Trophodynamic and biogeochemistry in the annual sea-ice at Terra Nova Bay (Ross Sea, Antarctica).

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BIOGEOCHEMISTRY AND ALGAL COMMUNITIES IN THE ANNUAL SEA ICE AT TERRA NOVA BAY (ROSS SEA, ANTARCTICA)

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During the fifteenth Italian Antarctic expedition, in the framework of the Pack Ice Ecosystem Dynamics programme, we investigated structure and functioning of the sympagic communities in the annual pack ice at Terra Nova Bay (74 °41.72′S, 164 °11.63′E). From November 1 to November 30 1999, we collected intact sea ice cores and platelet ice samples at an interval of 3 days. Ice samples were analysed for inorganic nutrients concentrations, algal biomass and productivity, pigment spectra, extracellular enzymatic activities and bacterial carbon production, micro-algal and metazoan community structure. Autotrophic biomass in the bottom ice increased more than two orders of magnitude from the beginning to the end of November 1999 (i.e. from *c.* 1–400 mg chlorophyll *a* m^{-3}). In the same temporal interval, inorganic nutrients concentrations as well as dissolved organic matter sharply increased. Pigment spectra and microscopic analyses revealed that bottom ice communities were different from those of the platelet ice. The bottom-ice sympagic flora was represented almost exclusively by cryobenthic species, whereas platelet ice was characterised by the presence of both cryopelagic and cryobenthic species. Metazoan community in the bottom sea ice was largely dominated by copepods. In particular, the calanoiod *Stephos longipes* and the harpacticoid *Harpacticus furcifer* accounted for more than 90% of the sympagic fauna. In the bottom sea ice concentrations of phaeophorbides and other degraded phytopigments were low indicating that most of the sympagic flora was active. These findings suggest that grazing pressure might be only a minor factor controlling or regulating inorganic nutrient concentrations. Conversely, potential degradation rates of organic carbon mediated by extracellular enzymatic activity were very high and largely exceeded organic matter production by photosynthesis.

Keywords: Sea ice; Nutrients; C:N ratio; Microalgae; Sympagic meiofauna

1 INTRODUCTION

Sea ice surrounding the Antarctic continent varies in extent from 4×10^6 km^2 in summer to 20×10^6 km^2 in winter, representing one of the largest and most dynamic ecosystems on Earth (Arrigo *et al.* 1997). Sea ice formation and melting are major factors affecting

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physical–chemical characteristics and biological processes of the entire Southern Ocean (Garrison and Buck, 1991; Smetacek *et al.*, 1992; Dieckmann *et al.*, 1998; Gleitz *et al.*, 1998; Brierley and Thomas, 2002).

Annual primary production in the Antarctic sea ice ranges between 30 and 70 Tg C (Arrigo *et al.*, 1997). Although primary production in the sea ice has been estimated to account for only a minor fraction (1–4%) of the total biogenic carbon production in the Southern Ocean, sea ice algal biomass plays a fundamental role representing a highly concentrated food source for higher trophic levels, both during the period of autotrophic biomass accumulation in the sea ice and during ice melting in summer (Legendre *et al.*, 1992).

Sea ice biota includes a variety of micro-organisms, such as micro-algae and small metazoans, living within the ice (i.e. sympagic organisms) and larger animals living at the sea ice–water interface (Spindler, 1994).

During austral spring, dense auto- and heterotrophic populations accumulate within the annual sea ice where algal biomass and primary production may reach values as high as 400 mg chlorophyll *a* (Chl-*a*)m^{-2} and 1 g C m^{-2} d^{-1}, respectively (Günther *et al.*, 1999; McMinn *et al.*, 1999; Guglielmo *et al.*, 2000; Thomas *et al.*, 2001). During summer, this biomass is released into the water column after ice melting (Leventer and Dunbar, 1996; Fischer *et al.*, 1988), fuelling both the pelagic and benthic coastal environments with huge amounts of bioavailable organic carbon (Fabiano and Pusceddu, 1998; Pusceddu *et al.*, 2000).

However, at Terra Nova Bay it has been recently reported that the considerable accumulation of algal biomass in the sea ice during austral spring is not followed by the depletion of inorganic nutrient concentrations, which, in contrast, remain very high (Guglielmo *et al.*, 2000).

Several biological factors have been invoked to explain such a discrepancy; zooplankton grazing on micro-algal cells and very high organic matter degradation rates have been recently proposed (Günther *et al.*, 1999; Guglielmo *et al.*, 2000). The comprehension of factors involved in such an apparently paradoxical condition of high nutrient–high biomass is of paramount importance for clarifying trophodynamic and biogeochemical pathways in the Antarctic sea ice.

In the frame of the fifteenth Italian Antarctic Expedition, the Pack Ice Ecosystem Dynamics project aimed at investigating whether transfer of matter and energy within the sea ice trophic web are top–down (grazing) and/or bottom–up (nutrient) controlled. To do this, we investigated vertical distribution and temporal changes of inorganic nutrient concentrations, pigment spectra and species composition of the algal sympagic communities in the annual pack ice and platelet ice as well as organic matter content and extracellular enzymatic activities in its bottom layer and in the platelet ice. In the bottom-ice layer, we also investigated the composition of metazoan populations.

2 MATERIALS AND METHODS

The sampling area, ca. 100 m^2, was located in the offshore annual pack ice at Terra Nova Bay (74 °41.72′ S, 164 °11.63′ E) (Fig. 1). Sea ice cores (10 cm i.d.) were collected at 2–3-day intervals from 1 November to 30 November 1999, using an aluminium corer. Sea ice thickness (about 2.4 m) remained constant during the sampling period.

Immediately after collection, sea ice cores were sliced (in dim light conditions to avoid photodamage) into 3-, 6- and 12-cm thick sections, according to the considered variables. Four cores were collected at each sampling date and used for nutrient measurements, photosynthetic pigment analyses, bacterial carbon production, extracellular enzymatic activities and primary production measurements.

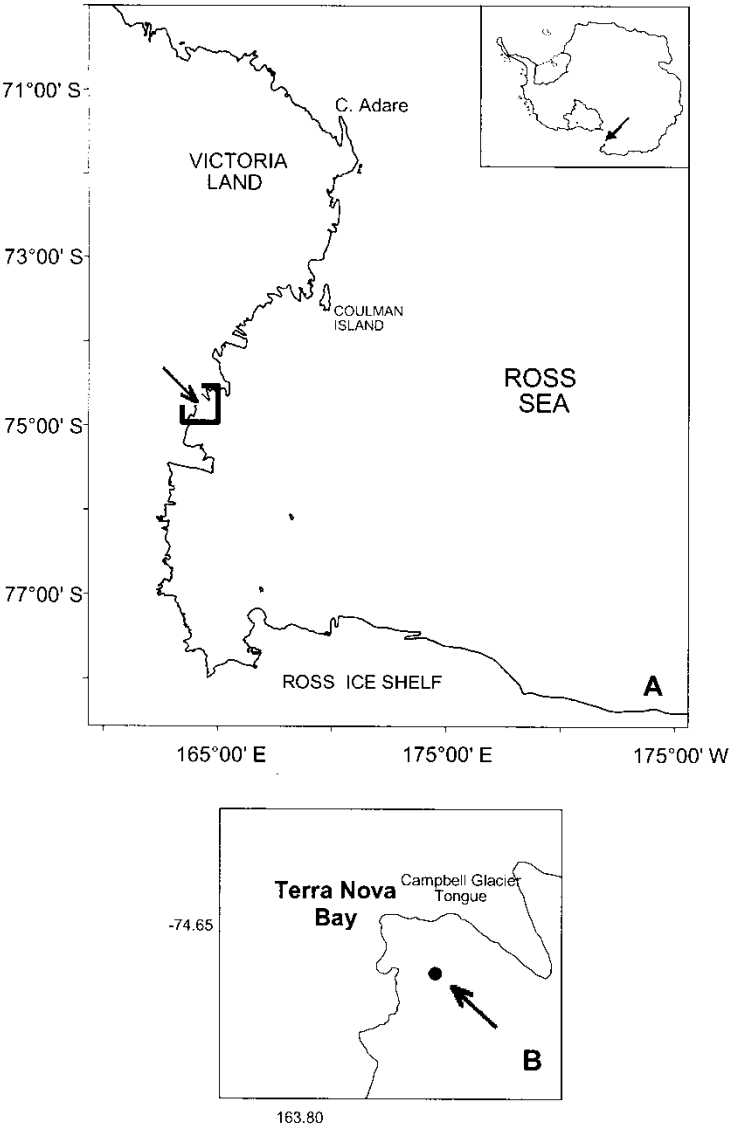

FIGURE 1 Sampling area (A) and station location (B).

For the determination of inorganic nutrient concentrations ($NO_3 = NO_2$, NH_4, PO_4, $Si(OH)_4$), the lowest 50 cm of each sea ice core was sliced into sections of 10 cm thickness, whereas the remaining upper part of the core was sliced into sections of 20 cm. Sections were then melted in a thermostatic bath at a temperature close to 0 °C; after melting, samples were pre-filtered onto Whatman GF/C filters (Guglielmo *et al.*, 2000). Nutrient concentrations ($\mu mol\,dm^{-3}$) were determined by means of a segmented-flow autoanalyser ALPKEM, according to the methods of ALPKEM Flow Solution (ALPKEM, 1992a–c; 1994), while practical salinity units (UNESCO, 1981) were obtained by means of an Autosal Guildline salinometer.

In order to investigate sea ice formation processes occurring during winter, tritium concentrations expressed as Tritium Units (TU; $1\,TU = 0.118\,Bq\,dm^{-3}$) were determined along sea

ice cores. Radioactive content of sea ice samples was measured, after acidification with 200 µl of 0.1 N HCl, within 24 h from filtration, in a Wallac 1400 liquid scintillator, using 10 ml of Aquasol II as a scintillation cocktail. The radioactive content of different sea ice layers has been used to provide information on the different water masses that originated the sea ice, following the technique already applied on ice-free water masses (Michel *et al.*, 1979; Roether, 1989; Bayer and Schlosser, 1991; Schlosser *et al.*, 1991).

For particulate organic carbon and nitrogen analyses, sea ice was melted in the dark at *c.* 0 °C and filtered onto Whatman GF/F filters. Filters were analysed by a CHN analyser.

For the analysis of extracellular aminopeptidase activity, three to five replicates (about 5 cm^3 of sea ice broken up into small pieces) for each section were treated immediately as reported by Guglielmo *et al.*, (2000). Briefly, sea ice samples were incubated 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. 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, sea ice samples were melted at room temperature in dim light conditions and filtered through Whatman GF/F glass fibre filters. Spectrofluorometric analyses of Chl-*a*, phaeopigments (Phaeo) and spectrophotometric determination of chlorophaeopigments (Chl) were carried out within a maximum of 12 h after collection. Results of both analyses indicate the presence of a strong correlation between Chl-*a* and Chl concentrations ($r^2 = 0.975$); therefore, only Chl data are presented here. Filters were placed in neutralised 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 for the spectrofluorometric calibration procedure and for the spectrophotometric (Kontron, Uvikon) analyses are given in Lazzara *et al.* (1997). The HPLC analyses were carried out according to Mantoura and Llewellyn (1983) using an HPLC Beckman System 166.

Micro-algal community composition was analysed microscopically with a Zeiss invertoscope (IM35, ob. 40 ×); taxa were identified according to Hasle (1964), Balech (1976), Priddle and Fryxell (1985), Ricard (1987), Chretenniot-Dinet (1990) and Medlin and Priddle (1990).

For metazoan counting, ice cores were sliced into three to five layers and then melted in a thermostatic bath at 0 °C. After melting, samples were preserved in a 2% buffered formalin solution. In the laboratory, all metazoans were identified under a dissecting microscope. All copepods were identified at species level and assigned to the correct development stage. In this article, only data on copepods are included.

3 RESULTS AND DISCUSSION

The Ross Sea is characterised by the largest continental shelf of the entire Antarctic ocean and is one of the most productive areas of the Southern Ocean (Comiso *et al.*, 1993; Arrigo and McClain, 1994; Saggiomo *et al.*, 1998; Saggiomo *et al.*, 1999).

Remarkable differences in the structural characteristics of the sea ice and the presence/absence of an unconsolidated platelet layer under the congelation ice have been observed along the Ross Sea coastline. In particular, Terra Nova Bay has been reported as a site of formation of platelet ice, while this layer is absent in the adjacent Woods Bay (Guglielmo *et al.*, 2000). Therefore, we suggest that the formation of a platelet ice layer in Terra Nova Bay could be a triggering mechanism leading to different algal assemblages inhabiting these two adjacent areas.

In November 1999, the thickness of the pack ice at Terra Nova Bay was about 240 cm, notably thicker than the average thickness of 140 cm observed in 1997 in the same area (Guglielmo *et al.*, 2000) and exhibited a different structure between the upper 120 cm and the lower part of sea ice cores. The analysis of vertical profiles of tritium and crustal radionuclide concentrations in the sea ice (Fig. 2) indicates that higher values of tritium (on average 4.7 ± 1.1 TU), coupled with the presence of other radionuclides (^{214}Bi-^{214}Pb) of crustal origin, were found in the ice core below 120 cm horizon rather than in the upper one (1.6 ± 0.5 TU). Despite the lack of classic textural analysis of the sea ice, this result suggests that the formation of the lower part of sea ice might have occurred after an intense aeolian advection of terrestrial material, whereas the upper sea ice column was formed under different meteorological conditions.

Figure 3 illustrates Chl-*a* vertical distribution in the ice cores at the beginning and at the end of November 1999. On 4 November, algal biomass in the upper 220 cm of the pack ice was <1 μg Chl-*a* l^{-1}, and slightly higher values – up to 1.30 μg Chl-*a* l^{-1}– were measured in the bottom 20 cm. Conversely, algal biomass in the platelet ice at the beginning of November was very high (90 μg Chl-*a* l^{-1}; Fig. 3). At the end of November, algal biomass concentrations increased significantly throughout the ice core including platelet ice. With the exception of the bottom-ice layer, the maximum increase was observed in the upper layer of the intact sea ice. Biomass accumulation exceeded 400 μg Chl-*a* l^{-1} in the bottom-ice layer and 350 μg Chl-*a* l^{-1} in the platelet ice (Fig. 3). Vertical and temporal changes in the composition of the photosynthetic pigment pools clearly indicated the presence of significant changes in the taxonomic composition and photophysiological adaptation of algal assemblages in the different layers of the ice cores.

Fucoxanthine was by far the most abundant pigment, in particular in the bottom ice, indicating the dominance of diatoms. Relatively high concentrations of Chl-*b* were observed, with a decreasing pattern from the top to the bottom layers of sea ice; Chl-*b* concentrations in both the bottom and platelet ice were almost undetectable. Peridinin, a diagnostic pigment for dinoflagellates, was recorded throughout the ice core in variable concentrations but dinoflagellates never dominated the sympagic assemblages. As far as photoprotective pigments

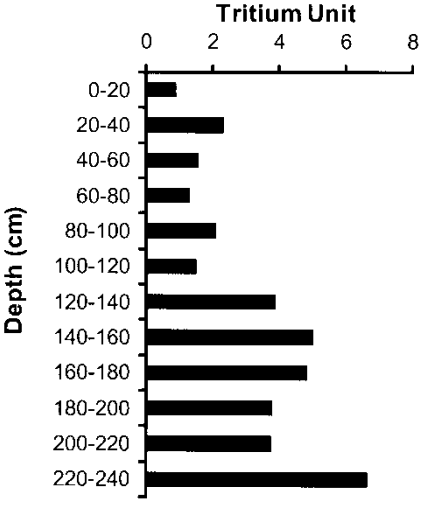

FIGURE 2 Vertical profile of tritium concentrations ($1\ \text{TU} = 0.118\ \text{Bq dm}^{-3}$) in the sea ice cores collected at Terra Nova Bay in November 1999.

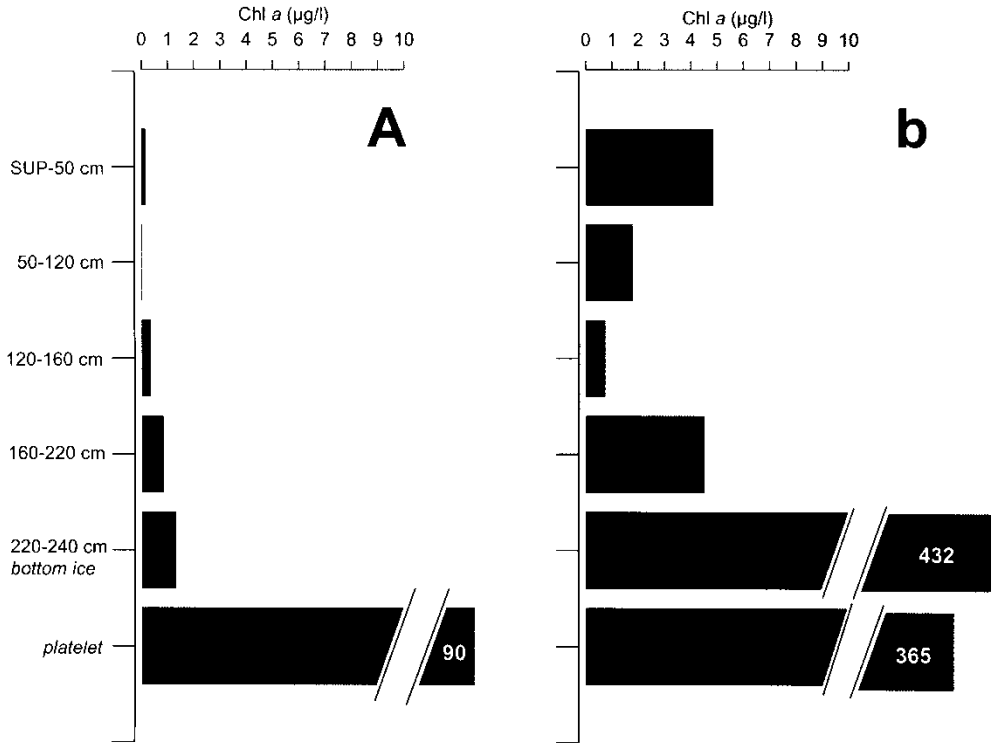

FIGURE 3 Chl-*a* distribution along the ice cores on November 4 (A) and November 28 (B) 1999.

concentration is concerned, diadinoxanthin occurred throughout the ice core, whereas diatoxanthin was observed only in the top layer of the sea ice. At the end of November, the dominance of fucoxanthine was even more pronounced (about 70% of total pigments with exception of Chl-*a*) along the entire ice core. Chl-*b* was found at very low concentrations and only in the top layer. Peridinin concentrations were even lower than at the beginning of November.

Algal biomass accumulation in the bottom layer of intact sea ice in 1999 was notably lower than in 1997 (Fig. 4; Guglielmo *et al.*, 2000). Such difference may be related to the much thicker pack ice in 1999 (240 *vs.* 140 cm in 1997). Furthermore, thicker snow coverage

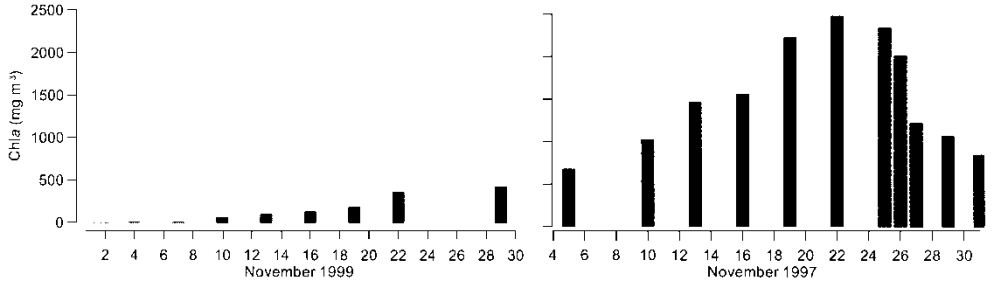

FIGURE 4 Temporal evolution of micro-algal biomass ($\mu g\, l^{-1}$ Chl-*a*) in the bottom ice during spring in 1999 and in 1997.

(>20 cm) was observed in 1999, so that lower light availability likely occurred in 1999 (Arrigo *et al.*, 1991). In 1999, snow coverage progressively decreased during November, thus, allowing light to reach deeper ice layers and, therefore, enhancing algal growth. Clearly, different environmental conditions (in terms of light availability and snow cover) in 1999 resulted in a delay of micro-algal accumulation in the pack ice as occurred in 1997 (Fig. 4). As the sampling period in 1999 was limited to November, we do not know whether sympagic algal biomass reached values comparable to those recorded in 1997 in a later period. Previous investigations in the same area reported that photosynthetic capacity of the bottom-ice sympagic flora are very low, suggesting that algal growth should have occurred at very low rates. These findings suggest that the increase in bottom-ice micro-algal biomass might be the result of both colonization and accumulation of micro-algae entering intact sea ice from platelet (Guglielmo *et al.*, 2000), rather than deriving from *in situ* algal growth.

Microscopic analyses of the bottom and platelet ice layers showed the presence of very different algal assemblages in these two layers. The bottom-ice flora was mainly composed by cryobenthic diatoms, of which the most abundant species was *Entomoneis kjellmanni* (e.g. *Amphiprora* sp.). On the other hand, the platelet layer was characterised both by pelagic and benthic species.

Previous studies carried out in Terra Nova Bay reported that diatoms largely dominate both the pelagic and the sympagic flora, with clear differences in species composition. *Fragilariopsis curta* generally dominated the pelagic flora (Marino *et al.*, 1995), whereas cryobenthic diatoms, such as *Amphiprora* sp. and *Nitzschia* cf. *stellata*, accounted for more than 90% of the entire bottom sea ice flora. Further, the possible role of sea ice melting in triggering summer phytoplankton blooms has been highlighted (Saggiomo *et al.*, 1998, 1999, 2002).

Such composition of the sympagic algal community has been previously reported in the Terra Nova Bay sea ice, irrespective of sea ice thickness (Guglielmo *et al.*, 2000). Therefore, the algal assemblages observed in this study appear as a distinctive feature of the Terra Nova Bay sea ice, while sea ice algal assemblages in the nearby Wood Bay are largely dominated by chromophyceans (Moro *et al.*, 2000).

During the austral spring, most of the autotrophic biomass in the annual sea ice was concentrated near the sea ice–water interface in Terra Nova Bay, as previously reported in other Antarctic sites (Brierley and Thomas, 2002). As outlined above, in the present study a continuous significant increase of autotrophic biomass (by a factor of about 400) in the bottom sea ice was observed from 1 November to 30 November (Fig. 4). Contemporarily, while a clear increase in particulate organic nitrogen concentrations was observed, no clear patterns in particulate organic carbon (POC) concentrations occurred (Fig. 5(a) and (b)). As a consequence, the C : N ratio values (Fig. 5(c)) clearly decreased from early November (about 10) to the end of the sampling period (about 4). Such pattern suggests that, at the end of November, nitrogen-rich organic compounds accumulated in the bottom sea ice, thus, potentially guaranteeing high amounts of fresh and bioavailable organic matter for heterotrophic metabolism.

From the beginning to the end of November 1999 (Tab. I, Fig. 6), particulate organic nitrogen (PON) concentrations increased both in the lowest 10 cm of sea ice (from 6.6 to 107 $\mu mol\,dm^{-3}$, i.e. about 15 times) and, to a lower extent, in the 1 m layer above (from 4.1 ± 0.9 to $11.0 \pm 2.0\,\mu mol\,dm^{-3}$). A similar trend was observed in the bottom sea ice layer for all inorganic nutrients investigated. At the end of November, nitrite plus nitrate and PO_4 concentrations in the bottom sea ice layer reached values as high as 70.6 and 14.1 $\mu mol\,dm^{-3}$, respectively. These concentrations were well above those observed in the underlying seawater and much higher than those expected from the

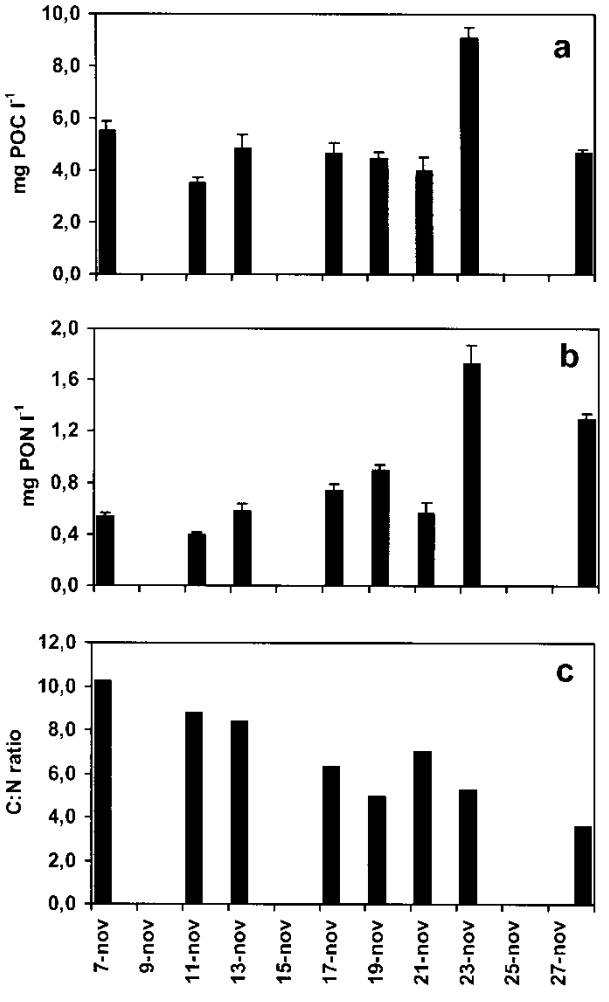

FIGURE 5 Temporal changes of particulate organic carbon (a) and nitrogen (b) concentrations and C : N ratios (c) in the bottom ice at Terra Nova Bay during November 1999.

observed increase of salinity, confirming previous findings in the annual pack ice at Terra Nova Bay (Guglielmo *et al.*, 2000). Conversely, inorganic nutrient concentrations in the sea ice layer comprised between 130 and 230 cm displayed an inverse temporal pattern, characterised by a clear depletion of nitrate plus nitrite, PO_4 and $Si(OH)_4$ concentrations, that resulted below the expected values normalised to salinity. These findings suggest that autotrophic processes in the upper sea ice layer (i.e. 120–230 cm) lead to a clear nutrient

TABLE I Inorganic and organic nutrients concentrations in the bottom sea ice at the beginning and at the end of November 1999.

Date	*DIN (μM N)*	*PO_4 (μM P)*	*SiO_2 (μM Si)*	*DOP (μM P)*	*DON (μM N)*
November 1	19.18	0.35	9.6	0.13	0.18
November 25	87.15	14.11	22.9	5.22	107.16

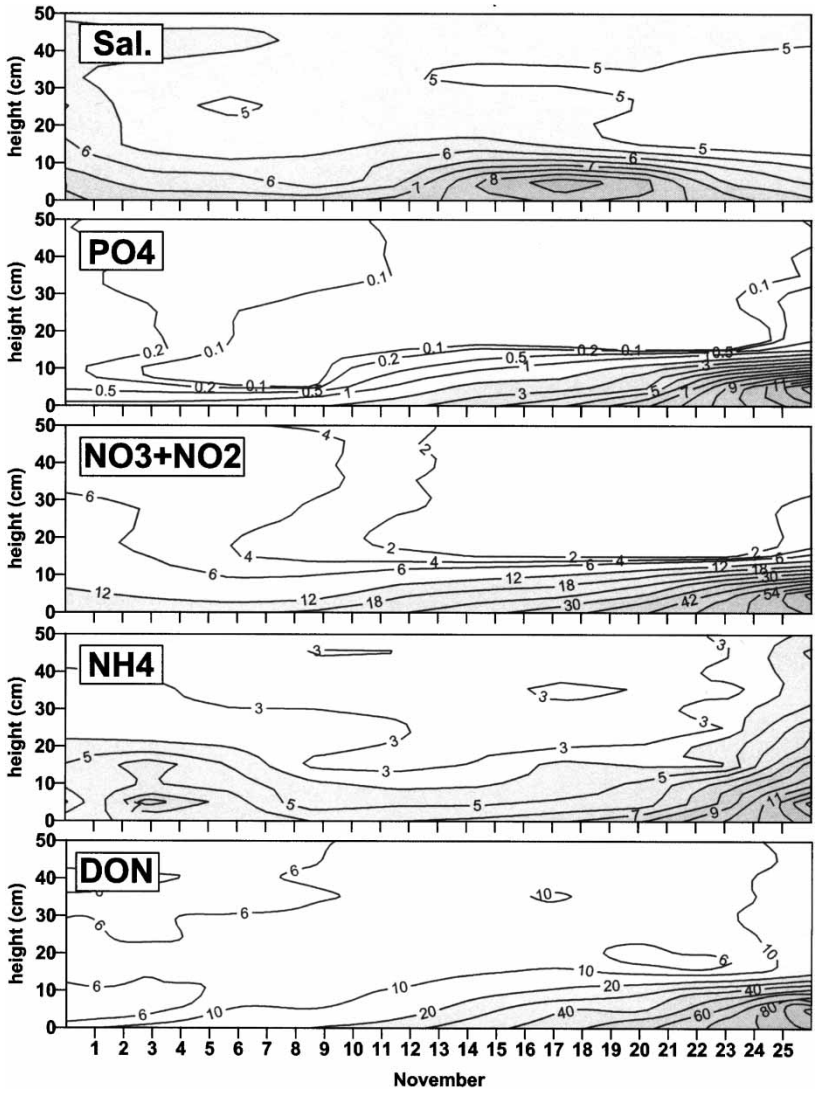

FIGURE 6 Temporal changes in nutrient concentrations in the sea ice at Terra Nova Bay during November 1999.

depletion, while in the bottom sea ice a paradoxical increase of inorganic and organic nutrients and algal biomass is observed. This apparent paradox has been previously reported in the same area and in other coastal sea ice regions of the Southern Ocean (Guglielmo *et al.*, 2000; Brierley and Thomas, 2002). Such a discrepancy has been previously ascribed to the occurrence of remineralisation activities much higher than primary production, able to maintain inorganic nutrient supply to sympagic micro-algae always above their requirements (Guglielmo *et al.*, 2000). Extracellular enzymatic activity are a key step in organic matter cycling (Azam, 1998). In this study, we found aminopeptidase activity values in the bottom sea ice and in the platelet ice much higher than those in the surrounding ice-free waters (Fig. 7).

Based on dissolved organic nitrogen concentrations, we tentatively estimated the potential degradation rate of the dissolved organic nitrogen pool in the bottom sea ice. To do this, we

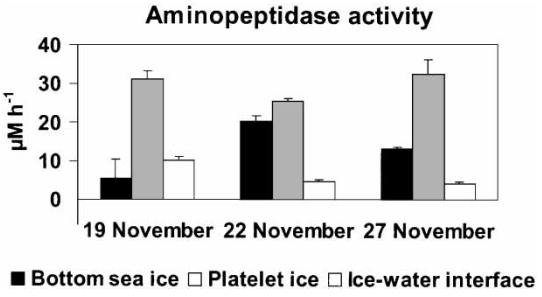

FIGURE 7 Aminopeptidase activities in the bottom sea ice, platelet ice and ice–water interface in 1999.

assumed DON entirely represented by dissolved proteins (Keil and Kirchman, 1993) and, by dividing the proteinaceous C pool potentially liberated by aminopeptidase activity (assuming 72 $\mu g\,C\,\mu mol^{-1}$ of MCA as a conversion factor; Fabiano and Danovaro, 1998) for the carbon equivalents of dissolved proteins (assuming 0.49 $\mu g\,C\,\mu g^{-1}$ as a conversion factor; Fabiano *et al.*, 1995), we estimated that the entire dissolved organic nitrogen pool in the bottom sea ice could be potentially degraded (i.e., mobilised) in a few hours (1–5 h). Although based on the maximal aminopeptidase activity (i.e. at saturating substrate concentrations) and on conversion factors, these results suggest that rates of bacterial-mediated degradation of organic matter in the bottom sea ice may be extremely fast. Such high potential degradation rates of organic carbon ($>10\,g\,C\,m^{-2}\,d^{-1}$ only for the protein pool) largely exceed organic matter production by photosynthesis, possibly leading to the observed accumulation of inorganic nutrients.

Another possible factor involved in the accumulation of inorganic nutrients in the bottom sea ice concurrently with the accumulation of algal biomass could be identified in the grazing pressure by planktonic herbivores, which, however, were present in relatively low numbers. Metazoan community associated with the bottom sea ice was largely dominated by

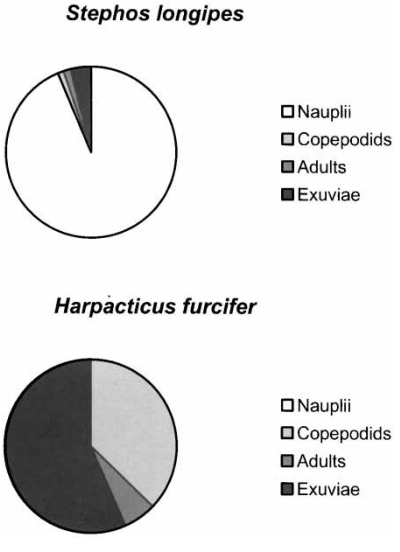

FIGURE 8 Life stages of *S. longipes* and *H. furcifer* in the sea ice at Terra Nova Bay during spring in 1999.

TABLE II Range of abundance of *S. longipes* and *H. furcifer* life stages in the sea ice at Terra Nova Bay during spring in 1999.

	Min (ind. l^{-1})	*Max (ind. l^{-1})*
S. longipes		
Nauplii	3.5	509.5
Copepodids	0.0	7.9
Adults	0.0	13.1
Exuviae	0.0	21.0
H. furcifer		
Nauplii	0.0	0.0
Copepodids	0.0	60.1
Adults	0.0	12.0
Exuviae	0.0	71.1

copepods. In particular, the calanoiod *Stephos longipes* and the harpacticoid *Harpacticus furcifer* accounted together for more than 90% of the entire sympagic meiofauna. While *S. longipes* was mostly represented by nauplli (Costanzo *et al.*, 2002), *H. furcifer* individuals were mainly present as copepodids (Fig. 8, Tab. II). This result confirms previous findings on the life-cycle strategy of the Antarctic calanoid copepods (Schnack-Schiel *et al.*, 1995, 2001). Both species displayed widely fluctuating temporal patterns. A peak in *S. longipes* abundance was observed on 19 November, whereas *H. furcifer* displayed much lower abundance for the entire sampling period (Fig. 9). The two dominant ice-associated copepod species in the Weddell Sea are the calanoid *S. longipes* and the harpacticoid *Drescheriella glacialis* (Dahms *et al.*, 1990; Schnack-Schiel *et al.*, 1995, 1998, 2001). In the sea ice of Terra Nova Bay, the highest copepod abundance was observed in the lower part of the ice cores (i.e. bottom 10 cm), where highest Chl-*a* concentrations were measured (up to 400 $\mu g\, l^{-1}$; Guglielmo *et al.*, 2000), as reported in the Eastern Weddell Sea (Dahms and Dieckmann, 1987; Kurbjeweit *et al.*, 1993; Schnack-Schiel *et al.*, 1995). The HPLC analyses indicated that concentrations of phaeophorbides and other degraded phytopigments were extremely low in the bottom sea ice, thus, indicating that most of the sympagic flora was active. These findings suggest that grazing pressure may be only a minor factor controlling or regulating inorganic nutrient concentrations in the bottom sea ice.

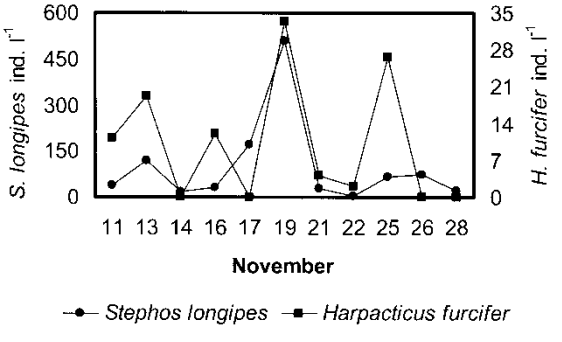

FIGURE 9 Temporal changes of *S. longipes* and *H. furcifer* abundance (ind. l^{-1}) in the bottom ice in Terra Nova Bay, November 1999.

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References

ALPKEM (1992a). Nitrate plus nitrite in seawater. In: ALPKEM (ed.), *The Flow Solution Methodology Doc. No. 000630, 8/92 Rev. B*. Wilsonville, OR, USA, 19 pp.

ALPKEM (1992b). Orthophosphate in seawater. In: ALPKEM (ed.), *The Flow Solution Methodology Doc. No. 000626, 4/92 Rev. A*. Wilsonville, OR, USA, 16 pp.

ALPKEM (1992c). Silica in seawater. In: ALPKEM (ed.), *The Flow Solution Methodology Doc. No. 000671, 5/92 Rev. A*. Wilsonville, OR, USA, 16 pp.

ALPKEM (1994). Ammonia in seawater. In: ALPKEM (ed.), *The Flow Solution Methodology. Doc. No. 000674, 5/94 Rev. E*. Wilsonville, OR, USA, 20 pp.

Arrigo, K. R., Sullivan, C. W. and Kremer, J. N. (1991). A bio-optical model of Antarctic sea ice. *Journal of Geophysical Research*, **96**, 10581–10592.

Arrigo, K. R. and McClain, C. R. (1994). Spring phytoplankton production in the western Ross Sea. *Science*, **266**, 261–263.

Arrigo, K. R., Lizotte, M. P., Worthen, D. L., Dixon, P. and Dieckmann, G. (1997). Primary production in Antarctic sea ice. *Science*, **276**, 394–397.

Azam, F. (1998). Microbial control of oceanic carbon flux: the plot thickens. *Science*, **280**, 694–696.

Balech, E. (1976). Clave ilustrada de Dinoflagelados Antarcticos. *Publicaciones Instituto Antartico Argentino*, **11**, 1–99.

Bayer, R. and Schlosser, P. (1991). Tritium profiles in the Weddell Sea. *Marine Chemistry*, **35**, 123–126.

Brierley, A. S. and Thomas, D. N. (2002). Ecology of Southern Ocean pack ice. *Advances in Marine Biology*, **43**, 171–276.

Chretiennot-Dinet, M. J. (1990). Chlorophycées, Cryptophycées, Euglenophycées, Eustigmatophycées, Prasinophycées, Prymnesiophycées et Tribophycées. In: Sournia, A. (ed.), *Atlas du phytoplancton marin*. Editions du CNRS, Paris.

Comiso, J. C., McClain, C. R., Sullivan, C. W., Ryan, J. P. and Leonard, C. L. (1993). Coastal zone color scanner pigment concentrations in the Southern Ocean and relationships to geophysical surface features. *Journal of Geophysical Research*, **98**, 2419–2451.

Costanzo, G., Zagami, G., Crescenti, N. and Granata, A. (2002). Naupliar development of *Stephos longipes* Giesbrecht, 1902 (Copepoda: Calanoida) from the annual sea ice of Terra Nova Bay, Antarctica. *Journal of Crustacean Biology*, **22**, 855–860.

Dahms, H. U. and Dieckmann, G. S. (1987). *Drescheriella glacialis* gen. Nov., sp. Nov. (Copepoda, Harpacticoida) from Antarctic sea ice. *Polar Biology*, **7**, 329–337.

Dahms, H. U., Bergmann, M. and Sehminke, H. K. (1990). Distribution and adaptations of sea ice inhabiting Harpacticoida (Crustacea, Copepoda) of the Weddell Sea (Antarctica). *Marine Ecology*, **11**, 207–226.

Dieckmann, G. S., Eicken, H., Haas, C., Garrison, D. L., Gleitz, M., Lange, M., Nothing, E., Spindler, M., Sullivan, C. W., Thomas, D. N. and Weissenberger, J. (1998). A compilation of data on sea ice algal standing grop from the Bellingshausen, Amudsen, and Weddell Seas from 1983 to 1994. In: Lizotte, M. P. and Arrigo, K. R. (eds.), *Antarctic Sea Ice Biological Processes, Interactions and Variability.* Antarctic Research Series, Vol. 73, pp. 85–92.

Fabiano, M., Danovaro, R., Crisafi, E., La Ferla, R., Povero, P. and Acosta-Pomar, L. (1995). Particulate matter composition and bacterial distribution in Terra Nova Bay (Antarctica) during summer 1989–1990. *Polar Biology*, **15**, 393–400.

Fabiano, M. and Danovaro, R. (1998). Enzymatic activity, bacterial distribution and organic matter composition in sediments of the Ross Sea. *Applied and Environmental Microbiology*, **64**, 3838–3845.

Fabiano, M. and Pusceddu, A. (1998). Total and hydrolizable particulate organic matter (carbohydrates, proteins and lipids) at a coastal station in Terra Nova Bay (Ross Sea, Antarctica). *Polar Biology*, **19**, 125–132.

Fisher, G., Fütterer, D., Gersond, R., Honjo, S., Ostermann, D. and Wefer, G. (1988). Seasonal variability of particle flux in the Weddell Sea and its relation to ice cover. *Nature*, **306**, 363–365.

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

Gleitz, M., Bartsch, A., Dieckmann, G. S. and Eicken, H. (1998). Composition and succession of sea ice diatom assemblages in the eastern and southern Weddell Sea, Antarctica. In: Lizotte, M. P. and Arrigo, K. R. (eds.), *Antarctic Sea Ice Biological Processes, Interactions and Variability*, Antarctic Research Series, Vol. 73, pp. 107–120.

Guglielmo, L., Carrada, G. C., Catalano, G., Dell'Anno, A., Fabiano, M., Lazzara, L., Mangoni, O., Pusceddu, A. and Saggiomo, V. (2000). Structural and functional properties of sympagic communities in the annual sea ice at Terra Nova Bay (Ross Sea, Antarctica). *Polar Biology*, **23**, 137–146.

Günther, S., Gleitz, M. and Dieckmann, S. (1999). Biogeochemistry of Antarctic sea ice: a case study on platelet ice layers at Drescher Inlet, Weddell Sea. *Marine Ecology Progress Series*, **177**, 1–3.

Hasle, G. R. (1964). *Nitzschia* and *Fragilariopsis* species studied in the light and electron microscopes. 1: Some marine species of the groups *Nitzschiella* and *Lanceolatae*. *Skrifter utgitt av Det Norske Videnskaps-Academi Oslo*, **16**, 1–48.

Keil, R. G. and Kirchman, D. L. (1993). Dissolved combined aminoacids: chemical form and utilization by marine bacteria. *Limnology and Oceanography*, **38**, 1256–1270.

Kurbjeweit, F., Gradinger, R. and Weissenberger, J. (1993). The life cycle of Stephos longipes – an example for cryopelagic coupling in the Weddell Sea (Antarctica). *Marine Ecology Progress Series*, **98**, 255–262.

Lazzara, L., Massi, L., Nuccio, C., Biondi, N. and Innamorati, M. (1997). Phytoplankton ecology: irradiance, particles, gilvin, pigments, absorption, fluorescence, production and species density in Terra Nova Bay, Ross Sea. Nat. Progr. Ant. Res., ROSSMIZE 93–95, Data Report I, pp. 229–279.

Legendre, L., Ackley, S. F., Dieckmann, G. S., Gulliksen, B., Horner, R., Hoshiai, T., Melnikov, I. A., Reeburg, D. S., Spindler, M. and Sullivan, C. W. (1992). Ecology of sea ice biota. 2. Global significance. *Polar Biology*, **12**, 429–444.

Leventer, A. and Dunbar, R. B. (1996). Factors influencing the distribution of diatoms and other algae in the Ross Sea. *Journal of Geophysical Research*, **101**, 18489–18500.

Mantoura, R. F. C. and Llewellyn, C. A. (1983). The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse phase HPLC. *Analytica Chimica Acta*, **151**, 297–314.

Marino, D., Montresor, M., Mazzella, L. and Saggiomo, V. (1995). Diatom flora in faecal pellets from Terra Nova Bay (Antarctica), *Proceedings of the 13th International Diatom Symposium*. pp. 229–239.

McMinn, A., Skerratt, J., Trull, T., Ashworth, C. and Lizotte, M. (1999). Nutrient stress gradient in the bottom 5 cm of fast ice, McMurdo Sound, Antarctica. *Polar Biology*, **21**, 220–227.

Medlin, L. K. and Priddle, J. (1990). *Polar Marine Diatoms*. British Antarctic Survey, Cambridge.

Moro, I., Paccagnella, R., Barbante, C. and Andreoli, C. (2000). Microalgal communities of the Sea Ice, ice-covered and ice-free waters of Wood Bay (Ross Sea, Antarctica) during the austral summer 1993–94. *P.S.Z.N. Marine Ecology*, **21**, 233–245.

Pusceddu, A., Dell'Anno, A. and Fabiano, M. (2000). Organic matter composition in coastal sediments at Terra Nova Bay (Ross Sea) during summer 1995. *Polar Biology*, **23**: 288–293.

Ricard, M. (1987). Diatomophycées. In: Sournia, A. (ed.), *Atlas du Phytoplankton Marin*. Edition du CNRS, Paris.

Roether, W. (1989). On oceanic boundary conditions for tritium, on tritiugenic ^{3}He, and the tritium–^{3}He age concept. In: Anderson, D. L. T. and Willebrand, J. (eds.), *Oceanic Circulation Data and Dynamics*. Kluwer Academic Publishers, Dordrecht, pp. 377–407.

Saggiomo, V., Carrada, G. C., Mangoni, D., D'Alcala, M. R. and Russo, A. (1998). Spatial and temporal variability of size-fractionated biomass and primary production in the Ross Sea (Antarctica) during austral spring and summer. *Journal of Marine Systems*, **17**, 115–127.

Saggiomo, V., Carrada, G. C., Mangoni, O., Marino, D. and Ribera d'Alcalà, M. (1999). Physiological and ecological aspects of primary production in the Ross Sea. In: Faranda, F. M., Guglielmo, L. and Ianora, A. (eds.), *Ross Sea Ecology – Italian Antarctic Expeditions (1987–1995)*. Springer-Verlag, Berlin, pp. 247–258.

Saggiomo, V., Catalano, G., Mangoni, O., Budillon, G. and Carrada, G. C. (2002). Primary production processes in ice-free waters of the Ross Sea (Antarctica) during the austral summer 1996. *Deep-Sea Research II*, **49**, 1787–1801.

Schlosser, P., Bullister, J. L. and Bayer, R. (1991). Studies of deep water formation and circulation in the Weddell Sea using natural and anthropogenic tracers. *Marine Chemistry*, **35**, 97–122.

Schnack-Schiel, S. B., Thomas, D., Dieckmann, G. S., Eiken, H., Gradinger, R., Spindler, M., Weissenberger, J., Mizdalski, E. and Beyer, K. (1995). Life cycle strategy of the Antarctic calanoid copepod Stephos longipes. *Progress in Oceanography*, **36**, 45–75.

Schnack-Schiel, S. B., Thomas, D., Dahms, H. U., Haas, C. and Mizdalski, E. (1998). Copepods in Antarctic sea ice. *Antarctic Research Series*, **73**, 173–182.

Schnack-Schiel, S. B., Thomas, D. N., Haas, C., Dieckmann, G. S. and Alheit, R. (2001). The occurrence of the copepods *Stephos longipes* (Calanoida) and *Drescheriella glacialis* (Harpacticoida) in summer sea ice in the Weddell Sea, Antarctica. *Antarctic Science*, **13**, 150–157.

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

Spindler, M. (1994). Notes on the biology of sea ice in the Arctic and Antarctic. *Polar Biology*, **14**, 319–324.

Thomas, D. N., Kennedy, H., Kattner, G., Gerdes, D., Gough, C. and Dieckmann, G. S. (2001). Biogeochemistry of platelet ice: its influence on particle flux under fast ice in the Weddell Sea, Antarctica. *Polar Biology*, **24**, 486–496.

UNESCO (1981). Background papers and supporting data on the Practical Salinity Scale (1978). *UNESCO Technical Papers in Marine Science*, **77**, 144 pp.