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## Spring-time dynamics of diatom communities in landfast and underlying platelet ice in Terra Nova Bay, Ross Sea, Antarctica

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### ABSTRACT

We investigated the composition of diatom communities in annual fast ice and their variations over time during the 1999 austral spring in Terra Nova Bay (Ross Sea, Antarctica). Diatoms varied along the ice core in both cell abundance and species composition, with a minimum in the lower layer and a peak in the platelet ice. Planktonic species constituted in total about 98% of the diatom assemblage in the surface layers of the ice core down to the thickness of 220 cm. In the bottom ice and the underlying platelet-ice layer, the contribution of planktonic diatoms was lower (60% and 65%, respectively) at the beginning of the sampling period, and then decreased further to reach 30% in the bottom ice, where a remarkable biomass increase over time was caused by in situ growth and accumulation of benthic species.

By contrast in the platelet-ice layer only small changes were recorded in the composition of the diatom assemblage, which was mainly constituted by the bloom of *Fragilariopsis nana*. The benthic species are generally not found in the water column, while species in the platelet-ice layer presumably constitute the seed for the initial plankton bloom during the ice-free periods in Terra Nova Bay.

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### 1. Introduction

Annually formed sea ice is the main feature of the polar regions and plays a fundamental role in structuring marine ecosystems at high latitudes, thus affecting the interactions between the ocean and the atmosphere as well as influencing global climate (Eicken, 1992; Thomas and Dieckmann, 2002; Smetacek and Nicol, 2005). Sea ice is a complex matrix containing channels, capillaries and pores, intimately connected with the underlying water column, and represents a harsh physico-chemical environment characterized by steep gradients in temperature, salinity, light and nutrient concentrations (Eicken, 1992; McMinn et al., 1999; Thomas and Dieckmann, 2002). Nevertheless, diverse microbial communities, known as the sympagic biota, are able to survive in the brine inclusions and interstices of the sea ice habitat (e.g. Arrigo, 2014).

The most conspicuous members of the sea ice microbial communities are the microalgae that are adapted to live in extreme conditions and flourish within the distinct micro-habitats that are created when

the sea ice forms and develops (Lizotte, 2003; Arrigo and Thomas, 2004; Lavoie et al., 2005; Mock and Thomas, 2005; Matsuoka et al., 2009). The microalgae living in the annual pack ice may contribute ca. 10–30% of the annual primary production in the Antarctic regions (Arrigo et al., 1998) and up to 57% in the central Arctic Ocean (Gosselin et al., 1997). Although landfast ice occupies only 1 to 5% of the total ice cover around Antarctica, standing crops of microalgae are three orders of magnitude greater than those reported for the multi-year pack ice autotrophic communities (Ackley and Sullivan, 1994; Archer et al., 1996; Guglielmo et al., 2000; Róžańska et al., 2008).

In landfast ice, microalgae form distinct surface, interior and bottom communities that originate and develop over time under the influence of different environmental variables (e.g. Horner, 1985; Horner et al., 1992; Arrigo, 2014). Surface communities occurring at the snow–ice interface mainly result from seawater infiltration (Meguro, 1962). The internal horizons are probably the most inhospitable habitats for microalgal life, because they are constituted by columnar ice (Arrigo, 2014). Although these horizons can receive sufficient light for photosynthesis, they are characterized by brine salinities that are too high to allow microalgal growth (Arrigo and Sullivan, 1992), while the low brine volumes in the interior ice layers restrict nutrient exchange

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with the water column underneath (Archer et al., 1996; Golden et al., 1998, 2007). Following temperature increase in springtime, the decline of brine salinities and the nutrient exchange promoted by the increase of brine volumes make net microalgal growth possible in these layers (Garrison et al., 2003; Mundy et al., 2011; Arrigo, 2014). The microbial communities inhabiting the bottom few centimeters of landfast ice and the underlying platelet-ice layer differ markedly from the interior communities in taxonomic composition and biomass, and in the timing and fate of production (Bunt, 1963; Horner et al., 1992; Günther and Dieckmann, 2001; Arrigo and Thomas, 2004; Fiala et al., 2006; Lazzara et al., 2007). The platelet ice is a semi-consolidated layer of disk-shaped ice crystals mixed with seawater, ranging from a few centimeters to several meters in thickness, which develops under the landfast ice in several Antarctic coastal areas (Garrison et al., 1986; Smetacek et al., 1992; Mangoni et al., 2009a). The bottom- and platelet-ice microhabitats are frequently the most biologically productive sea ice habitat owing to their ubiquity, proximity to seawater nutrients, and mild temperature and salinity gradients (Archer et al., 1996; Arrigo, 2014). The ice-associated microalgae in these layers are well adapted to low irradiances and variations in the light regime during the winter–spring transition (Lizotte and Sullivan, 1991; Lazzara et al., 2007; Mangoni et al., 2009a, 2009b; Róžańska et al., 2009). In the Ross Sea during the spring bloom, in the bottom- and platelet-ice microhabitats the chlorophyll *a* biomass showed an increase up to three orders of magnitude higher than the one in the upper ice horizons, while the microalgal communities occurring throughout the ice thickness were always characterized by a relatively low biomass increase (Arrigo, 2003; Guglielmo et al., 2000; Lazzara et al., 2007; Mangoni et al., 2009a).

The most abundant microalgal taxa in sea ice, in both the Arctic and the Antarctic, are the diatoms (Bacillariophyceae) (Medlin and Priddle, 1990; Palmisano and Garrison, 1993; Ikävalko and Thomsen, 1997; Tuschling et al., 2000; Thomas and Dieckmann, 2002; McMinn et al., 2007; Riaux-Gobin et al., 2011). In Antarctic landfast ice, planktonic diatoms, such as *Chaetoceros* Ehrenberg and *Fragilariopsis* Hustedt species, are usually observed in the surface-ice horizon, whereas benthic taxa, belonging to the genera *Berkeleya* Greville, *Entomoneis* Ehrenberg, *Nitzschia* Hassall and *Pleurosigma* W. Smith, dominate the bottom ice and the platelet-ice layer communities (Palmisano and Sullivan, 1983, 1985; Lazzara et al., 1995, 2007; Arrigo et al., 1998; Dieckmann et al., 1998; Guglielmo et al., 2000). Pennate diatom taxa, namely of the genera *Nitzschia*, *Fragilariopsis*, *Entomoneis*, and *Navicula* Bory, are common in the bottom ice (Ratkova and Wassmann, 2005; Fiala et al., 2006), but have also been noted in surface ice (Whitaker and Richardson, 1980; Lizotte and Sullivan, 1991; Ryan et al., 2006), interior ice (Garrison, 1991), and in the platelet-ice layer (Arrigo et al., 1995). Centric diatoms (e.g., *Thalassiosira* Cleve, *Porosira* Jørgensen and *Chaetoceros* Ehrenberg) are also found in the ice habitats in the Antarctic but generally dominate in recently formed ice or in the platelet-ice layer (Lizotte and Sullivan, 1991; Smetacek et al., 1992; Riaux-Gobin et al., 2003). The benthic diatoms, namely *Amphiprora kufferathii* Manguin, *Berkeleya adeliensis* Medlin and *Navicula glaciei* Van Heurck, which cannot survive in ice-free pelagic waters, may be considered a sea ice signature (Mangoni et al., 2009b; Riaux-Gobin et al., 2011).

The Ross Sea is an interesting site to study the role of sea ice habitats in polar regions for the high seasonal variability, the presence of several distinctive polynya systems and the conspicuous biological processes linked to sea ice (Zwally et al., 1983; Arrigo et al., 1998; Saggiomo et al., 1998, 2002; Mangoni et al., 2004). Landfast ice in the Ross Sea shows an underlying layer of semi-consolidated platelet ice that can range up to several meters (Arrigo et al., 1998). In Terra Nova Bay (TNB), a thick landfast ice (100–250 cm) is often associated in springtime with a highly dynamic platelet-ice layer, which has served several studies on ice-associated microalgae (Guglielmo et al., 2000; Lazzara et al., 2007; Mangoni et al., 2009a, 2009b). In this area, microalgal biomass reaches its maximum

value in the ice, being even higher than the whole water column biomass during the summer bloom (Guglielmo et al., 2000; Lazzara et al., 2007). However, no information is available on the microalgal communities inhabiting the different sea ice horizons, nor on the spring dynamics of diatoms in the bottom- and platelet-ice layers, while their implications in bloom-seeding processes remain unclear.

The aim of this study was to investigate the vertical distribution of the diatom communities throughout the entire annual landfast ice and its changes over time through the analysis of two complete ice cores collected during the austral spring in TNB. Additional samples were collected to assess the temporal dynamics of diatom communities in bottom- and platelet-ice layers.

## 2. Materials and methods

### 2.1. Sampling

The sampling area is located on the landfast ice in Gerlache Inlet at TNB, Ross Sea, Antarctica (74°41.20' S, 164°10.73' E) at about 4 km from the Italian 'Mario Zucchelli Station'. Sea ice cores were collected on six occasions from 7 to 27 November 1999, within a 100 m<sup>2</sup> surface area using an aluminum ice corer (10 cm internal diameter). At the start of the sampling operations, the bottom and underlying platelet-ice biomass was measured on several cores collected across the sampling area in order to assess the level of spatial variability. The biomass varied between 2% and 16% over the sampling area. Sea ice thickness was about 240 cm and remained almost constant during the sampling period. Two complete ice cores were collected on 7 and 27 November corresponding to the beginning and the end of the sampling period, and cut with a carpenter saw. These two cores were cut in five sections: 0–55 cm (top), 56–110 cm, 111–165 cm, 166–220 cm and 221–240 cm (bottom). Unfortunately the samples of the two sections (56–110 cm and 166–220 cm) of the core collected on 27 November were lost. The semi-consolidated ice crystals forming the underlying platelet-ice layer (about 140 cm thickness by visual scuba-diver inspection) were collected (crystals and interstitial sea water mixture) through the core holes with a plastic ladle on each sampling occasion.

Four additional cores were collected on 13, 19, 21 and 22 November; in this case only the bottom- (221–240 cm) and the platelet ice were sampled. Ice and platelet-ice samples were kept in plastic vessels at low light intensity, and slowly melting in a thermostatic bath at 2–4 °C for 4–6 h.

Physical data were collected by the meteo-radiometric weather station and underwater sensors in the sampling area (Lazzara et al., 2007) during the study period. Temperature and salinity values along the ice core were measured on a sea-ice core which was collected on 15 November 1999 in the same area of the sea-ice cores examined. Results concerning the main environmental features are synthetically described in the Results section, while for detailed information on air/water/ice temperatures, water/ice salinities and irradiances above and below the ice column can be found in Lazzara et al. (2007).

### 2.2. Analyses

In the laboratory, melted ice subsamples were filtered through Whatman GF/F glass fiber filters for chlorophyll *a* (chl *a*) determination. Filters were ground and extracted in 90% acetone at –20 °C for at least 12 h in the dark. Chl *a* concentration was measured with a PerkinElmer LS 50 spectrofluorometer (Holm-Hansen et al., 1965).

For the identification and enumeration of diatoms, melted ice subsamples from each ice core section and platelet-ice layer were preserved in 4% formaldehyde final concentration. Diatom cells were identified to the lowest possible taxonomic rank (Medlin and Priddle, 1990; Hasle and Syvertsen, 1997; Scott and Thomas, 2005). In case of doubtful identifications, specimens were classified at a higher taxonomic rank. Cells were counted using a Zeiss Axiophot inverted microscope

(Carl Zeiss, Oberkochen, Germany) at 400× magnification, operating with phase contrast optics (Utermöhl, 1958; Lund et al., 1958; Zingone et al., 2010). Empty diatom frustules were counted separately from those containing cytoplasm.

For electron microscopy examination, subsamples were oxidized with 70% nitric acid at 60 °C for 1 h, washed several times with distilled water, oxidized again with concentrated sulphuric acid and washed again. A few drops of cleaned diatom material were air-dried onto aluminum stubs and coated with platinum for scanning electron microscopy (SEM) (JEOL JSM-6700F, Peabody, USA) or put on formvar-coated grids for transmission electron microscopy (TEM) (LEO 912AB, Carl Zeiss, Oberkochen, Germany).

The Shannon diversity index ( $H'$ ,  $\ln$ ) was calculated to characterize the species diversity of sea-ice diatom communities (Magurran, 1988). A non-metric multidimensional scaling (MDS) ordination of a Bray-Curtis similarity matrix, with a group-average cluster analysis, was performed to identify groups of samples with similar taxonomic composition (Clarke and Warwick, 2001). Before calculating the similarity matrix, the abundance data were standardized (i.e., relative abundance data) and  $\log(x + 1)$  transformed to reduce the influence of the most dominant taxa. All these analyses used the PRIMER v5 software (Clarke and Gorley, 2001).

### 3. Results

The snow coverage in the sampling area varied between 8 and 15 cm. From 1 to 30 November, air temperature varied from  $-2$  °C to  $-18$  °C with a mean value of  $-6$  °C. Values of incident irradiance varied between 1487 and 505  $\mu\text{E m}^{-2} \text{s}^{-1}$ , with pronounced oscillations. The mean values of the two typical sunny and cloudy days, 9 and 22 November, were 656 and 505  $\mu\text{E m}^{-2} \text{s}^{-1}$ , respectively. Values immediately under the bottom ice varied between 1.1 and 1.6% of surface values, while under the platelet ice they ranged between 0.4 and 0.9% of surface incident irradiance values. On 15 November 1999 temperature minima were recorded in the first 2 horizons and salinity minima in the following 2 layers (Table 1).

There was a great variability among the different ice horizons of the landfast ice in TNB also for biomass distribution. At the beginning of the sampling, chl *a* concentrations showed a marked gradient throughout the ice thickness, ranging from  $0.10 \mu\text{g l}^{-1}$  in the top-ice horizon to  $8.20 \mu\text{g l}^{-1}$  in the bottom ice (Fig. 1A). In the platelet-ice layer, the chl *a* biomass reached a maximum concentration of  $105 \mu\text{g l}^{-1}$ , giving an intense, bright-brown coloration to this semi-consolidated ice layer (Fig. 1A). At the end of the sampling season, chl *a* concentrations along the ice core had increased to  $4.84 \mu\text{g l}^{-1}$  in the top-ice horizon and  $410 \mu\text{g l}^{-1}$  in the bottom ice, with  $360 \mu\text{g chl } a \text{ l}^{-1}$  recorded in the platelet-ice layer (Fig. 1B).

The abundance of diatoms along the ice core sampled early in the springtime varied considerably among the various ice horizons and the platelet-ice layer (Fig. 1). Diatom abundances reached  $3.9 \times 10^6 \text{ cells l}^{-1}$  in the surface-ice horizon (0–55 cm) and  $3.6 \times 10^6 \text{ cells l}^{-1}$  in the immediate next ice horizon (56–110 cm). A sharp and steady decline in diatom abundances with

$1.4 \times 10^6 \text{ cells l}^{-1}$  and  $0.30 \times 10^6 \text{ cells l}^{-1}$  were recorded in the 111–165 cm and 166–220 cm ice horizons, respectively. In the lowest bottom-ice horizon (221–240 cm), diatom abundance increased to  $2.1 \times 10^6 \text{ cells l}^{-1}$ , while reaching  $11.6 \times 10^6 \text{ cells l}^{-1}$  in the 140-cm thick platelet-ice layer (Fig. 1A). In the late springtime sampling, the abundance of diatoms increased to  $10.4 \times 10^6 \text{ cells l}^{-1}$  in the top-ice horizon (0–55 cm) and to  $2.6 \times 10^6 \text{ cells l}^{-1}$  in the middle horizon (111–165 cm) (Fig. 1B). In the bottom-ice horizon (221–240 cm), cell abundance increased to  $77 \times 10^6 \text{ cells l}^{-1}$ , while the maximum diatom abundance was recorded in the platelet-ice layer with  $106 \times 10^6 \text{ cells l}^{-1}$  (Fig. 1B). On 7 November, the number of empty diatom frustules gradually decreased throughout the ice matrix from top to bottom, dropping from  $4.0 \times 10^6 \text{ cells l}^{-1}$  in the 0–55 cm ice layer to  $0.33 \times 10^6 \text{ cells l}^{-1}$  in 166–220 cm ice horizon, where no empty frustules were recorded in either the bottom ice (221–240 cm) and the platelet-ice layer (Fig. 1A). A similar trend was observed on 27 November, except that the numbers of empty frustules were higher, with  $11.3 \times 10^6$  empty cells  $\text{l}^{-1}$  in the surface ice and  $2.6 \times 10^6$  empty cells  $\text{l}^{-1}$  in the 166–220 cm ice horizon (Fig. 1B). No empty cells were observed in the bottom ice and platelet-ice layer.

The diatoms recorded from the various ice horizons and the platelet-ice layer in TNB included 39 taxa belonging to 23 genera, of which 39 were identified at the species level (Table 2). In both ice cores, >90% of the surface (0–55 cm) and interior (56–165 cm) diatom communities were represented by 20 planktonic taxa (Fig. 2). Several planktonic taxa were present along the entire ice thickness, such as *Chaetoceros* spp. (Fig. 5F), *Cylindrotheca closterium* (Fig. 5E) and *Fragilariopsis curta* (Fig. 5D), while others, like *Thalassiosira* spp., were only recorded in the bottom ice and the platelet-ice layer (Fig. 2).

In the surface (0–55 cm) layers, initially the most abundant species were the weakly silicified *Dactylosolen tenuijunctus* (Fig. 5A) with  $2.3 \times 10^6 \text{ cells l}^{-1}$  and the ice-associated species *Fragilariopsis curta* with  $0.82 \times 10^6 \text{ cells l}^{-1}$ , accounting for 57% and 21% of the total diatom community, respectively (Table 2, Fig. 2a). At the end of the sampling period, both species dramatically dropped in numbers to  $0.07 \times 10^6 \text{ cells l}^{-1}$  and  $0.60 \times 10^6 \text{ cells l}^{-1}$ , contributing 1% and 6% of the entire diatom community, respectively (Table 2, Fig. 2B). These taxa were replaced by *Fragilariopsis nana* (Fig. 5B and C), which became the predominant planktonic species increasing from  $0.16 \times 10^6 \text{ cells l}^{-1}$  (4% of the diatom community) on 7 November to  $65 \times 10^6 \text{ cells l}^{-1}$  (62% of the diatom community) on 27 November. Other species in this top-ice horizon were unidentified *Chaetoceros* (Fig. 5F) in the 7 November core and *Nitzschia* spp. in the 27 November core. Due to the predominance of *D. tenuijunctus* and *F. curta* in early spring and of *F. nana* and *Nitzschia* spp. in late spring, the Shannon diversity index in both top-ice layers was relatively low ( $H' = 1.3$ ).

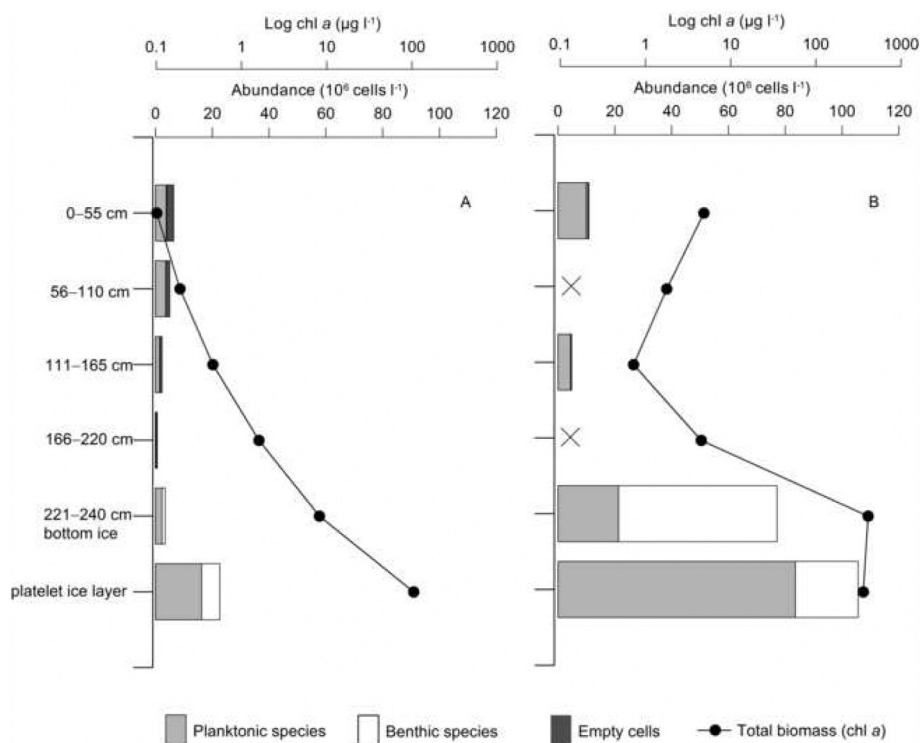
On 7 November, the interior diatom community of the three ice horizons, from 56 to 220 cm, was scarcely diversified and mainly characterized by high cell abundances of *Fragilariopsis curta* and *Cylindrotheca closterium*, which varied from  $0.16$  to  $1.8 \times 10^6 \text{ cells l}^{-1}$  and from  $0.09$  to  $1.1 \times 10^6 \text{ cells l}^{-1}$ , accounting for 48–50% and 27–46% of the total diatom community, respectively (Table 2, Fig. 2A) and with  $H'$  varying between 1.3 and 0.9 across the ice interior. Several benthic species were recorded in the 166–220 cm horizon, such as *Amphiprora kufferathii* (Fig. 5J), *Navicula perminuta* (Fig. 5M), *Berkeleya adeliensis* (Fig. 5L), *Entomoneis* spp., *Nitzschia lecointei* (Fig. 5H) and *Nitzschia taeniiformis* (Fig. 5I) (Table 2, Fig. 2A), although they were scarcely represented and contributed only 2% of the total diatom community. The interior horizon of the 27 November ice core was characterized by the dominance of *F. curta*, with  $2.0 \times 10^6 \text{ cells l}^{-1}$  accounting for 86% of the total diatom community (Table 2, Fig. 2B), and a still lower diversity index ( $H' = 0.6$ ).

In the early sampling dates, compared to the overlying layers the bottom ice (221–240 cm) and the platelet-ice layer showed more diverse diatom assemblages ( $H' = 2.1$  and 1.9, respectively), which

**Table 1**

Temperature and salinity values in a sea-ice core collected on 15 November within the same restricted area as the other sea-ice cores.

Horizons	Temperature °C Average (min/max)	Salinity Average (min/max)
Snow (15 cm)	( $-3.5/-7$ )	
0–55 cm	$-7.2$ ( $-7/-7.4$ )	7.36 (7.4/8.5)
56–110 cm	$-7.4$ ( $-6.9/-7.5$ )	6.65 (6.4/7.9)
111–165 cm	$-6.2$ ( $-6.9/-5.4$ )	5.07 (4.7/5.2)
166–220 cm	$-4.9$ ( $-5.4/-4.1$ )	4.90 (4.8/5.0)
Bottom ice	$-3.9$ ( $-4.1/-3$ )	7.85 (5.8/9.9)
Platelet ice	$-2$	10



**Fig. 1.** Vertical distribution of chlorophyll *a* (chl *a*) concentration and diatom cell abundance of planktonic and benthic species, and empty cells from various landfast ice horizons and the platelet-ice layer in Terra Nova Bay, Antarctica on (A) 7 November and (B) 27 November 1999.

were similar in species composition despite a remarkably higher cell abundance in the platelet-ice layer (Table 2, Fig. 2A). In both the bottom ice and the semi-consolidated ice crystal layers, *Fragilariopsis nana* and *Nitzschia stellata* (Fig. 5G) were predominant, along with other sympagic and ice-related species, e.g., *Amphiprora kufferathii*, *Berkeleya adeliensis*, *Nitzschia lecointei* and *Synedropsis recta* (Fig. 5K) (Table 2, Fig. 2A). In the bottom ice, *F. nana*, *Navicula perminuta* and *Synedropsis recta* attained  $0.40 \times 10^6$  cells  $l^{-1}$ ,  $0.03 \times 10^6$  cells  $l^{-1}$  and  $0.38 \times 10^6$  cells  $l^{-1}$ , respectively, the three species representing together 55% of the total diatom community (Table 2, Fig. 2A). The predominance of *F. nana* was maximum in the platelet-ice layer, where they contributed 61% of the total diatom community, both initially with  $4.6 \times 10^6$  cells  $l^{-1}$  and at the end of the sampling period with  $64.8 \times 10^6$  cells  $l^{-1}$  (Table 2, Fig. 2A). In both the bottom- and platelet-ice layers, specimens of *F. nana* always showed a reduced cell size (apical axis < 5  $\mu m$ , antapical axis < 2.5  $\mu m$ ) and was recorded as solitary or paired cells.

In the bottom ice, the abundance of diatom cells notably increased from the initial to the final spring sampling date, in which the contribution of benthic diatoms increased from 40% to 72% and *Amphiprora kufferathii*, *Berkeleya adeliensis* and *Nitzschia stellata* became the dominant benthic species with  $26 \times 10^6$  cells  $l^{-1}$ ,  $4.5 \times 10^6$  cells  $l^{-1}$  and  $18.7 \times 10^6$  cells  $l^{-1}$ , respectively. Among the planktonic species, *Synedropsis recta* and *Fragilariopsis nana* also increased notably, up to  $9.4 \times 10^6$  cells  $l^{-1}$  and  $6.6 \times 10^6$  cells  $l^{-1}$ , respectively (Fig. 3A). In the platelet-ice layer, cell abundance increased between the 7 and 27 November, but only small changes were observed in the relative importance of the dominant taxa (Fig. 3B).

Some planktonic species (e.g., *Fragilariopsis curta*, *Cylindrotheca closterium* and *Dactyliosolen tenuijunctus*) were relatively abundant in the different ice horizons, showing a peak and a higher proportion of dead cells in the upper ice horizons and representing only a minor part of the total community in the bottom ice and the platelet-ice layer. Some benthic and planktonic species, however, were almost

or completely absent from the upper ice horizons (e.g., *Entomoneis* spp., some *Thalassiosira* species) while they reached high cell abundances in the bottom ice and the platelet-ice layer.

The cluster analysis identified five groups of samples in landfast ice and platelet-ice layer of TNB (Fig. 4). MDS analyses, based on the taxonomic composition across the entire thickness of the ice cores and over time, showed that the two surface samples of 7 and 27 November (IV and I) differed between them and from all the other samples. The samples from the interior core horizons (V) grouped together. All platelet samples also grouped together, along with the bottom samples collected on the first two sampling dates (II), which had essentially the same taxonomic composition as the platelet-ice layer. The last group (III) was formed by the remnant bottom samples.

#### 4. Discussion

In this first recognition of diatom communities in Terra Nova Bay (TNB) landfast ice, diatoms showed a clearly distinct distribution throughout the ice thickness and marked temporal variations in the bottom horizon and the platelet-ice layer, with patterns often similar to those previously reported from other Antarctic areas.

Low diatom abundances were recorded in the interior ice horizons as opposed to high cell numbers in the top and mainly in the bottom-ice horizons, displaying the typical C-shaped vertical pattern reported in the Weddell Sea by Günther and Dieckmann (2001), who also found peak abundances in the platelet-ice micro-habitat. Chlorophyll *a* biomass increased over the spring in the entire ice thickness, and especially in the bottom- and platelet-ice layers. In these horizons, chl *a* increased up to three orders of magnitude more than in the upper ice horizons, while remaining more or less constant in the internal ice, a pattern shared with many other areas (e.g. vicinity of the Australian Antarctic Davis, Archer et al., 1996). The higher microalgal increase in landfast ice (Fiala et al., 2006), bottom ice (Garrison et al., 2003) and platelet-ice layer (Arrigo et al., 1993) can be explained by the enhanced



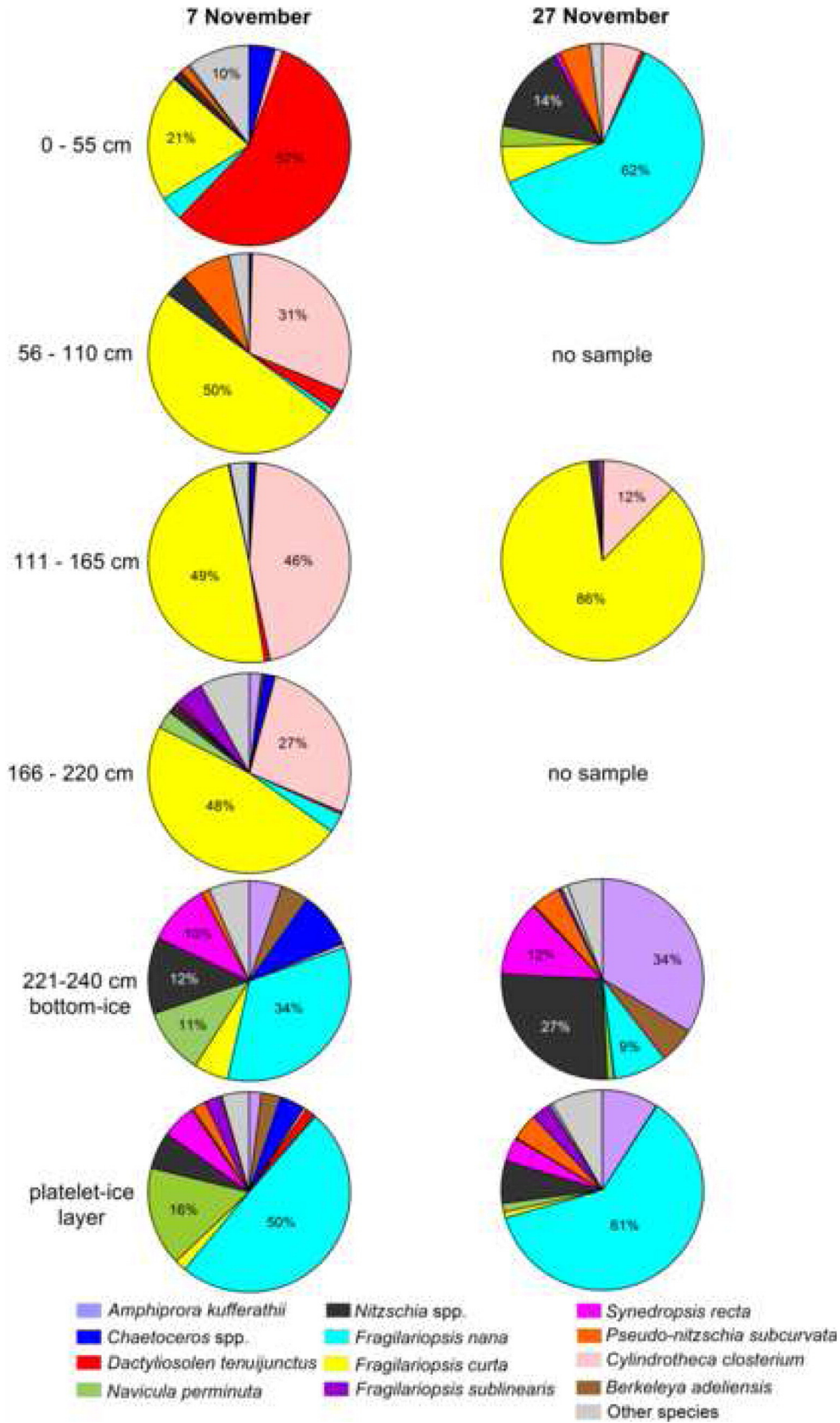
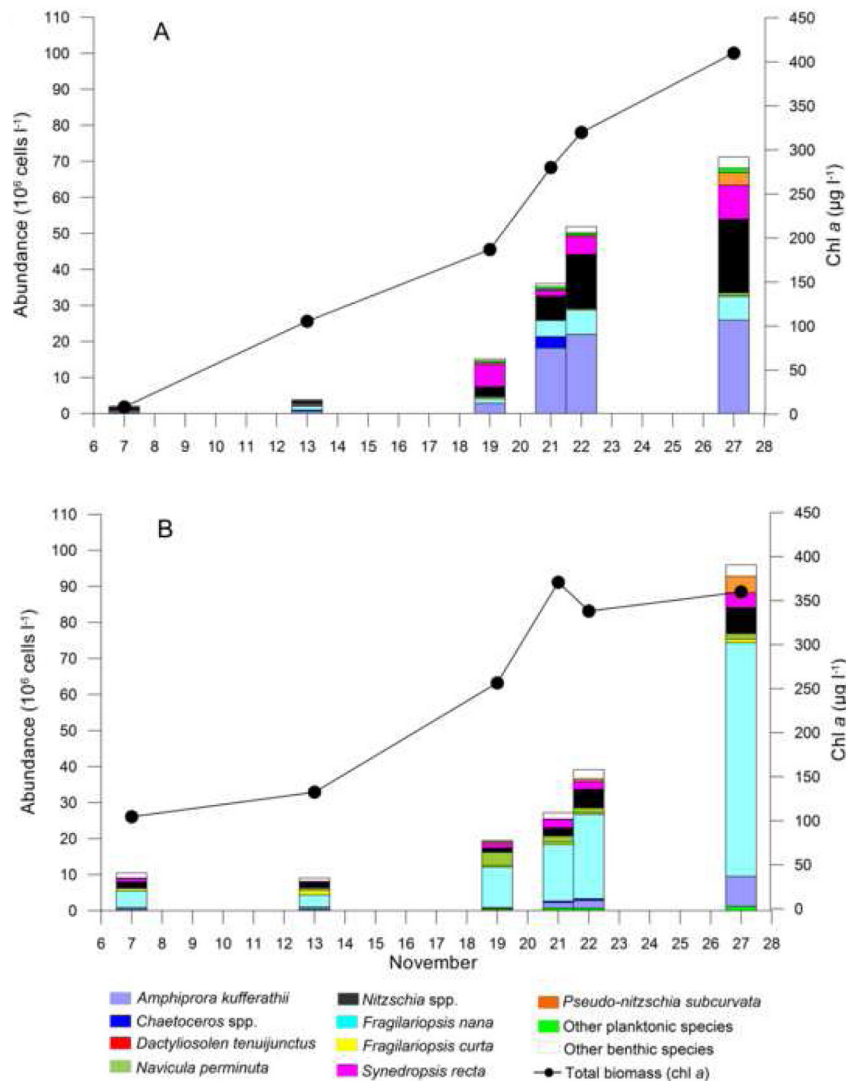


Fig. 2. Relative abundance (%) of diatom taxa from various landfast ice horizons and the platelet-ice layer in Terra Nova Bay, Antarctica on 7 and 27 November 1999. Other species include taxa with a relative abundance <3% in each horizon.



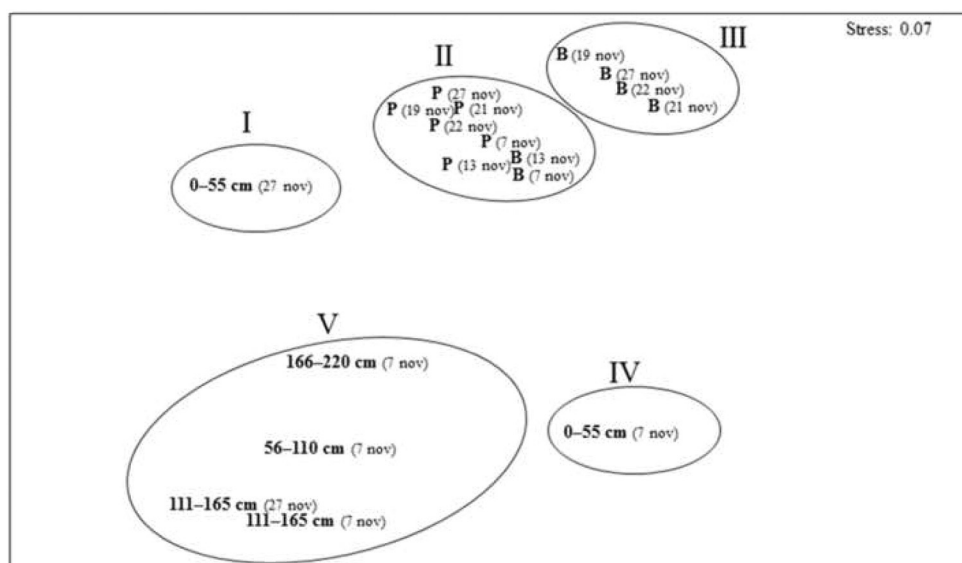
**Fig. 3.** Temporal variation of diatom cell abundance and chlorophyll (chl) a concentration in (A) the bottom ice and (B) the platelet-ice layer in Terra Nova Bay, Antarctica in November 1999.

nutrient availability in these horizons (Melnikov et al., 2002; Michel et al., 2003).

In TNB, five species, namely *Dactyliosolen tenuijunctus*, *Cylindrotheca closterium*, *Fragilariopsis curta*, *F. nana* and *Navicula perminuta*, made up between 20% and 50% of the total diatom abundance of the top to interior ice horizons (down to 220 cm) in both early and late spring. Such high contribution from these species does not find a match in any other reports from Antarctica. Gleitz et al. (1998) and Günther and Dieckmann (2001) did record these species but with much lower abundances in the Weddell Sea, where large *Chaetoceros* spp. and flagellates predominated. The five dominant species mentioned above have also been recorded in seawater in the first phases of ice formation in subsequent years (M. Saggiomo, unpubl. data), supporting the idea that TNB hosts a phytoplankton community which differs from other Antarctic areas.

Two non-mutually exclusive hypotheses have been formulated regarding planktonic diatoms recorded in high numbers in ice cores (Hoshiai, 1977; Grossi and Sullivan, 1985). These pelagic taxa may have been already present in high abundance in the water column at the time the ice was forming in autumn, or they may eventually have grown better than other entrapped diatom species. In the case of *Dactyliosolen tenuijunctus*, the species was already reported in ice-free waters of TNB during the second half of February 1999, which

corresponded to the first freezing steps of the surface waters, and in a later fall bloom (Nuccio et al., 2000). In our study, the low chl a biomass in the top-ice horizon and the high number of empty frustules of *D. tenuijunctus* indicate that the cells were either already dead at the moment of their entrapment or died right after their incorporation into the ice. This is also supported by the fact that *D. tenuijunctus* almost disappeared in the landfast ice in the second ice core sampled three weeks later. Indeed, in the upper ice horizon, total cell abundance more than doubled but the species composition changed completely compared to 20 days before, highlighting that most of the species dominating at the beginning of the sampling period were unable to grow in the ice. *Cylindrotheca closterium*, another common planktonic diatom, was among the dominant ones in the interior-ice community, and had also been observed previously in TNB (Innamorati et al., 1990; Nuccio et al., 1992; Andreoli et al., 1995). An increase of *C. closterium* over time occurred only in the surface layer of the core, matching the observations from Adélie Land, where it was found only in the upper ice horizon and supporting the hypothesis that it requires high light levels for growth (Fiala et al., 2006). The distribution of *C. closterium* in Antarctica varies markedly through time and space (Sung Ho and Fryxell, 1992; Günther and Dieckmann, 2001), but the species has never been found with such high abundances as those reported here for TNB.



**Fig. 4.** Two-dimensional non-metric multidimensional scaling (MDS) of 18 diatom samples collected from landfast ice horizons and platelet-ice layer in Terra Nova Bay, Antarctica. The five groups of samples with taxonomically similar diatoms assessed with a group-average clustering are superposed to the MDS. The similarity matrix was created on the log ( $x + 1$ ) transformed relative abundance of diatoms. Each sample is identified by the ice thickness horizon or a letter (B: bottom ice, P: platelet-ice layer) followed by the sampling date.

*Fragilariopsis curta* was relatively abundant across the entire ice sheet in TNB, and was hence presumably present in the water column during the whole period of ice formation. This species is predominant in ice-free waters in TNB in the austral spring (Saggiomo et al., 2000) as well as in austral summer (Innamorati et al., 1990; Nuccio et al., 1992, 2000; Andreoli et al., 1995). *Fragilariopsis curta* was also abundant in faecal pellets from inshore TNB waters (Marino et al., 1995) and in yearly moored sediment traps from the southwest Ross Sea (Leventer and Dunbar, 1996). Along with *Fragilariopsis cylindrus*, *F. curta* is considered the most abundant species in the coastal polynya of Victoria Land (Garrison et al., 2003). The latter species also is the most abundant species of ice edge environment (Smith and Nelson, 1985; Wilson et al., 1986), pack ice (Leventer et al., 1993) and landfast ice (Fiala et al., 2006; Günther and Dieckmann, 2001) in several polar areas and can hence be considered typical of the whole Antarctic coastal areas. *Fragilariopsis nana*, already abundant in the bottom ice and the platelet ice layer on the first sampling date, by the end of November dominated both the platelet and the surface-ice communities in TNB, reaching the highest specific abundances ( $>60 \times 10^6$  cells  $l^{-1}$ ). The distinction of the species from *F. cylindrus* is not obvious, but the width of the valve and the poroid density of our specimens matched *F. nana* (Lundholm and Hasle, 2008) although the rows of poroids were two or three, and never four, as at times reported for *F. nana*. Records of *F. nana* have certainly been included in those of *F. cylindrus* (Lundholm and Hasle, 2008), which is commonly reported in sea-ice algal communities from both the Arctic (Horner and Schrader, 1982; Poulin et al., 1983; von Quillfeldt et al., 2003; Róžańska et al., 2009) and the Antarctic (Garrison and Buck, 1985; Gleitz et al., 1998; Lizotte, 2001), and is considered typical for the plankton of the Southern Ocean (Clarke and Ackley, 1984; Ackley, 1985; Sung Ho and Fryxell, 1992). *Fragilariopsis nana* is the first species to bloom as the ice melt. Under experimental conditions it showed sustained growth at both high and low irradiance, and in nutrient-depleted as well as nutrient-repleted conditions, which demonstrates the versatile physiology of this species (as *F. cylindrus*, Mangoni et al., 2009a) and explains its increase over time in both the upper ice horizon and in the platelet-ice layer.

Benthic species were restricted to the lower ice horizon and consisted of taxa (e.g., *Amphiprora kufferathii*, *Synedropsis recta* and several *Nitzschia* species) already known to be part of the ice-associated diatom community in several polar areas (von Quillfeldt

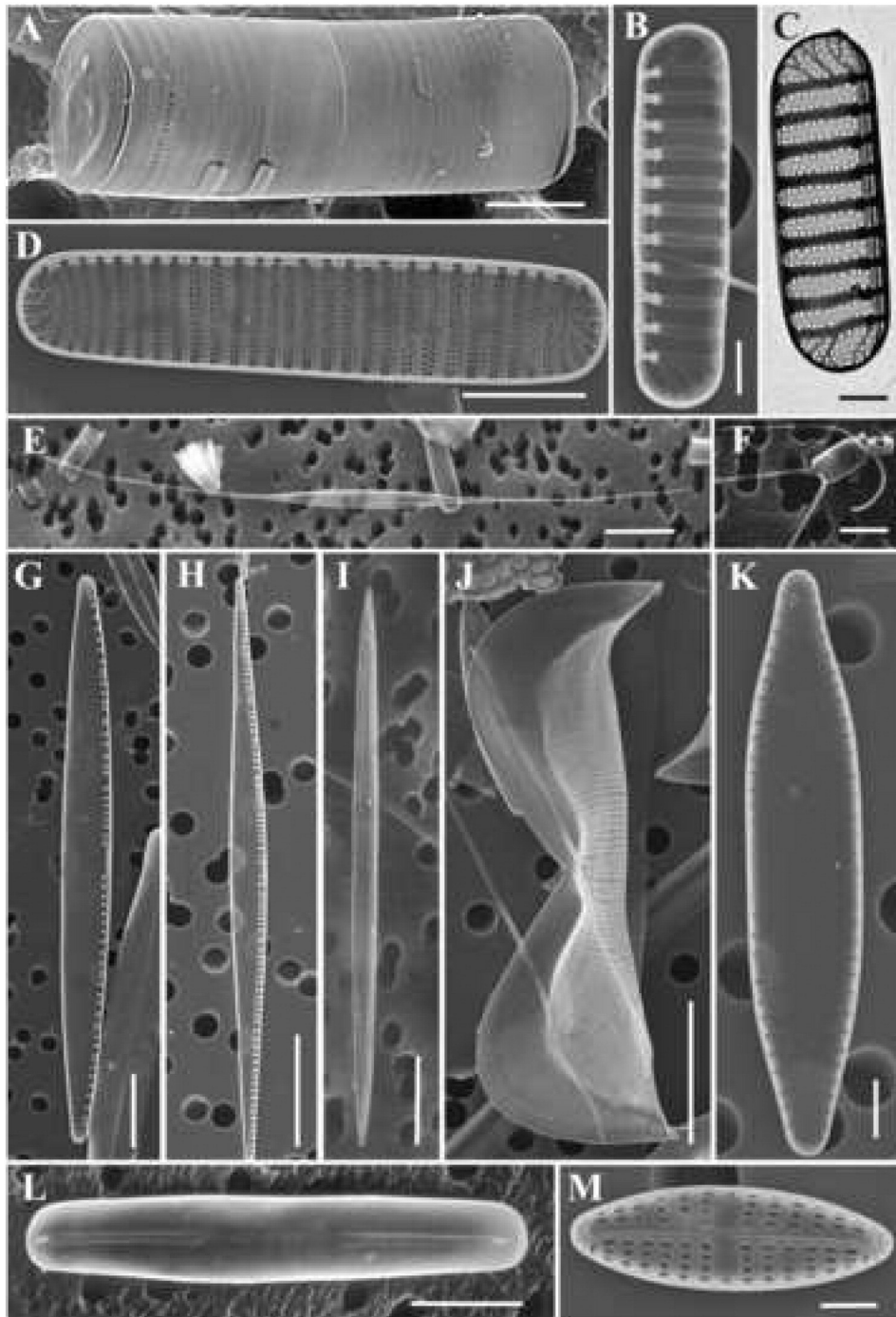
et al., 2003; Guglielmo et al., 2004; Lazzara et al., 2007; Róžańska et al., 2009). Some species of the genus *Navicula* are also commonly found in the sea ice but, notably, the small *Navicula perminuta* is here reported for the first time in this environment. However, the identification of small specimens of *Navicula* may be difficult with light microscopy and, therefore, *N. perminuta* may have been misidentified as *N. glaciei* Van Heurck (Kang et al., 2002).

A peculiarity of the landfast ice emerging from our results was the relatively high abundance of planktonic species in the bottom-ice horizon, which were not reported previously for TNB. The bottom-ice microalgal species are among the most shade-adapted photosynthetic organisms on earth (Thomas and Dieckmann, 2002) and grow well at low irradiance, where they are acclimated to normal salinity sea water with a regular supply of nutrients from the underlying seawater (Garrison, 1991; Ryan et al., 2004). Over the spring period, benthic species showed a much higher increase (from 30% to 70% of the total population) than planktonic ones, resulting in a shift in the diatom community composition. The increase of benthic diatoms in bottom ice was accompanied by low specific production values of 0.12–0.13 mg C (mg chl  $a$ ) $^{-1}$  h $^{-1}$ , thus indicating a major role of migration from platelet ice rather than in situ growth, as proposed by Lazzara et al. (2007).

Interestingly, a different bottom-ice algal community was reported from Woods Bay, 80 km north of TNB, where the xanthophyte *Pseudopleurochloris antarctica* Andreoli et al. represented 50% of the total algal community, and most common diatoms were *Amphiprora kufferathii*, *Chaetoceros dicaeta* Ehrenberg, *Fragilariopsis curta* and *F. cylindrus* (Moro et al., 2000). This difference is likely due to hydrological factors which, in Woods Bay, prevent the development of a platelet-ice layer (Moro et al., 2000).

In contrast to the compositional shift in the bottom ice, the semi-consolidated platelet-ice layer showed a considerable biomass increase with a dominance of planktonic species, mainly *F. nana*, throughout the sampling period. High cell abundances in these layers were comparable to the ones reported from other Antarctic regions (Arrigo et al., 1995; Dieckmann et al., 1998; Guglielmo et al., 2000; Arrigo, 2003; Lazzara et al., 2007), which is remarkable considering that the under-ice irradiance was often  $<1\%$  of the surface downwelling irradiance during the sampling period. Similar to what observed for bottom ice communities, the taxonomic composition of the platelet-ice community in TNB was quite different from the one reported in other areas. For example,





**Fig. 5.** Scanning (A, B, D–M) and transmission (C) electron micrographs of the most representative diatom species in the landfast ice and the underlying platelet-ice layer in Terra Nova Bay, Antarctica in November 1999. (A) *Dactyliosolen tenuijunctus*, entire frustule in perivalvar view, scale bar: 5  $\mu\text{m}$ . (B) *Fragilariopsis nana*, internal valve view, scale bar: 1  $\mu\text{m}$ . (C) *Fragilariopsis nana*, valve, scale bar: 5  $\mu\text{m}$ . (D) *Fragilariopsis curta*, internal valve view, scale bar: 5  $\mu\text{m}$ . (E) *Cylindrotheca closterium*, entire frustule, scale bar: 20  $\mu\text{m}$ . (F) *Chaetoceros* sp., single cell in perivalvar view, scale bar: 10  $\mu\text{m}$ . (G) *Nitzschia stellata*, internal valve view, scale bar: 10  $\mu\text{m}$ . (H) *Nitzschia lecontei*, internal valve view, scale bar: 10  $\mu\text{m}$ . (I) *Nitzschia taeniiformis*, entire frustule in valve view, scale bar: 20  $\mu\text{m}$ . (J) *Amphiprora kufferathii*, valve in girdle view, scale bar: 10  $\mu\text{m}$ . (K) *Synedropsis recta*, external valve view, scale bar: 2  $\mu\text{m}$ . (L) *Berkeleya adeliensis*, internal valve view, scale bar: 10  $\mu\text{m}$ . (M) *Navicula perminuta*, internal valve view, scale bar: 2  $\mu\text{m}$ .

centric diatoms were the most abundant algae in the platelet-ice layer from the Weddell Sea (Smetacek et al., 1992), whereas the dinoflagellates, *Amphidinium* Hulbert and *Gymnodinium* (Bergh) Lankester, dominated off Elephant Island, with diatoms representing only a minor fraction of the sea-ice algal community (Helbling et al., 1993).

Overall, the dynamics of the different ice horizons over the spring season is quite similar across the Antarctic region. However, remarkable variations among the species responsible for the spring increase emerge from the observations in the different areas. Differences could partly

depend on the interannual and/or seasonal variability, considering that the above-mentioned studies were conducted in different years or different stages of the ice melting process. However, the observed differences could well be the reflection of local physical and biological characteristics, including the interplay of light and salinity variations and possibly different predator communities, whose specific effects on microalgal communities would deserve deeper investigations.

As to the origin of the different populations, the truly planktonic species of the upper ice layers may have been trapped in late autumn–early

winter during the first steps of sea-ice formation. Considering the different phases of ice formation, a bloom of *Dactyliosolen tenuijunctus* dominating the upper ice horizon was probably trapped as first, whereas planktonic species such as *Fragilariopsis curta* and *Cylindrotheca closterium*, found in the interior-ice horizons, may have been trapped also or only in subsequent phases of the ice formation, thus showing to belong to a later stage of the succession in the area. The planktonic species *Fragilariopsis nana*, along with *Navicula perminuta* and other benthic species such as *A. kufferathii*, probably colonized the bottom ice and the platelet-ice layer over the winter and early spring. The benthic species were most likely transported by the small ice crystals that formed on the sea floor and then floated freely upwards (Gough et al., 2012), thus forming the platelet-ice layer, probably in relation with the super-cooled water masses driven by local topography.

The different assemblages evolved differently during the spring algal bloom. The upper layers showed only a modest increase produced by species that are able to grow/survive in the ice with its associated environmental features, such as high fluctuations of irradiance and salinity. In the bottom ice, the change in the physical structure favored the accumulation of benthic species. In the platelet-ice layer, the abundance increase was rather due to a bloom of planktonic species, dominated by *Fragilariopsis nana*, together with the benthic species *A. kufferathii* and *Nitzschia* spp. These benthic species were only present in the bottom ice and the platelet-ice layer where they grow in low light conditions in spring, while they were unable to grow in the planktonic habitat under experimental conditions (Mangoni et al., 2009b). Indeed these species, have never been reported in ice-free waters of Terra Nova Bay. While platelet-ice communities evolved maintaining an almost constant dominance of species with planktonic traits, bottom-ice communities were increasingly dominated by benthic diatoms.

Finally, diatoms accumulating in the bottom horizon of the landfast ice also undergo different fate in the subsequent phases of the system. The benthic species do not contribute to the late spring phytoplankton blooms, and the high biomass they produce in the bottom ice constituting an important food source for both pelagic and benthic food webs. By contrast, the planktonic species of the platelet-ice layer are the first to be found in high concentrations in open waters (Mangoni et al., 2009a), showing that this peculiar ice form constitutes an incubator for the late spring bloom of TNB.

The schematic representation of the origin and fate of different microalgal communities given above finds some confirmations in data collected in other years in the area. However, due to the significant spatial variability which is found in the landfast ice, additional studies are warranted to ascertain to what extent our data are representative with respect to other areas and other phases of ice development and to further delineate diatom taxonomy of ice assemblages in TNB.

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