

A study of the diatom-dominated microplankton summer assemblages in coastal waters from Terre Adélie to the Mertz Glacier, East Antarctica (139°E–145°E)

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Abstract In January 2004 the microplankton community from the coastal waters of Terre Adélie and Georges V Land (139°E–145°E) was studied. Results showed a diatom-dominated bloom with chlorophyll *a* levels averaging $0.64 \mu\text{g l}^{-1}$ at 5 m depth (range $0.21\text{--}1.57 \mu\text{g l}^{-1}$). Three geographic assemblages of diatoms were identified, based on principal diatom taxa abundances. The stratified waters near the Mertz Glacier presented highest phytoplankton biomasses ($0.28\text{--}1.57 \mu\text{g Chl } a \text{ l}^{-1}$ at 5 m) and diatom abundances ($6,507\text{--}70,274 \text{ cells l}^{-1}$ at 5 m), but low diversity, dominated by *Fragilariopsis* spp. Lower biomasses ($0.38\text{--}0.94 \mu\text{g Chl } a \text{ l}^{-1}$ at 5 m) and abundances ($394\text{--}9,058 \text{ cells l}^{-1}$ at 5 m) were observed in the mixed waters around the Astrolabe Glacier with a diverse diatom community characterised by larger species *Corethron*

pennatum and *Rhizosolenia* spp. Finally an intermediate zone between them over the shallower shelf waters of the Adélie Bank represented by *Chaetoceros criophilus*, where biomasses ($0.21\text{--}0.35 \mu\text{g Chl } a \text{ l}^{-1}$ at 5 m) and abundances ($1,190\text{--}5,431 \text{ cells l}^{-1}$ at 5 m) were lowest, coinciding with the presence of abundant herbivorous zooplankton.

Keywords East Antarctica · Terre Adélie · Phytoplankton · Diatoms

Introduction

Studies of Antarctic plankton dating back to some of the earliest polar expeditions in the mid-1880s already mention the omnipresence and importance of phytoplankton in the water, and an interest in polar phytoplankton and its essential role in the primary production has generated much data over the past century (Knox 1994; El-Sayed 2005). Nevertheless, although the microplankton communities in Southern Ocean waters have been studied extensively, most studies have been located in waters off the Antarctic Peninsula and the Ross, Weddell, Bellingshausen and Scotia Seas (Froneman et al. 1997; El-Sayed 2005; Fonda Umani et al. 2005; Garibotti et al. 2005) and were done in relation to the general oceanic circulation. This contrasts with the rarity of studies in Eastern Antarctica (particularly in the western Pacific Ocean Sector), partly due to the frequent persistence of sea-ice along the coast in the austral summer and the low biomass of krill present in the region, lessening the economic interest of the region (Nicol et al. 2000; Harris et al. 2003).

The rarely studied shelf waters of Terre Adélie and King Georges V Land (from 139°E to 146°E) are of interest notably due to the formation of Antarctic Deep Water in

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the Mertz Glacier region and bays (Bindoff et al. 2000) and to the presence of two coastal polynyas, biologically productive areas of open water or reduced sea-ice cover within the ice pack, near Dumont d'Urville and the Mertz Glacier (Arrigo and van Dijken 2003; Sambrotto et al. 2003). In the Mertz Glacier Polynya, which opens up before the Dumont d'Urville Polynya, the phytoplankton bloom has been observed to last 3 months, although there are usually two peaks: late December and early March (Arrigo and van Dijken 2003).

Early studies of the phytoplankton off Terre Adélie by Manguin in 1949–1950 and Franguelli in 1950–1952 (in Riaux-Gobin et al. 2003) were centred on diatom taxonomy. Since then, subsequent surveys in the region have studied the microplankton community in offshore waters north of the shelf break and close to the Polar Front (Chiba et al. 2000; Waters et al. 2000). Studies near the coast have centred on the sea-ice communities (Delille et al. 1995; Riaux-Gobin et al. 2000, 2003, 2005) or concentrated on phytoplankton biomass and primary production in the Mertz Polynya (Sambrotto et al. 2003; Vaillancourt et al. 2003).

Most of the recent oceanographic studies done in Terre Adélie (including the present one) have taken place within the framework of the French ICOTA (Ichthyologie Côtière en Terre Adélie) programme, funded by the French Polar Institute (IPEV). This has been in place since 1996, with yearly summer campaigns located over the continental platform off the coast from Dumont d'Urville Station in Terre Adélie to the Mertz Glacier in East Antarctica (139°E–146°E). The more recent surveys have been set up to study plankton, fish larvae and fish. In this paper we present the microplankton results from the January 2004 campaign, of particular interest because of the rarity of studies on this group in Terre Adélie and neighbouring waters. This will include the abundances and spatial distribution of the dominant taxa present, as well as the assemblages they form, in relation to the main physical–chemical parameters.

Material and methods

Sampling and analyses

The ICOTA campaign took place on-board the French R.V. Astrolabe from 19 to 31 January 2004. Prominent features along the coast are three large bays (Commonwealth, Watt and Buchanan Bays), the presence of small glaciers (the Astrolabe and the Zéléé), as well as the largest glacier in the region: the Mertz Glacier. Relatively shallow waters can be found over the Adélie Bank, a large plateau (~200 m depth) between the Astrolabe Glacier and Commonwealth Bay. On either side of this bank, innershelf depressions are found,

most notably north of Terre Adélie and west of the Mertz Glacier. The deepest (1,200 m maximum) is known as the Adélie Depression, and is located between the Mertz Glacier and Watt Bay (142°E–146°E). It is limited to the north by a sill at the edge of the shelf break. During the campaign, the water was free of sea-ice, with icebergs observed only near the glaciers. We sampled at a total of 38 stations in the waters over the continental platform between 139°E–145°E and 66°S–67°S (Fig. 1).

Throughout the survey, regular measurements of sea surface temperature (SST) and salinity (SSS) were taken with an on-board surface thermosalinometer (managed by CSIRO under the SURVOSTRAL programme) and were used to calculate sea surface density.

Water samples for each station were obtained using an 8-l Niskin at 5 m depth in order to study levels of nutrients, photosynthetic pigments and the microplankton community.

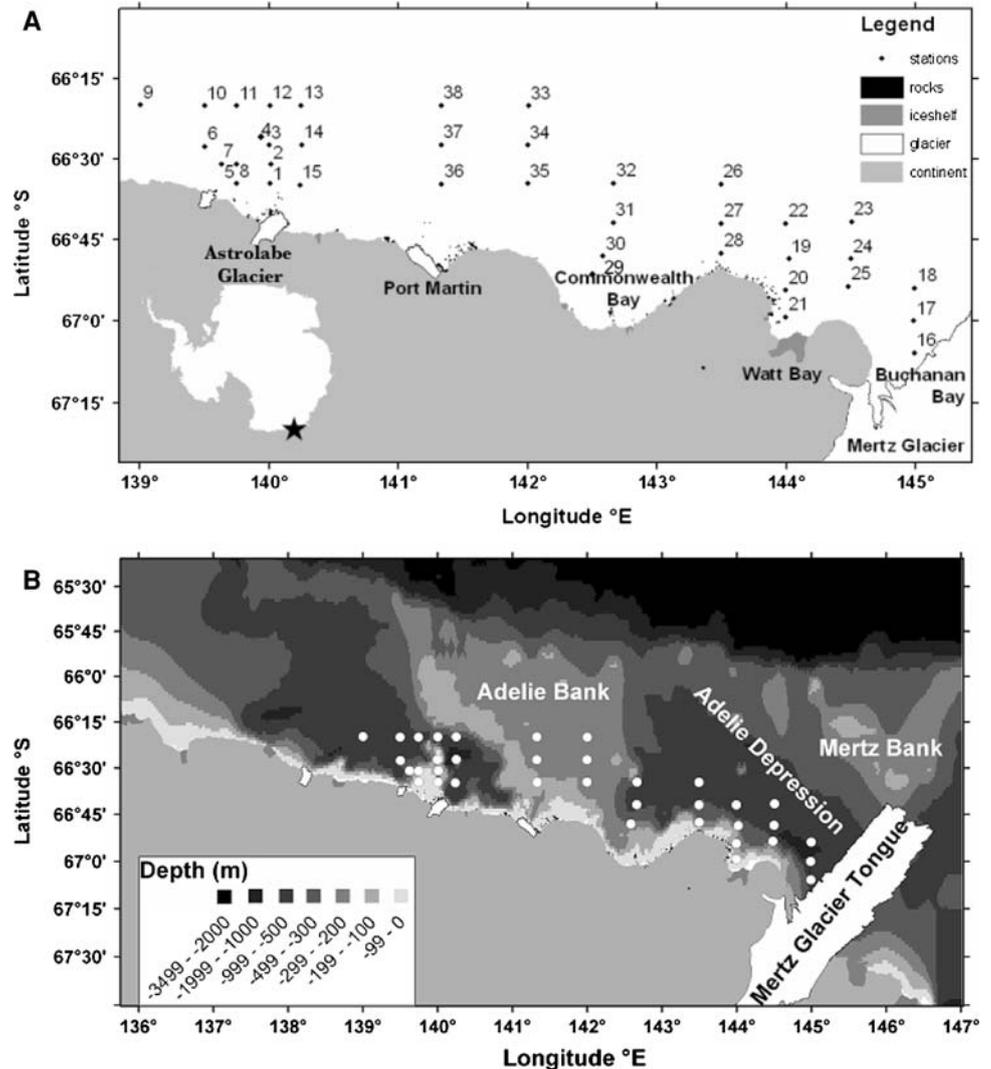
Water samples for nitrate NO_3^- , nitrite NO_2^- and silicic acid $\text{Si}(\text{OH})_4$ (20 ml) were collected directly from the Niskin Bottles using polyethylene syringes. Polyethylene flasks were filled ca. 2/3 full, immediately frozen vertically and stored at -20°C until analysis. Syringes and flasks had previously been soaked in 10% HCl for 24 h and rinsed thrice with Milli-Q water and sample water. Nutrients were determined by means of a Technicon AutoAnalyser II. Nitrate and nitrite were analysed according to working procedures of Tréguer and Le Corre (1975), while silicate was determined according to Gordon et al. (1993). OSIL marine nutrient standards were used for calibrations.

Phytopigment analysis has been described in Swadling et al. (2008). In brief, seawater was filtered through 13-mm GF/F filters and then frozen in liquid nitrogen for return to Australia where pigments were extracted and analysed by HPLC (Zapata et al. 2000).

Microplankton samples were obtained at each station by filtering 2–5 l of seawater from the Niskin bottle through a 20 μm mesh net. The resulting sample was rinsed into a flask and preserved in 2.5% buffered formalin for a final volume of 100 ml.

The microplankton assemblages were later studied in Belgium using an Olympus IX50 inverted microscope. Subsamples of between 10 and 15 ml were collected and allowed to sediment in a 20 ml chamber for at least 18 h and then observed using a 20 \times and 40 \times objectives. Microplankton (>20 μm) were identified using the recent work published by Scott and Marchant (2005). Diatoms were identified at the genus level wherever possible. A similar in-depth identification of dinoflagellates, silicoflagellates and ciliates was not done for this study. Cells were counted and identified (to the lowest taxon possible for diatoms) in order to estimate abundances (expressed as cells l^{-1}). In the case of *Thalassiothrix antarctica*, a long narrow pennate diatom that was only found broken in the

Fig. 1 Map of Terre Adélie and Georges V Land with position of sampling stations (a) and bathymetry (b)



samples, only fragments $>100\ \mu\text{m}$ long were counted in order to limit overestimation of this species. A minimum of 100 fields per sample were counted using the $20\times$ objective.

Community diversity based on abundances was estimated by calculating the Shannon–Weaver diversity index H' (log-base) using the BioDiversity Pro software package.

A complementary qualitative study of some samples was done in order to better identify the diatom taxa present. For this 1-ml sub-samples were filtered and rinsed with distilled water. Each filter was put on a carbon tape attached to a metal stub (25 mm diameter). Sub-samples were dried, carbon-coated and observed with a LEO (438VP) scanning electron microscope (SEM).

GIS mapping and statistical analysis

Geographic Information Systems (GIS) (ArcGis 9.1; ESRI) were used to produce distribution maps of the microplankton

and environmental variables. Environmental and biological data were imported into the GIS as point georeferenced data. Interpolations of surface temperature and salinity were calculated to generate raster layers (based on pixels) by kriging using the Geostatistical Analyst extension of ArcGis. Geostatistics are methods which allow the estimation of a value at unsampled locations (Rivoirard et al. 2000). Areas where interpolations are not accurate enough are withdrawn from the map depending on the standard deviation map obtained as well when kriging is processed.

Statistical analyses were done using the Statistica (for scatter plots and relationships between diatom abundance and water surface density) and Microsoft Xlstat (for correspondence analyses) software packages. The affinity of assemblages both among sites and principal diatom taxa (square root of abundance) was established from the (sites \times taxa) matrix using a correspondence analysis. Sites and taxa groups were distinguished by automatic hierarchical classification.

Results

Environmental variables

A density gradient was observed in surface waters over this region (Fig. 2a), following quite closely the gradient in sea surface salinities (SSS) (Fig. 2b). In general higher densities were observed closer to shore than further out to sea. Denser waters (and saltier, $SSS > 34.2$) were to be observed around and offshore from the Astrolabe Glacier, and east along the coast until Commonwealth Bay from where less dense (and fresher, $SSS < 33.9$) waters predominated towards the Mertz Glacier and further offshore. Waters were coldest ($SST < -1^{\circ}C$) in the proximity of the Mertz Glacier, whereas relatively warm waters were observed over the plateau ($SST > 0.2^{\circ}C$) (Fig. 2c).

Nutrients

Nutrients measured, nitrate NO_3^- , nitrite NO_2^- , and silicic acid $Si(OH)_4$, showed (Fig. 3a–c) variations throughout the site. At 5 m depth, both NO_3^- and SiO_3^{2-} showed a gradient from higher concentrations in the west (maxima of $34.4 \mu M$ at station 8 and $56.1 \mu M$ at station 5, respectively) to lower ones over the Adélie Bank and the Adélie Depression (minima of $30.4 \mu M$ at station 16 and $50.2 \mu M$ at station 31, respectively). NO_2^- on the other hand, showed highest concentrations over the Adélie Bank ($0.24 \mu M$ at station 33), with values slightly decreasing both to the east and west of this area (minimum of $0.15 \mu M$ at station 7).

Chl *a*

Chlorophyll concentrations (Fig. 4) were highest near the Astrolabe and Mertz Glaciers and over the Adélie Depression, with a maximum near the Mertz Glacier ($1.57 \mu g l^{-1}$ at station 16). Much lower values were observed over the plateau (minimum $0.21 \mu g l^{-1}$ at station 35). Vertically, there was little variation in concentrations in the waters surrounding the Astrolabe Glacier, whereas in the eastern region concentrations dropped considerably with depth.

Microplankton

Microplankton abundances varied widely. Total microplankton abundances averaged $11,754 \pm 15,312 \text{ cells } l^{-1}$ with a maximum of $71,154 \text{ cells } l^{-1}$ (station 23) over the Adélie Depression. Values then decreased towards the coast and the west, with a minimum of $417 \text{ cells } l^{-1}$ (station 9) in the westernmost region. The Shannon index H' values were minimal near the Mertz Glacier and over the

Adélie Depression (0.12 in stations 17 and 23) but then increased towards the west with a maximum of 1.01 near the Astrolabe Glacier (station 2) and varied little in the surrounding waters or over the Adélie Bank.

From Terre Adélie to the Mertz Glacier, the microplankton community (Fig. 5) was completely dominated by diatoms (ranging from 394 to $70,274 \text{ cells } l^{-1}$), with abundances 1–2 orders of magnitude greater than the other components: dinoflagellates (0 – $624 \text{ cells } l^{-1}$), silicoflagellates (0 – $460 \text{ cells } l^{-1}$) and ciliates (0 – $628 \text{ cells } l^{-1}$).

Non-diatom microplankton

Dinoflagellates identified included members of the genera *Dinophysis*, *Gymnodinium*, *Gonyaulax* and *Protoperidinium*. Results from dinoflagellates (Fig. 5a) have all been pooled into a single category with an average of $218 \pm 178 \text{ cells } l^{-1}$. In general, higher concentrations of dinoflagellates were seen close to shore in Commonwealth Bay and over the Adélie Depression (with a maximum of $625 \text{ cells } l^{-1}$ at station 29). Cell concentrations were lowest away from the coast, west of the Astrolabe Glacier (indeed, no dinoflagellates were observed in several samples from this area).

Silicoflagellates (Fig. 5b) presented the lowest abundances of all the microplankton, $35 \pm 86 \text{ cells } l^{-1}$, except in the waters just west of the Astrolabe Glacier (maximum of $460 \text{ cells } l^{-1}$ at station 6) where they frequently outnumbered dinoflagellates and ciliates. Their numbers decreased drastically towards the east (absent from several samples). *Dictyocha speculum* was the only silicoflagellate species observed.

A large majority of the ciliates observed during this study were tintinnids ($71.6 \pm 32\%$ of all ciliates), amongst which the genus *Codonellopsis* was abundant. At 5 m, ciliates averaged $102 \pm 126 \text{ cells } l^{-1}$, higher levels were observed just off the Astrolabe (with a maximum of $628 \text{ cells } l^{-1}$ at station 2) and Mertz Glaciers (in particular over the Adélie Depression), and then lower over the Adélie Bank (Fig. 5c). There were several samples in which no ciliates were observed.

Diatom abundances and species composition

As stated previously, diatoms were the overwhelmingly dominant component of the microplankton community. Results at 5 m depth (Fig. 5d), averaging $11,398 \pm 15,161 \text{ cells } l^{-1}$, showed large variations over the area surveyed, with very high abundances observed over the Adélie Depression (maximum of $70,275 \text{ cells } l^{-1}$ at station 23) and generally in the waters neighbouring the Mertz Glacier, whereas in waters over the Adélie Bank and the western part of the region the diatom population showed a

Fig. 2 Sea-surface (a) density, (b) salinity and (c) temperature (°C) in Terre Adélie and Georges V Land (from continuous measurements at 3 m depth)

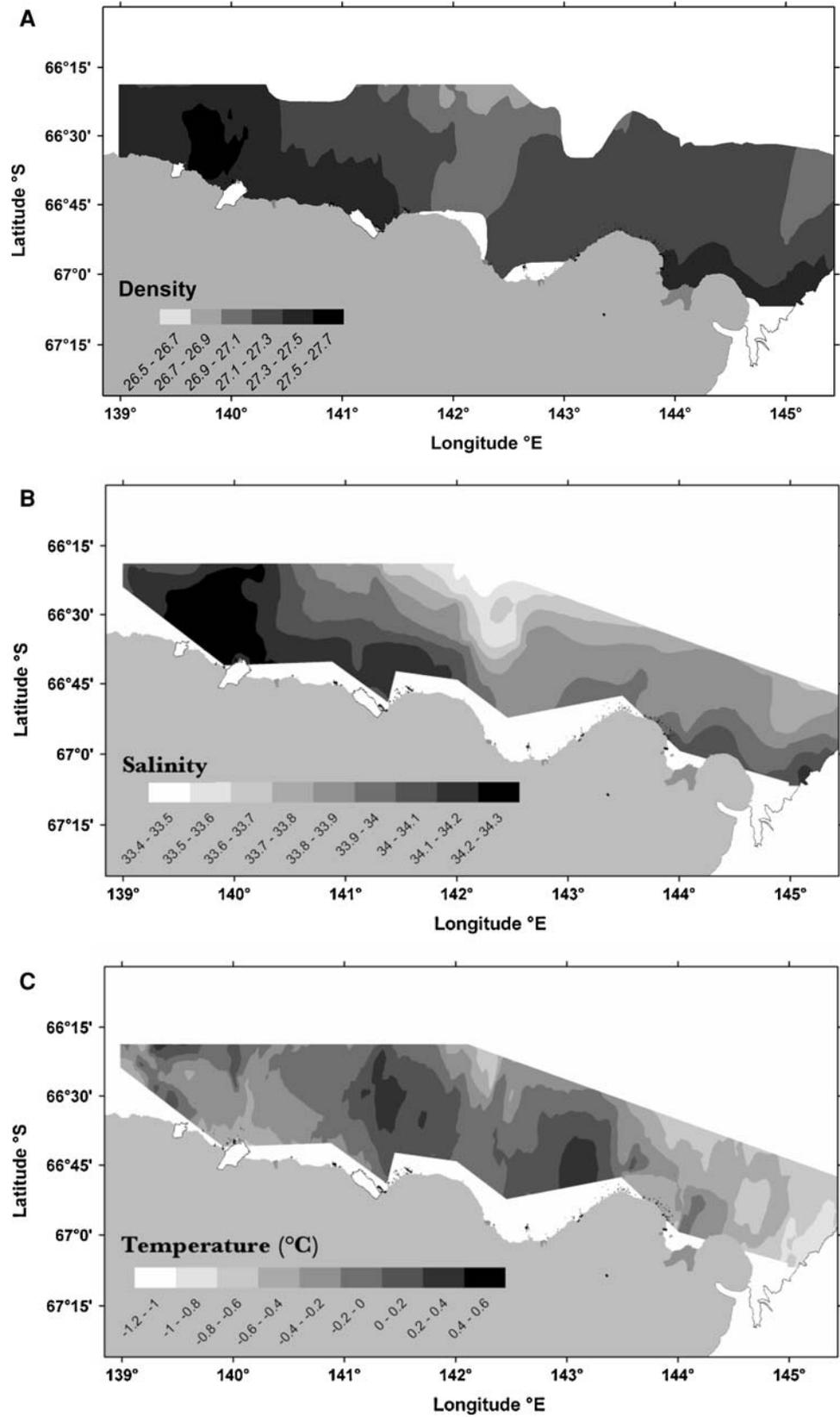


Fig. 3 Nutrient concentrations (μM) at 5 m depth. **a** Nitrite NO_2^- , **b** nitrate NO_3^- , **c** silicic acid $\text{Si}(\text{OH})_4$

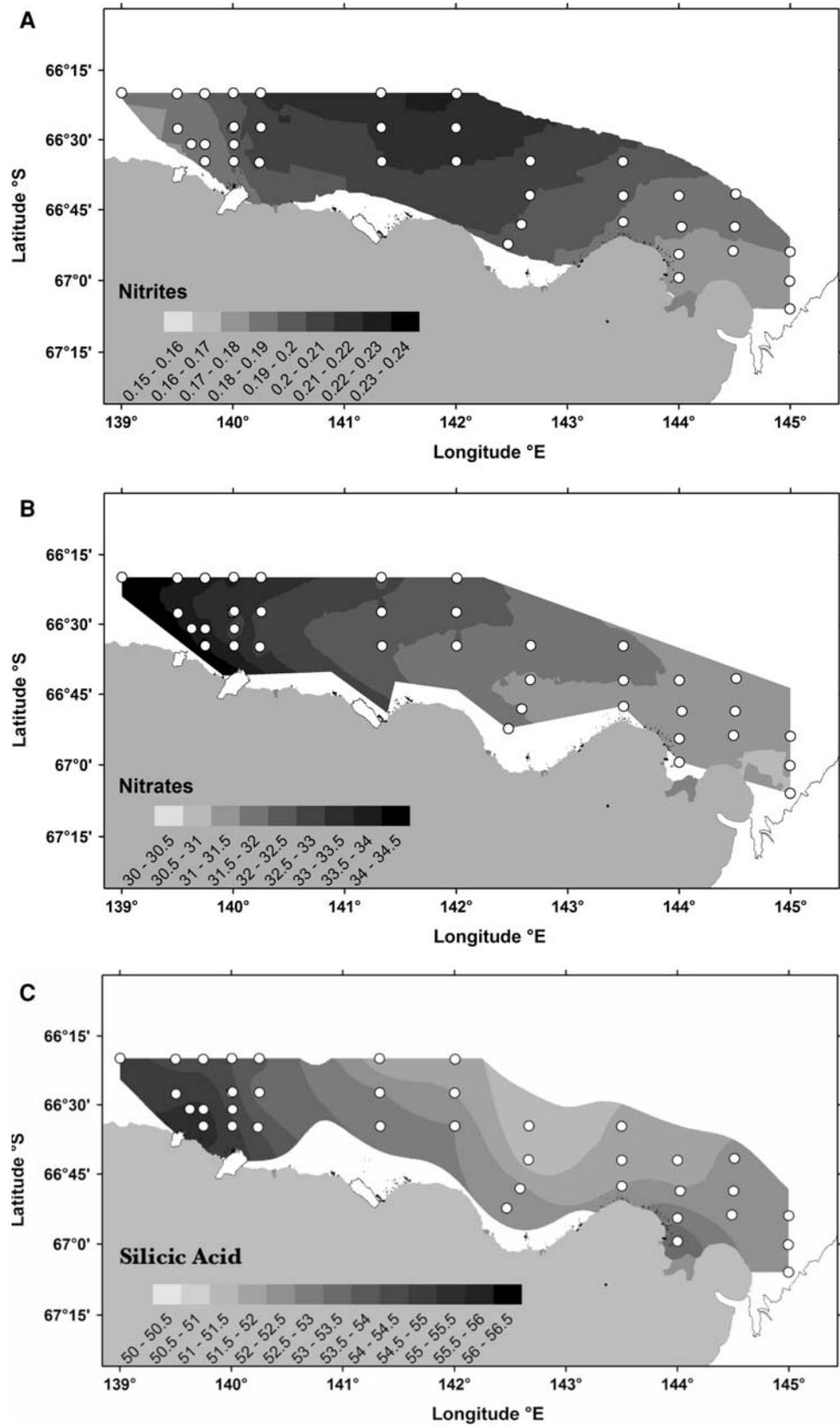
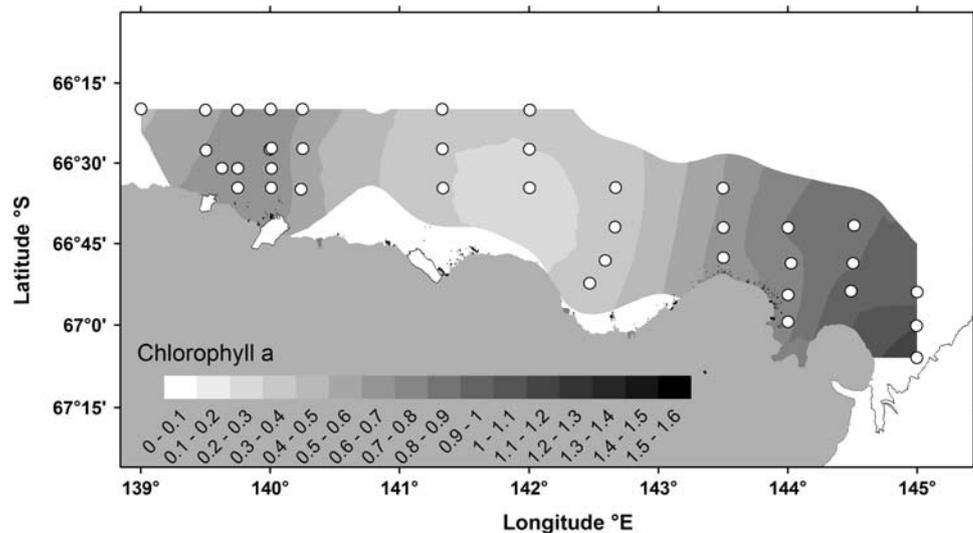


Fig. 4 Total Chl *a* concentrations $\mu\text{g l}^{-1}$ at 5 m depth



marked decrease in numbers (minimum of 48 cells l^{-1} at station 38).

The most common diatom species, counted and identified using optical microscopy, are listed in Table 1, along with their frequency of occurrence. Among the most widespread groups, only four ever individually constituted more than 10% of the diatom population at more than one station and could be considered a dominant group. These were *Fragilariopsis* spp., *Chaetoceros criophilus*, *Rhizosolenia* spp. and *Corethron pennatum* (Fig. 6). Occasionally, *Thalassiothrix antarctica* also approximated this 10% level. The use of SEM allowed to identify other diatom species that were not included in the counts. Among these were the centric diatoms, *Chaetoceros atlanticus*, *Coscinodiscus bouvet*, *Stellarima microtrias*, several *Thalassiosira* species (such as *T. ritscheri*, *T. lentiginosa*, *T. gravida*, *T. gracilis*, *T. tumida*, *T. ritscheri*), *Porosira glacialis*, *Asteromphalus hookeri*, *Actinocyclus actinochilus*, *Rhizosolenia antennata* and the pennate diatoms, *Achnanthes vicentri*, and *Cocconeis* spp., as well as several *Fragilariopsis* species (such as *F. kerguelensis*, *F. curta*, *F. pseudonana*, *F. rhombica*).

The small, rectangular-shaped, colonial pennate diatom *Fragilariopsis* spp. (sizes approximately $5 \times 30 \mu\text{m}$, with occasional larger forms reaching up to $8 \times 100 \mu\text{m}$) was by far the most widely distributed and abundant group (Fig. 7a). Abundances (often an order of magnitude greater than other groups) varied a lot throughout the zone, with an average of $9,335 \pm 15,170$ cells l^{-1} and a maximum of 68,222 cells l^{-1} at station 23. Generally *Fragilariopsis* spp. comprised $>80\%$ of the diatoms (ranging from 60 to 90%), in the eastern region of our site, in particular over the Adélie Depression. In the western region, although they frequently remained abundant (but an order of magnitude less), they were no longer as dominant (ranging from 0 to

50% of diatoms) due to the large number of other species present. None were observed in two offshore stations (10 and 11).

The chain-forming centric diatom *Chaetoceros criophilus* ($\sim 25 \times 30 \mu\text{m}$) was also present throughout the region (Fig. 7b), with an average abundance of 478 ± 422 cells l^{-1} . *Chaetoceros criophilus* was most abundant close to the coast over the Adélie Bank (maximum of 1,701 cells l^{-1} at station 36) and near the Astrolabe Glacier (peak of 1,344 cells l^{-1} at station 6). Further offshore and to the east, abundances decreased, to the point that none were observed at certain stations (16, 17 and 25). Several other *Chaetoceros* species were observed (Table 1), but the only other one to reach relatively high abundances was *C. dictyota* (51 ± 54 cells l^{-1}).

The centric diatoms *Rhizosolenia* spp. and *Corethron pennatum*, with sizes ranging from 5×140 to $40 \times 500 \mu\text{m}$ and 20×90 to $50 \times 350 \mu\text{m}$, respectively, were two of the largest species present (apart from a few *Thalassiosira* spp. of $\phi > 100 \mu\text{m}$). They showed similar distributions and abundances (Fig. 7c, d), averaging 378 ± 359 cells l^{-1} and 206 ± 281 cells l^{-1} , respectively, and were frequently dominant species in the western part of the area (maximum 24.3% of all diatoms for *Rhizosolenia* spp. and 31.3% for *C. pennatum*). Both groups showed their highest abundances close to the Astrolabe Glacier (1,841 cells l^{-1} for *Rhizosolenia* spp. at station 6 and 1,395 cells l^{-1} for *C. pennatum* at station 2), but where *Rhizosolenia* spp. distribution seemed to remain close to the coastline, continuing eastward a bit over the Adélie Bank, *C. pennatum* abundances peaked directly to the north of the Astrolabe Glacier. Over the bank, *Rhizosolenia* spp. could constitute approximately 10% of the diatom population, whereas in this same area *C. pennatum* was always below 10%. Both groups were occasionally present in the

Fig. 5 Microplankton abundances (cells l^{-1}) at 5 m depth. **a** dinoflagellates, **b** silicoflagellates, **c** ciliates, **d** diatoms

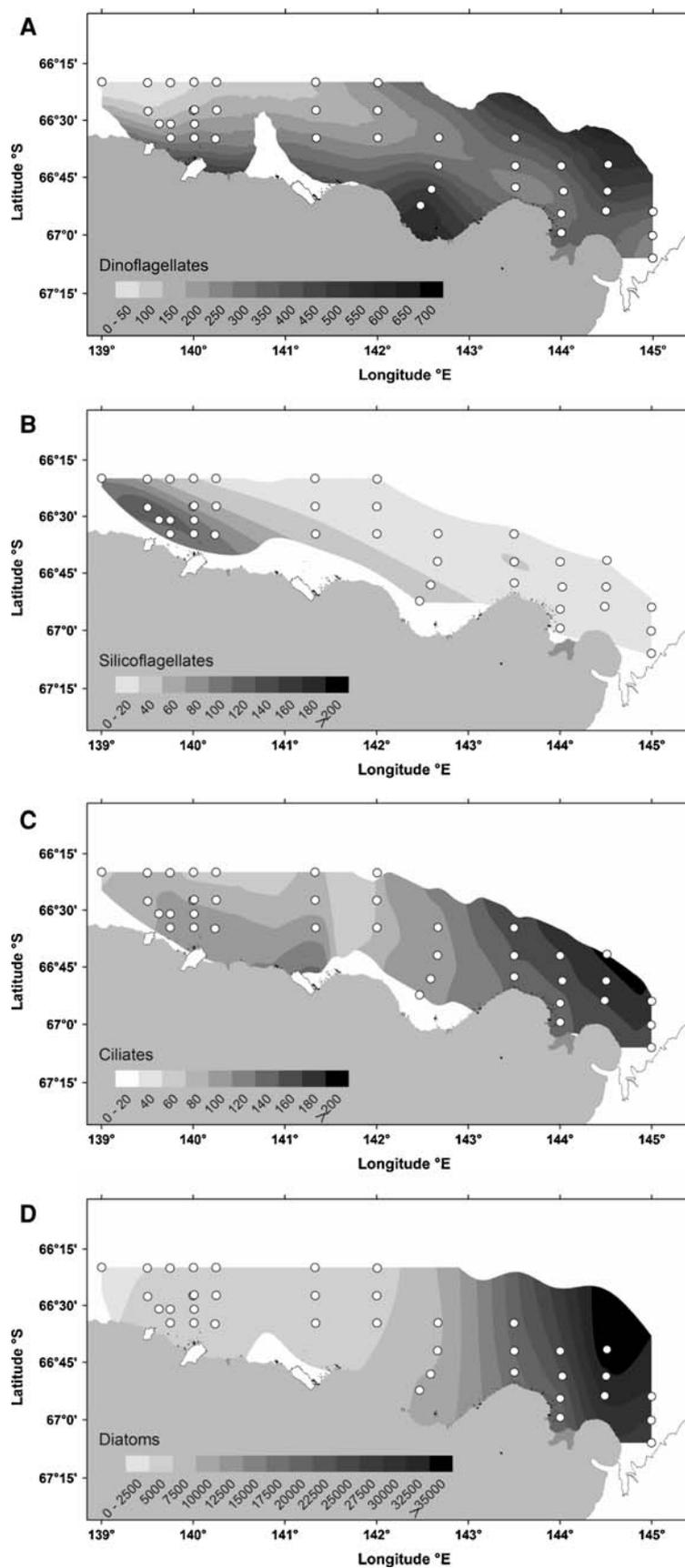


Table 1 Frequency of occurrence (FO) of common diatom species found in samples (all depths) from Terre Adélie to the Mertz Glacier

Taxon	FO (%)
<i>Actinocyclus</i> spp.	98.9
<i>Thalassiothrix antarcticum</i>	97.1
<i>Fragilariopsis</i> spp.	96.6
<i>Rhizosolenia</i> spp.	96.6
<i>Thalassiosira</i> spp.	91.4
<i>Chaetoceros</i> spp.	90.2
<i>Chaetoceros criophilus</i>	88.5
<i>Corethron pennatum</i>	88.5
<i>Asteromphalus</i> spp.	72.4
<i>Nitzschia</i> , <i>Pseudo-nitzschia</i> , <i>Navicula</i> group	67.8
<i>Chaetoceros dichchaeta</i>	61.5
<i>Coscinodiscus</i> spp.	41.4
<i>Eucampia antarctica</i>	33.9
<i>Banquisia belgica</i>	25.3
<i>Odontella</i> spp.	14.9
<i>Chaetoceros curvisetus</i>	9.2

east, but were rare (between 0.3 and 7% of diatoms for *Rhizosolenia* spp. and 0–1% for *C. pennatum*).

Thalassiothrix antarctica was quite abundant in certain areas (albeit to a lesser degree than the four groups mentioned previously), sometimes representing >10% of the diatom population over the Adélie Bank. The average abundance was 236 ± 191 fragments l^{-1} , with a rather uniform distribution throughout the region, except for peaks of abundance close to shore near the Astrolabe Glacier and at either side of Watt Bay (maximum of 755 fragments l^{-1} at station 28).

Two ice associated species were also counted: *Eucampia antarctica* and *Odontella* sp. *Odontella* sp. was extremely rare (2.8 ± 8 cells l^{-1} at 5 m), but could have been underestimated due to the difficulty of observing its weakly silicified cells with the optical microscope. It was more noticeably present near the Astrolabe Glacier. *Eucampia antarctica* averaged 8.3 ± 24 cells l^{-1} and was most abundant near the Astrolabe Glacier (maximum 127 cells l^{-1} at station 1) as well as to a lesser degree near the Mertz Glacier. In the former region it comprised up to 3% of the diatom population.

Diatom assemblages

Correspondence analysis was done on the abundances of the principal diatom taxa at 5 m depth (Fig. 8). The first two axes accounted for 90.7% of the variation. These results allowed similar stations to be gathered into three groups, each characterised by the dominance of a certain

taxon. The first axis, which accounted for 77.66% of the variation, shows a clear separation of the stations in the Mertz Glacier and Adélie Depression region (stations 16, 17, 18, 19, 20, 21, 24, 25, 27) as well as the two coastal Commonwealth Bay stations (29 and 30) from the rest of the study area. In this group *Fragilariopsis* spp. is the overwhelmingly abundant and dominant taxon. The second axis (13.04% of the variation) allows for the separation of the Adélie Bank stations (15, 31, 32, 33, 34, 35, 36, 38) from those near the Astrolabe Glacier and further east (1, 2, 3, 6, 7, 10, 11, 13). The Adélie Bank group appears to have been determined by the presence of *Chaetoceros criophilus*, whereas the Astrolabe Glacier group was determined by the larger species *Corethron pennatum* and *Rhizosolenia* spp. Based on this grouping of stations, average abundances of the main microplankton groups for each zone have been presented in Table 2.

Diatoms and water surface densities

We compared the distribution at 5 m depth of the four dominant taxa observed in this study (*Corethron pennatum*, *Rhizosolenia* spp., *Chaetoceros criophilus* and *Fragilariopsis* spp.) with the surface water densities (Fig. 9). For this we did a correlation between diatom abundances and density values at each station. *Fragilariopsis* spp. (Fig. 9a) showed a distinct preference for stratified waters with a lower surface density. Although present throughout the region, *Fragilariopsis* spp. abundances exploded within a limited range of surface water densities: between 27.2 and 27.3.

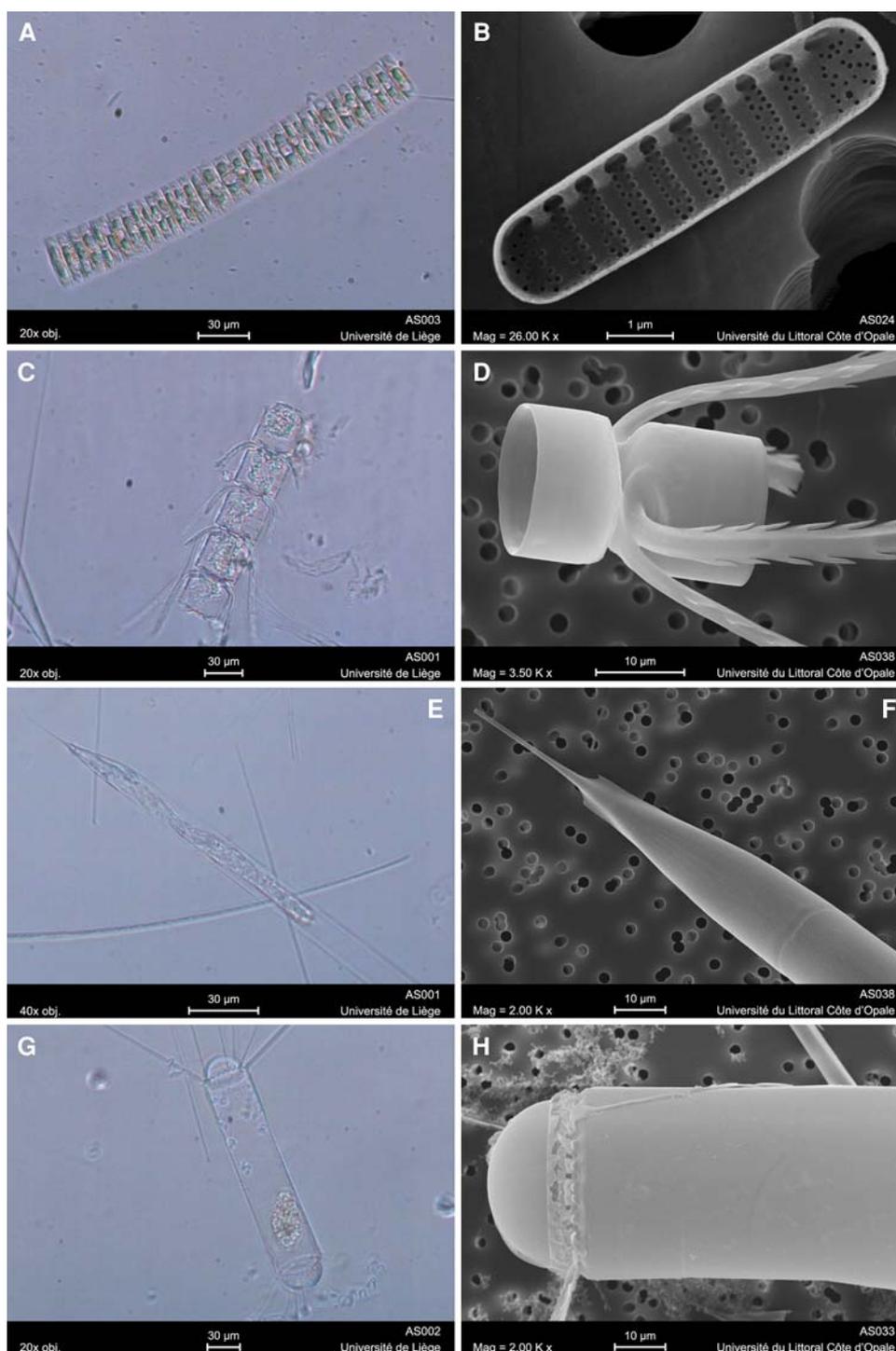
Corethron pennatum and *Rhizosolenia* spp. (Fig. 9b) also showed a clear relationship with surface water densities ($P < 0.01$), but in their case we observe a marked preference for more mixed waters with higher surface densities.

Chaetoceros criophilus (Fig. 9b), on the other hand, does not have a significant relationship with surface water density ($P = 0.9$), although its highest abundances were observed in waters with intermediate surface densities.

Discussion

Although certain studies (Reay et al. 2001) have shown water temperature to influence phytoplankton production, it does not seem to have been a deciding factor in our region as the coldest waters (around the Mertz Glacier and Adélie Depression) are those that show the highest abundances and biomass. This could be due to the low variation in temperatures present in our region (barely 1.5°), or to the higher influence of other factors, such as the water column stability as estimated by surface water densities (higher

Fig. 6 Principal diatoms from Terre Adélie and the Mertz Glacier region. Photos taken with an inverted microscope (**a, c, e, g** by C.Beans) and a scanning electron microscope (**b, d, f, h** by C.Vallet & L.Courcot). **a, b** *Fragilariopsis* spp.; **c, d** *Chaetoceros criophilus*; **e, f** *Rhizosolenia* spp.; **g, h** *Corethron pennatum*. Magnification for SEM photos, objective used for inverted microscope photos are specified



abundances and biomass were observed in the more stable waters of the Mertz Glacier region).

With chlorophyll *a* concentrations averaging $0.64 \mu\text{g l}^{-1}$ at 5 m depth, and ranging between 0.04 and $1.57 \mu\text{g l}^{-1}$ throughout the zone (at all depths), the waters from Terre Adélie to the Mertz Glacier appear to support a significant summer standing crop of phytoplankton, comparable to the $0.6 \mu\text{g l}^{-1}$ average in Antarctic waters (Table 3). Although

it could be possible that we missed the peak of the summer bloom, similar levels were presented by Arrigo and van Dijken 2003, Sambrotto et al. (2003) and Vaillancourt et al. (2003) at the peak of the blooms in the Dumont d'Urville Polynya, Commonwealth Bay and the Mertz Polynya. Nevertheless, although presenting similar diatom cell abundances to neighbouring regions (Table 3), these values are lower than those observed in the coastal waters of

Fig. 7 Abundances (cells l^{-1}) of dominant diatoms at 5 m depth: **a** *Fragilariopsis* spp., **b** *Chaetoceros criophilus*, **c** *Rhizosolenia* spp., **d** *Corethron pennatum*

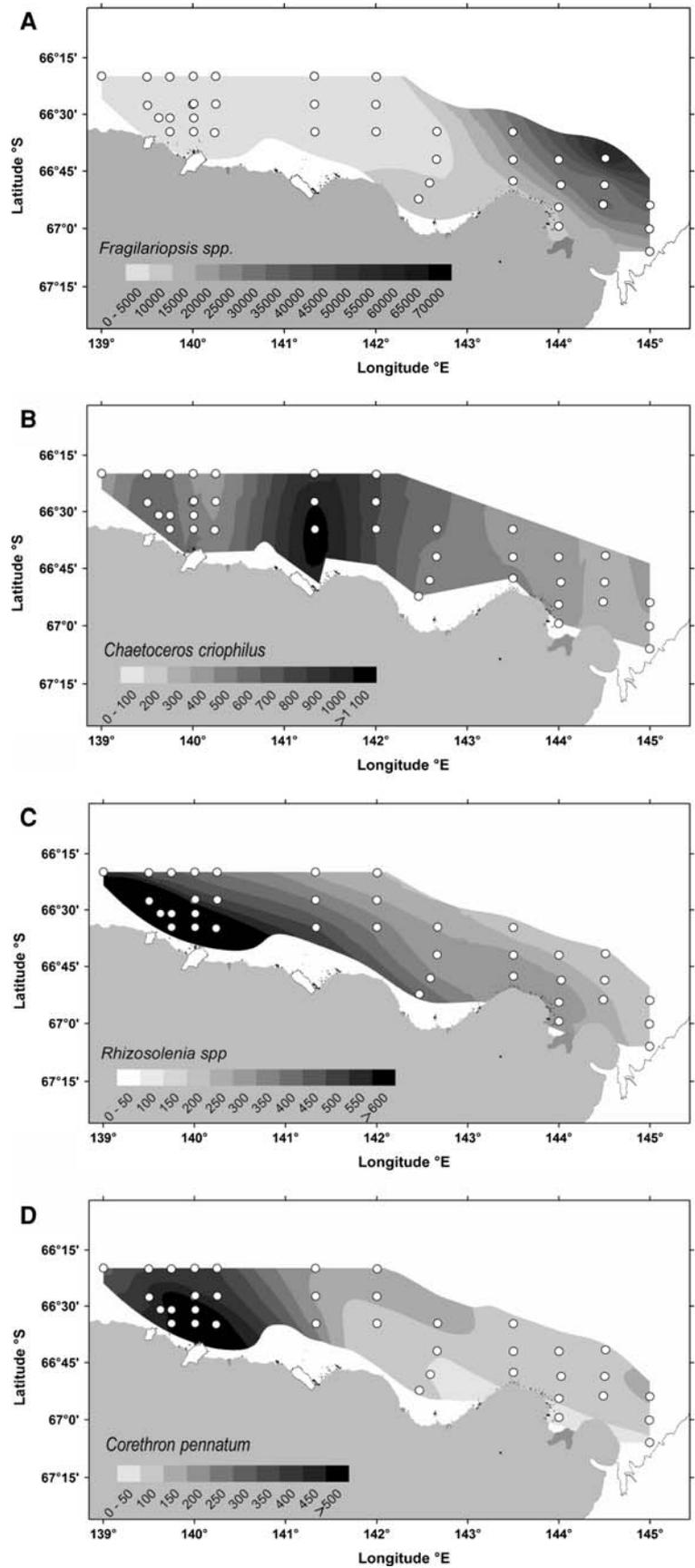
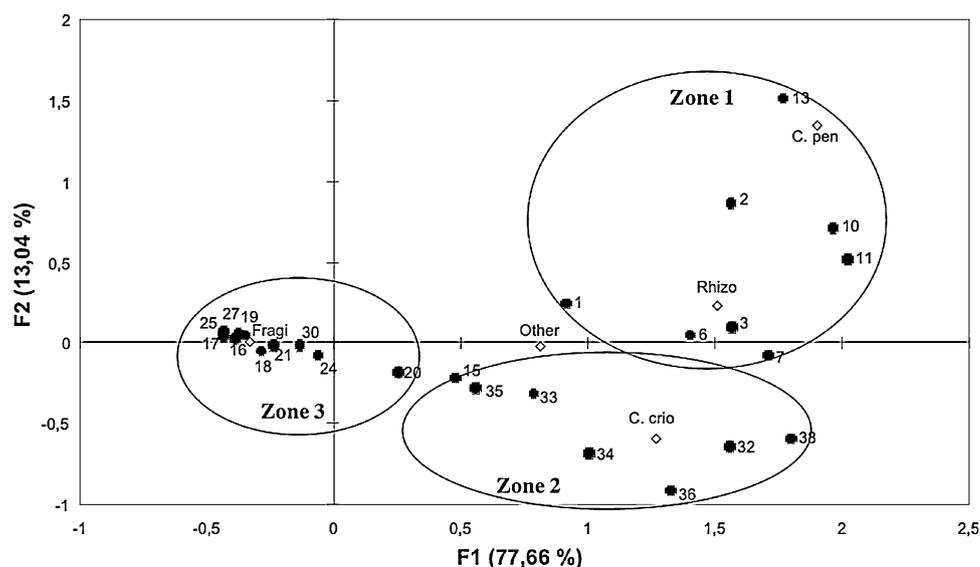


Fig. 8 Correspondence analysis of dominant diatom groups at 5 m depth and sampling stations



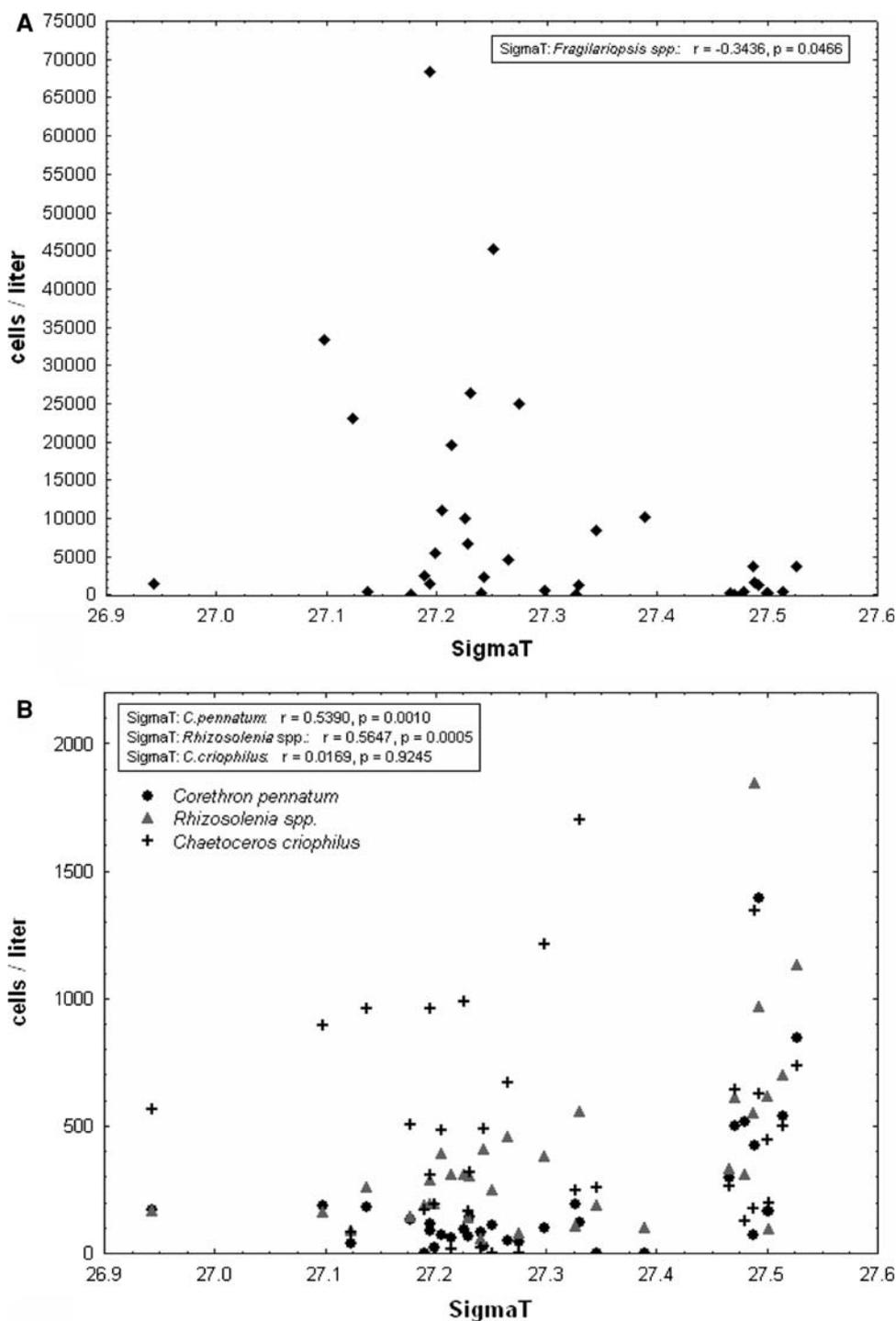
Prydz Bay ($2.1 \mu\text{g l}^{-1}$) (Jacques and Fukuchi 1994) and Terra Nova Bay ($0.1\text{--}4 \mu\text{g l}^{-1}$) (Goffart et al. 2000). Also, in a major survey of the region, Wright and van den Enden (2000) found that waters from 128°E to 150°E were considerably less productive than waters from 93°E to 120°E .

It appears then that phytoplankton biomasses are lower in the Terre Adélie–George V Lands than in those neighbouring regions. The Chl *a* concentrations measured during this study were higher than those of the waters north of the Terre Adélie shelf break (yet still south of the Polar Front)

Table 2 Nutrients (μM), Chl *a* ($\mu\text{g l}^{-1}$), microplankton (cells l^{-1}) and Shannon–Weaver diversity index *H'* in Terre Adélie and Georges V Land surface waters (5 m depth) (average \pm SD, maximum–minimum)

	Astrolabe Glacier	Adélie Bank	Mertz Glacier + Adélie Depression
Nitrite	0.19 ± 0.02 (0.15–0.22)	0.21 ± 0.01 (0.19–0.24)	0.19 ± 0.02 (0.16–0.22)
Nitrate	33.45 ± 0.84 (31.65–34.37)	32.22 ± 0.4 (31.38–32.64)	31.29 ± 0.48 (30.38–31.91)
Silicic Acid	54.42 ± 1.05 (51.51–58.08)	51.81 ± 1.21 (50.22–53.23)	52.23 ± 0.80 (51.15–54.21)
Chl <i>a</i>	0.68 ± 0.14 (0.38–0.94)	0.29 ± 0.05 (0.21–0.35)	0.79 ± 0.37 (0.28–1.57)
Ciliates	80 ± 180 (0–628)	42 ± 30 (14–97)	156 ± 82 (40–312)
Dinoflagellates	102 ± 105 (0–352)	154 ± 82 (61–269)	354 ± 180 (78–624)
Silicoflagellates	71 ± 139 (0–460)	12 ± 12 (0–35)	17 ± 22 (0–67)
Diatoms	$3,317 \pm 2,790$ (394–9,058)	$3,360 \pm 1,271$ (1,190–5,432)	$22,919 \pm 18,249$ (6,507–70,274)
<i>Fragilariopsis</i> spp.	$954 \pm 1,346$ (0–3,669)	1216 ± 850 (76–2,459)	$21,159 \pm 18,064$ (4,448–68,222)
<i>Rhizosolenia</i> spp.	608 ± 516 (56–1,841)	298 ± 142 (145–555)	226 ± 115 (76–456)
<i>Corethron pennatum</i>	433 ± 380 (72–1395)	107 ± 64 (0–183)	70 ± 53 (0–187)
<i>Chaetoceros criophilus</i>	444 ± 380 (72–1395)	821 ± 488 (168–1,701)	312 ± 331 (0–989)
Other <i>Chaetoceros</i> spp.	311 ± 307 (18–973)	385 ± 331 (139–1,463)	434 ± 356 (34–1,145)
<i>Thalassiothrix antarctica</i> (fragments/l)	204 ± 215 (0–696)	171 ± 123 (42–425)	300 ± 193 (96–755)
<i>Eucampia antarctica</i>	12 ± 36 (0–127)	0	10 ± 15 (0–44)
<i>Asteromphalus</i> spp.	37 ± 54 (0–175)	58 ± 66 (0–208)	81 ± 54 (0–160)
<i>Acinocyclus</i> spp.	97 ± 96 (0–316)	101 ± 63 (17–215)	139 ± 84 (16–323)
<i>Thalassiosira</i> spp.	69 ± 95 (0–337)	41 ± 34 (0–97)	61 ± 42 (0–161)
<i>Coscinodiscus</i> spp.	16 ± 33 (0–105)	8 ± 11 (0–28)	11 ± 15 (0–54)
<i>Odontella</i> spp.	6 ± 13 (0–37)	0	1 ± 5 (0–18)
<i>NitzschialPseudo-nitzschia</i> group	6 ± 21 (0–74)	0	0
Other diatoms	120 ± 130 (0–337)	107 ± 109 (0–334)	164 ± 110 (0–418)
<i>H'</i>	0.85 ± 0.08 (0.74–1.01)	0.3 ± 0.19 (0.12–0.63)	0.31 ± 0.17 (0.12–0.63)

Fig. 9 Surface water density (sigmaT) vs. abundances of four diatom species at 5 m depth: **a** *Fragilariopsis* spp. and **b** *Chaetoceros criophilus*, *Rhizosolenia* spp. and *Corethron pennatum*



as studied by Chiba et al. in 1996 (2000) and Gomi et al. in 2000 (2005) (Table 3), indicating that the shelf waters remain an important location for primary production in the region.

As in other regions around Antarctica (Jacques and Fukuchi 1994; Chiba et al. 2000; Waters et al. 2000; Fonda Umani et al. 2005), the microplankton communities in Terre Adélie are strongly dominated by diatoms (over 80% of the

microplankton). Within this group, the dominance of pennate diatoms (in particular *Fragilariopsis* spp.) is consistent with other eastern Antarctic and Ross Sea studies (Kopczynska et al. 1986; Goffart et al. 2000; Waters et al. 2000). Previous studies in the waters just north of the shelf break also noted the importance of *Fragilariopsis* spp. and related species in the region, with abundances similar to those reported here ($0\text{--}6.8 \times 10^5$ cells l^{-1} at

Table 3 Chl *a* and microplankton abundances in the region

Location	Period	Chl <i>a</i> ($\mu\text{g l}^{-1}$)	Diatom abundances (cells l^{-1})	Reference
Southern Ocean average (BIOMASS cruises)	Summer	0.6		El-Sayed (2005)
Prydz Bay	Summer	2.1		Jacques and Fukuchi (1994)
Terre Adélie + Georges V Land	January 2004	0.21–1.57	1.14×10^5	This study
Dumont d'Urville Polynya	November 1995	0.69	2×10^3	Riaux-Gobin et al. (2000, 2003)
Dumont d'Urville Polynya	Summer peak	1.17		Arrigo and van Dijken, (2003)
Mertz Polynya		0.93		
Terre Adélie + Commonwealth Bay	December 2000–January 2001	1.33 1.03		Sambrotto et al. (2003) and Vaillancourt et al. (2003)
Mertz Region				
Terre Adélie–offshore	January–February 1996	0.4 – 0.6		Chiba et al. (2000)
Terre Adélie–offshore	February–March 2000	0.3 – 0.5		Gomi et al. (2005)
Terra Nova Bay (Ross Sea)	January–February 1998		Maximum 6×10^5	Fonda Umami et al. (2005)
Western Ross Sea	January 1990	0.1–4		Goffart et al. (2000)

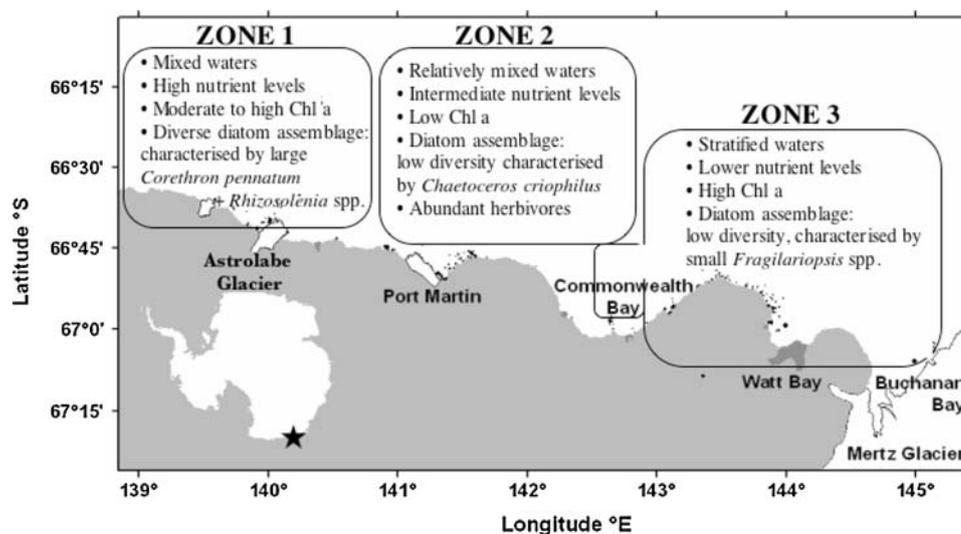
5 m): in Gomi's study (2005) the dominant diatoms were *Fragilariopsis* spp. ($0.5\text{--}1 \times 10^5$ cells l^{-1}); Waters et al. (2000) noted the most frequent diatoms in our zone were a group composed of *F. curta*, *Nitzschia lecontei* and other related species larger than $20 \mu\text{m}$ (3.6×10^4 to 5.6×10^5 cells l^{-1}), while in the Terre Adélie waters close to the Polar Front (Chiba et al. 2000), the dominant diatom was *F. kerguelensis*. These authors also mentioned the presence of *Corethron pennatum*, *Rhizosolenia* spp. and the frequently abundant *Thalassiothrix antarctica* and *Chaetoceros criophilus*, which are all abundant species in our study.

Both the cartographic representations and the correspondence analysis done on the abundances of the principal

diatom species allowed us to distinguish three separate zones in our region (Fig. 10): the Mertz Glacier and Adélie Depression zone, the Adélie Bank zone and the Astrolabe Glacier zone.

Beginning in the East, the Mertz Glacier and Adélie Depression stations are shown to be very different from the remaining zones. The region (Zone 3 in Fig. 10) is characterised by the presence of a polynya which begins to open in mid-September and is usually fully developed by mid-October, allowing for a phytoplankton bloom early in the season (Sambrotto et al. 2003; Vaillancourt et al. 2003). During our study we found there was maximum depletion of nutrients in this region and a stratified water column, probably due to the ice melt. Stratified

Fig. 10 schematic representation of the differences between the three zones



waters have been previously observed to be locations of high phytoplankton biomass (Priddle et al. 1994). The nutrient depletion would appear to indicate that the bloom had begun earlier in this region than in the others. Chl *a* levels were highest in this zone (with an average of $0.79 \mu\text{g l}^{-1}$ and a maximum of $1.57 \mu\text{g l}^{-1}$). Diatom, ciliate and dinoflagellate abundances were at a maximum (70,274, 312 and 624 cells l^{-1} , respectively). Among the diatom community, a very low diversity ($H' = 0.31 \pm 0.17$) was observed of principally small diatoms (*Fragilariopsis* spp. dominated the community, *Chaetoceros* spp. were also relatively abundant). In a recent classification (Sambrotto et al. 2003) this zone was also distinguished from the rest of the region based on bathymetry, distribution of pack-ice and fast-ice, and chlorophyll levels. Studies by Samyshev in 1991 (Waters et al. 2000) have suggested that the smaller ice-seeded diatoms *Fragilariopsis* spp. and *Chaetoceros* spp. are typical of spring/early summer, when the sea-ice begins to melt and the waters are stratified. Other authors have also mentioned the importance of stratified waters for diatoms, noting that diatoms showed a positive correlation with water column stability, as stratification increases the time a cell spends in an environment with high available light for photosynthesis (Gibson et al. 1997; Goffart et al. 2000; Moro et al. 2000). In their studies diatom blooms appeared to be much more abundant in stratified waters and were frequently dominated by small pennate diatoms such as *Fragilariopsis* spp. or *Nitzschia* spp. Cores taken from the sediment near the Mertz Glacier showed abundant frustules from *Fragilariopsis* species, making this group the dominant diatom in recent times (Maddison et al. 2006).

Stations in the other two zones were less stratified possibly due to the mixing by the summertime katabatic winds, which are more frequent and intense in Terre Adélie and Commonwealth Bay than near the Mertz Glacier (Sambrotto et al. 2003; Vaillancourt et al. 2003). They showed similar abundances and diversity, but were separated into two groups based on the importance of certain diatom taxa.

The Astrolabe Glacier zone (Zone 1 in Fig. 10) comprised 15 stations with less nutrient-depleted waters than elsewhere in the region. This zone was characterised by average to high Chl *a* concentrations ($0.68 \pm 0.14 \mu\text{g l}^{-1}$ at 5 m), high diatom diversity ($H' = 0.85 \pm 0.08$) and average abundances ($3,317 \pm 2,790$ cells l^{-1} at 5 m), and dominance of predominantly larger species such as *Corethron pennatum* and *Rhizosolenia* spp. These species are typically associated with open ocean conditions (Armand et al. 2005; Crosta et al. 2005; Maddison et al. 2006) and would thrive better in these mixed waters than the smaller pennate diatoms due to drag-inducing adaptations that

reduce their sinking rate, such as long appendages (in the case of *C. pennatum*) or their needle-like morphology (for *Rhizosolenia* spp.). This zone is also where the highest abundances of silicoflagellates were found (maximum 460 cells l^{-1}), being very rare in the other two zones.

The Adélie Bank zone (Zone 2 in Fig. 10) was comprised of stations that were located over the shallower and warmer shelf waters. These had intermediate nutrient concentrations, yet much lower Chl *a* concentrations ($0.29 \pm 0.05 \mu\text{g l}^{-1}$ at 5 m) than the surrounding zones, and average diatom abundances ($3,360 \pm 1,271$ cells l^{-1} at 5 m) with a low diversity ($H' = 0.3 \pm 0.19$). These stations were characterized by the presence and high abundance of *Chaetoceros* spp., in particular *C. criophilus*. The differences between the surface water densities and nutrient concentrations of this zone and those of the Astrolabe Glacier zone being so low suggest that some other factor could help explain the differences in diatom abundances between the two zones. Studies done during the same campaign found the waters over the plateau to hold the largest abundances of potential grazers in the region. These include various copepods (calanoid and cyclopoid) (Swadling et al. 2008), appendicularians, euphausiids (Vallet et al., pers. communication) and fish larvae (particularly *Pleuragramma antarcticum*, Koubbi et al. 2008a, b), which have been known to prey on microplankton (Smetacek et al. in Marchant and Murphy 1994). The low biomass observed here may therefore very well be due to the larger grazing pressure in this zone.

Finally, the distribution of the microzooplankton component shows a preference for the waters around the Mertz Glacier and Adélie Depression where the highest average abundances of both dinoflagellates (354 ± 180 cells l^{-1}) and ciliates (156 ± 82 cells l^{-1}) were observed. This distribution coincides with the highest diatom abundances characterised by small *Fragilariopsis* spp. (usually not much bigger than $30 \times 5 \mu\text{m}$). Although Chl *a* levels are also very high to the north and west of the Astrolabe Glacier, the area is dominated by larger and chain-forming diatoms such as *Corethron pennatum*, *Rhizosolenia* sp. or *Chaetoceros* spp., and grazing studies have shown a net preference by microherbivores for the smaller primary producers (preferably below the $20 \mu\text{m}$ fraction) and an avoidance of the larger, chain-forming diatoms (Froneman and Perissinotto 1996).

Conclusions

The microplankton communities in the coastal waters between Terre Adélie and the Mertz Glacier were dominated by diatoms. Both the cartographic representations and the

correspondence analysis of the species composition allowed the region to be separated into three zones each represented by a dominant group: the Mertz Glacier–Adélie Depression zone with stratified waters characterised by low diversity due to very high abundances (chl *a* 0.79 ± 0.37 ; diatoms $22,919 \pm 18,249$ cells l^{-1} at 5 m) and dominated by the small colonial *Fragilariopsis* spp.; the Astrolabe Glacier zone where diversity was high, abundances average (chl *a* 0.68 ± 0.14 μg l^{-1} ; diatoms $3,317 \pm 2,790$ cells l^{-1} at 5 m) and the diatom community was principally composed of larger species such as *Corethron pennatum* and *Rhizosolenia* spp; and the Adélie Bank zone over the shallower shelf waters where biomasses were lower (chl *a* 0.29 ± 0.05 μg l^{-1} ; diatoms $3,360 \pm 1,271$ cells l^{-1} at 5 m), coinciding with a large presence of herbivorous zooplankton, and where the small chain-forming *Chaetoceros criophilus* and similar species were dominant.

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