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ORIGINAL PAPER

Biogeochemistry and microbial community composition in sea ice and underlying seawater off East Antarctica during early spring

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Abstract Pack ice, brines and seawaters were sampled in October 2003 in the East Antarctic sector to investigate the structure of the microbial communities (algae, bacteria and protozoa) in relation to the associated physico-chemical conditions (ice structure, temperature, salinity, inorganic nutrients, chlorophyll *a* and organic matter). Ice cover ranged between 0.3 and 0.8 m, composed of granular and columnar ice. The brine volume fractions sharply increased above −4°C in the bottom ice, coinciding with an important increase of algal biomass (up to 3.9 mg C l^{-1}), suggesting a control of the algae growth by the space availability at that period of time. Large accumulation of NH_4^+ and PO_4^{3-} was observed in the bottom ice. The high pool of organic matter, especially of transparent exopolymeric particles, likely led to nutrients retention and limitation of the protozoa grazing pressure, inducing therefore an algal accumulation. In contrast, the heterotrophs dominated in the underlying seawaters.

Keywords Sea ice · Brine volume fraction · Nutrients · Organic carbon · Sympagic organisms

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Introduction

The seasonal occurrence of sea ice is an important feature in the Southern Ocean, with sea ice extending from 4×10^6 km^2 in summer to 20×10^6 km^2 in winter (Zwally et al. 1983; Comiso 2003). Sea ice plays a key role in the Earth Climate system, by governing the deep water formation, in addition to heat and gas exchanges between the lower atmosphere and sea surface (Dieckmann and Hellmer 2003). From a biological point of view, sea ice is a rich environment for microbial communities (algae, bacteria, protozoa) and for a wide variety of life forms of vital importance for the whole Antarctic ecosystem (Lizotte 2003). The "frozen ocean" provides extreme and highly variable habitats both spatially and temporally. Microorganisms are indeed subject to contrasted chemical and physical constraints (e.g. temperature, salinity, space, light, pH, nutrients), which vary in space (horizontally and vertically) and time (ice formation and melting, Eicken 1992; Thomas and Dieckmann 2002). On a micro-scale, the biomass is essentially confined to the brine pockets and channels (Eicken 2003), representing less than 10% of the sea ice volume in the winter–spring period. Microorganisms within the sea ice are physically constrained in such a way that many of the biological and chemical interactions are likely to be comparable to those reported for aquatic biofilm studies (Mock and Thomas 2005).

The distribution, concentration and taxonomic composition of sympagic communities are related, on one hand, to the abundance and species composition of the planktonic microorganisms present in the water column at the time and location of sea ice formation and, on the other hand, to sea ice properties such as age and texture (Spindler et al. 1990). The structuring of the sea ice communities starts initially by the incorporation of pelagic organisms upon sea ice formation. Most of the cells are passively incorporated in the ice, being harvested during frazil ice formation and/or by the percolation pumping mechanism (Shen and Ackermann 1990). Cells with the capability to adhere to the ice matrix might also be introduced into the bottom skeletal layer of columnar/congelation ice later in the season, as water underneath the ice cover is continually exchanged due to tidal currents and the thermohaline circulation (Lizotte 2003).

As the season progresses, the evolution of the sympagic communities depends on two major physical factors: light and temperature. First, light conditions in the ice environment depend on seasonal changes in solar radiation, ice thickness and snow cover, which can lead to reflection and attenuation of incident irradiance (Arrigo 2003). Then temperature controls volume as well as salinity of the brines. The microorganisms living within the ice therefore not only have to cope with low temperatures but also to withstand high osmotic pressures and low space availability. Moreover, due to temperature variations, the size and the degree of connection between brine pockets and channels change with time (Perovich and Gow 1996). The sea ice porosity is consequently affected and the exchanges between the atmosphere, the sea ice and the underlying water are altered. For instance, sea ice can be considered as permeable and brines can move through the solid when the brine volume fraction represents 5% of the total ice volume for a temperature of −5°C and a bulk ice salinity of 5 (Golden et al. 1998).

The reduction of permeability also has an important impact on the structure of the microbial community (Granskog et al. 2003). Sea ice thermodynamics may constrain the migration of organisms and alter trophic relationships e.g. by preventing predation by large organisms. The permeability stage of ice cover may also control the growth of autotrophs by limiting the supply of nutrients from the underlying water, as well as restraining transports of contaminants and heat.

Finally, biological processes taking place in sea ice may potentially regulate the pelagic ecosystem. During winter, the organic matter accumulated in the sea ice may represent an important food source for large consumers such as krill (Garrison 1991). When the ice melts, the material incorporated within the ice matrix can be ultimately released into the water column. The organisms released from decaying sea ice may settle rapidly as aggregates (Riebesell et al. 1991) and feed the benthic trophic web, being quickly grazed by zooplankton and incorporated into fast settling pellets (Scharek et al. 1994), or act as an inoculum for the planktonic blooms (Garrison et al. 1987). Moreover, nutrients such as iron (Fe) and dissolved organic matter (DOM) sequestrated in the sea ice in winter time can be released in the under ice water and in turn stimulate the planktonic microorganisms growth in the high nutrient low chlorophyll (HNLC) Southern Ocean (Lannuzel et al. 2007; Dumont et al. 2009). These processes may influence the carbon biological pump, e.g. by increasing the carbon export from surface to the deep waters.

The objectives of the present study were to investigate the relationships between physical, chemical and biological properties in the sea ice environment. We present results on the microbial community (abundance and biomass of algae, bacteria and protozoa) in the sea ice and in the underlying seawater (0, −1 and −30 m depths) in relation to physical (ice structure, salinity, temperature and brine volume fraction) and chemical (inorganic nutrients, dissolved and particulate organic carbon and transparent exopolymeric particles) parameters at the end of winter–early spring season in the pack ice zone of the western Pacific Ocean sector.

Materials and methods

Sampling and study area

Samples were collected during the research cruise AA-03-V1 "Arise in the East" aboard the Australian RV Aurora Australis, between 1 and 27 October 2003 in the area 63–66°S/109–118°E (Table 1). Sea ice, brines and under-ice water samples were collected under trace metal clean conditions (Lannuzel et al. 2006).

At each station, a set of closely spaced ice cores (maximum 20 cm between each consecutive core, on a homogeneous level ice floe) were collected with an electropolished stainless steel ice corer (14 cm internal diameter). While one core was wrapped in plastic bags and kept frozen (−28°C) for later analysis of ice texture and salinity, ice cores dedicated to biological and chemical parameters were stored in plastic bags at −28°C in the dark until further processing. Within 24 h after sampling, these cores were cut into four sections of 6 cm height. These 6-cm sections were sub-sampled from the full length of the core, chosen so that a top, two intermediate and a basal sections were included from every core. The sections were transferred into acid washed polyethylene containers and further treated as described below for the analysis of inorganic nutrients [NO_3^-/NO_2^-, NH_4^+, PO_4^{3-}, $Si(OH)_4$], chlorophyll *a* (Chl *a*), and microscopic investigations. For dissolved organic carbon (DOC), particulate organic carbon (POC) and transparent exopolymeric particles (TEP)

Table 1 Physical (texture: G = granular, C = columnar; temperature; salinity and brine volume fraction) and chemical [brine volume-normalized concentrations of $Si(OH)_4$, NO_3^-/NO_2^-, PO_4^{3-} and NH_4^+] characteristics along with chlorophyll *a* (Chl *a*) and transparent exopolymeric particles (TEP) concentrations in sea ice core sections

	Depth (cm)	Snow (cm)	Texture	Temperature (°C)	Salinity	Brine volume (%)	$Si(OH)_4$ (μM)	NO_3^-/NO_2^- (μM)	PO_4^{3-} (μM)	NH_4^+ (μM)	Chl *a* (μg l^{-1})	TEP-C[b] (mg l^{-1})
Station IV	0–6	2	G	−8.9	8.6	4.7	270.0	111.7	7.15	5.14	0.22	0.42
1 October 2003	20–26		C	−5.9	3.6	2.9	153.2	34.7	0.14	19.20	0.14	0.25
64°37.7′S	36–42		C	−3.7	4.4	5.8	21.6	17.2	0.74	29.23	0.58	0.06
117°44.5′E	42–48[a]		C	−3.0	6.0	13.1	61.8	109.9	79.44	65.70	19.25	2.02
Station V	7–13	40–50	G	−5.2	6.6	6.9	140.0	26.6	4.74	11.66	3.92	0.44
7 October 2003	40–46		C	−3.5	3.1	3.4	80.9	29.5	0.50	29.23	1.00	0.02
64°34.0′S	69–75		G/C	−1.9	2.3	6.3	20.7	15.8	0.35	15.56	1.96	0.04
116°37.8′E	75–81[a]		C	−1.8	3.3	8.9	72.2	49.3	46.54	19.97	27.98	0.94
Station VII	11–17	5–10	G	−6.2	9.1	6.9	169.8	41.8	0.71	6.70	0.36	ND
9 October 2003	32–38		C	−4.7	4.5	3.4	191.0	22.4	2.88	25.07	2.10	ND
64°38.0′S	56–62		C	−3.2	3.8	6.3	26.0	12.3	0.59	8.19	2.16	ND
116°40.7′E	62–68[a]		C	−2.7	7.3	8.9	105.4	109.2	85.86	72.10	34.26	ND
Station IX	6–12	40–50	G	−4.3	5.2	6.4	140.1	15.6	1.47	16.48	1.22	0.24
11 October 2003	20–26		C	−3.6	4.7	6.6	49.2	15.3	0.52	8.76	0.62	0.15
64°24.1′S	39–45		C	−2.8	4.9	8.4	26.8	12.0	1.09	6.59	0.93	0.37
115°17.5′E	45–51[a]		C	−2.4	6.1	16.3	62.5	34.6	24.76	11.52	12.98	0.78
Station XII	0–6	6	G	−6.7	7.7	4.7	299.6	131.8	12.66	9.94	0.16	0.18
14 October 2003	24–30		C	−4.7	5.2	6.8	111.6	91.1	1.19	12.37	0.28	0.04
63°56.2′S	40–46		G/C	−3.4	5.9	11.8	23.9	8.5	2.07	9.10	0.73	0.13
114°19.4′E	60–66[a]		C	−1.9	4.1	12.0	48.6	8.3	20.61	11.86	14.67	0.36
Station XIII	0–6	4	G/C	−7.9	9.0	5.8	342.9	113.5	6.00	17.61	0.04	ND
20 October 2003	8–14		G/C	−6.1	5.3	4.3	274.9	89.8	2.02	5.59	0.22	ND
65°16.1′S	14–20		G/C	−5.1	4.7	3.5	254.4	89.8	1.01	35.39	0.39	ND
109°27.8′E	20–26[a]		G/C	−4.0	6.2	6.2	176.7	151.9	15.38	13.11	9.10	ND

[a] Bottom sections

[b] Data from Dumont et al. (2009) converted to carbon equivalents according to Engel and Passow (2001)

ND not determined

determination, sea ice sections were transferred into glass beakers precombusted at 450°C for 4 h.

In addition, access holes "sack holes" were drilled into the sea ice cover at two depths (ice levels above or below −5°C, a first-order proxy of the permeability threshold, Golden et al. 1998) to allow the gravity driven brine collection. Brines and under-ice seawater (0, −1 and −30 m) were collected using a portable peristaltic pump (Cole-Parmer, Masterflex E/P) and acid cleaned tubing. Seawater and brines samples were transferred into acid washed bottles successively rinsed with ultra high purity water (UHP) (18.2 MΩ Millipore milli-Q system) and the collected samples.

Ice structure, temperature and salinity

The ice structure was determined by thin section analysis and photographs taken under polarized light. Based on ice crystal size and orientation, two stratigraphic units were distinguished: granular ice and columnar ice. High-resolution analyses of the $\delta^{18}O_{ice}$ allowed further discrimination between snow ice and frazil ice within the granular facies (Jeffries et al. 1989; Eicken 1998). Ice temperature was measured on site using a calibrated probe (TESTO 720) inserted every 5 or 10 cm along the freshly sampled core. Bulk ice salinity was determined by conductivity using WP-84-TPS meter. The brine volume fraction in the sea ice ($\frac{V_b}{V}$ = brine volume/bulk sea ice volume ratio) was calculated on the basis of temperature and salinity values following the equations of Cox and Weeks (1983) and Lepparänta and Manninen (1988), revisited in Eicken (2003).

Nutrients

Ice sections were melted in the dark at 4°C and filtered in the same way as the "sack holes" brine and seawater samples through 0.4-µm polycarbonate filters. Inorganic nutrients [NO_3^-/NO_2^-, NH_4^+, PO_4^{3-} and $Si(OH)_4$] were analyzed in the filtrates by colorimetry following the methods described in Grasshoff et al. (1983). To avoid matrix effect, standards used for calibration were prepared in artificial seawater solutions with salinities similar to those of the samples analyzed.

Chlorophyll *a*

For the determination of Chl *a*, ice core sections were melted in the dark at 4°C in seawater prefiltered through 0.2-µm polycarbonate filters (1:4 volume ratio), to avoid rupture of the sympagic microorganisms cells due to osmotic shocks during sample melting (Garrison and Buck 1986). Subsamples were filtered onto Whatman GF/F filters and Chl *a* was extracted in 90% v:v acetone in the dark at 4°C for 24 h, and quantified fluorometrically according to Yentsch and Menzel (1963).

Organic matter

For the determination of organic matter, sea ice sections were melted at 4°C in the dark in precombusted (450°C, 4 h) glass beakers. This process took no longer than 24 h. In samples dominated by diatoms, this melting process has been shown as not to be problematic with respect to the release of intracellular content (Thomas et al. 1998). Particulate organic carbon (POC) was collected on precombusted (450°C, 4 h) Whatman GF/F filters, stored at −20°C until analysis. After drying the filters at 60°C, POC was analyzed with a Fisons NA-1500 elemental analyzer following carbonate removal from the filters by HCl fumes overnight. Filtered samples for DOC were stored in precombusted (450°C, 4 h) 20-ml glass ampoules with 25 µl H_3PO_4 (concentration 50%), which were sealed to avoid contact with air. Samples were kept in the dark at 4°C until analysis. The DOC was measured by high temperature catalytic oxidation (HTCO; procedure of Sugimura and Suzuki 1988) with a Shimadzu TOC-5000 analyzer. Triplicate TEP subsamples were determined according to the spectrophotometric method of Passow and Alldredge (1995). Briefly, 10–15 ml subsamples were filtered onto 0.4 µm pore size polycarbonate filters (Nuclepore) using a vacuum pressure <150 mm Hg. TEP were stained with Alcian Blue solution (0.02% Alcian Blue, pH 2.5). Filters were then extracted with 6 ml of 80% H_2SO_4 for 2 h, in the dark with constant stirring. Absorbance was measured against a distilled water blank at 787 nm. TEP concentrations were recorded as µg gum Xanthan equivalents and converted into carbon equivalents according to Engel and Passow (2001).

Bacteria, algae and protozoa abundance and biomass

Ice core sections sampled for the determination of the microorganism abundance and biomass were melted according to the same procedure as for the Chl *a* analysis described above.

Algae and protozoa were enumerated by inverted light microscopy (100× magnification and 320× magnification) according to the method of Utermölh (1958) and by epifluorescence microscopy (400× magnification) after DAPI staining (Porter and Feig 1980). Autotrophic species were distinguished from heterotrophs by the red autofluorescence of Chl *a* observed under blue light excitation. A minimum of 100 organisms was counted per taxonomic group. Microscopic size measurements were converted to cell volumes, according to a set of geometric correspondences (Hillebrand et al. 1999). Algae and protozoan biomass was calculated from the abundance and the specific carbon

biomass (carbon per cell) estimated from the relationships established by Menden-Deuer and Lessard (2000).

Bacteria were enumerated by epifluorescence after DAPI staining (Porter and Feig 1980). A minimum of 1,000 cells was counted in at least 10 different fields at 1,000× magnification. A relative standard deviation of 15% ($n = 20$ filters from the same sample) was estimated on the bacterial abundance determination. Bacterial biovolumes were determined by image analysis (Lucia 4.6 software) and calculated by treating rods and cocci as cylinders and spheres, respectively (Watson et al. 1977). They were converted to carbon biomass by using the relation established from data measured by Simon and Azam (1989): $C = 92\ V^{0.598}$ where C is the carbon per cell (fg C cell^{-1}) and V is the biovolume (μm^3).

Brine concentration estimation

The actual habitat of sea ice organisms, the brine channel system, is very difficult to sample. The most widely applied method to collect brines by drainage into "sack holes" cored in the ice (Thomas and Papadimitriou 2003) was used in the present study (see "Sampling and study area"). However, brines samples collected by sack hole sampling do not really sample the particulate phase which is mostly retained in the ice matrix and will be underestimated in the sampled brines. Moreover, the brines collected in sack holes are collected from an undefined area of sea ice (Thomas and Papadimitriou 2003). We confronted hereafter measured brine concentration with brine concentration estimated (C_b^{est}) on the basis of the ratio of the depth-integrated calculated brine volume (V_b^{int}) to depth-integrated bulk sea ice concentrations ($C_{\text{ice}}^{\text{int}}$):

$$C_b^{\text{est}} = \frac{C_{\text{ice}}^{\text{int}}}{V_b^{\text{int}}} \times 100$$

The values were depth-integrated from the top of ice core to the brine collection depths.

Results

Physical environment

Detailed results of the ice texture, temperature, salinity and brine volume of sea ice cores collected during the "Arise in the East" Antarctic cruise during September–October 2003 are presented elsewhere (Tison et al. 2005; Lannuzel et al. 2007). The main physical characteristics of the sea ice sections considered in the present paper are summarized in Table 1. The six sampled stations were located within the seasonal marginal ice zone. Sea ice thickness ranged between 0.3 and 0.8 m. The top of the core was characterized by a layer of granular ice originating from frazil ice growth during the early stages of ice formation and/or snow ice formation due to seawater infiltration in the snow cover. Granular ice accounted for between 15 and 51% of the total ice thickness. The lowermost layer of the ice presented a columnar structure formed through congelation growth at the base of the ice sheet. At stations XII and XIII, the cores presented more complex textural sequences with some bands of granular ice observed along the sea ice core, suggesting rafting had occurred (Lannuzel et al. 2007).

Ice temperature varied between −8.9 and −1.8°C (Table 1). Minimum temperatures were observed in the upper ice section of the cores. At station IV, more than 50% of the ice cover was below −5°C, while most of the ice cover was above −5°C at stations V and IX. Intermediate temperature regimes were observed at the other stations (VII, XII and XIII). This considerable inter-station variability of the temperature profiles clearly results from contrasted surface snow thicknesses (2–50 cm, Table 1). For most of the stations, salinity values showed the typical C-shaped salinity profile, characteristic of first-year ice in winter–spring period (e.g. Weeks and Ackley 1986). Bulk ice salinities ranged between 2.3 and 9.1, whereas brine salinities varied between 61.5 and 103.5. Sea ice brine volumes ranged between 2.9 and 16.3%. Maximum values were observed in the bottom sections (median 10.5%). In the upper layers, brine volumes were <5% at stations IV and XII, and >5%, the permeability threshold for the other stations. Station IX displayed generally higher porosity, with brine volumes being >5% along the whole core.

Chemical environment

Nutrient concentrations measured in the sea ice and water column are gathered in Tables 1 and 2, respectively. In sea ice, brine volume-normalized $Si(OH)_4$ concentrations ranged from 20.7 to 342.9 μM, with values measured in the upper layers (median 219.9 μM) higher than the intermediate and bottom layers (median 65.1 and 67.4 μM, respectively). Bulk ice silicate values were highly correlated with salinity values (Pearson correlation: $r = 0.97$, $P < 0.001$, $n = 51$; Fig. 1a). Brine volume-normalized NO_3^-/NO_2^- concentrations in the ice varied between 8.3 and 151.9 μM. Like silicate, nitrate (and nitrite) concentrations followed relatively well the theoretical dilution lines (TDL), except in some brines and intermediate sea ice sections, where several nitrate (and nitrite) values obtained were below the TDL (Fig. 1b). For PO_4^{3-}, the brine volume-normalized concentrations in the bottom layers (median 35.7 μM) were up to 45 times greater than surface seawater levels. This enrichment is illustrated in Fig. 1c, where bulk ice concentrations clearly lie above the seawater dilution curve. In contrast, the PO_4^{3-} concentrations measured

directly in the brines were remarkably low in comparison to expected values from the TDL. Likewise, NH_4^+ concentration analyzed in the brine samples were low (Fig. 1d) but concentrations in the ice were always above the TDL.

Dissolved organic carbon concentrations ranged between 0.85 and 8.22 mg C l^{-1} (median 1.49 mg C l^{-1}) in the bulk sea ice samples (Fig. 2). Maximum concentrations were observed in the bottom layers (median 4.37 mg C l^{-1}). Concentrations in brine samples (median 1.94 mg C l^{-1}, range 1.52–5.03 mg C l^{-1}; Table 3) were in the same range as those measured in the bulk ice samples (Fig. 2).

Table 2 Chemical and biological characteristics of the seawaters, $n = 17$

	Range	Median
Nutrients		
$Si(OH)_4$ (μM)	49.6–67.4	62.1
NO_3^-/NO_2^- (μM)	18.8–29.9	29.1
PO_4^{3-} (μM)	1.6–2.1	1.96
NH_4^+ (μM)	<0.056–0.4	<0.056
Chlorophyll *a* (μg l^{-1})	0.02–0.10	0.03
Organic carbon		
Dissolved (mg l^{-1})	0.52–3.26	1.08
Particulate (mg l^{-1})	0.02–0.11	0.06
TEP-C (mg l^{-1})	0.10–0.64	0.31
Organism biomass		
Algae (μg C l^{-1})	<0.01–1.59	0.13
Bacteria (μg C l^{-1})	0.61–5.15	2.08
Protozoa (μg C l^{-1})	<0.01–2.32	0.08

Concentrations measured in brines were therefore lower (13 times in average) than the brine concentrations estimated from bulk ice DOC and calculated brine volumes (Table 3). In the underlying seawater (Table 2), DOC concentrations (median 1.08 mg C l^{-1}, range 0.52–3.26 mg C l^{-1}) were lower than in the sea ice. Estimated TEP-C ranged from 0.02 to 2.02 mg C l^{-1} (median 0.25 mg C l^{-1}) in bulk sea ice samples (Table 1) with maximum values in the bottom layers (median 0.86 mg C l^{-1}). Measured brines concentrations were very low (median 0.12 mg C l^{-1}) and two order of magnitude lower than estimated brines concentrations (Table 3). In the underlying waters, the TEP concentrations remained high, between 0.10 and 0.64 mg C l^{-1} (Table 2).

POC and microorganisms distribution

Particulate organic carbon concentrations ranged between 0.35 and 4.78 mg C l^{-1} in bulk sea ice samples (Fig. 2). Maximum values were always measured in the bottom layers (median 3.41 mg C l^{-1}), while lower values, but still high as compared to seawater, were observed in the intermediate layers (median 0.66 mg C l^{-1}). Concentrations measured in the brine samples were much lower (57 times, in average) than the expected estimated values based on bulk ice POC and calculated brine volumes (Table 3). The POC concentrations measured in the underlying seawater (Table 2) ranged between 0.02 and 0.11 mg C l^{-1} (median 0.06 mg C l^{-1}). Measured total POC contains a biotic component (the biomass of microorganisms estimated by microscopy) and a detrital component ($POC_{detrital} = POC_{total} - POC_{biotic}$).

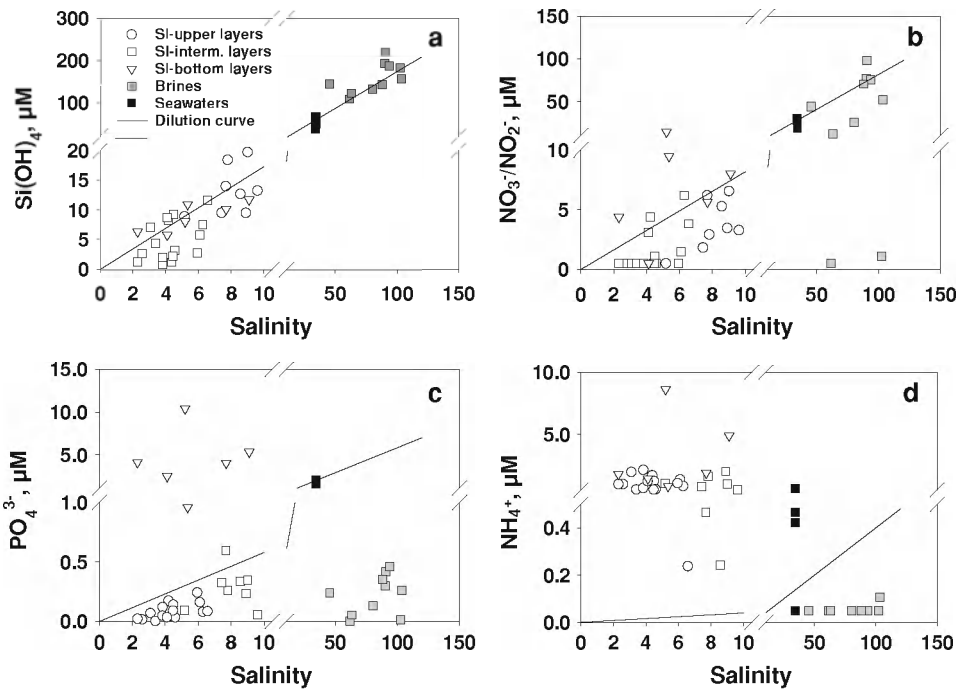

Fig. 1 Nutrients: **a** Silicate, **b** nitrate/nitrite, **c** phosphate and **d** ammonium, as a function of salinity in melted cores (bulk ice concentration), brine and seawater samples. The theoretical dilution line (TDL) was established from the nutrient concentration in under-ice water (−30 m) of the same station

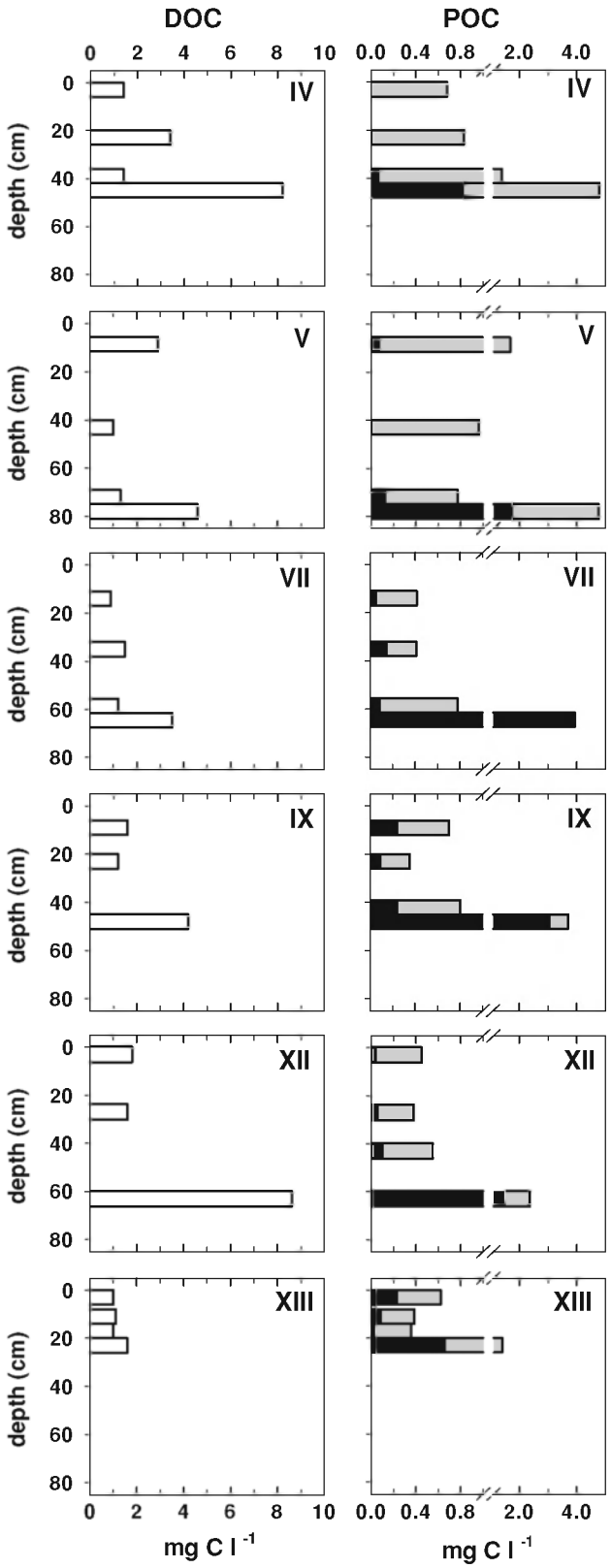

Fig. 2 Vertical distribution of organic carbon (dissolved and particulate) in the four sea ice sections. Particulate including biotic (*in black*) and detrital (*in gray*) organic carbon

Table 3 Dissolved organic carbon (DOC), particulate organic carbon (POC), transparent exopolymeric particles carbon (TEP-C), bacteria, algae and protozoa biomasses in the brine samples

	Measured values	Estimated values
DOC (mg l^{-1})	1.94	25.4
$n = 8$	1.52–5.03	10.9–68.9
POC (mg l^{-1})	0.18	10.2
$n = 9$	0.09–0.29	5.3–26.3
TEP-C (mg l^{-1})	0.12	12.3
n = 8	0.09–0.55	6.8–66.7
Bacteria (μg l^{-1})	9.75	484.8
$n = 9$	1.52–74.69	108.5–708.2
Algae (μg l^{-1})	8.99	551.1
$n = 9$	1.81–39.35	117.7–3076.7
Protozoa (μg l^{-1})	1.04	127.7
$n = 9$	0.02–6.54	68.3–1771.9

Measured (collected by sack hole) and estimated values based on bulk ice concentration and calculated brine volume (see "Materials and methods"). Median and range are given; n = number of samples

The latter is not directly associated to living organisms but results from previous biological activities. However, it is worthwhile to note that the biomass estimation by microscopy is not a very precise measurement of the microorganism standing crop. The conversion from the abundance of the microorganisms to carbon involves regression analyses and conversion factors that are subject to errors. If detritus content is high as compared to the biotic fraction (which can be observed in the microscopy samples), the carbon content of detritus can be estimated by difference without being strongly affected by the error on the microscopic estimate. The detrital POC pool generally dominated the POC in sea ice (Fig. 2; range 61–99%, median 81%), except in the bottom layer where the biotic pool could represent as much as 100% of the total POC. In seawater, POC was mainly detrital (Table 2; 87–99% of total POC, median 9%).

The biotic POC in the bottom layer was largely dominated by algal C biomass (Table 4). In sea ice, algal biomass ranged from 0.8 to 3,906 μg C l^{-1}, with values higher than 310 μg C l^{-1} in bottom ice (Fig. 3). Maximum concentrations of Chl *a* were recorded in bottom section as well (Table 1) and a sharp increase of algal biomass is observed from brine volume fraction higher than 8% (Fig. 5). In underlying seawater, Chl *a* concentrations were below 0.10 μg l^{-1} (Table 2). Similarly to POC, algal biomass in brine samples was lower than the estimated algal biomass based on bulk ice algal biomass and calculated brine volume (Table 3). The algal biomass in the bulk ice was largely dominated (median 82% of total algae biomass) by large algae (ESD > 20 μm) whereas the proportion of small algae was higher in the brine samples

Table 4 Contribution (%) of algae, bacteria and protozoa biomass in total biotic carbon; ratio of heterotroph to autotroph biomass (HB/AB ratio) in the sea ice samples, brines and seawater samples

	Algae (%)	Bacteria (%)	Protozoa (%)	HB/AB ratio
Upper layer	48	28	22	1.07
$n = 6$	7–85	9–73	<1–41	0.18–12.67
Intermediate layers	58	30	4	0.73
$n = 12$	46–92	7–52	<1–41	0.85–1.23
Bottom layer	97	2	<1	0.03
$n = 6$	47–99	1–4	<1–50	0.01–1.15
Brines	9	83	9	10.13
$n = 8$	2–39	32–97	<1–47	1.53–54.11
Seawaters	8	82	11	8.50
$n = 17$	<1–31	46–100	<1–46	2.21–525.53

Median and range are given, n = number of samples

(median 53% of total algae biomass, $n = 24$). In seawater, the algal biomass was also dominated by <20 μm cells with some exceptions (median 73% of total algal biomass, $n = 17$).

The autotrophic composition in sea ice was highly variable and showed a patchy distribution of biomass, reflecting the heterogeneity of the ice environment (Fig. 4). Autotrophic dinoflagellates could represent most of the autotrophic biomass in the upper layer, whereas diatoms (pennates and centrics) largely dominated in the other ice layers. Pennates generally dominated the diatomaceous biomass, with long chains of *Fragilariopsis* sp. only observed in the bottom ice. Centrics (mainly *Corethron* sp. and *Eucampia* sp.) were occasionally observed. In bottom ice, large autotrophic ciliates >10 μm were abundant at station IX, representing 58% of the autotrophic biomass (Fig. 4). Autotrophic nanoflagellates biomass was not significant in the ice assemblage. In the water column below, the autotrophic biomass was on average three orders of magnitude lower than in the sea ice and the autotrophic nanoflagellates represented a large contribution (median 36% of algal biomass, $n = 17$) of the pelagic autotrophic biomass.

Bacterial biomass ranged between 2.1 and 108.0 μg C l^{-1} in sea ice, with maximum values recorded at the maximum of algal carbon in the bottom layers (Fig. 3; median 26.0 μg C l^{-1}). However, in this ice section, their contribution to total C biomass stayed below 4% (Table 4). In the upper and intermediate layers, bacterial biomass represented from >9% up to 73% and from 7% up to 52%, respectively of the total biomass. In the brines and seawater samples, their contribution reached 83 and 81% (median values) respectively (Table 4). As estimated for algae, only a small fraction of bacteria were sampled in the brines (Table 3) as compared to the expected values estimated from bulk ice samples.

Protozoan biomass ranged between 0.7 and 331.0 μg C l^{-1} (Fig. 3). As for algae and bacteria, the maximum of biomass was reported in the bottom layer. Again, the biomass distribution among each group of protozoa was remarkably variable (Fig. 4). Dinoflagellates and ciliates generally dominated the ice protozoa biomass. The equivalent spherical diameter (ESD) ranged between 2 and 51 μm (median 11 μm, $n = 550$) and between 11 and 39 μm (median 17 μm, $n = 120$) for dinoflagellates and ciliates, respectively. In seawater, flagellates (including nano- and dino-flagellates) with ESD $\leq$ 10 μm dominated (range 2–10; median 4 μm, $n = 400$). In sea ice, the protozoa contribution to biotic carbon ranged between <1 and 50% (Table 4). In the brines and seawaters samples, their contribution varied between <1–47% and <1–46%, respectively.

The ratio of heterotroph (i.e. bacteria and protozoa) to autotroph biomass (HB/AB ratio) ranged between 0.01 and 12.7 in the sea ice (Table 4), with very low values in the bottom layer (median 0.03, $n = 6$). On the opposite, in the underlying seawater, the heterotrophs largely dominated with HB/AB varying between 2.21 and 525.53 (median 8.50, $n = 17$).

Discussion

The sampling period of the ARISE cruise (October) corresponds to the austral late winter–early spring. Values of salinities in the ice cores collected were similar to those previously observed in Antarctic sea ice for end-of-winter conditions (Clarke and Ackley 1984). Higher bulk ice salinity values were found in top layers of the ice cores, indicating that no significant brine drainage had already taken place from the top, as it is often the case later in the season (Tison et al. 2008). The collected ice cores consisted of granular and columnar ice textures, which is characteristic of first-year Antarctic pack ice. Sea ice growth processes are key mechanisms for the incorporation and distribution of microorganisms (Horner et al. 1992; Weissenberger and Grossmann, 1998; Lizotte 2003). Granular ice is associated with dynamic turbulent conditions and forms usually at high growth rates, while columnar ice forms more slowly (Eicken 2003). A rapid growth involves the concentration of cells, by nucleation of frazil ice crystal or by scavenging of cells as frazil crystals float up through the water column (Garrison et al. 1989; Horner et al. 1992). In contrast, columnar ice formation has tendency to reject algal cells in the initial growth period (Palmisano and Garrison 1993; Weissenberger and Grossmann 1998). Consequently, sympagic communities found

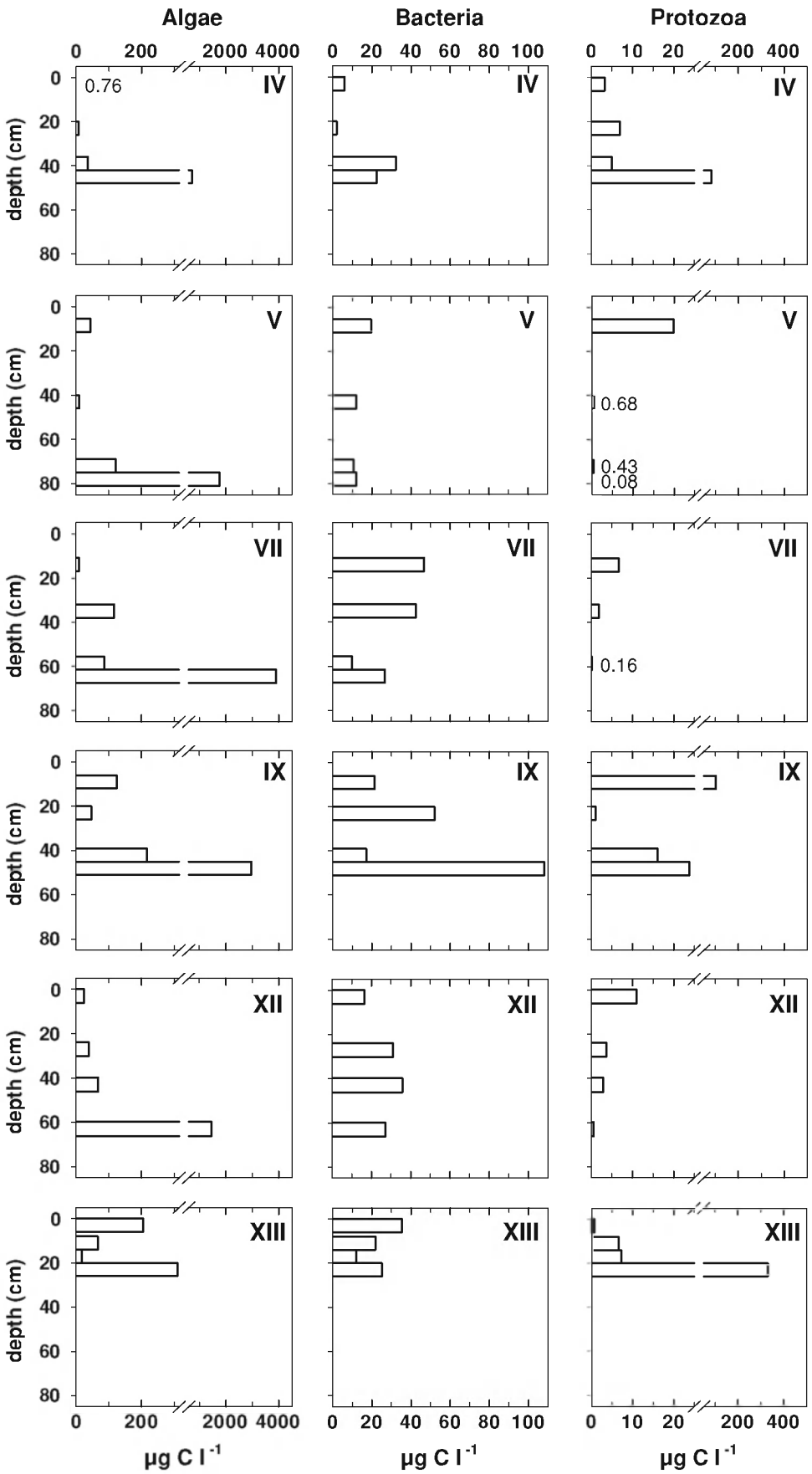

Fig. 3 Vertical distribution of sympagic microorganisms (algae, bacteria and protozoa) in the four sea ice sections

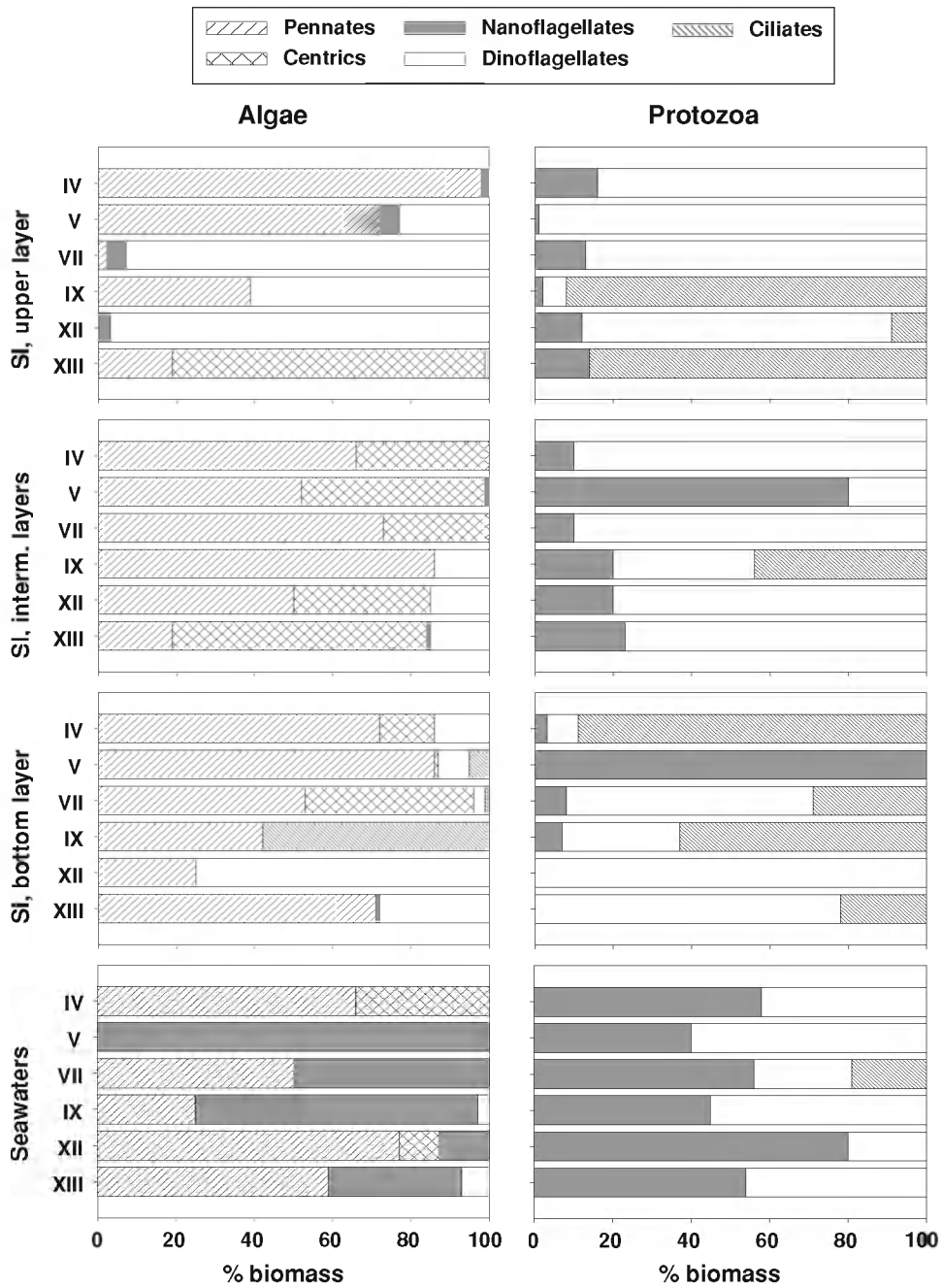

Fig. 4 Distribution of major algae and protozoa taxonomic groups in the sea ice [*upper*, *intermediate* (average values) and *bottom layers*] and underlying seawaters

in granular ice could be composed of organisms from the previous autumn, such as dinoflagellates forming cysts (Garrison and Close 1993). Nevertheless, contrasts in the initial concentration between various textural units were probably damped as time goes by, from autumn to the winter–spring (Eicken et al. 1991). In the late winter, the slowly growing bottom skeletal ice layer of the columnar ice provides a unique habitat where large accumulations of organisms, in particular algae, are observed (Garrison and Mathot 1996). In our samples, no clear relationship between biological occurrence and textural type (granular and columnar ice) was observed.

Generally, abiotic factors, i.e. light, temperature, salinity, nutrients are considered to control ice algal growth and explain spatial and temporal distribution of sea ice organisms (Arrigo and Sullivan 1994). Temperature, which controls the brine salinity and the brine volume fraction, structures the sea ice ecosystem (Eicken 1992). The brine volume fractions reported in this study were relatively stable (between 3 and 8%) but increased sharply, when a threshold temperature of −4°C was reached in the columnar ice and mainly in the bottom section. The brine volumes and more specifically the internal surfaces of brine channels and pockets could be a key factor in controlling

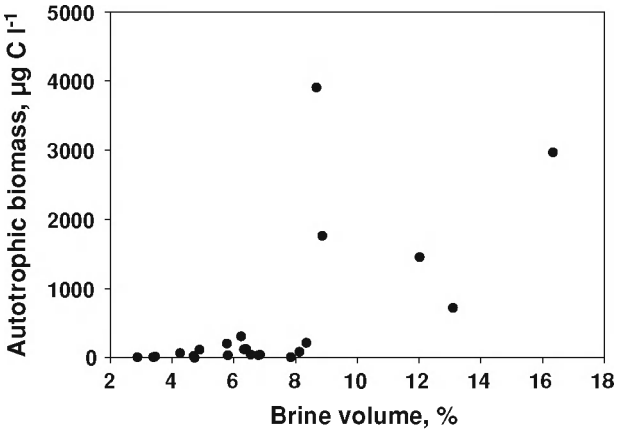

Fig. 5 Autotrophic biomass as a function of brine volume fraction in the pack ice

the accumulation and colonization of microorganisms in the sea ice (Krembs et al. 2000). As reported by Perovich and Gow (1996), for brine volumes of 3–8%, the mean surface area of the brine pockets remains essentially constant. As the ice further warms, the mean area gradually increases as the brine volume increases from 8 to 20%, and then sharply from 20 to 40%, due to the connection of pockets by the brine channels. In our study, a sharp increase of algal biomass is indeed observed from brine volume fraction higher than 8%, suggesting a control by the brine volume fraction on the algae accumulation at the beginning of the productive season in the sea ice (Fig. 5). For brine volumes ranging from 3 to 8%, the autotrophic biomass remained relatively constant, but above the limit of 8%, which roughly corresponds to −4°C, autotrophic organisms can accumulate (Fig. 5). During tank experiments, it has been shown that diatom biomass could accumulate when ice temperatures increased from −4 to −3°C (Krembs et al. 2001).

Both the ice–water exchanges and the environmental space available for sympagic organisms are driven by the brine volume. The percolation theory for columnar ice shows that, below a critical brine volume of 5%, which corresponds to a temperature and salinity of −5°C and 5 respectively, sea ice becomes impermeable, thus limiting the circulation of brines. This phenomenon is of prime importance for ice algal growth which becomes rapidly macro-nutrient limited (Arrigo 2003). When the ice is impermeable, nutrients found in the sea ice internal habitat mainly originate from their initial entrapment during ice formation or from recycling. As the ice starts to warm up, gravity brine drainage allows the transport of nutrients from the underlying water across the ice–water interface via convection mechanisms. Alternatively, nutrients replenishment can also occur when flooding introduces seawater within the surface layers. Nutrient concentrations in the sea ice cores will therefore result from a subtle balance between physical processes (permeability and brine drainage/convection) and/or biological activity (uptake and remineralization) depending on the temporal thermodynamic stage of the ice cover. Parameters governed by physical mechanisms should vary with salinity, because the latter depends on temperature and brine drainage/convection processes only. In order to reveal a potential biological control on nutrient concentrations in the ice cover as compared to those in the water column, theoretical dilution lines (TDL) have been plotted for each nutrient (Fig. 1). The estimated TDL can only be considered as a rough guide to processes involved in concentrating nutrients from seawater into brines. Since we do not have any data on nutrients concentrations in the water column when the sea ice was formed, we assume that the initial nutrient concentration was similar to the one measured in the seawater at −30 m. We also have to assume that no nutrient fractionation occurs during ice growth and during further desalination processes, which is a plausible approximation given the fact that molecular diffusion (with specific diffusion coefficients) contributes partly to these processes. Results obtained by Meese (1989) for cations that are not involved in biotic processes seem to indicate that this approximation is valid. Briefly, a negative deviation of TDL is associated to the biological uptake while a positive deviation indicates remineralization processes. Our results show that silicate concentrations are centered on the dilution curve and nitrates, although roughly increasing with salinity, already show some signs of depletion, with most of the ice samples slightly below the TDL and some of the brine samples clearly exhibiting strong deficits. Other studies showed that nitrate and silicate concentrations in the winter sea ice were centered on TDL, indicating that little nutrient uptake had taken place prior to the sampling time (Dieckmann et al. 1991; Arrigo et al. 1993). As the season progresses, nutrient concentrations fell increasingly below TDL presumably due to algae uptake (Arrigo et al. 1993; Papadimitriou et al. 2007). Although phosphate and ammonia are not correlated with salinity, a large accumulation of these two nutrients in the bottom section is observed. The very high correlation between PO_4^{3-} and NH_4^+ ($r^2 = 0.938$, $P < 0.001$, $n = 22$) suggests that their accumulation could result from similar processes. High accumulation of PO_4^{3-} and NH_4^+ are also observed in other sea ice studies (Dieckmann et al. 1991; Arrigo et al. 1995; Thomas et al. 1998). The remineralization of the observed large accumulated organic pools in the ice as well as the direct release of algal osmolytes due to cell lysis (Cota et al. 1990; Lizotte 2003; Thomas and Papadimitriou 2003) could lead to these very high concentrations.

In early spring, the major nutrients concentrations in the microenvironment where the algae are living, i.e. the brine

volume-normalized nutrients concentrations, are very high (Table 1, this study) as well as for micronutrients like iron (Lannuzel et al. 2007). The concentrations are at least 5 (range 5–88) times higher for Si, 18 (range 18–165) times for N and 122 (range 122–1,570) times for DFe above the average values of the half-saturation constant [Ks(Si) = 3.9 ± 5.0 μM, Ks(N) = 1.6 ± 1.9 μM, Kμ(Fe) = 0.35 ± 0.44 nM] characterizing diatoms nutrient uptake in oceanic waters (Sarthou et al. 2005). The PO_4^{3-} availability could however be sometimes limiting in the intermediate layers where its concentration reached values lower than diatoms estimated half-saturation constant [Ks(P) = 0.24 ± 0.29 μM]. Nevertheless, the PO_4^{3-} brine concentrations in the upper and bottom sea ice samples were at least six times above the value of the half-saturation constant. These results suggest that the algae growth was not limited by nutrients availability at the beginning of the productive season. The growth of the sympagic organisms at low temperature can however be limited by reduced affinity for substrates such as for nitrate and silicate (Thomas and Papadimitriou 2003). For instance, the half-saturation constant for the uptake of silicic acid is known to be high for diatoms from the Southern Ocean as compared to other region (Ks > 60 μM, Sommer 1986; Nelson et al. 2001).

Diatoms which dominated the algae community in sea ice are nevertheless relatively flexible in their intracellular Si content, and near-maximum cell division rates can be sustained even when ambient concentrations of silicic acid limit Si uptake by diminishing the cellular Si content (Martin-Jézéquel et al. 2000). Hence Si uptake rates may appear to be limited by ambient silicic acid concentrations, but this does not necessarily imply limitation of growth.

During our investigation, high concentration of TEP have been observed in sea ice samples, in agreement with the range of values reported for Antarctic pack ice (Meiners et al. 2004) and in Arctic fast and pack ice (Krembs and Engel 2001; Krembs et al. 2002; Meiners et al. 2003; Riedel et al. 2006, 2007a). Pennate diatoms have been reported to secrete high TEP concentrations for both adhesion and mobility by gliding (Wetherbee et al. 1998). The ability to move vertically should be an advantage in the sea ice environment in order to gain access to better light and nutrients conditions. Bacteria are also capable of producing TEP (Simon et al. 2002), but in a lower amount as compared to algae (Meiners et al. 2004; Riedel et al. 2006). Previous studies on sea ice have reported high numbers of bacteria attached to algal cells (Grossmann and Gleitz 1993; Grossmann 1994; Grossmann and Dieckmann 1994) and algal derived TEP (Meiners et al. 2004). During the present cruise, TEP were fairly well correlated with Chl *a* (Dumont et al. 2009). The high measured concentrations of TEP likely have the potential to anchor the cells to the ice surface and retain ice components into this viscous phase. The difference between values measured in brine samples (sack holes) and values estimated from bulk ice values and brine volume could result from the attachment or entrapment of the microorganisms in the ice matrix. A large fraction of microorganisms would therefore not be sampled by the drainage collection into "sack holes".

Also, dissolved organic carbon seems to have been retained on the brine pockets and channels walls in sea ice, as suggested by the large difference between concentration measured in the "sack holes" samples and estimated brines concentrations based on bulk ice DOC concentrations and brine volume fractions. These results corroborate the view of Krembs et al. (2000) and Mock and Thomas (2005) who consider that the sea ice internal habitat resembles that of a biofilm adhering to the brine channel walls, with an overlying flowing liquid phase i.e. the brine fraction. Biofilms can be defined as microorganisms attached to a surface and embedded in an extracellular gel-like matrix of polymeric substances (Fischer 2003). TEP are clearly an integral part of the structural organization of the biofilm. TEP have also been shown to adsorb dissolved organic compounds from the bulk fluid (Davey and O'Toole 2000). DOC concentrations were within the range previously observed in the sea ice (Thomas et al. 1995; Krembs et al. 2002), with very high values in the bottom layers (Meiners et al. 2008; this study). These DOC concentrations reached values close to those of POC in the bottom ice. Sea ice DOC/POC ratio ranged from 1:1 to 4:1, whereas seawater ratio typically varied from 5:1 to 61:1. These measured DOC/POC ratio in the sea ice environment are very low in comparison to traditional oceanic water value of 15:1 (Millero 1996; Kepkay 2000). An explanation for that might be the abiotic transformation of DOC into POC when a DOC threshold is reached, maintaining a constant DOC/POC ratio. In Antarctic summer ice floe, DOC concentrations up to five times lower than those of POC have even been reported (Kattner et al. 2004). POM and/or TEP formation from DOM can indeed be described using coagulation dynamics (Chin et al. 1998; Mari and Burd 1998). Low DOC/POC ratio are typically observed in biofilms and aggregates (Giani et al. 2005), due to high biotic DOC consumption and remineralization or transformation through coagulation process into TEP and/or POC (Passow 2000). Moreover, when reaching salinities as high as those measured in the brine pockets (in this study >61), a substantial increase of cations such as Na^+, Ca^{2+}, Mg^{2+} and Fe^{3+} may enhance floc formation and aggregation of suspended dissolved organic carbon (Decho 2000).

In addition to the accumulation of DOC and TEP, high inorganic nutrients such as PO_4^{3-} and NH_4^+ concentrations were measured. A proportion of the inorganic nutrients produced by the remineralization of organic matter might not instantly turned over but remains in the

biofilm, which acts as a reservoir and buffers the direct effects of major nutrients depletions. For instance, Fe (oxy)hydroxides associated with DOM may bind PO_4^{3-} (Maranger and Pullin 2003). Such an association could have promoted the accumulation of DOM-Fe–P complex in the sea ice, as suggested by the parallel accumulation of TEP, DOC, Fe and PO_4^{3-} in the sea ice bottom layers. This could allow the maintenance of an eutrophicated environment (sea ice environment) in a HNLC region such as the Southern Ocean. The median heterotrophic/autotrophic (HB/AB) ratio measured in our sea ice samples, <0.73 (median, $n = 24$), is characteristic of eutrophic environments (Gasol et al. 1997) where autotrophic biomass is largely composed of micro-sized (>20 μm) diatoms, while bacteria and protozoa biomass stays much more modest, as observed in this study. When the season progresses, later in spring and summer, sea ice samples can present lower HB/AB ratios (Garrison et al. 1986; Mathot et al. 1992), as it is observed for bottom ice samples in the present study (Fig. 6).

The gel structure characterizing the brine system could also modify typical trophic relationships observed in marine ecosystems. Several authors have found a positive relationship between bacterial and algal biomass/production in sea ice during spring/summer (Grossi et al. 1984; Kottmeier et al. 1987; Kottmeier and Sullivan 1990; Stewart and Fritsen 2004). However, as it is the case in the present study, Kottmeier et al. (1987) found no significant relationship between algae and bacteria in late winter sea ice. Maximum bacterial biomass was observed at maximum algal biomass, but the relative contribution to total C biomass was very low (Table 4). On the contrary, their contribution was relatively higher at low level of total microorganism biomass. Although we observed very high TEP and DOC concentrations, bacterial biomass remained relatively low and there was no relationship with these potential substrates (Pearson correlation: $r = 0.130$, $P > 0.10$, $n = 16$ for bacteria vs. TEP; $r = 0.125$, $P > 0.10$, $n = 26$ for bacteria vs. DOC). It has been proposed that sea ice can be an environment where the development of a microbial loop is often hampered, leading to the accumulation of POM and DOM (Lizotte 2003). As observed previously by Meiners et al. (2004), the integrated sea ice TEP in our study represented 687–12,343% of the integrated bacterial biomass, with very high percentage at the most winter station (station IV as defined in Lannuzel et al. 2007). Sea ice TEP seems nevertheless potentially to serve as a carbon source for sympagic bacteria, as suggested by a coupling between TEP and NH_4^+ regeneration (end-product of bacterial remineralization; Riedel et al. 2007a). Confirming this, a very high correlation between TEP and NH_4^+ concentrations (Pearson correlation: $r = 0.89$, $P < 0.001$, $n = 14$) is also observed in the present study. However, as observed in annual sea ice in the Ross Sea, rapid turnover of nitrogen-organic compounds is not always associated to high bacterial growth (Guglielmo et al. 2000).

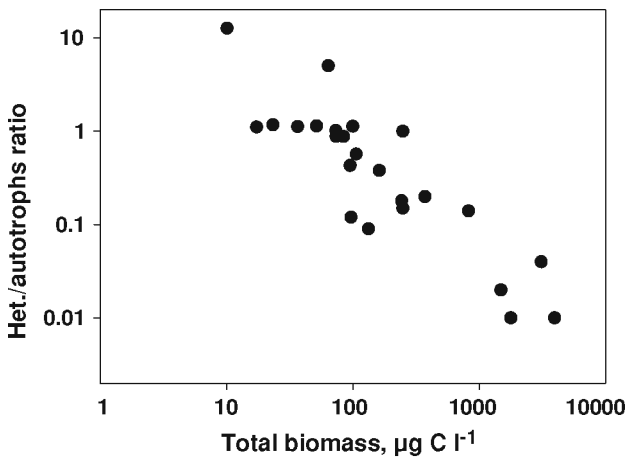

Fig. 6 Heterotrophic to autotrophic biomass ratio as a function of total microorganism (algae, bacteria and protozoa) biomass in the pack ice zone

Despite the fact that bacteria are exposed to very high substrate concentrations, protozoa grazing might control their biomass accumulation. Protozoa can indeed consume bacteria as well as small-sized algae. Our current understanding of sea ice grazing activity is however limited by the lack of appropriate investigation methods (Lizotte 2003). Given these limitations, sea ice feeding relationships could be analyzed from the absence/presence of prey and grazers and numerical response curves. Ciliates and dinoflagellates, as observed in this study, dominated the protozoa biomass in sea ice (Garrison and Mathot 1996). The particle size spectrum ingested by ciliates appears to be determined by their cell size (Fenchel 1987), a ratio between predator and prey size of 1:10 is usually observed. In our studies, ciliates with ESD < 40 μm dominated and those ciliates could consequently only graze on cells smaller than 4 μm i.e. bacteria and flagellates. However, Scott et al. (2001) reported a wide range of food particles biomass from femto- to nano-sized cells for an Antarctic sea ice ciliate (*Pseudocohnilembus* sp., ESD < 12 μm). Dinoflagellates, dominating the protozoa biomass in the sea ice, have been shown to feed on particles that approach or exceed their own sizes (Gaines and Elbrächter 1987). In the Antarctic marginal ice zone, the size range of autotrophic prey and predators overlaps. The ESD of dinoflagellates enumerated in our samples is around 11 μm (median). Those dinoflagellates are therefore likely to consume nano-sized particles. In Antarctic seawaters protozoa biomass linearly increased with the availability of potential food such as bacteria and small algae (<20 μm, Becquevort et al. 1992; Becquevort 1997). In the present study, protozoa biomass significantly

correlated with the food biomass (Pearson correlation: $r = 0.620$, $P < 0.001$, $n = 22$) but increased only when a food threshold was reached (Fig. 7). There would be a range of food concentrations over which ingestion cannot offset maintenance metabolism, so that consumer growth rate would be ≤ 0. If mobility needed for the capture of food represents a substantial energy cost, it would seem advantageous to limit predation activity when food concentration is too low to provide a compensating energy return (Taylor 1978). The presence of high TEP concentration altering the physical conditions by setting a gel, could change grazer mobility (Joubert et al. 2006), and then regulate the prey–grazer interactions. Accordingly, Riedel et al. (2007b) found a negative correlation between TEP concentration and experimentally derived ingestion rates of bacterivores in Arctic sea ice.

During seasonal melting, the accumulated components will be released from the sea ice to the seawater and some of them may serve as inoculum. Aggregated ice algae might be quickly grazed by krill (Scharek et al. 1994) or rapidly settle (Riebesell et al. 1991). The released algal cells would then never have the chance to serve as an inoculum for open water blooms. In the present study, diatoms dominated in the ice environment, whereas flagellates dominated in the water column. The similarity between sea ice and water column algal assemblages is indeed not demonstrated in all studies (Leventer 2003). The planktonic organisms could have the opportunity to grow thanks to the release of Fe and OM concentrated in the sea ice. In the underlying seawater, the DFe (Lannuzel et al. 2007), DOC and TEP concentrations were lower than in the sea ice; but were still relatively high for Antarctic seawaters (for DFe: 0.05–0.3 nM, de Baar and de Jong 2001; for DOC: <0.72 mg C l^{-1}, Ogawa and Tanoue 2003). The OM release seems actively consumed by bacteria which largely dominated biotic C biomass (Table 3). DOM released during ice melting is indeed known to be rapidly used by bacteria (Kähler et al. 1997; Giesenhagen et al. 1999). Consequently, extremely high values of HB/AB ratios were reported. These ratios reflected the community structure dominating in sea ice underlying waters at the end of winter (Garrison and Mathot 1996).

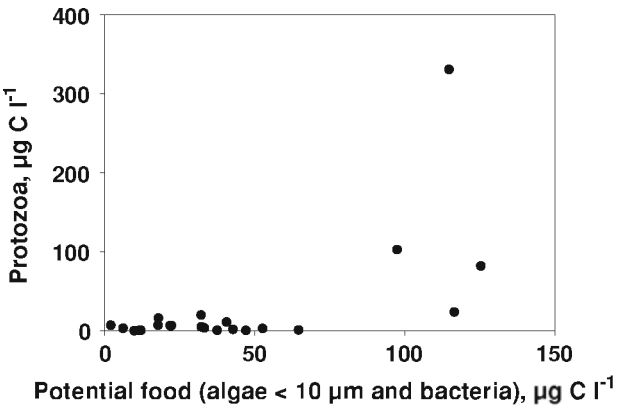

Fig. 7 Relationship between protozoa biomass and potential food, i.e. algal <20 µm and bacterial biomass

Conclusion

Sea ice algal growth at the beginning of the productive season was not limited by nutrients, but rather by available brine space and surface. A large fraction of microorganisms embedded in TEP, were retained to the brine channel/pockets, forming a gel "biofilm". It constitutes specific microenvironments for microorganisms (algae, bacteria and protozoa) where the high retention of nutrients and the low presence of their grazers allowed a large accumulation of algae. The increased autotrophic biomass was largely dominated by micro-sized diatoms. Despite large substrate concentration, the observed bacteria and protozoa biomass increase was much more modest. The accumulated OM could then be released in the seawater at the time of ice melting, stimulating the planktonic microbial loop.

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