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Light environment and seasonal dynamics of microalgae in the annual sea ice at Terra Nova Bay, Ross Sea, Antarctica

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Abstract: We investigated the physical conditions of the Spring pack ice environment at Terra Nova Bay to understand their influence on the structure and physiology of sympagic microalgae. Bio-optical methods were used to study the availability and spectral quality of solar radiation, both inside and underneath the ice cover. Pack ice thickness was around 2.5 m, with a temperature between -2 and -7°C. On average, only 1.4% of surface PAR penetrated to the bottom ice and less than 0.6% below platelet ice level. Surface UV-B radiation under the bottom ice was 0.2–0.4%. Biomass concentrations up to 2400 mg Chl *a* m^{-3}, dominated by two species of diatoms (*Entomoneis kjellmannii* and *Nitschia* cf. *stellata*), showed marked spatial and temporal patterns. Maximum values were in the platelet ice during the first half of November, and in the bottom ice two weeks later. Strong shade adaptation characteristics emerged clearly and explained the relevant abundance of microalgae within the sea ice, with specific absorption coefficients (a*) as low as 0.005 m^2 (mg Chl *a*)$^{-1}$ and the photo-acclimation index (E_k) in the range of *in situ* irradiance. The biomass specific production values were low, around 0.12–0.13 mg C mg Chl a^{-1} h^{-1}. The hypothesis suggesting bottom ice colonization by platelet ice microalgae is supported here.

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Key words: bottom ice, diatoms, irradiance, platelet ice, shade adaptation

Introduction

Sea ice is a site of primary production with a seasonal pattern of biomass accumulation and production that both extends and increases regional productivity (Lizotte 2003). Production and accumulation of biomass, including both autotrophic and heterotrophic forms and detritus, occur within the ice. In particular, sea ice biota includes large animals living on the sea ice and at the sea ice-water interface, as well as a variety of micro-organisms such as microalgae and metazoans, living within the ice (sympagic organisms) (Spindler 1994). Sea ice assemblages include those growing at the sea ice surface and within a sub-ice platelet layer. Platelet ice, a semi-consolidated layer of ice ranging from a few centimetres to several metres in thickness, is at times observed immediately beneath the pack ice. Platelet ice is the most porous of all sea ice types, being composed of approximately 20% ice and 80% seawater by volume (Arrigo & Thomas 2004).

The ice-water interface constitutes an important habitat for polar organisms, with highest abundances and biomass in the bottom few centimetres of the sea ice (bottom ice community, Horner *et al.* 1988). The porous nature of sea ice allows fluid exchange across different horizons inside the ice and across the ice-water interface from where nutrients are replenished. The bottom ice freely exchanges with seawater, resulting in stable conditions and unlimited supply of nutrients. Few biological studies have considered the exchange process across the ice-water interface as a possible cause for the variability of ice-associated organisms (Cota & Horner 1989, Cota *et al.* 1991). Availability of nutrients, room for growth and the presence of ice as a protection against zooplankton grazing, make this structure an ideal habitat for many microorganisms. Through a suite of physiological adaptations, the assemblages thrive inside the ice itself, some in fact living their entire life cycles within the ice (Thomas & Dieckman 2002).

A major limiting factor for sympagic autotrophic growth is light availability, which depends on the attenuation by the ice itself as well as by the snow cover on top of the ice. Sea ice algae possess extreme low light adaptations, which they show as unique photophysiological characteristics (Cota & Sullivan 1990, Arrigo 2003) in the light-harvesting pigment concentration and composition, in the photosynthesis/irradiance response (PE curves), and through other inherent bio-optical properties, like the chlorophyll specific absorption coefficient (a*). Sea ice diatoms, which often dominate the assemblages, typically react to the sympagic light environment with the increase of Chl *a* concentration, as well as accessory pigments Chl *c* and fucoxanthin, to balance the selective absorption of portions of the light spectrum by ice and snow (Arrigo *et al.* 1991, Robinson *et al.* 1995, Thomas 2004). The parameters of the PE curves, as a consequence of shade adaptation, should

present the lowest photoacclimation indexes (E_k) and P_{max}, but high values of the light-utilization efficiency (α) and photoinhibition index (β). Protection against photodamage due to high visible or UV radiation, can be achieved through carotenoids or specific mycosporin-like amino acids (MAAs) (Karsten *et al.* 1998, Arrigo 2003).

Due to the low light levels, microalgal communities of this habitats can only bloom at the core of the summer (Dieckmann *et al.* 1998), often associated with populations living further down in the ice column (platelet ice), with concentration exceeding 1000 mg Chl *a* m^{-3} (Palmisano & Sullivan 1983). These high values of biomass are more typical in the coastal ice, where the photosynthetic capacity of sympagic microorganisms is about one order of magnitude lower than in offshore sea ice communities (Palmisano *et al.* 1987, Arrigo *et al.* 1997, Guglielmo *et al.* 2000) or in phytoplankton (Lizotte & Sullivan 1992, Saggiomo *et al.* 2002).

Annual primary production in the Antarctic sea ice has been estimated between 30 and 70 Tg C (Arrigo *et al.* 1997, Arrigo & Thomas 2004), a large amount of which occurs during the summer. In that season, the sea ice autotrophic biomass reaches values as high as 400 mg Chl *a* m^{-2}, and primary production is *c.* 1 g C m^{-2} d^{-1}. Similar values are reported for the ice-free waters of the most productive oceanic regions. Primary production in the sea ice accounts for only a minor fraction (1–4%) of the total biogenic carbon production in the Southern Ocean, but it represents a fundamental concentrated food source for higher trophic levels, both during the period of autotrophic biomass accumulation in the sea ice and during ice melting (Legendre *et al.* 1992).

Though differentiated, the populations of sympagic microalgae are mainly composed of diatoms. In particular, *Berkeleya* cf. *rutilans*, *Entomoneis* spp., *Nitschia* cf. *stellata*, *Pleurosigma* spp. dominate the bottom ice layer (Palmisano & Sullivan 1983, Lazzara *et al.* 1995, Guglielmo *et al.* 2000), while dinoflagellates or prymnesiophytes may appear in the surface layers (Ackley & Sullivan 1994), in lower concentrations. With respect to the extreme environmental conditions of the pack ice where they live, these photoautotrophic communities are expected to possess unique ecophysiological features. This study investigates the peculiar conditions of the sympagic Antarctic environment and the photophysiological adaptations of the sea ice microalgae to the light field, as a contribution to identifying the reasons for the presence of an important autotrophic biomass within the sea ice.

Material and methods

During the XIII and XV Italian Expeditions to Antarctica, in the springs of 1997 and 1999, we investigated the distribution, abundance and taxonomic composition of sympagic phytoplankton, in the vicinity of Terra Nova Bay.

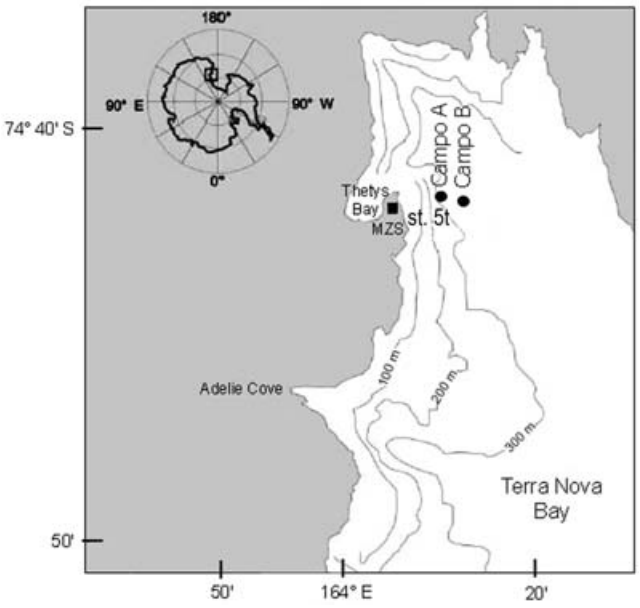


Fig. 1. Map of the investigated area at Terra Nova Bay, Antarctica, with location of the sampling stations, on the pack ice: Campo A (1999) and St. 5t (1997), Campo B (1999). MZS indicates the Italian Station.

We adopted optical techniques to study the availability and the spectral quality of the solar radiation, when it passes through ice, snow, and seawater. Ice core samples were collected as described in Guglielmo *et al.* (2000), every two or three days, in a defined sampling area of 100 m^2, where we established: station 5t (74°41.72'S, 164°11.63'E), from 5 November–1 December 1997; Campo A (74°41.2'S, 164°10.73'E) and Campo B (74°42.15'S, 164°14.60'E), from 30 October–29 November 1999 (Fig. 1). All ice cores revealed a multiple horizon structure. Horizon thickness varied, but the structure of the cores appeared identical in the two seasons: a surface layer, an intermediate one, a bottom ice layer and the platelet ice. For each section of the ice cores, we analysed photosynthetic pigments and phytoplankton composition. Spectral absorption and attenuation measurements (AC-9-25, Wetlabs) were performed on intact, diluted and filtered samples (Whatman, GFF) of bottom and platelet ice. Detailed measurements of temperature and salinity in the pack ice were obtained from an ice core at Campo A (on 15 November 1999). Immediately after the removal of each ice layer from the top, a thermocouple (Pt100, Delta Ohm, ± 0.1°C) measured the temperature within the ice, at a depth of 1–2 cm from the surface. Salinity was derived from measures of temperature and conductivity (Mod. 30, YSI) on 16 melted sections of the ice core.

Atmospheric temperature, relative humidity and irradiance were assessed at the pack ice surface using a combination of a LI-193SA quantum sensor (LICOR) for downwelling PAR irradiance; a global-irradiance meter CM6B (Kipp & Zonen); two band filtered sensors for

ultraviolet irradiance, UV2/AP-373 ± 2 nm, and UV2/BP-313 ± 2 nm (DELTA-T) and a temperature and relative humidity sensor, HMP35AC (Vaisala). Measurements were automatically collected every 5 minutes and stored in the CR10X data logger (Campbell Scientific). The following equations allowed conversion and subsequent comparison among the different light sensors (quantum and energetic): PAR ($\mu E\ m^{-2}\ s^{-1}$) = 4.46 PAR (Wm^{-2}), following Morel & Smith (1974); and PAR ($\mu E\ m^{-2}\ s^{-1}$) = 2.30 E_{glob} (Wm^{-2}).

The spectroradiometric probe PUV 500/510 (Biospherical Ltd.) measured irradiance, fluorescence and temperature, in seawater and through the ice. The device consists of two units for coincident acquisition of underwater and surface irradiance. Both units are equipped with one PAR irradiance quantum sensor, with four UV-irradiance energetic sensors (305, 320, 340, 380 nm), with sensors for temperature and pressure, and one radiance sensor (687 nm) to measure the natural fluorescence of Chl *a*. Vertical profiles of descending underwater irradiance (Ed) were performed by lowering the probe through holes in the pack-ice (∅ 40 cm). The mean vertical diffuse attenuation coefficients (K_d) of downwelling PAR and UV irradiance were calculated, according to the relation: $K_d = 1 / (z_2 - z_1) * \ln [Ed(z_1) / Ed(z_2)]$, where: $(z_2 - z_1)$ is the thickness of the considered layer; Ed (z_1) and Ed (z_2) are levels of downwelling irradiance, respectively referred to the preceeding (z_1) and subsequent (z_2) depth of the measuring probe. For absolute measurements of under ice irradiance, a custom-built structure (ASTICE), which consisted of a mobile under-ice arm, allowed deployment of the PUV probe almost at a right angle, 250 cm away from the central vertical axe of the hole. In this position, the probe's uplooking sensors could measure the unaltered light field below the pack ice and the platelet ice.

The amount of microalgal biomass was estimated from spectrophotometric analysis (Kontron, Uvikon 930) on acetone-extracted Chl *a* plus phaeopigments (chloro-phaeopigments, according to Lazzara *et al.* 1997), within a few days of sampling. A spectrofluorimetric technique (Neveux & Panouse 1987) was also adopted for samples of the XV Expedition, taken after 20 November. A conditional regression of the values obtained with the two methods on the same samples ($n = 61$) gave a regression coefficient $r = 0.97$. The chlorophaeopigments concentrations of all samples could thus be homogeneously referred to the spectrophotometric technique.

HPLC analyses were performed (Hewlett Packard HPLC, mod. 1100) according to the method of Mantoura & Llewellyn (1983) as modified by Brunet *et al.* (1993). For the determination of chlorophylls and carotenoids, we used a spectrophotometer with a diode array detector (DAD) set at 440 nm. In addition, a spectrofluorimeter was employed for the determination of chlorophyll degradation products. Calibration of the HPLC was carried out using 20 different pigments, provided by the International Agency for ^{14}C Determination (VKI, Water Quality Institute).

The optical microscopy observations allowed quantitative and taxonomic analysis on phytoplankton, by means of the Uthermöl method (Hasle 1978) and the inverted optical microscopes IM-35 (Zeiss), Diaphot (Nikon) and OPTECH, all with 40x optics and phase contrast. Taxonomy was based on Balech (1976), Hasle (1964, 1965a, 1965b), Manguin (1960), Medlin & Priddle (1990), Priddle & Fryxell (1985), and Round *et al.* (1990).

We investigated the PvsE relationship of the sympagic communities in the bottom pack ice. Sea ice samples were melted in 0.2 µm filtered seawater (T -1.5°C, dilution from 1:20 to 1:100). Subsamples were placed in 50 ml bottles, inoculated with 20 µCi of $NaH^{14}CO3$, and then exposed to 12 different irradiance levels, for one hour, using a radial photosynthetron with circulating seawater (Babin *et al.* 1994). The irradiance inside each incubation bottle was measured using a 4π sensor (QLS-101, Biospherical Instruments). To control the process of dark fixation, one subsample was added with four drops of saturated seawater DCMU solution and placed in the dark inside the incubator (Legendre *et al.* 1983). Filtration on the 25 mm Whatman GF/F filters was carried out immediately after incubation in the same light conditions as for core sectioning operations. All ^{14}C samples were acidified with 200 µl of 0.1 N HCL and, after adding 10 ml of Aquasol II scintillation cocktail, read within 24 hours of filtration with a Beckman LS 1801 liquid scintillator. The parameters of the Production/Irradiance relationships (PvsE) were derived from the model of Platt *et al.* (1980): $P^B(E) = P^Bs\ [1 - \exp(-\alpha E / P^Bs)]\exp(-\beta E / P^Bs)$, where: P^B = biomass specific carbon fixation rate [mg Carbon (mg Chl *a*)$^{-1}$ hr $^{-1}$]; E = actinic irradiance level [µmol photons $m^{-2}\ s^{-1}$]; P^Bs = maximum specific carbon fixation rate at saturating irradiances [mg Carbon (mg Chl *a*)$^{-1}$ hr^{-1}]; α = the initial slope of the PvsE curve [mg Carbon (mg Chl *a*)$^{-1}$ hr^{-1} (µmol photons $m^{-2}\ s^{-1}$)]; β = photoinhibition factor [mg Carbon (mg Chl *a*)$^{-1}$ hr^{-1} (µmol photons $m^{-2}\ s^{-1}$)$^{-1}$].

Results

Light environment and optical properties in seawater and ice

Short-wave daily insolation (E_{glob}) were higher in October and November 1999 than in 1997 (Fig. 2), especially after mid November, due to reduced cloud coverage. Daily means of air temperature were low in the second half of October 1997, from -8°C to -16°C (monthly minimum) but they increased strongly afterwards, reaching the maximum value 1.05°C, on 21 November. In the same period of 1999, temperature was generally lower. Starting from -17.5°C, it showed a similar rapid increase during the first week of November, up to -2°C. The differences between the two years are more evident after mid November: in 1997, temperature was never below -6°C, whereas in 1999, values

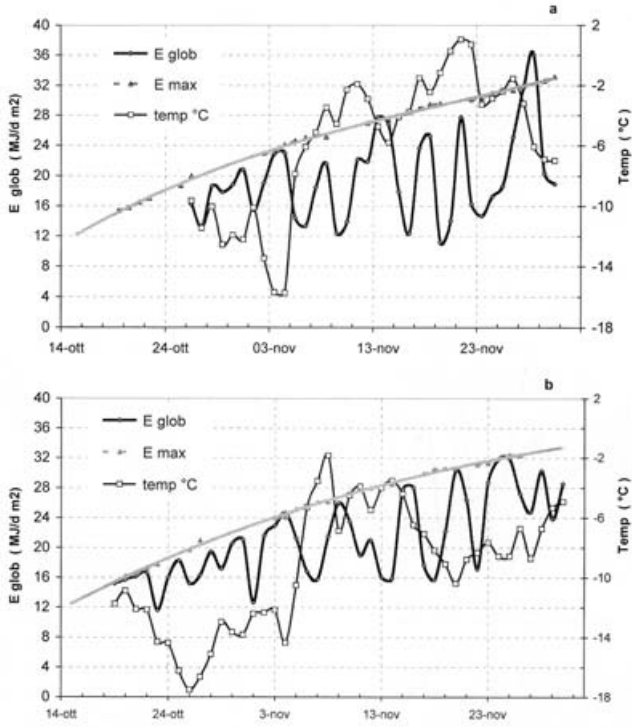


Fig. 2. Temporal variations of mean daily temperature (°C) and global daily irradiance (MJ m^{-2} d^{-1}), during the spring **a.** 1997, and **b.** 1999. The dotted line expresses the theoretical mean daily irradiance in "clear-sky" conditions (Lazzara *et al.* 2000), with a mean atmospheric transmission of 80 %.

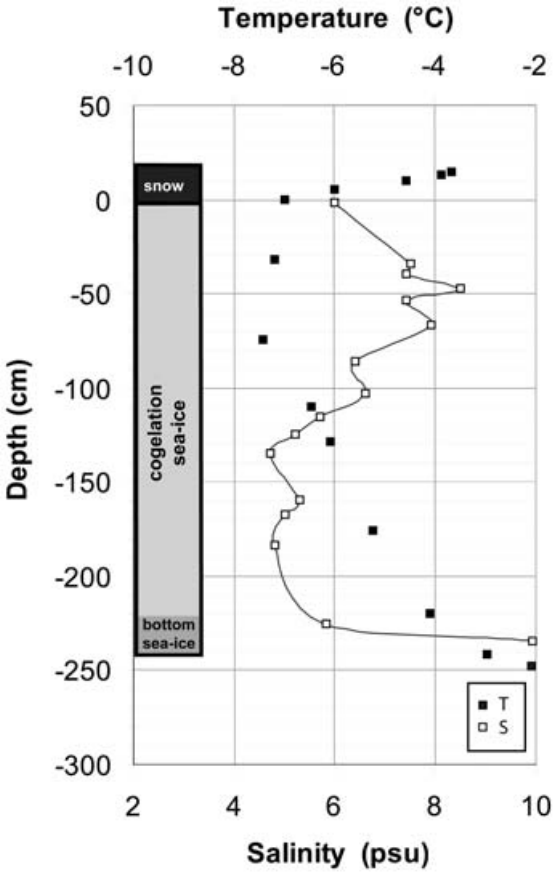


Fig. 3. Bathymetric profiles of temperature (°C) and salinity (psu), measured along an ice core from Campo A, on 15 November 1999.

were between -10°C and -6°C. A long-wave feedback associated with the cloud coverage may explain these differences. In fact, air temperature at sea level is remarkably warmer after mid November 1997.

The ice cores sampled during the XIII Expedition (1997) revealed a multiple horizon structure: surface = 0–80 cm, intermediate = 80–130 cm, bottom = 130–140 cm, platelet ice. Two years later, in the same season, the sea ice structure was unchanged, but each layer showed a different thickness: the surface layer was 110 cm; the intermediate between 110 and 220 cm; the bottom, which was sampled as a two-layer system, 220–240 cm. Profiles of temperature and salinity, measured on the ice cores of Campo A, on 15 November 1999 (Fig. 3), revealed three main features in temperature and salinity. Minimum values of temperature (-7°C) were measured in the surface section, 0–100 cm, with salinity values as high as 8.5 psu. From 110 to 240 cm, the ice temperature was higher and salinity at its minimum. In the lowest 10–20 cm, corresponding to the bottom ice, both temperature and salinity values increased, owing to the proximity of free sea water.

We derived the temporal variation of the diffuse attenuation coefficient for PAR irradiance ($K_{d\ PAR}$) in the water column, from the light profiles measured from 3–29 November 1999 (Fig. 4). We have distinguished three parts of the water column: 3–5 m, comprehensive of the platelet layer; 5–10 m, just below the platelet; from 10 m down to 25 m. The mean $K_{d\ PAR}$, measured in the water column, shows highest values under the pack, at the platelet ice level, from 0.39 to 0.78 m^{-1}. Minimum values occurred in the layer 5–25 m, ranging between 0.05 and 0.35 m^{-1}. From our observations, $K_{d\ PAR}$ varies in time according to variations in biomass (see further; Fig. 5b). During November 1999, initial values of $K_{d\ PAR}$ increased in all layers, up to 2–4 times. The maximum value of 0.78 m^{-1} was reached as early as mid November, in the shallow layer, in correspondence with a peak of biomass concentration in the platelet ice. In the same period, the deeper layers still showed minimum values, only up to 0.05 m^{-1}. Maximum values of K_d in the lowest level, 10–25 m, occurred only at the end of the month, suggesting that the bottom ice biomass progressively deepened in the water column, along with the melting of pack ice.

The optical measurements obtained under the platelet ice in combination with K_d values derived from the irradiance profiles measured in the platelet ice layer, allowed estimation of the levels of irradiance experienced by the sympagic microalgal populations (Table I). From our measurements, under the platelet ice, PAR ranged between

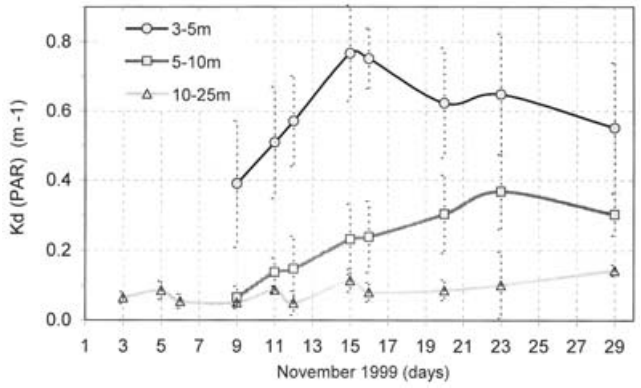


Fig. 4. Temporal variations of the mean diffuse attenuation coefficient for PAR radiation (Kd PAR ; m^{-1} mean ± SD), in the seawater under the pack ice. The diagram shows average values of Kd PAR relative to three different ranges of depths: 3–5 m, 5–10 m, 10–25 m.

0.4–0.9% of surface values, corresponding to 6 and 13 µE m^{-2} s^{-1}, when the maximum value of surface PAR was recorded (1487 µE m^{-2} s^{-1}). The K_d coefficients, measured within the platelet layer between 10–16 November 1999, have been used to estimate PAR and UV irradiance levels under the bottom layer. PAR irradiance under the bottom ice, ranges between 1.1 and 1.6% of surface values, which as daily average in absolute values becomes 5.6 to 10.5 µE m^{-2} s^{-1}. The percentage of the surface UV-B radiation that

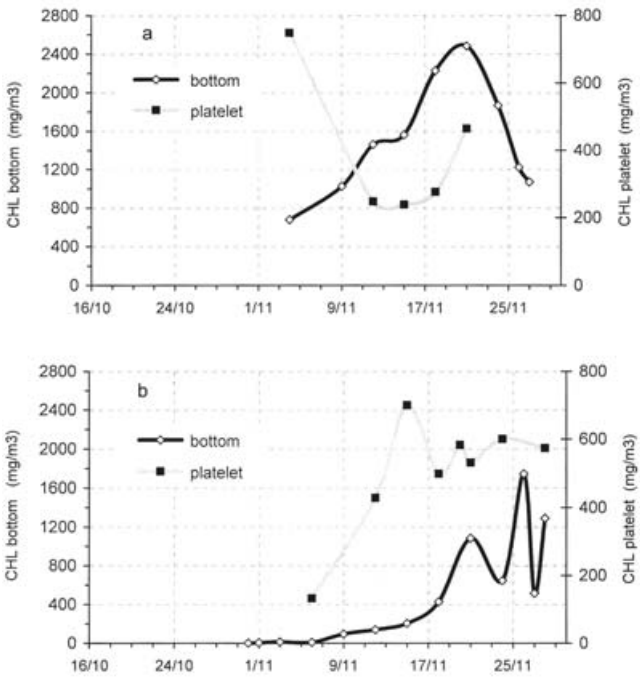


Fig. 5. Temporal variations of chlorophaeopigments concentration (CHL; mg m^{-3}) in the bottom-ice and in the platelet ice during the spring of 1997 and 1999.

Table I. Levels of PAR and UV-B irradiance, within and below the thickest sea ice (240 cm of congelation ice and 160 cm platelet ice), in 1999. The mean values of two typical days, sunny (9 November) and cloudy (22 November), have been chosen to represent the experienced environmental range. Light levels under the bottom layer (240 cm) have been calculated from attenuation of irradiance measured within the platelet (on 10–16 November 1999).

	E/Eo range%	Eo max	9 Nov '99 avg.	22 Nov '99 avg.
PAR (µE m^{-2} s^{-1})				
at surface	100	1487	655.97	505.42
at 240 cm under bottom	1.1–1.6	16.4–23.8	7.2–10.5	5.6–8.1
at 400 cm under platelet	0.4-0.9	5.9-13.4	2.6–5.9	2–4.5
UV-B (mW m^{-2} nm^{-1})				
at surface	100	53.2	20.38	20.99
at 240 cm under bottom	0.18–0.36	0.10–0.19	0.04–0. 07	0.04–0.08
at 400 cm under platelet	0.04–0.08	0.02–0.04	0.01–0.02	0.01–0.02

penetrates under the platelet ice, at 400 cm depth, is reduced on average to only 0.06% and under the bottom ice it is about 0.18–0.36% , so that one of the maximum values here recorded is 0.76 µW cm^{-2} 40 nm^{-1}.

Dynamics of the autotrophic biomass

During November, both in 1997 and 1999, we observed a strong increase in microalgal biomass in all layers of the sea ice, and particularly in the bottom and platelet ice (Fig. 5). In 1997, in the bottom ice, chlorophaeopigment concentrations increased from 680 to 2480 mg m^{-3}, then decreased to *c.* 1000 mg m^{-3}, by the end of the month. In the platelet ice layer, concentration ranged between 748 and 248 mg m^{-3}, with maximum values at the beginning of November. In 1999, pigment concentration was generally lower than in 1997. The maximum concentration was 1740 mg m^{-3} in the bottom ice, at the end of the month, and 716 mg m^{-3} in the platelet ice, in mid November. Cell density values agreed with the chlorophaeopigment concentration. In 1997, cell density ranged from $95*10^6$ cell dm^{-3}, on 10 November, to $156*10^6$ cell dm^{-3}, on 22 November. In 1999, density increased gradually, from $2*10^6$ cell dm^{-3}, at the beginning of the month, to $70*10^6$ cell dm^{-3}, at the end of the same month. An abundant microalgal sympagic community was thus present in springtime in the pack and platelet ice of Terra Nova Bay. The concentration of this biomass ranged over three orders of magnitude along the ice column, showing relatively low concentrations in the surface layers and high values in the bottom layers.

Physiological features of the sympagic community

During both expeditions (XIII and XV), pennate diatoms clearly appeared as the prevalent taxonomic group of the sympagic microalgal communities. In particular, two cryobenthic species dominated: *Entomoneis kjellmanni* (ex *Amphiprora* sp.) and *Nitschia* cf. *stellata*. We also found

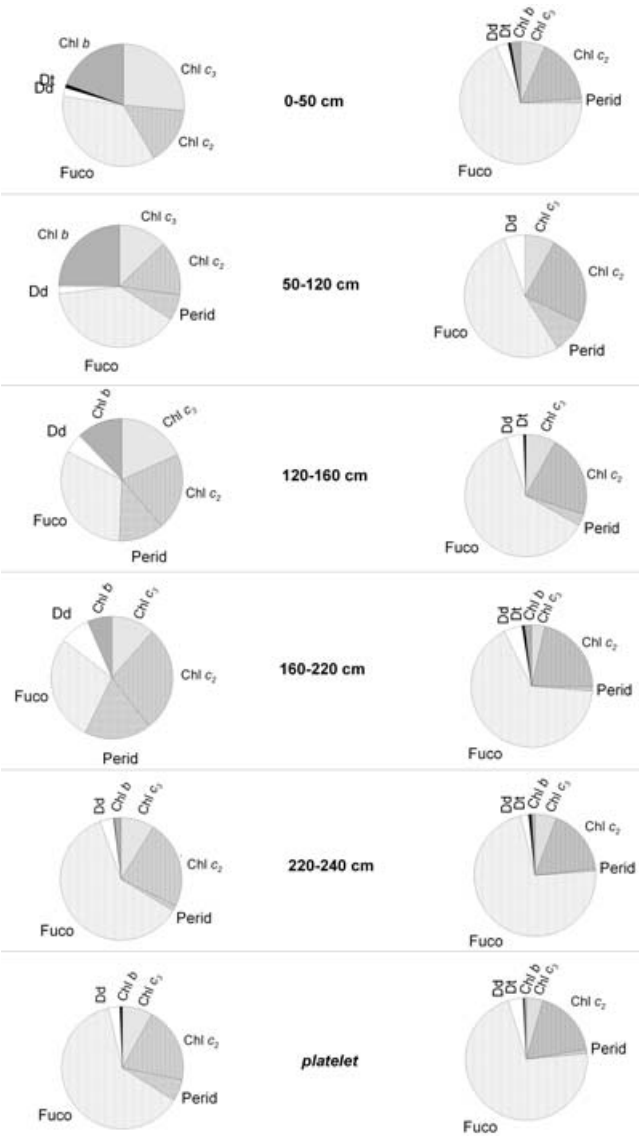
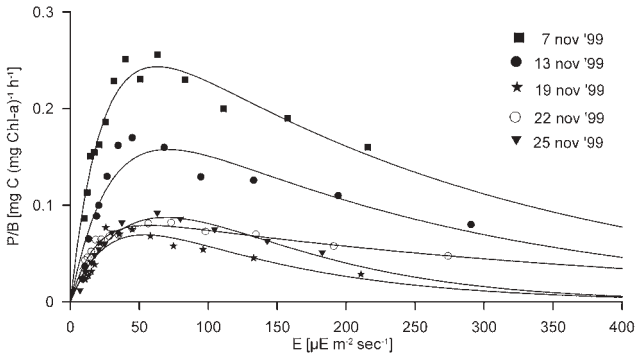


Fig. 6. Relative pigment composition of the sympagic assemblages of microalgae, in the different layers of two ice-cores, sampled at Campo A (6 and 26 November 1999).



day	P^B_{max}	α	β	E_m	E_k
7 Nov. '99	0.243	0.01313	0.00123	63	19
13 Nov.	0.158	0.00721	0.00099	70	22
19 Nov.	0.069	0.00380	0.00123	54	18
22 Nov.	0.079	0.00520	0.00025	57	15
25 Nov	0.087	0.00350	0.00394	69	25

Fig. 7. PvsE curves and photosynthetic parameters of the bottom-ice assemblages (P/B: mg C (mg chl h)$^{-1}$; E: E m^{-2} s^{-1}).

other species in the ice column, which appeared much less abundant, such as *Coscinodiscus* cf. *furcatus* and *Fragilariopsis* cfr. *curta*. Various species of the genera *Nitschia*, e.g. *N*. cf. *taeniiformis*, and *Fragilariopsis* cf. *cylindrus* were representative of the platelet ice assemblage. All cells showed abundant and evident chloroplasts.

The absorption measurements performed on the microalgal suspensions, from 25–28 November 1997 and 1999, revealed quite low values of specific absorption, both for the bottom and the platelet ice communities. At 676 nm, the chlorophyll specific absorption a*, ranged between 0.005 and 0.017 m^2 (mg Chl *a*)$^{-1}$; the blue to red ratio (440/676 nm) was between 1.36 and 2.36. For the bottom ice microalgae, the mean spectral average of a* was respectively 0.0083 ± 0.0021 m^2 (mg Chl *a*)$^{-1}$ (n = 4) in 1997 and 0.0104 ± 0.0043 m^2 (mg Chl *a*)$^{-1}$ (n = 6) in 1999.

Figure 6 summarizes the pigment composition (except Chl *a*), of samples collected at the beginning and at the end of November 1999. This analysis provides an approximate indication of the taxonomic composition and of the photo-acclimation characteristics of the population in the different layers of the pack ice. At the beginning of the month, the high concentrations of Fucoxanthin (Fuco) in all layers confirmed the dominance of diatoms, especially in the bottom ice. Chlorophyll *b* concentration was fairly constant in all ice core layers throughout the sampling period (0.055 ± 0.047 mg m^{-3}), whereas the percent contribution to the total pigment pool varied considerably (Fig. 6). Peridinin (Perid) and Chl c_3 concentrations varied but were always low (mean 0.340 and 0.555 mg m^{-3}, respectively); no particular pattern could be discerned along the ice core. Other diagnostic pigments were always below the detection limit. By the end of November, the pigment spectrum was substantially different mainly due to a considerable increase in Fuco concentrations. Fuco represented 70% of the sum of all pigments (Chl *a* excluded) along the ice core.

The sum of photoprotective pigments of brown algae (Diadinoxanthin, Diatoxanthin) showed a fairly even distribution at all levels throughout the ice cores. It is noteworthy that the contribution of these pigments to the total pigment pool increased during the period of study, from 6–7% at the beginning of November to about 12 % at the end of the month.

We conducted PvsE experiments on the sympagic microalgal population of the bottom ice, on 7, 13, 19 and 22 November 1999 (Fig. 7). A gradual decrease in P^B_{max} and an increase in α was observed from 7 to 19 November,

thereafter these parameters changed little but along an opposite gradient. The photoacclimation index, E_k, was low from 18 to 25 μE m^{-2} s^{-1}, with a small increase by the end of the experimental series. The PvsE curves showed a very strong photoinhibition (average β = 0.00127 mg carbon (mg Chl *a*$^{-1}$ hr^{-1} (μE m^{-2} s^{-1})$^{-1}$).

Discussion

Low light levels are typical of the under ice environment. The attenuation coefficients in the sea ice are at least one order of magnitude higher than in water (Maykut & Grenfell 1975) and a snow cover of 10 cm can further reduce transmission of light by a factor of two. The presence of a highly concentrated microalgal biomass also produces a strong and selective attenuation of PAR irradiance. Very few direct measurements exist of irradiance inside and under the Antarctic sea ice, owing to the technical difficulties related to the presence of the pack ice itself. This variable, which is essential for understanding most of the ecological processes, is usually calculated through radiative transfer models (Maykut & Grenfell 1975, Arrigo *et al.* 1991), starting from direct measurements mainly undertaken on Arctic sea ice (Perovich 2003).

Our measurements of daily average PAR irradiance, at surface and under the pack ice of Terra Nova Bay, in mid November, showed a range of 5.6 to 10.6 μE m^{-2} s^{-1} for the bottom sea-ice environment, and of 2 to 5.9 μE m^{-2} s^{-1} for the platelet ice. Robinson *et al.* (1998; figs 3 & 4) estimated an irradiance reaching the platelet ice assemblage at McMurdo, during November 1989, between 1 and 9 μE m^{-2} s^{-1}, (0.6–1.0% of surface PAR). Similar values (0.4%) were reported by Palmisano & Sullivan (1985). In the Arctic, in April and May, bottom ice algal communities living under 2 m of ice were reached by 0.1 to 1.0% of surface PAR, which was between 1.5 and 8.6 μE m^{-2} s^{-1} at noon (Suzuki *et al.* 1997). Much higher values, up to *c.* 3% of surface PAR, reached the platelet ice layer in other measurements of Robinson *et al.* (1995, table 1). The under ice irradiance range is then quite wide, as it is mainly influenced by the snow cover and the biomass density of the bottom ice microalgae. In fact, the values estimated through a bio-optical model by Arrigo (1991) range between 0.15 and 5% of surface PAR, from October to the beginning of December.

Sympagic microflora is highly abundant in the coastal sea ice of Terra Nova Bay in springtime, especially in the bottom and platelet ice (Guglielmo *et al.* 2000). In these layers, biomass concentration reaches values which are up to three orders of magnitude higher than in the surface ice layer or in the seawater below the pack ice, as currently observed in coastal Antarctic sea ice (Arrigo *et al.* 1995, Dieckmann *et al.* 1998, Arrigo 2003). In 1997, the increase of autotrophic biomass in the bottom ice appears to be in phase with the initial increase in irradiance levels. Only after a period of high temperature and a further increase of irradiance was a decline in biomass concentration observed. This decrease was probably linked to ablation of the annual pack ice and the dispersion/sinking of the sympagic biomass. In 1999, conversely, both solar radiation and biomass concentration showed a rising trend throughout November. The average values of temperature were quite low and stable, around -10°C, and the pack ice was one metre thicker than in 1997. These environmental factors probably affected the blooming season in 1999, which appeared delayed by two weeks with respect to our observations in 1997. The temporal dynamics of the algal biomass was the same in 1997 and in 1999, similar concentrations were reached, with a two weeks shift.

The spectral averages of specific absorption (ā*), measured on the bottom and platelet microalgal communities during both years, ranged between 0.006 and 0.017 m^2 (mg Chl *a*)$^{-1}$. Other authors describe mean specific absorption coefficients between 0.006 and 0.010 m^2 (mg Chl *a*)$^{-1}$, for the platelet and the congelation ice microalgae of McMurdo Sound (SooHoo *et al.* 1987). Values of ā* inferior to 0.009 m^2 (mg Chl *a*)$^{-1}$ were found in extremely shade-adapted platelet ice algae of McMurdo (Robinson *et al.* 1998). These values are all rather low if compared with the photic layer of pelagic environments, where light availability is not a limiting factor for phytoplankton growth. As an example to express a range of variability for a*, in different oceanic regions, Bricaud *et al.* (1995) give values of a_{676}* between 0.005 and 0.0550 m^2 (mg Chl *a*)$^{-1}$. Our values for a_{676}* are at the lower end of this range, between 0.005–0.017 m^2 (mg Chl *a*)$^{-1}$, and are a clear consequence of low light acclimation in a nutrient replete environment, as generally expected in Antarctic waters (Mitchell & Holm-Hansen 1991). Chlorophyll cellular content typically increases, in these conditions, to improve light harvesting ability (Falkowski & Raven 1997, MacIntyre *et al.* 2002). In the diatom *Chaetoceros protuberans* chlorophyll cellular content up to 5 pg Chl *a* cell^{-1} was observed under acclimation to light intensities as low as 35 μE m^{-2} s^{-1} (Morel *et al.* 1987, table 2). In the polar environment, Arctic sympagic diatoms showed 5 to 10 pg cell^{-1} (Barlow *et al.* 1988, fig. 3), and 28 pg cell^{-1} in diatoms from the bottom ice of McMurdo Sound (Sullivan *et al.* 1985, fig. 4). In our observations, we measured a range of 10–25 pg Chl *a* cell^{-1}. Despite the general assumption that cellular light absorption is proportional to cellular Chl *a* concentration, the efficiency of absorption (a*) declines in low light acclimated cells, because of increased pigment packaging and consequent self-shading (Morel & Bricaud 1981).

The PvsE experiments and the analyses of photoprotective pigments revealed further physiological adaptations to the sympagic environment. Photoinhibition was evident in all the experiments and in addition to the specific carotenoids, some evidence of photoprotecting

substances like MAAs, appeared in these microalgae: only populations of the upper metre of the sea ice core showed an absorption peak at 380 nm (Lazzara *et al.* 2004).

The photoacclimation index E_k was in the same range (15–25 µE m^{-2} s^{-1}) as the very low irradiance levels measured in the bottom ice, indicating the capacity of the microalgal assemblages to adapt to these extreme low light conditions (Table I, Fig. 7). Values of photosynthetic capacity (P^B_{max}) were accordingly low, as expected from sympagic communities (Lizotte & Sullivan 1991, 1992, Guglielmo *et al.* 2000). P^B_{max} values decreased with time during the season of 1999, in contrast with our observations of 1997 (Guglielmo *et al.* 2000), when the photosynthetic parameters remained fairly constant over the entire sampling period, but the means are essentially identical for the two years, 0.119 mg C mg Chl a^{-1} h^{-1}, in 1997 and 0.127 mg C mg Chl a^{-1} h^{-1}, in 1999.

We relate the decrease in the photosynthetic capacity (P^B_{max}) over time to the accumulation of biomass (Fig. 7), and to the observed changes in the taxonomic composition of the sympagic communities. In fact, a mixed algal assemblage was found in the pack ice at the beginning of November, while, by the end of the month, diatoms were by far the most abundant group, as shown by the pigment composition. A significant increase of Fucoxanthin (diatoms diagnostic pigment) occurred in all layers of the ice core from the pre-bloom period to the full-bloom phase. The Fuco:Chl *a* ratio increased while the pigment:Chl *a* ratios of Peridinin, Chl *b*, Chl c_3 sharply decreased in all layers, over the sampling period. These findings indicate that the notable increase in algal biomass was mainly due to diatoms. However, the increase in Fuco:Chl *a* ratio was also due to the need to optimize light harvesting as shown by the maximum values of this ratio that were always recorded in the bottom ice (0.92 on 4 November, 0.82 on 28 November). When we consider the mean molar ratios of the accessory pigments we have 1.25 and 0.37 for Fuco: Chl *a* and Chl *c*:Chl *a*, respectively. These are high values, only expected for cultures grown in low light (Falkowski & Raven 1997) and also observed in shade adapted platelet ice algae, at McMurdo (Robinson *et al.* 1995, table 2).

The minor variability of the photosynthetic parameters, in November 1997 as compared to the 1999 findings, may be explained by the shift in algal succession stage, i.e. the study period in 1997 occurred when the assemblages were already dominated by diatoms, as clearly indicated by the taxonomic and pigment analyses. In particular cryobenthic species (*Entomoneis kjellmanni* and *Nitschia* cf *stellata*) dominated the bottom sympagic flora whilst the platelet assemblage was mainly cryopelagic (e.g. *Fragilariopsis* cf *cylindrus*) with only a minor contribution of cryobenthic species .

Finally the integrated sympagic biomass values at Terra Nova Bay, up to 280 mg m^{-2}, were in the upper range of those reported from thirteen cruises in the Southern Ocean (Dieckmann *et al.* 1998), and in the review of Arrigo (2003, table 5.1), for bottom-ice communities. Interestingly, these values are even higher than the maximums reached in the water column integrated biomass observed at Terra Nova Bay (Lazzara *et al.* 2000).

The low light conditions observed in and beneath the ice, the high content of accessory pigments, the low photosynthetic parameters and specific absorption coefficients, the pigments ratios and the abundance of chloroplasts in the algal cells, all these are strong indications of the shade-adapted condition of these sympagic microalgal communities. The decreasing trend of photosynthetic capacity, which follows the high levels of photosynthetic yield at the onset of biomass accumulation, may be due to self-shading; the modest enhancement of the productive processes recorded at the end of the sampling period, might be related to photoacclimation. Biomass growth rates, estimated from the temporal variation of pigment concentration and cell density, appear higher than those suggested by the PvsE experiments. For both campaigns, the estimates of growth rates do not agree with the measurements of ice colour and of microalgal biomass concentration. This was presumably due mainly to the inevitable differences between *in situ* and experimental conditions; the experiments were performed on melted ice and the organisms experienced a rapid change from sympagic to pelagic conditions. However, the increase in algal biomass in the platelet ice occurred about three weeks prior to the accumulation of biomass in the bottom ice. In our opinion this discrepancy between observed cell densities and the ^{14}C measurements could be explained if, in addition to *in situ* growth, we consider the functional capacity of cryobenthic species to colonize the ice channels of the bottom ice layer with active migration, as previously suggested by Guglielmo *et al.* (2000, 2004).

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