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Nutrients, algal biomass and communities in land-fast ice and seawater off Adélie Land (Antarctica)

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Abstract: Land-fast ice in the vicinity of Adélie Land was sampled during spring 1995. The ice was annual, thin, with no consistent snow cover, and exposed to oceanic conditions. Temporal and spatial variations of the vertical pigment distribution were studied in relation to environmental factors, during the break up of the ice. Different levels were sampled in the congelation ice and the platelet ice-like layer (PLI). Under-ice water and open water masses were also sampled. The algal biomass was greater in the PLI (24 ± 14 µg chl *a* l^{-1} offshore and up to 9 mg chl *a* l^{-1} near-shore), than in the under-ice water, and fell to 0.9 ± 0.64 µg chl *a* l^{-1} in open water masses. Homogenous low pigment concentrations were detected in the upper levels of congelation ice. A gradient was identified along a 7 km seaward transect, sampled in November, with the lowest biomass offshore. The integrated pigment concentrations in fast ice reached very high levels (> 500 mg chl *a* m^{-2} near the coast and 0.8 mg m^{-2} offshore), with apparently no relationship with either the ice thickness or snow cover. In the congelation ice nutrient concentrations were low and their distribution homogenous, whereas in the PLI high concentrations of nitrate (up to 100–300 µM NO_3^-) and silicic acid [30–100 µM $Si(OH)_4$] were detected, often related to high pigment concentrations and proximity to islands. The sea ice algae communities were diverse, but mostly composed of chain-forming and tube-dwelling pennate diatoms (*Amphiprora*, *Berkeleya*, *Nitzschia* and *Navicula*). Cell densities in PLI reached up to 10^{10} cells l^{-1}. At very low biomass and cell densities ($2\ 10^4$ cells l^{-1}) the phytoplankton also had a low diversity; some species were similar to those of the PLI, such as *Navicula glaciei*, but other were typically planktonic (*Chaetoceros*). At sea ice break-up it is estimated that a significant proportion of particulate matter (up to 0.5 g chl *a* m^{-2} near-shore) was transferred to the underlying water masses (on an average 15 t POC km^{-1} shoreline).

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Key words: Annual land-fast ice, nutrients, phytoplankton, pigment biomass, sea ice microalgae

Introduction

Ice associated algal blooms and "superblooms" in Antarctic regions have been described and their importance tentatively quantified. These blooms have different origins (Smetacek *et al.* 1990 and reference therein) as well as multiple developmental cycles. Some are associated with the receding pack ice edge (Sullivan *et al.* 1990 and references therein), whilst others are directly associated with the ice itself, particularly the bottom ice or an unconsolidated under-ice layer such as the so-called "platelet layer" (references in Table I). There is only limited information about such unconsolidated layer blooms which have been mostly observed under land-fast ice, but also under pack ice. Their implication in the Antarctic food chain is as yet unclear.

The ice algal communities are complex and continually changing. McGrath Grossi *et al.* (1987) described a strand community in McMurdo Sound growing loosely attached to the bottom ice, after disappearance of the platelet ice. These strands are difficult to sample with a conventional corer and show great spatial heterogeneity (Sasaki & Watanabe 1984, Watanabe 1988). Cota & Sullivan (1990) described diatom successions in bottom ice where *Nitzschia stellata* was dominant, and *Amphiprora* declined as *Berkeleya* sp. increased late in the season. Watanabe *et al.* (1990), also observed succession in bottom ice and suggested that the presence of pelagic diatoms in an interior assemblage could be considered as a fingerprint of the planktonic cells entrapped during ice establishment (see also Günther & Dieckmann 1999). The physiology of the communities is inconsistent. The trapped pelagic algae do not grow well, whereas the pennate diatoms in the bottom ice are apparently highly productive when irradiance is sufficient. In addition, heterotrophy has also been inferred in a platelet ice community by Palmisano & Sullivan (1985).

Physical and biological interactions are also apparent (Garrison *et al.* 1986 and references therein). During melting ice crystal structure changes as does the circulation of pore water. High concentrations of diatoms may initiate, or increase, melting in the platelet layer (Sullivan *et al.* 1983). Variations in nutrient concentrations within the ice, and in the underlying

Table I. Land-fast ice maximum microalgal standing stocks associated with the ice–water interface in Antarctica.

Site	Fast ice character	Biomass layer	Max. biomass	Reference
McMurdo Sound		platelet ice	500–1000 mg C m^{-2}	Bunt & Lee 1970
Syowa	annual	bottom ice	1000 mg chl *a* m^{-3}	Hoshiai 1977
McMurdo Sound		bottom congelation ice	309 mg chl *a* m^{-2}	Palmisano & Sullivan 1983
Lützow-Holm Bay (North Syowa)	1.40 m	under ice epontic strands	32.7 mg chl *a* m^{-2}	Sasaki &Watanabe 1984
McMurdo Sound	annual	platelet layer bottom congelation ice	76 mg chl *a* m^{-2} 9 mg chl *a* m^{-2}	Grossi McGrath *et al.* 1987
Syowa	multiyear	bottom ice	125 mg chl *a* m^{-2}	Watanabe *et al.* 1990
McMurdo Sound	annual	bottom ice	565 mg chl *a* m^{-2}	*in* Knox 1990
McMurdo Sound	second year 2.50 m	platelet ice 0.65–0.75 m	6500 mg chl *a* m^{-3} 37.4 g C m^{-2}	Arrigo *et al.* 1995
Weddell Sea	annual 2.10 m	platelet ice 1 m	210 mg chl *a* m^{-2}	Günther & Dieckmann 1999
Adélie Land	annual 1.20 m	platelet ice-like 0.10–0.30 m	9000 mg chl *a* m^{-3} 500 mg chl *a* m^{-2}	present study

Table II. Sampling sites, dates and observations.

Sampling site/date	Lat.	Long.	Congelation ice thickness cm	Platelet layer colour
Chenal de Pedersen, 12/11/95				
P_1	66°40'.00	140°01'.00	75	no colour
Coast to offshore transect, 15/11/95				
R_1	66°39'.477	140°00'.500	78	deep coloured
R_2	66°38'.557	140°00'.050	67	deep coloured
R_3	66°37'.978	140°00'.094	66	no colour
R_4	66°37'.235	140°00'.176	77	light colour
R_5	66°36'.571	140°00'.214	100	light colour
R_6	66°36'.305	140°00'.281	105	light colour
R_7	66°33'.980	140°00'.357	98	no colour
DDU/Prud'Homme transect, 20/11/1995				
S_1	66°40'.170	139°59'.943	110	deep coloured
S_2	66°40'.683	139°58'.133	114	deep coloured
S_3	66°40'.878	139°56'.882	110	deep coloured
S_4	66°41'.207	139°55'.693	103	deep coloured
S_5	66°41'.331	139°54'.809	115	less coloured
Coast to offshore transect, 26/11/95				
T_1	66°39'.477	140°00'.500	60	deep coloured
T_2	66°38'.557	140°00'.050	64	pinkish
T_3	66°37'.978	140°00'.094	74	no colour
T_4	66°37'.235	140°00'.176	70	no colour columnar ice melting
DDU/Prud'Homme transect, 26/11/1995				
U_1	66°40'.20	139°59'.90	96	deep coloured
U_2	66°40'.00	139°58'.00	107	deep coloured
U_3	66°41'.00	139°57'.00	114	no colour
U_4	66°41'.00	139°56'.00	82	no colour
U_5	66°41'.00	139°55'.00	110	deep coloured
Polynya Water, 7 to 16/12/1995				
W Lion	66°39'.45	140°01'.10		
Mas Iono	66°40'.05	140°00'.50		
N Poissons	66°40'.50	139°59'.40		
lead N Lion	66°39'.12	140°00'.60		

water during the bloom, are also high and depend upon many physical and biological factors (e.g. Cota & Sullivan 1990, Grossmann *et al.* 1996). Dieckmann *et al.* (1992) observed accumulation of ammonia in the platelet layer.

The relationships between communities that develop within under-ice layers and in water masses are not often considered (Perrin *et al.* 1987, Smetacek *et al.* 1992). In pack ice the same species assemblages occur as in the underlying water (Garrison & Buck 1985) whilst in the fast ice environment the assemblages seem to be different to the plankton with aggregation and sedimentation of pennate diatoms occuring during melting (Sasaki & Hoshiai 1986). As far as fluxes of particulate matter are concerned, Matsuda *et al.* (1990) and Knox (1990) have pointed out the importance of these blooms for benthos.

Adélie Land is a coastal area largely open to the ocean, the land-fast ice is annual, less than 2 m thick and predictable. In contrast with other Antarctic study areas (e.g. Günther & Dieckmann 1999), the snow cover is thin. Oceanographic data for the coastal shelf of Adélie Land are scarce: some hydrological data are available from a summer cruise (Tchernia 1951) and taxonomic investigations, mostly for pelagic diatoms, were conducted during the same cruise by Manguin (1960). The phytoplankton is characterized by low biomass (on an average 1.23 µg chl *a* l^{-1} in summer; Fiala & Delille 1992), and the ice pigment biomass, studied over one year at a neritic site sheltered between islands, is also low (maximum 40 µg chl *a* l^{-1} at spring; Delille *et al.* 1995).

The present study was conducted on land-fast ice from coastal to deeper water sites representative of offshore conditions. We aim to test relationships between ice (particularly the platelet ice), under-ice water and open water from small polynyas (cf. Armstrong *et al.* 1966) opening during ice break up, in term of pigment biomass, community diversity and nutrient dynamics [NO_3^- and Si $(OH)_4$].

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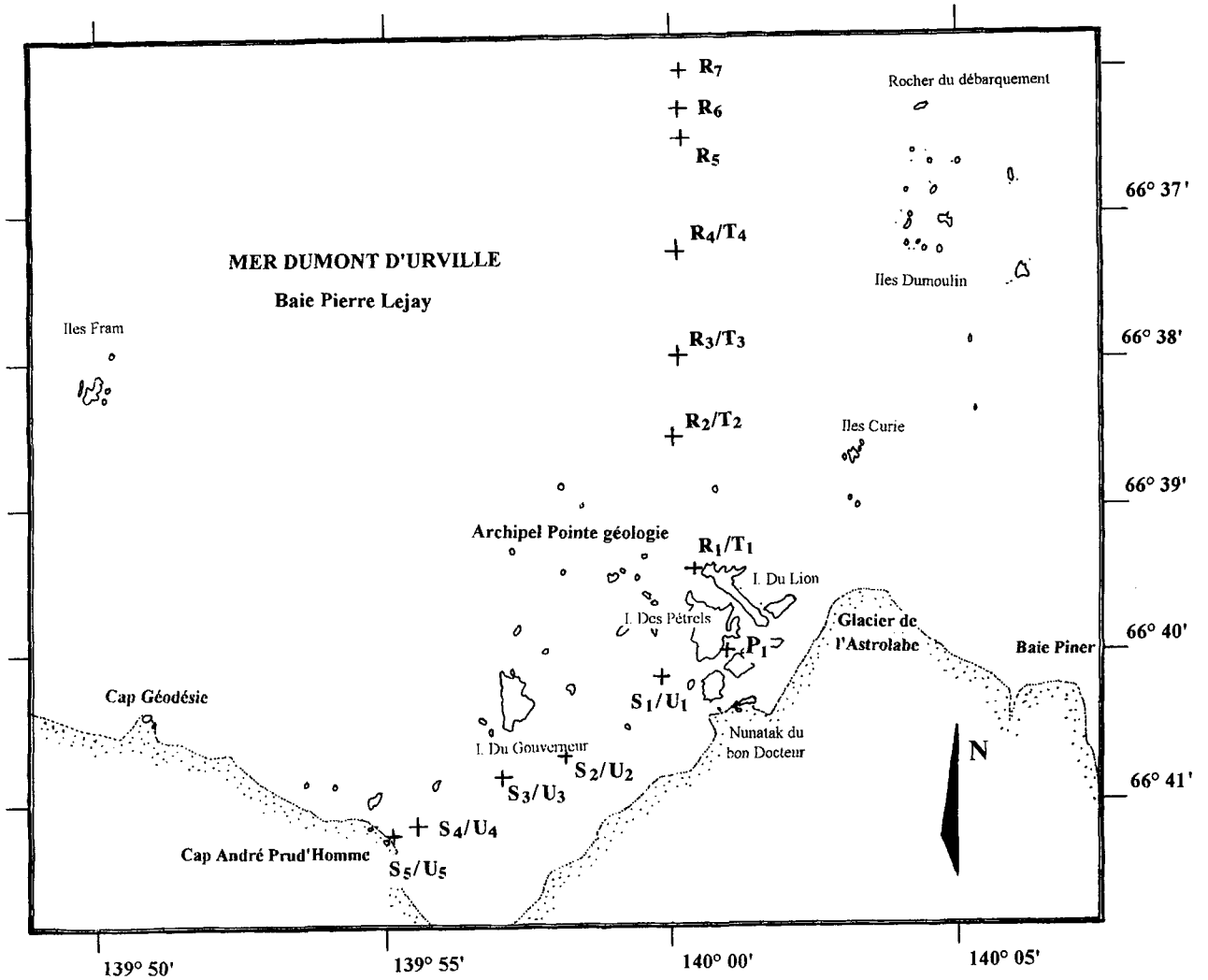

Fig. 1. Sample location (coast to offshore transect: R_1 to R_7/T_1 to T_4; near shore transect: S_1 to S_5/U_1 to U_5 and Chenal de Pedersen: P_1)

Sampling sites and methods

Ice conditions

During the passage through pack ice off Adélie Land with the *Astrolabe* (5–10 November 1995), the basal part of the ice sheet was often brownish (characteristic of Bacillaryophyceae). The under-ice water, mixed with brash ice, was then significantly coloured. Occasionally it was yellowish or pinkish (probably due to bacteria or *Mesodinium rubrum*). The brown coloration was very patchily distributed, as has often been described in this environment. Thin and translucent newly formed ice was not coloured and the large deep-blue polynyas were not discoloured by phytoplankton blooms.

The study area on the west side of the Astrolabe Glacier included an archipelago close to the continent, with shallow channels. The open sea gradually deepens to the north (140 m at R_7; Fig. 1, cf. SHOM map no 6285, ed. 1989). There are strong tidal currents. The pattern of local water circulation is related to the submarine topography (glacial valleys oriented SW–NE and separated by ridges) and is probably also affected by the Astrolabe Glacier. A land-fast sea ice cover develops each year from March until December/January. During the study period the ice sheet appeared mostly uniform and unfractured. It was never thicker than 1.20 m and began to melt and become unstable by mid-December. Small polynyas appeared close to islands and bergs, as well as along channels between the islands, and, offshore leads developed rapidly (Fig. 2).

Sampling sites and strategies

1) To test the effect of the distance from the coast, a 7 km transect from Dumont d'Urville to open sea (R_1 to R_7; (from 66°39'.48"S, 15 m deep to 66°35'.98"S, 140 m deep; Fig. 1 & Table II) was undertaken on 15 November. To test the melting effect, it was repeated two weeks

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later as melting was rapidly developing (T_1 to T_4; the northern offshore T_5 to T_7 stations were not enough safe to be sampled).

2) To test the land fast ice near-shore homogeneity and *in situ* melting effects, a 5 km transect near the coast, from Dumont d'Urville to Cap André Prud'Homme (S_1 to S_5) was undertaken on 20 November and was repeated one week later (U_1 to U_5).

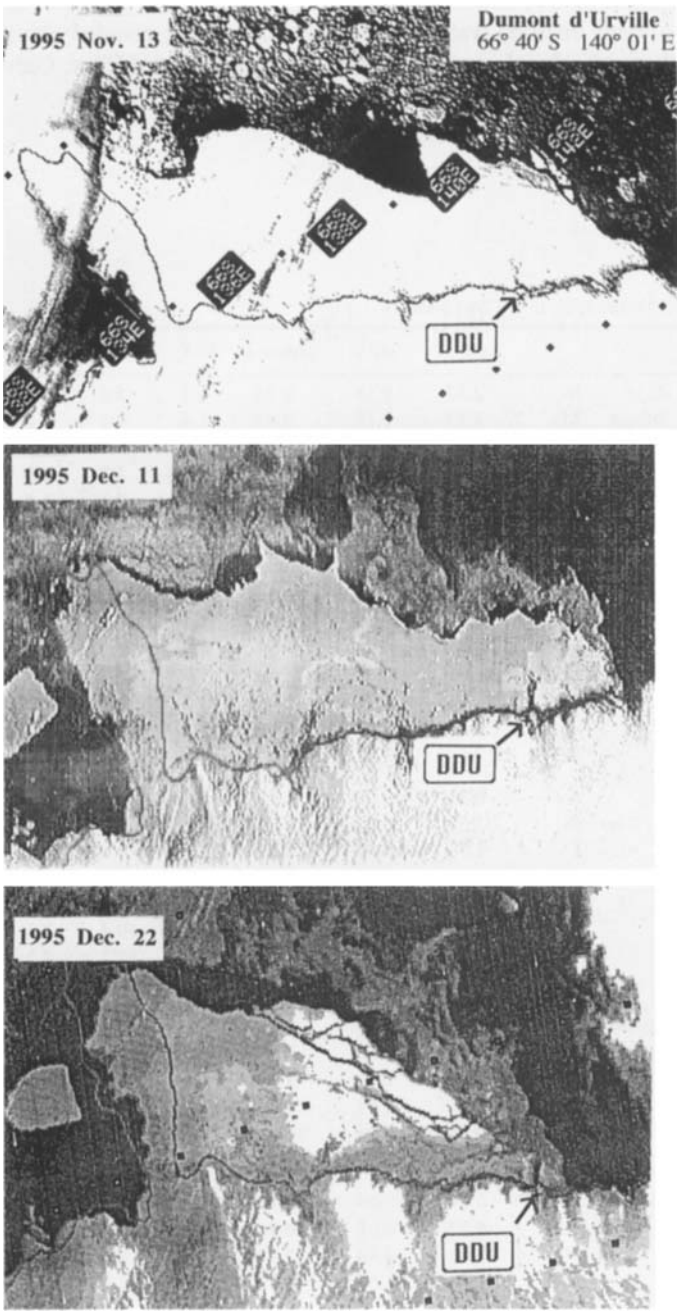

Fig. 2. Sea ice spatial distribution and change during ice break up (satellite images from November and December 1995, near Dumont d'Urville).

3) As a control, one core was collected at Chenal de Pedersen (P_1, a neritic station located between two islands, previously sampled by Delille *et al.* 1995).

These land-fast ice transects, and particularly those from Pointe Géologie Achipelago to the open sea (R_1 to R_7), were the first to be undertaken in this part of Antarctica. This transect was situated at the west side of the Astrolabe Glacier, away from the influence of bergs and islands. During this study, the ice cover developed leads that restricted the scope of investigations further northward.

Sample collection

A motorized SIPRE corer was used (Medlin & Priddle 1990). The sampling sites were located by GPS. The whole cores were measured on extraction and placed into dark plastic bags. After the ice core was removed, the platelets from the unconsolidated layer under the congelation ice (platelet ice-like layer) that rose into the hole, were rapidly sampled into plastic containers (these platelets will be named PLI in the present work, bearing in mind that sampling undisturbed PLI is only possible by diving). After removing all the remaining platelets, the free water (under-ice water, UIW) was collected with a glass bottle. At the end of the sampling period, when ice was melting and small polynyas were appearing, some lead and polynyas water (PW) was collected into polyethylene bottles from 20 cm under the surface. PLI, UIW and PW were immediately analysed in the laboratory at Dumont d'Urville station. However the cores were kept frozen (-20°C) for one night before analysis, possibly inducing an under-evaluation of pigment content in the ice by way of cell disruption.

From each core, 5 cm slices were cut from the surface (S), middle (M) and bottom layers (F_1, F_2, F_3). For pigment analysis, ice subsamples were melted at 4–7°C in the dark in 250 ml of filtered seawater to avoid any cell breakage. Final volumes were recorded for volumetric corrections. A subsample was preserved using Lugol or formaldehyde (2% final concentration) for microscopic identification (light microscopy and SEM) and enumeration (the volumetric correction was applied in the final calculations). Samples were kept in the dark before analysis. Another subsample was filtered (GF/F fibre filters) for microphyte pigment measurements. Immediately after sampling UIW and PW samples were filtered. Chlorophyll *a* (including isomers), *b* and *c* (chl *a*, *b* and *c*) and associated phaeopigments (phaeo *a*, *b*, *c*) were measured in acetone extracts (Neveux & Lantoine 1993). GF/F filters (stored at -20°C at Adélie Land) were kept frozen until analysis (University of Montpellier, six months later). Filters were homogenized in 100% acetone (*pro analysis* Merck) and kept cool and dark for 2 h before measurement. The melted ice samples were filtered and analysed in the same way (the filtered sea water, used for ice melting, was sampled, filtered and analysed in the same way as other samples: the chl *a* concentrations were insignificant).

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UIW and PW subsamples were preserved with Lugol or formaldehyde for microscopic identification and enumeration. Ice, PLI, UIW and PW subsamples were collected and kept frozen (-20°C) for nutrient measurements. Nitrate [NO_3+NO_2] and silicic acid [$Si(OH)_4$] were determined (precision: 1%) six months later at the Brest laboratory (Tréguer & Le Corre 1975). Unfortunately neither temperature nor salinity were measured on these samples and as a consequence the nutrients concentrations were not normalized. The microalgal carbon biomass transferred to underlying water masses during ice break up was calculated from PLI chl *a* concentrations (around 20 cm deep), neglecting the other ice levels and the other pigments, and using only samples from the first kilometre from coast to offshore (S_1–S_5, U_1–U_5, R_1–R_2, T_1–T_2). This estimate, expressed as t POC km^{-1} shoreline, is probably too low.

Some samples were selected and examined by light microscopy and in Scanning Electron Microscopy (SEM) to accurately identify microalgae at the lowest possible taxonomic rank. The identification of sea ice microalgae were done according to Manguin (1957, 1960), Priddle & Fryxell (1985), Medlin & Priddle (1990), Hasle *et al.* (1994), and Hasle & Syvertsen (1996). The enumeration of microalgal cells followed a slightly modified version of the Utermöhl method using a Leica Diaplan phase contrast microscope (Utermöhl 1958, Lund *et al.* 1958, Hamilton 1990). Depending on the concentration of microalgae in the sample, a certain aliquot was poured in a settling chamber (10 ml, 25 ml) and filled up with distilled water. Microalgal cells were counted along randomly selected transects at a magnification of 500 x. Only cells with plastids were counted.

Table III. Transect Dumont d'Urville to Cap André Prud'Homme (S_1 to S_5, 20/11/1995; U_1 to U_5, 26/11/1995).

		chl *a*	chl *b*	phaeo *a*	NO_3	$Si(OH)_4$	Si/NO_3			chl *a*	chl *b*	phaeo *a*	NO_3	$Si(OH)_4$	Si/NO_3
S_1	S	0.20	0.02	0.03	9.6	13.7	1.4	U_1	S	2.32	0.14	0.26	4.7	5.6	1.2
110 cm	M	2.33	0.14	0.28	2.9	4.8	1.7	96 cm	M	3.52	0.19	0.43	1.4	4.2	3.0
	F1	16.76	0.84	1.71	4.8	2.7	0.6		F1	4.96	0.27	0.50	1.1	1.6	1.5
	F2	127.94	7.30	13.99	2.9	2.2	0.8		F2	7.06	0.41	1.01	1.0	1.7	1.7
	F3	181.41	10.79	23.15	5.9	3.3	0.6		F3	35.82	1.83	4.15	2.8	4.1	1.5
	PLI	9875	722	747.24	299.5	102.8	0.3		PLI	5377	301	1002	201.2	51.9	0.3
	UIW	1550	72.89	293.21	87.2	74.7	0.9		UIW	1140	69.09	183.17	83.7	48.3	0.6
S_2	S	9.83	0.64	1.39	9.1	13.0	1.4	U_2	S	1.14	0.08	0.16	5.0	7.0	1.4
114 cm	M	0.53	0.04	0.06	3.5	4.3	1.2	107 cm	M	4.00	0.29	0.68	1.5	4.1	2.7
	F1	78.48	4.16	8.66	3.0	2.7	0.9		F1	4.41	0.26	0.53	0.9	1.5	1.7
	F2	14.79	0.83	1.63	4.2	1.7	0.4		F2	11.31	0.68	1.40	1.6	1.3	0.8
	F3	49.36	2.69	4.96	3.6	2.1	0.6		F3	29.91	1.71	3.96	2.1	2.1	1.0
	PLI	3881	257.3	532.33	102.9	60.4	0.6		PLI	932.6	56.85	95.26	69.1	19.7	0.3
	UIW	807.27	57.61	40.37	51.0	66.9	1.3		UIW	517.64	32.13	59.45	–	–	–
S_3	S	7.16	0.76	1.32	6.8	8.4	1.2	U_3	S	0.22	0.02	0.03	6.6	13.7	2.1
110 cm	M	1.81	0.10	0.24	3.3	5.6	1.7	114 cm	M	3.38	0.027	0.056	2.7	8.5	3.2
	F1	47.20	2.58	5.16	1.7	3.9	3.3		F1	1.76	0.10	0.22	1.7	3.0	1.8
	F2	28.97	1.57	3.12	4.2	3.5	0.8		F2	2.87	0.18	0.38	1.8	2.5	1.4
	F3	50.20	2.75	5.90	3.8	3.6	0.9		F3	15.74	0.86	1.14	3.1	4.6	1.5
	PLI	673.01	34.61	69.16	40.9	28.6	0.7		PLI	49.70	2.38	5.78	26.4	60.4	2.3
	UIW	471.0	37.55	42.25	44.8	61.0	1.4		UIW	61.99	3.56	5.06	24.1	52.2	2.2
S_4	S	3.22	0.16	0.33	7.1	10.9	1.5	U_4	S	15.82	0.78	2.59	4.9	7.9	1.6
103cm	M	1.44	0.08	0.17	1.2	5.4	4.5	82 cm	M	6.66	0.35	0.56	1.6	2.6	1.6
	F1	7.00	0.38	0.62	1.8	1.3	0.7		F1	6.14	0.33	0.53	1.6	2.6	1.6
	F2	14.19	0.67	1.79	1.8	1.9	1.1		F2	22.13	1.31	1.96	1.9	3.0	1.6
	F3	142.19	7.56	14.75	2.0	3.1	1.6		F3	18.9	1.01	1.85	10.2	13.6	1.3
	PLI	2477	114.0	204.5	40.9	45.7	1.1		PLI	139.16	8.56	16.69	16.1	23.2	1.4
	UIW	1066	49.39	77.13	25.0	47.2	1.9		UIW	150.07	8.54	13.35	16.3	35.9	2.2
S_5	S	7.85	0.45	0.69	6.7	10.2	1.5	U_5	S	0.69	0.04	0.10	4.3	6.4	1.5
115cm	M	3.59	0.21	0.39	1.4	3.8	2.7	110 cm	M	0.77	0.05	0.10	2.2	4.3	2.0
	F1	8.82	0.46	0.81	0.9	0.6	0.7		F1	78.43	4.64	12.03	2.3	2.2	1.0
	F2	16.83	0.98	1.88	0.9	0.8	0.9		F2	272.66	18.37	37.27	4.6	2.2	0.5
	F3	102.82	5.71	11.69	1.5	2.1	1.4		F3	150.52	8.13	11.51	–	6.6	–
	PLI	3509	267.6	397.45	10.9	53.0	4.9		PLI	1172.7	79.97	205.03	46.5	26.6	0.6
	UIW	812	38.20	67.38	6.9	32.7	4.7		UIW	984.62	74.03	104.12	–	–	–

Pigment units: $\mu g\ l^{-1}$; Nutrient units: µM (not normalized).

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Results

Climatic conditions

In October, November and December 1995, insolation was higher than normal, yet precipitation was low compared to the mean for the reference period (1966–95). Day air temperature (°C) became positive in late November 1995, resulting in increased melting (small polynyas appeared near Dumont d'Urville). During the entire sampling period the weather was stable (maximum mean daily wind speed rarely exceeded 80 km h^{-1}).

Ice conditions

The land-fast ice was composed of

1) irregular and often shallow snow cover, melting at the end of the study period,
2) congelation ice composed of a) columnar ice (from 40–100 cm, with no infiltration layers or other intercalar coloured layers) showing that the conditions for ice formation are more calm than in offshore pack ice and b) bottom-ice (from 1–5 cm granular ice, composed of irregular crystals, often - but not always - coloured by microphytes), and
3) an underlying unconsolidated "platelet ice"-like layer (PLI) more or less developed (from 10–30 cm, average 20 cm), often brownish. This PLI was not composed of well defined plate-like crystals but of soft crystals, perhaps due to melting during sampling. Nevertheless, the proximity of the Astrolabe Glacier and continental shelf, supports the suggestion that this layer originated from platelet ice.

As melting rapidly increased, the PLI regressed (probably due to the melting during the day and the effects of bottom currents), whereas the bottom-ice layer became soft and porous, particularly for the northern stations (T_3, T_4; Fig. 1). A thin layer of translucent ice (from 0.5–1 cm thick) appeared at the basal part of the bottom ice, showing vertical channels, often colonized by diatoms. This thin layer probably resulted from diurnal variations in temperature (causing melting and freezing), and also from regression of the PLI that was protecting the bottom-ice from direct contact with supercooled water masses. Because it was loosely connected to the bottom-ice this brittle layer was difficult to sample. When sampled it was considered as part of the bottom-ice.

Near-shore transect from Dumont d'Urville to Cap André Prud'Homme

Along the near-shore transect (S_1 to S_5, U_1 to U_5; Fig. 1, Table III), the thickness of the annual ice sheet averaged 107 cm (S_1 to S_5) and 100 cm one week later (U_1 to U_5). The snow cover was irregular, thicker than offshore but never exceeding 20 cm. Nutrient concentrations were very low and homogeneous in the different congelation-ice layers (Table III, Fig. 4), whereas in PLI and UIW concentrations reached very high levels [up to 300 µM NO_3^- and 100 µM $Si(OH)_4$], often associated with high pigment concentrations (Table III). The chl *a*/NO_3^- ratio varied from 10–321 in F_3 and PLI and from 2–100 in UIW. The pigment biomass reached very high levels in PLI, up to 9.8 mg chl *a* l^{-1}, with apparently no relationship with the snow cover thickness. Chlorophyll *a*/phaeo *a* was high, ranging from 11 during the first samplings to 9 two weeks later (in F_3, PLI, UIW), whereas the ratio was lower in PW (5.5; Table IV), showing the bottom ice communities were growing intensively (and/or not grazed), until ice break up, which was different from the underlying phytoplankton (low biomass).

Along this transect (sampling sites very close to the continent), a spatial gradient in bottom ice nutrients was obvious, reflecting the variable influence of land – and particularly islands. Although spatial variations in NO_3^- and $Si(OH)_4$ concentration were roughly linked, the $Si(OH)_4/NO_3^-$ ratios exhibited large variations within the ice sheet and between sampling sites (Table III, Fig. 4). The $Si(OH)_4/NO_3^-$ ratio increased markedly from S_1 to S_5 in PLI (from 0.3 to 4.9) and in UIW (from 0.9–4.7). Nutrient and pigment concentrations decreased between the two sampling periods (S: 20/11/1995, U: 26/11/1995), probably due to melting ice and ablation.

At the neritic station Chenal de Pedersen (P_1) pigments and nutrients concentrations were low, even in the PLI [20 µg chl *a* l^{-1}, 15.7 µM NO_3^- and 34.4 µM $Si(OH)_4$] probably due to the low exchanges with open ocean water masses. Furthermore, the bottom of the ice (F_3 layer) contained macroalgae debris, that may interfered with microalgal pigment measurements.

Coast to offshore transect, north of Dumont d'Urville

During the 7 km "coast to offshore" transect (R_1 to R_7, T_1 to T_4; Figs 3 & 5) no "infiltration layer" or coloured zone was observed either for the columnar ice, or under the snow cover. The ice sheet was relatively thin (less than 1.20 m), and the snow cover, when present, was less than 10 cm during the study period, favouring penetration of solar radiation. Unfortunately no under-ice irradiance measurement are available. Nevertheless, here again a spatial gradient appeared. At stations close to the islands (R_1 to R_2, T_1 to T_2; except for silicic acid in PLI and UIW) higher concentrations were observed for both nutrients and pigments (Fig. 3) in PLI and UIW, and also in surface congelation ice (S). In PLI, the $Si(OH)_4/NO_3^-$ ratio increased markedly from coast to offshore (from 0.3–0.7 at R_1 to R_2, to 1.7–2.4 at R_3 to R_7), whereas the chl *a* concentrations ranged from 4 mg l^{-1} at R_1 to 5 µg l^{-1} at R_7.

The chl *a*/chl *b* ratio, ranging from 7–24, also exhibited a geographical gradient (with higher ratios close to the islands) and was slightly higher in the top layers of the ice, illustrating

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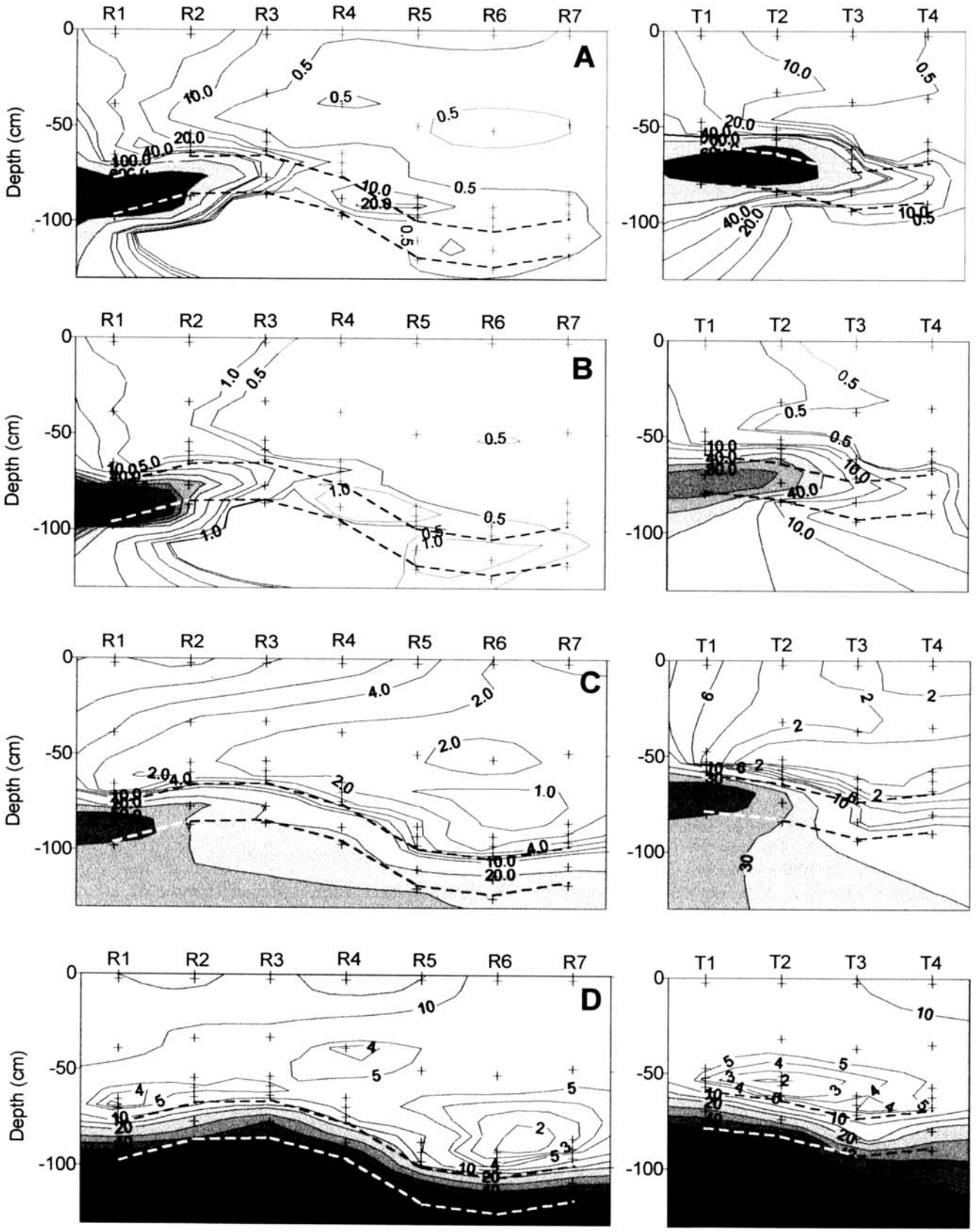

Fig. 3. **a.** Chl *a*, **b.** phaeo *a*, **c.** NO_3^- and **d.** $Si(OH)_4$ spatial patterns along the two "coast to offshore" transects (R_1 to R_7, 15/11/1995 and T_1 to T_4, 26/11/1995). Pigment units: mg m^{-3}; Nutrient units: µM (not normalized). Dashed lines indicate the PLI extent. Shading is proportional to concentration.

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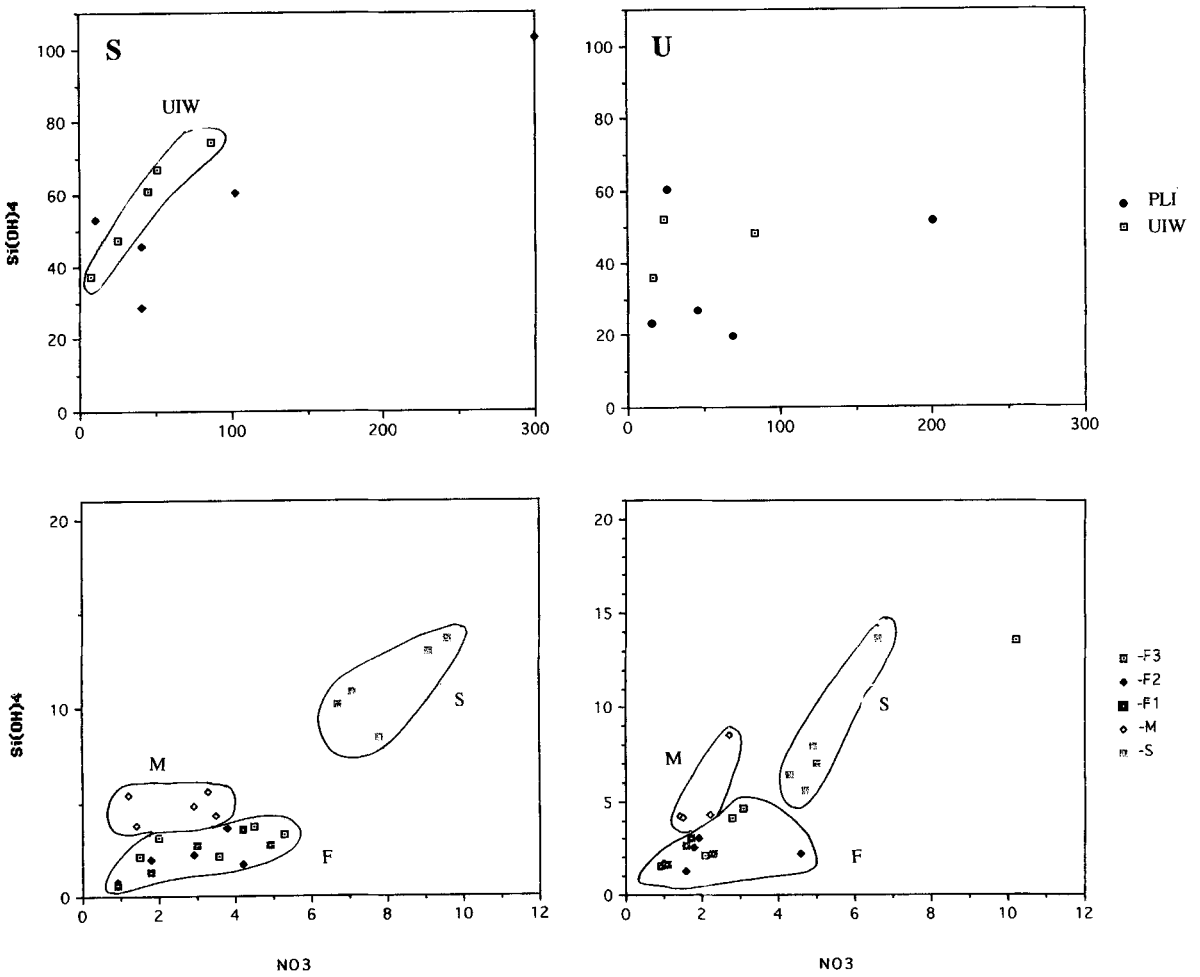

Fig. 4. $Si(OH)_4$ and NO_3^- relationships along the near shore transect (S = S_1 to S_5 sampling stations, 20/11/1995 and U = U_1 to U_5 sampling stations, 26/11/1995). Units: µM (not normalized).

probable differences in microphyte assemblages.

Polynyas and leads

Water samples (PW) from leads and polynya collected at the beginning of the ice break up (Table IV) illustrate the chemical and biological characteristics of the coastal underlying water-masses at that time. The phytoplankton biomass (average 0.69 µg chl *a* l^{-1}) was low compared with PLI or UIW, and the chl *a*/phaeo *a* ratios were also lower. $Si(OH)_4$ and NO_3^- mean concentrations reached respectively 63.93 and 27.13 (Table IV).

Assemblages

The microphyte assemblages for the F_3, PLI and UIW layers were very similar to those described previously (Table V). Diatoms were dominant (> 25 species), and particularly the pennates, in which the most abundant species were *Navicula glaciei*, *Nitzschia stellata*, *Berkeleya adeliensis*, *Amphiprora kufferathii*. Some centric diatoms were also present, such as *Porosira pseudodenticulata*. In some PLI samples (particularly at the end of the study period) clumps and strands were observed, mainly composed of tube-dwelling colonies of *Berkeleya adeliensis*. This observation is in agreement with other descriptions, and may reflect succession within the community.

In the bottom layers (F_3, PLI and UIW, R_1 to R_7; Table VI) a good relationship existed between cell numbers, biomass and NO_3^- concentrations, whereas two weeks later (T_1 to T_4) these links were less strong (not illustrated), probably due to ablation of a part of the platelet ice and cell sedimentation. Nevertheless, the same geographical gradient was evident at the two sampling dates, supporting the existence of a land effect. The highest cell concentration and species number were observed near the coast, whilst some species were only encountered offshore (*Nitzschia* sp2) and others were more abundant near shore (such as *Porosira pseudodenticulata*). The PW community was characterized by very low species numbers and cell densities (on an average 2 x 10^3 cells l^{-1}); among these species some were common in PLI such as *Navicula glaciei* or *Amphiprora kufferatii* whereas others,

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Table IV. Samples from small polynyas and leads.

	chl *a*	chl *b*	phaeo *a*	chl *a*/ phaeo *a*	NO_3^-	$Si(OH)_4$	Si /NO_3
R_7E lead	0.22	0.01	0.04	5.5	28.4	63.9	2.25
Mas Ionosph.	0.66	0.06	0.13	5.07	29.8	72.1	2.42
N. Poisson	1.95	0.13	0.30	6.5	27.3	65.4	2.40
N. Lion	0.26	0.02	0.08	3.25	23.0	54.3	2.36
W. Lion	0.36	0.02	0.11	3.27	n d	n d	n d
$\bar{x}$	0.69	0.05	0.13		27.13	63.93	
s d	0.73	0.05	0.10		2.93	7.34	

Pigment units: µg l^{-1}; Nutrient units: µM (not normalized).
n d = no data

observed but not enumerated, were pelagic (Table V).

Discussion

Unconsolidated under-ice layers (especially the "platelet ice") are apparently a favourable habitat for microphyte development. Whereas Bunt (1963) described a productive layer in McMurdo as a "loosely aggregated matrix of large, plate-like ice crystals", Palmisano & Sullivan (1985) followed Lewis & Weeks (1970) in describing a "mixture of congelation-type crystals and lamellate plates". Cota & Sullivan (1990) enlarged the term to "partially consolidated underwater frazil ice". Such a layer is classically present under land-fast ice but also under pack ice or floes (Eicken & Lange 1989, Smetacek *et al.* 1992, Grossmann *et al.* 1996). Its formation may occur *in situ* under bottom ice (Smetacek *et al.* 1992) or drift (Dieckmann *et al.* 1986). Recent papers and reviews (Ackley & Sullivan 1994, Arrigo *et al.* 1995, Grossmann *et al.* 1996) have pointed out the specific texture of this layer, but confirm it is not restricted to fast ice. There is, at present, no general agreement about the microphytes associated with this layer. Described as typically benthic (Smetacek *et al.* 1992, platelet under fast ice), or planktonic (Smetacek *et al.* 1992: platelet under pack ice), these communities may also be mixed (Bunt 1963, Palmisano & Sullivan 1985). Cota & Sullivan (1990) pointed out that the interface between congelation ice and platelet ice is often not well defined and that contamination or incorporation may exist within the two substrates (Spindler *et al.* 1990, Günther & Dieckmann 1999). Thus, microalgae of the bottom-ice and of platelet ice layers may demonstrate different origins, seasonal successions, biological variations, following or induced by the physical variations in the substrate. A further complication is that platelet ice has a different history and evolution below the fast-ice and below the pack-ice. Significant algal biomass is apparently linked to fast-ice (Table I), with especially high values in the Adélie Land area, and has to be incorporated into Southern Ocean carbon balances.

Table V. A checklist of the dominant species from the R_1 to R_7/T_1 to T_4 transects and small polynyas.

	F_3	PLI	UIW	PW
Amphiprora kufferathii Manguin	+	+	+	
A. oestrupii Van Heurck	+			
Asteromphalus heptactis (Brébisson) Ralfs in Pritchard		+		
A. hookeri Ehrenberg		+		
Berkeleya adeliensis Medlin	+	+	+	+
Cylindrotheca closterium (Ehrenberg) Reimann & Lewin	+	+		
Fragilariopsis curta (Van Heurck) Hustedt	+			+
F. kerguelensis (O'Meara) Hustedt		+	+	
F. rhombica (O'Meara) Hustedt		+	+	
F. sublinearis (Van Heurck) Heiden	+	+		
Manguinia rigida (M. Peragallo) Paddock	+	+		
Navicula glaciei Van Heurck	+	+	+	+
N. sp_1		+		
Nitzschia lecointei Van Heurck	+	+	+	
N. stellata Manguin	+	+	+	+
N. taeniiformis Simonsen	+	+		
N. sp_1		+	+	
N. sp_2		+	+	
Odontella litigiosa (Van Heurck) Hoban		+		
Porosira pseudodenticulata (Hustedt) Jousé	+	+		
Proboscia truncata (Karsten) Nöthig & Ligowski	+			
Pseudo-nitzschia subcurvata (Hasle) Fryxell				+
P. turgiduloides (Hasle) Hasle	+		+	
Rhizosolenia sp		+		
Synedropsis fragilis (Manguin) Hasle, Syvertsen & Medlin	+	+		+
S. recta Hasle, Medlin & Syvertsen		+		+
Thalassiosira gracilis (Karsten) Hustedt			+	
Others : Flagellate spp.	+	+	+	+

F_3 = Bottom of the congelation Ice, PLI = Platelet ice, UIW = under-ice water, PW = polynya water

The Adélie Land land-fast ice ecosystem contains considerable biomass particularly concentrated in the PLI during summer 1995 (up to 9.8 g chl *a* m^{-3}; 1.9 g chl *a* m^{-2}). The ice algae assemblages, dominated by pennate diatoms and showing strands in the coastal sites during melting, are comparable to previous descriptions (Palmisano & Sullivan 1983 (McMurdo Sound platelet layer), McGrath Grossi & Sullivan 1985 (McMurdo Sound bottom congelation community), Watanabe 1988 (subice assemblage), Cota & Sullivan 1990). Compared with chl *a*/phaeo *a* ratios obtained in McMurdo by Palmisano & Sullivan (1983; 1.25 in PLI, 0.3 in UIW), these Adélie Land ratios were very high even during melting. Other points may also be more specific to Adélie Land, such as the presence of flagellates in coastal samples, but with no clear pattern or preference for one particular ice layer. This in contrast to observations by Günther & Dieckmann (1999, in Weddell Sea land-fast ice). The dispersal of these flagellates seemed to occur during ice break up. In addition

Table VI. Linear regression coefficients between pigments, nutrient concentrations (not normalized) and microphyte cell counts (F_3, PLI and UIW for the transect R_1 to R_7; $n = 21$; *significant at $P = 0.01$).

	NO_3	$Si(OH)_4$	chl *a*	phaeo *a*	cells
NO_3	–	0.178	0.787*	0.782*	0.748*
$Si(OH)_4$		–	0.001	0.001	0.005
chl *a*			–	0.999*	0.984*
phaeo *a*				–	0.982*
cells					–

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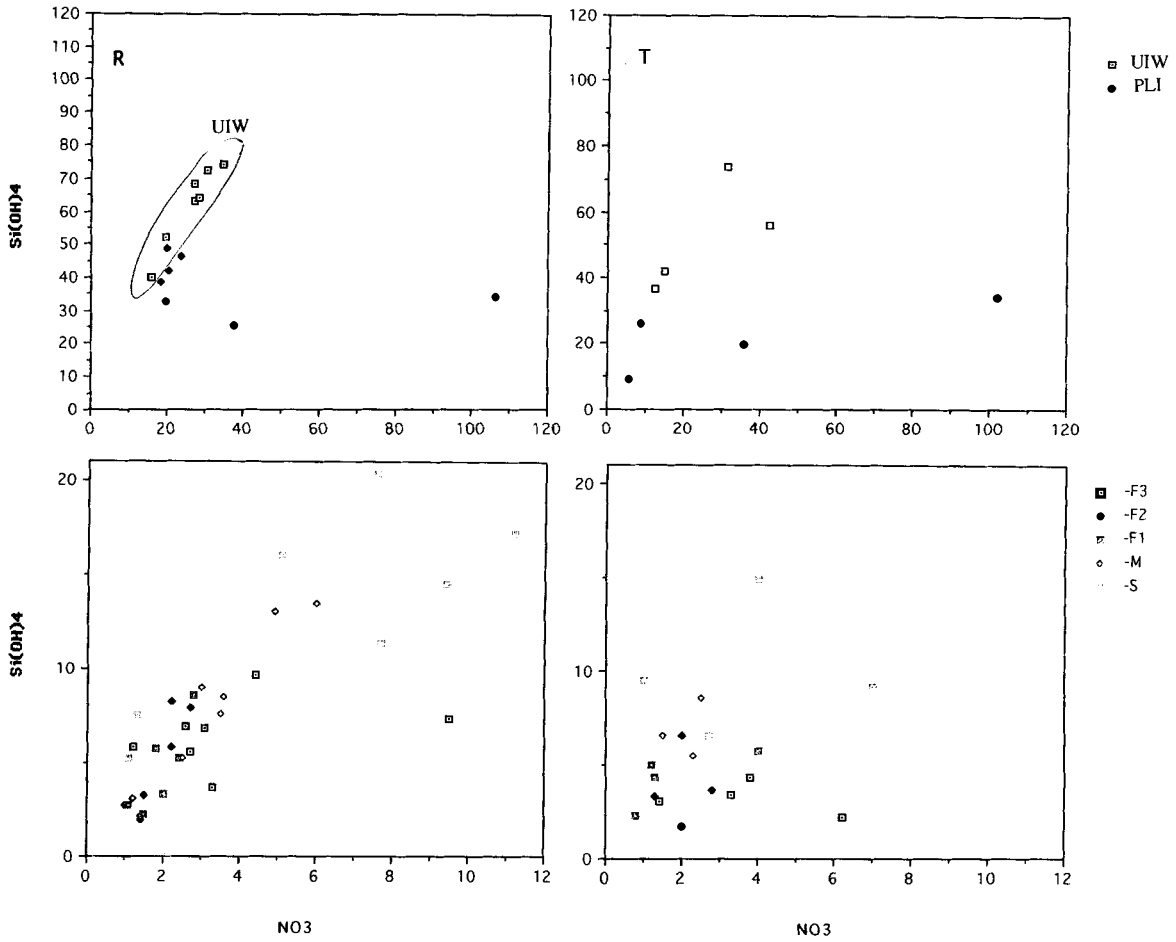

Fig. 5. $Si(OH)_4$ and NO_3^- relationships along the "coast to offshore" transect (R = R_1 to R_7 sampling stations, 15/11/1995 and T = T_1 to T_4 sampling stations, 26/11/1995). Units: µM (not normalized).

the coastal to offshore gradient of nutrients and microalgae argues in favour of a "land effect" for at least part of the year, but probably not with respect to coastal areas with rookeries.

Another point concerns the nutrient dynamics. $Si(OH)_4$ was generally in lower concentrations in the PLI than in the underlying water (UIW) or in the PW (small polynyas; Table IV), as result of a Si consumption by algae at a higher rate than the regeneration of this nutrient in these productive layers. Nitrate seems to have been actively regenerated. Nitrate may be recycled at a higher rate than silicic acid since the concentrations in PLI are very high (up to 100 µM) compared to UIW. NO_3^- and chl *a* are highly correlated (r^2 = 0.787. n = 21; Table VI), whereas no obvious relationship exists between $Si(OH)_4$ and chl *a* concentrations. These results suggest an active microbial loop in the platelet-like layer leading to high primary production within a 1–2 km wide belt of the coast and the islands. The mucopolysaccharides and/or other organic products (such as amino acids) excreted by the dense tube-dwelling diatoms (such as *Berkeleya* present as clumps in the melting platelets) may be ammonified and nitrified, regenerating the nitrate stock available to primary producers (Arrigo *et al.* 1995). Such nitrifying processes, after being underestimated for Antarctic environments, have now been demonstrated as effective in the open waters of the Southern Ocean (Bianchi *et al.* 1997). Silicate, incorporated into diatom frustules and exported via sedimentation, may act as a limiting factor (depletion and low regeneration rate in the PLI). In addition, diatom heterotrophy shown by the platelet communities (Palmisano & Sullivan 1985) suggest that this platelet-like layer might be considered as a specific ecosystem, adapted to low irradiance and able to generate significant biomass during short time periods.

Export by sedimentation of a high proportion of particulate silica and carbon is suspected to occur at ice break up in the Adélie Land environment. Applying the ratio C/chl *a* of 30 (cf. 31 in Palmisano & Sullivan 1983; 34.0 ± 12.1 in Arrigo *et al.* 1995), an estimated average annual production of *c.* 15 g C m^{-2} (0.4–0.6 g chl *a* m^{-2}) within 1 km uniform coastal belt such as in Adélie Land would correspond to at least 15 t C km^{-1} coast (this excludes losses due to grazing, sinking during the bloom or the existence of other fast-ice blooms

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during the year). This biomass is probably mass-sedimented, and/or scattered by strong currents, during ice break up and melting.

Conclusion

The ice/water interface exhibited a high microphytic biomass near the Adélie Land shore before ice break up, probably induced by the relative thinness of the ice sheet enhancing the under ice irradiance available to microphytes. Antarctic models may perhaps under-estimate the POC biomass available to underlying water masses during ice break up, when they only take into account pack-ice data (Arrigo *et al.* 1997). The land-fast ice represents only a narrow coastal belt adjacent to the pack ice area, but its algal biomass is high. The present study has also illustrated the potential for nitrate to be abruptly injected in the underlying water masses during ice break up: 100 μM NO_3^- in the PLI (minimum 10 cm thick) corresponds to an average of 20 kg NO_3^- km^{-1} coast. During sea-ice break up a sharp increase in irradiance may trigger off the coastal phytoplankton bloom for which there is no evidence of microphyte seeding from the fast ice in this region. During the sampling period (1995 late winter) the phytoplankton biomass (on an average 0.69 μg chl *a* l^{-1}) was low compared with those of the PLI or UIW, and the chl *a*/phaeo *a* ratios also were lower, suggesting differences in the origin and maturity level of the communities. On the other hand, the PW $Si(OH)_4/NO_3^-$ ratios (on an average 2.36; Table IV) are in agreement with ratios previously reported for coastal surficial Antarctic waters (i.e. Tréguer & Jacques 1992).

No strong relationship between platelet assemblages and underlying phytoplankton was found during this study. Previous descriptions of the phytoplankton composition of this coastal and neritic area (Manguin 1960) did not mention the pennate diatoms present (except for *Fragilariopsis kerguelensis* and *Nitzschia curta*). The presence of *Navicula glaciei* or *Nitzschia stellata* in the phytoplankton, along with *Archaeomonas* cf. *areolata* (suspected to be a good sea ice indicator species, Mitchell & Silver 1982), illustrate the ice proximity, whilst on the other hand *Chaetoceros* spores and vegetative cells (*Chaetoceros* cf. *neglectus*) argue for a habitat specificity for the plankton assemblage.

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