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Biogeochemistry of Antarctic sea ice: a case study on platelet ice layers at Drescher Inlet, Weddell Sea

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ABSTRACT: Interstitial water samples collected from sea-ice platelet layers at a coastal site in the eastern Weddell Sea, Antarctica, were analyzed for total alkalinity, pH, major nutrient, oxygen, dissolved inorganic carbon (DIC) concentrations and biomass. Based on the data obtained here and in previous studies on sea-ice ecosystems, a conceptual description of biogeochemical processes during maturation of algal blooms in semi-enclosed sea-ice habitats is presented. The concept invokes an initial phase of nitrate-based 'new' production during which nutrient replenishment from the surrounding seawater surpasses algal demand, leading to rapid accumulation of algal biomass in excess of what is accounted for by the apparent DIC and nutrient depletion. As long as nitrate is present in non-limiting quantities, primary production proceeds in close agreement with Redfield ratios. During later stages of the bloom, algal nutrient demand exceeds replenishment, and nitrate is completely consumed, where the photosynthetic quotient indicates utilization of ammonium. Following nitrate exhaustion, photosynthetic carbon fixation is maintained, but is directed towards production of carbon-rich metabolites and excretion of dissolved organic matter, leading to further DIC drawdown and alteration of algal biochemical composition from the nitrate-replete state. During both phases, cell mortality and lysis in conjunction with inefficient feeding of metazooplankton (if present) lead to liberation and subsequent accumulation of dissolved matter including major nutrients. The co-occurrence of phosphate accumulation, strong oxygen supersaturation and depleted DIC concentration thus suggest that heterotrophic oxidation of organic matter may not represent the major pathway by which nutrients are regenerated in sea-ice ecosystems.

KEY WORDS: Antarctic · Platelet ice · Nutrient cycling · Carbon flux · DIC

INTRODUCTION

During balanced growth, phytoplankton absorb major nutrients and dissolved inorganic carbon (DIC) in stoichiometric quantities known as the Redfield ratios (C:N:P = 106:16:1, Redfield 1958). In biological oceanography, these ratios have been used extensively to model phytoplankton productivity as a function of a limiting nutrient, and to describe ocean biogeochemical cycles (Broecker & Peng 1982, Falkowski & Woodhead 1992). In the winter mixed layer of the Southern Ocean, nitrate, silicate and phosphate concentrations of approximately 30, 75 and 2 µmol l^{-1} respectively (Jennings et al. 1984, Scharek et al. 1994) could convert to maximum phytoplankton standing stocks of about 200 µmol particulate organic carbon (POC) l^{-1} (equals 2400 µg (POC) l^{-1}) and, assuming a POC to chlorophyll *a* (chl *a*) ratio of 50 (w/w), a concentration of ca 50 µg chl *a* l^{-1} Yet, due to a combination of light, micronutrient, downward export and grazing controls on phytoplankton growth, these values are never attained in the open ocean (Burkill et al. 1995, de Baar et al. 1995).

Antarctic sea-ice biological communities, however, represent a notable exception to conditions observed in the water column. Algal standing stocks >100 µg chl *a* l^{-1} have been reported from the bottom part of the congelation ice, from platelet layers, and other habitats closely associated with ice sheets (Palmisano & Garrison 1993). Apparently, bottom-up and top-down controls constraining phytoplankton biomass accumula-

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tion in the open ocean are at least temporarily ineffective in sea-ice habitats. From a biogeochemical perspective, this observation is remarkable insofar as ice habitats provide the means for phytoplankton to accumulate to concentrations far in excess of maximum standing stocks predicted from complete utilization of major nutrients present in the open water. The obvious explanation is replenishment of nutrients from the surrounding water column, while the algal cells are retained within the physical boundaries of the habitat due to attachment to ice crystal surfaces, thus preventing a proportional dilution of the algal crop during water exchange.

Rates of exchange with the surrounding seawater can be constrained, however, by density stratification due to meltwater input and the physical barrier imparted by the ice matrix, particularly during the advancing summer season (Dieckmann et al. 1992, Smetacek et al. 1992, Fritsen et al. 1994, Arrigo et al. 1995, Gleitz et al. 1995). Subsequently, ice algal nutrient demand may exceed rates at which nutrients are resupplied, resulting in gradients of dissolved constituents between interstitial waters of ice habitats and the surrounding seawater. When nutrient exchange has completely subsided, algal growth relies on rates of *in situ* nutrient regeneration. As heterotrophic nutrient remineralization is inevitably associated with a release of dissolved carbon dioxide, in this situation one would not expect to find DIC depletion far in excess of 200 µmol l^{-1}, even if primary production based on regenerated nutrients is sustained. Yet, the few published data on DIC concentrations in sea-ice ecosystems are often at odds with these predictions. Gleitz et al. (1996a) recorded DIC deficiencies of up to 700 µmol l^{-1} in pools of meltwater trapped between melting ice floes. Similar results were also reported from analyses of brine samples collected from intact sea ice during summer (Gleitz et al. 1995). These discrepancies have up to now not been the focus of detailed investigation.

Here we report on a biogeochemical study of interstitial water samples collected from platelet layers at Drescher Inlet, Weddell Sea. Layers of platelet ice are commonly found underlying land-fast and pack ice in coastal regions of the high Antarctic (Ackley & Sullivan 1994). Individual ice platelets measure up to several centimeters in diameter, and are up to several millimeters thick. Upon accumulation underneath an existing ice cover, ice platelets consolidate into a more or less rigid lattice that may attain a thickness of up to several meters. In addition to its significance for coastal sea-ice mass balances (Eicken & Lange 1989), platelet layers have been shown to provide a most favorable habitat for phytoplankton growth (Dieckmann et al. 1992, Smetacek et al. 1992, Arrigo et al. 1993a, Grossmann et al. 1996). As this semi-enclosed system is comparable with other highly productive sea-ice ecosystems such as meltpools (Gleitz et al. 1996a), freeboard layers (Fritsen et al. 1994) and internal bands of rotten ice (Thomas et al. 1998), it was thus considered a suitable model habitat for a detailed case study of biogeochemical cycles during sea-ice algal blooms.

MATERIALS AND METHODS

Location of study sites. The study was conducted between 23 January and 23 February 1995 (Julian days 23 to 54) at Drescher Inlet, a roughly 20 km long and 1 to 2 km wide indentation in the Riiser-Larsen Ice Shelf at 72° 52' S, 19° 25' W (Vestkapp, Eastern Weddell Sea, Antarctica; Fig. 1) half way between the Antarctic Stations Neumayer (Germany) and Halley Bay (UK). The inlet was completely covered by fast ice during the

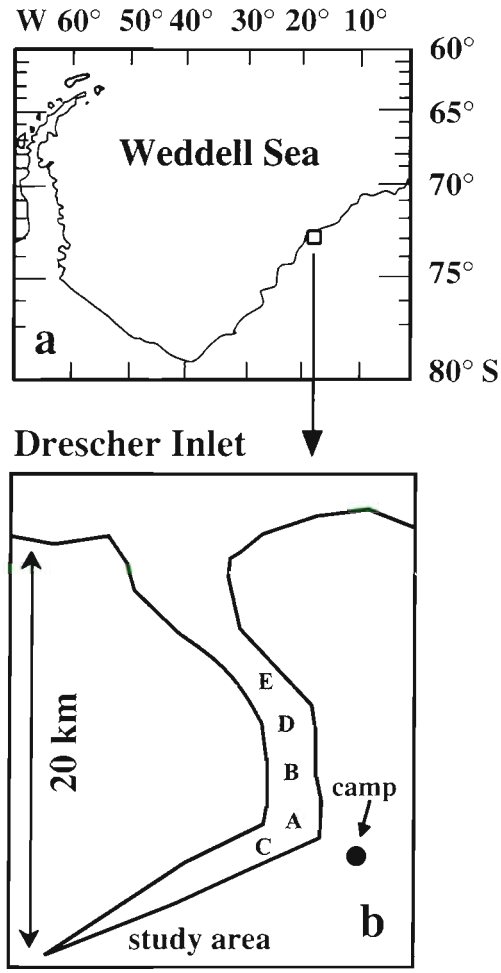

Fig. 1. (a) Location of Drescher Inlet in the eastern Weddell Sea, (b) location of the 5 sites from which samples were collected

study period. Samples were collected from platelet layers in the midportion of the inlet, approximately 10 to 15 km away from the coast. In this area, platelet ice layers with thickness ranging between 3 and 7 m were observed underneath the congelation ice. At several locations, platelet ice had also upwelled in small, 1 to 2 m wide cracks (leads) pervading the intact ice cover. These cracks were often covered by a thin (1 to 3 cm) layer of ice, which was either free of snow, or was covered by a dome of snow leaving a void several decimeters between the ice cover and the snow.

At 3 sites, samples were collected from platelet layers that had accumulated in cracks (Fig. 1; Sites A to C). Ice thickness of 260 cm and internal discolored bands of ice biota indicated the presence of second-year sea ice. Snow depths ranged from 80 to 100 cm. Additional samples were collected from platelet layers underlying the congelation ice (Fig. 1; Sites D to E). In this region, the sea ice was 200 to 220 cm thick, and was covered with 20 to 50 cm of snow, both typical for Weddell Sea fast ice. The biomass maximum was located in the bottom 20 cm, denoting the presence of first-year sea ice.

Sample collection. Surface samples from the interstitial water of platelet layers upwelled in cracks were collected after cautiously breaking the thin ice cover and submersing a glass bottle 5 cm into the platelet layer, taking care that no ice platelets became incorporated during collection. One set of bottles was filled to the rim, and stoppered without leaving an air space. These samples were stored in insulated boxes until return to the laboratory, where they were split for alkalinity and nutrient determinations approximately 1 h later. A second set of bottles was filled in a similar manner for oxygen determinations. A total of 11 surface samples were collected on 3 dates from randomly selected locations approximately 20 m apart, and 2 surface samples were collected on 2 dates from a different site at locations about 10 m apart.

In addition to collecting samples from the platelet layer surface, interstitial water samples were obtained from depths of 5 to 105 cm or 5 to 225 cm at 20 cm intervals using a modified version of the high-resolution sampler (ADONIS) described by Dieckmann et al. (1992). The apparatus consists of a plastic pipe holding 6 polyethylene tubes (i.d. 0.5 cm) which are extruded after lowering the device into position in the platelet layer. Tubes are connected to a collection unit consisting of a vacuum pump applying a low vacuum of −150 hPa and 2 sampling bottles per tube. The first sampling bottle was filled completely by pumping water through it into the second bottle. Because the first bottle was 4 times smaller than the second one, it was sufficiently rinsed, preventing the exposure of sampled water to the atmosphere at the same time. Subsamples for alkalinity and oxygen determinations were collected from the first bottle, nutrient subsamples were taken from the second bottle. On 2 occasions, seawater was collected from a depth of 20 m by lowering a 5 l Niskin bottle into the sub-ice water column. At each sampling, ice platelets were scooped with a ladle and sieved through a household sieve to separate them from the interstitial water.

Physical and chemical analyses. Throughout the study area, and over the entire study period, variations of interstitial water temperature were small; the temperature ranged between −1 and −2°C. Salinity was measured routinely at laboratory temperature (ranging between 5 and 10°C) using a microprocessor conductivity meter, calibrated prior to the study with standard seawater. On 15 February, we measured a light profile of a crack platelet layer using a Licor LI-1000 datalogger equipped with a submersible 4π SA192 sensor and a 2π SZ190 insolation sensor.

Oxygen concentrations were determined according to the Winkler method (Grasshoff 1983). A volume-calibrated glass reagent bottle (ca 50 ml) was filled either by immersing directly into the surface platelet layer or by carefully decanting water from the first ADONIS collection bottle. Winkler reagents were added, the bottle was stoppered, vigorously shaken, and transferred to the camp laboratory. For determination of *in situ* primary production we took 2 additional initial bottles and deployed 2 light bottles and a single dark bottle for 24 h at 10 cm depth. All 5 bottles were analyzed for oxygen concentrations as described above.

Comparison of dissolved oxygen concentrations of interstitial water obtained with the ADONIS and from samples rinsed directly into Winkler bottles (Fig. 2) clearly reveals that our modified sampling unit is well suited for profiling dissolved gases in aquatic systems. The slight underestimation of oxygen at extraordinary high concentrations may arise from the fact that gradients there were very steep and sampling depth differed slightly (5 to 10 cm with the ADONIS compared to 0 cm with the 'production' bottles).

After taking the oxygen sample, a second glass bottle was filled to the rim, and stoppered without leaving an air space. Upon return to the camp, the sample was allowed to warm to laboratory temperature. Subsequently, the pH of the sample was measured using a combination electrode connected to a microprocessor pH meter, calibrated daily before determinations commenced with NBS standard buffers, and allowing >1 h to adjust to low ionic strength. Prior to each measurement series, the electrode was allowed to adjust to sample salinity for at least 1 h using interstitial water of known salinity. Thereafter, the electrode was immersed in the (previously stoppered) sample, and a stable pH reading (drift <0.1 mV $30\,s^{-1}$) was recorded.

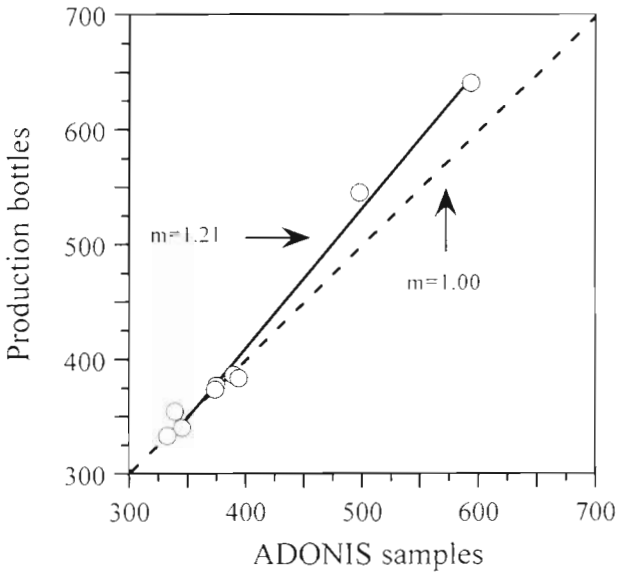

Fig. 2. Oxygen concentrations of interstitial water samples obtained with the modified ADONIS and from 'production' bottles. Solid line and slope denote results of linear regression analysis, hatched line represents 1:1 relationship. Unit is µmol O_2 kg^{-1} for both axes

Total alkalinity (TA) was determined using a potentiometric titration method (Almgren et al. 1983). Samples (50 ml) were titrated with 0.05 N hydrochloric acid, the normality of which had been determined beforehand by iodometric titration, using an automatic burette. The second equivalence point of carbonic acid was calculated by linear regression analyses of Gran plots constructed from 25 pH measurements in the range of pH 4 to 3, determined by adding 75 µl increments of acid and recording pH. The carbonate system was calculated from TA and pH, using the carbonic acid dissociation constants of Mehrbach et al. (1973). Concentrations of dissolved carbon dioxide and pH were calculated for a temperature of 0°C.

Nutrient subsamples (60 ml) were filtered (0.45 µm pore size) at low vacuum, transferred to polyethylene bottles, fixed with mercuric chloride, and stored outside the laboratory in a metal box dug 50 cm into the meteoric ice. Temperatures inside the box varied between −8 and −12°C. Upon return to the ship and subsequently, nutrient samples were stored at 4°C. Concentrations of nitrate, nitrite, phosphate and silicate were measured after 6 mo in the home laboratory using a Technicon autoanalyzer, following standard methods of Technicon modified as described in Spies et al. (1988). Storage of samples in a similar manner has been shown not to affect the inorganic nutrient concentrations (Kirkwood 1992). Each sample was analyzed twice and values averaged. Attempts to measure ammonium immediately after collection in the camp laboratory were unsuccessful due to malfunction of the spectrophotometer. Due to prolonged storage, ammonium concentrations were not determined thereafter.

Subsamples were filtered on GF/C filters for chl *a* determination and on precombusted GF/C filters for POC and PON determinations respectively. In the camp, filters were stored along with the nutrient samples. Upon return to the ship and subsequently, filters were kept frozen at −27°C. Chlorophyll filters were analyzed according to the method of Evans & O'Reilly (1983). Prior to determinations, filters for POC and PON analysis were acidified with 1 N hydrochloric acid, and dried overnight at 60°C. They were then transferred into tin vials, and analyzed using a CHN analyzer calibrated with acetanilide standards.

Microscopic investigations. Samples from the interstitial water were poured into brown flasks and fixed with hexamethylentetramine-buffered formalin to a final concentration of 0.5%. Bottles were stored in wooden boxes inside the lab-hut. Upon return to the ship and subsequently, samples were stored along with the nutrient samples. Ice platelets were allowed to melt in GF/C filtered seawater and subsequently treated as the interstitial water samples. At the institute, samples were counted using a Zeiss ICM 405 inverted microscope after settling in 3 to 10 ml chambers (Utermöhl 1958). Cell concentrations of bacteria were determined by epifluorescence microscopy of acridine orange-stained samples as described by Grossmann (1994).

Zooplankton were caught on 6 occasions at Sites A and B. Surface samples were scooped with a 5 l plastic jar and consecutively sieved through a household sieve to separate interstitial water from ice platelets. The platelets were allowed to melt in filtered seawater and both the interstitial water and the melted platelets were concentrated using a plankton net with 30 µm mesh size. Samples were preserved using the same formalin-solution as for the phytoplankton samples but to a final concentration of 5%. Species identification was performed to family level for less abundant taxa and to species level and their developmental stages for the more abundant calanoid and harpacticoid copepods.

RESULTS

During February and March 1995 biomass rich algal assemblages developed in platelet layers upwelled in fast ice cracks of the Drescher Inlet. The algal community was dominated by chain-forming diatoms of the genera *Fragilariopsis* and *Entomoneis* with dinoflagellates and the prymnesiophyte *Phaeocystis* contributing

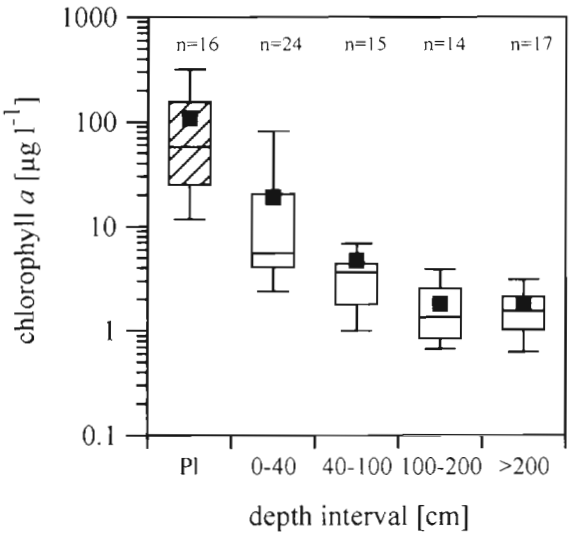

Fig. 3. Box plot of chlorophyll *a* concentrations of ice platelets and interstitial water samples collected from sea-ice platelet layers at Drescher Inlet during austral summer (Julian days 23 to 54). Squares denote mean concentrations, horizontal bars denote 10th, 25th, 50th, 75th and 90th percentiles (from bottom to top). PI: ice platelets

less than 30% of algal abundances on average. The proportion of empty cells were generally less than 20% in surface samples. In contrast the proportion of empty cells in under-ice samples varied between 40 and 75%, this proportion ranged from 20 to 50% in samples with high phosphate concentrations. Mean chlorophyll concentrations of the interstitial water peaked at 10 µg l^{-1} near the surface and decreased with depth (Fig. 3). Algal standing crop attached to ice platelets exceeded that in the interstitial water by approximately 1 order of magnitude. Highest standing stocks in interstitial waters of 26.7 mg m^{-2} were found on 7 February at Site A. This amounts to a total of 150 mg m^{-2} if corrected for the contribution of attached biomass (assuming a water/ice platelet ratio of 1:1). POC concentrations of surface interstitial water vary between 43 and 800 µmol C l^{-1}. Again, this is an underestimation of the total POC as the attached proportion was not determined. Bacterial numbers ranged from 0.7×10^7 to 1.6×10^9 cells l^{-1} and were positively correlated to algal biomass (Spearmann rank correlation $r_s = 0.77$; $n = 45$; $p < 0.0001$) with the exception of Site C, where bacterial numbers were in the same range despite consistently low chl *a* concentrations. The zooplankton consisted primarily of copepods ranging in abundance from 140 to 400 individuals l^{-1}. Relative abundances between calanoids and harpactacoids or their developmental stages revealed no obvious trend.

A light profile was measured only once on 15 February at Site B where the crack was shielded by a bridge of snow with a thickness of 10 cm, ca 70 cm above the sea-surface. Incident light levels at 5 cm depth were 8% (107 µE m^{-2} s^{-1}) of the surface insolation and decreased exponentially to 0.1% at 1 m depth corresponding to 1 µE m^{-2} s^{-1} at that date. Two time series were recorded: first between 1 February and 6 February, under 2 m of fast ice covered by 1 m of snow (Site D) where PAR never exceeded values of 0.25 µE m^{-2} s^{-1}, and second from 15 February to 19 February at Site B. Noon light levels there ranged between 30 and 34 µE m^{-2} s^{-1} at a depth of 30 cm.

Salinity varied between 25.8 and 33.5 (Table 1), indicating the influence of meltwater on concentrations of dissolved constituents in many samples. This was corrected for by normalizing all data to a salinity of 35. We do not expect air/sea exchange of gaseous constituents to have significantly influenced the composition of samples collected from cracks, because the upper platelet layer was shielded from direct contact with the atmosphere by a thin cover of solid ice that had to be broken prior to sample collection.

The salinity-normalized, average composition of the sub-ice seawater at 20 m depth (2 samples collected on Julian days 52 and 53) was 2158 µmol DIC kg^{-1}, 375 µmol O_2 kg^{-1}, 21.3 µmol NO_3 kg^{-1}, 48.1 µmol $Si(OH)_4$ kg^{-1}, and 1.54 µmol PO_4 kg^{-1}. These concentrations coincided with those prevalent in platelet layers below a depth of 1 m. In contrast, silicate and especially nitrate were exhausted in many surface samples whereas phosphate attained extraordinary high accumulations of up to 15.3 µmol kg^{-1} (Fig. 4).

Salinity-normalized dissolved inorganic carbon concentrations of interstitial water samples ranged from 1545 to 2184 µmol kg^{-1}. This is reflected by the normalized dissolved oxygen concentrations ranging between 348 and 980 µmol kg^{-1} indicating intense photosynthetic carbon fixation (Table 1). Thus, carbon uptake at Redfield ratio would only account for a DIC depletion of 145 µmol kg^{-1} (at present nitrate concentrations of 21 µmol kg^{-1}); this theoretical limit predicted from complete nutrient consumption was exceeded in most interstitial surface water samples (Fig. 5) and considerable DIC depletion up to 100 µmol kg^{-1} was also recorded down to 1 m depth. Nevertheless, DIC depletion was almost always lower than interstitial POC concentrations; this result was even more pronounced if the attached proportion of POC was also taken into account.

DISCUSSION

Although platelet layers occur at many locations around the Antarctic underneath land-fast ice or under drifting pack ice (Ackley & Sullivan 1994), their pro-

Table 1. Excerpt of data of biotic and abiotic parameters measured on platelet layers in Drescher Inlet, 1995. Data are not corrected for salinity. Note different depth scale for Site E. ns: not sampled

Depth (cm)	Site B 07 Feb	Site B 15 Feb	Site B 23 Feb	Site C 09 Feb	Depth (cm)	Site E 22 Feb
Chlorophyll *a* (µg l^{-1})						
10	88.91	28.78	10.61	2.56	210	2.22
30	31.06	29.42	4.92	4.27	230	1.07
50	6.55	25.29	3.92	3.63	250	1.71
70	4.13	6.84	2.42	2.07	270	0.63
90	1.71	4.49	3.99	1.35	290	0.91
110	1.28	3.78	2.56	2.14	310	1.37
Nitrate (µmol l^{-1})						
10	5.54	20.40	22.99	0.47	210	20.92
30	19.98	21.16	22.60	5.65	230	20.36
50	20.35	20.88	22.32	13.30	250	20.42
70	20.32	21.55	22.61	15.59	270	20.90
90	21.04	21.63	22.87	15.58	290	20.89
110	20.63	21.90	21.56	15.47	310	20.58
Silicate (µmol l^{-1})						
10	18.59	43.81	48.31	17.65	210	45.05
30	43.56	46.91	47.84	22.30	230	43.93
50	44.59	48.49	47.29	34.12	250	44.69
70	45.43	47.64	48.01	37.12	270	45.01
90	45.69	47.40	48.87	37.38	290	44.53
110	44.73	47.61	45.72	36.49	310	44.37
Phosphate (µmol l^{-1})						
10	0.89	2.13	2.28	11.60	210	1.47
30	1.54	2.21	2.24	12.12	230	1.44
50	1.52	2.17	2.19	5.44	250	1.44
70	1.73	2.28	2.24	3.66	270	1.47
90	1.72	2.20	2.30	2.68	290	1.46
110	1.71	2.24	2.13	2.06	310	1.46
Salinity (psu)						
10	33.0	33.3	33.1	25.8	210	33.4
30	33.4	33.3	33.3	27.9	230	33.4
50	33.4	33.3	33.4	31.4	250	33.5
70	33.4	33.3	33.5	32.7	270	33.5
90	33.4	33.4	33.5	32.7	290	33.5
110	33.4	33.5	33.5	32.8	310	33.5
Oxygen (µmol l^{-1})						
10	498	394	348	743	210	376
30	387	367	ns	641	230	371
50	373	368	343	496	250	374
70	364	370	353	445	270	375
90	358	365	ns	438	290	380
110	360	356	352	435	310	374
POC (µmol l^{-1})						
10	609.9	242.3	59.5	59.2	210	23.0
30	174.1	151.2	56.8	67.2	230	44.5
50	39.7	117.4	27.4	49.6	250	10.9
70	36.1	39.7	22.4	55.3	270	13.1
90	13.2	32.3	39.5	57.2	290	10.7
110	7.2	28.1	22.6	43.2	310	14.0
PON (µmol l^{-1})						
10	89.7	35.3	7.5	7.2	210	2.5
30	26.4	22.2	9.0	9.3	230	3.5
50	5.8	17.5	3.7	7.9	250	1.2
70	6.6	6.4	3.3	9.7	270	1.5
90	4.0	5.0	5.7	9.8	290	1.2
110	1.9	4.4	2.8	7.2	310	1.7

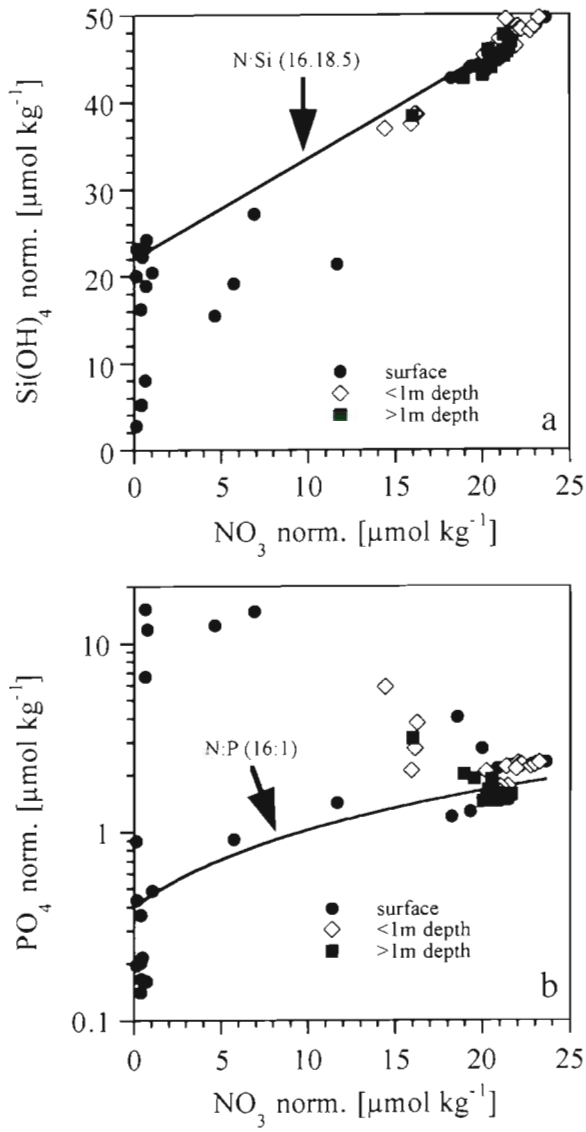

Fig. 4. Salinity-normalized (a) silicate ($Si[OH]_4$), and (b) phosphate (PO_4) vs nitrate (NO_3) concentrations of interstitial water samples collected from sea-ice platelet layers at Drescher Inlet during austral summer (Julian Days 23 to 54). Solid line in a denotes N:Si ratio for sea-ice diatoms (Arrigo et al. 1995), solid line in b denotes N:P ratio of 16:1. Note logarithmic scale in b

portion of the total sea-ice extent is relatively low. Furthermore the majority of samples collected for this study originated from platelet layers that had upwelled in cracks in the fast ice of the Drescher Inlet. Yet we consider the conditions we found to occur in a variety of semi-enclosed sea-ice habitats commonly found in Antarctica.

Platelet layers occurring in cracks are isolated laterally by the sea ice and from below by the ice platelets themselves. Therefore, seawater exchange is consider-

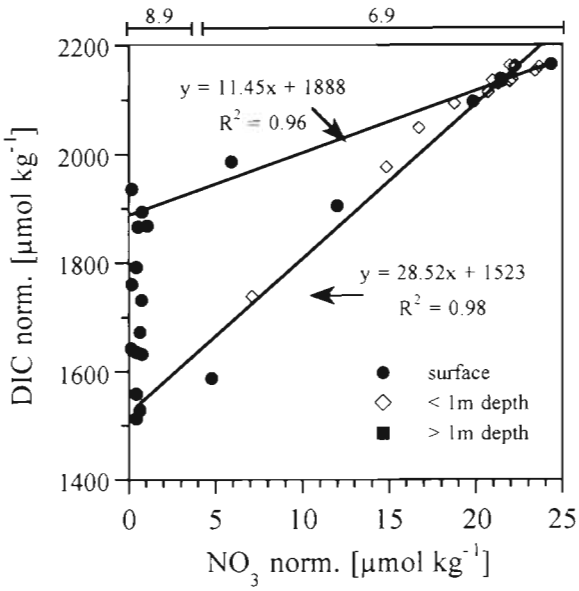

Fig. 5. Salinity-normalized dissolved inorganic carbon (DIC), vs nitrate (NO_3) concentrations of interstitial water samples collected from sea-ice platelet layers at Drescher Inlet during austral summer (Julian days 23 to 54). Solid lines and equations denote results of linear regression analyses of the 2 extreme trends in DIC to nitrate uptake ratios. Numbers above the graph denote mean POC:PON ratios of samples within the range of the bars; SD is 1.3 for C/N = 6.9 and 2.2 for C/N = 8.9

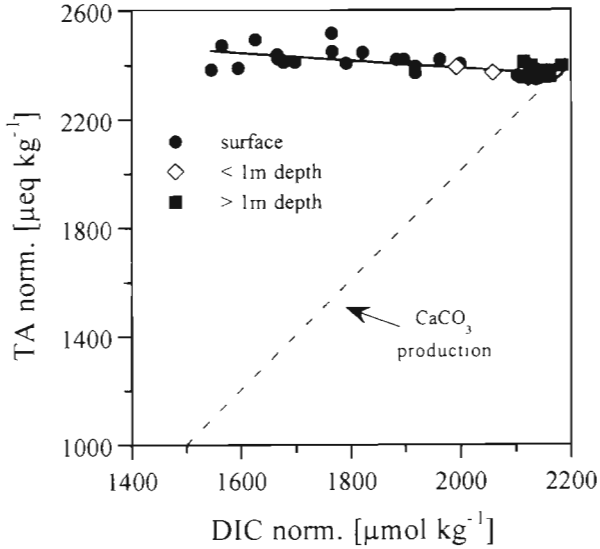

Fig. 6. Salinity-normalized total alkalinity (TA) vs dissolved inorganic carbon (DIC) concentrations of interstitial water samples collected from sea-ice platelet layers at Drescher Inlet during austral summer (Julian days 23 to 54). Solid line and equation denote results of linear regression analysis, hatched line denotes the TA vs DIC relationship expected from calcium carbonate production

ably restricted, as it is in melt pools (Gleitz et al. 1996a), free board layers within ice floes (Fritsen et al 1994), internal layers of rotten ice (Thomas et al. 1998), pack ice platelet layers (Smetacek et al. 1992), and the bottom zone in sea ice immediately above the ice/water interface (Smith et al. 1989). We discuss here nutrient and DIC dynamics in crack platelet layers and develop a conceptual model representative for semi-enclosed sea-ice ecosystems where nutrients and not light limit algal growth.

Biological and geochemical boundary conditions

Biomass data imply that considerable algal growth within platelet layers at Drescher Inlet occurred primarily in cracks in the fast ice where platelets rose to the surface. This is supported by *in situ* light measurements that revealed light levels beneath snow covered fast ice to be below the photosynthetic compensation point for sea-ice algae (Bunt 1964, Cota 1985). As in platelet layers elsewhere (Dieckmann et al. 1992), algal biomass is not only freely suspended within the interstitial water but a large proportion is also attached to the ice platelets. Therefore, the majority of algae are confined within the habitat. In accord with other studies on taxonomic composition of platelet layers in the southern Weddell Sea (Smetacek et al. 1992, Grossmann et al. 1996), the algal biomass at Drescher Inlet consists predominantly of diatoms.

Salinity-normalized concentrations of dissolved inorganic carbon and dissolved oxygen of surface interstitial water reflect various stages of productivity within crack platelet layers. Concentrations of these gases may be influenced by advection of sub-ice water into platelet layers in addition to local production and respiration. Atmospheric exchange was probably negligible because all cracks were shielded from direct contact with the atmosphere by a thin layer of solid ice that had to be broken prior to sample collection. Furthermore, precipitation of calcium carbonate could be excluded, as it is associated with a reduction of total alkalinity (TA); for each mol of calcium carbonate formed, 1 mol of DIC and 2 equivalents of alkalinity are removed from the water. In the samples analyzed here, TA actually increased slightly with decreasing DIC concentrations (Fig. 6; $p = 0.018$), as would be expected when nitrate is taken up by primary production (Brewer & Goldman 1976). However, the photosynthetic quotient (PQ) revealed ammonium to be an additional nitrogen source. Laws (1991) showed that PQ normally ranges between 1.1 and 1.4 depending on the redox state of the nitrogen source where lower values indicate uptake of ammonium. Our data reveal a PQ of 0.9 (Fig. 7), but when corrected by the result of the

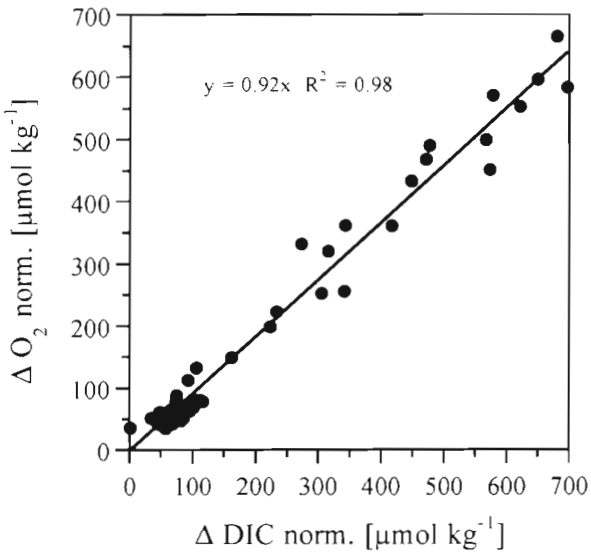

Fig. 7 Salinity-normalized molecular oxygen (O_2) vs dissolved inorganic carbon (DIC) concentrations of interstitial water samples collected from sea-ice platelet layers at Drescher Inlet during austral summer (Julian days 23 to 54). Solid line and equation represent results of linear regression analysis

regression in Fig. 2, PQ increases to 1.1, substantiating the uptake of ammonium.

Nutrient concentrations of the water column are lower than typical winter mixed layer values in the southeastern Weddell Sea (Scharek et al. 1994), indicating that the composition of the sub-ice seawater was affected by primary production that had presumably taken place in surface waters of the ice-free coastal current prior to advection beneath the sea ice of Drescher Inlet. Furthermore, water column nutrient concentrations equal those of platelet layers underneath fast ice, showing that nutrient uptake there is lower than the rate of replenishment. This is in accord with investigations of platelet layers under fast ice in McMurdo Sound where nutrients are replete even at algal standing stocks of 1 g chl *a* l^{-1} (Arrigo et al. 1995). The same is true for nutrient concentrations of interstitial crack water were algal biomass is low. However, during maturation of the bloom the biogeochemical situation in crack platelet layers differs significantly from those platelet layers in which mixing takes place as is discussed below.

Biogeochemical conditions in crack platelet layers

As the exchange of seawater is substantially restricted, nutrient uptake by algae in crack platelet layers surpasses rates of replenishment. In many surface samples nitrate is completely exhausted or at least below the half-saturation constant for Antarctic fast ice algae (Priscu & Sullivan 1998). Smetacek et al. (1992) found the same situation in platelet layers under drifting pack ice that is not affected by tidal currents. Assuming a nutrient replete biochemical composition of C:N:Si:P = 107:16:18.5:1 for ice diatoms (Arrigo et al. 1995), and comparing this with ratios of winter mixed layer nutrients (C:N:Si:P = 1100:15:38.5:1), we expect nitrate depletion to occur first, taking into account that experiments with natural Antarctic algal assemblages (Nelson & Tréguer 1992) revealed much higher silicate uptake affinities than found in laboratory experiments (Jacques 1983, Arrigo et al. 1993b). Furthermore, nitrate and silicate are removed from the water at a ratio of 16:18.5 (Arrigo et al. 1995) as long as nitrate is sufficient and even then silicate concentrations still decrease (Fig. 3a) which indicates further algal growth. But as nitrate is essential for cell division, nitrogen has to be resupplied in some form to support continuing silicate removal. At the same time phosphate often surpasses winter seawater concentrations by an order of magnitude or at least exceeds that predicted from nitrate consumption at a Redfield ratio of 16:1 (phosphate should decrease from 1.5 µmol kg^{-1} to 0.2 µmol kg^{-1} if nitrate decreases from 22 µmol kg^{-1} to 1 µmol kg^{-1}). Salinity-corrected phosphate concentrations surpassing seawater values were also measured in samples collected from platelet layers beneath fast ice (Dieckmann et al. 1992, Arrigo et al. 1995), as well as pack ice (Garrison et al. 1990, Dieckmann et al. 1991), pointing to efficient *in situ* regeneration and accumulation of regenerated nutrients. A conceptual model is shown below, explaining these unusual nutrient concentrations.

While phosphate is at extraordinarily high concentrations the contrary is the case for dissolved inorganic carbon. If carbon and nitrogen were taken up at Redfield ratios (Redfield 1958), nitrate concentrations of the water column would allow DIC uptake of 146 µmol kg^{-1} resulting in concentrations of 2012 µmol DIC kg^{-1} which does not explain the DIC concentrations of down to 1500 µmol kg^{-1} that are observed here. Banse (1994) re-evaluated 2 experiments performed by McAllister et al. (1961) and Antia et al. (1963) regarding the uptake of DIC and nitrate and found that carbon uptake was uncoupled from nitrate uptake as DIC was removed at a constant rate even when nitrate consumption had ceased. However, DIC depletion by up to several hundred µmol kg^{-1} beyond the theoretical limit is not restricted to crack platelet layers. For example, Gleitz et al. (1995) analyzed the chemical composition of brine collected from pack ice in the Southern Weddell Sea during the summer, and later analyzed water collected from pools of meltwater trapped between ice floes in the same investigation area (Gleitz et al. 1996a). In both

studies, the authors found the same elevated phosphate concentrations as well as extraordinarily high DIC depletion. Therefore, data presented here reflect stages in the developmental history of ice algal blooms representative for other sea-ice habitats.

Based on ours and other data we provide a conceptual model of biogeochemical processes in semi-enclosed sea-ice ecosystems. Major parameters in this concept are the physical boundary conditions, which determine the rate of exchange between the ice ecosystem and the surrounding seawater, and the physiological capacity of the ice biota to remain metabolically active despite shifts in environmental conditions. We propose a temporal succession characterized by a phase dominated by algal utilization of nutrients advected into the system (phase of nitrate-based, 'new' production), followed by a phase during which primary production relies on liberated internal nutrient pools and algal metabolism is directed towards production and accumulation of carbon-rich metabolites. This model is elaborated in the following sections.

Table 2. Concentrations of particulate organic carbon (POC) and dissolved inorganic carbon (DIC) at Drescher Inlet (Site B). POC attached to ice platelets not included. ΔDIC was calculated by subtracting each concentration from water column value

Julian day	Depth (cm)	POC (μmol l^{-1})	DIC (μmol l^{-1})	ΔDIC (μmol l^{-1})
30	5	747	1795	342
37	5	676	1830	307
38	5	534	1926	211
38	25	165	2096	41
38	45	67	2099	38
38	65	51	2089	48
38	85	45	2098	39
38	105	22	2135	2
46	5	242	2088	49
46	25	151	2113	24
46	45	117	2116	21
46	105	28	2110	27
54	5	60	2105	32
54	45	27	2112	25
54	65	22	2127	10
52	2000	17	2137	water column

Phase I (nitrate-based production)

During the early stages of sea-ice algal blooms, sustained replenishment of nutrients from the surrounding water column through convection or turbulent diffusion will lead to rapid accumulation of organically bound carbon, nitrogen, and phosphorus as well as biogenic silica in excess of what is accounted for by instantaneous DIC and nutrient deficiencies. In our study, this is documented by concentrations of POC exceeding the DIC depletion in many samples collected at Site B (Table 2). Our data also show that during maturation of the bloom, the nutrient demand of the accumulating algal biomass exceeds replenishment, leading to variations of DIC, O_2 and the 'new' nutrients advected into the system. Apparently, nitrate-based production proceeds in general accord with Redfield stoichiometries, which is indicated by the close correlation between silicate versus nitrate depletion (Fig. 4a) and POC/PON ratio (Fig 5), as long as 'new' nutrients (represented by nitrate) are present in non-limiting quantities. The phosphate versus nitrate relationship observed here (Fig. 4b) also suggests that nutrient regeneration during this phase can already be substantial, leading to accumulation of regenerated nutrients. In accord with our data, pronounced accumulation of regenerated nutrients was observed in platelet layers underlying fast ice at McMurdo Sound, despite frequent exchange with the sub-ice seawater (Arrigo et al. 1995). However, DIC versus nitrate relationship already points to non-Redfield uptake metabolism even at nutrient replete state (Fig. 5).

If exchange with the surrounding seawater is sufficient to always maintain nutrients at non-limiting concentrations, the phase of 'new' production can be sustained until self-shading due to the dense concentration of algal pigments will terminate the bloom. This situation has been documented for platelet layers underlying fast ice at McMurdo Sound (Arrigo et al. 1993b, 1995). At Drescher Inlet, the special crack situation and a thicker platelet layer was apparently responsible for lower rates of nutrient fluxes from the sub-ice seawater, and consequently, lower rates of algal biomass accumulation. Accordingly, 'new' nutrients can be fully consumed before light levels become limiting.

Phase II (production directed towards carbon-rich metabolites)

The pronounced DIC overconsumption relative to nitrate (Fig. 5) indicates that ice algal carbon fixation continues even after nitrate is exhausted. Previous studies have shown that one mechanism by which this can be achieved is alteration of cellular biochemistry during phases of nitrate deprivation. In a laboratory study using a clone of *Thalassiosira antarctica* isolated from the Southern Ocean, Peters & Thomas (1996a) observed resting cell formation, decline (but not cessation) of photosynthetic activity, and production of nitrogen-poor metabolites during a 21 d nitrate exhaustion experiment, resulting in C/N ratios of the algal organic matter as high as 34. Similar observations were also

reported from natural ice algal assemblages collected in the field. Gleitz et al. (1996a) measured C/N ratios of up to 15 in the (diatom-dominated) samples collected from the pools of meltwater referred to above, which was associated with massive lipid accumulation within algal cells (Fahl & Kattner 1993). Similarly, C/N ratios of up to 25 were recorded by Priscu & Sullivan (1998) in samples collected from fast ice at McMurdo Sound, Ross Sea. An 'overflow production' of carbon-rich reserve material of the same magnitude as observed by Peters & Thomas (1996a) would in fact be sufficient to explain the surplus DIC depletion observed in the present study. C/N ratios of particulate matter varied between 4.5 and 12.8, and often exceeded the 'balanced' ratio of 6.6 even at high nitrate concentrations (Fig. 5). A maximum C/N ratio of 13 as measured here would only account for a DIC overconsumption of roughly 200 µmol kg^{-1}, and would thus explain only part of the observed depletion of up to 450 µmol DIC kg^{-1} recorded at Site A (Fig. 5). Although it is known that phytoplankton release organic compounds extracellularly (Larsson & Hagström 1982, Lignell 1990), there are not enough data sets of *in situ* DOM concentrations to sufficiently explain the fate of the excessive carbon fixation. Arrigo et al. (1995) detected simple sugars and amino acids in platelet layers in much higher concentrations than in the underlying water column. Within internal sea-ice slush layers, Thomas et al. (1998) measured DOC concentrations up to 600 µmol l^{-1} strongly correlated with chl *a*. Furthermore, in Arctic sea ice Thomas et al. (1995) found DOC to be uncoupled from DON concentrations but there DOC was not correlated with chl *a*. From this we surmise a shift of fixed carbon from cell growth to dissolved organic matter (DOM) with a high C/N ratio at nutrient deplete state.

This is notable also because current estimates of total ice-related carbon production (Legendre et al. 1992, Arrigo et al. 1997) do not take dissolved organic matter into account. Thus, the study of Thomas et al. (1998) and the data presented here strongly suggest that consideration of DOM production by sea-ice microalgae is likely to result in a significantly higher total production estimate.

In the remainder of the discussion, we will focus on possible pathways by which nutrients may have been regenerated.

Pathways of nutrient recycling within sea-ice ecosystems

Previous accounts of nutrient dynamics in sea-ice habitats have frequently invoked heterotrophic remineralization as a foremost explanation for elevated phosphate or ammonium concentrations (Garrison et al. 1990, Dieckmann et al. 1991, 1992, Arrigo et al. 1995). The main heterotrophic consumers in sea-ice ecosystems are bacteria and phagotrophic flagellates (Garrison 1991). A specialized crustacean fauna, in particular small copepods, has also been observed within the solid sea ice and at the ice/seawater interface, where they feed on ice algae (Dahms et al. 1990, Conover & Huntley 1991, Kurbjeweit et al. 1993, Schnack-Schiel et al. 1995, Tanimura et al. 1996). However, previous studies have failed to detect metazoan grazers in platelet layers in any significant numbers (Dieckmann et al. 1992, Smetacek et al. 1992, Grossmann et al. 1996). In the light of these reports, a most remarkable finding of this study is the presence of large stocks of metazooplankton in platelet layers at Drescher Inlet. In contrast, numbers of heterotrophic protozoans were negligible so bacteria and copepods were the main consumers of algal primary production here.

It is well established that feeding copepods release inorganic phosphorus and ammonium, as well as dissolved organic matter into the surrounding water (Butler et al. 1969, Ikeda & Mitchell 1982, Le Borgne 1986). It must be emphasized, however, that over longer (seasonal) time scales, heterotrophic production of ammonium and phosphate, would consume oxygen (while releasing carbon dioxide) in about the same proportions in which it was removed from the water during primary production, as, with the exception of silicon, the biochemical composition of the heterotrophs does not differ fundamentally from that of the phytoplankton (Conover & Huntley 1991, Fagerbakke et al. 1996). In our study, however, phosphate accumulation was associated with substantial DIC depletion (Fig. 3b) and strong oxygen oversaturation. Based on this data, we suspect that heterotrophic oxidation of algal organic matter and excretion of metabolic endproducts may not represent a major pathway by which nutrients are regenerated in similar sea-ice ecosystems. In contrast to previous speculation, we suggest that liberation of dissolved matter including nutrients from the large biomass pool that had accumulated during a phase when nutrient replenishment exceeded algal uptake must have been a major process by which nutrients were released into interstitial waters without proportional oxygen consumption or carbon dioxide release. Subsequently, we will refer to this way of nutrient release as 'liberation', opposed to 'regeneration', which implies assimilation and excretion of metabolic end products. Such nutrient liberation may partly be related to algal mortality and cell lysis, and may also be amplified by inefficient ('sloppy') feeding when metazoan grazers are present.

In the presence of large prey sizes (e.g. large cells or algal chains) and high food concentrations, copepods

have been shown to feed inefficiently, resulting in algal cell fragmentation and ingestion of only a fraction of the cellular debris produced (O'Connors et al. 1976, Roy et al. 1989). In samples considered here, the dominant diatoms growing attached to ice platelets as well as suspended in the interstitial waters were chain-forming species belonging to the genera *Fragilariopsis* and *Entemoneis*, which are likely to be disrupted during copepod feeding. Mechanical disruption of food particles will lead to liberation of particulate and dissolved organic matter as well as fragmentation of silica frustules. The higher proportion of empty cells in samples where phosphate concentrations were also elevated gives an indication that this process occurred here. In diatom-dominated samples collected from various sea-ice habitats at McMurdo Sound, Priscu & Sullivan (1998) measured millimolar intracellular concentrations of nitrate, ammonium and soluble reactive phosphorus, indicating that ice algae contain substantial internal inorganic nutrient pools, possibly related to high-affinity uptake systems but less efficient assimilation into metabolites. These nutrients would be liberated and made available to the phytoplankton upon cell disruption and lysis. Clearly, liberation of phosphorus (and presumably ammonium) must have greatly exceeded reutilization by algae (and bacteria), giving rise to the exceptional enrichment of phosphate measured in several samples at Site A (Fig. 4b). Thomas et al. (1998) observed highly concentrated sea-ice communities in internal voids penetrating perennial sea ice in the Bellingshausen Sea during summer. Supporting our line of arguments, salinity-normalized ammonium and phosphate concentrations exceeding seawater values along with substantial DOM accumulation were interpreted as indication for efficient *in situ* nutrient regeneration mediated by copepods, which were found in similar numbers as in our study. Unfortunately, DIC and oxygen concentrations were not reported in this study. However, it has to be mentioned that liberation of internal pools can explain the elevated phosphate concentrations only to a certain point. Phosphate concentrations of more than 10 µmol kg^{-1} as found in this study are yet not understood.

In addition, cell mortality and subsequent lysis of polar diatoms can also be induced by a combination of nitrate exhaustion, high pH, strong oxygen oversaturation, and low concentrations of dissolved carbon dioxide (Gleitz et al. 1996b, Peters & Thomas 1996a). Such conditions may regularly be attained during advanced stages of ice algal blooms when exchange with the surrounding seawater is greatly restricted (Gleitz et al. 1995, 1996a, this study).

It has been shown that small-sized siliceous debris produced by grazing zooplankton experiences significantly higher dissolution rates than intact diatom frustules or biogenic silica enclosed within fecal pellets (Tréguer et al. 1989, Nelson et al. 1991). Additionally, alkalinisation of the medium due to intense primary productivity up to pH values >9 (as present here) will have also enhanced dissolution rates of biogenic silica (Kamatani et al. 1988). However, compared with liberation of phosphate due to disintegration, dissolution of biogenic silica is a slow process and therefore does not lead to elevated silicate concentrations (Fig. 4a). Moreover, silicate is removed continuously when liberated nitrate and phosphate are taken up for cell growth. The main features of the proposed inorganic carbon, oxygen and nutrient relationships proposed here are summarized in Fig. 8.

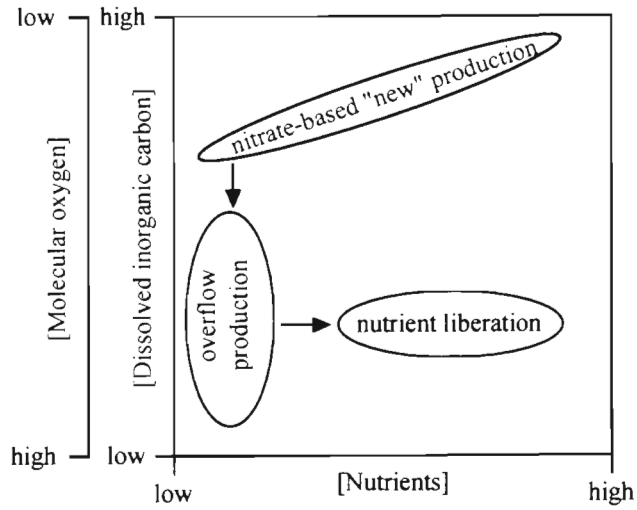

Fig. 8. Hypothetical relationship between molecular oxygen, dissolved inorganic carbon, and nutrient concentrations (arbitrary units) in sea-ice ecosystems during different stages of ice algal blooms (for detailed description see text)

In conclusion, it is clear that geochemical dynamics in semi-enclosed sea-ice ecosystems are complex, and many of the processes discussed above await further verification. Nevertheless, the concept proposed here highlights the potential importance of several features not adequately accounted for in previous studies. In addition to the alternative pathways of nutrient recycling laid out above, our data and results presented elsewhere indicate high rates of DOM production during advanced stages of ice algal blooms where replenishment of nutrients is restricted. The significance of DOM for ice-based productivity and carbon turnover, however, represents a major unknown in current concepts of sea-ice ecosystem functioning. Altogether, the scenario developed here should help to direct future research to key processes that need to be clarified. In this respect, complete data sets including time-series measurements of all particulate and dissolved organic and inorganic constituents of sea-ice biogeochemical cycles are required.

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