Large scale importance of sea ice biology in the Southern Ocean

KEVIN R. ARRIGO[1] and DAVID N. THOMAS[2]

[1]*Department of Geophysics, Stanford University, Stanford, CA 94305-2215, USA*
[2]*School of Ocean Sciences, University of Wales-Bangor, Menai Bridge, Anglesey LL59 5AB, UK*
arrigo@stanford.edu

Abstract: Despite being one of the largest biomes on earth, sea ice ecosystems have only received intensive study over the past 30 years. Sea ice is a unique habitat for assemblages of bacteria, algae, protists, and invertebrates that grow within a matrix dominated by strong gradients in temperature, salinity, nutrients, and UV and visible radiation. A suite of physiological adaptations allow these organisms to thrive in ice, where their enormous biomass makes them a fundamental component of polar ecosystems. Sea ice algae are an important energy and nutritional source for invertebrates such as juvenile krill, accounting for up to 25% of total annual primary production in ice-covered waters. The ability of ice algae to produce large amounts of UV absorbing compounds such as mycosporine-like amino acids makes them even more important to organisms like krill that can incorporate these sunscreens into their own tissues. Furthermore, the nutrient and light conditions in which sea ice algae thrive induce them to synthesize enhanced concentrations of polyunsaturated fatty acids, a vital constituent of the diet of grazing organisms, especially during winter. Finally, sea ice bacteria and algae have become the focus of biotechnology, and are being considered as proxies of possible life forms on ice-covered extraterrestrial systems. An analysis of how the balance between sea ice and pelagic production might change under a warming scenario indicates that when current levels of primary production and changes in the areas of sea ice habitats are taken into account, the expected 25% loss of sea ice over the next century would increase primary production in the Southern Ocean by approximately 10%, resulting in a slight negative feedback on climate warming.

Introduction

Sea ice structure

During each autumn, the surface of the ocean surrounding the Antarctic continent begins to freeze, eventually forming a layer of sea ice up to approximately a metre thick, but averaging about 0.4 m (Worby *et al*. 1996, 2001). This ice cover generally extends over an area ranging from 4 x 10^6 km^2 in the summer to approximately 19 x 10^6 km^2 in late winter, most of which consists of annual pack ice (Cavalieri *et al*. 1999). The presence of sea ice increases surface albedo, restricts air-sea gas exchange, and provides a stable habitat for diverse microbial assemblages.

In the early stages of pack ice formation, dense concentrations of frazil ice can develop rapidly under turbulent conditions as large quantities of heat are extracted from the near-surface ocean during strong wind events (Eicken 2003, Haas 2003). As winds diminish and the sea surface calms, ice crystals float to the sea surface where they coalesce into semi-consolidated grease ice, and eventually, into thicker nilas and pancake ice (Ackley & Sullivan 1994). Additional freezing and horizontal movement fuses ice pancakes together to form a continuous ice pack. Frazil ice is more common in the Antarctic than in the Arctic, due primarily to the fact that more first-year ice forms in the southern hemisphere.

The initial stage of sea ice formation generally begins in the autumn when there are still substantial microbial populations left over in surface waters from the preceding spring blooms. As a result, during early frazil ice formation, particles such as microalgae, heterotrophic protists, and bacteria are often scavenged from the water column as the newly-formed frazil ice crystals rise to the surface (Garrison *et al*. 1990). In some cases, enrichment factors for chlorophyll *a* (Chl *a*) calculated from the ratio between the concentrations in ice and underlying water have been reported to be as high as 53, with the incorporation of large diatoms being observed most commonly (Weissenberger & Grossmann 1998).

Subsequent ice growth beyond the consolidated pancake stage proceeds vertically as heat is extracted from the sea ice surface by the cold atmosphere. This is also true for land-fast ice which does not have an appreciable frazil ice stage. Columnar ice crystals extend from the lower ice margin into the water column. The bottom boundary of the growing columnar ice, referred to as the skeletal layer, is highly porous and has a temperature that is just below the freezing point of seawater. Rafting of ice floes, as sea ice is moved by the wind and tides, causes breakage and occasionally forces parts of the floe below freeboard, flooding the ice surface with seawater (Fritsen *et al*. 1998).
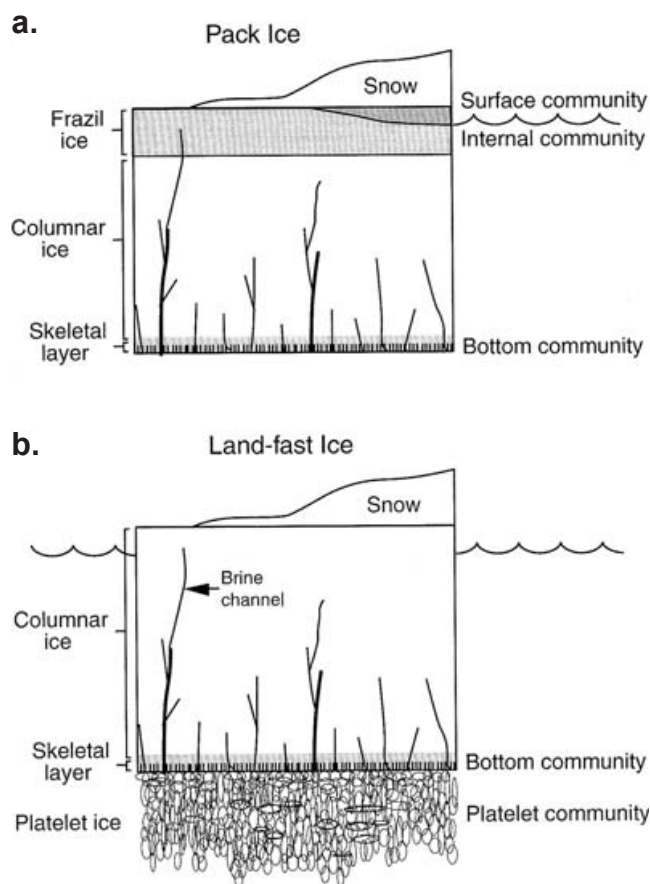
a.

b.

Fig. 1. Schematic illustration of pack ice and land-fast ice showing the major physical features and locations of microbial habitats.

Similarly, heavy snow cover can also force the ice floe below freeboard, resulting in surface flooding and the formation of snow ice and ultimately surface gap layers (Haas *et al*. 2001, Massom *et al*. 2001).

Sea ice biota

Since the first descriptions of sea ice biology by Ehrenberg (1841) and Hooker (1847), a diverse and complex assemblage consisting largely of microorganisms has been described from sea ice habitats (Palmisano & Garrison 1993, Staley & Gosnik 1999, Lizotte 2003). As summarized by Lizotte (2003), at least in its early stages, the biodiversity contained within sea ice is likely to be comparable to that found in the waters from which the ice is formed and the organisms recruited. However, clearly within the ice there are obvious shifts in population and dominance of species. As sea ice ages there are distinct changes from diverse populations of bacteria towards a greater predominance of psychrophilic species (Staley & Gosnik 1999, Junge *et al*. 2004). Within consolidating and ageing ice there is a gradual reduction in the numbers of large centric diatom species, older ice often being dominated by small pennate diatom species such as *Fragilariopsis curta* (van Heurck)

Hustedt (Gleitz & Thomas 1993, Leventer 1998). It is curious as to why the ubiquitous species *F. kerguelensis* (O'Meara) Hustedt is not found more commonly in sea ice samples. It would appear that many of the features that would select for success in the ice, in particular an extremely robust frustule (Hamm *et al*. 2003) would make this species suitable to life in the ice. Clearly modern molecular and biomarker techniques will play a more central role in future investigations of microbial diversity of sea ice, especially for determination of bacteria and archaea species (Nichols & McMeekin 2002, Junge *et al*. 2004). A good example has been the recent numeration of viruses in sea ice. Although viruses have been known to be present in sea ice, until recently reports about virus numbers in Antarctic sea ice were rare. However, Gowing (2003) and Gowing *et al*. (2002) have clearly demonstrated that just like bacteria and algae, viruses can be highly enriched in Antarctic sea ice.

By far the most studied organisms in sea ice are the algae, and for this short review it is the primary production and algal ecology that are mostly considered. Several reviews have been published recently where more detailed discussions about sea ice ecobiogeochemistry are discussed (Thomas & Dieckmann 2002a, 2002b, Brierley & Thomas 2002, Lizotte 2003).

Algal communities, especially diatoms, flourish within the distinct micro-habitats which are created when sea ice forms and ages (Fig. 1). The primary advantage afforded by sea ice is that it provides a platform from which sea ice algae can remain suspended in the upper ocean where light is sufficient for net growth. Sea ice habitats are often characterized by steep gradients in temperature, salinity, light, and nutrient concentration (Eicken 1992, McMinn *et al*. 1999a, Thomas & Dieckmann 2002a, 2002b). It is in those regions of the ice floe that are most closely associated with the underlying seawater that sea ice microalgae flourish. This is because two of the primary factors controlling the growth of algae in sea ice are elevated salinity (Kottmeier & Sullivan 1988, Arrigo & Sullivan 1992) and access to nutrients (Thomas & Papadimitriou 2003). Except for those areas where snow cover exceeds approximately 0.3 m, light is usually sufficient for net photosynthesis during the spring and summer (Grossi *et al*. 1987, Arrigo *et al*. 1991, 2003). The greatest fraction of sea ice microalgae often reside in the bottom 20 cm of the ice sheet where environmental conditions are generally stable and more favourable for growth. Here, algal biomass has been observed to exceed 200 mg Chl *a* m^{-2} (Palmisano & Sullivan 1983, Palmisano *et al*. 1985, Riaux-Gobin *et al*. 2000, 2003, Trenerry *et al*. 2002), a value comparable to a productive water column yet contained within a much smaller volume. Bottom ice communities form in the skeletal layer (Fig. 1a) and extend upwards as far as 0.2 m, their upward distribution generally being limited by nutrient availability and high brine salinity characteristic of the sea

ice interior when temperatures are low (Arrigo & Sullivan 1992, Mock *et al.* 2003).

Under certain conditions, microalgae may also be found in internal layers, where they infiltrate the ice at the freeboard level (Fritsen *et al.* 2001) or are seeded by the particles scavenged during frazil ice formation (Fig. 1a). Internal communities are often subjected to large environmental fluctuations (Lizotte & Sullivan 1991). For example, brines with salinities as high as 173 psu and temperatures as low as -16°C have been collected from the upper 1.0 to 1.5 m of the sea ice in McMurdo Sound, high enough to prevent detectable metabolic activity in most sea ice algae (Arrigo & Sullivan 1992). Because of the generally restricted nutrient supply to the internal sea ice habitats, microbial biomass is generally low. The highest biomass accumulation recorded for internal communities is 50 mg Chl *a* m^{-2} (Garrison, unpublished), with most ranging from 0.5–30 mg Chl *a* m^{-2} (Ackley *et al.* 1979, Garrison & Buck 1982, Clarke & Ackley 1984, Fritsen *et al.* 1994, Stoecker *et al.* 2000).

The extensive production of extracellular polymeric substances (EPS) within ice has led to speculation as to the nature of sea ice brines and the biological–physical interaction at the ice-liquid interface (Krembs *et al.* 2002, Deming 2002). Clearly the microbial food web, dominated by the production and hydrolyses of dissolved organic matter, will be very much altered from that we understand from open waters. The close proximity of bacteria and fungi to the primary producers, with a high amount of DOM production, probably means that the interactions known from biofilms or interstitial sediment systems are more typical of those processes taking place within the ice (Krembs *et al.* 2000, Brierley & Thomas 2002). Of particular note in this context, is the finding that ice algae release extracellular macromolecules that are thought to alter recrystallization of ice (Raymond & Fritsen 2001, Raymond & Knight 2003). It is an intriguing concept that diatoms (and bacteria) may be causing physical changes to their immediate environment, enabling survival at the coldest temperatures (Junge *et al.* 2001, Krembs *et al.* 2002, Deming 2002, Junge *et al.* 2004).

Less common sea ice assemblages include those that grow at the sea ice surface and within a sub-ice platelet layer. Surface communities form in regions of the pack that become flooded with seawater, either as a result of sea ice rafting (when one ice floe is pushed into and then over another) or snow loading (Fig. 1a). In areas where snow loading is important, algal growth is a function of the balance between reduced light levels due to shading by the snow cover and increased nutrient input due to the weight of the snow causing the surface to flood (Arrigo *et al.* 1997). Such surface flooding occurs over 15–30% of the ice pack in Antarctica (Wadhams *et al.* 1987). Despite its snow cover, light is sufficiently high at the ice surface that in regions with substantial flooding, surface communities

exhibit photosynthetic rates comparable to those of open ocean Antarctic phytoplankton (Lizotte & Sullivan 1992a). As a result, surface communities can attain high levels of algal biomass, with reported levels of Chl *a* ranging from 80 mg Chl *a* m^{-2} (Kottmeier & Sullivan 1990) to 244 mg Chl *a* m^{-2} (Whitaker 1977).

Platelet ice, a semi-consolidated layer of ice ranging from a few cm to several metres in thickness, is commonly observed beneath land-fast ice in regions adjacent to floating ice shelves where surface waters can become super-cooled (Fig. 1b). Platelet ice is the most porous of all sea ice types, being composed of approximately 20% ice and 80% seawater by volume. Although the extent of platelet ice habitats is not known, 45% of the continental margin in the Antarctic is associated with an ice shelf (Bindschadler 1990, Kipfstuhl 1991), suggesting this habitat may be relatively common there.

Platelet ice provides approximately five times more surface area for algal attachment than the skeletal layer where most of the biomass within the congelation ice is concentrated. The platelet ice is also characterized by relatively rapid nutrient exchange. In contrast to much of the congelation ice, where physical nutrient replenishment is controlled by thermodynamic processes within the ice (e.g. convection and brine drainage), the rate of nutrient exchange within platelet ice covaries with tidal height and may be influenced by sub-ice currents (Arrigo *et al.* 1995). The interstitial seawater within the platelet ice layer is estimated to turn over once every 1.6 to 12.0 days depending on tidal cycle (Arrigo *et al.* 1995). As a result of
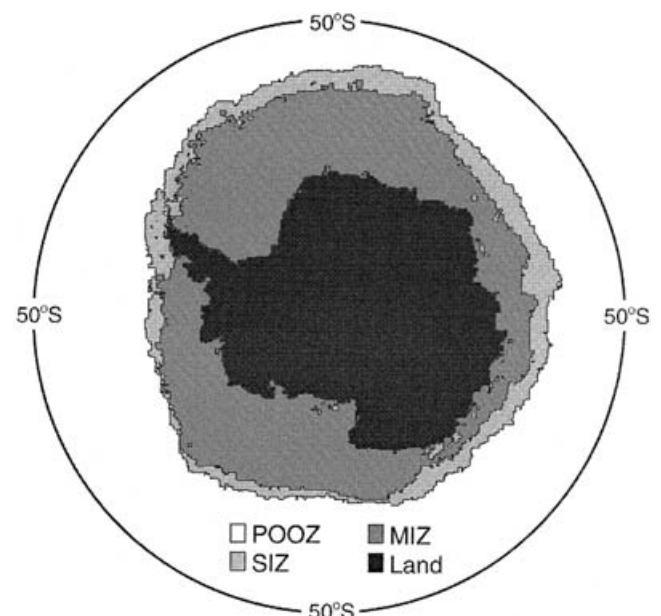

Fig. 2. Map of sea ice cover in the Southern Ocean during the month of November showing the extent of the major regimes, including the permanently open ocean zone (POOZ), marginal ice zone (MIZ), and the sea ice zone (SIZ).

its high surface area and high porosity, platelet ice harbours some of the highest accumulations of sea ice algae found anywhere on Earth, occasionally exceeding 1000 mg Chl *a* m^{-2} (Bunt & Lee 1970, Arrigo *et al*. 1993).

Contrasting annual water column production with that estimated for sea ice suggests that ice microalgae contribute a small fraction to total production in the Southern Ocean. Annual primary production in waters of the Southern Ocean (south of 50°S) calculated from satellite ocean colour, sea ice cover, and sea surface temperature data ranges from 2900–4414 Tg C yr^{-1} (Arrigo *et al*. 1998a, Moore & Abbott 2000). Annual production is greatest in the permanently open ocean zone (POOZ), the region not impacted by sea ice (Fig. 2), contributing approximately 88% of the annual primary production. Because of their small size, the marginal ice zone (MIZ) and the continental shelf contribute only 10% and 2%, respectively, despite exhibiting markedly higher daily production rates (Arrigo *et al*. 1998a).

In contrast, the annual rate of primary production within Antarctic sea ice zone (SIZ) is calculated to range from 30–70 Tg C (Legendre *et al*. 1992, Mathot *et al*. 1996, Arrigo *et al*. 1997, 1998b). Total primary production is a function of both the sea ice extent and the rate of carbon fixation per unit surface area (Arrigo *et al*. 1998b) and has an error associated with it of ± 30%. Although sea ice is at its maximum extent in October, because of low production rates during this time, the spatially integrated rate of production is calculated to be only 4 Tg C month^{-1} (Arrigo *et al*. 1998b). Primary production in Antarctic sea ice is greatest in November (13 Tg C month^{-1}) as areal rates of production increase by a factor of four and sea ice coverage remains high. Annually, over 90% of the biogenic carbon is produced within first-year sea ice and approximately 60% of it is produced during November and December. Spatially integrated production declines between December and April, due to the dramatic decrease in first-year sea ice coverage. The rate of production per unit area peaks in January in both first-year (2.2 g C m^{-2} month^{-1}) and multi-year sea ice (1.1 g C m^{-2} month^{-1}), respectively. In February, spatially averaged rates of production in first-year sea ice exceed those in multi-year ice; however, due to the continued melting of first-year sea ice, the bulk of the biogenic carbon is produced in multi-year ice. Although first-year sea ice increases in coverage again during March and April, the low productivity rates in this newly formed sea ice result in a lower amount of production than in the established multi-year ice.

The production rate of 30–70 Tg C yr^{-1} for Antarctic sea ice is about 1–2% of the annual biogenic carbon production in the Southern Ocean. However, sea ice primary production is a much larger fraction (10–28%) of total production in the ice covered waters of the Southern Ocean, which ranges from 141 to 383 Tg C yr^{-1} (Smith & Nelson 1986, Legendre *et al*. 1992, Arrigo *et al*. 1998a) and includes the highly productive marginal ice zones. Therefore, in those waters that are ice covered for part of the year, algae growing within sea ice can be an important component of the marine food web.

Grazers in the ice

Although rates of primary production by sea ice algae are generally low compared to their phytoplankton counterparts, they are often virtually the sole source of fixed carbon for higher trophic levels in ice-covered waters. Furthermore, sea ice algae have been shown to sustain a wide variety of protozoan and metazoans (Schnack-Schiel 2003), including krill, through the winter months when other sources of food are lacking (Brierley & Thomas 2002, Schnack-Schiel 2003, Lizotte 2003). As populations shift within developing ice in conjunction with changing physico-chemical conditions, it is clear that the interactions between producers and grazers will also change accordingly. Although it is not known whether the diversity of organisms in ice differs from that of the open water, the interactions between organisms in the ice food web will clearly be very different. For the protozoan and metazoan grazers the ice provides a highly concentrated food source where at times minimal energy needs to be expended to exploit the resource. However, the brine channel system also provides areas within the ice where grazers are totally excluded (Krembs *et al*. 2000). In turn the organisms such as krill, (often referred to as the 'keystone' organisms in the overall Southern Ocean pelagic food web) is a vital food source for 'higher trophics' including squid, birds, seals and whales (Ainley *et al.* 2003 and citations therein).

There have been decades of research into the dynamics of krill (*Euphausia superba* Dana) populations, and it is beyond the scope of this review to make a detailed synopsis of the available information. Brierley & Thomas (2002) and Schnack-Schiel (2003) review the significance of sea ice to krill dynamics on both short time scales and decadal periods. The extent and duration of sea ice has been linked to krill recruitment and spawning (Siegel & Loeb 1995, Loeb *et al*. 1997). Although adult krill can withstand periods of starvation, juvenile krill cannot withstand periods without food, and therefore sea ice production is vital to their survival. During heavy sea ice years and late opening of the seasonal pack ice in spring, an earlier onset of the krill spawning season is favoured and recruitment of krill is high. In contrast, after winters with reduced ice extent and duration when krill recruitment is consequently low, high salp densities are recorded. It is evident that extended sea ice cover fosters increased krill.

The connection between krill distributions and sea ice have been recently highlighted by Brierley *et al*. (2002) who used an autonomous underwater vehicle (AUTOSUB-2) to conduct long transects from open waters into sea ice regions. Approximately three times more krill were found

under the ice with the majority of the krill being found in a band between 1 and 13 km inside the sea ice edge, consistent with earlier findings by Nicol *et al*. (2000). These authors stress that it is not the ice extent that may be important for krill, but rather the extent of the ice edge. As they comment, a 25% decrease in sea ice area would in fact only equate to a 9% reduction in the overall length of sea ice edge.

Although much has been written of krill in the Southern Ocean, sea ice is also an important food resource for a wide range of other zooplankton. Within the ice matrix itself these include turbellarians and harpacticoid, calanoid, and cyclopoid copepods (Schnack-Schiel *et al*. 2001a, 2001b). Although turbellarians dominate the within ice fauna, three species of copepod, *Drescheriella glacialis* Dahms & Dieckmann, *Paralabidocera antarctica* (Thompson) and *Stephos longipes* Geisbrecht are found in very high numbers within sea ice, and have life history strategies that are evidently linked to the seasonal sea ice cycle (Schnack-Schiel 2003).

At the ice-water boundary, larger organisms such as fish (mainly *Pagothenia borchgrevinki* (Boulenger)), amphipods and euphausiids dominate along with other copepod species that are not found within the ice (Brierley & Thomas 2002, Schnack-Schiel 2003). Those organisms recorded from within the ice are evidently feeding directly on bacteria, protists, and algae within the brine channel system, although the size of the channels effectively limits how much of the ice these grazers are able to exploit (Krembs *et al*. 2000). Those organisms living below the ice feed on algae and bacteria covering the peripheries of ice floe surfaces, but also on the flux of particulate material being released from the ice.

Flux of biogenic matter from sea ice

The release of the high concentrations of biological matter contained within the ice upon ice melt is an important event in the seasonal sea ice cycle (Leventer 2003). The fate of this material has consequences for biogeochemical cycling, bentho-pelagic coupling and ultimately for the sequestration of organic carbon into sediments (Armand & Leventer 2003). Biological material released from sea ice can be in the form of dissolved or particulate organic matter, living cells or aggregations of dead and living cells. In many sediment trap studies, the flux of matter to depth is often enhanced by packaging of the ice diatoms by the grazers into faecal pellets (reviewed by Brierley & Thomas 2002, Leventer 2003). Whereas diatom frustules encased in krill faecal pellets are often broken and damaged, there are numerous reports of other faecal pellet forms, produced by smaller metazoans and protozoan grazers from other grazers, containing unbroken frustules, often of monospecific origin, reaching the sediments (Armand & Leventer 2003).

There is a widely held view that released sea ice organisms may act as "seed" populations for ice edge plankton blooms, the development of which is facilitated by melt water stabilization of the shallow mixed layer (Leventer 2003 and citations therein). Such seeding is not ubiquitous, but is dependent among other things on interactions of prevailing winds and vertical mixing. However, where sea ice edge blooms are found, they are often associated with high rates of grazing by krill and other zooplankton that, in turn, attract intense feeding by higher trophics.

Generally, the rates of flux of biogenic material to depths in the Southern Ocean are very low (Leventer 2003 and citations therein) and this flux is mostly restricted to short bursts that are associated with the break up of sea ice and/or with sea ice retreat. These short pulses of organic material from overlying sea ice may have resulted in adaptive feeding strategies for benthic feeders (Gili *et al.* 2001, Beaulieu 2002).

Major ecobiogeochemical characteristics of sea ice

Chemical signatures

The generally restricted seawater exchange and large build-up of algal biomass within the various sea ice habitats results in a number of chemical changes within the sea ice environment (in addition to nutrient depletion) that the ice algae must cope with. These include elevated O_2 and low CO_2 concentrations, and pH levels as high as 11 (Thomas & Dieckmann 2002a, Thomas & Papadimitriou 2003 and citations therein). Such extreme changes are not just associated with closed or semi-closed ice systems, but strong gradients across the diffusive boundary layers associated with bottom ice assemblages with high algal standing stocks can also be striking (Trenerry *et al*. 2002).

These chemical changes in the carbonate system, oxygen concentrations, and pH present an unusual suite of factors that, coupled with declining nutrient conditions in the ice, may in part control species composition. In particular, physiological adaptations that sustain photosynthesis at high O_2 and low CO_2 in a strongly alkaline environment are a critical prerequisite for survival in the ice. It is also possible that toxic photochemical products, including hydrogen peroxide and hydroxyl radicals, may accumulate in the high oxygen regions (Vincent & Roy 1993, Prézelin *et al*. 1998). Diatoms have been shown to have high activities of antioxidative enzymes, such as catalase, glutathione peroxidase, and glutathione reductase, to cope with these potentially damaging conditions (Raven 1991, Raven *et al*. 1994, Rijstenbil 2001), and activities of these enzymes in diatoms isolated from sea ice are also high (Schriek 2000).

It should be noted that the conditions described above are typical of most studies to date. However, in some cases, oxygen levels are greatly reduced, and sea ice may actually

become anoxic, as evidenced by the presence of bacteria normally associated with anoxic environments (Petri & Imhoff 2001). Results of ice tank experiments would indicate that during ice formation degassing of oxygen and CO_2 from growing ice floes may also considerably reduce the concentrations of these compounds available for photosynthesis and respiration (Mock *et al.* 2003, Papadimitriou *et al.* 2004).

Naturally, high standing stocks of sea ice algae have large demands on other inorganic nutrients. Nitrogen, phosphorus and silicate exhaustion is frequently associated with algal growth within ice and in bottom ice assemblages. However, prolific standing stocks of diatoms are also reported where nitrogen, silicate and phosphorus concentrations are still high and not reflecting the build up of algal biomass (Thomas & Dieckmann 2002b and citations therein). These findings lead to the conclusion that microbial dynamics within sea ice are such that rates of organic matter turnover and nutrient regeneration are high. Frequently, high concentrations of ammonium, up to 178 µM, are recorded in sea ice, together with high concentrations of nitrate (300 µM) and phosphate (42 µM). Such concentrations are far in excess of surface seawater values (< 1 µM, < 30 µM and < 2 µM respectively), and clearly support the hypothesis that nutrient regeneration within ice systems is extensive. These values were taken from the synopsis of Thomas & Dieckmann (2002b), where the anomalies in nutrient status of sea ice and the implications of such high levels are discussed in detail.

Closely linked to this hypothesis is that extremely high concentrations of dissolved organic carbon and nitrogen (DOC/DON) have been reported from Antarctic sea ice (Thomas & Dieckmann 2002b and citations therein). DOC and DON concentrations up to 1.8 mM and 0.78 mM respectively have been measured, or 30 and 8 times higher than surface water concentrations, respectively. However, when concentrations within the brine channel/pore space are calculated from estimated brine volumes, actual concentrations of DOC in brines were up to 23.3 mM and DON up to 2.2 mM (Thomas *et al.* 2001). Little work has been conducted to date to characterise DOM from within the ice, although as discussed by Brierley & Thomas (2002) and Thomas & Papadimitriou (2003) the production of DOM is closely linked with the production of EPS by algae and bacteria (Krembs *et al.* 2002), as well as low temperature effects on substrate affinity (Pomeroy & Wiebe 2001).

As well as there being high rates of nutrient remineralization, it should be noted that the highest algal standing stocks recorded from sea ice are actually measured at parts of floes where re-supply of nutrients from the surrounding seawater is possible. This may be true of internal assemblages, and is certainly true for surface gap layers (Kennedy *et al.* 2002) as well as platelet ice systems underlying fast ice (Arrigo *et al.* 1995). In these cases it would appear that the ice is acting as a physical structure on which the algae preferentially grow. The supply of nutrients is then produced from the flushing of the exposed ice surfaces to seawater, either via ocean swell (Fritsen, personal observation), tidal forcing (Arrigo *et al.* 1995), or internal convection (Fritsen *et al.* 1994). In the case of bottom ice assemblages, this flushing will be frequent, but for those ice layers associated with surface gaps in the interior of an ice floe or deep within a thick platelet ice layer, the degree of nutrient replenishment will be dependent on factors such as ocean swell and tidal amplitude

Restricted CO_2 exchange and depletion of the dissolved inorganic carbon (DIC) pool is accompanied by an enrichment of the stable carbon isotopes ^{13}C in the remaining DIC leading to more positive carbon isotope values of $\delta^{13}C_{DIC}$ (Kennedy *et al.* 2002 and citations therein). The ^{13}C enrichment in DIC is, in turn, reflected in an enrichment in the stable carbon isotope composition of the particulate material, $\delta^{13}C_{POC}$, values up to -8‰ having been measured in field samples (McMinn *et al.* 1999a, Kennedy *et al.* 2002, Arrigo *et al.* 2003, Thomas & Papadimitriou 2003). In contrast, open water values in the Southern Ocean range from -21‰ to -30‰. Enrichment of ^{13}C in sediments has been suggested as a proxy for past carbon dioxide concentrations in surface waters (Gibson *et al.* 1999, McMinn 2000, McMinn *et al.* 2001). However, if POC enriched in ^{13}C is being produced in sea ice it is reasonable to predict that material sinking out from sea ice may result in ^{13}C-enriched sediments, irrespective of regional surface water variations in the partial pressure of carbon dioxide (reviewed by Leventer 2003, Armand & Leventer 2003).

Enhanced/modified lipid synthesis

Inorganic nutrients, irradiance, and the growth status of bacteria and algae greatly influence their biochemical composition and those inhabiting sea ice evidently have a carbon metabolism that is different from algae from less physiologically demanding environments (Thomas & Dieckmann 2002a and citations therein). Conspicuous lipid droplets in sea ice diatoms are frequently observed (Nichols *et al.* 1989) and increased lipid production is often accompanied by dynamic changes in lipid class abundances during the development of sea ice assemblages (Nichols 2003). It is evident that the overriding processes governing changes in lipid quality and quantity are related to inorganic nutrient limitation (Lizotte & Sullivan 1992b, Palmisano *et al.* 1988), but changes in salinity, and light levels have all been implicated in the causes of changed lipid biosynthesis of both sea ice bacteria and algae (Nichols *et al.* 1999, 2000, Staley & Gosink 1999, Mock & Kroon 2002a, 2002b, Nichols 2003).

Naturally, the biochemical composition of the ice biota

has profound implications for their quality as a food source for protozoan and metazoan grazers. This is particularly true of polyunsaturated fatty acids (PUFA) produced by both bacteria and microalgae. Many marine organisms cannot produce PUFA, and require them to be supplied in their diet (Nichols 2003). Enhanced PUFA production (up to orders of magnitude increases) by sea ice algae and bacteria has been measured, induced by the low irradiances, low temperatures, and high salinities found within sea ice (Nichols *et al*. 1999, Mock & Kroon 2002a, 2002b, Nichols 2003), and therefore sea ice assemblages are a richer source of essential PUFA for grazing organisms. Since the conditions that stimulate PUFA production in sea ice microbes are most extreme in winter, it is probable that PUFA production in the ice organisms will be maximal at that time. Those organisms grazing within winter sea ice will therefore have a diet greatly enriched in PUFA, which may be a significant factor in maintaining viable stocks, especially of larval stages of zooplankton species, and maintaining the fitness of these to exploit more favourable feeding conditions upon ice melt in spring.

UV protecting compounds

Organisms living beneath the Antarctic ozone hole are often exposed to high levels of ultraviolet radiation (UVR). Despite strong attenuation by snow, sea ice, detritus, and dissolved organic matter, a substantial fraction of ultraviolet radiation (UV, 280–400 nm) can be transmitted through the ice to the ice algal community (Trodahl & Buckley 1989) where it can contribute to oxidative damage (McMinn *et al*. 1999b, Belzile *et al*. 2000). In addition, fluorescence-based studies show that UV radiation, particularly UVB (280–320 nm), inhibits photosynthesis in sea ice diatoms by diminishing photosystem II performance (Schofield *et al*. 1995), presumably via direct impacts on binding proteins or the primary electron acceptor. During high UV events, such as the spring development of the Antarctic ozone hole, increased DNA damage has also been detected, which could also impact recovery of the photosynthetic apparatus (Meador *et al.* 2002).

To protect themselves from UVR, many organisms produce chemical sunscreens such as mycosporine-like amino acids (MAAs). HPLC analysis of sea ice samples from the pack ice of the Ross Sea indicated the presence of the MAAs porphyra-334, shinorine, mycosporine-glycine, and palythine, within the ice algal population (Erickson 2000). The most common suite of MAAs utilized for UVR photoprotection was likely to consist of porphyra-334 and/or shinorine together with palythine.

There was a highly significant relationship between the MAA content of a given sample and the depth within the ice from which that sample was collected ($P < 0.01$), with the MAA content consistently decreasing with increasing depth at all stations where ice was thick enough for such

differences to be resolved (Arrigo, unpublished). Interior and surface communities, which usually had lower algal biomass, often exhibited higher MAA content per cell than bottom ice communities. This is consistent with previous results showing that MAA content per cell decreases with the depth of the water for both phytoplankton and macroalgal communities (Jeffery *et al*. 1999, Hoyer *et al*. 2001). However, studies to verify UV induction of MAAs and their ability to protect against UV damage in sea ice algae have been inconclusive (Ryan *et al*. 2002).

It has been proposed that in some algae, such as halophilic cyanobacteria, MAAs are used as osmolytes (Oren 1997), with MAA production being synergistically enhanced by a combination of osmotic and UVR stress (Portwich & Garcia-Pichel 1999). Algae growing within the sea ice interior and near the sea ice surface can also experience dramatic osmotic shifts as variations in ambient temperature drive large changes in sea ice brine salinity (Assur 1958), and perhaps high MAA content is an adaptive strategy to maintain osmotic balance in these organisms as well. It should be noted, however, that despite the correlation between MAA content and osmotic stress, MAAs were found to be insignificant in maintaining osmotic balance in cyanobacteria when compared to intracellular concentrations of sugar osmolytes (Portwich & Garcia-Pichel 1999). Whether or not MAA production in sea ice algae is in part an osmoregulatory strategy is not known, but the benefits of high MAA absorption with respect to enhanced UVR radiation near the sea ice surface and even within the interior are clear. In the Ross Sea, ice algae growing near the sea ice surface during the spring require high intracellular MAA content to survive the relatively high and constant fluxes of UVR to which they are exposed throughout the 24 hour long photoperiod.

Sea ice algae have been shown to be an important energy and nutritional source for invertebrates such as juvenile krill (Stretch *et al*. 1988). However, sea ice algae may provide an additional benefit for the grazer population as well. Increased solar UVR has been shown to reduce zooplankton recruitment and adversely affect trophic transfer of material by affecting heterotrophic species as well as primary producers (Malloy *et al*. 1997). Levels of UVR radiation that are typical of those found within the upper 15 m of the water column have been found to be lethal to krill (Newman *et al*. 1999) which, due to their nucleotide base composition, are particularly susceptible to UVR damage (Jarman *et al*. 1999). Because marine invertebrates, including krill (Newman *et al*. 2000), must obtain MAAs from their algal diets (Carroll & Shick 1996, Karentz *et al*. 1997, Carefoot *et al*. 1998, Whitehead *et al.* 2001), sea ice algae represent a highly concentrated source of MAAs that can be exploited by organisms within the upper trophic levels. Grazers can obtain at least ten times more MAAs per unit of Chl *a* ingested by consuming sea ice algae than they can from consumption of Antarctic phytoplankton. An ice algal MAA

source may be particularly important to krill during the austral spring when ozone levels are still low, sea ice algae are actively growing, and the major phytoplankton blooms of the Southern Ocean have yet to develop (Arrigo *et al*. 1998a). Sea ice algae also may provide the MAAs found in the tissues of shallow benthic organisms in areas like McMurdo Sound, where no other likely MAA source has been found (McClintock & Karentz 1997). Because MAAs can be transferred from grazers to their predators (Whitehead *et al.* 2001), UVR photoprotectants produced by ice algae have the potential to benefit organisms at a variety of trophic levels.

Enhanced DMSP (& DMS) production

Dimethylsulfoniopropionate (DMSP) is a precursor of dimethylsulphide (DMS). The flux of DMS from the oceans to the atmosphere is of great significance since it is the main source of marine derived sulphates, and in turn, cloud condensation nuclei. DMSP is produced by marine algae as an intracellular osmolyte for osmoregulation. At low temperatures, it is thought to have antifreeze properties and intracellular concentrations are also known to be controlled by light, nutrients, and pH (Malin & Kirst 1997). The breakdown of DMSP to DMS can be greatly enhanced by high grazing activity.

Both pack ice and fast ice studies have shown that very high concentrations of DMSP can be produced by ice algae assemblages (Trevena *et al*. 2003 and citations therein) reaching concentrations of over 1500 nM, much higher than seawater values which typically range from 0 to 50 nM. All the environmental factors mentioned above will contribute to sea ice algae producing high DMSP reserves, although high brine salinities are thought to be the predominant controlling factor. In their synopsis of the rather limited number of studies of DMSP within sea ice conducted to date, Trevena *et al*. (2003) estimated that the overall mean concentration of DMSP in sea ice to be in the order of 178 nM. They then extrapolated their findings to estimate that the Antarctic sea ice zone contains up to 9 Mmole sulphur in the form of DMSP. The ultimate fate of this large reservoir of DMSP for the production of considerable fluxes of DMS to the atmosphere, especially during ice melt, may have important impacts for localized and global climate patterns. The production of DMSP, and its breakdown products of DMS and acrylic acid, have important implications for biological interactions and chemical properties of the ice itself. Brierley & Thomas (2002) and Thomas & Papadimitriou (2003) have reviewed some of these including the supply of metabolites to bacteria and/or inhibition of bacterial activity at high concentrations, the inhibition of both protozoan and metazoan grazers, as well as having an important role in the scavenging of potentially toxic hydroxyl radicals (Sunda *et al*. 2002) and other reactive oxygen species within brines described above.

Biotechnology

Cold adapted organisms have potential in a broad range of biotechnological applications and in recent years, there has been considerable attention placed on sea ice microbes as a source of viable products for industrial, agricultural and medical processes (Nichols *et al*. 1999, Cavicchioli *et al*. 2002). One of the major thrusts is to look for microorganisms suitable for commercial production of PUFA to be utilized as dietary supplements in aquaculture, agriculture, and for human consumption. As stated above, sea ice bacteria and algae produce high levels of PUFA within sea ice, and are logical candidates for screening activities to look for organisms to help maximize essential fatty acid production.

Applications exist in a range of industries for cold-active enzyme applications, e.g. cleaning agents, leather processing, degradation of xenobiotic compounds in cold climes, food processing (fermentation, cheese manufacture, bakery, confectionery, meat tenderisation) and molecular biology. Clearly sea ice organisms are a potentially good source of such cold-active enzymes (Nichols *et al*. 1999, Cavicchioli *et al*. 2002).

Zaslavskia *et al*. (2001) have shown that diatoms have all the necessary activities for glucose metabolism, and the potential to transform from obligate photoautotrophy to full heterotrophy can be achieved through metabolic engineering. It has been speculated that in winter, sea ice diatoms switch from autotrophy to heterotrophy (Palmisano & Sullivan 1985, Rivkin & Putt 1987, Palmisano & Garrison 1993), although whether such switches to heterotrophy by sea ice algae are really possible is still open to much speculation. The findings of Zaslavskia *et al*. are rather provocative for more rigorous investigations of the possibility for non-engineered heterotrophic growth of diatoms in sea ice. Naturally the implications for using heterotrophic diatoms in industrial fermentation processes is an intriguing goal (Kröger 2001)

In addition to enzyme applications and PUFA production, cold adapted archaea, bacteria and eukaryotes from sea ice have other potential biotechnological applications, ranging from sources of cryoprotectants, bioremediation of oil spills, frost protection and low temperature waste treatment. As stressed by Cavicchioli *et al*. (2002) "the vastness of sea ice extent and the diversity of abiotic regimes that are found within the sea ice zone, clearly promise tremendous potential for the discovery of novel low temperature extremophiles and their exploitation for future biotechnological applications".

Proxies for astrobiology

In recent years, the development of the research field of astrobiology has been a strong driving force in the study of extremophiles (Cavicchioli 2002). Hoover *et al*. (1986)

were probably some of the first to make the direct link between diatoms in sea ice and the possibility that diatoms are part of microbiological systems in comets, Europa, and interstellar space. The ice-covered seas of Europa and Ganymede, Mars, as well as the ice covered 'snowball earth', are all systems in which sea ice, and the organisms that live within it, may serve as appropriate proxies (Marion *et al.* 2003). However, the ice on these systems is tens to 100s of kilometres thick, compared to the 1–10 m thick ice we know from Polar oceans, and the life forms that potentially can/could survive these conditions are likely to be very different from the dominant sea ice organisms. On the other hand, the discoveries such as those by Sharma *et al.* (2002) who demonstrated that bacteria can remain viable under immense pressure within liquid phases of ice-VI, a form of ice in which the solid phase of water is heavier than the liquid phase, certainly makes a strong case for continuing this work (Deming 2002). In contrast to many of the large scale processes discussed in this review, it is curious to note that it is likely to be ultra fine scale investigations into the nature of the interfaces between solid and liquid phases within ice where these investigations will profitably concentrate - a somewhat surprising scale considering the enormous distances and timescales on which the field of astrobiology is used to dealing with.

Future changes in ice cover

Changing sea ice in the Southern Ocean

Thus far, sea ice in the Arctic and Antarctic differ in their specific responses to changes in climate. The extent of Arctic sea ice has shrunk at an annual rate of 0.35% since the 1970s, for a total reduction of *c.* 14% (Johannessen *et al.* 1995, 1999), consistent with observations that the Arctic Ocean and its peripheral seas are presently warming (Dickson 1999). In addition, the thickness of the multi-year ice pack that covers the central Arctic Ocean has decreased by 40% in 30 years, from 3.1 m on average in the period 1958–76, to 1.8 m in the 1990s (Rothrock *et al.* 1999). In contrast, sea ice extent in the Antarctic has been much less heavily impacted. Despite a slightly shortened sea ice season for some of the Antarctic (Parkinson 2002), sea ice extent has increased by 1% per decade between 1979 and 1998 (Zwally *et al.* 2002). The only region where sea ice extent has exhibited a decrease is in the Bellingshausen–Amundsen Sea sector, which, in contrast to the rest of the Antarctic, has experienced a 4–5°C increase in temperature over the last 60 years.

Gloersen (1995) was among the first to show that statistically significant periodicities (quasi-biennial and quasi-quadrennial) exist in the time series of Antarctic sea ice extent and that these periodicities could be related to variations in the climate cycle, in this case, ENSO. In a more detailed study, Kwok & Comiso (2002) noted strong correlations between the polar climate anomalies and sea ice extent in both the Bellingshausen–Amundsen Sea and the Ross Sea, and that these anomalies are coupled to climate patterns in the tropical latitudes. At a local scale, analyses of sea ice concentration data with European Centre for Medium-Range Weather Forecasts (ECMWF) operational fields by Hanna (2001) indicate that the unusually extensive sea ice in the Ross Sea in 1997/98 was associated with a northward shift of the circumpolar westerly surface winds over the southern Pacific Ocean. In contrast to conditions in the Ross Sea, Ackley *et al.* (2001) reported anomalous southerly winds in the Weddell Sea during the 1997–98 El Niño, which resulted in lower sea ice concentrations than normal. Similar anomalies associated with ENSO have also been reported for Antarctic precipitation (Bromwich *et al.* 2000). Together, these and other studies indicate that a teleconnection exists between climate patterns in the southern low latitudes and in the high latitude Southern Ocean and that these climate patterns exert primary control over sea ice distributions throughout much of the region.

Impacts on primary production

What net change in Antarctic sea ice distributions and associated primary production would accompany a marked increase in global temperature? Even if temperatures were to increase by the predicted 1–6°C over the next century, Antarctic winters will still be cold and annual sea ice will continue to form. In addition, increased precipitation associated with higher temperatures may reduce rates of sea ice melt, thereby stabilizing the sea ice cover (Zwally *et al.* 2002). It is likely, however, that the fraction of the annual ice cover experiencing a shortened sea ice season will eventually increase in response to warming temperatures.

Under the most extreme conditions, the maximum extent of Antarctic sea ice may diminish, as it has already done in the Arctic. Antarctic sea ice cover is predicted to shrink by 25% over the next 100 years in a GCM where atmospheric CO_2 was increased 1% yr^{-1} (Meehl *et al.* 2000). This is in good agreement with the 17–31% loss in southern hemisphere sea ice predicted by Rind *et al.* (1997) in response to a doubling of atmospheric CO_2 over the next century. If sea ice extent were to diminish as result of increased global temperatures, then the relative sizes of the POOZ, the MIZ, including waters over the continental shelves, and the SIZ would shift. Because the planet is already in the midst of an interglacial period, a time of historically high temperatures, further reductions in ice from the present state are unprecedented over the last few million years. Consequently, little information exists in the historical record that can be compared to predictions of how reduced sea ice would impact Southern Ocean primary production. However, we may be able to gain some insight into how climate change may alter productivity in the Southern Ocean by utilizing existing models of primary
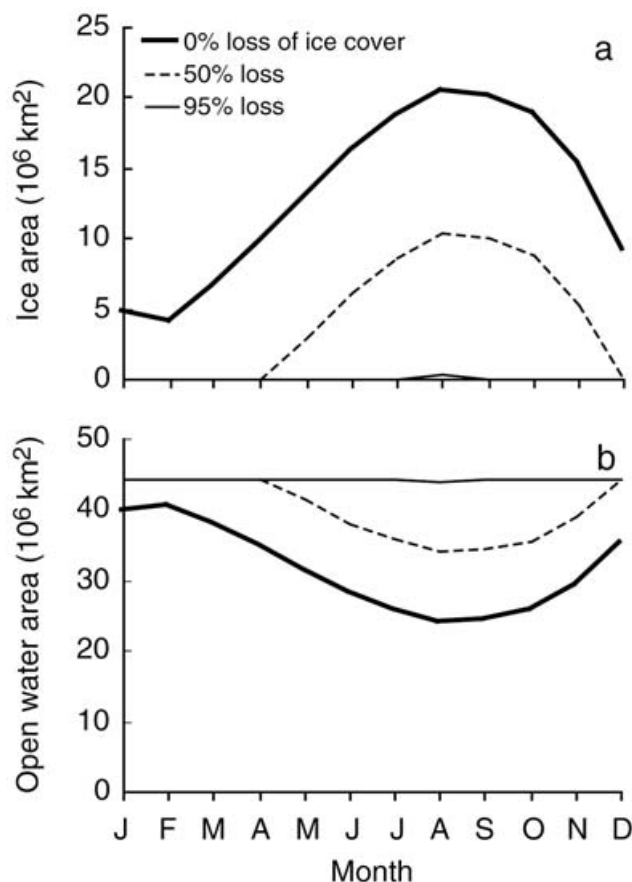
Fig. 3. Monthly changes in the area of **a.** sea ice cover, and **b.** open
water for model runs simulating different degrees of sea ice
cover loss.

Fig. 4. Monthly changes in total primary production (sea ice plus
water column) in the **a.** SIZ, **b.** MIZ, and **c.** the POOZ for model
runs simulating different degrees of sea ice cover loss.

production within the sea ice (Arrigo *et al.* 1997) and the
open Southern Ocean (Arrigo *et al.* 1998a). The simple
analysis presented below assumes that rates of production
are not substantially altered within the three habitats of
interest (SIZ, MIZ, POOZ) because of global climate
change. Furthermore, these models do not take into account
changes in hydrography and ocean circulation that may also
accompany climate changes. The major factor driving
changes in production is assumed simply to be a change in
the relative size of each of the three regimes.

Although doubling of atmospheric CO_2 concentrations is
expected to reduce ice cover by up to 30% (Rind *et al.* 1997,
Meehl *et al.* 2000), we chose to test scenarios with a loss of
ice cover ranging from 0–100% in order to include both best
and worst case scenarios. Only results for 0%, 50% and
95% loss are shown here. In those simulations where
warming resulted in a net loss of sea ice, the length of the
sea ice season was shortened as well. For example, in the
case of a 50% loss of ice, the Antarctic was assumed to
remain ice-free for a full three months of the year (Fig. 3a).
The area of the POOZ was evaluated from the ice edge to
50°S (the approximate mean latitude of the Antarctic Polar
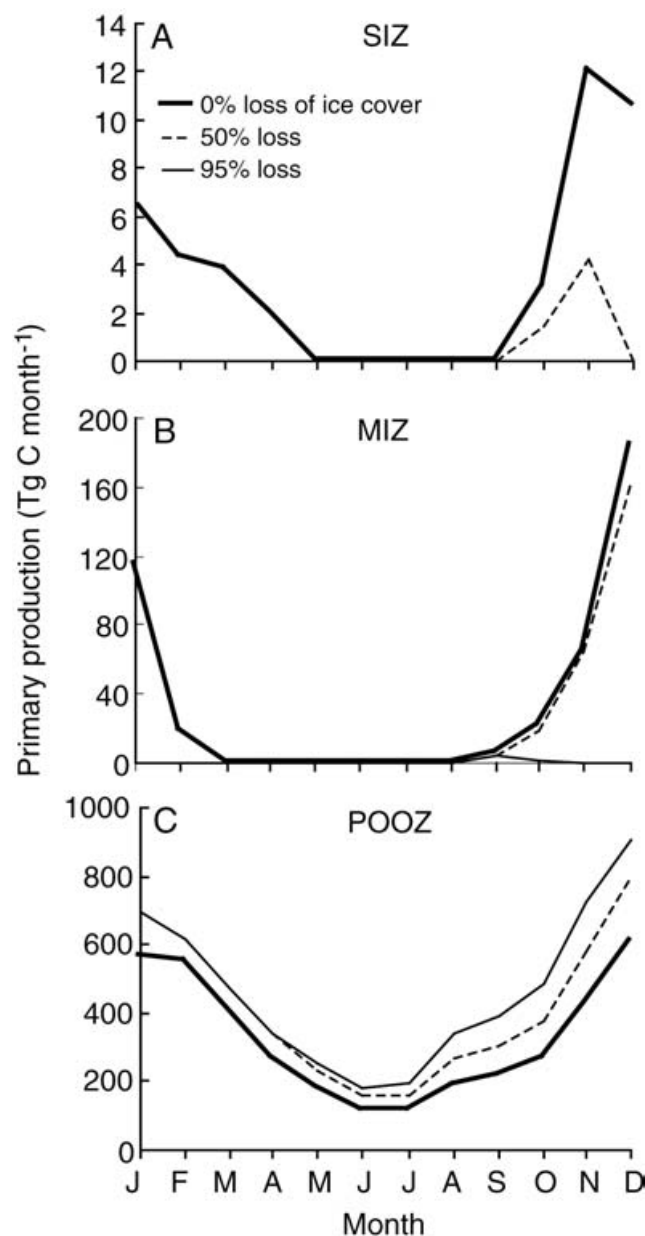Front). Because the POOZ is relatively large, changes in

open water area in response to diminishing ice cover
(Fig. 3b) were not as extreme as the changes in sea ice
extent.

Currently, primary production in the Antarctic SIZ peaks
in November and December (Fig. 4a, 0% loss case), the
time of year when there is ample light for growth and still an
extensive sea ice cover. Production continues throughout
the autumn as sea ice extent increases, but eventually drops
to zero at the end of May as the Southern Ocean enters its
long austral night. Total primary production throughout the
Southern Ocean MIZ is estimated to be approximately
43 Tg C yr^{-1} (Arrigo *et al.* 1997, 1998b). A 50% loss of sea

Table I. Southern Ocean Primary Production (Tg C yr^{-1}).

Regime	Today	50% ice cover	5% ice cover
Sea Ice	43	6	0
Marginal Ice Zone	409	250	5
Open Ocean	3919	5012	5616
Total	4371	5268	5621

ice cover still provides sufficient ice cover (Fig. 3a) for a spring and early summer ice algal bloom (Fig. 4a), although it covers a smaller area and is much less productive than today. In the late summer and fall, however, primary production in the case of a 50% loss of sea ice is near zero (Fig. 4a) due to the early disappearance and late formation of the annual ice pack (Fig. 3a). As a result, a 50% loss in sea ice cover translates into an 86% loss in annual sea ice primary production (Table I). A 95% loss of sea ice would reduce annual sea ice primary production to zero because ice would only form in the middle of the southern hemisphere winter when there is no light available for photosynthesis.

This temporal pattern of primary production in the MIZ (Fig. 4b) is qualitatively similar to that of the SIZ (Fig. 4a). Under normal ice conditions (0% loss in ice cover), primary production in the MIZ peaks a little later (late spring and early summer) and declines a little sooner than in the SIZ. Despite the similar temporal dynamics, annual production is approximately an order of magnitude higher in the MIZ than in the SIZ, totalling approximately 400 Tg C yr^{-1}. A 50% loss of sea ice cover results in only slightly lower production during the late spring and early summer. However, because sea ice (and hence the MIZ) disappears by January in the 50% loss scenario, primary production in the MIZ during late summer and autumn drops to zero. As a result, production in the MIZ after a 50% loss of ice cover would be reduced by approximately 40% from the present case (Table I). Primary production in the 95% ice loss scenario was nearly as low in the MIZ (5 Tg C yr^{-1}) as it was in the SIZ (0 Tg C yr^{-1}), with production in the MIZ being restricted to the month of September (Fig. 4a), following the melt of entire Antarctic ice pack which had formed the month before (Fig. 3a).

In contrast to the SIZ and the MIZ, where a decline in sea ice cover is predicted to result in a corresponding reduction in annual primary production, loss of sea ice over in the POOZ should increase annual production in that habitat. This is due to the fact that, by definition, the size of the POOZ increases as sea ice extent is reduced; as its area increases, so should its contribution to total Southern Ocean production. A decrease in ice extent from 0% to 50% is predicted to increase production in the POOZ for all months of the year, with the largest increases coming in the spring and summer (Fig. 4c). Annually, a 50% loss in sea ice cover is expected to yield a ~28% increase in production within the POOZ, from approximately 3900 to 5000 Tg C yr^{-1}. This
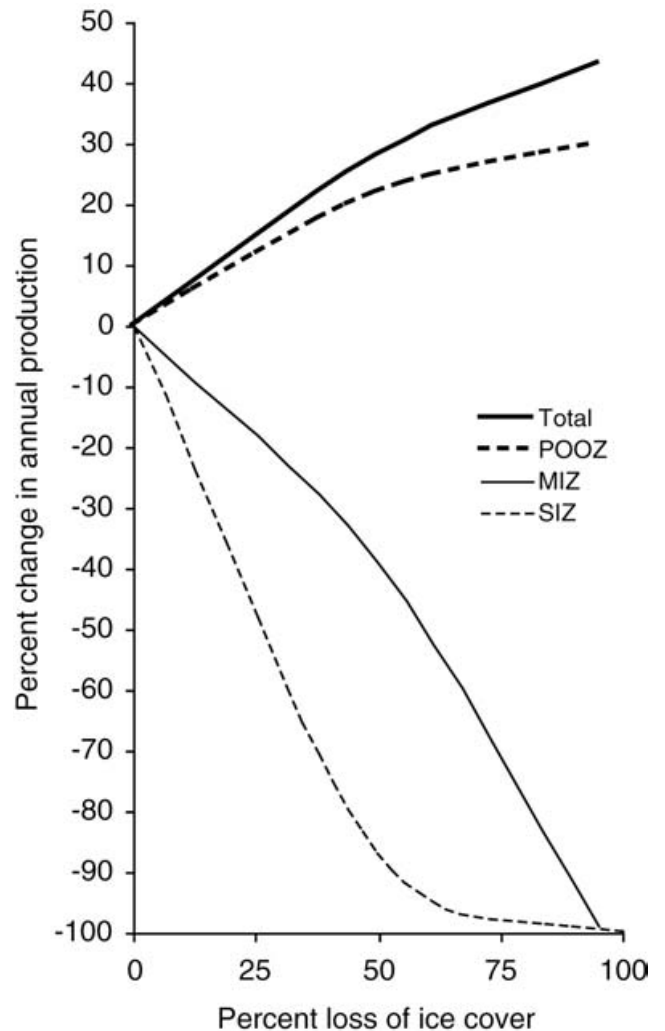

Fig. 5. Calculated percent change in annual production on the Southern Ocean (south of 50°S) as a function of the percent loss of sea ice cover.

increase (1100 Tg C yr^{-1}) more than compensates for the combined losses in production expected within the MIZ and the SIZ (~200 Tg C yr^{-1}). The net gain in production for the Southern Ocean resulting from a 50% loss of ice cover is approximately 900 Tg C yr^{-1} (Table I), or an increase of 21%. For a 95% loss of sea ice, production increases by another 7%, from 5270 to 5620 Tg C yr^{-1}, not quite as dramatic an increase as in the 50% loss case because during the summer, open water was already at its maximum extent (Fig. 3b). Increases in production between the 50% and the 95% ice loss cases were restricted to the months of April–December.

Considering the effects of a sea ice loss on all three habitats simultaneously, it is clear that a net change in production over the Southern Ocean will be a function of the production rate per unit area in each habitat (SIZ, MIZ, POOZ) and the extent of that habitat. Daily production per unit area is relatively low in the SIZ compared to the MIZ

and the POOZ, and as a result, the loss of production within a diminishing sea ice cover is more than compensated for by the gain in production in the increasingly large POOZ. Although daily rates of production are greatest per unit area in the MIZ (Arrigo *et al*. 1998a), because it is relatively short lived and covers the smallest area (Fig. 2), the loss was also more than compensated for by the gain in production in the POOZ. By plotting the specific reduction in sea ice cover against the resulting change in annual production for all the model runs, it is possible to assess the expected impact of the full possible range of sea ice losses (0–100%). Initially, each 25% loss of sea ice will result in a 10% increase in total primary production, with increases in POOZ production outpacing losses in the MIZ and SIZ. The increase in total production begins to level off, however, as more sea ice is lost, with the maximum possible increase in total production (assuming a 100% ice cover loss) being approximately 30% (Fig. 5).

This analysis indicates that when current levels of primary production and changes in the areas of the three different sea ice habitats are taken into account, the expected 25% loss of sea ice over the next century would increase primary production in the Southern Ocean by approximately 10%, resulting in a slight negative feedback on climate warming. There are a number of factors that would be expected to modify this estimate, however. For example, the loss of sea ice and reduction in the area of the MIZ could favour non-diatom species such as *Paralabidocera antarctica* (Arrigo *et al*. 1999). Such a change in community composition could increase nutrient utilization efficiency and further increase rates of production in the Southern Ocean. This is because *P. antarctica* is estimated to fix twice as much carbon per unit phosphate removed than its diatom counterparts (Arrigo *et al*. 1999). Because *P. antarctica* could pull more CO_2 out of surface waters, and indirectly, out of the atmosphere, such a switch in community composition would represent a negative feedback to climate change.

Second, because sea ice harbours algae that can seed phytoplankton blooms, the loss of sea ice and this seed population could reduce primary production in the MIZ. However, because the size of MIZ should shrink in proportion to the loss of sea ice, the impact of a loss of seed stock will be minimized. Still, this effect would represent a weak positive feedback to climate change in that more CO_2 would be allowed to accumulate in the atmosphere.

Third, because iron accumulates in sea ice and is released in a concentrated pulse to surface waters in the spring as the ice melts, a reduced ice cover could lower surface Fe levels and, hence, primary production. It has been proposed that Fe released from melting sea ice can increase surface water Fe concentrations by almost an order of magnitude (Sedwick & DiTullio 1997, Sedwick *et al*. 2000). This release may be an efficient mechanism for stimulating phytoplankton production because it adds Fe in right place (at the sea surface) and at the right time (in the austral spring). A loss of ice cover could reduce concentrations of Fe in surface waters in spring, causing a decline in phytoplankton productivity, representing a positive feedback to climate change. The severity of this loss depends on relative importance of aeolian and deep-water Fe sources, which is not yet fully understood.

It should be noted, however, that, Thomas (2003) has raised fundamental questions about the Fe content and sea ice. If iron is limiting to Southern Ocean phytoplankton growth, and sea ice is formed from iron-deficient waters, is it not reasonable to conclude that the ice based primary production is also iron limited? There is little evidence for this since sea ice algal growth is rapid within new sea ice and in spring and summer iced based primary production remains high. Maximum growth of ice algae is often concentrated on the bottom few centimetres of ice floes, where replenishment of inorganic nutrients from the underlying water sustains high standing crops. Again this replenishment is with iron-deficient water, and the prolific growth of bottom ice algae exhibits no obvious signs of iron limitation. Admittedly Fe will be concentrated into brines in a conservative fashion as ice floes thicken, but as ice sheets expel brines from the time they are first formed, it is not clear if sea ice will contain elevated quantities of Fe to be released into the water column on melting.

Finally, increased global temperatures over the next century are expected to increase surface stratification in the Southern Ocean (Sarmiento *et al*. 1998). Because stratification reduces vertical mixing between surface and deep waters, increased stratification would result in higher mean daily light levels in surface waters and reduced nutrient exchange with deeper waters. Under increased stratification, productivity in areas that are currently light-limited would increase while productivity in areas that are currently nutrient limited would decrease. Obviously, these two effects will offset each other to some degree, with the net result being determined by the relative area of nutrient and light limited waters. It is not yet known which of these water types predominates, so the net effect of increased stratification is not yet known. In addition, increased stratification could favour the growth of diatoms (Arrigo *et al*. 1999), which would reduce nutrient utilization efficiency and rates of primary production in nutrient limited waters. In this case, stratification would represent a positive feedback to climate change, with carbon fixation rates declining and additional CO_2 accumulating in the atmosphere.

References

ACKLEY, S.F. & SULLIVAN, C.W. 1994. Physical controls on the development and characteristics of Antarctic sea-ice biological communities: a review and synthesis. *Deep-Sea Research Part 1*, **41**, 1583–1604.

ACKLEY, S.F., BUCK, K.R. & TAGUCHI, S. 1979. Standing crop of algae in the sea ice of the Weddell Sea region. *Deep-Sea Research*, **26**, 269–281.

ACKLEY, S.F., GEIGER, C.A., KING, J.C., HUNKE, E.C. & COMISO, J. 2001. The Ronne polynya of 1997/98: observations of air-ice-ocean interaction. *Annals of Glaciology*, **33**, 425–429.

AINLEY, D.G., TYNAN, C.T. & STIRLING, I. 2003. Sea ice; a critical habitat for polar marine mammals and birds. *In* THOMAS, D.N. & DIECKMANN, G.S., *eds. Sea ice – an introduction to its physics*, *chemistry*, *biology and geology*. Oxford: Blackwell Science, 240–266.

ARMAND, L.K. & LEVENTER, A. 2003. Palaeo sea ice distribution - reconstruction and paleoclimatic significance. *In* THOMAS, D.N. & DIECKMANN, G.S., *eds. Sea ice – an introduction to its physics*, *chemistry*, *biology and geology*. Oxford: Blackwell Science, 333–372.

ARRIGO, K.R. & SULLIVAN, C.W. 1992. The influence of salinity and temperature covariation on the photophysiological characteristics of Antarctic sea ice microalgae. *Journal of Phycology*, **28**, 746–756.

ARRIGO, K.R., SULLIVAN, C.W. & KREMER, J.N. 1991. A bio-optical model of Antarctic sea ice. *Journal of Geophysical Research*, **96**, 10581–10592.

ARRIGO, K.R., ROBINSON, D.H. & SULLIVAN, C.W. 1993. A high resolution study of the platelet ice ecosystem in McMurdo Sound, Antarctica: Photosynthetic and bio-optical characteristics of a dense microalgal bloom. *Marine Ecology Progress Series*, **98**, 173–185.

ARRIGO, K.R., DIECKMANN, G., GOSSELIN, M., ROBINSON, D.H., FRITSEN, C.H. & SULLIVAN, C.W. 1995. A high resolution study of the platelet ice ecosystem in McMurdo Sound, Antarctica: Interpretation of biomass and nutrient profiles within a dense microalgal bloom. *Marine Ecology Progress Series*, **127**, 255–268.

ARRIGO, K.R., LIZOTTE, M.P., WORTHEN, D.L., DIXON, P. & DIECKMANN, G. 1997. Primary production in Antarctic sea ice. *Science*, **276**, 394–397.

ARRIGO, K.R., WORTHEN, D.L., SCHNELL, A. & LIZOTTE, M.P. 1998a. Primary production in Southern Ocean waters. *Journal of Geophysical Research*, **103**, 15 587–15 600.

ARRIGO, K.R., WORTHEN, D.L., DIXON, P. & LIZOTTE, M.P. 1998b. Primary productivity of near surface communities within Antarctic pack ice. *Antarctic Research Series*, **73**, 23–43.

ARRIGO, K.R., ROBINSON, D.H., WORTHEN, D.L., DUNBAR, R.B., DITULLIO, G.R., VANWOERT, M. & LIZOTTE, M.P. 1999. Phytoplankton community structure and the drawdown of nutrients and CO_2 in the Southern Ocean. *Science*, **283**, 365–367

ARRIGO, K.R., ROBINSON, D.H., DUNBAR, R.B., LEVENTER, A.R. & LIZOTTE, M.P. 2003. Physical control of chlorophyll *a*, POC, and PON distributions in the pack ice of the Ross Sea, Antarctica. *Journal of Geophysical Research*, **108**, 3316, doi:10.1029/2001JC001138.

ASSUR, A. 1958. Composition of sea ice and its tensile strength. *In Arctic Sea Ice. Washington, DC:* US National Academy of Sciences, National Research Council, Publication No. 598, 106–138.

BEAULIEU, S.E. 2002. Accumulation and fate of phytodetritus on the sea floor. *Oceanography and Marine Biology Annual Review*, **40**, 171–232.

BELZILE, C., JOHANNESSEN, S.C., GOSSELIN, M., DEMERS, S. & MILLER, W.L. 2000. Ultraviolet attenuation by dissolved and particulate constituents of first-year ice during late spring in an Arctic polynya, *Limnology and Oceanography*, **45**, 1265–1273.

BINDSCHADLER, R. 1990. *SeaRISE: a multidisciplinary research initiative to predict rapid changes in global sea level caused by collapse of marine ice sheets*. College Park, MA: NASA Conference Publication 3075, 47 pp.

BRIERLEY, A.S. & THOMAS, D.N. 2002. Ecology of Southern Ocean pack ice. *Advances in Marine Biology*, **43**, 171–276.

BRIERLEY, A.S., FERNANDES, P.G., BRANDON, M.A., ARMSTRONG, N.W., MCPHAIL, S.D., STEVENSON, P., PEBODY, M., PERRETT, J., SQUIRES, M., BONE, D.G. & GRIFFITHS, G. 2002. Antarctic krill under sea ice: elevated abundance in a narrow band just south of ice edge. *Science*, **295**, 1890–1892.

BROMWICH, D.H., ROGERS, A.N., KALLBERG, P., CULLATHER, R.I., WHITE, J.W.C. & KREUTZ, K.J. 2000. ECMWF analyses and reanalyses depiction of ENSO signal in Antarctic precipitation. *Journal of Climate*, **13**, 1406–1420.

BUNT, J.S. & LEE, C.C. 1970. Seasonal primary production in Antarctic sea ice at McMurdo Sound in 1967. *Journal Marine Research*, **28**, 304–320.

CAREFOOT, T.H., HARRIS, M., TAYLOR, B.E., DONOVAN, D. & KARENTZ, D. 1998. Mycosporine-like amino acids: possible UV protection in eggs of the sea hare *Aplysia dactylomela*. *Marine Biology*, **130**, 389–396.

CARROLL, A.K. & SHICK, J.M. 1996. Dietary accumulation of UV-absorbing mycosporine-like amino acids (MAAs) by the green sea urchin (*Strongylocentrotus droebachiensis*). *Marine Biology*, **124**, 561–569.

CAVALIERI, D.J., PARKINSON, C.L., GLOERSEN, P., COMISO, J.C. & ZWALLY, H.J. 1999. Deriving long-term time series of sea ice cover from satellite passive-microwave multisensor data sets. *Journal of Geophysical Research*, **104**, 15 803–15 814.

CAVICCHIOLI, R. 2002. Extremophiles and the search for extraterrestrial life. *Astrobiology*, **2**, 281–292.

CAVICCHIOLI, R., SIDDIQUI, K.S., ANDREWS, D. & SOWERS, K.R. 2002. Low-temperature extremophiles and their applications. *Current Opinion in Biotechnology*, **13**, 253–261.

CLARKE, D.B. & ACKLEY, S.F. 1984. Sea ice structure and biological activity in the Antarctic marginal ice zone. *Journal of Geophysical Research*, **89**, 2087–2095.

DEMING, J.W. 2002. Psychrophiles and polar regions. *Current Opinion in Microbiology*, **5**, 301–309.

DICKSON, B. 1999. Oceanography - all change in the Arctic. *Nature*, **397**, 389–391.

EICKEN, H. 1992. The role of sea ice in structuring Antarctic ecosystems. *Polar Biology*, **12**, 3–13.

EICKEN, H. 2003. From the microscopic, to the macroscopic, to the regional scale: growth, microstructure, and properties of sea ice. *In* THOMAS, D.N. & DIECKMANN, G.S., *eds. Sea ice – an introduction to its physics*, *chemistry*, *biology and geology*. Oxford: Blackwell Science, 22–81.

EHRENBERG, C.G. 1841. Einen Nachtrag zu dem Vortrage über verbreitung und Einfluß des mikroskopischen Lebens in Süd- und Nordamerika. *Deutsche Akademie der Wissenschaften zu Berlin, Monatsberichte 1841*, 202–207.

ERICKSON, M.J. 2000. *Ultraviolet-absorbing compounds in phytoplankton of the Ross Sea, Antarctica*. MSc thesis, University of Wisconsin Oshkosh, 50 pp. [Unpublished].

FRITSEN, C.H., LYTLE, V.I., ACKLEY, S.F. & SULLIVAN, C.W. 1994. Autumn bloom of Antarctic pack-ice algae. *Science*, **266**, 782–784.

FRITSEN, C.H., ACKLEY, S.F., KREMER, J.N. & SULLIVAN, C.W. 1998. Flood-freeze cycles and microalgal dynamics in Antarctic pack ice. *Antarctic Research Series*, **73**, 1–22.

FRITSEN, C.H., COALE, S.L., NEENAN, D.R., GIBSON, A.H. & GARRISON, D.L. 2001. Biomass, production and microhabitat characteristics near the freeboard of ice floes in the Ross Sea, Antarctica, during the austral summer. *Annals of Glaciology*, **33**, 280–286.

GARRISON, D.L. & BUCK, K.R. 1982. Sea-ice algae in the Weddell Sea. I. Biomass distribution and the physical environment. *Eos, Transactions of the American Geophysical Union*, **63**, 47.

GARRISON, D.L., CLOSE, A.R. & REIMNITZ, E. 1990. Algae concentrated by frazil ice: evidence from laboratory and field measurements. *Antarctic Science*, **1**, 313–316.

GIBSON, J.A.E., TRULL, T., NICHOLS, P.D., SUMMONS, R.E. & MCMINN, A. 1999. Sedimentation of C-13-rich organic matter from Antarctic sea-ice algae: a potential indicator of past sea-ice extent. *Geology;* **27**, 331–334.

GILI, J.-M., COMA, R., OREJAS, C., LÓPEZ-GONZÁLEZ, J. & ZABALA, M. 2001. Are Antarctic suspension-feeding communities different from those elsewhere in the world. *Polar Biology*, **24**, 473–485.

GLEITZ, M. & THOMAS, D.N. 1993. Variation in phytoplankton standing stock, chemical composition and physiology during sea ice formation in the southeastern Weddell Sea, Antarctica. *Journal of Experimental Marine Biology and Ecology*, **173**, 211–230.

GLOERSEN, P. 1995. Modulation of hemispheric sea-ice cover by ENSO events. *Nature*, **373**, 503–506.

GOWING, M.M. 2003. Large viruses and infected microeukaryotes in Ross Sea summer pack ice habitats. *Marine Biology*, **142**, 1029–1040.

GOWING, M.M., RIGGS, B.E., GARRISON, D.L., GIBSON, A.H. & JEFFRIES, M.O. 2002. Large viruses in Ross Sea late autumn pack ice habitats. *Marine Ecology Progress Series*, **241**, 1–11.

GROSSI, S.M., KOTTMEIER, S.T., MOE, R.L., TAYLOR, G.T. & SULLIVAN, C.W. 1987. Sea ice microbial communities. VI. Growth and primary production in bottom ice under graded snow cover. *Marine Ecology Progress Series*, **35**, 153–164.

HAAS, C. 2003. Dynamics versus thermodynamics: the sea ice thickness distribution. *In* THOMAS, D.N. & DIECKMANN, G.S., *eds*. *Sea ice – an introduction to its physics, chemistry, biology and geology*. Oxford: Blackwell Science, 82–111.

HAAS, C., THOMAS, D.N. & BAREISS, J. 2001. Surface properties and processes of perennial Antarctic sea ice in summer. *Journal of Glaciology*, **47**, 613–625.

HAMM, C.E., MERKEL, R., SPRINGER, O., JURKOJC, P., MAIER, C., PRECHTEL, K. & SMETACEK, V. 2003. Architecture and material properties of diatom shells provide effective mechanical protection. *Nature*, **421**, 841–843.

HANNA, E. 2001. Anomalous peak in Antarctic sea-ice area, winter 1998, coincident with ENSO. *Geophysical Research Letters*, **28**, 1595–1598.

HOOKER, J.D. 1847. *The botany of the Antarctic voyage of H.M. Discovery ships* Erebus *and* Terror *in the years 1838–1843. Part 1. Flora Antarctica*. London: Reeve Brothers.

HOOVER, R.B., HOYLE, F., WICKRAMASINGHE, N.C., HOOVER, M.J. & AL-MUFTI, S. 1986. Diatoms on Earth, comets, Europa and interstellar space. *Earth, Moon and Planets*, **35**, 19–45.

HOYER, K., KARSTEN, U., SAWALL, T. & WIENCKE, C. 2001. Photoprotective substances in Antarctic macroalgae and their variation with respect to depth distribution, different tissues and developmental stages. *Marine Ecology Progress Series*, **211**, 117–129.

JARMAN, S., ELLIOTT, N., NICOL, S., MCMINN, A. & NEWMAN, S. 1999. The base composition of the krill genome and its potential susceptibility to damage by UV-B. *Antarctic Science*, **11**, 23–26.

JEFFREY, S.W., MACTAVISH, H.S., DUNLAP, W.C., VESK, M. & GROENEWOUD, K. 1999. Occurrence of UVA- and UVB-absorbing compounds in 152 species (206 strains) of marine microalgae. *Marine Ecology Progress Series*, **189**, 35–51.

JOHANNESSEN, O.M., MILES, M. & BJORGO, E. 1995. The Arctic's shrinking sea-ice. *Nature*, **376**, 126–127.

JOHANNESSEN, O.M., SHALINA, E.V. & MILES, M.W. 1999. Satellite evidence for an Arctic sea ice cover in transformation. *Science*, **286**, 1937–1939.

JUNGE, K., KREMBS, C., DEMING, J.W., STIERLE, A. & EICKEN, H. 2001. A microscopic approach to investigate bacteria under *in situ* conditions in sea ice samples. *Annals of Glaciology*, **33**, 304–310.

JUNGE, K., EICKEN, H. & DEMING, J.W. 2004. Bacterial activity at-2 to -20°C in Arctic wintertime sea ice. *Applied Environmental Microbiology*, **70**, 550–557.

KARENTZ, D., DUNLAP, W.C. & BOSCH, I. 1997. Temporal and spatial occurrence of UV-absorbing mycosporine-like amino acids in tissues of the Antarctic sea urchin *Sterechinus neumayeri* during springtime ozone-depletion. *Marine Biology*, **129**, 343–353.

KENNEDY, H., THOMAS, D.N., KATTNER, G., HAAS, C. & DIECKMANN, G.S. 2002. Particulate organic carbon in Antarctic summer sea ice: concentration and stable carbon isotopic composition. *Marine Ecology Progress Series*, **238**, 1–13.

KIPFSTUHL, J. 1991. On the formation of underwater ice and the growth and energy budget of the sea ice in Atka Bay, Antarctica. *Reports on Polar Research*, **85**, 89 pp.

KOTTMEIER, S.T. & SULLIVAN, C.W. 1988. Sea ice microbial communities. IX. Effects of temperature and salinity on metabolism and growth of autotrophs and heterotrophs. *Polar Biology*, **8**, 293–304.

KOTTMEIER, S.T. & SULLIVAN, C.W. 1990. Bacterial biomass and bacterial production in pack ice of Antarctic marginal ice edge zones. *Deep-Sea Research*, **37**, 1311–1330.

KREMBS, C., GRADINGER, R. & SPINDLER, M. 2000. Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice. *Journal of Experimental Marine Biology and Ecology*, **243**, 55–80.

KREMBS, C., EICKEN, H., JUNGE, K. & DEMING, J.W. 2002. High concentrations of exopolymeric substances in Arctic winter sea ice: implications for the polar ocean carbon cycle and cryoprotection of diatoms. *Deep-Sea Research 1*, **49**, 2163–2181.

KRÖGER, N. 2001. The sweetness of diatom molecular engineering. *Journal of Phycology*, **37**, 657–658.

KWOK, R. & COMISO, J.C. 2002. Southern Ocean climate and sea ice anomalies associated with the Southern Oscillation. *Journal of Climate*, **15**, 487–501.

LEGENDRE, L., ACKLEY, S.F., DIECKMANN, G.S., GULLICKSEN, B., HORNER, R., HOSHIAI, T., MELNIKOV, I.A., REEBURGH, W.S., SPINDLER, M. & SULLIVAN, C.W. 1992. Ecology of sea ice biota. 2. Global significance. *Polar Biology*, **12**, 429–444.

LEVENTER, A. 1998. The fate of Antarctic "sea ice diatoms" and their use as paleoenvironmental indicators. *Antarctic Research Series*, **73**, 121–137.

LEVENTER, A. 2003. Particulate flux from sea ice in Polar waters. *In* THOMAS, D.N. & DIECKMANN, G.S., *eds*. *Sea ice – an introduction to its physics, chemistry, biology and geology*. Oxford: Blackwell Science, 303–332.

LIZOTTE, M.P. 2003. Microbiology of sea ice. *In* THOMAS, D.N. & DIECKMANN, G.S., *eds*. *Sea ice – an introduction to its physics, chemistry, biology and geology*. Oxford: Blackwell Science, 184–210.

LIZOTTE, M.P. & SULLIVAN, C.W. 1991. Photosynthesis-irradiance relationships in microalgae associated with Antarctic pack ice: evidence for *in situ* activity. *Marine Ecology Progress Series*, **71**, 175–184.

LIZOTTE, M.P. & SULLIVAN, C.W. 1992a. Photosynthetic capacity in microalgae associated with Antarctic pack ice. *Polar Biology*, **12**, 497–502.

LIZOTTE, M.P. & SULLIVAN, C.W. 1992b. Biochemical-composition and photosynthate distribution in sea ice microalgae of McMurdo Sound, Antarctica - evidence for nutrient stress during the spring bloom. *Antarctic Science*, **4**, 23–30.

LOEB, V., SIEGEL, V., HOLM-HANSEN, O., HEWITT, R., FRASER, W., TRIVELPIECE, W. & TRIVELPIECE, S. 1997. Effects of sea ice extent and krill or salp dominance on the Antarctic food web. *Nature*, **387**, 897–900.

MALIN, G. & KIRST, G.O. 1997. Algal production of dimethyl sulfide and its atmospheric role. *Journal of Phycology*, **33**, 889–896.

MALLOY, K.D., HOLMAN, M.A., MITCHELL, D. & DETRICH, H.W. 1997. Solar UVB-induced DNA damage and photoenzymatic DNA repair in Antarctic zooplankton. *Proceedings of the National Academy of Science*, **94**, 1258–1263.

MATHOT, S., GARRISON, D.L. & LANCELOT, C. 1996. *Eos, Transactions of the American Geophysical Union*, **76**, 143.

MARION, G.M., FRITSEN, C.H., EICKEN, H. & PAYNE, M.C. 2003. The search for life on Europa: limiting environmental factors, potential habitats, and Earth analogues. *Astrobiology*, **3**, 785–811.

MASSOM, R.A., EICKEN, H., HAAS, C., JEFFRIES, M.O., DRINKWATER, M.R., STURM, M., WORBY, A.P., WU, X., LYTLE, V.I., USHIO, S., MORRIS, K., REID, P.A., WARREN, S. & ALLISON, I. 2001. Snow on Antarctic sea ice. *Reviews of Geophysics*, **39**, 413–445.

MCCLINTOCK, J.B. & KARENTZ, D. 1997. Mycosporine-like amino acids in 38 species of subtidal marine organisms from McMurdo Sound, Antarctica. *Antarctic Science*, **9**, 392–398.

MCMINN, A. 2000. Late Holocene increase in sea ice extent in fjords of the Vestfold Hills, eastern Antarctica. *Antarctic Science*, **12**, 80–88.

MCMINN, A., SKERRATT, J., TRULL, T., ASHWORTH, C. & LIZOTTE, M. 1999a. Nutrient stress gradient in the bottom 5 cm of fast ice, McMurdo Sound, Antarctica. *Polar Biology*, **21**, 220–227.

MCMINN, A., ASHWORTH, C. & RYAN, K. 1999b. Growth and productivity of Antarctic Sea ice algae under PAR and UV irradiances. *Botanica Marina*, **42**, 401–407.

MCMINN, A., HEIJNIS, H., HARLE, K. & MCORIST, G. 2001. Late-Holocene climatic change recorded in sediment cores from Ellis Fjord, eastern Antarctica. *Holocene*, **11**, 291–300.

MEADOR, J., JEFFREY, W.H., KASE, J.P., PAKULSKI, J.D., CHIARELLO, S. & MITCHELL, D.L. 2002. Seasonal fluctuation of DNA photodamage in marine plankton assemblages at Palmer Station, Antarctica, *Photochemisrty and Photobiology*, **75**, 266–271.

MEEHL, G.A., COLLINS, W.D., BOVILLE, B.A., KIEHL, J.T., WIGLEY, T.M.L. & ARBLASTER, J.M. 2000. Response of the NCAR climate system model to increased CO_2 and the role of physical processes. *Journal of Climate*, **13**, 1879–1898.

MOCK, T. & KROON, B.M.A. 2002a. Photosynthetic energy conversion under extreme conditions. I. Important role of lipids as structural modulators and energy sink under N-limited growth in Antarctic sea ice diatoms. *Phytochemistry*, **61**, 41–51.

MOCK, T. & KROON, B.M.A. 2002b. Photosynthetic energy conversion under extreme conditions. II. The significance of lipids at low temperature and low irradiances in Antarctic sea ice diatoms. *Phytochemistry*, **61**, 53–60.

MOCK, T., KRUSE, M. & DIECKMANN, G.S. 2003. A new microcosm to investigate oxygen dynamics at the sea-ice water interface. *Aquatic Microbial Ecology*, **30**, 197–205.

MOORE, J.K. & ABBOTT, M.R. 2000. Phytoplankton chlorophyll distributions and primary production in the Southern Ocean. *Journal of Geophysical Research*, **105**, 28 709–28 722.

NEWMAN, S.J., NICOL, S., RITZ, D. & MARCHANT, H. 1999. Susceptibility of Antarctic krill (*Euphausia superba* Dana) to ultraviolet radiation. *Polar Biology*, **22**, 50–55.

NEWMAN, S.J., DUNLAP, W.C., NICOL, S. & RITZ, D. 2000. Antarctic krill (*Euphausia superba*) acquire a UV-absorbing mycosporine-like amino acid from dietary algae. *Journal of Experimental Marine Biology and Ecology*, **255**, 93–110.

NICOL, S., PAULY, T., BINDOFF, N.L., WRIGHT, S., THIELE, D., HOSIE, G.W., STRUTTON, P.G. & WOEHLER, E. 2000. Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature*, **406**, 504–507.

NICHOLS, D.S. 2003. Prokaryotes and the input of polyunsaturated fatty acids to the marine food web. *FEMS Microbiology Letters*, **219**, 1–7.

NICHOLS, D.S. & MCMEEKIN, T.A. 2002. Biomaker techniques to screen for bacteria that produce polyunsaturated fatty acids. *Journal of Microbiological Methods*, **48**, 161–170.

NICHOLS, D., BOWMAN, J., SANDERSON, K., NICHOLS, C., LEWIS, T., MCMEEKIN, T. & NICHOLS, P.D. 1999. Developments with Antarctic microorganisms: culture collections, bioactivity screening, taxonomy, PUFA production and cold adapted enzymes. *Current Opinion in Biotechnology*, **10**, 240–246.

NICHOLS, D.S., OLLEY, J., GARDA, H., BRENNER, R.R. & MCMEEKIN, T.A. 2000. Effect of temperature and salinity stress on growth and lipid composition of *Shewanella gelidimarina*. *Applied Environmental Microbiology*, **66**, 2422–2429.

NICHOLS, P.D., PALMISANO, A.C., RAYNER, M.S., SMITH, G.A. & WHITE, D.C. 1989. Changes in the lipid composition of Antarctic sea ice diatom communities during a spring bloom: an indication of community physiological status. *Antarctic Science*, **1**, 133–140.

OREN, A. 1997. Mycosporine-like amino acids as osmotic solutes in a community of halophilic cyanobacteria. *Geomicrobiology Journal*, **14**, 231–240.

PALMISANO, A.C. & GARRISON, D.L. 1993. Microorganisms in Antarctic sea ice. *In* FRIEDMAN, E.I., *ed. Antarctic microbiology*. New York: Wiley-Liss, 167–218.

PALMISANO A.C. & SULLIVAN, C.W. 1983. Sea ice microbial communities (SIMCO). I. Distribution, abundance, and primary production of ice microalgae in McMurdo Sound, Antarctica in 1980. *Polar Biology*, **2**, 171–177.

PALMISANO, A.C. & SULLIVAN, C.W. 1985. Growth, metabolism, and dark survival in sea ice microalgae. *In* HORNER, R.A., *ed. Sea ice biota*. Boca Raton, FL: CRC Press, 131–146.

PALMISANO, A.C., SOOHOO, J.B. & SULLIVAN, C.W. 1985. Photosynthesis-irradiance relationships in sea ice microalgae from McMurdo Sound, Antarctica. *Journal of Phycology*, **21**, 341–346.

PALMISANO, A.C., LIZOTTE, M.P., SMITH, G.A., NICHOLS, P.D., WHITE, D.C. & SULLIVAN, C.W. 1988. Changes in photosynthetic carbon assimilation in Antarctic sea-ice diatoms during spring bloom - variation in synthesis of lipid classes. *Journal of Experimental Marine Biology and Ecology*, **116**, 1–13.

PAPADIMITRIOU, S., KENNEDY, H., KATTNER, G., DIECKMANN, G.S. & THOMAS, D.N. 2004. Experimental evidence for carbonate precipitation and CO_2 degassing during sea ice formation. *Geochimica et Cosmochemica Acta*. In Press.

PARKINSON, C.L. 2002. Trends in the length of the Southern Ocean sea-ice season, 1979–99. *Annals of Glaciology*, **34**, 435–440.

PETRI, R. & IMHOFF, J.F. 2001. Genetic analysis of sea-ice bacterial communities of the Western Baltic Sea using an improved double gradient method. *Polar Biology*, **24**, 252–257.

POMEROY, L.R. & WIEBE, W.J. 2001. Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. *Aquatic Microbial Ecology*, **23**, 187–204.

PORTWICH, A. & GARCIA-PICHEL, F. 1999. Ultraviolet and osmotic stresses induce and regulate the synthesis of mycosporines in the cyanobacterium Chlorogloeopsis PCC 6912. *Archives of Microbiology*, **172**, 187–192.

PRÉZELIN, B., MOLINE, M.A. & MATLICK, H.A. 1998. ICECOLORS '93: spectral UV radiation effects on Antarctic frazil ice algae. *Antarctic Research Series*, **73**, 45–83.

RAVEN, J.A. 1991. Plant responses to high O_2 concentrations: relevance to previous high O_2 episodes. *Palaeogeography*, *Palaeoclimatology*, *Paleaoecology*, **97**, 19–38.

RAVEN, J.A., JOHNSTON, A.M., PARSONS, R. & KÜBLER, J. 1994. The influence of natural and experimental high O_2 concentrations on O_2-evolving phototrophs. *Biological Review*, **69**, 61–94.

RAYMOND, J.A. & FRITSEN, C.H. 2001. Semipurification and ice recrystallization inhibition activity of ice-active substances associated with Antarctic photosynthetic organisms. *Cryobiology*, **43**, 63–70.

RAYMOND, J.A. & KNIGHT, C.A. 2003. Ice binding, recrystallization inhibition, and cryoprotective properties of ice-active substances associated with Antarctic sea ice diatoms. *Cryobiology*, **46**, 174–181.

RIAUX-GOBIN, C., TREGUER, P., POULIN, M. & VETION, G. 2000. Nutrients, algal biomass and communities in land-fast ice and seawater off Adélie Land (Antarctica). *Antarctic Science*, **12**, 160–171.

RIAUX-GOBIN, C., POULIN, M., PRODON, R. & TREGUER, P. 2003. Land-fast ice microalgal and phytoplanktonic communities (Adélie Land, Antarctica) in relation to environmental factors during ice break-up. *Antarctic Science*, **15**, 353–364

RIJSTENBIL, J.W. 2001. Effects of periodic, low UVA radiation on cell characteristics and oxidative stress in the marine planktonic diatom *Ditylum brightwellii*. *European Journal of Phycology*, **36**, 1–8.

RIND, D., HEALY, R., PARKINSON, C. & MARTINSON, D. 1997. The role of sea ice in $2 \times CO_2$ climate model sensitivity. 2. Hemispheric dependencies. *Geophysical Research Letters*, **24**, 491–1494.

RIVKIN, R.B. & PUTT, M. 1987. Heterotrophy and photoheterotrophy in Antarctic microalgae: light-dependent incorporation of amino acids and glucose. *Journal of Phycology*, **23**, 442–452.

ROTHROCK, D.A., YU, Y. & MAYKUT, G.A. 1999. Thinning of the Arctic sea-ice cover. *Geophysical Research Letters*, **26**, 3469–3472.

RYAN, K.G., MCMINN, A., MITCHELL, K.A. & TRENERRY, L. 2002. Mycosporine-like amino acids in Antarctic sea ice algae, and their response to UVB radiation. *Zeitschrift Fur Naturforschung*, **57**, 471–477.

SARMIENTO, J.L., HUGHES, T.M.C., STOUFFER, R.J. & MANABE, S. 1998. Simulated response of the ocean carbon cycle to anthropogenic carbon warming. *Nature*, **393**, 245–249.

SCHNACK-SCHIEL, S.B., DIECKMANN, G.S., GRADINGER, R., MELNIKOV, I.A., SPINDLER, M. & THOMAS, D.N. 2001a. Meiofauna in sea ice of the Weddell Sea (Antarctica). *Polar Biology*, **24**, 724–728.

SCHNACK-SCHIEL, S.B., THOMAS, D.N., HAAS, C., DIECKMANN, G.S. & ALHEIT, R. 2001b. The occurrence of the copepods *Stephos longipes* (Calanoida) and *Drescheriella glacialis* (Harpacticoida) in summer sea ice in the Weddell Sea, Antarctica. *Antarctic Science*, **13**, 150–157.

SCHNACK-SCHIEL, S.B. 2003. The macrobiology of sea ice. *In* THOMAS, D.N. & DIECKMANN, G.S., *eds*. *Sea ice – an introduction to its physics, chemistry, biology and geology*. Oxford: Blackwell Science, 211–239.

SCHOFIELD, O., KROON, B.M.A. & PREZELIN, B.B. 1995. Impact of ultraviolet-b radiation on photosystem-II activity and its relationship to the inhibition of carbon fixation rates for Antarctic ice algae communities. *Journal of Phycology*, **31**, 703–715.

SCHRIEK, R. 2000. Effects of light and temperature on the enzymatic antioxidative defense systems in the Antarctic ice diatom *Entomoneis kufferathii* Manguin. *Reports on Polar Research*, **349**, 1–130.

SEDWICK, P.N. & DITULLIO, G.R. 1997. Regulation of algal blooms in Antarctic shelf waters by the release of iron from melting sea ice. *Geophysical Research Letters*, **24**, 2515–2518.

SEDWICK, P.N., DITULLIO, G.R. & MACKEY, D.J. 2000. Iron and manganese in the Ross Sea, Antarctica: seasonal iron limitation in Antarctic shelf waters. *Journal of Geophysical Research*, **105**, 11321–11336.

SHARMA, A., SCOTT, J.H., CODY, G.D., FOGEL, M.L., HAZEN, R.M., HEMLEY, R.J. & HUNTRESS, W.T. 2002. Microbial activity at gigapascal pressures. *Science*, **295**, 1524–1516.

SIEGEL, V. & LOEB, V. 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Marine Ecology Progress Series*, **123**, 45–56.

SMITH, W.O. & NELSON, D.M. 1986. The importance of ice–edge phytoplankton blooms in the Southern Ocean. *BioScience*, **36**, 251–257.

STALEY, J.T. & GOSNIK, J.J. 1999. Poles apart; biodiversity and biogeography of sea ice bacteria. *Annual Reviews of Microbiology*, **53**, 189–215.

STOECKER, D.K., GUSTAFSON, D.E., BAIER, C.T. & BLACK, M.M.D. 2000. Primary production in the upper sea ice. *Aquatic Microbial Ecology*, **21**, 275–287.

STRETCH, J.J., HAMNER, P.P., HAMNER, W.M., MICHEL, W.C., COOK, J. & SULLIVAN, C.W. 1988. Ice algae foraging behavior of the Antarctic krill, *Euphausia superba* Dana. *Marine Ecology Progress Series*, **44**, 131–139.

SUNDA, W., KIEBER, D.J., KIENE, R.P. & HUNTSMAN, S. 2002. An antioxidant function for DMSP and DMS in marine algae. *Nature*, **418**, 317–320.

THOMAS, D.N. 2003. Iron limitation in the Southern Ocean. *Science*, **302**, 565.

THOMAS, D.N. & DIECKMANN, G.S. 2002a. Antarctic sea ice - a habitat for extremophiles. *Science*, **295**, 641–644.

THOMAS, D.N. & DIECKMANN, G.S. 2002b. Biogeochemistry of Antarctic sea ice. *Oceanography and Marine Biology: Annual Review*, **40**, 143–169.

THOMAS, D.N. & PAPADIMITRIOU, S. 2003. Biogeochemistry of sea ice. *In* THOMAS, D.N. & DIECKMANN, G.S., *eds. Sea ice – an introduction to its physics, chemistry, biology and geology*. Oxford: Blackwell Science, 267–302.

THOMAS, D.N., ENGBRODT, R., GIANNELLI, V., KATTNER, G., KENNEDY, H., HAAS, C. & DIECKMANN, G.S. 2001. Dissolved organic matter in Antarctic sea ice. *Annals of Glaciology*, **33**, 297–303.

TRENERRY, L.J., MCMINN, A. & RYAN, K.G. 2002. *In situ* oxygen microelectrode measurements of bottom-ice algal production in McMurdo Sound, Antarctica. *Polar Biology*, **25**, 72–80.

TREVENA, A.J., JONES, G.B., WRIGHT, S.W. & VAN DEN ENDEN, R.L. 2003. Profiles of dimethylsulphoniopropriionate (DMSP), algal pigments, nutrients, and salinity in the fast ice of Prydz Bay, Antarctica. *Journal of Geophysical Research*, **108**(C5), 3145, doi: 10.1029/2002JC001369.

TRODAHL, H.J. & BUCKLEY, R.G. 1989. Ultraviolet levels under sea ice during the Antarctic spring, *Science*, **245**, 194–195.

VINCENT, W.F. & ROY, S. 1993. Solar ultraviolet-B radiation and aquatic primary production: damage, protection and recovery. *Environmental Reviews*, **1**, 1–12.

WADHAMS, P., LANGE, M. & ACKLEY, S.F. 1987. The ice thickness distribution across the Atlantic sector of the Antarctic Ocean in midwinter. *Journal of Geophysical Research*, **92**, 14535–14552.

WEISSENBERGER, J. & GROSSMANN, S. 1998. Experimental formation of sea ice: importance of water circulation and wave action for incorporation of phytoplankton and bacteria. *Polar Biology*, **20**, 178–188.

WHITAKER, T.M. 1977. Sea ice habitats of Signy Island (South Orkneys) and their primary productivity. *In* LLANO G.A., *ed. Adaptations within Antarctic ecosystems*. Washington, DC: Smithsonian Institution, 75–82.

WHITEHEAD, K., KARENTZ, D. & HEDGES, J.I. 2001. Mycosporine-like amino acids (MAAs) in phytoplankton, a herbivorous pteropod (*Limacina helicina*), and its pteropod predator (*Clione antarctica*) in McMurdo Bay, Antarctica. *Marine Biology*, **139**, 1013–1019.

WORBY, A.P., JEFFRIES, M.O., WEEKS, W.F., MORRIS, K. & JANA, R. 1996. The thickness distribution of sea ice and snow cover during late winter in the Bellingshausen and Amundsen seas, Antarctica. *Journal of Geophysical Research*, **101**, 28441–28455.

WORBY, A.P., BUSH, G.M. & ALLISON, I. 2001. Seasonal development of the sea-ice thickness distribution in East Antarctica: measurements from upward-looking sonar. *Annals of Glaciology*, **33**, 177–180.

ZASLAVSKIA, L.A., LIPPMEIER, J.C., SHIH, C., EHRHARDT, D., GROSSMAN, A.R. & APT, K.E. 2001. Trophic conversion of an obligate phototrophic organism through metabolic engineering. *Science*, **292**, 2073–2075.

ZWALLY, H.J., COMISO, J.C., PARKINSON, C.L., CAVALIERI, D.J. & GLOERSEN, P. 2002. Variability of Antarctic sea ice 1979–1998. *Journal of Geophysical Research*, **107**, 3041, doi:10.1029/2000JC000733.