Structural and functional properties of sea ice communities in the first year sea ice at Terra Nova Bay (Ross Sea, Antarctica).

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Structural and functional properties of sympagic communities in the annual sea ice at Terra Nova Bay (Ross Sea, Antarctica)

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Abstract Studies on the chemical and biological properties of annual pack ice at a coastal station in Terra Nova Bay (74°41.72′S, 164°11.63′E) were carried out during austral spring at 3-day intervals from 5 November to 1 December 1997. Temporal changes of nutrient concentrations, algal biomasses, taxonomic composition, photosynthetic pigment spectra and P–E relationships were studied. Quantity, composition and degradation rates of organic matter in the intact sea ice were also investigated. In addition, microcosm experiments were carried out to evaluate photosynthetic and photo-acclimation processes of the sympagic flora in relation to different light regimes. High concentrations of ammonia were measured in four ice-cores (weighted mean values of the cores ranged from 4.3 ± 1.9 μM to 7.2 ± 3.4 μM), whereas nitrate and phosphate displayed high concentrations (up to 35.9 μM and 7.6 μM, respectively) only in the bottom layer (135–145 cm depth). Particulate carbohydrate and protein concentrations in the intact sea ice ranged from 0.5 to 2.3 mg l^{-1} and 0.2 to 2.0 mg l^{-1}, respectively, displaying a notable accumulation of organic matter in the bottom colored layer, where bacterial enzymatic activities also reached the highest values. Aminopeptidase activity was extremely high (up to 19.7 μM l^{-1} h^{-1} ± 0.05 in the bottom layer), suggesting a rapid turnover rate of nitrogen-enriched organic compounds (e.g. proteins). By contrast, bacterial secondary production was low, suggesting that only a very small fraction of mobilized organic matter was converted into bacterial biomass (< 0.01‰). The sympagic autotrophic biomass (in terms of chlorophaeopigments) of the bottom layer was high, increasing during the sampling period from 680 to 2480 μg l^{-1}. Analyses of pigments performed by HPLC, as well as microscope observations, indicated that diatoms dominated bottom communities. The most important species were *Amphiprora* sp. and *Nitschia* cfr. *stellata*. Bottom sympagic communities showed an average P^{B}_{max} of 0.12 mgC mg Chl^{-1} and low photoadaptation index (E_k = 18 μE m^{-2} s^{-1}, E_m = 65 μE m^{-2} s^{-1}). Results of the microcosm experiment also indicated that communities were photo-oxidized when irradiance exceeded 100 μE m^{-2} s^{-1}. This result suggests that microautotrophs inhabiting sea ice might have a minor role in the pelagic algal blooms.

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Introduction

The Antarctic Ocean is characterized by low year-round temperature and by the seasonal formation of pack ice at the sea surface. In the last decade, several studies have shown that ice formation-melting processes are responsible for changes in quantity and composition of planktonic communities (Garrison and Buck 1991; Dieckmann et al. 1998; Gleitz et al. 1998) and they are recognized as the major factors conditioning the availability of suspended particles for planktonic and benthic suspension feeders, especially during the austral summer

(Smith and Nelson 1985; Nelson and Smith 1986; Fabiano et al. 1993).

The first studies in this region were carried out in coastal areas where ice communities of the bottom layer play an important role. The major contribution to the knowledge of the biological and ecological dynamics of the sympagic flora in coastal sites was provided by Sullivan and collaborators for McMurdo Sound (Palmisano and Sullivan 1983, 1985; Sullivan 1985). In recent years, however, the offshore sea ice has received much more attention (Arrigo et al. 1998; Dieckmann et al. 1998).

Microalgal growth within the coastal sea ice, which is usually thicker when compared to offshore sea ice, is controlled by salinity (Arrigo and Sullivan 1992) and by the thickness of the snow layer, which attenuates irradiance (Arrigo et al. 1991). Coastal sea-ice algal communities display a photosynthetic capacity about 1 order of magnitude lower than that measured in offshore sea ice (Palmisano et al. 1987; Arrigo et al. 1993) or for phytoplankton (Lizotte and Sullivan 1992). Algal communities at the top layers of sea ice grow at high light levels even though nutrients are limiting. Under such conditions, salinity of the ice cavities, whose volume, in turn, depends upon the ice porosity, indicates possible nutrient exchange with the underlying water (Ackley and Sullivan 1994). Species composition of ice-algal communities is extremely variable and pigment ratios seem to be completely different in the Antarctic as compared to those reported for other polar areas (Lizotte et al. 1998).

A general review of these topics is given by Knox (1994) and recent information on the variability of physical and biological processes occurring in the sea ice has been presented by Lizotte and Arrigo (1998) and Jeffries (1998). These studies indicate that light is the major factor limiting primary production of the sympagic communities. In addition, data reported for the Ross Sea (SooHoo et al. 1987) indicate a wide spatial heterogeneity in irradiance values, due to the patchiness of sympagic communities and snow coverage.

Some papers have dealt with the nutritional quality of suspended particles in the Antarctic Ocean (Handa et al. 1992; Fabiano et al. 1993, 1996; Fabiano and Pusceddu 1998), and the fate of particulate organic matter (POM) under the pack ice (Matsuda et al. 1990). However, to our knowledge, no data are available on the biochemical composition of POM within the sea ice. While some papers have dealt with bacterial abundance and biomass in the sea ice (Sullivan and Palmisano 1984; Archer et al. 1996; Delille and Rosiers 1996), others have reported on bacterial secondary production associated with Antarctic pack ice (Kottmeier et al. 1987; Grossmann 1994; Grossmann and Dieckmann 1994; Archer et al. 1996).

Information on the functioning of microbial enzymatic activity is fundamental for the comprehension of the microbial loop in aquatic systems (Chrost 1990). Few data on enzymatic activity in Antarctic sea ice are available in the literature (Helmke and Weyland 1995; Misic et al. 1998). These studies clearly indicate that extra-cellular enzymatic activities are strictly linked to organic matter availability.

The main aims of this study were: (1) to gather information on short-term changes in nutrient concentrations and algal biomass, taxonomic composition, photosynthetic pigment spectra and primary production, and (2) to estimate the quantity, composition and degradation rates of labile organic compounds and bacterial secondary production in the intact annual sea ice at a coastal station in Terra Nova Bay, during late spring 1997. We also evaluated photosynthetic and photo-acclimation processes of the sympagic flora in relation to different experimental light levels, to test the role of sympagic flora in conditioning the composition of the spring phytoplankton bloom.

Materials and methods

The sampling area was located in the offshore annual pack ice of Terra Nova Bay (74 41.72′S, 164 11.63′E) at 2 nautical miles from the Italian Base (Fig. 1). Sea-ice cores (10 cm Ø) were collected, at 3-day intervals, in a 100-m^2 delimited area, from 5 November to 1 December 1997, using an aluminum corer. Sea-ice thickness (about 1.4 m) remained constant during the entire sampling period.

Meteorological (air temperature, relative humidity) and radiometric measurements (surface downwelling solar irradiance, quantum photosynthetically active radiation (PAR), UV-A 380 ± 5 nm and UV-B 320 ± 5 nm) were recorded (Campbell Scientific CR10X data logger, 5 min of acquisition frequency) during the whole month of November at the sampling site. In-water spectral downwelling irradiances at two UV and four VIS wavelengths (Satlantic, OCI-200) and quantum PAR (LI-Cor, 192SA)

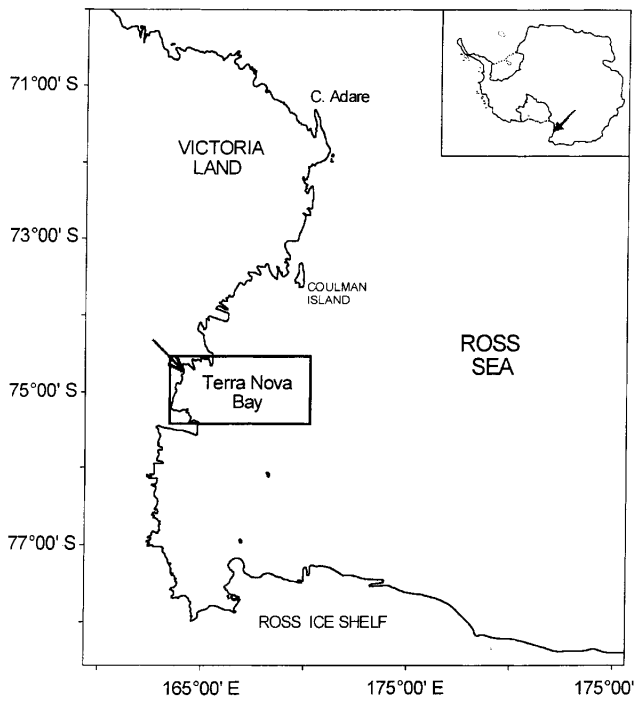


Fig. 1 Location of the ice cores sampling site

were measured under the pack ice with the radiometer alternately towed by an ROV or by a SCUBA diver.

Immediately after collection, sea-ice cores were sliced, in light conditions just sufficient to carry out operations, into 3-, 6-, and 12-cm-thick sections, according to the parameters to be considered. Four cores were collected at each sampling date and used for nutrient and salinity measurements, biochemical determination of organic matter and photosynthetic pigments, secondary bacterial production and eso-enzymatic activity and for measurement of primary production, respectively.

For the determination of the vertical distribution of chemical parameters [inorganic nutrients, N-NO_3, N-NO_2, N-NH_4, P-PO_4, Si-Si$(OH)_4$ and salinity], the cores were cut in 10-cm slices. Each slice was melted in a low-power microwave oven. A comparison among different melting techniques (in microwave oven, in the dark at room temperature, in tapwater bath) was carried out using the first cores collected. The microwave yielded the lowest nutrient content found in the sea ice. Nutrient data reported in the present paper have been obtained using the microwave technique, which caused the loss of the first cores collected and gave concentrations that must be considered as underestimated. However, the microwave allowed us to reduce to about 5 h the time between sampling and analysis. After melting, each sample was filtered onto a glass fibre Whatman GF/C. Nutrient concentrations were determined with an autoanalyser ALPKEM with segmented flow, according to the methods of ALPKEM Flow Solution (ALPKEM 1992a, 1992b, 1992c, 1994), and salinity was determined with a salinometer AGE Minisal 2100.

Data for the biochemical composition of organic matter, bacterial production and enzymatic activity reported in this study relate to the sampling performed on 22 November 1997. For biochemical analyses, sea-ice cores were sliced into six 25-cm sections, melted in the dark at room temperature and filtered onto Whatman GF/F filters. Filters were stored at −25°C until analysis (about 1 month). Concentrations of particulate carbohydrates (CHO) and proteins (PRT) were measured according to Dubois et al. (1956) and Hartree (1972), respectively. Protein and carbohydrate concentrations were converted into carbon equivalents using 0.49 and 0.4 as conversion factors, respectively (Fabiano and Pusceddu 1998).

For the analysis of bacterial production and eso-enzymatic activity, three to five replicates (about 10 cm^3 of sea ice broken up into small pieces) for each section were treated immediately as follows: for the determination of bacterial production, sea-ice samples were incubated at −1.8°C in the dark with 2.5 ml of filtered (0.22 μm) and sterile seawater containing 10 nM of L-4-5 ^{3}H Leucine (2.85 TBq mM^{-1}) for 4 h. Linearity of leucine incorporation over the incubation period was checked from 1 to 6 h. Incubations were stopped with formaldehyde (0.4% final concentration). Three formaldehyde pre-killed sub-samples for each horizon were treated identically and used as blanks. At the end of the incubation period, samples were melted and analysed as described by Simon and Azam (1989). For the determination of enzymatic activity, sea-ice samples were incubated separately at −1.8°C in the dark for 4 h with 2.5 ml of filtered, sterile seawater containing 200 μM l-leucine-4-methylcumarinyl-7-amide (Leu-MCA) and 75 μM MFU-β glucopyranoside for aminopeptidase (LA) and β-glucosidase (BG) activities, respectively. After incubation, samples, once melted, were centrifuged and analysed fluorometrically according to Fabiano and Danovaro (1998).

For spectrophotometric, spectrofluorometric and HPLC determinations of photosynthetic pigments, three different sections (0–80 cm, 80–130 cm, 130–140 cm, starting from top of the core and named alpha, beta and gamma, respectively) of the ice cores were melted at room temperature and in dim light and filtered through Whatman GF/F glass fibre filters.

Spectrofluorometric analyses of chlorophyll a (Chla) and phaeopigments (phaeo) and spectrophotometric determination of chlorophaeopigments (Chl) were carried out within a maximum of 12 h after collection. Filters were placed in neutralized 90% v/v acetone, minced with a glass stick and allowed to extract for 24 h. The extract was read before and after acidification; the spectrofluorometer (Spex Fluoromax) was checked daily with a solution of Chl *a* from *Anacystis nidulans* by Sigma. Details of the spectrofluorometric calibration procedure and the spectrophotometric (Kontron, Uvikon) analyses are given in Lazzara et al. (1997). HPLC analyses were carried out in Italy 1 month later according to Mantoura and Llewellyn (1983) using an HPLC Beckman System 166.

Measurements of primary production were performed in simulated *in situ* conditions. Each sample was poured into light and dark Pyrex 150-ml bottles and incubated with 1 ml (20 μCi) of $NaH^{14}CO3$. Incubations of 4–6 h were carried out in incubators cooled by circulating surface seawater, at 1% of incident light obtained by means of neutral light screens. After incubation, separation into size fractions (total, micro-, nano- and picophytoplankton) was obtained by differential filtration.

The P-E relationship was studied in the bottom community of pack ice. Sea-ice samples were melted in 0.2 μm filtered seawater (temperature −1.5°C, dilution 1:20). Sub-samples were placed in 50-ml bottles, inoculated with 20 μCi of $NaH^{14}CO3$ and then submitted, for 1 h, to 12–24 irradiance levels using a radial photosynthetron (Babin et al. 1994). In order to check for dark fixation, one sub-sample of each sample was incubated in darkness with the addition of four drops of a saturated solution of DCMU in seawater (Legendre et al. 1983). Filtration on the 25-mm Whatman GF/F filters was carried out immediately after incubation, in the same light conditions as for core-sectioning operations.

Radioactive content for each sample, as well as for the samples of size-fractionated primary production, was measured, after acidification, with 200 μl of HCL 0.1 N, within 24 h of filtration, in a Wallac 1400 liquid scintillator, using 10 ml of Aquasol II scintillation cocktail.

Attenuation and absorption coefficients at nine wavelengths in the VIS domain (412, 440, 488, 510, 555, 630, 650, 676, 715 nm) were recorded (Wetlabs, AC-9) in a few selected samples corresponding with the primary production incubation experiments. Spectral absorption of colored dissolved organic matter and the microalgal communities was measured (following Bricaud et al. 1981 and Kishino et al. 1986, respectively) with a spectrophotometer (LiCor-1800UW) and an integrating sphere. Microalgal community composition was analysed microscopically with a Zeiss invertoscope (IM35, ob. ×40); taxa were identified according to Balech (1976), Chretenniot-Dinet (1990), Hasle (1964), Medlin and Priddle (1990), Priddle and Fryxell (1985) and Ricard (1987).

To follow temporal changes of the sympagic flora once released in the pelagic environment, a mesocosm experiment was carried out as follows. The gamma sections of four cores were immediately submitted to incubations for 12 days in about 500 l of filtered surface seawater. The experiment was conducted in two different light conditions: at natural incident light, and at incident light reduced by 90% by means of a neutral screen. Sub-samples were taken daily for photosynthetic pigment analysis (HPLC) and for deriving P-E curves.

Results

Light, nutrients and salinity

The daily integrated solar irradiance (VIS + IR, Fig. 2) increased from 10 to 35 MJ m^{-2} day^{-1} at the end of November, while air temperatures (daily mean) increased between 4 and 7 November, reaching the highest value (1.2°C) on 22 November. Figure 3 shows the vertical profiles of nutrients and salinity for the ice core of 28 November when, immediately below the ice, seawater displayed the following characteristics: Si-Si$(OH)_4$ = 72.6 μM, N-(NO_3 + NO_2) = 27.5 μM, P-PO_4 = 1.96 μM and salinity = 34.75. With regard to

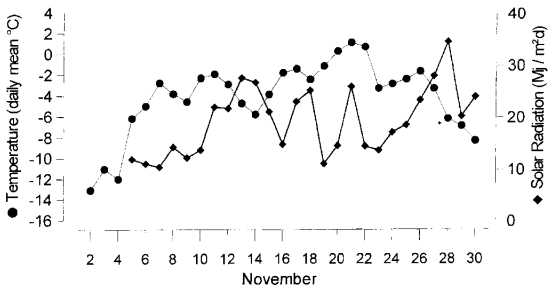


Fig. 2 Daily evolution of mean air temperature and daily integrated solar radiation (VIS+IR) during November 1997 at the ice cores sampling site

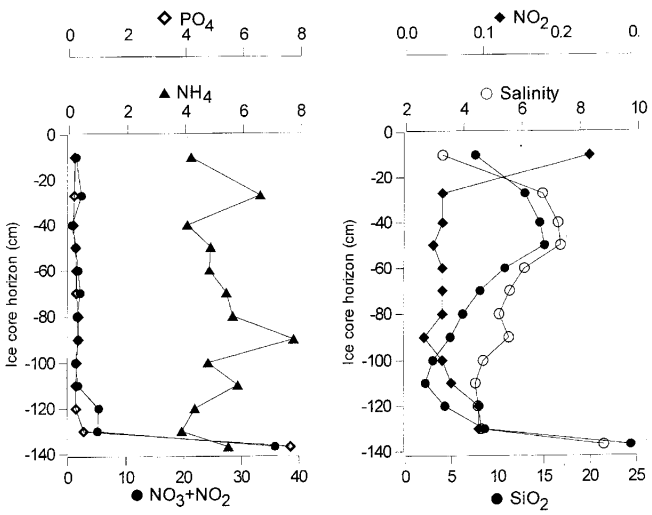


Fig. 3 Vertical distribution of nutrients and salinity in the ice core (scale: 0–8 μM, phosphate and ammonia; 0–40 μM nitrate + nitrite and silicate; 0–0.40 μM nitrite and 0–10 PSU salinity)

the ice core, concentrations of $Si\text{-}Si(OH)_4$ ranged from 7.5 to 24.4 μM (average for the entire core 9.4 μM). Among the nutrients, only silicate showed a relatively good correlation with the salinity values ($R^2 = 0.77$). The vertical profile of silicate concentrations showed a relative maximum in the upper part, at about 50 cm from the ice surface, and an absolute maximum at the bottom of the core. The concentrations of $N\text{-}(NO_3 + NO_2)$ varied between 0.7 and 35.9 μM (on average 5.7 ± 12.9 μM). $P\text{-}PO_4$ concentrations varied between 0.1 and 7.7 μM (on average 1.0 ± 2.8 μM). Maximum phosphate, nitrate and silicates concentrations were recorded at the bottom of the core. Vertical distribution of $N\text{-}NO_2$ and $N\text{-}NH_4$ displayed a wider pattern; nitrite concentrations were highest at the surface, just beneath the snow layer, in contrast to all other nutrients, and varied between 0.02 and 0.24 μM (on average 0.06 ± 0.6 μM). Ammonium concentrations for the entire ice core varied from 4.1 to 7.8 μM (on average 5.5 ± 1.8 μM).

The vertical profiles of $N\text{-}(NO_3 + NO_2)$ and $P\text{-}PO_4$ were well correlated ($R^2 = 0.98$, $n = 13$, $P < 0.001$) with an average N/P ratio of 4.6 ± 0.2, but they did not display significant correlation with salinity. Only silicate, among all the nutrients considered in this study, showed a low correlation with salinity values ($R^2 = 0.77$, $P = 0.40$).

Particulate organic matter, enzymatic activity and bacterial production

Particulate carbohydrate and protein concentrations, protein to carbohydrate ratio, aminopeptidase and β-glucosidase activities and bacterial production values are summarized in Table 1. Carbohydrate and protein concentrations in the sea ice at Terra Nova Bay ranged from 0.5 to 2.3 mg l^{-1} and from 0.2 to 2.0 mg l^{-1}, respectively. Vertical distribution of both carbohydrate and protein concentrations indicated a remarkable accumulation of organic matter in the bottom colored layer (Fig. 4) with a highest to lowest ratio of 4.3 and 7.5, for carbohydrate and protein, respectively.

Vertical patterns of bacterial enzymatic activities (Fig. 5a, b) were characterized by a strong increase in the bottom layers (100–140 cm depth) of the ice core, where values of aminopeptidase and β-glucosidase activities were 14 and 7 times higher, respectively, than values in the top layers (0–100 cm depth). Aminopetidase activity (on average 7.2 ± 3.36 μgM l^{-1} h^{-1}, highest to lowest ratio = 17.9) displayed values about 40 times higher than β-glucosidase activity (on average 0.18 ± 0.09 μgM l^{-1} h^{-1}, highest to lowest ratio = 42).

Bacterial production also showed a vertical pattern characterized by the highest values in the colored layer (Fig. 5c). Nevertheless, although enzymatic activities measured in the sea ice at Terra Nova Bay were very

Table 1 Carbohydrate (*CHO*) and protein (*PRT*) concentrations (μgC l^{-1}), protein to carbohydrate ratio, aminopeptidase (*LA*) and β-glucosidase (*BG*) activities (μM l^{-1} h^{-1}) and bacterial production (*BP*, ngC l^{-1} h^{-1}) in the sea ice at Terra Nova Bay on 22 November 1997

Horizon (cm)	CHO	PRT	PRT:CHO	LA	SE	BG	SE	BP	SE
0–20	214.3	133.0	0.51	1.68	0.04	0.07	0.07	1.2	0.8
20–40	321.8	302.7	0.77	1.63	0.12	0.02	0.02	1.2	0.7
40–60	462.8	464.3	0.82	1.18	0.05	0.05	0.05	1.5	1.1
60–80	302.0	417.6	1.13	1.10	0.50	0.11	0.01	1.4	1.2
80–100	496.5	591.1	0.97	17.91	0.72	0.66	0.08	5.5	1.3
100–140	927.4	997.7	0.88	19.75	0.05	0.20	0.00	8.5	0.5
Avg	454.1	484.4	0.8	7.2		0.2			
ES	94.9	110.1	0.1	3.4		0.1			

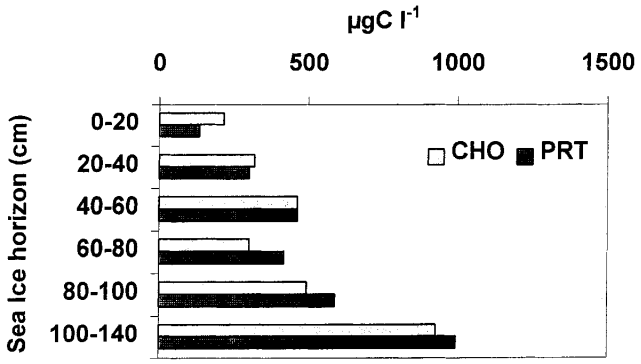


Fig. 4 Vertical distribution of carbohydrates (*CHO*) and proteins (*PRT*) in the sea ice at Terra Nova Bay. Data are reported as carbon equivalents (µgC l^{-1})

high, bacterial secondary production values were very low, ranging from 1.2 to 8.5 ngC l^{-1} h^{-1} (highest to lowest ratio of about 7).

Autotrophic biomass and primary production

The temporal dynamics of sympagic autotrophic biomass as chlorophaeopigments (Chl) are shown in Fig. 6 for the three different horizons. A marked increase was evident up to 22 November, which implied active growth of the microalgal sympagic community and indicated the presence of a bloom in the sea ice. A rough estimate of the mean growth rate gives 0.12 doublings day^{-1} during 2 weeks in the bottom layer, and up to 0.57 doublings day^{-1} in the surface layer. The three layers showed temporally differentiated patterns and were characterized by concentrations of Chl ranging within 3 orders of magnitude: in the alpha layer they varied between 0.9 and 16 µg l^{-1}, in the beta layer between 13 and 40 µg l^{-1} and in the gamma layer from 680 to 2480 µg l^{-1}.

The sympagic flora showed different size spectra in the three horizons considered. In the alpha horizon the percentage contribution of the three size classes were equivalent, while for the beta and gamma horizons, the microphytoplanktonic fraction largely dominated (90% of the biomass, Table 2). The dominance of this size fraction also increased over time up to 95%, in particular within the gamma horizon.

The concentration of most of the pigments analysed was very low; the ratio pigment/Chla indicated the absolute dominance of the brown algae, in particular of diatoms. The ratio fucoxanthin/Chla remained fairly constant over time within the three sections, as shown in Fig. 7, while the 19′hexanoiloxifucoxanthin (Prymnesiophyceae) increased only within the alpha horizon. These observations indicate that the less abundant algal groups also maintained their contribution, although with minor variations in time.

Microscopical observations showed that diatoms always dominated the sympagic microalgal community of the whole ice column, with two numerically equivalent

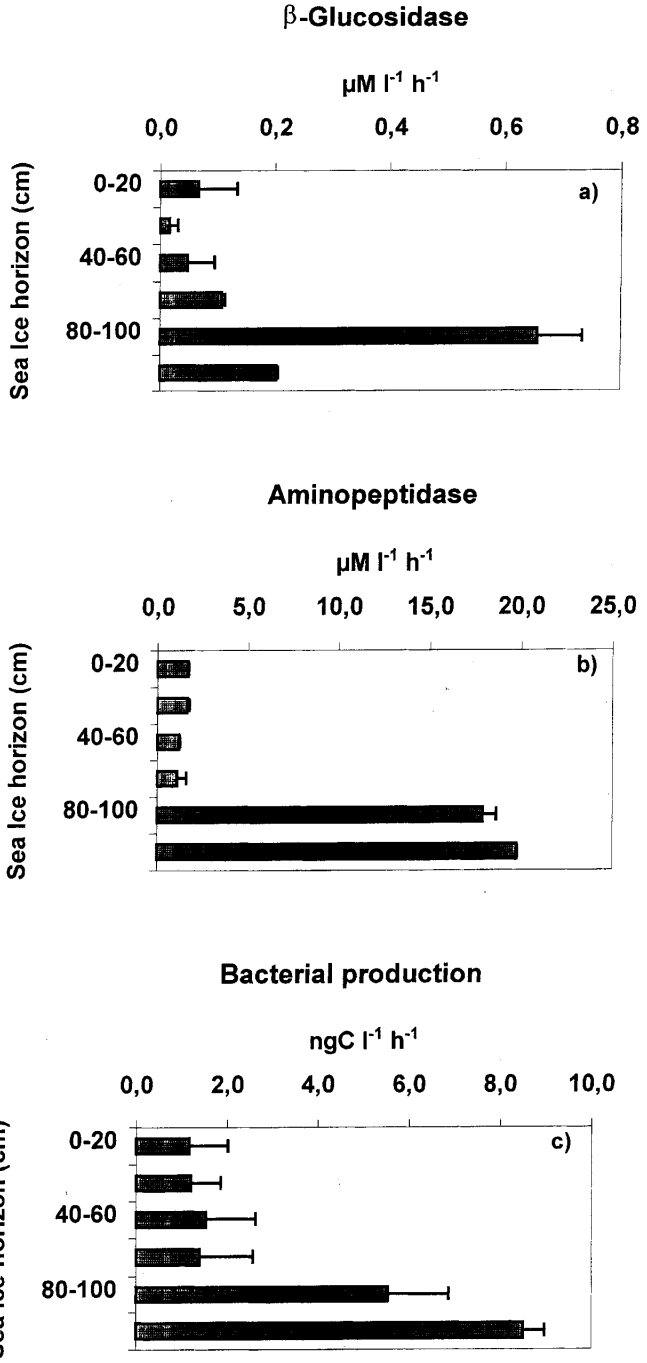


Fig. 5 Vertical distribution of aminopeptidase (**a**), β-glucosidase (**b**) and bacterial secondary production (**c**) in the sea ice at Terra Nova Bay. *Error bars* denote standard deviations ($n = 5$)

species characterizing the bottom community: *Amphiprora* sp. and *Nitschia* cfr. *stellata*. The latter was more important at the beginning of November and the former at the end of November. Other species, much less frequently observed in the three horizons, were always diatoms: *Actynocyclus* cfr. *actinochilus*, *Fragilariopsis* cfr. *curta*, *Pleurosigma* sp., *Nitschia* spp. (cfr. *subcurvata*, cfr. *closterium* and cfr. *promare*). Cell abundances varied in accordance with Chla concentrations, from 0.542 10^6

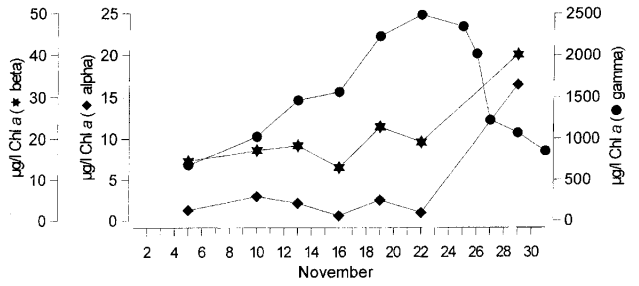


Fig. 6 Temporal evolution of chlorophaeopigments in the three sea-ice sections: alpha (0–80 cm), beta (80–130 cm) and gamma (130–140 cm)

Table 2 Percent contribution (*AVG, MIN, MAX*) of size-fractions (micro-, nano- and pico-) in the three different horizons during sampling period

	AVG	MIN	MAX
Alpha			
Micro- %	41.6	37.5	45.6
Nano- %	18.9	7.8	30.0
Pico- %	39.5	32.5	46.6
Beta			
Micro- %	85.8	82.5	89.0
Nano- %	9.0	6.7	11.2
Pico- %	5.3	4.3	6.3
Gamma			
Micro- %	92.3	87.9	96.8
Nano- %	5.6	1.1	10.3
Pico- %	2.1	0.4	4.6

cells dm^{-3} in the surface layer to 8.67 10^6 cells dm^{-3} in the intermediate layer, and 156 10^6 cells dm^{-3} in the bottom layer.

The photosynthetic processes within the gamma layer showed that during the study period the photosynthetic capacity was fairly constant, whereas both the efficiency and the adaptation index displayed temporal changes (Fig. 8). In particular, the efficiency increased and photoinhibition decreased, at increasing incident light levels; both the optimal light levels for photosynthesis and the photosaturation index decreased. It is noteworthy that the E_k of the sympagic flora was similar to that reported for the pelagic populations of phytoplankton during the austral spring and summer (Lazzara et al., in press; Saggiomo et al., in press).

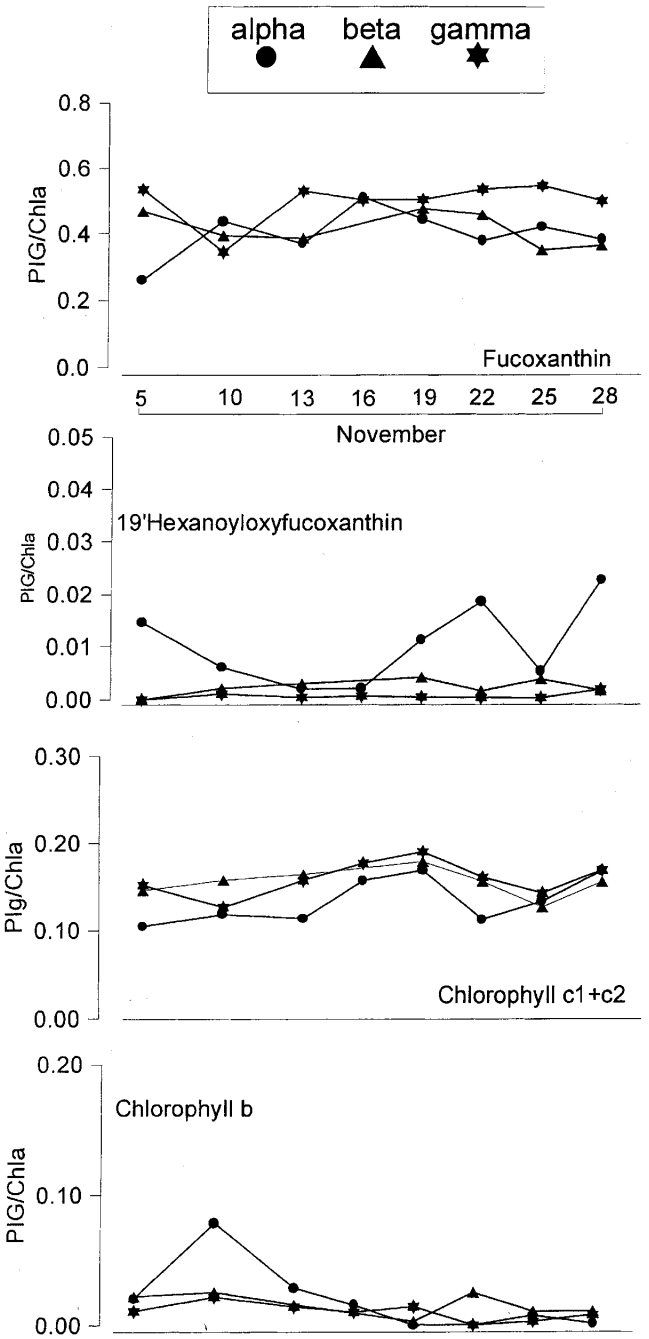


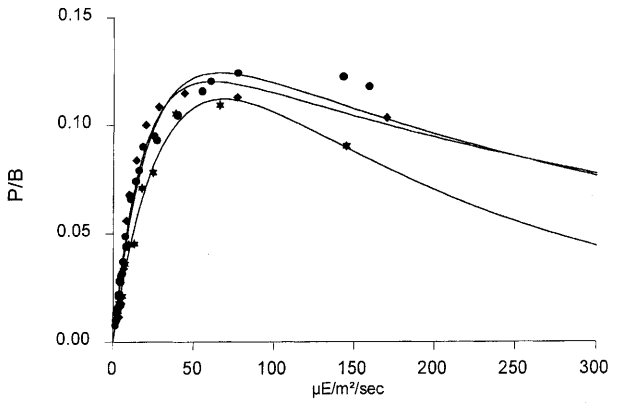
Fig. 7 Temporal evolution of ratio PIG/Chla in alpha, beta and gamma sections

The photo-acclimation experiment

Figure 9 shows the variation in time for the two experiments of total biomass and diatoxanthine, the latter representing the photoprotective pigment of brown algae to high light levels. At incident surface irradiance the population appeared to be photo-oxidized, but even at 10% of incident natural irradiance the phytoplankton population decreased and growth was observed to occur only after 8 days. A sample exposed to an average PAR of 854 µE m^{-2} s^{-1} showed a reduction of chlorophyll concentration of 27% after 5 min and 75% after 2 h, due probably to photobleaching.

Discussion

Salinity seems to be the only parameter that was completely controlled by physical forcing. Among the other parameters, potentially controlled by the interaction



Date	α	β	P^B_{max}	E_m	E_k
★ 13 Nov	0,0052	0,0008	0,112	68,25	21
● 16 Nov	0,0071	0,0004	0,124	65,54	17
◆ 25 Nov	0,0078	0,0003	0,121	60,85	15

Fig. 8 P-E curves of bottom communities (gamma) in different days

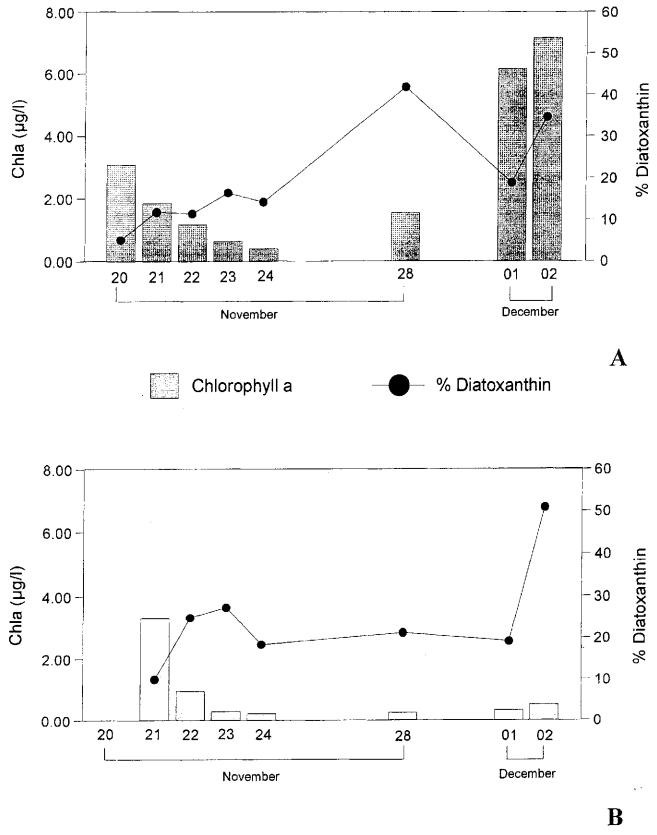


Fig. 9 Temporal evolution of biomass (Chla) and diatoxanthine in the two mesocosm experiments; **A** 10% of incident irradiance; **B** 100% incident irradiance

between physical and biological factors, silicate concentrations alone showed a significant correlation with salinity. On the base of the dilution curve given by Thomas et al. (1998), we can interpret our silicate values as the result of biological removal, except for the deepest horizon showing the highest levels of biomass and a slight excess of silicate. The more rapid regeneration processes of nitrogen and phosphorus, as compared to that of silicate, would thus result in the relatively higher levels shown by their profiles in the lowest ice layer. Remineralization processes exceeding autotrophic assimilation might explain this apparent paradox. The hypothesized importance of biological activities as the base of the correlation between remineralization time and the concentrations of dissolved nitrogen and phosphorus is further supported by the good correlation between these two nutrients, as well as by an N/P ratio of 4.6, much lower than the value of about 12 reported by Catalano et al. (1997) for the surrounding seawater. The high N-NH_4 concentrations, as abundant as N-NO_3 within the ice, as well as the fact that both these nitrogen forms showed concentrations well above the dilution curve in the bottom layer of the cores, may represent an indication of an intense heterotrophic activity.

The high values of inorganic nutrients found in this study could be partially biased by the release of intracellular material from melting ice (Günther et al. 1999). However, the above illustrated role of heterotrophic activity is supported by the extremely high values of enzymatic activities measured in this study. In fact, they are from 50 to 100 times higher than those reported by Misic et al. (1998) for melting sea ice, up to 1000 times higher than those given by the same authors for ice-free waters, and 10–75 times higher than the values found in winter in the intact sea ice of the Weddell Sea (Helmke and Weyland 1995). From a comparison between melting sea ice and ice-free waters with pack ice, the latter appears as a highly active system able to rapidly exploit the high amounts of available organic matter. The protein and carbohydrate carbon potentially liberated by aminopeptidase and β-glucosidase activities were compared to the total protein and carbohydrate concentrations in the sea ice. On average, about 490 µgC l^{-1} h^{-1} of protein carbon and 12 µgC l^{-1} h^{-1} of carbohydrate carbon should have been liberated. These values, compared to protein concentrations converted to carbon equivalents (484 µgC l^{-1}), indicate that the entire protein pool could be mobilized within 0.5 and 5.8 h (on average 2.7 h). By contrast, the total carbohydrate pool mobilization would occur within 11 and 300 h (on average 102 h). This rapid turnover rate, due to the preferential utilization of nitrogen-enriched organic compounds (e.g. proteins), may have important implications in cycling of inorganic nutrients, which can be actually utilized by the large resident autotrophic community. Moreover, such accumulation of inorganic nitrogen, in a promptly available form (NH_4), might represent an important gain for planktonic primary producers during the sea-ice melting processes.

We calculated that only a very small fraction of mobilized particulate organic carbon was converted into bacterial biomass (<0.01%). In fact, bacterial

secondary production values reported in this study are much lower (about 10–15 times) than those reported in the Weddell sea-ice winter (Helmke and Weyland 1995) but comparable to those found in the Weddell Sea by Grossmann (1994), during sea-ice formation. These results suggest that a possible inhibiting mechanism of bacterial secondary production might be present in the sea ice. Since grazing activity is negligible in the intact sea ice (Grossmann and Dieckmann 1994; Grossmann et al. 1996), other processes limiting bacterial secondary production, including dissolved organic compounds produced by micro-algae and possible stress effects of high oxygen concentrations, should be explored in the future.

Protein and carbohydrate concentrations (on average 0.9 and 1.1 mg l^{-1}, respectively) were about 23 and 4 times higher than in surrounding ice-free waters (Fabiano and Pusceddu 1998), indicating a clear accumulation of organic matter in the sea ice. The dominance of proteins and high values of the PRT:CHO ratio are, generally, distinctive characteristics of high productive areas (Pusceddu et al. 1996), while the dominance of carbohydrates is frequently observed in nutrient-depleted systems (Danovaro et al., in press). In Antarctic waters, the PRT:CHO ratio has been found to reach values of > 1 during maximum autotrophic activity, and decreases during particulate organic matter degradation and consumption processes (Fabiano et al. 1993; Fabiano and Pusceddu 1998). Similarly, Misic et al. (1998), by means of laboratory experiments, demonstrated a short-term decrease of the PRT:CHO ratio during the decomposition of particulate organic matter deriving from different sources. Values of the protein to carbohydrate (PRT:CHO) ratio (on average 0.8 ± 0.1) within the pack ice at Terra Nova Bay were comparable to those observed in fresh organic detritus-depleted waters, such as in the oligotrophic Ligurian Sea (Fabiano et al. 1984), reaching values > 1 only in the middle of the ice core. From this comparison and taking into account the rapid OM turnover rates estimated by means of enzymatic activity measurements, it might be inferred that the OM matter accumulated within the sea ice in this study was already partially degraded. Further analyses of the digestible fraction (Fabiano and Pusceddu 1998) of OM in the sea ice will help to prove this hypothesis.

The diatoms that dominated the microalgae observed in this study have been previously described as typical of coastal bottom-ice communities in Terra Nova Bay (Lazzara et al. 1995, 1997) and also at McMurdo Sound (Palmisano and Sullivan 1983).

The onset of autotrophic biomass growth in the bottom horizon (Fig. 6) appeared to be in phase with the first increase in solar radiation (Fig. 2), whereas the decline of the bloom began after a long period of high temperatures and newly increased irradiance. It seems likely that both processes of progressive ice melting and higher photoinhibition can entail, for extremely low-light adapted cells, the final phase of the sympagic microalgal bloom.

It should be noted that the microalgal biomass integrated for the whole sea-ice column reached quite high values (up to 280 mg Chl m^{-2}), which are similar to or higher than those characteristic of the bloom period in the ice-free water column at Terra Nova Bay (180 mg Chl m^{-2} for the whole euphotic zone, Lazzara et al., in press). This first spring sympagic bloom occurring in the sea ice seems at least as important as the following one or two summer blooms in the water column.

The average P^B_{max} of 0.12 mgC $(mgChla)^{-1}$ agrees with the biomass growth observed within the lower ice layer. These P^B_{max} values fall in the same range as those reported for other Antarctic coastal areas (Lizotte and Sullivan 1991, 1992). The high algal biomass coupled with P^B_{max} values reported within the sea ice suggest that the sympagic algal communities, especially in the bottom ice layers, are well adapted to growth at very low light values. When bottom sea-ice algal communities are experimentally exposed to low light levels (100 $\mu E\ m^{-2}\ s^{-1}$) they are greatly damaged due to the lack of adequate photoprotective systems.

This observation is further supported by the results of short-time incubations (from 5 min to 2 h), which showed that high irradiance levels induced drastic reductions of Chla concentration, a probable indication of photobleaching. Prézelin et al. (1998) obtained similar great reductions in Chla concentrations in frazil ice communities from Palmer Station (Antarctic Peninsula). Our results, therefore, suggest that microautotrophs inhabiting sea ice might have a minor role in the pelagic algal blooms. Moreover, as shown by the low phaeopigment concentrations, which characterize the bottom sympagic microalgal community, the community of the bottom ice layer does not seem to experience strong grazing pressure within this compartment.

We emphasize that microalgal blooms within the sympagic system represent the first finding of this kind for Terra Nova Bay. This bloom is comparable with or even greater than summer blooms reported in ice-free waters in the same area. (Lazzara et al., in press). As shown by Lazzara et al. (1996) for open-water phytoplankton communities during summer, the light regime represents an important factor in also controlling sympagic primary production during spring by an algal community adapted to an extremely low-light regime.

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