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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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article info abstract

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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;](#page--1-0) [Thomas and Dieckmann, 2002; Smetacek and Nicol, 2005\)](#page--1-0). 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 [\(Eicken, 1992;](#page--1-0) [McMinn et al., 1999; Thomas and Dieckmann, 2002\)](#page--1-0). 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\)](#page--1-0).

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

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<http://dx.doi.org/10.1016/j.jmarsys.2016.06.007> 0924-7963/© 2016 Elsevier B.V. All rights reserved. the sea ice forms and develops ([Lizotte, 2003; Arrigo and Thomas,](#page--1-0) [2004; Lavoie et al., 2005; Mock and Thomas, 2005; Matsuoka et al.,](#page--1-0) [2009](#page--1-0)). The microalgae living in the annual pack ice may contribute ca. 10–30% of the annual primary production in the Antarctic regions [\(Arrigo et al., 1998\)](#page--1-0) and up to 57% in the central Arctic Ocean [\(Gosselin et al., 1997\)](#page--1-0). 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,](#page--1-0) [1994; Archer et al., 1996; Guglielmo et al., 2000; Ró](#page--1-0)żańska 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.,](#page--1-0) [1992; Arrigo, 2014](#page--1-0)). Surface communities occurring at the snow–ice interface mainly result from seawater infiltration [\(Meguro, 1962](#page--1-0)). The internal horizons are probably the most inhospitable habitats for microalgal life, because they are constituted by columnar ice ([Arrigo,](#page--1-0) [2014\)](#page--1-0). 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](#page--1-0)), 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.,](#page--1-0) [1998, 2007](#page--1-0)). 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 [\(Garrison et al., 2003; Mundy et al., 2011; Arrigo, 2014\)](#page--1-0). 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](#page--1-0) [Dieckmann, 2001; Arrigo and Thomas, 2004; Fiala et al., 2006; Lazzara](#page--1-0) [et al., 2007](#page--1-0)). The platelet ice is a semi-consolidated layer of diskshaped 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](#page--1-0) [et al., 1992; Mangoni et al., 2009a](#page--1-0)). 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 [\(Archer et al., 1996; Arrigo, 2014](#page--1-0)). The ice-associated microalgae in these layers are well adapted to low irradiances and variations in the light regime during the winter–spring transition ([Lizotte and Sullivan, 1991; Lazzara et al., 2007; Mangoni](#page--1-0) [et al., 2009a, 2009b; Ró](#page--1-0)żańska et al., 2009). In the Ross Sea during the spring bloom, in the bottom- and platelet-ice micro-habitats the chlorophyll a biomass showed an increase up to three orders of magnitude higher than the one in the upper ice horizons, while the microalgal communities occurring throughout the ice thickness were always characterized by a relatively low biomass increase ([Arrigo,](#page--1-0) [2003; Guglielmo et al., 2000; Lazzara et al., 2007; Mangoni et al., 2009a\)](#page--1-0).

The most abundant microalgal taxa in sea ice, in both the Arctic and the Antarctic, are the diatoms (Bacillariophyceae) [\(Medlin and Priddle,](#page--1-0) [1990; Palmisano and Garrison, 1993; Ikävalko and Thomsen, 1997;](#page--1-0) [Tuschling et al., 2000; Thomas and Dieckmann, 2002; McMinn et al.,](#page--1-0) [2007; Riaux-Gobin et al., 2011](#page--1-0)). 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 [\(Palmisano and](#page--1-0) [Sullivan, 1983, 1985; Lazzara et al., 1995, 2007; Arrigo et al., 1998;](#page--1-0) [Dieckmann et al., 1998; Guglielmo et al., 2000\)](#page--1-0). Pennate diatom taxa, namely of the genera Nitzschia, Fragilariopsis, Entomoneis, and Navicula Bory, are common in the bottom ice ([Ratkova and Wassmann, 2005;](#page--1-0) [Fiala et al., 2006](#page--1-0)), but have also been noted in surface ice [\(Whitaker](#page--1-0) [and Richardson, 1980; Lizotte and Sullivan, 1991; Ryan et al., 2006](#page--1-0)), interior ice [\(Garrison, 1991\)](#page--1-0), and in the platelet-ice layer ([Arrigo et al.,](#page--1-0) [1995](#page--1-0)). 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 [\(Lizotte and Sullivan, 1991; Smetacek et al., 1992;](#page--1-0) [Riaux-Gobin et al., 2003\)](#page--1-0). 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](#page--1-0) [et al., 2011](#page--1-0)).

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;](#page--1-0) [Saggiomo et al., 1998, 2002; Mangoni et al., 2004\)](#page--1-0). 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](#page--1-0)). 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 [\(Guglielmo et al., 2000; Lazzara et al., 2007; Mangoni et al., 2009a,](#page--1-0) [2009b\)](#page--1-0). 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](#page--1-0) [et al., 2007\)](#page--1-0). However, no information is available on the microalgae 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 $m²$ 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 [\(Lazzara et al.,](#page--1-0) [2007\)](#page--1-0) 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](#page--1-0) 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. \(2007\)](#page--1-0).

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\)](#page--1-0).

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,](#page--1-0) [1990; Hasle and Syvertsen, 1997; Scott and Thomas, 2005](#page--1-0)). In case of doubtful identifications, specimens were classified at a higher taxonomic rank. Cells were counted using a Zeiss Axiophot inverted microscope

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