RESEARCH ARTICLE

Spring phytoplankton onset after the ice break-up and sea-ice signature (Adélie Land, East Antarctica)

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Abstract

The phytoplankton onset following the spring ice break-up in Adélie Land, East Antarctica, was studied along a short transect, from 400 m off the continent to 5 km offshore, during the austral summer of 2002. Eight days after the ice break-up, some large colonial and solitary diatom cells, known to be associated with land-fast ice and present in downward fluxes, were unable to adapt in ice-free waters, while some other solitary and short-colony forming taxa (e.g., *Fragilariopsis curta*, *F. cylindrus*) did develop. Pelagic species were becoming more abundant offshore, replacing the typical sympagic (ice-associated) taxa. Archaeomonad cysts, usually associated with sea ice, were recorded in the surface waters nearshore. Rough weather restricted the data set, but we were able to confirm that some microalgae may be reliable sea-ice indicators and that seeding by sea ice only concerns a few taxa in this coastal area of East Antarctica.

The onset of the spring phytoplankton bloom, following the ice break-up in Antarctica, has received more attention for the pack ice edge than in coastal circumpolar regions. The edge of the marginal ice zone was considered an ideal environment for phytoplankton blooms (e.g., Sullivan et al. 1988; Fonda Umani et al. 2005; Garrity et al. 2005). However, a large part of the Antarctic shelf and seasonal ice zone remains poorly investigated due to logistical and technical constraints. Predictive models are currently developed based on sea-ice and ice-edge blooms to assess carbon export in seasonally ice-covered regions (e.g., Rodriguez y Baena et al. 2008), but in situ work still remains essential for validating such models, especially in poorly surveyed regions. While differences are noticed in the position and composition of the productive layers in pack and land-fast ice (Palmisano & Garrison 1993), the phytoplankton community also differs in composition, origin and development between coastal and offshore sites (Leventer 2003).

In the land-fast ice off Adélie Land, several surveys have provided an overview of the bottom-ice protist communities, which are composed of diatoms among other organisms (Riaux-Gobin et al. 2000; Riaux-Gobin et al. 2003; Fiala et al. 2006; Poulin et al. 2006). Land-fast ice forms annually in March and is relatively thin along the Adélie Land coast. In spring, the sympagic (ice-associated) community is restricted to a thin layer at the proximate part of the bottom ice and showed a taxonomic composition similar to other sea-ice communities reported from other Antarctic coastal regions (e.g., Cota & Sullivan 1990; Watanabe et al. 1990; Ackley & Sullivan 1994; Günther & Dieckmann 2001). Increasing irradiance and air temperature in springtime, along with ice melting processes, contribute to flush out the protist cells from the bottom ice layer, which are then scattered in the under-ice water column and eventually contribute to the vertical sinking flux of particulate organic material to deep waters and benthic communities (Leventer 2003).

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The coastal phytoplankton off Adélie Land following the ice break-up is less documented than the bottom land-fast ice communities (e.g., Beans et al. 2008), but the spatial distribution of the phytoplankton biomass has previously been described (Fiala & Delille 1992). However, the taxonomic composition is only briefly reported in the latter paper, with the presence of large diatom taxa at coastal stations such as *Corethron criophilum*, *Chaetoceros dichaeta* and *Fragilariopsis kerguelensis*, while they observed a reduction in the phytoplankton biomass and a shift in the taxonomic composition with small-sized flagellate cells at offshore stations.

The present study focuses on a restricted data set of the phytoplankton off Adélie Land, one week after the spring break-up of 2002. The objective was to compare the taxonomic phytoplankton composition along an offshore gradient in parallel with a survey of some biogeochemical parameters. Sea-ice signature species and possible seeding processes of the phytoplankton are discussed.

Material and methods

Study site and sampling

Due to rough weather, water sampling was only conducted once, on 18 January 2002, eight days after the ice break-up off the Adélie Land, East Antarctica. Water samples were collected with a 4-L Niskin bottle at 0, 5, 10 and 20 m along an offshore transect at four stations (Fig. 1) from A ($66°39.22'$ S, $140°00.14'$ E) to D

($66°36.81'$ S, $139°59.56'$ E) to determine the following variables: chlorophyll (Chl) a, b and phaeopigments (Phaeo) a, b; nitrite (NO_2); nitrate + nitrite ($NO_3 + NO_2$); phosphate (PO_4) and silicic acid ($Si[OH]_4$); and the identification and enumeration of phytoplankton cells.

Unfortunately, conductivity–temperature–depth instruments and current meters were not available for us to use along the prospected transect, which limited our understanding of hydrographic parameters. Nevertheless, we studied the under-ice current regime and the Lagrangian north-western drift (mainly governed by the tidal regime and in favour of an offshore export of particles) before the ice break-up on the same area, during the same campaign (Riaux-Gobin et al. in press).

Analytical methods

Biogeochemistry. Samples for nutrient determination were frozen immediately at $-20°C$ prior to be analysed in Banyuls-sur-Mer, France, using an AutoAnalyzer III (Technicon Corporation, New York, NY, USA; Tréguer & Le Corre 1975). Water samples for pigment analysis were filtered through 47-mm GF/F grade filters (Whatman, Maidstone, Kent, UK) and kept frozen at $-20°C$ prior to being analysed in Banyuls-sur-Mer. Following a 3-hour extraction in 5.4 mL of 100% acetone at 4 to 7°C in the dark, the concentrations of Chl a, b and Phaeo a, b were determined with an LS 55 Flourescence Spectrometer (PerkinElmer, Wellesley, MA, USA; Neveux & Lantoine 1993).

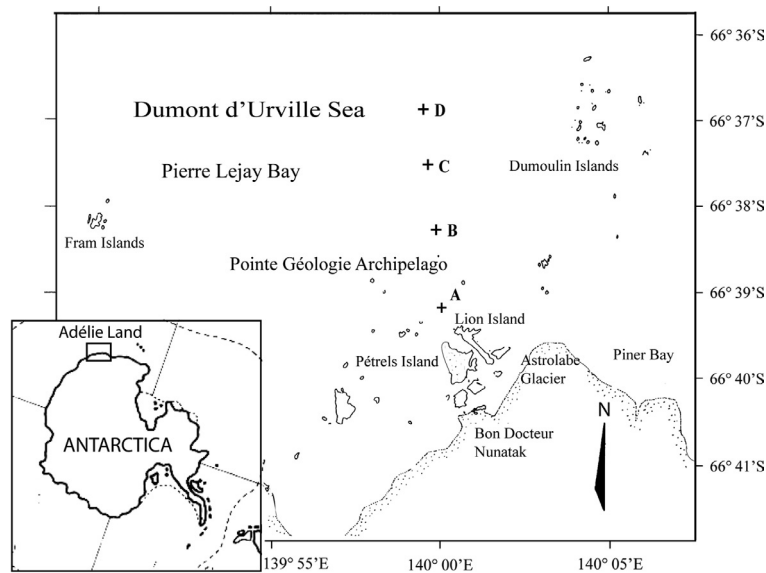**Fig. 1** Map of Adélie Land in Dumont d'Urville Sea, East Antarctica, showing the location of the four stations (A – D) along an offshore transect.

Identification and cell enumeration. Samples for the identification and enumeration of phytoplankton cells were preserved with acidic Lugol's solution. Cells were identified to the lowest possible taxonomic rank and enumerated under an inverted microscope (Wild, Heerbrugg, Switzerland) operating with phase contrast optics (Lund et al. 1958). Empty diatom cells were recorded separately as centric or pennate forms. The main taxonomic references used to identify the phytoplankton were Manguin (1957, 1960), Priddle & Fryxell (1985), Medlin & Priddle (1990), Hasle et al. (1994) and Hasle & Syvertsen (1997).

Statistical analysis. A covariance-based principal component analysis (PCA), using Statistica® software, was applied to the set of log-transformed data (log [x + 1]) corresponding to abundance data at each of the four sampling sites and at each of the four sampled depths (excluding unidentified taxa and morphological groups; see Table 1). This analysis tentatively discriminates taxonomic communities along axes and illustrates their relationship with the sampling sites.

Table 1 List of phytoplankton recorded in ice-free conditions offshore Adélie Land on 18 January 2002. Four-character abbreviations stand for each taxonomic entry. Asterisks mark species used in principal component analysis and Fig. 3.

BACILLARIOPHYCEAE

Centric
*asho *Asteromphalus hookeri* Ehrenberg
*chdi *Chaetoceros dichaeta* Ehrenberg
*chne *C.* cf. *neglectum* Karsten
*spch *Chaetoceros* spores
*cocr *Corethron criophilum* Castracane
*cosp1 *Coscinodiscus* sp.
*euan *Eucampia antarctica* (Castracane) Mangin
*odwe *Odontella weissflogii* (Janisch) Grunow
*pops *Porosira pseudodenticulata* (Hustedt) Jousé
thsp *Thalassiosira* spp.
*cesp1 Centric diatom sp. 1

Pennate
*amku *Amphiprora kufferathii* Manguin
*bead *Berkeleya adeliensis* Medlin
*cofa *Cocconeis fasciolata* (Ehrenberg) Brown
*cycl *Cylindrotheca closterium* (Ehrenberg) Reimann & Lewin
*frcu *Fragilariopsis curta* (Van Heurck) Hustedt
*frcy *F. cylindrus* (Cleve) Frenguelli
*frke *F. kerguelensis* (O'Meara) Hustedt
*frrh *F. rhombica* (O'Meara) Hustedt
*frsu *F. sublinearis* (Van Heurck) Heiden
*hama *Haslea major* (Heiden) Simonsen
*hatr *H. trompii* (Cleve) Simonsen
*mech *Membraneis challengeri* (Grunow) Paddock

*nadi *Navicula directa* (W. Smith) Ralfs
*nagl *N. glaciei* Van Heurck
*nasp *N.* sp. 1
*nas2 *N.* sp. 2
*nile *Nitzschia lecointei* Van Heurck
*nist *N. stellata* Manguin
*nite *N. taeniiformis* Simonsen
*plac *Plagiotropis acuta* (M. Peragallo) Simonsen
*psli *Pseudo-nitzschia lineola* (Cleve) Hasle
*pssu *P. subcurvata* (Hasle) Fryxell
*pstu *P. turgiduloides* (Hasle) Hasle
*pssp *P.* sp. 1
psspp *Pseudo-nitzschia* spp.
*syre *Synedropsis recta* Hasle, Medlin & Syvertsen
CHOANOFLAGELLIDEA
*mono *Monosiga* sp.
chos *Choanoflagellate* spp.
CHRYSOPHYCEAE
*kych *Archaeomonas* (cysts)
*ocsp *Ochromonas* sp.
CRYPTOPHYCEAE
*lesp *Leucocryptos* sp.
*rhsp *Rhodomonas* sp.
crys Cryptophyceae spp.
DICTYOCHOPHYCEAE
*disp *Dictyocha speculum* Ehrenberg
DINOPHYCEAE
*amsp *Amphidinium* cf. *sphenoides* Wülff
*gyfi *Gymnodinium* cf. *filum* Lebour
*gyga *G.* cf. *galeatum* Larsen
*prbi *Protoperidinium bipes* (Paulsen) Balech
*prsp *P.* sp. 1
*dis1 Dinoflagellate sp. 1
*dis3 Dinoflagellate sp. 3
*dis4 Dinoflagellate sp. 4
gybi Gymnodinioids ≥20 μm
gysm Gymnodinioids <20 μm
dism Dinoflagellates ≤20 μm
dibi Dinoflagellates ≥20 μm
EUGLENOPHYCEAE
eugl Euglenophyceae spp.
KINETOPLASTIDEAE
*pstr *Pseudobodo* cf. *tremulans* Griessmann
PRYMNESIOPHYCEAE
*phan *Phaeocystis antarctica* Karsten
UNIDENTIFIED FLAGELLATES
F11 Flagellates 11–20 μm
F20 Flagellates ≥20 μm
F5 Nanoflagellates ≤5 μm
F6 Nanoflagellates 6–10 μm
*fl1 Flagellate sp. 1
*fl2 Flagellate sp. 2

Results

Biogeochemistry

The photosynthetic pigment biomasses and nutrient concentrations measured at four depths along the

offshore transect (Fig. 1) were relatively homogeneous throughout the water column (Table 2). Phosphate concentrations were slightly higher nearshore in the surface water at station A, while remaining relatively homogeneous elsewhere. Nitrite, nitrate and silicic acid concentrations were homogeneous. Chlorophyll *a* concentrations were generally low but slightly higher in surface waters averaging at 2.22 µg L^{-1}, with no offshore spatial gradient, while Chl *b* showed low concentrations everywhere averaging at 0.12 µg L^{-1}, but with the lowest concentrations nearshore (on average 0.09 µg L^{-1}). Phaeopigment *a* concentrations were low (0.47–0.98 µg L^{-1}) and homogeneous from 0 to 20 m. The Chl *a*:Phaeo *a* ratios were high (2.0–2.5) at all depths.

Taxonomic composition

A total of 66 phytoplankton taxa (including two spore groups), representing 49 species in nine algal classes, were recorded for the water column off Adélie Land in mid-January 2002 (Table 1). Some taxa, mainly sea-ice indicators, are illustrated in Fig. 2. Several microalgae and morphometric groups (Table 1), not ranked to species level, have been recorded and enumerated. The cell abundance concerning the dominant microalgal taxa from the surface samples are listed with a rough ranking following the spatial abundances along the A – D transect (Table 3). Three groups are tentatively categorized (Table 3): (1) taxa mainly found in nearshore waters, close to ice melt (station A); (2) taxa mostly abundant at station D, close to offshore water masses; and (3) taxa without spatial preference.

The PCA was applied on a set of data (concerning all depths sampled) with the 49 species and 16 samples (Fig. 3). Some species, commented in the discussion, are in bold in Fig. 3 (see corresponding full names in Table 1). The first three axes explain 36.0% of the variance in the species data and the first two axes explain 25.6%. Even if

these scores are not that high, the PCA allows for the separation of samples or groups of samples (delineated by ellipses/lines in Fig. 3) and the identification of some associated/linked species.

The first PCA axis explains 14.3% of the variance in the microalgal assemblage data set, the coastal sample A5 being the major associated site. The associated species (higher negative scores on axis 1) are the flagellate sp. 2, *Navicula* sp. 1 and *Plagiotropis* acuta. The second PCA axis explains 11.4% of the variance in this assemblage. The species with the highest positive score on axis 2 are vegetative cells of the pelagic taxa *Chaetoceros* cf. *neglectum, C. dichaeta* and *Porosira pseudodenticulata*. The species with the highest negative score on axis 2 are the chain-forming diatoms *Berkeleya adeliensis* (Fig. 2e, h), *Amphiprora kufferathii* (Fig. 2d, g) and *Pseudo-nitzschia* sp. 1. The third PCA axis (not illustrated) explains 10.4% of the variance and discriminates pelagic taxa with a positive score such as *Odontella weissflogii* and centric sp. 1, from the taxon *Nitzschia taeniiformis* known to be a sympagic taxon. The PCA analysis discriminates relatively clearly the offshore sites D (positive scores on axis 2; Fig. 3) opposite to the more coastal and surface water sites (negative scores on axes 1 and 2).

Discussion

Spatial gradient in biogeochemical parameters

These newly ice-free waters showed no stratification down to 20 m for nutrients (see standard deviations in Table 2), possibly due to rough sea conditions and tidal mixing after the spring ice break-up. The low concentration of phaeopigments and the high Chl *a*:Phaeo *a* ratio (Table 2) tend to show a relatively fresh and ungrazed standing stock of microalgal cells. After eight days following the ice break-up, the phytoplankton community is still in a pre-bloom period with very low Chl *a*

Table 2 Chloropigments (µg L^{-1}) and nutrients (µm) in water samples, sites stations A – D (see Fig. 1) only showing the mean value of the water column from 0 m to 20 m.

| Station		Chl *a*	Chl *b*	Phaeo *a*	Phaeo *b*	Chl *a*:Phaeo *a*	Si(OH)$_4$	NO$_2$	NO$_3$+NO$_2$	PO$_4$
A	Mean	1.73	0.09	0.75	0.23	2.35	52.8	0.15	26.8	1.64
	SD	0.36	0.02	0.20	0.04	0.33	1.37	0.01	1.63	0.18
B	Mean	2.21	0.13	0.93	0.32	2.38	54.36	0.17	27.83	1.55
	SD	0.22	0.02	0.06	0.02	0.29	1.63	0.01	1.56	0.07
C	Mean	2.04	0.13	0.96	0.28	2.12	52.13	0.15	24.95	1.58
	SD	0.09	0	0.02	0.02	0.07	6.10	0.02	3.38	0.05
D	Mean	2.04	0.13	0.85	0.30	2.14	52.73	0.17	25.75	1.67
	SD	0.25	0.01	0.03	0.04	0.36	6.44	0.01	4.37	0.14
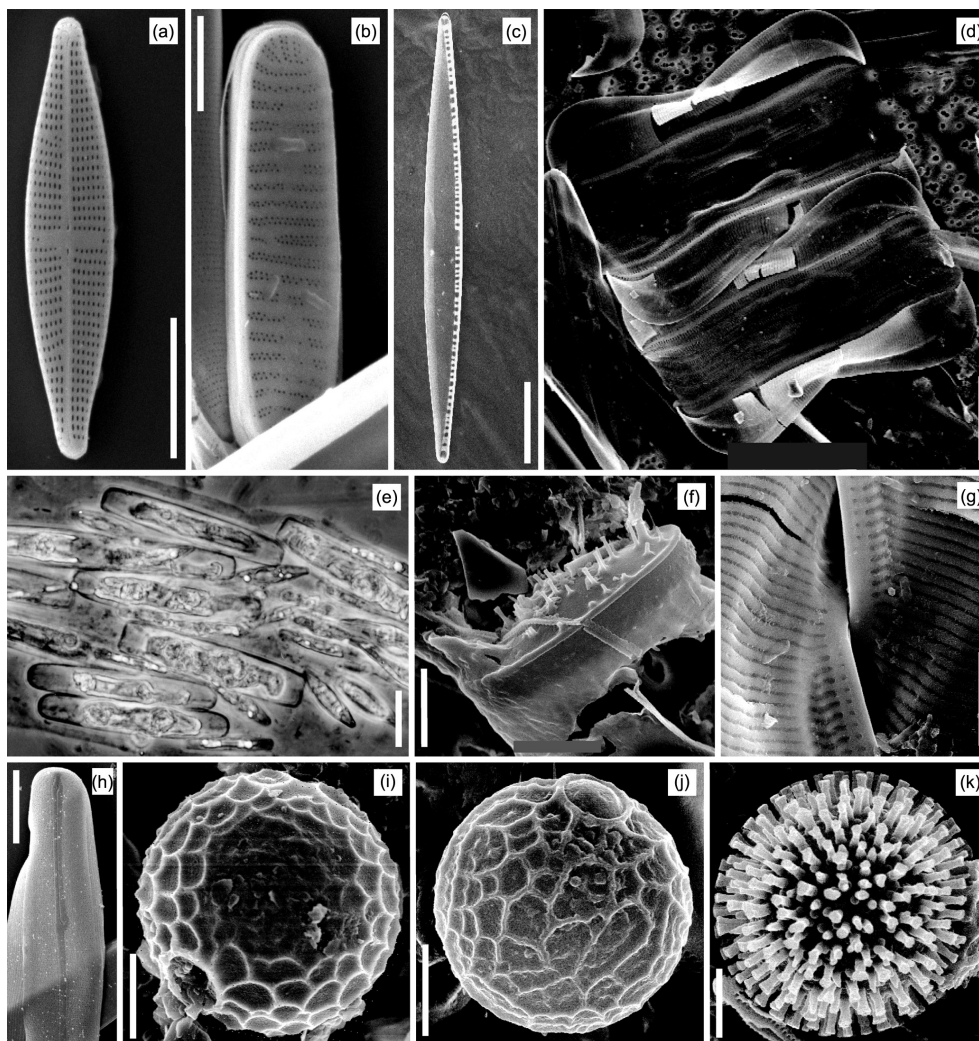
Fig. 2 Micrographs of some protist taxa, mainly sea-ice indicators, from Adélie Land, in light (e) and scanning electron microscopy (a – d, f – k). (a) *Navicula glaciei*; (b) *Fragilariopsis curta*; (c) *Nitzschia stellata*; (d, g) *Amphiprora kufferathii*; (e, h) *Berkeleya adeliensis*; (f) spore of *Chaetoceros* cf. *neglectum*; (i – k) Archaeomonadaceae (cysts): (i) *Archaeomonas* cf. *areolata*, (j) *A.* cf. *speciosa* Deflandre, and (k) *Litheusphaerella* cf. *spectabilis*. Scale bars: 3 μm (i – k); 5 μm (b, f, g); 10 μm (a, e, h); 20 μm (c, d).

biomass in surface waters decreasing at 5 m. However, the Chl *a* biomass measured at 5 m is higher than the concentrations recorded in the under-ice water the week before (C. Riaux-Gobin, pers. obs.).

NO_3 and $Si(OH)_4$ concentrations (Table 2, mean 26 and 53 μM, respectively) were very similar to data recorded during the summer of 1995 in the same area, in small polynyas opened before the complete ice break-up at coast (Riaux-Gobin et al. 2000; Table 4; mean 27 and 64 μM, respectively). The Chl *a* concentrations were lower in 1995 (mean 0.69 μg L^{-1}) than in the present study, possibly due to the fact that the sampling took place before the break-up.

Phytoplankton spatial distribution and origin of sea-ice protist taxa

The ice-free phytoplankton taxonomic composition (Table 2) slightly differed from the one reported from the land-fast ice and the under-ice surface water before the ice break-up in the same area (Riaux-Gobin et al. 2003). Several ice-associated taxa such as *Banquisia belgica* and *Entomoneis kjellmanii* were absent in the ice-free conditions, and several microalgae present in the phytoplankton were absent from the sea ice some weeks before (i.e., *Membraneis challengeri*, *Pseudo-nitzschia lineola*, *Fragilariopsis kerguelensis*, most of the centric diatoms,

Table 3 Rough ranking of cell abundance (10^3 cells L^{-1}) of the dominant taxa recorded in the surface waters (0 m) along the transect A – D (see Fig. 1) in Adélie Land, East Antarctica (January 2002). Taxa not detected are indicated with the abbreviation nd. Squared assemblages per station are representative of (1) nearshore and (2) offshore the dominance. The third group (3) shows no obvious spatial gradient. Asterisks mark species used in principal component analysis and Fig. 3.

Protist taxon	Abundance at station			
	A	B	C	D
(1) More abundant nearshore				
*Chaetoceros spores	274.5	127.7	137.3	63.9
*Amphiprora kufferathii	3.5	nd	nd	nd
*Berkeleya adeliensis	31.9	nd	nd	nd
*Pseudo-nitzschia lineola	28.4	5.3	nd	17.7
*P. subcurvata	106.4	5.3	21.1	53.2
Choanoflagellate spp.	49.7	nd	nd	21.3
*Archaeomonas (cysts)	14.2	nd	nd	nd
Flagellates spp. 11–20 µm	14.2	16.0	7.1	nd
Dinoflagellates ≤20 µm	17.7	5.3	7.1	3.5
Gymnodinioids ≥20 µm	10.6	2.7	nd	7.1
(2) More abundant offshore				
*Chaetoceros cf. neglectum	844.6	497.5	760.2	1355.2
*Porosira pseudodenticulata	nd	nd	nd	10.6
Thalassiosira spp.	nd	nd	nd	10.6
*Fragilariopsis cylindrus	168.9	196.9	232.3	340.6
*F. kerguelensis	nd	nd	7.1	17.7
Nanoflagellates spp. 6 – 10 µm	168.9	199.5	147.8	312.1
Nanoflagellates spp. ≤5 µm	950.2	651.9	1288.0	1525.4
Gymnodinioids <20 µm	17.7	21.3	24.8	46.1
(3) No obvious spatial gradient				
*Chaetoceros dichaeta	138.4	66.5	53.2	113.5
*Eucampia antarctica	17.7	2.7	14.2	10.6
*Fragilariopsis curta	70.9	58.5	127.0	85.1
*Pseudo-nitzschia turgiduloides	49.7	42.6	42.6	24.8
*Pseudo-nitzschia sp. 1	nd	23.9	17.7	nd
*Synedropsis recta	nd	nd	10.6	nd
*Monosiga sp.	nd	nd	95.0	nd
Cryptophyceae spp.	nd	2.7	10.6	nd
*Amphidinium cf. sphenoides	nd	5.3	10.6	7.1
Euglenophyceae spp.	nd	2.7	3.5	nd
*Phaeocystis antarctica	1161.4	428.363	1171.9	776.9

particularly species of *Chaetoceros*, and several dinoflagellates; M. Poulin, pers. comm.).

The large and colonial pennate diatoms, *Amphiprora kufferathii* and *Berkeleya adeliensis*, recognized as sympagic taxa (Garrison et al. 1986; Leventer 1998; McMinn 1998; Knox 2006) were only present at the nearshore station A, and *Navicula glaciei* (Fig. 2a) was also rarely recorded in the plankton (it was not recorded at the offshore stations C and D). In contrast, *Fragilariopsis cylindrus* and *F. curta* (Fig. 2b) were relatively abundant in the pelagic waters, with up to 55×10^4 cells L^{-1} at station A (5 m) and 16×10^4 cells L^{-1} at station B (10 m), respectively (see discussion of *Fragilariopsis cylindrus* and *F. curta* in Leventer 1998). Archaeomonad cysts (Fig. 2i – k), also recog-

nized as sea-ice inhabitants (Mitchell & Silver 1982), are not rare on the Adélie Land bottom ice, platelet ice layer and adjacent waters (Riaux-Gobin & Stumm 2006) and were only recorded at the coastal station A.

Pelagic species were abundant offshore throughout the water column, particularly with vegetative cells of *Chaetoceros dichaeta* and *C.* cf. *neglectum reaching* up to 22×10^4 cells L^{-1} and 16×10^5 cells L^{-1}, respectively. These taxa seem to rapidly develop, particularly *C.* cf. *neglectum*, while they were absent from the land-fast ice and rare or absent from the under-ice surface water before the ice break-up (Riaux-Gobin et al. 2003). A particular mention can be drawn for the spores of *Chaetoceros*: during the 1995 campaign in Adélie Land,
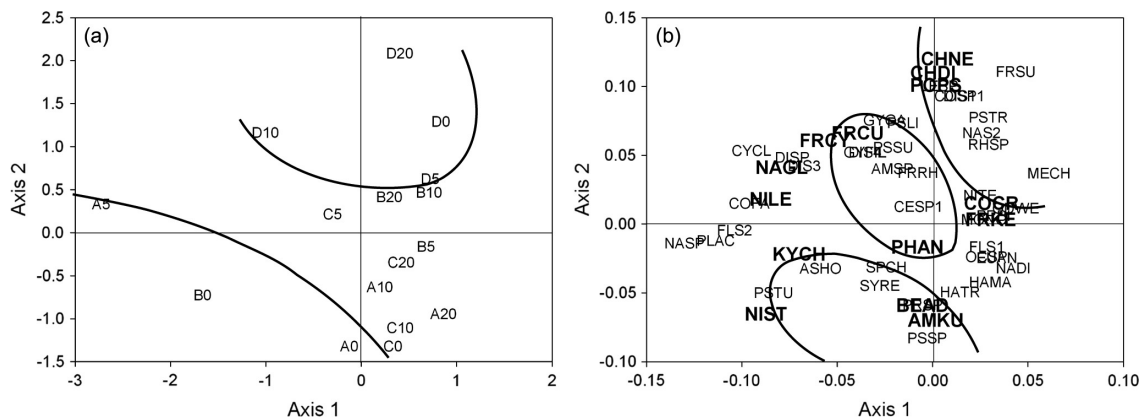
Fig. 3 Principal component analysis of (a) stations: nearshore and surface samples (stations A and B, with negative scores on axes 1 and 2 are individualized). The analysis also groups the offshore and deeper samples (particularly station D, positive score on axis 1). Principal component analysis of (b) species distribution with a group of sympagic taxa (e.g., BEAD, AMKU and KYCH, negative score on axis 1), a group of typical pelagic taxa (e.g., CHNE, CHDI, POPS, positive scores on axis 1), and an intermediate group of well-adapted taxa to ice-free water conditions (e.g., FRC, FCRU and PHAN). See Table 1 for abbreviations.

spores of *Chaetoceros* were recorded, along with vegetative cells of *C.* cf. *neglectum*, only in small adjacent polynyas but apparently not in sea ice (Riaux-Gobin et al. 2003). Before the ice break-up in 2002, spores of *Chaetoceros* were only recorded at 5-m water depth under the ice sheet, but never in the bottom or platelet ice (M. Poulin, pers. comm.). After the ice break-up (present study), these *Chaetoceros* spores were surprisingly slightly more abundant at station A than at offshore stations: they may have been overlooked in sea-ice samples (Fig. 2f).

Fragilariopsis kerguelensis, which is reported to be an indicator species of open water conditions with no correlation to sea ice (Pike et al. 2008), was absent at nearshore stations A and B and was present only in the surface waters at offshore stations C and D.

Dinoflagellates and the prymnesiophyte *Phaeocystis antarctica*, with 11×10^5 cells L^{-1}, were abundant in the surface waters at coastal stations denoting their relationship with cold waters and ice melting conditions (slightly lower salinity at station A; data not shown), as previously demonstrated by Moisan & Mitchell (1999). In our study, *P. antarctica* dominated the surface water phytoplankton community representing 16% of the total phytoplankton assemblage.

PCA analysis

As shown from the PCA analysis (Fig. 3) and the rough ranking in Table 3 (only surface samples), one week after the effective ice break-up the water masses, if referred to taxonomy, show a strong gradient from coast to offshore. The coastal stations A and B (0 m) scored negatively on

the PCA axes 1 and 2 (Fig. 3) and they were characterized by the presence of typical sympagic pennate diatoms such as *Amphiprora kufferathii*, *Berkeleya adeliensis* and *Nitzschia stellata* (Fig. 2c), while these taxa apparently did not survive at offshore ice-free stations. The station A is also characterized by the presence of archaeomonad cysts that were absent from offshore stations.

In contrast, the colonial protist taxa *Fragilariopsis cylindrus*, *F. curta* and *Phaeocystis antarctica* classically present in the bottom layer of the land-fast ice seemed well adapted to open water conditions (central group of taxa in Fig. 3) as previously shown in ice-edge open waters (Hegseth & von Quillfeldt 2002). The same conclusion was recently given for *Fragilariopsis cylindrus* from a platelet ice community at Terra Nova Bay, which was also well adapted to planktonic conditions (Mangoni et al. 2009). *Fragilariopsis curta* showed an adaptation to decreasing salinity due to sea-ice melting (Ryan et al. 2004), and both *F. cylindrus* and *F. curta* were the most common flourishing microalgae in the marginal ice zone (Leventer 1998), which was also the case for *P. antarctica* (Fryxell & Kendrick 1988; Kang et al. 2001).

The PCA first and second axes discriminate relatively clearly the origin of the cells: (1) a sympagic coastal origin for several taxa (negative scores of A0, B0 and C0 on axis 2; signature of the land-fast ice present a few days before on the sampling area, particularly in surface coastal waters); in opposition to (2) a pelagic origin for several others taxa (positive scores of all depths at D and deep waters at B on axis 2). The ice break-up was effective at coast only a few days before sampling and drifting ice was

still present, implying a strong sympagic component to the coastal diatom community.

Sea-ice proxies

The preservation of phytoplankton and sea-ice diatoms in sediments, particularly in the Southern Ocean and their use for palaeo sea-ice reconstructions (Armand & Leventer 2010), has been commented upon and questioned (Leventer 1998) and remains a topic of current interest (Pike et al. 2008). Pike et al. showed the complexity of studies comparing contemporary and fossil Antarctic diatom communities, but they concluded that the summer community is largely not preserved in the sediments. Tanimura et al. (1990) compared the diatom communities in the water column after the ice break-up with communities from sea ice and the surface sediments in Lützow-Holm Bay, Antarctica. They showed that several weakly silicified diatom taxa that were abundant in the water column and sea-ice (e.g., *Berkeleya* sp. a, *Chaetoceros* spp., *Cylindrotheca closterium*, *Navicula glaciei*, *Nitzschia lecointei*, *N. stellata*, *Pleurosigma* sp. and *Tropidoneis* sp.) were not recorded in the sediments. On the other hand, two more strongly silicified species associated with sea ice and the underlying waters, namely *Fragilariopsis curta* and *F. cylindrus*, were well-preserved in sediments (see Leventer 1998; Armand et al. 2005). Tanimura et al. (1990) also pointed out that *F. kerguelensis* in addition to *F. obliquecostata* (Van Heurck) Heiden, *F. separanda* Hustedt and *F. sublinearis* were usually recorded in greater numbers in the sediments than in sea-ice environments, which can be explained by their resistance to corrosion and, for *F. kerguelensis*, the penetration of open ocean currents under the land-fast ice.

Sympagic land-fast ice pennate diatoms (e.g., *Amphiprora kufferathii*, *Berkeleya adeliensis* and *Navicula glaciei*) that cannot survive in ice-free waters may be considered a land-fast sea-ice signature. However, with respect to diatoms, a reliable signature means that the frustules need to be well preserved in the fossil record, which is not often the case, like for *Navicula glaciei* (Krebs et al. 1987; Tanimura et al. 1990).

Cysts of *Archaeomonas* preserved well in sediments (Deflandre 1932; Tynan 1971). In the coastal area of Adélie Land, *Archaeomonas* cf. *areolata* Deflandre and *Litheusphaerella* cf. *spectabilis* Deflandre were present in sea ice and under-ice waters (Fig. 2i, k) (Riaux-Gobin & Stumm 2006) but preferentially in sea-ice layers. In this study, cysts only occurred in the surface waters at the coastal stations. These observations confirmed the use of these archaeomonad cysts as a signature or a "proxy" of the presence of annual land-fast ice and support previous

findings by Mitchell & Silver (1982). The receding ice may seed these organisms in the under-ice water, but as their life cycle is so far unknown this cannot conclusively be inferred.

The presence of *Chaetoceros* resting spores was interpreted as indicative of high primary production by Leventer (1998) and also as a proxy for spring sea-ice melting (Crosta et al. 2007), but these observations fail to provide details about spore formation in sea ice or adjacent cold waters.

Seeding by sea ice

It is of interest to evaluate the contribution of the land-fast ice to the phytoplankton seeding process. Several environmental variables affect the development of bottom ice protists and their fate following the ice melting events responsible for their release to the water column. It has been demonstrated that sympagic algae may contribute to the pelagic bloom in Ellis Fjord, in eastern Antarctica (McMinn 1996) and also in Terra Nova Bay (Mangoni et al. 2009). However, Ligowski et al. (1992), studying sea-ice diatoms and ice-edge plankton diatoms in the Weddell Sea, stated that sea-ice diatoms in their samples were not in good health and could not be regarded as an inoculum for the phytoplankton diatoms. They concluded the poor physiological state of these ice microalgae may be ascribed to the sampling period (summer) and the sampling region.

Depending on the ice type and history (land-fast ice, pack ice, drifting floes) and the presence/absence of platelet ice, seeding processes are bound to be highly variable. Ichinomiya et al. (2008) investigated the abundance and sinking flux of diatoms under fast ice at Syowa Station in East Antarctica and showed that species released from the ice exhibit differences in their buoyancy control and sinking characteristics.

The study reported here confirms our previous investigations in Adélie Land on small polynyas and leads just before the ice break-up event in the austral summer of 1995, where the under-ice phytoplankton was composed of some sympagic diatoms as well as vegetative cells of *Chaetoceros* that were not present in the land-fast ice (Riaux-Gobin et al. 2000). Here, the abundance of *Fragilariopsis cylindrus* and *F. curta* in ice-free waters indicates a possible seeding by sea-ice for these two taxa, previously demonstrated as successfully exploiting the water column adjacent to the ice as well as the ice itself (Leventer 1998).

The prymnesiophyte *Phaeocystis antarctica*, an opportunistic taxon (Fryxell & Kendrick 1988), has recently been shown to be capable of surviving in both the ice and the

water column (Tang et al. 2009) but with no prevalence of one environment as refuge. During the EPONTA 2001 survey, the communities present in the land-fast ice before the break-up and in the open water immediately after the break-up were investigated in Adélie Land. Before the ice break-up, *P. antarctica* was shown to grow preferentially in the platelet ice and in the under-ice waters but only during the last 10 days before the ice break-up (M. Poulin, pers. comm.). This observation may possibly imply that sea-ice trapped *P. antarctica* cells from the underlying water masses, before seeding them back at the ice break-up.

Conclusion

The sudden increase in irradiance after the ice break-up triggers the growth of the phytoplankton, but the origin of the ice-free protist community is not yet entirely understood. Such uncertainties have also been pointed out in other studies: the seeding attributed to the receding ice edge has been well documented, commented upon and questioned (Lizotte 2001), mostly in pack-ice environments but has never yielded the same conclusions (Leventer 2003). As Ishikawa et al. (2001) also conclude in their study of the origin, evolution and fate of diatom communities under fast ice near Syowa Station during the austral summer, further investigations are needed to clarify the findings. The present set of data is very restricted and only represents a one-time survey concerning Adélie Land. Such samplings have to be replicated several times before giving an accurate and reliable overview of: (1) the taxa present, their origin and relationship with the sea-ice history (having or not experienced winter break-up events); (2) the taxa that immediately sediment (fast vertical flux to the benthos) and do not participate to the pelagic cycle after the ice break-up; (3) the taxa that seed the water column; and finally (4) the taxa that may be good annual sea-ice proxies.

Acknowledgements

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