

# Primary production in the upper sea ice

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**ABSTRACT:** Observations and experiments were conducted on fast ice in McMurdo Sound, Antarctica, to investigate seasonal changes in primary production in the upper sea ice interior. In November and early December 1995, a dense phytoflagellate assemblage developed in the brine channels and pockets at a snow-free site. Primary production was calculated from  $^{14}\text{C}$  measurements of primary productivity in brine samples combined with estimates of the proportion of the ice volume occupied by brine. On 4 December 1995, when the dinoflagellate *Polarella glacialis* dominated, estimated daily production peaked at  $12.4 \text{ mg C m}^{-2}$  in the upper 50 cm of ice. On this date, brine temperature was  $\sim -3^\circ\text{C}$  and brine salinity was  $\sim 60$ . By mid-December, daily production declined by 77%, but chlorophyll-specific rates of photosynthesis remained high. The decline in production coincided with encystment of *P. glacialis* and nutrient depletion, the former triggered by the latter. Primary production continued to decrease during December and January. On 9 January 1996, when ice temperatures were  $\sim -1^\circ\text{C}$  and brine salinity was  $\sim 20$ , there was a brief bloom of small pennate diatoms in the upper ice interior, but chlorophyll-specific rates of photosynthesis were low and estimated daily production was  $< 1 \text{ mg C m}^{-2}$ . Based on  $^{14}\text{C}$  uptake and brine volume, algal production in the upper 50 cm of sea ice was  $181 \text{ mg C m}^{-2}$  for the season (mid-November through mid-January). Increases in phytoflagellate biomass in the upper 90 cm of ice for this same period indicated that production was  $\geq 256 \text{ mg C m}^{-2}$ . Brief early season blooms of cryo- and halo-tolerant phytoflagellates accounted for most of the primary production in the upper sea ice interior.

**KEY WORDS:** Sea ice · Antarctica · McMurdo Sound · Ice algae · Cysts · Hypnozygotes · Dinoflagellates · *Polarella* · Diatoms · Chrysophytes · Primary productivity

## INTRODUCTION

At its maximum extent, sea ice is estimated to cover  $18 \times 10^6 \text{ km}^2$  in the Antarctic and  $14.5 \times 10^6 \text{ km}^2$  in the Arctic, and thus it is an important feature of the world's ocean (Kirst & Wiencke 1995). Ice algae are estimated to contribute  $\sim 20\%$  of total primary production in both Antarctic and Arctic seas (Kirst & Wiencke 1995). There have been numerous studies of photosynthesis by microalgae collected from near the base of the sea ice. In contrast there have been relatively few studies

of photosynthesis by microalgae from the upper sea ice (Garrison & Buck 1991, Gleitz & Kirst 1991, Lizotte & Sullivan 1991, 1992, Fritsen et al. 1994, Archer et al. 1996, Robinson et al. 1997, Stoecker et al. 1997, Mock & Gradinger 1999).

Microalgae are common in the brine channels and pockets in the interior sea ice in polar seas (Ackley et al. 1979, Garrison & Buck 1989, 1991, Stoecker et al. 1992, Fritsen et al. 1994, Archer et al. 1996, Mock & Gradinger 1999). Interior sea ice microalgal assemblages occur in fast ice (sea ice that forms and remains attached to the coast) and pack ice (sea ice that is not attached along the coast). Although internal ice algal assemblages appear to be common in the upper ice, they are not as well documented as the diatom communities that occur near the base of the fast ice (Garrison & Buck 1989, Watanabe et al. 1990, Syvertsen & Kristiansen 1993, Archer et al. 1996). This is probably because the diatom assemblages near the base of the

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ice, although they are usually patchy in distribution, have a high biomass with a high chlorophyll content, and thus are of obvious importance. In land-fast ice, the melt pool and interior microalgal assemblages in the upper ice usually have a lower chlorophyll content and biomass per unit ice volume than the diatom-dominated assemblages that occur near the base of the ice. Therefore upper ice assemblages are less noticeable although they may be more widely distributed than the bottom of the ice assemblages (Archer et al. 1996, Mock & Gradinger 1999).

Estimates of primary production for both the Arctic and Antarctic sea ice (Legendre et al. 1992, Kirst & Wiencke 1995, Wheeler et al. 1996) suffer from lack of information on the spatial and seasonal extent of various assemblages and their productivity. However, numerical models have been developed to investigate regional differences in primary production in Antarctic pack ice (Arrigo et al. 1997, 1998). The contribution of the upper or interior sea ice assemblages to sea ice primary production has only been documented in a few instances (reviewed in Mock & Gradinger 1999). In many studies of sea ice primary production, the contribution of interior ice assemblages has not been addressed.

Phytoflagellates are often dominant in the upper sea ice and diatoms in sea ice infiltrated by seawater, particularly at the base of the sea ice (Hsiao 1980, Palmisano & Sullivan 1983, McConville & Wetherbee 1983, Garrison & Buck 1989, 1991, Gradinger et al. 1992, Arrigo et al. 1995, Archer et al. 1996, Ikävalko & Gradinger 1997, Buck et al. 1998, Stoecker et al. 1998). Phytoflagellate dominance is particularly common early in the growing season when temperatures are well below  $-2^{\circ}\text{C}$  and brines are hypersaline. Relatively little is known about the productivity and physiological ecology of sea ice phytoflagellates (Ikävalko & Gradinger 1997).

The sea ice interior near the ice-air interface is a more extreme environment than the base of the ice and the underlying water column (Kottmeier & Sullivan 1988, Archer et al. 1996). For example, in McMurdo Sound, Antarctica, interior ice temperatures can be as low as  $-20^{\circ}\text{C}$  in the upper 10 cm of ice at the beginning of the austral spring (late September), with calculated brine volumes  $<2\%$  and brine salinity as high as 220 (Stoecker et al. 1997). During the austral summer (late December and January), upper ice temperatures can reach  $-1.5^{\circ}\text{C}$ , brine volume may exceed 15%, and the brine within the upper sea ice is usually  $<32$  psu (Stoecker et al. 1998). A set of halo- and cryo-tolerant phytoflagellates grow in the upper fast ice interior in mid- to late November when upper ice temperatures are still below  $-4^{\circ}\text{C}$  and brine salinity is elevated (Stoecker et al. 1997, 1998).

In McMurdo Sound fast ice, the dominant phytoflagellates are a small photosynthetic dinoflagellate *Polarella glacialis*, an ochromonad-like chrysophyte, and a prasinophyte *Mantoniella* sp. (Stoecker et al. 1992, Montresor et al. 1999). The dinoflagellate and chrysophyte excyst during austral spring, bloom briefly, and then encyst during December and early January (Stoecker et al. 1992, 1997, 1998). Small diatoms bloom in mid- to late December and January in the upper sea ice interior (Stoecker et al. 1998). Similar patterns have been seen in fast ice in East Antarctica (Archer et al. 1996).

Changing light, temperature, brine salinity and nutrient availability probably play important roles in species succession in the upper ice interior. It has been speculated that nutrient depletion stimulates sexuality and cyst formation by *Polarella glacialis* (Stoecker et al. 1998). Life history transitions can be important in species succession. Encystment may be the cause or effect of rapid decreases in primary production (growth) in assemblages dominated by cyst-forming species.

Physical factors (temperature, salinity, light and nutrient availability), as well as biological factors (species composition and abundance, and physiological state), should interact in controlling primary production in the upper sea ice interior as in other aquatic environments. However, because of low diversity in the upper ice, species succession and life history events should be more strongly associated or have a larger impact on primary production in the upper sea ice than these phenomena have in more diverse assemblages in more seasonally stable habitats.

Herein we report on *in situ* and simulated *in situ* incubations with brine collected from the interior of first year (less than 1 yr old) fast ice at a snow-free location in McMurdo Sound, Antarctica, between late November 1995 and mid-January 1996 (austral spring-summer). Samples were incubated at approximately 30 cm depth in the ice or under environmental conditions that approximate those at 30 cm depth in the ice. We manipulated inorganic nutrient concentrations to determine if nutrient depletion triggers cyst formation. Photosynthetic carbon fixation in brine collected from the upper sea ice interior was measured at approximately weekly intervals. We determined physical, chemical and biological parameters for the brine and compared the brine data to similar data obtained from sea ice cores taken at the same location and dates (Stoecker et al. 1998). We used both data sets in interpretation of results from the incubations. Estimates of spring-summer primary production in the upper sea ice interior based on photosynthetic performance and on changes in standing stocks are compared.

## MATERIALS AND METHODS

**Sampling.** Brine sampling was carried out in conjunction with a seasonal study of micro-environmental conditions and algal population dynamics in the upper land-fast sea ice at a windswept, snow-free area on the annual sea ice just north of Inaccessible Island in McMurdo Sound, Antarctica (77° 39.18' S, 166° 25.67' E). At approximately weekly intervals between mid-November 1995 and mid-January 1996, triplicate coring sites were randomly chosen within the approximately 10000 m<sup>2</sup> study area, and 90 cm cores were obtained at each of the sites using a Siple corer (Rand & Mellor 1985, Stoecker et al. 1998). Core holes were covered with small pieces of plywood, and brine was allowed to accumulate. Brine was collected after the brine level in a hole had become stable. Brine samples were transported in coolers to the laboratory for chemical and biological analyses.

**Determination of environmental parameters.** The depth of brine from the ice surface was measured with a meter stick and *in situ* temperature of brine was measured with a digital thermometer. A Li-Cor 193SB spherical sensor was used to measure irradiance at the surface of the ice and just below the brine surface in the core holes with covers in place. Most of the irradiance in the ice is diffuse; thus use of small covers during the measurements, to exclude direct light from reaching the probe, works well.

In the laboratory, salinity of collected brine samples was determined using a YSI (Yellow Springs Instrument Co.) salinometer (some samples were diluted with distilled water for measurement). Duplicate subsamples from each brine sample were stored frozen for nutrient analyses (Lachat QuikChem AE Autoanalyzer). Standard addition experiments were performed to determine if the high brine salinity interfered with the nutrient analyses; when necessary, samples were diluted with Milli-Q water prior to analysis. Duplicate subsamples were filtered onto GF/F Whatman glass fiber filters, extracted in 90% acetone with grinding and chlorophyll *a* (chl *a*) determined by fluorometry (Parsons et al. 1984).

**Microscopic analysis of microalgal assemblages.** To enumerate microalgae, subsamples of brine were fixed and preserved with 1% glutaraldehyde. The fixed samples were stained with proflavine and examined using epifluorescence microscopy (Stoecker et al. 1992). Chlorophyll-containing cells and cysts were enumerated and cysts were distinguished from vegetative cells by the penetration of proflavine into vegetative cells but not into cysts as well as by differences in morphology.

**Cyst formation experiments.** Two experiments were performed to determine if addition of inorganic nutrients would affect cyst formation by *Polarella glacialis*

and chrysoflagellates. On 2 dates in December, approximately 600 ml brine samples were collected from core holes at the Inaccessible Island site. At the time of collection, *in situ* brine temperature was measured with a digital thermometer and subsamples were taken for determination of brine salinity and for microscopic analyses. The brine samples were transported in a cooler to a site on the fast ice closer to McMurdo Station (the Hut site, Stoecker et al. 1997), where experimental manipulations were done.

For each experiment, duplicate control and +nutrient flasks were employed. We gently dispensed 100 ml of brine into each of four 250 ml polycarbonate screw-cap flasks. Nitrate (0.1 ml of a stock solution of 7.5% [w/v] NaNO<sub>3</sub> in distilled water) and phosphate (0.1 ml of a stock solution of 0.5% [w/v] NaH<sub>2</sub>PO<sub>4</sub>·H<sub>2</sub>O in distilled water) were added to the + nutrient flasks to achieve added concentrations of 883 μM nitrate and 36 μM phosphate. The control flasks were not amended. The experimental and control flasks were incubated together in brine in covered core holes at the Hut site. Light levels during incubation were approximately 33% of surface incident irradiance. Temperature in the incubation holes was measured each time the bottles were sampled. For the first incubation, the bottles were retrieved at approximately weekly intervals and 20 ml subsamples were removed for microscopic analyses before the bottles were replaced in the holes. In the second experiment, the bottles were sampled after 4 and 13 d. Both experiments were ended on 27 December.

For statistical analyses, a square-root transformation was applied to counts and an arcsine transformation was applied to proportions (Sokal & Rohlf 1995). The difference between treatments was tested for statistical significance with a 2-tailed *t*-test with equal variances unless the variances were unequal, then a 2-tailed *t*-test with unequal variances was employed (Sokal & Rohlf 1995). Statistical analyses were carried out using Jandel SigmaStat version 2.0.

**Photosynthesis experiments.** Photosynthesis by upper sea ice microalgae was investigated by measuring <sup>14</sup>C uptake by brine samples collected from core holes in the ice and incubated at a range of irradiances under *in situ* or simulated *in situ* conditions for ~24 h. We chose 1 d field incubations over short-term laboratory measurements because our objective was to estimate primary production in the upper ice. Short-term laboratory measurements are good for measuring physiological responses of microalgae, but they do not necessarily extrapolate accurately to daily *in situ* production (Henley 1993).

Approximately 2 l of brine were collected for each experiment, then transported in a cooler to a site where incubations could be conducted. A hut or tent

on the land-fast ice at the Hut site (Stoecker et al. 1997) was used during November and December to set up the incubation bottles, but by January it was no longer possible to access the Hut site because of surface ice decay. In January, the incubations were set up in the Crary Laboratory at McMurdo Station.

$^{14}\text{C}$  bicarbonate ( $57.3 \text{ mBq mmol}^{-1}$ ) was added to 1400 ml of the brine to achieve activities of  $\sim 0.1 \text{ mBq ml}^{-1}$ . Aliquots (100 ml) of the spiked brine were dispensed under low light conditions into duplicate Teflon bottles with 0 to 5 layers of screening, which transmitted 92 to 3% of photosynthetically active radiance (PAR). Duplicate black Teflon bottles were used as dark controls. The remaining 600 ml of brine was used for determination of dissolved inorganic carbon (DIC) (iO Model 700 Carbon analyzer), salinity, chl *a*, and for enumeration of microalgae.

Because of the snow cover and ice thickness at the hut site, the upper ice temperatures and light levels during late November and early December were much lower than at the snow-free Inaccessible Island site (Stoecker et al. 1997, 1998). We chose not to incubate the bottles directly in the ice. Instead we immersed the incubation bottles in a water-filled translucent fiberglass tub sunk in the sea ice; sodium chloride was added to the tub to keep the bottles from freezing-in, which facilitated their retrieval. During late November and early December, the temperatures in the tub were close to the ice temperatures at the Inaccessible Island site, but by 14 December the temperatures in the tub were higher than in the upper ice at the Inaccessible Island site. On 19 December we switched to incubating the bottles in an uncovered core hole. By the beginning of January, it was no longer possible to get to the hut site, so incubations were performed in an outdoor flowing seawater incubator at McMurdo Station. By this time, surface ice temperatures were close to seawater temperature. In all cases, the experiments were set up within 2 to 3 h of brine collection.

Incubation temperatures were measured with a digital thermometer at the beginning and end of incubation. Surface irradiance and irradiance in the brine or seawater surrounding the incubation bottles were measured with a Li-Cor 193SB spherical quantum sensor; from these data, percent incident irradiance reaching the surface of the bottles was calculated. For each experiment, average surface PAR was modeled from hourly 400 to 600 nm radiance ( $\mu\text{W cm}^{-2}$ ) measured at McMurdo Station by Biospherical Instruments, Inc. To obtain average surface PAR during an experiment, average  $\mu\text{W cm}^{-2}$  radiance (400 to 600 nm) was PAR corrected and then converted to  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . Percent incident irradiance for each treatment was calculated as the product of percent incident irradiance reaching the surface of the incubation bottles and

the% transmittance of the treatment bottles, which ranged from 92 to 3% of PAR for the light treatments. Average PAR for a treatment was calculated as percent incident irradiance for the treatment multiplied by average surface PAR for the incubation.

After incubation for  $\sim 24 \text{ h}$ , the bottles were retrieved and transported in insulated chests to the laboratory. To measure total activity (TA) of  $^{14}\text{C}$ , 100  $\mu\text{l}$  of brine was added to a scintillation vial containing 100  $\mu\text{l}$  of phenylethylamine and then 7 ml of scintillation cocktail (Ecolume, ICN Biochemicals, Inc.) was added. Triplicate samples were taken. The samples were counted on a Beckman LS 6800 liquid scintillation counter with automatic quench correction. The TA ( $\text{dpm ml}^{-1}$ ) was calculated as average dpm in the 100  $\mu\text{l}$  samples multiplied by 10. Fixed  $^{14}\text{C}$  was measured on duplicate 50 ml samples from each incubation bottle. In very low light, each 50 ml sample was filtered ( $< 25 \text{ mm Hg}$  pressure) onto a 2.5 cm diameter Whatman GF/F filter, the filter was placed in a scintillation vial and dampened with 10% HCl to kill the cells and remove residual  $^{14}\text{C}$  bicarbonate. The filters were dried at  $60^\circ\text{C}$  in a hood and then 1 ml of distilled water and 7 ml Ecolume were added. The activity on the filters was measured with a Beckman LS 6800 liquid scintillation counter with automatic quench correction.

For each light bottle, the carbon fixed was calculated as:

$$\mu\text{g C l}^{-1} \text{ d}^{-1} = (R_x - R_d) \times 20 \times (\text{DIC}/\text{TA}) \times 1.05$$

where  $R_x$  is the average dpm for the light bottle (50 ml filtered sample),  $R_d$  is the average dpm for the dark bottles (50 ml filtered samples), DIC is the dissolved inorganic carbon ( $\mu\text{g ml}^{-1}$ ), TA is the total activity ( $\text{dpm ml}^{-1}$ ) and 1.05 is the isotope discrimination factor for  $^{14}\text{C}$  (Welschmeyer & Lorenzen 1984).

The photosynthesis-irradiance ( $P-I$ ) data were fitted to a hyperbolic tangent function (Jassby & Platt 1976) using commercial software (SigmaPlot version 4.0, Jandel Scientific).

Standard errors for estimates of maximum rate of photosynthesis ( $P_{\text{max}}$ ) and initial slope of the photosynthesis versus irradiance curve ( $\alpha$ ) were determined by the fitting algorithm.

## RESULTS

### Environmental conditions

The physical and chemical properties of the collected brine changed dramatically due to warming between late November and mid-December 1995, and then remained relatively constant between late December and mid-January 1996 (Table 1). The last sam-

Table 1. Physical-chemical conditions in brine collected from triplicate core holes at the Inaccessible Island study site. Mean  $\pm$  standard error. NS = no sample collected

Date	Temp. (°C)	Salinity	Chl a ( $\mu\text{g l}^{-1}$ )	NH <sub>4</sub> ( $\mu\text{M}$ )	NO <sub>2</sub> + NO <sub>3</sub> ( $\mu\text{M}$ )	PO <sub>4</sub> ( $\mu\text{M}$ )	Brine vol <sup>a</sup> (%)
27 Nov 95	-4.4 $\pm$ 0.3	82.2 $\pm$ 4.7	10.0 $\pm$ 3.0	NS	NS	NS	10.7
4 Dec 95	-3.2 $\pm$ 0.03	60.5 $\pm$ 2.3	7.04	0.83 $\pm$ 0.02	5.84 $\pm$ 0.9	2.09 $\pm$ 0.6	11.4
14 Dec 95	-2.2 $\pm$ 0.1	38.4 $\pm$ 0.5	0.76 $\pm$ 0.07	0.41 $\pm$ 0.3	0.93 $\pm$ 0.1	0.13 $\pm$ 0.0	17.8
19 Dec 95	-1.9 $\pm$ 0.06	32.7 $\pm$ 0.9	0.95 $\pm$ 0.06	1.43 $\pm$ 0.6	0.70 $\pm$ 0.2	0.13 $\pm$ 0.01	14.7
27 Dec 95	-1.6 $\pm$ 0.03	25.5 $\pm$ 1.7	0.26 $\pm$ 0.04	1.07 $\pm$ 0.2	0.28 $\pm$ 0.14	0.03 $\pm$ 0.0	17.3
4 Jan 96	-1.4 $\pm$ 0.03	22.3 $\pm$ 0.7	0.29 $\pm$ 0.2	0.58 $\pm$ 0.2	0.17 $\pm$ 0.03	0.33 $\pm$ 0.1	13.4
9 Jan 96	-1.4 $\pm$ 0.07	20.4 $\pm$ 0.2	0.69 $\pm$ 0.5	0.21 $\pm$ 0.11	0.33 $\pm$ 0.05	0.19 $\pm$ 0.02	17.0
17 Jan 96	-1.6 $\pm$ 0.03	24.8 $\pm$ 0.1	0.06 $\pm$ 0.02	0.59 $\pm$ 0.5	0.40 $\pm$ 0.06	0.21 $\pm$ 0.03	14.8

<sup>a</sup>Estimated from ice temperatures and bulk salinities in upper 50 cm of ice cores (data from Stoecker et al. 1998)

ple was taken on 17 January and the ice at this location broke out between 20 and 22 January 1996.

Between 27 November and 14 December 1995, the brine collected from the core holes was hypersaline compared to seawater, and brine temperatures were below  $-2^{\circ}\text{C}$  (Table 1). On 19 December, brine salinity was near 32 and brine temperature was around  $-2^{\circ}\text{C}$ . Between the end of December and the last sampling on 17 January 1996, the brine was hyposaline compared to seawater, and brine temperatures were between  $-1.7$  and  $-1.3^{\circ}\text{C}$ . The lowest brine salinity ( $\sim 20$ ) and one of the highest brine temperatures ( $\sim -1.4^{\circ}\text{C}$ ) occurred in the 9 January samples.

Concentrations of nitrate and inorganic phosphate were low in brine samples collected after mid-December (Table 1). Ammonium concentrations were relatively high ( $>1 \mu\text{M}$ ) in some samples, and variability among samples collected from replicate core holes was high (Table 1). Chl a concentrations were highest in the November samples and mostly  $<1 \mu\text{g l}^{-1}$  from mid-December onward (Table 1).

### Abundance and composition of brine microalgal assemblage

Flagellated cells of photosynthetic chrysophytes were numerically dominant in the hypersaline brines collected in late November and early December, occurring at densities of  $\geq 10^7$  cells  $\text{l}^{-1}$ , but were rare in brines collected after 4 December (Table 2). However, coccoid chrysophyte cells were abundant in brine samples collected in mid-December when brine temperatures were between  $-2.4$  and  $-1.8^{\circ}\text{C}$  and brine salinity was between  $\sim 32$  and  $39$  (Tables 1 & 2). Chrysophyte statocysts were detectable in brine from mid-December onward, and their densities in the brine peaked in late December and January (Table 2).

The dominant photosynthetic dinoflagellate in the brine was a small gymnodinioid species, which has been recently described as *Polarella glacialis* gen. nov., sp. nov. (Montresor et al. 1999). It occurred at densities  $>10^6 \text{ l}^{-1}$  of brine between late November and early January (Table 2). Flagellated cells of this species

Table 2. Abundance of microalgae in brine collected from triplicate core holes at the Inaccessible Island site. Mean numbers of cells  $\times 10^3 \text{ l}^{-1} \pm$  standard error. ND = not detectable

Date	Chrysophytes			<i>Polarella glacialis</i>	Dinoflagellates		<i>Mantoniella</i> sp.	Diatoms	Others
	Flagellates	Coccoid cells	Statocysts		Larger dinoflagellate	Cysts			
27 Nov 95	11324 $\pm$ 3408	ND	ND	1797 $\pm$ 389	142 $\pm$ 33.5	ND	999 $\pm$ 589	ND	250 $\pm$ 250
4 Dec 95 <sup>a</sup>	10084	ND	ND	10313	ND	ND	ND	ND	ND
14 Dec 95	ND	3893 $\pm$ 994	26 $\pm$ 27	4978 $\pm$ 943	27 $\pm$ 27	728 $\pm$ 85	5458 $\pm$ 3047	ND	ND
19 Dec 95	ND	5190 $\pm$ 1815	714 $\pm$ 369	4450 $\pm$ 1703	48 $\pm$ 48	1172 $\pm$ 345	6720 $\pm$ 6189	ND	ND
27 Dec 95	ND	650 $\pm$ 232	4764 $\pm$ 1877	1707 $\pm$ 279	ND	24801 $\pm$ 546	506 $\pm$ 310	24 $\pm$ 24	ND
4 Jan 96	ND	388 $\pm$ 161	3601 $\pm$ 579	1364 $\pm$ 243	ND	1950 $\pm$ 283	1277 $\pm$ 1088	111 $\pm$ 60	664 $\pm$ 62
9 Jan 96	ND	240 $\pm$ 191	1847 $\pm$ 1114	123 $\pm$ 45	ND	1361 $\pm$ 520	2161 $\pm$ 64.4	735 $\pm$ 382	421 $\pm$ 47
17 Jan 96	ND	178 $\pm$ 67	5941 $\pm$ 596	141 $\pm$ 47	ND	1256 $\pm$ 467	891 $\pm$ 743	19 $\pm$ 18	284 $\pm$ 144

<sup>a</sup>No replicates, subsample from incubation

occurred only at low densities in the brine after 4 January. The resting cysts (hypnozygotes) of *P. glacialis* were not detectable in the brine until mid-December but they occurred at high densities from mid-December until the end of the sampling season. A larger, mixotrophic dinoflagellate was also detected (refer to Fig. 4b in Stoecker et al. 1992), but it was much rarer than *P. glacialis* (Table 2).

Other microalgae found in the brine included the small flagellated prasinophyte *Mantoniella* sp. and a mixture of small pennate diatoms (Table 2). *Mantoniella* sp. occurred at high densities in some brine samples throughout the sampling season. Diatoms were not detectable in the brine until late December, and diatom densities were low in the brine except in samples collected on 9 January.

### Cyst formation

The first nutrient addition incubation was started on 4 December, with brine of a salinity of 65 and a temperature, at the time of collection, of  $-3.3^{\circ}\text{C}$ . The brine contained vegetative cells of the dinoflagellate *Polarella glacialis* ( $\sim 2.8 \times 10^4 \text{ ml}^{-1}$ ) and chrysoflagellates ( $\sim 9 \times 10^3 \text{ ml}^{-1}$ ). No dinoflagellate or chrysophyte cysts were

found. The brine temperature during the 23 d incubation at the Hut site ranged from  $-3.4$  to  $-2.0^{\circ}\text{C}$  and irradiance was  $\sim 33\%$  of incident surface irradiance.

During the first week of the incubation, dinoflagellate numbers increased in both control and nutrient addition treatments (Fig. 1A). By 18 December, some of the dinoflagellates in the control treatment had a 'bubbly' surface texture, which often precedes cyst formation. On 27 December,  $>94\%$  of the dinoflagellate cells in the control treatment were encysted, but none of the dinoflagellate cells in the nutrient addition treatment were encysted (Fig. 1B). At the end of the experiment, the percent of the dinoflagellates which were cysts was significantly higher in the control than in the nutrient addition treatment ( $p < 0.05$ ).

After the initial sample, it was not possible to enumerate chrysoflagellates because the samples were not filtered immediately after fixation, and the chrysoflagellate autofluorescence faded in the later samples. However, the chrysophyte statocysts were readily distinguishable. Statocysts were observed in both the control and experimental treatments on 18 December. By the end of the incubation on 27 December, statocysts were present at mean densities of  $1.1$  to  $1.7 \times 10^3 \text{ cells ml}^{-1}$ . The difference in abundance of statocysts between treatments was insignificant ( $p > 0.05$ ) (Fig. 2A).

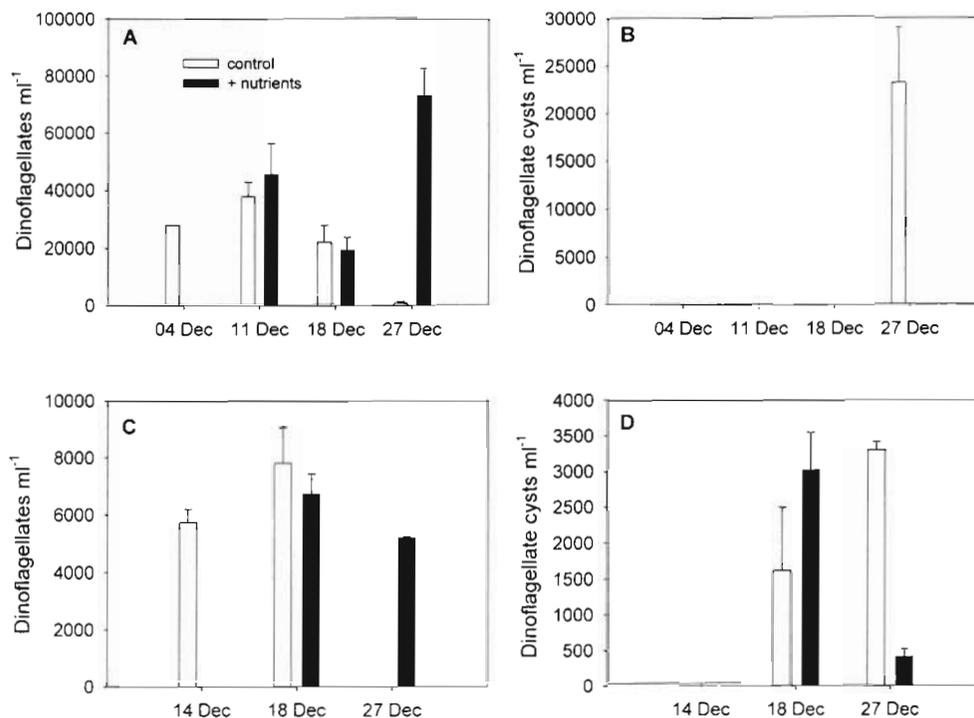


Fig. 1. *Polarella glacialis*. Abundance of (A,C) vegetative cells and (B,D) resting cysts (hypnozygotes) during *in situ* incubations with brine collected on 4 and on 14 December 1995.  $N = 2$  except for initial densities on 4 and 14 December for which  $N = 1$ . Means + standard error

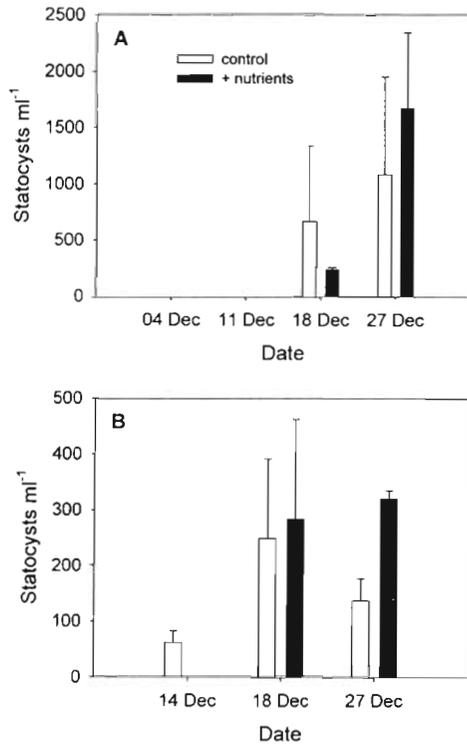


Fig. 2. Abundances of chrysophyte statocysts during *in situ* incubations with brine collected on (A) 4 December and (B) 14 December 1995.  $N = 2$  except for initial densities on 4 and 14 December for which  $N = 1$ . Means + standard error

In the second nutrient addition incubation, which was started 10 d later than the first, brine salinity was 37 and brine temperature at the time of collection was  $-2.4^{\circ}\text{C}$ . Initial densities of vegetative cells of dinoflagellates and chrysoflagellates were both  $\sim 6 \times 10^3$  cells  $\text{ml}^{-1}$  (Figs. 1C & 2B). In contrast to the first experiment, dinoflagellate cells with a 'bubbly' texture were evident at the beginning, indicating the initiation of cyst formation. Low numbers of statocysts were also present (Fig. 2B). Four days later, dinoflagellate cysts were present in both control and nutrient addition treatments at about equal numbers (Fig. 1D) with the difference in percent cysts not significantly different ( $p > 0.05$ ). At the end of the first incubation, dinoflagellate vegetative cells were low in abundance and cysts were abundant in controls, but in the nutrient addition treatment the number of dinoflagellate vegetative cells had risen and the number of cysts was low (Fig. 1 C,D). The percent of dinoflagellates which were encysted was significantly higher in the control than in the nutrient addition treatment ( $p < 0.01$ ). The number of statocysts increased in both treatments. The average number of statocysts was higher in the nutrient addition treatment (Fig. 2B), but the difference between treatments was not statistically significant ( $p > 0.05$ ).

## Photosynthesis and primary production

Initial temperature and salinity of brine samples used in the incubations (Table 3) were close to average values for the site sampled on the same day (Table 1). On 14 December, the incubation temperature at the Hut site was  $1.1$  to  $2.1^{\circ}\text{C}$  warmer than in the upper ice at the sampling site (Table 3). From 19 December to 17 January, incubation temperatures were only slightly warmer ( $<1^{\circ}\text{C}$ ) than in the upper ice at Inaccessible Island (Table 3).

At the sampling site near Inaccessible Island, PAR just below the brine surface in core holes (about 20 to 30 cm from ice surface) averaged 248 to 498  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . This was 22% ( $n = 8$ , range 17 to 31%) of the incident PAR at the ice surface around mid-day (Table 3). In the incubations done in the tub at the Hut site, light levels were lower than in brine at the sampling site, with only 6.9% of incident PAR reaching the unscreened treatments in the 30 November and 4 December experiments, and 9.25% in the 14 December experiment (Table 3). In the 19 December incubation, which was conducted in a core hole, the calculated irradiance for an unscreened bottle was  $\sim 27.6\%$  of incident PAR and thus was within the *in situ* range at the sampling site. In the January incubations, which were conducted in a flowing seawater incubator, the unscreened treatments were exposed to  $\sim 32.2\%$  incident PAR, which was slightly higher than the range observed *in situ*. Average PAR at the ice surface ( $I_0$ ) during the incubations ranged from 548 to 722  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Table 3).

Average chl *a* values in the brine were relatively high, 7.0 and 7.5  $\mu\text{g l}^{-1}$ , in the first 2 incubations, but chlorophyll values were  $<1 \mu\text{g l}^{-1}$  in the other incubations except for the 9 January incubation when the brine had 1.64  $\mu\text{g chl a l}^{-1}$ . In the first 2 incubations, light saturation was not evident (Fig. 3 A,B) and thus the maximum rate of photosynthesis ( $P_{\text{max}}$  and chl *a*-specific  $P_{\text{max}}$ ) is a minimum estimate (Table 3). However, rates of photosynthesis in the unscreened treatments were high, 72 and 218  $\mu\text{g C l}^{-1}$  of brine  $\text{d}^{-1}$ , on 30 November and 4 December, respectively (Table 3). For the other incubations, light saturation occurred and there was no evidence of photoinhibition (Figs. 3 & 4). Between 14 December and 17 January,  $P_{\text{max}}$  declined from 32 to 5  $\mu\text{g C l}^{-1}$  of brine  $\text{d}^{-1}$ . Chl *a*-specific  $P_{\text{max}}$  declined from 1.5  $\mu\text{g C } (\mu\text{g chl a})^{-1} \text{h}^{-1}$  on 14 December to  $<1.0$  during the rest of the sampling period (Table 3). The light adaption index ( $I_k$ ) was calculated as  $P_{\text{max}}$  divided by  $\alpha$ , the initial slope of the photosynthesis versus irradiance curve (Table 3).  $I_k$  values ranged from 11 to 48  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Table 3).

Experimentally measured  $I_k$  values were consistently lower than irradiance measured around mid-day in brine at 20 to 30 cm down from the ice surface at the

Table 3. Photosynthesis versus irradiance incubations with brine from the Inaccessible Island site. Photosynthetic parameters are determined from fitting data to the equation of Jassby & Platt (1976). T = tub in ice at the Hut site; H = uncovered core hole at the Hut site; I = flowing seawater incubator at McMurdo Station. Avg  $I_0$  = Average irradiances at the ice surface during the ~24 h incubations. At the time of brine collection (10:00 to 12:30 h), the *in situ* irradiance just below the brine level in the sea-ice at the Inaccessible Island site ranged from 248 to 498  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  (17 to 31 % the irradiance at the ice surface) (N = 8). Average irradiances for the treatments during the incubations are given in the *P-I* curves (Figs. 3 & 4)

<b>(A) Environmental conditions</b>						
Date	Incubation site	Temp. (°C)		Brine salinity	Avg $I_0$ ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ )	Chl a ( $\mu\text{g l}^{-1}$ brine)
		Initial brine	Incubation temp.			
30 Nov 95	T	-3.4	-5.0 to -3.0	68.0	641	7.0
4 Dec 95	T	-3.3	-4.0 to -3.0	65.0	712	7.5
14 Dec 95	T	-2.1	-1.0 to 0	37.5	612	0.90
19 Dec 95	H	-1.8	--1.0	31.5	722	0.92
4 Jan 96	I	-1.4	--1.0	21.6	636	0.66
9 Jan 96	I	-1.3	--1.0	20.0	566	1.64
17 Jan 96	I	-1.6	--1.0	24.8	548	0.36
<b>(B) Photosynthetic parameters</b>						
Date	$P_{\text{max}}^a$ ( $\mu\text{g C l}^{-1} \text{d}^{-1}$ )	Chl a-specific $P_{\text{max}}$ ( $\mu\text{g C } [\mu\text{g chl a}]^{-1} \text{h}^{-1}$ )	$\alpha^a$ ( $\mu\text{g C l}^{-1} \text{d}^{-1}$ )	$\alpha^a$ ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) <sup>-1</sup>	$I_k$ ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ )	
30 Nov 95	72 ± 14.7 <sup>b</sup>	0.4 <sup>b</sup>	NA	NA	NA	
4 Dec 95	218 ± 4.3 <sup>b</sup>	1.2 <sup>b</sup>	NA	NA	NA	
14 Dec 95	32 ± 1.6	1.5	2.9 ± 0.43		11	
19 Dec 95	19 ± 1.6	0.8	0.4 ± 0.10		48	
4 Jan 96	13 ± 1.4	0.8	0.7 ± 0.19		19	
9 Jan 96	10 ± 0.9	0.2	0.7 ± 0.15		14	
17 Jan 96	5 ± 0.4	0.6	0.2 ± 0.04		25	
<sup>a</sup> Mean ± standard error determined by the fitting algorithm						
<sup>b</sup> Minimum estimate based on photosynthetic rate in unscreened treatment						

snow-free Inaccessible Island site (Table 3). Thus, we took  $P_{\text{max}}$  as an estimate of photosynthetic performance in brine in the upper 50 cm of ice. Daily primary production ( $\text{mg C m}^{-2}$ ) in the upper 50 cm of sea ice was calculated as:

$$\text{mg C m}^{-2} = (P_{\text{max}}) \times (BV/100) \times 0.5$$

where *BV* is % brine volume from Table 1.

Estimated daily primary production ranged from a high of ~12  $\text{mg C m}^{-2}$  on 4 December 1995 to a low of 0.4  $\text{mg C m}^{-2}$  on 17 January 1996 (Fig. 5). The highest production took place in early December during a bloom of the dinoflagellate *Polarella glacialis*. Within 10 d, daily production dropped by 77% as the dinoflagellate encysted and as inorganic nutrients declined to low levels (Fig. 5, Tables 1 & 2). In January (austral summer), when diatoms were present in the upper ice and temperatures and brine volumes were relatively high (Tables 1 & 2), daily primary production was <1  $\text{mg C m}^{-2}$ .

## DISCUSSION

Sea ice consists of a complex matrix of ice and brine, with brine volume dependent on temperature

and sea ice salinity (Weeks & Ackley 1982, Maykut 1985, Weissenberger et al. 1992, Ackley & Sullivan 1994). With current techniques, it is not feasible to measure photosynthetic rates with intact sea ice, although experiments have been performed with sectioned cores (Mock & Gradinger 1999). Melting cores to release microalgae drastically changes the physical and chemical milieu to which the microalgae are exposed. For these reasons, we chose to collect brine from core holes and use it for <sup>14</sup>C uptake incubations to measure photosynthesis. This minimized damage to algal cells and changes in their chemical environment.

However, the brine that accumulates in core holes probably differs from the average brine in intact sea ice (Stoecker et al. 1997). The species composition of algae in collected brine often differs from that in ice cores. Early in the season, chrysoflagellate biomass in brine was higher than in ice cores (Table 4). In contrast, the coccoid, non-motile, chrysophyte life history stages were more abundant in cores than in brine (Table 4). Similar differences between brine and cores in the distribution of chrysophytes were observed at a snow-covered site on the sea ice (Stoecker et al. 1997). Flagellated stages of *Polarella glacialis* and the prasin-

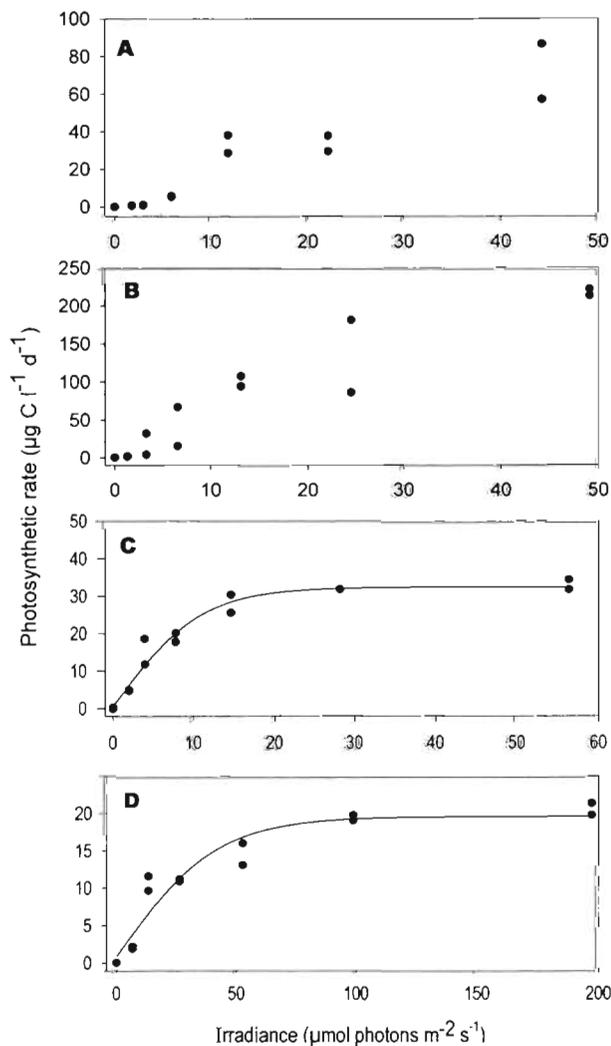


Fig. 3. Daily photosynthesis versus irradiance for *in situ* and simulated *in situ* brine incubations started on (A) 30 November, (B) 4 December, (C) 14 December, and (D) 19 December 1995. Curve fitting with hyperbolic tangent function (Jassby & Platt 1976)

ophyte *Mantionella* sp. were usually more abundant in brine than in ice cores (Table 4). Cyst formation was evident at the same time in both ice cores (Stoecker et al. 1998) and brine samples (Table 2). The brine obtained from core holes should best represent the ice depths with the greatest brine volume, between 25 and 55 cm in our investigation (Table 1c in Stoecker et al. 1998).

Although there are obvious differences between cores and brine, measurement of chl *a* and photosynthesis using brine assemblages, in concert with physical and chemical data, can provide useful information on seasonal changes in primary production in the upper sea ice. Chl *a* values in the brine peaked in late

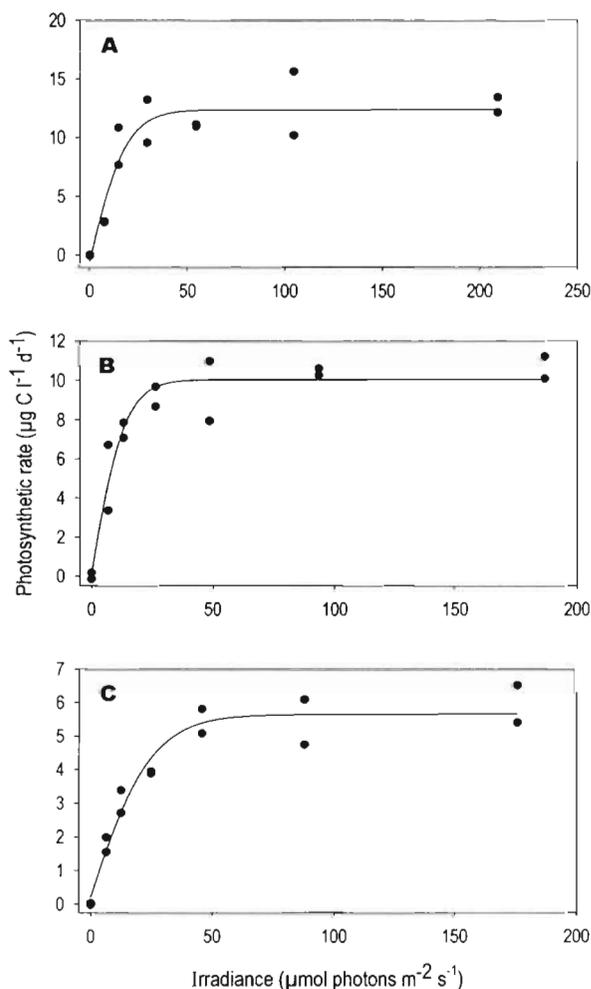


Fig. 4. Daily photosynthesis versus irradiance for *in situ* and simulated *in situ* brine incubations started on (A) 4 January, (B) 9 January, and (C) 17 January 1996. Curve fitting with hyperbolic tangent function (Jassby & Platt 1976)

November and early December (Table 3), coincident with dinoflagellate and chrysoflagellate blooms in the sea ice at this site (Stoecker et al. 1998). Chl *a* values dropped dramatically between 4 and 14 December, coincident with formation of non-motile stages and cysts. After 14 December, much of the color on filters was not extracted in 90% acetone with grinding (authors' unpubl. obs.), indicating that the chlorophyll contained in resting stages probably was not extracted. Thus, chl *a* values probably reflect the biomass of photosynthetically active life history stages.

During December, estimates of  $P_{\max}$  ranged from ~19 to 218  $\mu\text{g C l}^{-1}$  of brine  $\text{d}^{-1}$  (Table 3), which was higher than the 4.3 to 11.3 range of  $P_{\max}$  for brine from the snow-covered Hut site (Stoecker et al. 1997). In both cases  $P_{\max}$  should approximate *in situ* photosynthetic performance.

There were large differences in photosynthetic performance between the 2 sites in December 1995. The primary difference between the ice environment at the sites was age of the ice and snow cover. The Hut site was on second year ice and the Inaccessible Island site

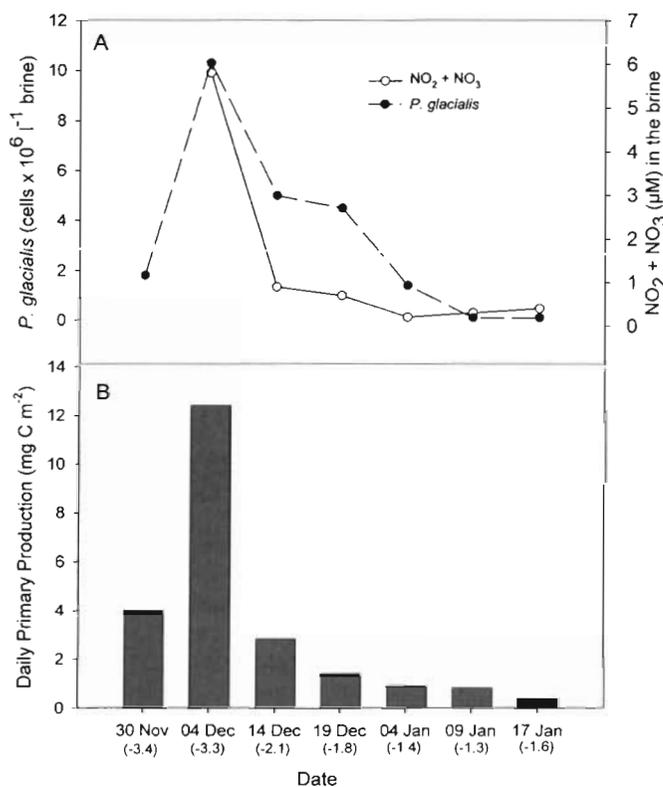


Fig. 5. Inaccessible Island site on snow-free first year sea-ice, spring-summer 1995-1996; (A) Abundance of *Polarella glacialis* (vegetative cells) and nitrate + nitrite concentrations in the brine; hypnozygotes (resting cysts) of *P. glacialis* were first noticed on 14 December 1995. (B) Estimated primary production in the upper 50 cm of sea-ice; brine temperatures in the upper sea ice are given in parentheses under each date

was first year ice. Multi-year ice is usually depleted in inorganic nutrients compared to first year ice and is usually thicker (Dieckmann et al. 1991, Gleitz et al. 1995). At the beginning of December, nitrate plus nitrite levels were high in the brine at both sites (Table 2 in Stoecker et al. 1997, Table 1 herein) and thus, in our case, nutrients do not appear to be the major cause of differences in productivity.

At the Hut site, the heavy snow cover (27 to 32 cm) and ice thickness ( $\geq 2$  m) (Stoecker et al. 1997) made the upper ice a very different habitat than at the Inaccessible Island site, where the ice was  $< 2$  m thick, wind-swept and almost devoid of snow cover (Stoecker et al. 1998). At the Hut site, brine temperatures in the upper ice during December remained  $< -5^\circ\text{C}$ , brine salinity remained  $> 99$ , and maximum irradiance in the upper ice brine was  $< 40 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . At the Inaccessible Island site, conditions in the upper ice were much less extreme in terms of temperature and brine salinity. At least 6 times as much light reached the brine assemblages in the upper ice at this site than at the Hut site (Stoecker et al. 1998 and Tables 1 & 3 herein). Dinoflagellates were much less abundant in brine at the Hut site than at the Inaccessible Island site, although chrysoflagellates and small diatoms were more abundant at the Hut site (Stoecker et al. 1998 and Table 2 herein). Due to higher ice temperatures at the snow-free site during December, brine volumes were about twice those at the Hut site. The lack of snow cover at the Inaccessible Island site made it a better habitat for growth of dinoflagellates and more productive than the Hut site. Previous studies have shown that snow cover has a dramatic impact on ice structure and its biota (reviewed in Gradinger et al. 1991, Ackley & Sullivan 1994).

Differences between dates in incubation procedures, errors in deriving average irradiance and brine volume from measurements, and differences between the biology of collected brine and intact ice all may

Table 4. Comparison of estimated biomass ( $\mu\text{g C l}^{-1}$ ) of phytoflagellates in the brine and in the upper 90 cm of the ice cores at the Inaccessible Island site. Biomass conversions and data for the cores from Stoecker et al. (1998). ND = no data

Date	Chrysoflagellates		Coccoid chrysophytes		<i>Polarella glacialis</i> <sup>a</sup>		Larger dinoflagellate		<i>Mantoniella</i> sp.	
	Brine	Cores	Brine	Cores	Brine	Cores	Brine	Cores	Brine	Cores
27 Nov 95	113.2	2.9	ND	ND	80.8	99.4	35.9	175.7	5.0	ND
4 Dec 95	101.8	126.6	ND	ND	464.1	154.9	ND	750.0	ND	ND
14 Dec 95	ND	4.4	62.3	138.8	224.0	92.1	6.8	11.6	27.3	1.6
19 Dec 95	ND	0.3	83	103.8	200.2	64.2	12.1	5.7	3.4	1.3
27 Dec 95	ND	0.4	10.4	50.4	76.8	31.4	ND	2.8	2.5	1.9
4 Jan 96	ND	0.1	6.2	11.4	61.4	19.0	ND	0.8	6.4	0.1
9 Jan 96	ND	ND	3.8	1.4	5.5	3.7	ND	ND	10.8	1.9
17 Jan 96	ND	ND	2.8	3.8	6.3	2.4	ND	ND	4.5	0.2

<sup>a</sup>Gymnodinioid dinoflagellate in Stoecker et al. (1998)

have influenced our estimates of primary production in the upper ice. However, it is clear from our data that snow-free upper fast ice is an ecologically dynamic and productive habitat. There were large changes in daily primary production between late November and mid-January (Fig. 5). The highest algal biomass and production were in late November and early December, when the ice surface was still very cold and the brine hypersaline (Tables 1 to 3). These peaks in biomass and production coincided with peaks in the population of *Polarella glacialis* (Table 2), which excysts in the ice during the austral spring while ice temperature is still low and brine salinity is high (Stoecker et al. 1997). Biomass and production were relatively low during late December and January, although environmental conditions were more moderate at this time.

Declines in  $P_{\max}$  but not chlorophyll-specific  $P_{\max}$  between 4 and 14 December coincided with encystment of photosynthetic dinoflagellates and chrysoflagellates and with a drastic decline in inorganic nutrients in the brine (Table 1) and ice (Stoecker et al. 1998). Resting cysts usually are not photosynthetically active and we found that their chlorophyll was not readily extracted. Thus, reductions in  $P_{\max}$  on 14 December were probably due to reductions in photosynthetically active biomass rather than to declines in chlorophyll-specific photosynthesis.

Nutrient depletion is a common trigger for sexuality and resting cyst formation in dinoflagellates (Pfiester & Anderson 1987). The *in situ* cyst formation experiments indicated that nutrient depletion, rather than changes in temperature, salinity or irradiance, triggered encystment of *Polarella glacialis* (Fig. 1). Laboratory experiments have confirmed that nutrient depletion, particularly inorganic nitrogen, is the primary stimulus for sexuality and cyst formation in this dinoflagellate (M.M.D.B. & D.K.S. unpubl. data). However, nutrient depletion did not trigger statocyst formation (Fig. 2). Chrysophytes often exhibit density-dependent control of sexuality and statocyst formation (Sandgren 1988), which may explain why statocyst densities were as high or higher in nutrient-amended treatments as in controls. It is interesting that declining nutrient levels apparently triggered sexuality and encystment in the dinoflagellates before community chlorophyll-specific rates of photosynthesis were affected.

The estimated carbon content of vegetative cells of *Polarella glacialis*, chrysoflagellates, and *Mantoniella* sp. are 45, 10, and 5 pg cell<sup>-1</sup>, respectively (Stoecker et al. 1998). Although *P. glacialis*, chrysophytes and *Mantoniella* sp. occurred at roughly similar cell densities in December (Table 2), the dinoflagellate dominated biomass. Chl *a* and  $P_{\max}$  declined before chlorophyll-specific  $P_{\max}$ , suggesting that cyst formation by the

dinoflagellate, triggered by declining nutrients, reduced photosynthetically active biomass (indicated by chl *a*). Thus cyst formation may have been an important factor in the drastic reduction in primary production in the upper sea ice during early December. After 14 December, chlorophyll-specific  $P_{\max}$  decreased sharply (Table 3) and nutrient levels declined further (Table 1). Reductions in photosynthetic performance due to nutrient stress (Gleitz et al. 1995) were undoubtedly important after 14 December.

In late December and January, inorganic nutrient concentrations remained low but fluctuated; this may have been due to a combination of nutrient regeneration within the ice and exchanges with the water column as brine drainage occurred and the ice decayed (Ackley & Sullivan 1994, Gleitz et al. 1995). In early to mid-January, a small bloom of pennate diatoms and prasinophytes occurred in the upper sea ice (Stoecker et al. 1998) and in the brine (Table 2). Light-saturated rates of photosynthesis per unit brine volume were low during the diatom and prasinophyte blooms (Table 3).

Our data indicate an average daily production of 3.24 mg C m<sup>-2</sup> in the upper 50 cm of sea ice at the snow-free Inaccessible Island site of our investigation (Fig. 5). If we assume an 8 wk growing period (i.e., significant production occurred a week before our first experiment in which production was already relatively high) (Fig. 5), the estimated seasonal production in the upper 50 cm of sea ice is ~181 mg C m<sup>-2</sup>. This probably underestimates production in the sea ice interior because as the ice warms in December and January, brine volumes increase and microalgae are found to ≥90 cm depth (Stoecker et al. 1998). Earlier we reported seasonal changes in biomass of phytoflagellates in ice cores from the Inaccessible Island site (Stoecker et al. 1998). On 14 November 1995, the total phytoflagellate biomass was near zero. The maximum biomass that developed in the upper ice of vegetative cells of *Polarella glacialis* was 155 μg C l<sup>-1</sup> ice, of chrysoflagellates was 127 μg C l<sup>-1</sup> ice and of prasinophytes was 2 μg C l<sup>-1</sup> ice (diatom biomass was not calculated). These data indicate algal production of at least 256 mg C m<sup>-2</sup>. The production estimate based on biomass is higher than the estimate based on <sup>14</sup>C uptake because it includes a greater depth of ice. Another factor that may contribute to the higher estimate based on biomass than primary productivity is the nutrition of phytoflagellates. Many dinoflagellates and chrysophytes are mixotrophs (Holen & Boraas 1995, Stoecker 1999), and thus it is possible that the phytoplankton biomass is partially supported by carbon from sources other than photosynthesis.

Production may occur during seasons not included in our study. Fritsen et al. (1994) observed an autumn bloom of sea ice algae within the upper layer of multi-

year pack ice. The bloom was driven by exchange of nutrient-depleted brine with nutrient-rich seawater as temperatures in the upper ice declined. Infiltration of seawater into the upper ice due to snow loading can also provide new nutrients and increase production (Ackley & Sullivan 1994). We don't know if primary productivity decreased or increased in the ice after it broke out. Estimates of production based only on austral spring and early summer are almost certainly underestimates of yearly production for a patch of ice.

Our estimates of primary production in the upper sea ice interior at a snow-free site are at least twice as high as an estimate of average microalgal production for interior sea ice assemblages ( $80 \text{ mg C m}^{-2}$ ) in the Antarctic (Table 1 in Legendre et al. 1992). Our estimate of production for the upper ice interior is lower than estimates of production by surface, freeboard and bottom assemblages from the Antarctic ( $4000$  to  $32\,000 \text{ mg C m}^{-2}$ ) (Table 1 in Legendre et al. 1992). However, it is difficult to evaluate the contribution of upper ice brine assemblages to total production in the Antarctic for several reasons. This habitat and its algal assemblages are often poorly defined in the literature (Horner et al. 1992). Chlorophyll must underestimate biomass in the upper ice relative to base of the ice because the upper ice is usually a colder, higher irradiance environment than the base of the ice (Kottmeier & Sullivan 1988, Arrigo et al. 1991). C:chl *a* ratio decreases with increases in irradiance and decreases in temperature (Geider et al. 1997). In the upper sea ice, production estimates based on standing stock of chlorophyll may considerably underestimate true production. Most field studies have not included primary production in the upper sea ice interior, particularly during austral spring, when upper ice temperature is low and brine salinity is high, but when these assemblages are most productive. Often it has been assumed that conditions are too harsh for the growth of microalgae in the upper sea ice interior early in the season (Kottmeier & Sullivan 1988).

There are large differences in the geophysics and biology of fast and pack ice. Both environments are extremely heterogeneous (Garrison et al. 1986, Ackley & Sullivan 1994). Year-to-year variation in the formation and decay of sea ice contributes to the problem of estimating the spatial extent of different sea ice assemblages and their productivity. For these reasons, it is not currently possible to determine the contribution of upper sea ice interior habitats to sea ice primary production. However, recent studies in the Arctic and Antarctic suggest that upper surface and interior sea ice assemblages, including those dominated by phytoflagellates, may make an important contribution to sea ice primary production, sometimes equaling or exceeding production by algae growing at the base of the sea ice (Mock & Gradinger 1999).

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