Antarctic Science 8 (2): 135–146 (1996)

# Ecology of diatom and bacterial assemblages in water associated with melting summer sea ice in the Weddell Sea, Antarctica

MARKUS GLEITZ, SÖNNKE GROSSMANN, RENATE SCHAREK and VICTOR SMETACEK

*Alfred-Wegener-Institut für Polar- und Meeresforschung, Bremerhaven, Germany*
*Postal address: AWI / BIO II, Postfach 12 01 61, D-27515 Bremerhaven, Germany*

**Abstract:** The fate of ice biota released via meltwater into pools of seawater trapped between melting ice floes (crack pools) was followed in late January in the southern Weddell Sea. Low salinity crack pools shared the following features: nitrate exhaustion, high pH and POC/PON ratios, high bacterial biomass composed of large cells, and a dense algal assemblage dominated to over 90% by only two diatom species. It is suggested that this "climax stage" evolved from a nutrient rich, moderate biomass situation prevailing in high salinity crack pools, and is representative of summer succession of sea ice biota. "Overflow" production following nitrate exhaustion by the algae resulted in internal (lipid) and external (presumably mucus) carbon pools. The latter must fuel bacterial biomass build-up, as algal mortality appeared to be low. The large algal and bacterial stocks point to low grazing pressure exerted by phagotrophic protists, presumably due to poor food quality (e.g. high C/N ratios) and/or excessive mucus production. It is concluded that environmental selection of the abundant ice algal species occurs under conditions prevailing in the disintegrating ice cover during summer, which differ drastically from those generally referred to as characteristic of the sea ice habitat at large (a combination of low temperature, low light and high salinity).

Received 8 July 1995, accepted 14 December 1995

**Key words:** grazing, ecology, physiology, nutrient limitation, sea ice algae, sea ice bacteria

## Introduction

Sea ice growth and retreat is a fundamental process in polar marine ecosystems (Eicken 1992, Knox 1994). Whereas light greatly reduces phytoplankton growth in ice-covered waters, high algal standing stocks have been observed in a variety of ice-associated (sympagic) habitats (Garrison 1991, Palmisano & Garrison 1993). It is now realized that sea ice enhances significantly the degree of ecological variability as well as the overall productivity of polar oceans (Eicken 1992, Legendre *et al.* 1992).

Four-fifths of the sea ice surrounding the Antarctic continent melt during summer (Zwally *et al.* 1983). During melt, the floes comprising the disintegrating ice cover break up into sizes from a few metres to tens of metres across and, as they are affected by swell, they tend to collide and break into smaller pieces. The honeycomb-like channels within the ice broaden by many orders of magnitude in the course of melting and render the floes crumbly (Eicken *et al.* 1988). As the floes rub against each other due to their differential movement, brash ice accumulates between them. The pieces of brash are irregularly shaped and cover the metre to decimetre size range. Such fields of disintegrating floes and brash have a distinctly brownish tinge indicating that they and the water trapped between them are sites of intense algal growth. Fields of brash ice are disrupted by passage of the ship and can neither be boarded nor entered by smaller boats. Hence, these habitats cannot be sampled by conventional ice coring.

Most studies on ice-associated habitats have been carried out during winter or spring from intact ice covers (Horner *et al.* 1992, Palmisano & Garrison 1993). Sea ice that persists through the summer has, on the other hand, not been studied systematically. Hence the ecology of brash ice fields is poorly known, partly because of their inaccessibility, but also because they represent a short-lived environment. This is unfortunate because, as evidenced by the brown discolouration, algal growth is probably most prolific in summer sea ice, when temperatures are mild and irradiances high (Burkholder & Mandelli 1965, Ackley *et al.* 1979).

A variety of ice habitats developing during summer at the pack ice surface have recently been described by Ackley & Sullivan (1994). In addition to snow-ice and freeboard layer habitats, the microenvironments that arise within disintegrating sea ice — exemplified in this study by water trapped between melting sea ice (crack pools) — will be a regular and wide-spread feature of brash ice fields deprived of snow cover. The greatest variation will be in the time span of a given ice-protected microenvironment and hence in the stage along the axis of maturation reached within it before dispersal by vigorous movement of the supporting ice cover.

The aim of the present study was to characterize the physical and chemical structure of this widespread but poorly known habitat, to examine the coupling of the primary and secondary production, and to follow the fate of this late

season biomass during the summer of 1991 in the southern Weddell Sea. The study period witnessed the most extensive accumulation of pack ice in the Weddell Sea since monitoring by remote sensing was commenced in 1974. Satellite images indicate that this was due to a southward compression of the pack ice field against the continent that prevented dispersal and large-scale melting of the ice cover (Lukin & Provorkin 1992). Unusual meteorological conditions appeared to be responsible for the phenomenon as, on the other side of the Antarctic Peninsula, in the Bellingshausen Sea, the sea ice cover retreated to a record minimum (Jacobs & Comiso 1993). Although the data presented here were collected during an exceptional ice year, they provide new information on the ecology of summer sea ice habitats, a site of intense ice-based primary and secondary production.

## Material and Methods

### *Sea ice conditions*

En route to the south-western Weddell Sea, *Polarstern* encountered a field of compressed brash ice interspersed by small intact floes with snow cover south of Halley Bay. This ice type, very aptly termed "porridge ice", is not unusual in the area (Captain S. Lawrence, *RRS Bransfield*, personal communication). Its extent and duration was the unusual feature of 1991.

The ship was caught in the ice for two weeks and drifted passively with the ice field south-west at *c.* 5 km $d^{-1}$. Tidal movement induced heavy ridging and brash formation between the melting floes. The ice thus exposed was tinged brown by algae, and consisted of a mixture of melting ice, snow and platelet ice. The latter forms in sub-surface layers of super-cooled water in the vicinity of floating ice shelves (Dieckmann *et al.* 1986). Platelet ice layers were generally present underneath larger, intact floes. In the course of ice-sheet deformation, seawater was exposed to the atmosphere in cracks between pieces of brash ice (Fig. 1). These "crack pools" ranged in size from decimetres to a few metres across. Their contact with the underlying seawater was either direct (these were used as blow holes by whales in the area) or via narrow channels that zigzagged downward between deformed floes. Brash ice fields represented *c.* 20–30% of the ice cover. Despite periodic compression of the ice sheet, some of the pools persisted for days.

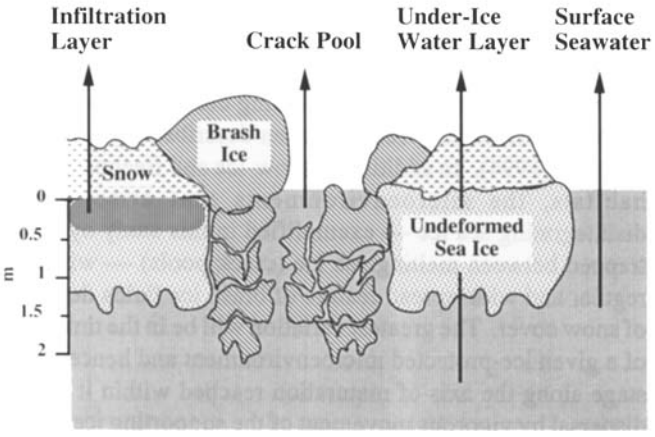


**Fig. 1.** Schematic illustration of various habitats associated with the summer sea ice. Samples were collected from crack pools, infiltration layers, under-ice water layers and surface seawater.

### *Sampling*

Water samples from crack pools, the under-ice water layer and the sea surface were collected between 76°20′S, 30°10′W and 76°40′S, 31°28′W from 21 January to 2 February 1991. Additional infiltration layer samples from intact floes were collected *c.* 500 km to the northeast between 6 and 11 February (for detailed cruise track see Bathmann *et al.* 1992). A total of eleven crack pool and six under-ice water layer, two infiltration ice, and two open water samples were collected.

Crack pool water was collected with a plastic bucket. In many cases, 0.5–1 cm of clear glassy ice covering crack pools had to be broken prior to sampling. The fragments of ice were discarded, and the water was used in the experiments without further treatment. On two occasions, only limited sample material could be obtained, and 0.25–0.5 l of water was diluted into 3–5 l of filtered seawater. The under-ice water layer was sampled from crevices between or from underneath ice floes by slowly sucking water into a 10 l glass bottle using an L-shaped plastic water pipe with a 2 m shaft connected to a vacuum pump. Water was collected through a series of small perforations (*c.* 3 mm diameter) at the tip of the pipe. The instrument and sampling technique have been described in detail by Smetacek *et al.* (1992). Samples from infiltration layers were collected with a beaker after removing 30 cm of snow cover. Surface water samples were taken with 12 l PVC Niskin bottles attached to a CTD rosette.

### *Physico-chemical measurements*

Salinity was measured using a conductivity salinometer calibrated with standard salt solutions provided by the manufacturer (WTW, Weilheim, Germany). Measurements of pH (on the NBS scale) and calculation of dissolved inorganic carbon (DIC) concentrations (for a temperature of 0°C) were carried out following Strickland & Parsons (1972). Nutrient subsamples were fixed with mercuric chloride and kept refrigerated until analysis in the home laboratory using a Technicon autoanalyser, following standard methods of Technicon modified as described in Spies *et al.* (1988). Each sample was analysed twice and values averaged.

### *Biochemical measurements*

Where chlorophyll (Chl *a*) concentrations were high,

https://doi.org/10.1017/S095410209600020X Published online by Cambridge University Press

measurements were made spectrophotometrically after homogenization and extraction in 90% acetone according to Jeffrey & Humphrey (1975). Chl *a* concentrations of all other samples were determined fluorometrically following Evans *et al.* (1987). Subsamples for determinations of particulate organic carbon (POC) and nitrogen (PON) were filtered onto precombusted GF/C filters, and stored at -27°C. Prior to measurement, filters were acidified with 0.1 N hydrochloric acid, dried at 60°C, and processed using a CHN analyser calibrated with acetanilide standards.

*Primary production*

Primary production measurements were carried out following Evans *et al.* (1987). Sample volumes of 50 or 100 ml were placed in borosilicate glass bottles, inoculated with 185–370 KBq of $^{14}$C-labelled sodium bicarbonate, and incubated for 5 or 10 h at -1°C in a temperature controlled deck incubator at 3 or 4 photon flux densities (50–400 $\mu$mol m$^{-2}$ s$^{-1}$), supplied by fluorescent tubes. Light was measured with a spherical light sensor. The incubations were terminated by filtering onto 0.45 µm cellulose nitrate filters. These were dried at room temperature, exposed briefly to fuming hydrochloric acid and dissolved in scintillation cocktail. Uptake rates were corrected by subtracting time-zero blanks. Samples were counted in a liquid scintillation counter, and quench correction was performed by automatic external standardization. The mean of light saturated photosynthetic rates was calculated to obtain an estimate of photosynthetic capacity.

*Microscopy and bacterial production*

Subsamples for diatom microscopy were preserved with hexamine buffered 20% formaldehyde. Cell counts were carried out with a Zeiss IM 35 inverted microscope using the Utermöhl method (Utermöhl 1958). Species were identified according to Priddle & Fryxell (1985) and Medlin & Priddle (1990).

Bacterial cell concentrations were determined by epifluorescence microscopy of acridine orange stained samples (Grossmann 1994). Estimates of bacterial biovolume were based on measurements of bacterial cell sizes and calculations of individual cell volumes (Grossmann & Reichardt 1991). Biomass of bacteria was derived from biovolume using a conversion factor of 3.0 × 10$^{-13}$ g C $\mu$m$^{-3}$ (Børsheim *et al.* 1990).

Bacterial production was determined from incorporation rate of [$^3$H]-thymidine into cold trichloroacetic acid extractable macromolecules (Fuhrman & Azam 1982). Triplicate samples of 4–20 ml were incubated for 4–6 h at -1°C. Since thymidine uptake was not saturated at the low concentration recommended by these authors, thymidine was added to give a final concentration of 50 nM ([methyl-$^3$H]-thymidine, diluted with cold thymidine to a specific activity of 0.3–1.4 TBq mmol$^{-1}$). Dependence of thymidine incorporation on incubation time was checked by time series and found to be linear up to 6 h. Extraction procedure and further processing of samples was carried out as described by Grossmann & Dieckmann (1994). Carbon production of bacteria was calculated from thymidine incorporation rate, conversion factor (1.89 × 10$^{18}$ cells per mole thymidine incorporated, Grossmann & Dieckmann 1994), and mean bacterial cell volume which was converted into units of carbon using the factor applied for biomass determinations.

## Results

*Environmental conditions*

Quantum irradiance (400–700 nm) over the study period, continuously recorded on the ship's upper deck with a hemispherical light sensor, ranged from 10–50 mol m$^{-2}$ d$^{-1}$ (Fig. 2). Irradiance measurements with a spherical light sensor mounted on an ice floe 10 cm above the surface on 30–31 January revealed that PAR incident on crack pools may be as high as 3500 $\mu$mol m$^{-2}$ s$^{-1}$, whereas maximum values recorded by the hemispherical sensor were approximately three times lower (Fig. 2). Since the hemispherical light sensor was set up in parallel to the ice surface, and, therefore,

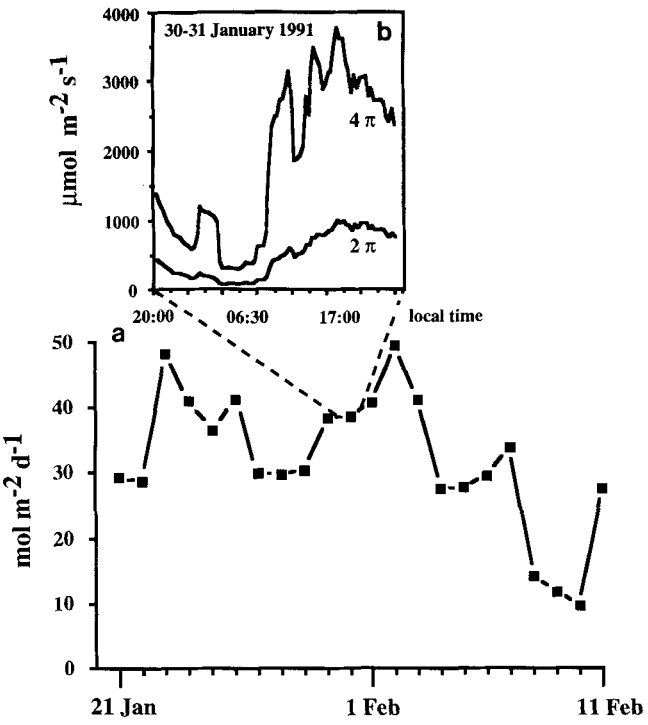


**Fig. 2.** **a.** Photosynthetically active radiation (PAR, wavelength 400–700 nm) measured continuously with a hemispherical (2π) light sensor, integrated over 24 h, during 21 January–11 February 1991. **b.** Instantaneous PAR recorded 10 cm above the snow surface with a hemispherical and spherical (4π) light sensor, on 30–31 January 1991 at 76°34'S/31°28'W.

https://doi.org/10.1017/S095410209600020X Published online by Cambridge University Press

did not record photons impinging at low angles adequately (e.g. at low sun angles or photons reflected from snow and ice), the reading of the spherical sensor presumably is a more realistic measure of quantum irradiance incident on crack pools. Mean daily air temperatures were in the range of -2.1 to -8.0°C.

### *Physical and chemical conditions*

Physico-chemical conditions were rather alike in samples collected from the sea surface and under-ice water layer (Table I). Similar values were also recorded in three crack pool samples (CP 9–11). On the other hand, salinity was significantly lower in eight samples obtained from narrow crack pools (CP 1–8), and low salinities were generally associated with low nitrate and DIC concentrations, but high pH values up to 9.3. Reduced salinities and DIC concentrations, and a pH value of 8.9 were also measured in the infiltration layer samples.

Phosphate and silicate concentrations in many samples exhibited a degree of variability that cannot readily be explained. A sampling artifact can be ruled out since other ice and water column samples taken during the same cruise and which received the same treatment in the home laboratory, gave reasonable results when compared with nitrate. For this reason, the anomalous values are presented in Table I, but they will not be discussed.

### *Phyto- and bacterioplankton composition, biomass, and productivity*

Subsamples were qualitatively analysed under a microscope immediately after collection onboard. These observations revealed that the open water phytoplankton community was numerically dominated by small autotrophic flagellates, mainly motile stages of *Phaeocystis* sp., indicating that winter conditions still prevailed in the pelagial (Scharek *et al.* 1994). Cell numbers of nanoflagellates and *Phaeocystis* sp. were substantially lower in all ice-associated habitats, contributing an estimated 20% to total phytoplankton abundance. In nitrate-depleted crack pools, flagellate abundance decreased to *c.* 10% of total phytoplankton cell numbers. The phagotrophic protists found in crack pools did not differ substantially, neither in species composition nor appearance under the microscope, from those in the water column. Protozoan abundance remained low (on average one to two orders of magnitude below diatom cell number) in all ice-associated habitats through all stages of maturation.

**Table I.** Chemical composition of samples collected from summer sea ice and open water (for description of habitats see text).

| | Sal. (‰) | pH | $NO_3$ (μM) | $PO_4$ (μM) | $SiO_4$ (μM) | DIC (mM) |
|---|---|---|---|---|---|---|
| Surface seawater | | | | | | |
| SW 1 | 34.0 | 8.17 | 28.9 | 1.19 | 57.7 | 2.29 |
| SW 2 | 34.0 | 8.30 | 21.9 | 1.42 | 40.8 | 2.19 |
| Under-ice water layer | | | | | | |
| UIWL 1 | 31.5 | - | - | - | - | - |
| UIWL 2 | 33.0 | 8.45 | 23.3 | 1.80 | 52.5 | 2.09 |
| UIWL 3 | 33.5 | 8.31 | 28.3 | 2.13 | 59.6 | 2.18 |
| UIWL 4 | 33.5 | 8.33 | 28.4 | 3.52 | 103.3 | 2.17 |
| UIWL 5 | 34.0 | 8.02 | 28.1 | 2.15 | 58.1 | 2.30 |
| UIWL 6 | 34.0 | 8.24 | 21.2 | 2.85 | 69.6 | 2.16 |
| Infiltration layer | | | | | | |
| IL 1 | 26.0 | 8.88 | - | - | - | 1.45 |
| IL 2 | 28.0 | 8.25 | - | - | - | 1.79 |
| Crack pool | | | | | | |
| CP 1 | 16.5 | - | 0.0 | 1.39 | 45.7 | - |
| CP 2 | 21.5 | 9.20 | 0.0 | 1.00 | 33.1 | 0.94 |
| CP 3 | 22.5 | 9.29 | 0.1 | 0.63 | 29.2 | 1.06 |
| CP 4 | 23.0 | - | 0.0 | 15.00 | 311.4 | - |
| CP 5 | 26.5 | 9.07 | 0.8 | 0.49 | 8.8 | 1.38 |
| CP 6 | 27.0 | 9.18 | 0.0 | 0.28 | 14.0 | 1.36 |
| CP 7 | 28.0 | 8.09 | 10.8 | 2.74 | 56.4 | 1.96 |
| CP 8 | 30.0 | 8.87 | - | - | - | 1.70 |
| CP 9 | 32.0 | 8.33 | 23.5 | 2.20 | 52.2 | 2.07 |
| CP 10 | 33.5 | 8.03 | 25.3 | 2.06 | 55.4 | 2.33 |
| CP 11 | 34.0 | 8.03 | 27.3 | 2.22 | 60.1 | 2.44 |

pH (on NBS scale) is given for 0°C.

**Table II.** Alphabetical list of diatoms found in samples collected from summer sea ice and open water.

*Amphiprora* sp.
*Banquisia belgicae* [VanHeurck] Paddock
*Chaetoceros neglectum* Karsten
*Chaetoceros dichaeta* Ehrenberg/*Chaetoceros bulbosum* "complex" (see Priddle & Fryxell 1985)
*Corethron criophilum* Castracane
*Eucampia antarctica* [Castracane] Mangin
*Fragilariopsis spp. (F. curta* [van Heurck] Hasle/*F. sublineata* Hasle/*F. obliquecostata* [van Heurck] Hasle/*F. vanHeurkiii* [M. Pergallo] Hasle)*
*Fragilariopsis cylindrus* (Grunow) Hasle*
*Fragilariopsis kerguelensis* (O'Meara) Hasle
*Haslea* sp.
*Manguinea fusiformis* (Manguin) Paddock
*Nitzschia angulata* Hasle
*Nitzschia closterium* [Ehrenberg] W. Smith
*Nitzschia heimii* Manguin
*Nitzschia prolongatoides* Hasle/*Nitzschia lecointei* VanHeurck*
*Nitzschia subcurvata* Hasle
*Nitzschia turgidula* Hustedt
*Odontella weissflogii* (Janisch) Grunow
*Plagiotropis gaussei* [Heiden in Heiden & Kolbe) Paddock/*Plagiotropis longa* [Cleve] Kuntze
*Pleurosigma* sp.
*Porosira pseudodenticulata* (Hustedt) Zhuse
*Proboscia* sp.
*Stellarima microtrias* [Ehrenberg] Hasle & Sims
*Thalassionema bacillaris* [Heiden] Kolbe
*Thalassiosira antarctica* Comber*
*Thalassiosira gracilis* [Karsten] Hustedt
*Tropidoneis* sp. (small form)

* species that dominate in high biomass situations.

https://doi.org/10.1017/S095410209600020X Published online by Cambridge University Press

Twenty seven diatom species were identified (Table II), and in all habitats, the diatom assemblage was dominated by species of *Fragilariopsis* (Fig. 3). However, in the open water and under-ice water layer, several other species also contributed significantly to total diatom abundance. *Fragilariopsis cylindrus* was by far the most abundant diatom in all crack pool samples. In nitrate-depleted crack pools, the relative abundance of *Thalassiosira antarctica* amounted to *c.* 20%.

Diatom and bacterial cell densities as well as POC, bacterial carbon, and Chl *a* concentrations were lowest in surface seawater (Table III). High salinity crack pool samples (CP 9–11) and three under-ice water layer samples (UIWL 2, 3, 5) had similarly low biomass concentrations. Low salinity crack pool samples, on the other hand, were characterized by high POC concentrations as well as high diatom and bacterial cell densities. High algal and bacterial concentrations were also observed in the infiltration layer samples. The mean ratio of POC to Chl *a* was 183 ± 83 ($n$=16), and did not vary much among samples collected from different habitats. Mean bacterial cell volumes were significantly larger in all ice-associated habitats, ranging from 0.15–0.45 $\mu m^3$, when compared to surface seawater, where cell volumes did not

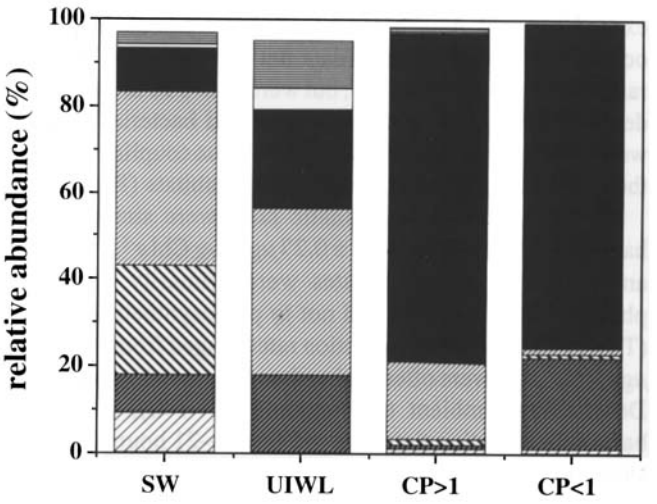


**Fig. 3.** Weighted relative abundance of diatoms in samples. SW=seawater, UIWL=under-ice water layer, CP>1=crack pools with $NO_3$>1 $\mu$M, CP<1=crack pools with $NO_3$<1 $\mu$M.

= *Nitzschia subcurvata*, = *N. prolongatoides*,
= *Fragilariopsis cylindrus*, = *Fragilariopsis* spp.,
= *Thalassiosira gracilis*, = *T. antarctica*,
= *Chaetoceros neglectum*

**Table III.** Chl *a*, bacterial and phytoplankton cell numbers and bacterial carbon biomass, POC and PON concentrations, and compositional ratios in samples collected from summer sea ice and the open water.

| | Chl *a* ($\mu g\ l^{-1}$) | Diatoms (cells $l^{-1} \times 10^6$) | Bacteria (cells $l^{-1} \times 10^9$) | BC ($\mu g\ l^{-1}$) | POC ($\mu g\ l^{-1}$) | PON ($\mu g\ l^{-1}$) | POC/ PON (m/m) | POC/ Chl *a* (w/w) |
|---|---|---|---|---|---|---|---|---|
| Surface seawater | | | | | | | | |
| SW 1 | 0.24 | 0.04 | 0.19 | 4.9 | - | - | - | - |
| SW 2 | 0.12 | 0.06 | 0.12 | 3.1 | 42 | 7 | 7.0 | 350 |
| Under-ice water layer | | | | | | | | |
| UIWL 1 | 3.08 | - | - | - | - | - | - | - |
| UIWL 2 | 0.73 | 0.17 | 0.17 | 3.3 | 198 | 29 | 8.0 | 271 |
| UIWL 3 | 0.49 | 0.11 | 0.23 | 4.3 | 113 | 18 | 7.3 | 231 |
| UIWL 4 | 18.10 | 2.14 | - | - | 1336 | 301 | 5.2 | 74 |
| UIWL 5 | 0.83 | 0.26 | 1.06 | 21.2 | 142 | 27 | 6.1 | 171 |
| UIWL 6 | 7.25 | 2.73 | 1.73 | 95.3 | 810 | 146 | 6.5 | 112 |
| Infiltration layer | | | | | | | | |
| IL 1 | 63.68 | - | 15.40 | 961 | - | - | - | - |
| IL 2 | 72.03 | 27.09 | 2.32 | 374 | - | - | - | - |
| Crack pool | | | | | | | | |
| CP 1 | 26.83 | - | 3.73 | 190 | 5991 | 496 | 14.1 | 223 |
| CP 2 | 24.08 | 15.23 | - | - | 4448 | 343 | 15.1 | 185 |
| CP 3 | 14.11 | 9.25 | 6.62 | 490 | 3603 | 305 | 13.8 | 255 |
| CP 4 | 230.02 | 130.84 | 18.20 | 2355 | 29187 | 2795 | 12.2 | 127 |
| CP 5 | 9.83 | 7.09 | - | - | 910 | 134 | 7.9 | 93 |
| CP 6 | 6.14 | - | 2.33 | 290 | 1426 | 134 | 12.4 | 223 |
| CP 7 | 23.51 | 14.02 | - | - | 741* | 130* | 6.7 | 32 |
| CP 8 | 4.58 | 0.71 | - | - | 1116 | 89 | 14.6 | 244 |
| CP 9 | 1.76 | 0.73 | - | - | - | - | - | - |
| CP 10 | 1.75 | 0.37 | - | - | 237 | 41 | 6.7 | 135 |
| CP 11 | 0.71 | 0.20 | - | - | 145 | 23 | 7.4 | 204 |

BC = bacterial carbon, POC = particulate organic carbon, PON = particulate organic nitrogen. * = possibly underestimated.

https://doi.org/10.1017/S095410209600020X Published online by Cambridge University Press

exceed 0.15 $\mu m^3$. Also, bacterial cells in crack pools frequently occurred in long filaments (data not shown). POC to PON ratios were usually close to 7, but were above 12 in six nitrate-depleted crack pool samples. Chl *a* and bacterial biomass were positively correlated, indicating a close coupling between the phyto- and bacterioplankton in all habitats (Fig. 4).

Light-saturated photosynthetic rates were similar in all habitats with a mean of 0.49 ± 0.27 $\mu g$ C $\mu g$ Chl $a^{-1}$ $h^{-1}$ ($n$=21), and primary production rates were primarily related to phytoplankton biomass, and not to photosynthetic capacity (Table IV). Bacterial production rates ranged from 0.03–151 $\mu g$ C $l^{-1}$ $h^{-1}$, and were often higher than the primary production. Despite low ambient temperatures (*c* -1°C), calculated bacterial generation times ranged from 4–21 hours (data not shown).

## Discussion

The environmental and biotic features encountered in seven different low-salinity and nitrate-exhausted crack pools (CP 1–6 and CP 8) were very similar to one another but differed strikingly from the conditions normally found in the water column following nitrate exhaustion by phytoplankton blooms (Smetacek 1985, Smetacek & Pollehne 1986). These crack pools shared the following unusual features: high pH (8.8–9.3) and POC/PON ratios (>10), high bacterial biomass composed of large, filamentous cells, and an equally dense algal assemblage dominated to over 90% by only two diatom species. We suggest that the range of conditions recorded in a fairly small area and under calm, sunny conditions indicates evolution of a nitrogen-deficient climax stage in low salinity

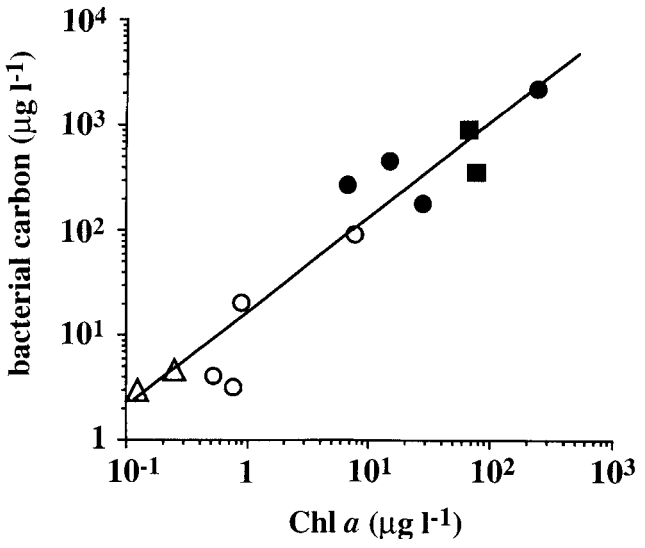


**Fig. 4.** Bacterial carbon vs. Chl *a* in samples collected from summer sea ice and open water. Δ denote surface seawater, O denote under-ice water layer, ● denote crack pool samples, and ■ denote infiltration layer samples. Line represents best fit of linear regression analysis.

**Table IV.** Photosynthetic capacity (Pmax; $\mu g$ C $\mu g$ Chl $a^{-1}$ $h^{-1}$), primary production (PP; $\mu g$ C $l^{-1}$ $h^{-1}$) and bacterial production (BP; $\mu g$ C $l^{-1}$ $h^{-1}$).

| | Pmax | PP | BP |
|---|---|---|---|
| Surface seawater | | | |
| SW 1 | 0.64 | 0.15 | 0.03 |
| SW 2 | 1.39 | 0.17 | - |
| Under-ice water layer | | | |
| UIWL 1 | 0.38 | 1.17 | - |
| UIWL 2 | 0.51 | 0.37 | - |
| UIWL 3 | 0.51 | 0.25 | - |
| UIWL 4 | 0.56 | 10.14 | - |
| UIWL 5 | 0.47 | 0.39 | - |
| UIWL 6 | 0.64 | 4.64 | - |
| Infiltration layer | | | |
| IL 1 | 0.68 | 43.30 | 31.6 |
| IL 2 | 0.18 | 12.97 | - |
| Crack pool | | | |
| CP 1 | 0.53 | 14.22 | 6.7 |
| CP 2 | 0.24 | 5.78 | - |
| CP 3 | 0.56 | 7.90 | 69.7 |
| CP 4 | 0.13 | 29.90 | 150.7 |
| CP 5 | 0.50 | 4.92 | - |
| CP 6 | 0.48 | 3.08 | 57.6 |
| CP 7 | 0.29 | 6.82 | - |
| CP 8 | 0.42 | 1.92 | - |
| CP 9 | 0.69 | 1.21 | - |
| CP 10 | 0.20 | 0.35 | - |
| CP 11 | 0.26 | 0.19 | - |

crack-pools (CP 1–6) from a nutrient rich, moderate biomass situation prevailing in high-salinity, "younger" pools (CP 7 and 9–11). This situation is not exceptional as large algal and bacterial biomasses together with high C/N ratios have been reported previously from intact sea ice (Cota & Sullivan 1990, Kottmeier & Sullivan 1990). Yet, a detailed analysis of the underlying processes has, to our knowledge, not been documented from sea ice associated habitats.

### *Origin and nutrient budgets of crack pools*

Water in a newly-formed crack pool will originate largely from the underlying seawater and will be subsequently diluted by meltwater emanating from the surrounding ice surfaces. The channel system within floes will also be enlarging, and pore water will be seeping into the crack pools from the sides but will also upwell from algal-rich platelet layers below the ice (Smetacek *et al.* 1992); these sources must have carried the organisms that were initially found within crack pools. Subsequent growth of these ice-associated species then resulted in the extreme conditions that characterize the crack pool climax stage. This climax stage developed fairly rapidly and was the result of a batch-culture-type development which we suggest is representative of summer succession of sea ice biota. The stage in the succession will be related to length of exposure of crack pool

https://doi.org/10.1017/S095410209600020X Published online by Cambridge University Press

water to full sunlight, and hence, will be reflected in its salinity for two reasons:

a) melting was due to solar radiation (air temperatures constantly sub-zero), hence the volume of meltwater is a measure of the solar radiation received and absorbed not only by ice but also algal populations,

b) buoyancy conferred by meltwater will prolong the lifetime of crack pool water by constraining vertical mixing despite movement of the ice field.

The combination of relatively high salinity, pH, and POC/PON ratio in the CP 8 sample (30‰, 8.87, and 14.6 respectively) indicates that even small amounts of meltwater input (<10%) are sufficient for the climax stage to develop. This relationship explains the surprisingly coherent correlation between salinity and POC found in crack pools (Fig. 5).

For budgetary purposes concentrations of nutrients and POC were normalized to a salinity of 34‰. This correction is necessary as ice melting is equivalent to diluting with distilled water. Winter nitrate concentrations in the Weddell Sea are *c.* 30 $\mu$M (Scharek *et al.* 1994). Conversion of this pool to phytoplankton biomass will yield *c.* 50 $\mu$g Chl *a* $l^{-1}$ and 2.4 mg algal POC $l^{-1}$ assuming C/Chl *a* and C/N ratios of 50 and 6.6 respectively. Assuming further that POC production is proportional to DIC uptake (no DIC replenishment from the atmosphere), initial DIC would decrease by *c.* 200 $\mu$M, and pH would increase from 8.2 to 8.6. Therefore, the pH values in excess of 8.8 recorded in five low salinity crack pools can only be accounted for by continued photosynthesis and accumulation of low nitrogen compounds (lipids and carbohydrates) following nitrate exhaustion ("overflow production"). In order to raise pH from 8.2 to 9.3 (the highest value), a conversion of *c.* 700 $\mu$M DIC would be required, resulting in a POC production of *c.* 8.4 mg $l^{-1}$. The time scales for complete nitrate exhaustion assuming a starting concentration of 1 $\mu$g Chl *a* $l^{-1}$ range between 7 and 13 days at maximum growth rates of 0.6 (Eppley 1972) and average rates of 0.3 $d^{-1}$ (determined in this study based on $^{14}C$ uptake) respectively.

A comparison of the amounts of DIC and nitrate removed with the levels of suspended POC and PON shows a reasonably close match in nitrate-replete waters (Fig. 6). However, nitrate-exhausted crack pools exhibited 60% loss of PON in two cases, slight gains in two others but increases by factors of 2 and 10 in crack pools with the lowest salinity. The corresponding POC losses calculated from DIC (where available) ranged from 20–80%. Whereas losses are easily explained by transfer to dissolved pools (DON and ammonia or DOC) and by sinking out of particles, the gains can only be due to input of POM from the surrounding ice. Attached organisms growing within ice channels will have concentrated nutrients from a larger volume of water than their immediate surroundings because, in the course of melting, the channels

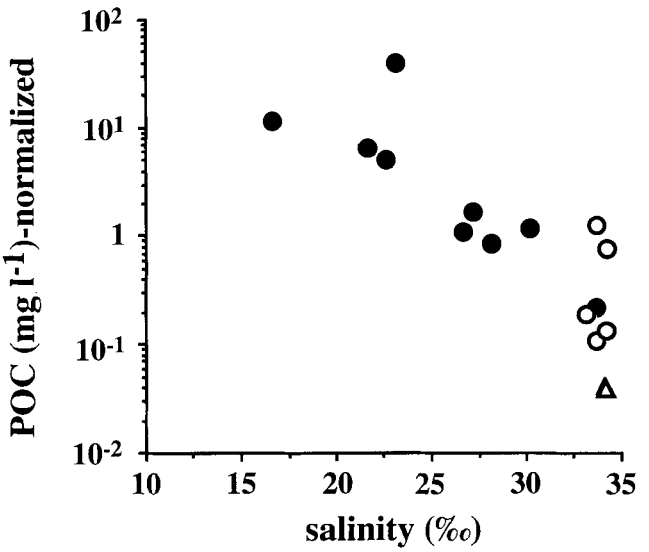


**Fig. 5.** Particulate organic carbon concentration (mg POC $l^{-1}$) vs salinity in samples collected from different habitats. POC was normalized to Sal=34 in order to correct for meltwater dilution. POC concentrations were not determined for infiltration layer samples. Symbols as in Fig. 4

will have been flushed by new water due to downward movement of brine and by vertical displacement of the ice floe. Melting and broadening of the channels will have then resulted in dislodgement and transport through lateral seepage into crack pools.

A dramatic change in POC/PON ratios occurred following nitrate exhaustion as demonstrated by crack pools 1–4, 6, and 8 (Fig. 7). Crack pool 5, despite its low salinity, still contained a trace of nitrate (0.8 $\mu$M), and a POC/PON ratio at 7.9 was only slightly elevated here. As high POC/PON ratios were accompanied by pH above 8.9 and DIC concentrations <1.7 mM (Table I, Fig. 7), it follows that the excess carbon was produced in the ambient water and was not a result of longer-term selective accumulation of refractory detritus with high C/N ratios. This conclusion is also supported by uniform ratios of POC/Chl *a* (Table III), and constant Pmax (Table IV). Furthermore, microscopical examination of nitrate-depleted crack pool samples showed that the majority of the *Thalassiosira* and *Fragilariopsis* cells contained conspicuous lipid droplets within their cytoplasm. Lipid analyses revealed that diatom fatty acids constituted between 3–14% of dry weight in nitrate-exhausted crack pools (CP 1–3, 8, and four other samples not considered in this study), compared to about 1% in nitrate-rich surface seawater (SW 1), (Fahl & Kattner 1993). The build-up of intracellular carbon relative to nitrogen will partly explain the high C/N ratios. However, a significant part of this excess organic carbon may have also been transported into extracellular pools — possibly mucus secreted by bacteria and algae (see below).

https://doi.org/10.1017/S095410209600020X Published online by Cambridge University Press

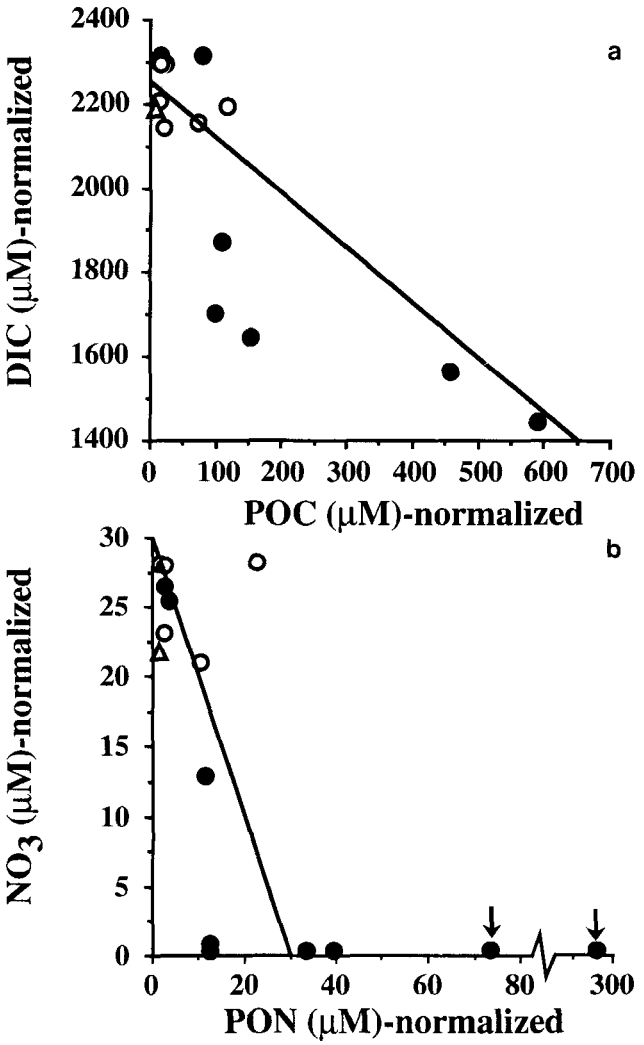


**Fig. 6. a.** Concentration of dissolved inorganic carbon ($\mu$mol DIC $l^{-1}$) vs. particulate organic carbon ($\mu$mol POC $l^{-1}$). **b.** concentration of nitrate ($\mu$mol $NO_3$ $l^{-1}$) vs. particulate organic nitrogen ($\mu$mol PON $l^{-1}$) of samples collected from different habitats. DIC concentrations for crack pool samples (●) marked with an arrow in (**b**) were not determined, and thus do not appear in (**a**). Lines represent hypothetical 1:1 conversion of DIC to POC (**a**) and $NO_3$ to PON (**b**). All concentrations were normalized to Sal=34. Symbols as in Fig. 4.

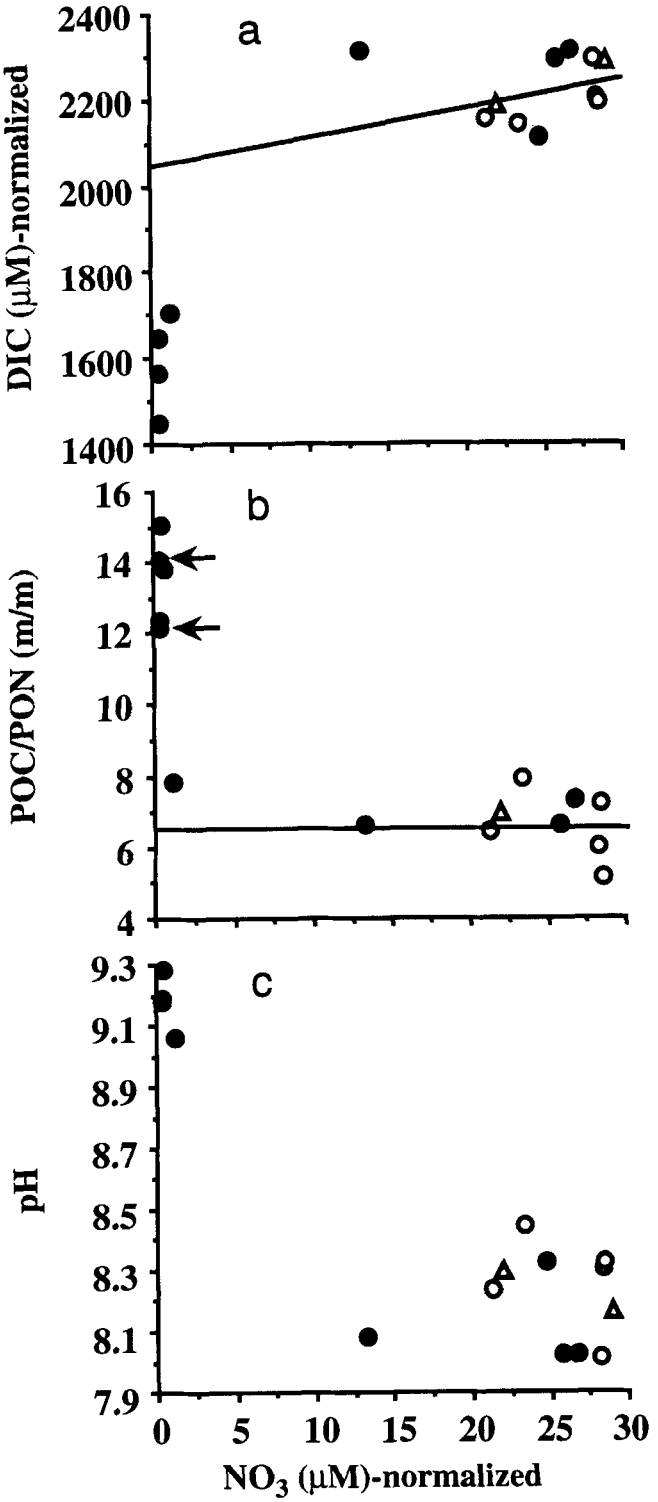


**Fig. 7. a.** Concentration of dissolved inorganic carbon ($\mu$mol DIC $l^{-1}$), **b.** POC/PON ratios (molar), **c.** pH (at 0°C), vs. nitrate ($\mu$mol $NO_3$ $l^{-1}$) concentration. DIC concentrations and pH for crack pool samples (●) marked with an arrow in (**b**) were not determined, and thus do not appear in (**a**) and (**c**). Line in (**a**) represents hypothetical molar uptake ratio of DIC:$NO_3$=6.6, line in (**b**) denotes molar POC/PON ratio of 6.6. All concentrations were normalized to Sal=34. Symbols as in Fig. 4.

*Bacterial biomass and growth rates*

Bacterial cell concentrations in matured crack pools were generally higher by one order of magnitude when compared to those of surface seawater and the under-ice water layer (Table III). Altogether, these bacterial densities range among the highest so far reported from a variety of sea ice habitats (McConville & Wetherbee 1983, Sullivan & Palmisano 1984, Kottmeier *et al.* 1987, Kottmeier & Sullivan 1990, Delille 1992). Accumulation of bacterial biomass in crack pools was caused by cell growth, which is documented by thymidine uptake. Rates of bacterial production (Table IV)

https://doi.org/10.1017/S095410209600020X Published online by Cambridge University Press

are comparable to those reported by Kottmeier & Sullivan (1990) from late summer "surface ponds", but clearly surpass values determined for bacterial assemblages of intact sea ice (Kottmeier & Sullivan 1987, 1990, Kottmeier *et al.* 1987, Rivkin *et al.* 1989, Grossmann & Dieckmann 1994).

Values for bacterial doubling times derived from standing stock and production rates in crack pools range from 4–20 h. These are remarkably short when considering the low incubation temperature of -1°C, but are similar to values at *in situ* temperature in other sea ice environments (doubling times of 12–14 h; Rivkin *et al.* 1989, Kottmeier & Sullivan 1990). In laboratory experiments, Wiebe *et al.* (1992) found that generation times of bacteria were substantially reduced at low temperature and high organic substrate concentrations. As pointed out above, the fact that the POC/DIC budgets balance reasonably well (Fig. 6) is an indication that comparatively little DOC accumulated in the water. Yet the bacterial substrate is likely to have come from this source via algal exudation as algal mortality, estimated from empty frustules (10–30% of diatoms), was low. Nitrogen-deficient cultures are known to exude more organic carbon than "healthy" algae (Hoagland *et al.* 1993), thus it is assumed that this was also occurring in the crack pools. The exudates are likely to have been in the form of mucous flakes sloughed off algal surfaces as postulated by Smetacek & Pollehne (1986) and observed and termed transparent exopolymers (TEP) by Alldredge *et al.* (1993). Conceivably, a significant portion of the detritus in crack pools will have been in the form of TEP that were retained by the GF/C filters used for POC determinations. These flakes together with smaller DOC will have been the substrate utilized by bacteria. That algal and bacterial growth were directly coupled is also indicated by the good correlation between Chl *a* and bacterial carbon concentrations (Fig. 4), recorded over a biomass range extending over two orders of magnitude. Sea ice bacteria maintained in laboratory culture are reported to secrete copious amounts of mucus (Helmke & Weyland 1995), which would represent an additional source of TEP. As in the case of nitrogen-deficient phytoplankton, these bacterial cells, possibly also protected by their slime sheathes, are likely to be of poor nutritive value for phagotrophs.

### *Algal growth physiology*

The variation in maximum Chl *a* - specific photosynthetic rates recorded in all samples from ice-associated habitats is relatively modest when compared with the very wide range in biomass and hence also abiotic conditions in the respective sites. This indicates that photosynthetic performance of the algal assemblages was not noticeably impaired by very high quantum irradiances incident on crack pools (Fig. 2), low salinity, high pH, and even nitrate exhaustion. The physiological capacity of sea ice microalgae to endure and even grow under extreme conditions is frequently cited although the conditions generally referred to are those characteristic of winter and spring sea ice (a combination of low temperature, low light, and high salinity environment; e.g. Palmisano & Sullivan 1982, Aletsee & Jahnke 1992) and hence at the other end of the spectrum to those recorded in association with summer sea ice. The data presented here confirm those of previous studies showing that sea ice microalgae continue to photosynthesize and grow under high light and low salinity conditions (Lancelot & Mathot 1989, Gleitz & Kirst 1991).

Release of ice biota to crack pools greatly favoured growth of only two diatom species, *Fragilariopsis cylindrus* and *Thalassiosira antarctica* in this study. These belong to the handful of algal species — almost exclusively diatoms and *Phaeocystis* sp. — which are responsible for the bulk of the biomass that is annually built up throughout the range of ice-associated habitats although more than 150 species can be considered as common in the ice habitat (Palmisano & Garrison 1993). Interestingly, these few species dominate ice-associated algal assemblages independent of the season, i.e. from early spring to late autumn, which contrasts strikingly with the well known pattern of species succession in the water column (Margalef 1978). This suggests that environmental factors pertaining to season (day length, irradiance, temperature, and salinity) but also changing nutrient concentrations and ratios do not impair growth performance of the dominants, and are hence not important in driving diatom succession in the ice habitat. Thus, *Thalassiosira antarctica* and *Fragilariopsis curta* dominated platelet ice habitats underlying drifting and fast ice respectively in the same area in October/November (Smetacek *et al.* 1992). The properties which enable these species to maintain high growth rates over an extraordinarily wide spectrum of environmental factors that apparently extends beyond that of co-occurring but less dominant species is not clear. Sommer (1986, 1991) observed interspecific differences among natural Antarctic phytoplankton in nutrient competition experiments. These studies confirmed that *F. cylindrus* and *T. antarctica* were successful competitors for nitrate and silicate in several experimental series. Recently, Riebesell *et al.* (1993) provided evidence for $CO_2$ limitation of common marine diatoms at $CO_2$ concentrations <10 $\mu$M (pH >8.5) which is much above ambient $CO_2$ concentrations in nitrate-exhausted crack pools. Indeed the ability to maintain photosynthesis by the fast-growing species at very high pH (9.2) and low $CO_2$ concentrations (<1.5 $\mu$M) suggests that these species may be able to directly utilize the large bicarbonate pool (Raven & Johnston 1991). Whether it is this ability which confers the competitive advantage over such a wide range of growth conditions remains to be examined.

### *Ecological role of disintegrating ice cover*

That dominant algae of sea ice and platelet ice habitats can also attain a similar status in water column blooms has been reported (Smith & Nelson 1985, Bodungen *et al.* 1986, Kang

https://doi.org/10.1017/S095410209600020X Published online by Cambridge University Press

& Fryxell 1992). As pointed out by Scharek *et al.* (1994), water column blooms in the marginal ice zone are dominated by typical ice algae where meltwater with its load of ice algae is transported away from the ice. Generally, a larger number of species and much greater variation in their dominance status is characteristic of water column blooms, although these rarely proceed to nitrate exhaustion in the Southern Ocean. One major difference between water column and ice-associated blooms is the much heavier grazing pressure exerted by phagotrophic protists and metazooplankton, particularly krill, in the former habitat (Nöthig & Bodungen 1989, Smetacek *et al.* 1990, Frost 1991), even though protozoa such as foraminifers (Dieckmann *et al.* 1991), thraustochytrids (Riemann & Schaumann 1993), heterotrophic dinoflagellates, choanoflagellates, and ciliates (Garrison & Buck 1989, 1991) have been found in large numbers in sea ice assemblages. Since, under favourable growth conditions, high algal and bacterial biomass accumulates within ice-associated habitats, the high protozoan grazing pressure on bacterial and algal populations now being shown to be the rule in pelagic environments (Garrison & Gowing 1993, Burkill *et al.* 1993) appears not to apply. The fact that grazing pressure apparently did not keep up with algal and bacterial growth rates in this study may be due to poor food quality of osmotrophs growing under nitrate-depleted conditions. Studies conducted in limnic environments have shown that growth rates of daphnids offered phosphate-depleted algae declined significantly (Sommer 1992). Malej & Harris (1993) have shown that grazing of copepods from the Adriatic Sea was inhibited by diatom slime secreted during stationary growth. Similarly, complex bacterial growth forms such as long filaments and mucous aggregates, which were frequently observed in crack pools, are less grazable by bactivores (Jürgens & Güde 1994).

The primary production in crack pools, calculated for an estimated 24 h period of light-saturated photosynthesis, falls in the range of values reported for assemblages collected from intact sea ice during spring (Garrison & Buck 1991). Average daily production per unit surface of the porous summer sea ice was calculated to be *c.* 100 mg C $m^{-2}$, a value similar to the integrated pelagic production measured in small stretches of open water pervading the closed sea ice cover (Gleitz *et al.* 1994). On the other hand, integrated production beneath the ice was estimated not to exceed 5 mg C $m^{-2}$ $d^{-1}$ due to low light levels (Gleitz *et al.* 1994). Therefore, in regions covered by summer sea ice, the bulk of primary production will come from algae growing in infiltration-, snow-ice- and freeboard layers (Ackley & Sullivan 1994), but also from brash ice and crack pools of deformed sea ice fields. Upon disintegration, this biomass will be released into the water column where it provides food for zooplankton and, upon sinking, also for the underlying benthos. The quantitative contribution to POC in the water column will be low but concentration in a narrow layer will enable efficient collection by suspension-feeding zooplankton such as krill and copepods known to feed on the undersurface of the ice (Marschall 1988, Kurbjeweit *et al.* 1993). Sediment traps suspended under the ice during this study collected substantial amounts of zooplankton — in particular krill faeces (González *et al.* 1994). Visual observations from the surface also indicated that krill was present and feeding under the ice. It follows that the disintegrating summer sea ice is an important source of food for metazooplankton.

Clearly, the common ice organisms will have developed adaptive mechanisms to withstand adverse environmental conditions in the confines of the winter ice habitat (Gleitz & Thomas 1993). However, effective and widespread colonization of the growing ice cover will be possible only if sufficient seed stocks are present in the autumnal water column. It follows that build-up of a large seed stock size prior to disappearance of the ice cover is a crucial aspect of adaptation to ice-associated habitats which can be achieved by maintenance of fast growth and/or low mortality rates under the conditions prevalent in summer sea ice. The large seeding stock which ensues will ensure effective and widespread colonisation of the autumnal ice sheet at its inception.

## Acknowledgements

We are grateful to U. Bathmann, K. Fahl, R. Gradinger, K. Lochte, S. Schröder and J. Weissenberger for their help in the field. We thank A. Bartel for doing the cell counts, G. Kattner and M. Stürcken-Rodewald for measuring nutrients, and H. Schwarz for her help with the POC analyses. Drs. D. Thomas, G. Dieckmann, S.F. Ackley, and one anonymous reviewer provided valuable comments on the manuscript. This is publication no. 990 of the Alfred-Wegener Institute for Polar and Marine Research, Bremerhaven.

## 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*, **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.

Aletsee, L. & Jahnke, J. 1992. Growth and productivity of the psychrophilic marine diatoms *Thalassiosira antarctica* Comber and *Nitzschia frigida* Grunow in batch cultures at temperatures below the freezing point of seawater. *Polar Biology*, **11**, 643–647.

Alldredge, A.L., Passow, U. & Logan, B.E. 1993. The abundance and significance of a class of large, transparent organic particles in the ocean. *Deep-Sea Research*, **40**, 1131–1140.

Bathmann, U., Schulz-Baldes, M., Fahrbach, E., Smetacek, V. & Hubberten, H.-W., *eds.* 1992. The expeditions ANTARKTIS IX/1–4 of the research vessel "Polarstern" in 1990/91. *Reports on Polar Research*, **100**, 403 pp.

v. Bodungen, B., Smetacek, V., Tilzer, M.M. & Zeitschel, B. 1986. Primary production and sedimentation during spring in the Antarctic Peninsula region. *Deep-Sea Research*, **33**, 177–194.

Børsheim, K.Y., Bratbak, G. & Heldal, M. 1990. Enumeration and biomass estimation of planktonic bacteria and viruses by transmission electron microscopy. *Applied Environmental Microbiology*, **56**, 352–356.

BURKHOLDER, P.R. & MANDELLI, E.F. 1965. Productivity of microalgae in Antarctic sea-ice. *Science*, **149**, 872–874.

BURKILL, P.H., EDWARDS, E.S., JOHN, A.W.G. & SLEIGH, M.A. 1993. Microzooplankton and their herbivorous activity in the northeastern Atlantic Ocean. *Deep-Sea Research*, **40**, 479–493.

COTA, G.F. & SULLIVAN, C.W. 1990. Photoadaptation, growth and production of bottom ice algae in the Antarctic. *Journal of Phycology*, **26**, 399–411.

DELILLE, D. 1992. Marine bacterioplankton at the Weddell Sea ice edge: distribution of psychrophilic and psychrotrophic populations. *Polar Biology*, **12**, 205–210.

DIECKMANN, G., ROHARDT, G., HELLMER, H. & KIPFSTUHL, J. 1986. The occurrence of ice platelets at 250 m depth near the Filchner Ice Shelf and its significance for sea ice biology. *Deep-Sea Research*, **33**, 141–148.

DIECKMANN, G.S., SPINDLER, M., LANGE, M.A., ACKLEY, S.F. & EICKEN, H. 1991. Antarctic sea ice: A habitat for the foraminifer *Neogloboquadrina pachyderma*. *Journal of Foraminifera Research*, **21**, 182–189.

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

EICKEN, H., GRENFELL, T.C. & STONEHOUSE, B. 1988. Sea ice conditions during an early spring voyage in the eastern Weddell Sea, Antarctica. *Polar Record*, **24**, 49–54.

EPPLEY, R.W. 1972. Temperature and phytoplankton growth in the sea. *Fishery Bulletin*, **70**, 1063–1084.

EVANS, C.A., O'REILLY, J.E. & THOMAS, J.P. 1987. A handbook for the measurement of chlorophyll *a* and primary production. *BIOMASS Scientific Series*, No. 8, 109 pp.

FAHL, K. & KATTNER, G. 1993. Lipid content and fatty acid composition of algal communities in sea-ice and water from the Weddell Sea (Antarctica). *Polar Biology*, **13**, 405–409.

FROST, B.W. 1991. The role of grazing in nutrient-rich areas of the open sea. *Limnology and Oceanography*, **36**, 1616–1630.

FUHRMAN, J.A. & AZAM, F. 1982. Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. *Marine Biology*, **66**, 109–120.

GARRISON, D.L. 1991. Antarctic sea ice biota. *American Zoologist*, **31**, 17–33.

GARRISON, D.L. & BUCK, K.R. 1989. The biota of Antarctic pack ice in the Weddell Sea and Antarctic Peninsula regions. *Polar Biology*, **10**, 211–219.

GARRISON, D.L. & BUCK, K.R. 1991. Surface-layer sea-ice assemblages in Antarctic pack ice during the austral spring: environmental conditions, primary production and community structure. *Marine Ecology Progress Series*, **75**, 161–172.

GARRISON, D.L., GOWING, M.M. (1993). Protozooplankton. *In* FRIEDMANN, I., *ed. Antarctic Microbiology.* New York: Wiley-Liss, 123–165.

GLEITZ, M. & KIRST, G.O. 1991. Photosynthesis-irradiance relationships and carbon metabolism of different ice algal assemblages collected from Weddell Sea pack ice during austral spring (EPOS 1). *Polar Biology* , **11**, 385–392.

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.

GLEITZ, M., BATHMANN, U.V. & LOCHTE, K. 1994. Build-up and decline of summer phytoplankton biomass in the eastern Weddell Sea, Antarctica. *Polar Biology*, **14**, 413–422.

GONZÁLEZ, H.E., KURBJEWEIT, F. & BATHMANN, U.V. 1994. Occurrence of cyclopoid copepods and faecal material in the Halley Bay region, Antarctica, during January-February 1991. *Polar Biology*, **14**, 331–342.

GROSSMANN, S. 1994. Bacterial activity in sea ice and open water of the Weddell Sea, Antarctica: a microautoradiographic study. *Microbial Ecology*, **28**, 1–18.

GROSSMANN, S. & DIECKMANN, G.S. 1994. Bacterial standing stock, activity, and carbon production during formation and growth of sea ice in the Weddell Sea, Antarctica. *Applied Environmental Microbiology*, **60**, 2746–2753.

GROSSMANN, S. & REICHARDT, W. 1991. Impact of *Arenicola marina* on bacteria in intertidal sediments. *Marine Ecology Progress Series*, **77**, 85–93.

HELMKE, E. & WEYLAND, H. 1995. Bacteria in sea ice and underlying water of the eastern Weddell Sea in midwinter. *Marine Ecology Progress Series*, **117**, 269–287.

HOAGLAND, K.D., ROSOWSKI, J.R., GRETZ, M.R. & ROEMER, S.C. 1993. Diatom extracellular polymeric substances: function, fine structure, chemistry, and physiology. *Journal of Phycology*, **29**, 537–566.

HORNER, R.A., ACKLEY, S.F., DIECKMANN, G.S., GULLIKSEN, B., HOSHIAI, T., LEGENDRE, L., MELNIKOV, I.A., REEBURGH, W.S., SPINDLER, M. & SULLIVAN, C.W. 1992. Ecology of sea-ice biota. 1. Habitat, terminology, and methodology. *Polar Biology*, **12**, 417–427.

JACOBS, S.S. & COMISO, J.C. 1993. A recent sea-ice retreat west of the Antarctic Peninsula. *Geophysical Research Letters*, **20**, 1171–1174.

JEFFREY, S.W. & HUMPHREY, G.F. 1975. New spectrophotometric equations for determining chlorophylls *a*, *b*, *c*1, *c*2 in higher plants, algae and natural phytoplankton. *Biochemie und Physiologie der Pflanzen*, **167**, 191–197.

JÜRGENS, K. & GÜDE, H. 1994. The potential importance of grazing-resistant bacteria in planktonic systems. *Marine Ecology Progress Series*, **112**, 169–188.

KANG, S.-H. & FRYXELL, G.A. 1992. *Fragilariopsis cylindrus* (Grunow) Krieger: the most abundant diatom in water column assemblages of Antarctic marginal ice edge-zones. *Polar Biology*, **12**, 609–627.

KNOX, G.A. 1994. *The Biology of the Southern Ocean.* Cambridge: Cambridge University Press, 444 pp.

KOTTMEIER, S.T. & SULLIVAN, C.W. 1987. Late winter primary production and bacterial production in sea ice and seawater west of the Antarctic Peninsula. *Marine Ecology Progress Series*, **36**, 287–298.

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

KOTTMEIER, S.T., GROSSI, S.M. & SULLIVAN, C.W. 1987. Sea ice microbial communities. VIII. Bacterial production in annual sea ice of McMurdo Sound, Antarctica. *Marine Ecology Progress Series*, **35**, 175–186.

KURBJEWEIT, F., GRADINGER, R. & WEISSENBERGER, J. 1993. The life cycle of *Stephos longipes* - an example for cryopelagic coupling in the Weddell Sea (Antarctica). *Marine Ecology Progress Series*, **98**, 255–262.

LANCELOT, C. & MATHOT, S. 1989. Phytoplankton: photosynthesis, growth and respiration. *In* HEMPEL, I., SCHALK, P. H., SMETACEK, V., *eds.* The expedition Antarktis VII/3 (EPOS LEG 2) of RV "Polarstern" in 1988/89. *Reports on Polar Research*, **65**, 78–86.

LEGENDRE, L., ACKLEY, S.F., DIECKMANN, G.S., GULLIKSEN, 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.

LUKIN, V. & PROVORKIN, A. 1992. Ice observations in the eastern Weddell and Lazarev Seas, January-March 1991. *In* BATHMANN, U., SCHULZ-BALDES, M., FAHRBACH, E., SMETACEK, V., HUBBERTEN, H.W., *eds.* The expedition ANTARKTIS IX/1–4 of the research vessel "Polarstern" in 1990/91. *Reports on Polar Research*, **100**, 107–124.

MALEJ, A. & HARRIS, R.P. 1993. Inhibition of copepod grazing by diatom exudates: A factor in the development of mucus aggregates? *Marine Ecology Progress Series*, **96**, 33–42.

MARGALEF, R. 1978. Life-forms of phytoplankton as survial alternatives in an unstable environment. *Oceanologica Acta*, **1**, 493–509.

MARSCHALL, H.-P. 1988. The overwintering strategy of Antarctic krill under the pack ice of the Weddell Sea. *Polar Biology*, **9**, 129–135.

MEDLIN, L. K. & PRIDDLE, J. 1990. *Polar marine diatoms.* Cambridge: British Antarctic Survey, 214 pp.

McConville, M.J. & Wetherbee, R. 1983. The bottom-ice microalgal community from annual ice in the inshore waters of East Antarctica. *Journal of Phycology*, **19**, 431–439.

Nöthig, E.-M. & v. Bodungen, B. 1989. Occurrence and vertical flux of faecal pellets of probably protozoan origin. *Marine Ecology Progress Series*, **56**, 281–289.

Palmisano, A.C. & Garrison, D.L. 1993. Microorganisms in Antarctic sea ice. *In* Friedmann, E.I., *ed. Antarctic Microbiology*. New York: Wiley-Liss, 167–218.

Palmisano, A.C. & Sullivan, C.W. 1982. Physiology of sea ice diatoms. 1. Response of three polar diatoms to a simulated summer–winter transition. *Journal of Phycology* **18**, 489–498.

Priddle, J. & Fryxell, G. 1985. *Handbook of the common plankton diatoms of the Southern Ocean: Centrales except the genus Thalassiosira.* Cambridge: British Antarctic Survey, 158 pp.

Raven, J.A. & Johnston, A.M. 1991. Mechanisms of inorganic-carbon acquisition in marine phytoplankton and their implications for the use of other resources. *Limnology and Oceanography*, **36**, 1701–1714.

Riebesell, U., Wolf-Gladrow, D.A. & Smetacek, V. 1993. Carbon dioxide limitation of marine phytoplankton growth rates. *Nature*, **361**, 249–251.

Riemann, F. & Schaumann, K. 1993. Thraustochytrid protists in Antarctic fast ice? *Antarctic Science*, **5**, 279–280.

Rivkin, R.B., Putt, M., Alexander, S.P., Meritt, D. & Gaudet, L. 1989. Biomass and production in polar planktonic and sea ice microbial communities: a comparative study. *Marine Biology*, **101**, 273–283.

Scharek, R., Smetacek, V., Fahrbach, E., Gordon, L.I., Rohardt, G. & Moore, S. 1994. The transition from winter to early spring in the eastern Weddell Sea, Antarctica: plankton biomass and composition in relation to hydrography and nutrients. *Deep-Sea Research*, **41**, 1231–1250.

Smetacek, V. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Marine Biology*, **84**, 239–251.

Smetacek, V. & Pollehne, F. 1986. Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. *Ophelia*, **26**, 401–428.

Smetacek, V., Scharek, R. & Nöthig, E.-M. 1990. Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill. *In* Kerry, K.R. & Hempel, G., *eds. Antarctic ecosystems: ecological change and conservation.* Berlin: Springer-Verlag, 103–114.

Smetacek, V., Scharek, R., Gordon, L.I., Eicken, H., Fahrbach, E., Rohardt, G. & Moore, S. 1992. Early spring phytoplankton blooms in ice platelet layers of the southern Weddell Sea, Antarctica. *Deep-Sea Research*, **39**, 153–168.

Smith Jr., W.O. & Nelson, D.M. 1985. Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. *Science*, **227**, 163–166.

Sommer, U. 1986. Nitrate- and silicate-competition among antarctic phytoplankton. *Marine Biology*, **91**, 345–351.

Sommer, U. 1991. Comparative nutrient status and competitive interactions of two Antarctic diatoms (*Corethron criophilum* and *Thalassiosira antarctica*). *Journal of Plankton Research*, **13**, 61–75.

Sommer, U. 1992. Phosphorus-limited *Daphnia*: Intraspecific faciliation instead of competition. *Limnology and Oceanography*, **37**, 966–973.

Spies, A., Brockmann, U.H. & Kattner, G. 1988. Nutrient regimes in the marginal ice zone of the Greenland Sea in summer. *Marine Ecology Progress Series*, **47**, 195–204.

Strickland, J.D.H. & Parsons, T.R. 1972. A practical handbook of seawater analysis, 2nd edn. *Bulletin of the Fishery Research Board of Canada*, **167**, 311 pp.

Sullivan, C.W. & Palmisano, A.C. 1984. Sea ice microbial communities: distribution, abundance, and diversity of ice bacteria in McMurdo Sound, Antarctica, in 1980. *Applied Environmental Microbiology*, **47**, 788–795.

Wiebe, W.J., Sheldon Jr., W.M. & Pomeroy, L.R. 1992. Bacterial growth in the cold: evidence for enhanced substrate requirement. *Applied Environmental Microbiology*, **58**, 359–364.

Zwally, H.J., Comiso, J.C., Parkinson, C.L., Campbell, W.J., Carsey, F.D. & Gloersen, P. 1983. *Antarctic Sea-ice, 1973–1976: Satellite passive-microwave observations.* Report SP-459, Washington DC. National Aeronautics and Space Administration (Scientific and Technical Information Branch).