

## Review

## Antarctic Marine Microorganisms and Climate Change: Impacts and Feedbacks

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**Abstract :** Global climate change will alter many such properties of the Southern Ocean as temperature, circulation, stratification, and sea-ice extent. Such changes are likely to influence the species composition and activity of Antarctic marine microorganisms (protists and bacteria) which play a major role in determining the concentration of atmospheric CO<sub>2</sub> and producing precursors of cloud condensation nuclei. Direct impacts of climate change on Antarctic marine microorganisms have been determined for very few species. Increasing water temperature would be expected to result in a southward spread of pelagic cyanobacteria, coccolithophorids and others. Growth rates of many species would be expected to increase slightly but nutrient limitation, especially micronutrients, is likely to result in a negligible increase in biomass. The extent of habitats would be reduced for those organisms presently living close to the upper limit of their thermal tolerance. Increased UVB irradiance is likely to favour the growth of those organisms tolerant of UVB and may change the trophic structure of marine communities. Indirect effects, especially those as a consequence of a diminution of the amount of sea-ice and increased upper ocean stratification, are predicted to lead to a change in species composition and impacts on both trophodynamics and vertical carbon flux.

**Key words :** Antarctica, marine microorganisms, climate change, temperature, UVB.

### 1. Introduction

Air temperatures have increased at rates of 0.9-1.2 °C per century at stations on the Antarctic continent and 0.7-1.0 °C on sub-Antarctic islands respectively (Jacka and Budd 1998). This warming is not uniform over the region. The temperature at stations on the Antarctic Peninsula is increasing at more than twice the average of all stations. Warming is greatest in winter and smallest in autumn at the Antarctic stations but largest in autumn and smallest in spring and summer at the sub-Antarctic stations. There have also been considerable changes in the sea around Antarctica over the last 30 years. Sub-Antarctic Mode Water and Antarctic Intermediate Water have cooled and freshened and are now deeper, implying warming of surface water and increased precipitation in their source areas (Wong *et al.* 1999).

During its peak in September, Antarctica sea-ice covers around  $20 \times 10^6$  km<sup>2</sup>. Although there has not been a significant change in the overall extent of Antarctic sea-ice during the satellite era (since 1973) there have been regional changes. The extent of sea-ice has increased in the 0°-40°E region while it has decreased in the region between 65 and 160°W (Jacka and Budd 1998). Using whaling records, de la Mare (1997) calculated that the Antarctic sea-ice retreated southwards by about 3 degrees of latitude between the mid 1950s and early 1970s, representing a reduction in area of sea-ice of around 25 %. Based on modelling studies, Wu and Budd (1998) concluded that a century ago, the sea-ice was thicker and extended 0.4 and 1.8 degrees of latitude north of its present position.

Direct and indirect effects of climate change in the biota have been reported from the terrestrial environments on the Antarctic continent and sub-Antarctic islands (Chown and Smith 1993; Kennedy 1995; Frenot *et al.*

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1997; Gremmen 1997; Bergstrom and Chown 1999). Increases in temperature and human activity in Antarctica will increase the likelihood of successful invasions by alien terrestrial organisms with consequences for indigenous communities (Bergstrom and Chown 1999). Such impacts are now the subject of increasing research activity.

In contrast to such studies on Antarctic terrestrial environments, evidence that climate change has impacted on the marine biota is sparse. Empirical evidence of such climate-induced change is hard to obtain due to the inherent spatial and temporal variability in the marine environment. The Antarctic Peninsula region is the most comprehensively studied using instrumental records as well as palaeoecological data from ice cores and marine sediments (Smith *et al.* 1999). These authors report elevated levels of organic carbon concentration in sediments during periods of minimal sea-ice conditions and low concentrations when sea-ice is persistent and that in recent times, changes in the abundance and distribution of penguin species coincides with warming in this region.

Marine microorganisms play a pivotal role in the global carbon cycle. The oceans contain some 40,000 Gt C of dissolved organic material, organic particulates and biota. In contrast, the terrestrial biota, soils and detritus contains about 2,200 Gt C. Evidence derived from simulation modelling indicates that the pre-industrial atmospheric concentration in the absence of the marine biota would have been 450 ppm rather than 280 ppm (Denman *et al.* 1996). Primary production by marine phytoplankton can conveniently be regarded to have two components—recycled production, depending on nutrients recycled in the surface layers of the ocean, and new or export production that is supported by nutrients supplied to the photic zone from the land, the atmosphere, or upwelled from the deep ocean. The biological carbon pump is the process by which export production is transported from the photic zone to the deep ocean where, over long time periods, the organic carbon is remineralized to inorganic forms. Only a small fraction of the carbon is incorporated into the sediments. Thus the biological carbon pump reduces the CO<sub>2</sub> concentration in the surface waters of the ocean and the atmosphere and increases the amount of carbon at depth.

In addition to their role in the global carbon cycle, marine microorganisms are a major source of climatically active gasses, especially dimethylsulfide (DMS). The atmospheric sulfur cycle over Antarctica is dominated by the emissions of DMS from marine sources. Although

highly seasonal, emissions from the sea-ice zone around Antarctica account for at least 17 % of the emission of sulphur from the global ocean (Curran and Jones 2000).

Here we give a brief overview of Antarctic marine microbial interactions before discussing the likely impacts, and potential feedbacks, of increasing concentrations of CO<sub>2</sub> and increasing temperature and UVB irradiation. We strive to separate the direct from the indirect effects of climate change. Species can differ substantially in their response to both temperature and UV stress. Thus, in order to assess impacts of climate change, it is essential to ascertain the effects of these stresses on key organisms and the consequences of these effects on community structure. However, much of the investigation on the ecophysiology of Antarctic marine organisms has concentrated on their adaptations to living at low temperature with relatively little attention being devoted to their response to increasing temperatures, hindering prediction of the direct and indirect impacts of climate change.

## 2. Microbial interactions in antarctic waters

The Antarctic marine environment has been conveniently divided into four zones, the Coastal and Continental Shelf Zone (CCSZ), the Seasonal Ice Zone (SIZ), Permanently Open Ocean Zone (POOZ), and the Polar Front Zone (PFZ) (Tréguer and Jacques 1992). These zones differ in their biology and nutrient fluxes.

Our understanding of marine microbial interactions and the dynamics of the Antarctic marine environment has increased dramatically over the last two decades. Once thought to be a simple food chain, it is now known that Antarctic marine food webs are no less complex than those in other parts of the world's oceans (Fig. 1) (Hewes *et al.* 1985; Marchant and Murphy 1994).

There is a fundamental difference between the microbial loop in temperate and Antarctic waters (Azam *et al.*

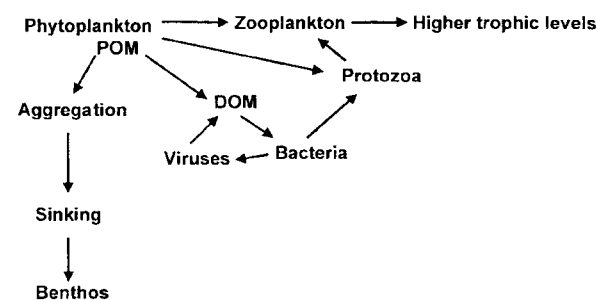


Fig. 1. Principal components of the marine pelagic food web.

1991). Picoplanktonic cyanobacteria are a major group of primary producers in temperate and tropical waters, but are essentially absent in Antarctic waters (Marchant *et al.* 1986). There are reports of size fractionated phytoplanktonic biomass and primary production in Antarctic waters that indicate a significant, and occasionally substantial, contribution by picoplankton (organisms in the size range 0.2-2.0  $\mu\text{m}$ ). Such studies are based on separating picoplankton from nanoplankton (organisms in the size range 2.0-20  $\mu\text{m}$ ) and microplankton (organisms > 20  $\mu\text{m}$ ) using filters of 2 and 20  $\mu\text{m}$  pore size respectively. Very few of these investigations have included details of the biodiversity of the organisms constituting the picoplanktonic contribution to productivity and biomass. Our studies reveal that Antarctic autotrophic "picoplankton" consists of highly asymmetric pennate diatoms including *Fragilariopsis curta*, *F. pseudonana*, *Pseudo-nitzschia prolongatoides*, *P. subcurvata*, *Cylindrotheca closterium*, and those nanoplanktonic flagellates that are able to pass through 2.0  $\mu\text{m}$  pore-sized filters including *Phaeocystis antarctica*, some chlorophytes and cryptophytes (Ishikawa *et al.* 2001).

Melting of the sea-ice during spring and summer generates a pycnocline, above which phytoplankton bloom in the nutrient-rich, high light environment. This southward moving region of high phytoplankton productivity in spring and early summer (Smith and Nelson 1986) is utilized by the higher trophic levels and contributes to high export production. However, some investigators (eg. Bathmann *et al.* 1994) have reported phytoplankton blooms between the major oceanographic fronts, not associated with the SIZ, as sites of substantial export production. Savidge *et al.* (1996) concluded that despite the extent of blooms elsewhere, the SIZ contributes at least 40 % of the phytoplankton biomass in the Southern Ocean.

In contrast to the highly productive coastal and ice edge environments that surround the Antarctic continent, the open ocean has a lower protistan biomass, consisting mainly of diatoms. Upwelling systems in the Southern Ocean maintain some of the highest near-surface macronutrient concentrations that have been recorded from oceanic waters, but micronutrients, especially iron, are likely to limit phytoplankton growth in some areas (de Baar *et al.* 1995; Coale *et al.* 1996). While many diatoms are adapted to low light conditions, wind-driven deep mixing carries cells below their compensation depth, limiting growth and accumulation of phytoplanktonic biomass.

### 3. Direct effects of climate change

#### CO<sub>2</sub> increase

While increased atmospheric CO<sub>2</sub> concentration is expected to promote production in terrestrial systems (Cao and Woodward 1998), marine production has not normally been considered to be limited by inorganic carbon. However Riebesell *et al.* (1993) and Hein and Sand-Jensen (1997) have challenged this view. They found that primary production increased by 15-19 % in response to the elevated CO<sub>2</sub> concentrations expected in surface oceanic waters over the next 100 to 200 years. Responses by phytoplankton differed dramatically between species, leading these authors to the conclusion that the overall increase in oceanic primary production would probably be small but the influence on phytoplankton species composition could be profound.

#### Temperature

An increase of 0.5-1 °C in sea surface temperature has been predicted for a doubling of atmospheric CO<sub>2</sub> concentration (Manabe *et al.* 1991). Priddle *et al.* (1992) considered that such a temperature increase is likely to have only a negligible direct impact on the Antarctic marine microorganisms. However more recent investigations in temperate areas of the world's ocean indicate small changes in ocean temperature can trigger interactions between key species that bring about substantial changes in natural communities (Sanford 1999). Many species of protists in Antarctic waters are living at temperatures below that required for maximum growth (see Vincent 1988 for review). Thus, an increase in water temperature is likely to cause species specific increases in growth rate, changing the relative abundance of microbial taxa and altering competitive interactions with ramifications for food web structure and function. Examples below illustrate this potential.

Chroococcoid cyanobacteria (blue-green algae) are an abundant and important group of picoplanktonic autotrophs in temperate and tropical waters where they have a growth rate of around 1.6 doublings per day (Johnson and Sieburth 1979). They also constitute a significant component of the food web with 30-40 % of their biomass being grazed per day (Iturriaga and Mitchell 1986). The abundance of these organisms decreases exponentially with temperature across the Southern Ocean (Marchant *et al.* 1987). Therefore any change in water temperature should lead to a predictable change in their abundance, and consequently a change in the species composition and

abundance of the microheterotrophs that graze them.

The distribution and abundance of some other phytoplankton such as coccolithophorids and Parmales are also temperature dependent. The distribution and abundance of these algae south of Australia has been well documented (Nishida 1986) and confirmed by our own observations. The abundance of coccolithophorids decreases with decreasing temperature so that south of 60°S, where the water temperature is below 4 °C, coccolithophorids are absent, other than the lightly calcified endemic polar taxa (Thomsen *et al.* 1988). Since coccolith production leads to a liberation of free CO<sub>2</sub> (Tyrrell and Taylor 1995), an increase in the abundance of coccolithophorids in the Southern Ocean to concentrations approaching those observed in the North Atlantic could have major influences on carbon flux. The Parmales are moderately abundant in polar waters and only very rarely found elsewhere (Booth and Marchant 1987; Kosman *et al.* 1993). Siliceous walls of Parmales have been found in sediment samples in Prydz Bay (Franklin and Marchant 1995) and were found to account for up to 32 % of the biogenic siliceous sediment close to the Ronne Ice Shelf in the Weddell Sea by Zielinski (1997). These authors conclude that Parmales are likely to be useful stratigraphic indicators of deposition from the coldest oceanic water namely, that which is seasonally ice covered. Any change in water temperature would be expected to have a direct effect on their distribution and abundance.

### Ultraviolet radiation

Stratospheric ozone concentration over Antarctica during spring commonly falls below 50 % and may decline below 30 % of pre-ozone-hole values (Weiler and Penhale 1994; Kerr 1998) and ozone depletion reportedly persists until February (Jones and Shanklin 1995). Thus, UVB (280-320 nm) radiation is enhanced throughout the period of greatest biological production in Antarctic waters. Antarctic ozone depletion is also predicted to increase in severity and duration in coming decades due to the greenhouse-induced cooling of the stratosphere (Shindell *et al.* 1998).

Concern regarding the effect of UVB on the Antarctic biota has led to an extensive literature on the photobiology of Antarctic organisms, most of which has focused on the impact of UVB on phytoplankton (eg. reviews by Voytek 1990; Karentz 1991; Häder and Worrest 1991; Vincent and Roy 1993; Karentz 1994; Marchant 1997; Davidson 1998). The evidence that UVB radiation can damage plankton is overwhelming: reducing production, growth,

and survival (eg. USEPA 1987; UNEP 1989, 1991). As discussed above, the sea-ice and seasonal ice zone support much of the primary production in the Southern Ocean (Smith and Nelson 1986; Voytek 1989). These environments are penetrated by biologically significant doses of UVB radiation (Trohadl and Buckley 1989; Karentz 1989; Ryan 1992; Smith *et al.* 1992; McMinn *et al.* 1997). Thus, enhanced UVB irradiances coincide with the seasonal bloom of plankton in environments that are susceptible to UVB radiation.

Large interspecific differences in the tolerance of phytoplankton to UVB exposure have been reported (Worrest *et al.* 1978; Calkins and Thordardottir 1980; Karentz *et al.* 1991; Helbling *et al.* 1994; Davidson and Marchant 1994; Davidson *et al.* 1994, 1996; Wängberg *et al.* 1996). Such differences in tolerance may be considerable, even between members of a single genus (Mitchell and Karentz 1990), or life stages of a single species (Marchant *et al.* 1991). Interspecific differences in the sensitivity of Antarctic phytoplankton to ambient UVB exposure has been shown to change species composition in mixed algal culture (Davidson *et al.* 1996) and in natural pelagic (Smith *et al.* 1992; Karentz and Spero 1995) and sea ice algal communities (McMinn 1997).

Many of the investigations of UVB impacts on marine microbes have been conducted on individual species. However, it has recently been recognized that the effect of UV radiation on the marine ecosystem is not the sum of its parts in isolation (Vernet and Smith 1997; Mostajir *et al.* 2000). Bothwell *et al.* (1994) showed that studies using a single trophic level could not predict the effect of UVB on an ecosystem since UVB induced changes in trophic-level interactions. Phytoplankton production supports planktonic microbial communities consisting of viruses, bacteria and protozoa, through which most of the organic matter in pelagic ecosystems is channeled (Azam 1998). Viruses, bacteria and protozoa can be damaged or killed by solar UVB radiation but species differ greatly in the sensitivity to UV exposure (for reviews see Jeffrey *et al.* 2000; Vernet 2000; Mostajir *et al.* 2000). Consequently, changes are likely in the production, growth, survival and species composition of these organisms. But very few studies have addressed UV-induced changes in dynamics of natural microbial assemblages (Sommaruga *et al.* 1999; Wickham and Carstens 1998; Keller *et al.* 1997; Bergeron and Vincent 1997; Mostajir *et al.* 1999) and none have been conducted in Antarctic marine waters. We have found that exposure of natural Antarctic microbial communities to ambient

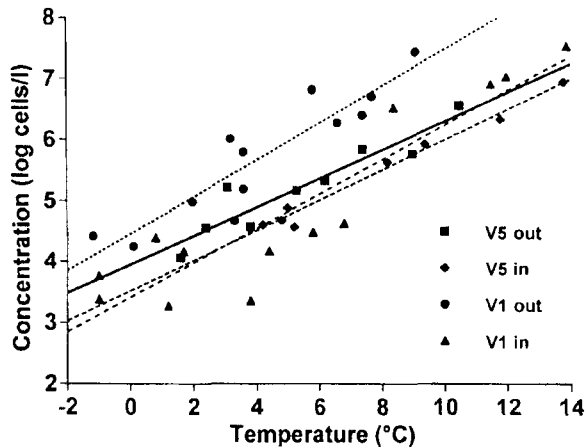


Fig. 2. Relationship between cyanobacterial concentration and temperature on 4 transects of the Southern Ocean between Tasmania and Antarctica (data from Marchant *et al.* 1987).

solar radiation causes UV dose and dose rate dependant phytoplankton mortality that enhanced activity of microheterotrophs (Davidson *et al.* unpublished).

UV-induced changes in the food available to higher trophic levels are the result of a complex array of biotic and abiotic feedback loops, the integrated effect of which is uncertain. Available literature suggests that increasing UVB may change the size, availability, nutritional value and palatability of plankton available to metazoan grazers (Marchant *et al.* 1991; Karentz 1994; Mostajir *et al.* 2000). Changes in the microbial community, its trophodynamics and availability to higher trophic levels, may significantly impact upon the biological pump (Mostajir *et al.* 2000), changing vertical carbon flux and altering the atmospheric accumulation of greenhouse gases.

#### 4. Indirect effects of climate change

As well as the direct effects of climate change described above, there are many indirect factors that may substantially affect the microbial ecology of the Southern Ocean. Climate change is likely to affect features of the Antarctic marine environment including sea-ice extent, ocean circulation, mixing regimes, cloud cover and nutrient input. An increase in water temperature would most likely lead to a decrease in the amount of sea-ice extent and/or its thickness. The effects of these changes on the biotic and abiotic environment are complex, wide-ranging and difficult to predict. Some of the likely consequences of this on the organisms of the Southern Ocean are shown

in fig. 2.

#### Sea ice and ocean circulation

In many areas around Antarctica, the formation of sea-ice during autumn and winter produces Antarctic Bottom Water. This cold dense saline water is excluded from the developing ice and sinks to the bottom. It flows well north of the equator, at least in the Atlantic Ocean, where it mixes with upper waters. A decline in the amount of Antarctic sea-ice would be expected to effect the production of Bottom Water and inhibit the present regime of vertical circulation south of the Polar Front. There is some evidence for a slowdown in the production of Antarctic Bottom Water (Broecker *et al.* 1999). Ocean-climate models predict reduction in the salt flux, less ocean convection and less deep water formation. This could well lead to a prolonged, major reduction in thermohaline circulation (O'Farrell *et al.* 1997; Budd and Wu, 1998; Hirst 1999) that would have profound consequences for marine microorganisms, because of inevitable changes in oxygen and nutrient supply.

#### Sea ice and mixing regimes

Release of low salinity water from the sea-ice in spring and summer leads to the development of the shallow mixed layer in the seasonal ice zone, the region of the highest productivity in the Southern Ocean. Reduction in the amount of sea-ice would limit the development of this layer with a consequential impact on the biota of this region. It follows that any reduction in the extent or stability of the shallow pycnocline of the marginal ice

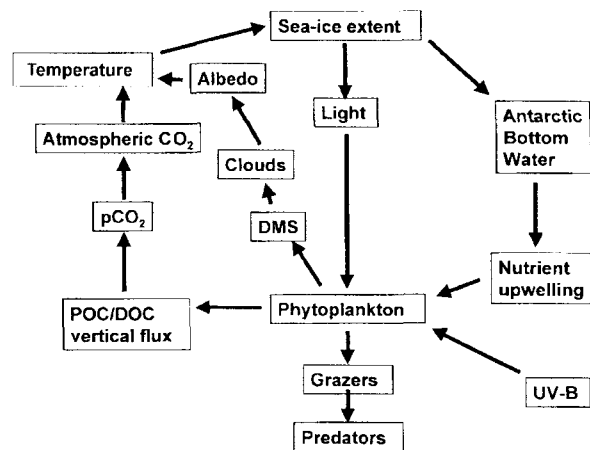


Fig. 3. Conceptual diagram of the principal indirect impacts of changes in temperature and UVB on Southern Ocean organisms and processes.

zone would lead to reduced production and vertical carbon flux.

Recent investigations in the Ross Sea indicate that phytoplankton community structure is related to the depth of the mixed layer (Arrigo *et al.* 1999). While diatoms were dominant in stratified waters, *Phaeocystis antarctica* dominated where there was more deeply mixed water. The drawdown of CO<sub>2</sub> and nitrate per mole of phosphate was found to be much lower for diatoms than for *Phaeocystis*. These authors concluded that the efficacy of the biological carbon pump in Southern Ocean could be reduced by around 36 % if stratification due to climate warming were to induce a change to phytoplankton communities dominated by diatoms rather than *Phaeocystis*. This illustrates the extent to which mixing regimes can cause changes in species composition that can significantly affect CO<sub>2</sub> drawdown.

The possible biological consequences of changes to mixing regimes in the seasonal ice zone have been considered above. In the open ocean, the standing crop and productivity of phytoplankton have been correlated with atmospheric conditions especially wind speed and direction (Dickson *et al.* 1988). Diatoms, the dominant phytoplanktonic organisms in the Southern Ocean, have high sinking rates and require turbulent mixing to remain in the photic zone (Smayda 1970). Thus any change in wind-induced surface mixing may alter the relative abundance of diatoms, the food available to higher trophic levels, and the vertical flux of carbon and silicon.

#### Sea ice and light climate

Reduced thickness of sea ice would result in higher light intensities reaching sea ice protist communities. Some protozoans are sensitive to light exposure (Chen and Chang 1999) and this may alter trophodynamics in this environment. Furthermore, UVB irradiances experienced by the sea-ice protist communities are likely to increase, reducing production and favouring species that have greater UV tolerance.

In contrast, light intensities are likely to be reduced in the absence of sea ice: the lack of sea-ice melt allowing deep mixing. While surface fluxes may be higher, increasing the impact of UVA and UVB radiation on organisms or larval stages that inhabit near-surface waters, deep mixing is likely to reduce exposure of planktonic organisms to UVB irradiation.

#### Sea ice and ice biota

A reduction in the amount of sea-ice would reduce the

habitat area for the sea ice microbial community, reducing total sea-ice microbial biomass available for krill and other grazers that feed on the under-ice organisms. In addition, since extensive sea-ice appears to favour the dominance of krill over salps (Nicol *et al.* 2000) reduction in sea-ice could significantly alter the patterns of grazing with profound consequences for higher predators. Additionally, reduced sea-ice would provide less inoculum to "seed" the bloom of phytoplankton of the marginal ice zone.

#### Cloud formation

*Phaeocystis antarctica* is particularly significant as the principal producer of dimethyl sulfide (DMS) in Antarctic waters (Gibson *et al.* 1990; Kang and Kang 1998). DMS is oxidized in the atmosphere to sulfate aerosol particles, the major source of cloud condensation nuclei (CCN) over the sea. As the albedo of clouds, and as a consequence global solar input, is determined by the concentration of CCN, indicating a mechanism for the regulation of climate by marine biological activity (Charlson *et al.* 1987). Projected climate changes in the Southern Ocean that affect the growth of *Phaeocystis*, may thus feed back on themselves through changes in cloudiness.

#### Nutrient input

Primary production in large areas of the Southern Ocean is limited by inadequate concentrations of nutrients, particularly iron and silica. One likely effect of global climate change is the production of airborne dust through the spread of deserts. Analysis of ice cores has shown a strong correlation between historic CO<sub>2</sub> concentrations and the input of iron and silica in dust, particularly during the last glacial maximum. It is likely that nutrient concentrations will increase downwind of continental dust sources. These would promote a change in ecosystem structure, especially when coupled with increased water temperatures and other factors described above.

Model results show that of all oceans, the Southern Ocean is likely to experience the greatest slowing in CO<sub>2</sub> uptake with climate change (Sarmiento and Le Quere 1996). Reduced down-welling will also limit the ability of the ocean to sequester anthropogenic CO<sub>2</sub> (Sarmiento *et al.* 1998). Changes in the marine biota also need to be considered. Using coupled climate model output under the IPCC-IS92a greenhouse gas scenario, Matear and Hirst (1999) calculate that by 2100 there could be a reduction in cumulative oceanic uptake of 56 Gt of carbon. This reduced

uptake is equivalent to a 4% per year increase in CO<sub>2</sub> emissions for the 1995-2100 period.

## 5. Conclusions

Although we know little about how different microbial systems respond to global warming, there is a growing body of evidence to suggest fundamental changes in community structure and trophic interactions will occur (Petchey *et al.* 1999). The direct effect of changes in temperature and the UVB climate are known for only few Antarctic organisms however increased temperature and CO<sub>2</sub> concentration is expected to enhance phytoplankton growth and increase species diversity due to the invasion of organisms presently unable to grow at the present low temperature regime. On the other hand, increased UVB and declining sea-ice and MIZ extent are expected to have the opposite effect. We consider that the overall impact of these competing influences of global warming is likely to be changes in microbial species composition with increased species diversity, and a net decline in biological production in the Southern Ocean, to the detriment of higher trophic levels.

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