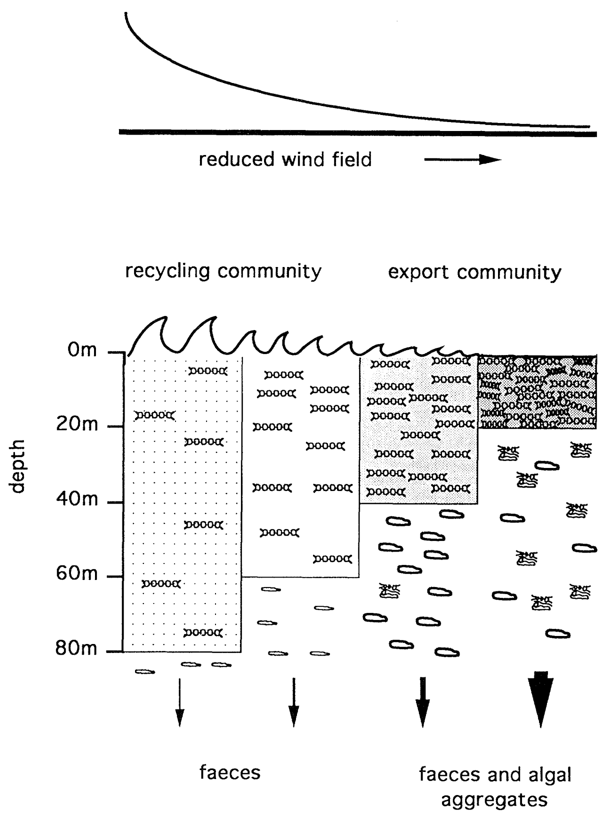

Figure 1. Schematic relationship between wind régime, mixed layer depth, and vertical particle flux. At high wind stress, the mixed layer is deep and phytoplankton biomass is low. Vertical flux of particles, predominately as small faecal pellets, is small. As the mixed layer becomes more shallow, under reduced wind forcing, algal biomass increases, and larger and colonial taxa become more important. Vertical particle flux also increases, and is dominated by flocs and faecal pellets of large grazers (based on Peinert *et al.* 1989).

4. THE FATE OF FIXED CARBON

The biological pump has a series of components, of which primary production by phytoplankton is only the initial part (Longhurst 1991). Particle transformation over the entire water column determines the route carbon follows through the cycle, and whether it enters long-lived or transient pools.

Community composition is a key determinant of the export of carbon from the euphotic zone. The structure of the plankton community results from a complex of environmental factors, some of which act directly on the grazing organisms themselves, whilst others act through intermediate levels of the food web. The fate of carbon may range from efficient recycling to effective export. Smetacek *et al.* (1990) review the extreme variation in vertical fluxes, as documented by sediment trap studies in the Bransfield Strait and Weddell Sea. At the one extreme, they point out that perhaps only 0.1% of primary production in the northern Weddell Sea may reach the seafloor, whereas krill grazing may produce rapid sedimentation of faecal material which represents significant proportions of annual production (perhaps 10%). E. Murphy & J. Priddle (unpublished data) reached similar conclusions from data for the South Georgia area, where the amount of carbon recycled in the euphotic zone was similar at stations dominated by diatom blooms or by microbial recycling, but represented 10 and 60% of total production, respectively.

Generalization of the effects of biological and physical variables on the flux from the euphotic zone is possible (Peinert *et al.* 1989), and is illustrated in figure 1. A shallow mixed layer is a prerequisite for build-up of high algal biomass. The shallower the layer, the faster the growth rate and the sooner the available nutrient pool is exhausted (Smetacek & Passow 1990). Nutrient exhaustion triggers aggregate formation and mass sinking out of diatom flocs. These flocs traverse the deep water column rapidly and represent a major source of organic carbon to the deep sea floor (Smetacek 1985; Jackson & Lochmann 1992; Riebesell & Wolf-Gladrow 1992). With increasing mixed layer depth, nutrient exhaustion no longer occurs. A recycling community dominates. Zooplankton faeces comprise an increasingly large proportion of sinking flux although overall export rates decline. This simplistic picture clearly ignores other significant events. For instance, mass sinking of a diatom bloom prior to nutrient exhaustion and following deep mixing by a passing storm has been observed in the Coastal Current adjoining the Weddell Sea (Bathmann *et al.* 1992).

5. POTENTIAL CHANGES IN THE SOUTHERN OCEAN ECOSYSTEM: IMPACT AND FEEDBACK

To understand the interaction between the Southern Ocean planktonic carbon cycle and future climate change, we need to focus on the controlling factors described above. However, four serious problems emerge when this approach is attempted.

1. It is difficult to obtain an unambiguous picture of the environmental changes which will impinge on the Southern Ocean ecosystem.
2. Although it is possible to make predictions of the effects of rapid environmental changes on the physiological response of living organisms, it is very much more difficult to assess the impact of long-term change. Here, biological response can include genetic drift and community change. These features are almost impossible to quantify experimentally.
3. The efficiency of the biological carbon pump in the ocean is determined by a matrix of biological processes, each with its own environmental controls and interrelationships with other processes. Although we might attempt to predict the impact of climate change on primary production, it is virtually impossible to translate this into carbon export.
4. The pelagic ecosystem can influence climate as well as being subject to climatic forcing. There is complex feedback, primarily through the effects of biogeochemical processes on the radiatively active gas composition of the atmosphere, but also subsidiary effects through the production of substances such as DMS (Charlson *et al.* 1987)

We have noted that phytoplankton production is controlled mainly by a range of physical and biological variables: light and vertical mixing, temperature-linked low growth rate, spatially varying micronutrient limitation, and the effects of grazing. These combined limitations give rise to the observed spatial pattern of low productivity in the permanently open water zone in the northern part of the Southern Ocean, and higher local productivity in association with the MIZ and coastal areas. We now examine likely climate-induced environmental changes, and attempt to assess their interaction with primary production in the Southern Ocean. This approach is the only viable option at present; numerical simulation of biogeochemical processes and climate change over large time- and space-scales is impractical with existing data and computers.

(*a*) *Temperature change*

There are several estimates of the magnitude of global warming, expected as a result of current and predicted anthropogenic changes. Early global simulations for a world with doubled atmospheric CO_2 concentrations suggested that both polar regions would exhibit the greatest warming. More recent models, which operate with a more realistic scenario of gradual increase in greenhouse gases and with more effective simulation of oceanic heat flux in coupled ocean-atmosphere models, indicate that warming in the Antarctic may not be as high as earlier predicted. Manabe *et al.* (1991) predict temperature change at the ocean surface of 0.5° to 1°C in the Southern Ocean under conditions of doubled atmospheric CO_2 concentration. In an examination of the seasonal pattern of this model, Manabe *et al.* (1992) also note that the annual temperature cycle would remain similar to contemporary behaviour.

If this relatively small change in temperature is realistic, then its direct effects on phytoplankton production can be assumed to be negligible. It would be unlikely to prompt significant changes in growth rates. Physiological studies of some poikilotherm herbivores suggest that this temperature change might be significant for them, thus either changing grazing rates or altering community composition.

(*b*) *Wind stress*

We would expect that major changes in wind stress would probably have consequences for phytoplankton primary production (Mitchell *et al.* 1991; Sakshaug *et al.* 1991). Long-period natural variability in wind forcing is implicated in changes in productivity in other parts of the world ocean (Dickson *et al.* 1988). Few published GCM results present explicit data on wind speed, although it might be surmised that changes in equator-to-pole temperature gradients might increase zonal winds. Manabe *et al.* (1991) predict only slight increase in wind stress in a doubled atmospheric CO_2 scenario. Peak windstress in this model was at 50°S, again similar to the contemporary pattern. Thus on the whole, we might expect slight increase in wind stress over the Southern Ocean, deepening mixed layers and thus continuing to inhibit phytoplankton bloom development.

(*c*) *Sea ice*

Ice formation and retreat are dominant processes in the Southern Ocean. They have a key biological role in providing stable conditions in which phytoplankton blooms may become established (Smith *et al.* 1988). Potential changes in extent, thickness and duration could all impinge on primary productivity. Climate change is expected to affect the extent of sea ice, and indeed changes in extent and thickness of Arctic sea ice have already been attributed to global warming (Gloersen & Campbell 1991). No such changes have been suggested for the Antarctic (Gloersen & Campbell 1991), and the model predictions of changes in Antarctic sea ice are ambiguous. Intuitively, we expect later formation of sea ice, and thinner ice cover, to increase heat flux to the surface water and thereby establish a positive feedback (Manabe & Stouffer 1980). Over periods of several decades, we would expect a decrease in total ice extent and a change in the timing of advance and retreat. These are crucial for the development of blooms in the marginal ice zone. Thus we would predict a decrease in Southern Ocean primary production associated with sea ice, although this might be offset partially by increased stability in the ice-free water column derived from stronger thermal stratification.

However, this simplified picture may not necessarily hold. Again, the model of Manabe *et al.* (1992) offers a somewhat surprising prediction. Here, sea-ice formation is critically influenced by the thermal effects of increased precipitation. In their model simulation under doubled atmospheric CO_2, sea-ice increases in extent, and thickens in the Weddell and Ross Seas. Were this situation to obtain, it could have important consequences for Southern Ocean carbon fluxes. The sea ice perimeter, and thus the area of the marginal ice zone ecosystem, would increase. The consequences for primary production depend on the importance of the spatio-temporal pattern of radiation flux to the MIZ. E. Murphy (personal communication) calculates that annual radiation input to the MIZ in the sector 0–90 W varies by 50% simply as a consequence of year-to-year variation in ice extent. At higher latitudes, the increased ice thickness in the simulation of Manabe *et al.* (1992) may impinge on the sea-ice community production, and could alter the importance of the under-ice community for overwintering herbivores, including krill (Smetacek *et al.* 1990).

(*d*) *Timescales and biological change*

Throughout this discussion, we have considered the effects of climatic change as if they were more or less instantaneous. Obviously, although the anticipated global changes will be more rapid than natural climate cycles, they are still slow in comparison with the physiological response of organisms. Other mechanisms can be invoked. It is clearly impossible even to guess at the possible manifestation of genetic selection within the existing populations. Change in community composition might also be expected, a process which might be exacerbated by the effects of other changes such as increasing UV-B fluxes and the impact of pelagic fisheries. Over longer time scales, we could anticipate more fundamental shifts in the character of the ecosystem, if taxa characteristic of higher latitudes are replaced by species from warmer waters. This could have key significance for the efficiency of the biological pump. For instance, the introduction of coccolithophorid blooms to the Southern Ocean (paralleling the North Atlantic) could change nutrient dynamics, decrease carbon drawdown, and increase cloud nucleation by DMS production.

6. INFORMATION FROM THE PALAEOENVIRONMENTAL RECORD

Potential changes and feedbacks between the oceanic biological pump and the global climate may have parallels in palaeoenvironmental record of oceanic production during glacial and interglacial periods. It is already clear that changes in global temperature were correlated strongly with atmospheric composition, especially CO_2 concentration. Barnola *et al.* (1987) have used data from ice cores to relate palaeotemperatures to atmospheric composition. They found that the concentrations of CO_2 varied by about 30% between glacial and interglacial periods. This indicates the role of radiatively active gases in determining global climate. It also indicates a natural mechanism for altering the content of these gases in the atmosphere, although whether this arises from climate-forcing of biogeochemical cycles or biogeochemical forcing of climate is not understood (e.g. Siegenthaler 1986). Alterations in Southern Ocean carbon export have been suggested as a potential mechanism for these changes, with elevated productivity reducing atmospheric CO_2 resulting in global cooling. Martin *et al.* (1990) propose a mechanism for changes in Antarctic marine productivity, based on aeolian iron input to the Southern Ocean, which could account for glacial–interglacial changes in atmospheric CO_2. Mortlock *et al.* (1991) contradict this supposition, indicating that palaeo-indicators of productivity in Antarctic marine sediments suggest that there was lower, rather than higher production in glacial periods.

7. EFFICACY OF ENHANCED SOUTHERN OCEAN PRIMARY PRODUCTION

Even if we are uncertain as to whether primary production in the Southern Ocean may change in response to alteration in global climate, it is useful to speculate on the potential effects of unspecified changes in the primary production of the Southern Ocean which might lead to increased utilization of the inorganic nutrient pool. The nature of the biological pump implies that it is not simply sufficient to increase carbon fixation by phytoplankton, but to export this to deep water where it will be removed from the global carbon cycle for a considerable length of time. Davies (1990) made a simplistic calculation to show that the surplus nitrate in the Southern Ocean should equate to 6.4 Gtonnes carbon fixed within phytoplankton. There are several grounds for doubting whether this theoretical enhancement of primary production would result in substantial and sustainable drawdown.

(*a*) *Losses within the euphotic zone*

The initial input to the biological carbon pump in the oceans is the fixation of carbon in particulate material by phytoplankton in the euphotic zone. This pool is comparatively short-lived, and only a very small proportion of it is exported to deeper water. The remainder is recycled within the ecological community of the euphotic zone, much of it returning rapidly, through respiration, to the dissolved inorganic pool where it can return to equilibrium with the atmosphere. At present, there is little quantitative information as to the proportion of primary fixation which is recycled within the euphotic zone. Huntley *et al.* (1991) suggest that the surface component of the biological pump is very inefficient, through the routing of much of the primary production along trophic pathways which involve air-breathing predators. Although their calculations and assumptions have been questioned, they serve to highlight both the small fraction of primary production which is normally exported from the euphotic zone, and the strong influence of ecosystem structure on the biological pump.

(*b*) *Counteracting processes*

Fuhrman & Capone (1991) point out that the stimulation or enhancement of Southern Ocean primary production would not simply result in greater carbon dioxide drawdown from the atmosphere. Other biogeochemical processes could be expected to change, with concomitant effects on atmospheric composition and climate. Among the key radiatively active gases which might also be generated are N_2O and CH_4. Fuhrman & Capone consider that the likely release of N_2O, with its greater greenhouse effect than CO_2, might alone more than counteract the climatic alleviation ‘bought’ by carbon dioxide reduction.

Other climatically important processes might be associated with the enhanced production. Algal production of dimethylsulphopropionate (DMSP) gives rise to dimethylsulphide (DMS), which in turn contributes to atmospheric sulphate aerosol, providing cloud nucleation sites (Charlson *et al.* 1987). Changes in cloud cover alter atmospheric albedo, heat flux to the ocean surface, and flux of photosynthetically available radiation. However, we are unclear at present both how important DMS production is in global climate, and whether Southern Ocean DMS production, which is restricted mainly to certain algal groups, might change. Gibson *et al.* (1989) reported DMS concentrations from Antarctic waters which were higher than previous measurements from other ocean areas, suggesting that DMS may play an important in cloud nucleation over Antarctic waters. Legrand *et al.* (1991) note high correlations between palaeotemperatures and biogenic sulphur emissions during a glacial–interglacial cycle, with indications of higher DMS output from Southern Hemisphere oceans during glacial periods. The authors emphasize the sensitivity of the ocean–atmosphere sulphur cycle to climate change, but there may also be feedback mechanisms as implied by Charlson *et al.* (1987).

(*c*) ***Effective carbon drawdown***

Following the suggestion that iron fertilization could produce result in complete or enhanced utilization of nitrate in the Southern Ocean, several numerical simulations have been attempted in order to assess the global consequences of such a change. All are derived from large-scale models, either box models or GCMs. Peng & Broecker (1990) concluded that the initial depression of atmospheric carbon dioxide concentration would rapidly be restored. They argued that deep water transport from the Southern Ocean was too small to continue to remove fixed carbon to the ocean interior. In a subsequent paper (Peng & Broecker 1991) they discuss this further, indicating that the rate of upwelling and the fate of upwelled water are the two key parameters in their model simulation. They also suggest that anoxia in deeper water may be significant. A similar modelling approach by Joos *et al.* (1991) produces slightly different results, indicating that complete nutrient utilization might remove 2 Gtonnes of CO_2 from the atmosphere. Both box models agree that the stimulus for primary production needs to be sustained: temporary fertilization will not produce long-term benefits. In a different modelling approach, Sarmiento & Orr (1991) used a three-dimensional ocean circulation model to simulate the effects of nutrient utilization in the Southern Ocean. They also found it to produce an effective reduction in atmospheric CO_2 and to induce some anoxia in deep waters. In their simulation, Southern Ocean nutrient utilization appears to have impacts on production at lower latitudes.

8. CONCLUSION

At present, numerical models cannot make direct prediction of the effects of climate on ocean biogeochemical carbon cycles, and consequent feedbacks. For the Southern Ocean, this problem is compounded by two factors: the biologists' inability to determine the factors which control oceanic primary production and the climate modellers' inability to provide robust estimates of the environmental conditions associated with predicted climate change. Taking the most recent GCMs with adequate simulation of oceanic heat fluxes, we note that changes in physical environmental conditions may have little direct impact on primary production, although ecosystem function may alter over slightly longer timescales. The impact of climate on Antarctic sea ice is not well-described, and thus the ecological consequences cannot be assessed.

There has been intense speculation over the possible effects of enhanced primary production in the Southern Ocean. This region has high nutrient concentrations and thus offers one of the major areas of the world where biogeochemical carbon flux could be increased. However, we can only note that enhanced primary production in the Southern Ocean, as envisaged as a consequence of Fe fertilization, would almost certainly not approach the carbon sequestration suggested by contemporary nutrient concentrations. It would certainly have repercussions on other parts of the world ocean, might have at most a neutral climatic effect due to associated climatically active components, and could only be effective if sustained. This conclusion appears to be borne out by the indication that Antarctic phytoplankton production during glacial periods was possibly lower, rather than higher, than in interglacial times.

We thank U. Riebesell, D. Wolf-Gladrow, E. Murphy and W. Connolly for valuable discussion and access to unpublished material.

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Discussion

J.-O. STRÖMBERG (*Kristinebergs Marinbiologiska Station, Fiskebäckskil, Sweden*). If we do get a marked reduction in the extent of Antarctic sea-ice because of climate change, how would this affect the higher faunal components?

J. P. CROXALL (*British Antarctic Survey, Cambridge, U.K.*). In response to Professor Strömberg's question we should note that ice-covered habitat is not necessary to the over-winter survival of krill because substantial populations occur in winter outside the marginal ice zone. However, the ice-covered habitat may be important for crucial aspects of krill life history (e.g. survival of juvenile krill) which form the basis for open-water populations. The relationships between ice cover and extent and krill demography is one of the key topics on which we urgently need quantitative data.