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# Interannual variability in the distribution of the phytoplankton standing stock across the seasonal sea-ice zone west of the Antarctic Peninsula

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*The spatial distribution of phytoplankton cell abundance, carbon (C) biomass and chlorophyll a (Chl a) concentration was analysed during three summers (1996, 1997 and 1999) in a seasonal sea-ice area, west of the Antarctic Peninsula. The objective of the study was to assess interannual variability in phytoplankton spatial distribution and the mechanisms that regulate phytoplankton accumulation in the water column. Phytoplankton C biomass and Chl a distributions were consistent from year to year, exhibiting a negative on/offshore gradient. The variations in C concentration had a close and non-linear relationship with the upper mixed layer depth, suggesting that the vertical mixing of the water column is the main factor regulating phytoplankton stock. The magnitude of C gradients was 5-fold higher during 1996 than during 1997 and 1999. This was ascribed to interannual variations in the concentration of diatom blooms in the region influenced by sea-ice melting. Vertical distribution of the phytoplankton, as estimated from Chl a profiles, also varied along an on/offshore gradient: Chl a was distributed homogeneously in the upper mixed layer in coastal and mid-shelf stations and concentrated in the deep layer (40–100 m) occupied by the winter waters (WW, remnants of the Antarctic surface waters during summer) in more offshore stations. The region with a deep Chl a maximum layer (DCM layer) was dominated by a phytoplankton assemblage characterized by a relatively high concentration of diatoms. The extent of this region varied from year to year: it was restricted to pelagic waters during 1996, extended to the shelf slope during 1997 and occupied a major portion of the area during 1999. It is hypothesized that iron depletion in near surface waters due to phytoplankton consumption, and a higher concentration in WW, regulated this vertical phytoplankton distribution pattern. Furthermore, we postulate that year-to-year variations in the spatial distribution of the DCM layer were related to interannual variations in the timing of the sea-ice retreat. The similarity between our results and those reported in literature for other areas of the Southern Ocean allows us to suggest that the mechanisms proposed here as regulating phytoplankton stock in our area may be applicable elsewhere.*

## INTRODUCTION

Phytoplankton standing stock is low throughout most of the Southern Ocean, and enhanced concentration is primarily found in sea-ice edge, coastal and frontal system zones (Sullivan *et al.*, 1993; Priddle *et al.*, 1994). The low phytoplankton concentration that characterizes this ocean, despite its high macronutrient availability, is considered to be a major 'paradox' (Knox, 1994; Marchant and Murphy, 1994). Therefore, over the last decades studies have aimed to understand the environmental conditions that regulate local variability in Antarctic phytoplankton composition, growth and accumulation.

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Some factors as water column vertical mixing, grazing and low iron concentration are invoked to explain low phytoplankton biomass (Priddle *et al.*, 1994; Varela *et al.*, 2002). However, there is still much controversy about the relevance of each one of these factors regulating phytoplankton, and how they interact determining the 'high-nutrient, low-chlorophyll' environment. Thus, more studies on the phytoplankton dynamics are of major importance to better understand the ecology of the Southern Ocean.

In particular, the seasonal sea-ice zone (SIZ) has drawn major attention, due to the large area of the Southern Ocean subjected to seasonal sea-ice advance and retreat (Tréguer and Jacques, 1992). The outstanding characteristic of this zone is a large phytoplankton bloom at the sea-ice edge (Smith and Nelson, 1986). In general, it is assumed that once the phytoplankton bloom has disappeared, the community developing in ice-free waters has the typical features of that found in permanently open waters, i.e. low biomass concentration and dominance of nanophytoflagellates (Smetacek *et al.*, 1990; Tréguer and Jacques, 1992). However, while the dynamics of ice-edge blooms has been extensively studied, the community developing in ice-free waters has received much less consideration. Thus, a complete understanding of phytoplankton dynamics in the SIZ is still lacking. Moreover, there remains a paucity of data corresponding to successive years, a fact that disallows to discriminate the yearly stable patterns of phytoplankton structure and dynamics in this zone. The assessment of these topics is essential to achieve a better characterization of the Antarctic phytoplankton. In turn, this information is of much relevance since phytoplankton, as the autotrophic component of the marine ecosystem, affects the structure and efficiency of the food web, the global biogochemical cycles and the biological pump of $CO_2$ in the Southern Ocean. Thus, a better understanding of these processes would only be possible if phytoplankton dynamics is well characterized.

This work focuses on the SIZ west of the Antarctic Peninsula (Fig. 1). This area showed a pronounced negative on/offshore gradient in chlorophyll *a* (Chl *a*) concentration during the summer (Smith *et al.*, 1998, 2001), which was associated to changes in phytoplankton composition, cell abundance and carbon (C) biomass during the 1997 summer (Garibotti *et al.*, 2003a). Furthermore, across-shelf changes in the vertical distribution of Chl *a* were also observed during the 1997 summer, and three regions were defined according to different Chl *a* profiles: a coastal region with high surface Chl *a* concentration in a shallow mixed layer (<15 m), a mid-shelf region with high Chl *a* concentration throughout a deeper upper mixed layer (30–40 m), and an oceanic region with a well-defined subsurface Chl *a* maximum in the water column (40–100 m depth). Various factors, such as water vertical mixing, iron concentration and grazing were postulated as controlling the observed spatial variability in phytoplankton concentration (Garibotti *et al.*, 2003a). These studies evidenced the extent of phytoplankton spatial variability in the area and gave clues about the mechanisms that control phytoplankton accumulation. However, the generality of these findings still remained unclear as only one year was analysed in detail.

Antarctic phytoplankton is usually described as concentrating in the upper portion of the water column (Holm-Hansen and Mitchell, 1991; Smith *et al.*, 1996; Varela *et al.*, 2002). Few studies have reported subsurface Chl *a* maxima, as observed in the Drake Passage (Holm-Hansen *et al.*, 1994, 1997; Berdalet *et al.*, 1997), in coastal SIZs (Yamaguchi *et al.*, 1985; Fiala *et al.*, 1998) and in the vicinity of South Georgia (Gilpin *et al.*, 2002; Korb and Whitehouse, 2004). Thus, the extensive presence of this atypical Chl *a* vertical profile within the shelf waters of the western Antarctic Peninsula during the 1997 summer (Garibotti *et al.*, 2003a) suggests that this phenomenon may be more widespread than previously reported. However, it must be determined whether this pattern is annually recurrent on the western coast of the Antarctic Peninsula, and if it is, a thorough analysis would be necessary to understand its dynamics and ecological relevance.

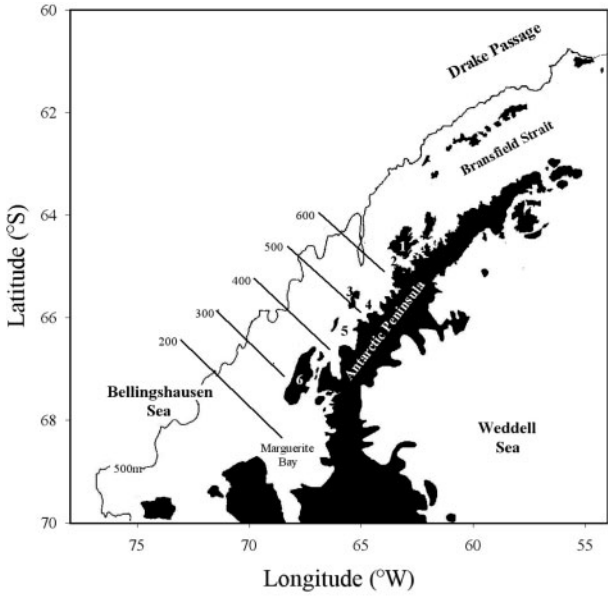


**Fig. 1.** Location of the sampling transects on the western coast of the Antarctic Peninsula during the summer cruises of 1996, 1997 and 1999. The 500-m isobath represents the continental shelf slope and 200–600 are the transect numbers. 1, Anvers Island; 2, Bismarck Strait; 3, Renauld Island; 4, Grandidier Channel; 5, Crystal Sound; 6, Adelaide Island.

The main objective of this study is to asses the interannual variability in Antarctic phytoplankton spatial distribution and to understand the mechanisms that regulate its accumulation in the water column during the summer. We analyse variability in the distribution of phytoplankton composition, cell abundance, C biomass and Chl *a* concentration, in relation to local environmental conditions. The study area is within the SIZ along the western Antarctic Peninsula (Fig. 1). The summers of 1996, 1997 and 1999 were included in this study since they are representative of the range of primary productivity observed during the 1990s (high productivity in 1996, intermediate in 1997 and low in 1999). Our main questions are (i) Is the distribution of the phytoplankton community consistent from year to year?, (ii) What are the main physicochemical parameters associated with the spatial distribution of the phytoplankton?, (iii) Are subsurface Chl *a* maxima an annually recurrent feature in the area?, if so (iv) What is the spatial distribution of subsurface Chl *a* maxima and how can their occurrence in the area be explained?

## METHOD

The study area is located in the continental shelf west of the Antarctic Peninsula, extending between Anvers Island and Marguerite Bay, and from the coast to approximately 200 km offshore (Fig. 1). Sampling was performed on board the R/V *Polar Duke* during the summer cruises (January and February) of 1996 and 1997, and on the ARV *L.M. Gould* in 1999. Stations were located at 20 km intervals along five across-shelf transect lines, plus additional coastal stations. At each station, temperature and salinity measurements were made down to 500 m (or to within a few meters of the bottom) with a Sea Bird CTD system (SBE 9/11) on a Bio-Optical Profiling System (BOPS). The BOPS included a conductivity-temperature-depth (CTD) sensor, a Biospherical Instruments MER 2040 system to determine spectral irradiance, a SeaTech profiling fluorometer for *in situ* fluorescence profiles and a General Oceanics rosette with 10 or 12 liter Go-Flow Niskin bottles for discrete water samples. Sampling depths were set at light levels, established by measuring the Photosynthetically Active Radiation (PAR) using a QSI 240 quantum sensor (Biospherical Instruments Inc.).

Sea-ice extent was derived from multifrequency passive microwave satellite sensing data supplied by the National Snow and Ice Data Center and processed using methods described by Smith and Stammerjohn (Smith and Stammerjohn, 2001). Monthly maps of sea-ice coverage across the continental shelf west of the Antarctic Peninsula (Smith and Stammerjohn, 2002) were comparatively analysed to evaluate variability in sea-ice cover during the winter and spring seasons preceding the summers studied.

Water density was estimated as sigma-*t* ($\sigma_t$). The bottom of the upper mixed layer (UML) was determined as the depth where a change in $\sigma_t > 0.05$ occurred in a 5-m depth interval. Water column vertical stability was calculated according to Mengesha *et al.* (Mengesha *et al.*, 1998): $E = d\sigma_t/dz \times 1/\sigma_{t(average)}$, where $d\sigma_t/dz$ is the density vertical gradient, $dz$ is a 50-m depth interval, and $\sigma_{t(average)}$ is the average density. The bottom of the euphotic zone was defined where the 1% incident light level occurs.

Water aliquots for microscopic analyses were taken from the 50% PAR depth and preserved with 2% acid Lugol's iodine solution. Phytoplankton cells were identified and counted with an inverted microscope (Iroscope IS-PH) according to the Utermöhl method (Utermöhl, 1958). Cell biovolumes were measured using the geometric shapes proposed by Hillebrand *et al.* (Hillebrand *et al.*, 1999) and corrected to account for cell shrinkage due to sample fixation (Montagnes *et al.*, 1994). Cell C content was calculated with two different C-to-volume ratios, one for diatoms (Montagnes and Franklin, 2001) and one for all the other algae groups (Montagnes *et al.*, 1994). These ratios are considered to be the best approach to estimate phytoplankton C biomass (Garibotti *et al.*, 2003b).

For the analysis of nutrient and Chl *a* concentration, water aliquots were taken from 6 depths within the euphotic layer (100, 50, 30, 13, 4 and 0.5% PAR). Water aliquots for measurements of nutrient concentrations were analysed within 12 h of sampling. Silicic acid, nitrate plus nitrite, phosphate and ammonium concentrations were measured according to the method of Johnson *et al.* (Johnson *et al.*, 1985). A Perstorp/Alpken segmented flow nutrient analysis system and a Labtronics data collection software were used. Due to technical problems phosphate concentrations were not estimated during the 1997 summer. Concentrations of Chl *a* and phaeopigments (pha) were estimated fluorometrically. Water aliquots were filtered through Millipore HA filters, the filters extracted in 90% acetone and stored frozen for 24 h (Smith *et al.*, 1981). Concentrations of pigments in acetone were measured using a digital Turner Designs fluorometer hat that was calibrated with pure Chl *a* dissolved in 90% acetone (SIGMA Co.). The ratio between pha and total pigment concentrations (Chl *a* + pha) was calculated as an index of phytoplankton health.

Contour plots of biological and physical variables were generated using the inverse distance–weighting algorithm for interpolation of the grid (Jongman *et al.*, 1995). These plots were used to analyse the horizontal spatial distribution patterns of variables.

# RESULTS

## Sea-ice, hydrographic and physicochemical characteristics

The study area is characterized by the seasonal coverage of the sea ice. Sea ice retreats progressively during spring and summer from the northwest to the southeast portion of the area, and at the studied periods the sea-ice edge was located in the southern part of Marguerite Bay. The summers of 1996, 1997 and 1999 were characterized by differences in the maximum extent of the sea-ice coverage during the previous winter and in the timing of the sea-ice retreat from the study area (Fig. 2; Smith and Stammerjohn, 2002). The 1996 summer was preceded by an extended sea-ice coverage, which started to retreat in October and partially covered the study area up to December. The 1997 summer was preceded by a winter with sea-ice coverage near the average for the period 1990–1999, which started to retreat in September, and disappeared from the area by December. The 1999 summer was preceded by low sea-ice coverage, which retreated early in spring and no longer remained in the area by November. Therefore, these summers can be considered as preceded by delayed (1996), average (1997) and advanced (1999) timing of sea-ice melting.

The hydrographic and water physicochemical characteristics were consistent from year to year. A major hydrographic feature detected throughout most of the area was a temperature minimum between 40 and 150 m depth (Fig. 3). This feature corresponds to the WW mass, which in turn corresponds to the Antarctic surface water mass that is restricted to the deep layer during summer (Hofmann *et al.*, 1996). Physicochemical properties in the upper 50 m of the water column (above the WW) showed great spatial variability (Table I). Water temperature and salinity increased gradually from the coast toward open ocean, with the highest degree of change in the zone outlined by Anvers, Renaud and Adelaide Islands, thus evidencing the presence of major differences between coastal and open waters (onshore and offshore from the islands, respectively). In fact, open waters were up to 1.5°C warmer and up to 0.8 psu more saline than those near the coast (Table I). The depth of the UML gradually increased from the coast towards offshore (Fig. 4; Table I). Accordingly, water column vertical stability decreased gradually from the coast to offshore (Table I). Coastal waters had a vertical profile characterized by a steep density gradient with depth (Fig. 3a, d and g), indicating a strong stratification of the water column and an UML shallower than 25 m depth. The density gradient was less pronounced in open waters, and the UML was deeper than 30 m (Fig. 3b, c, e, f, h and i). The UML was included within the euphotic zone at all stations (Fig. 3).

Macronutrient concentrations averaged over the UML were abundant throughout the area (Table I). Concentrations were well above limiting concentrations for phytoplankton growth and never dropped below detectable values.

## Distribution of phytoplankton standing stock

Phytoplankton biomass concentration was variable throughout the area. During the summers studied, phytoplankton C biomass concentrations were higher in coastal waters and steadily decreased towards offshore (Fig. 5a, d and g). More than 70 % of the sampling stations had relatively low phytoplankton concentrations, with less than 100 μg C $L^{-1}$. The highest phytoplankton concentrations were found at Marguerite Bay, reaching 1245, 967 and 1482 μg C $L^{-1}$ during 1996, 1997 and 1999, respectively. Another phytoplankton peak was found south of Anvers Island during the 1996 and 1999 summers, reaching 1618 and 418 μg C $L^{-1}$, respectively (Fig. 5a and g). Cell abundance distribution had also a negative on/offshore gradient during 1997 and 1999 (Fig. 5e and h), whereas during 1996 the highest cell numbers were found at mid-shelf (Fig. 5b). The similarity between the distribution patterns of C biomass and cell abundance for 1997 and 1999 indicates

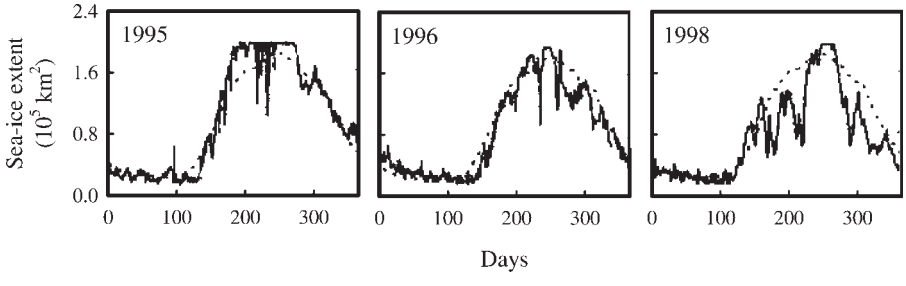


**Fig. 2.** Sea-ice extent in the western Antarctic Peninsula during the years that preceded the summers considered in this study. The dashed line represents the average values for the period between 1990 and 1999. Days from zero (1 January) to 365 (31 December). Adapted from Smith and Stammerjohn (Smith and Stammerjohn, 2001).

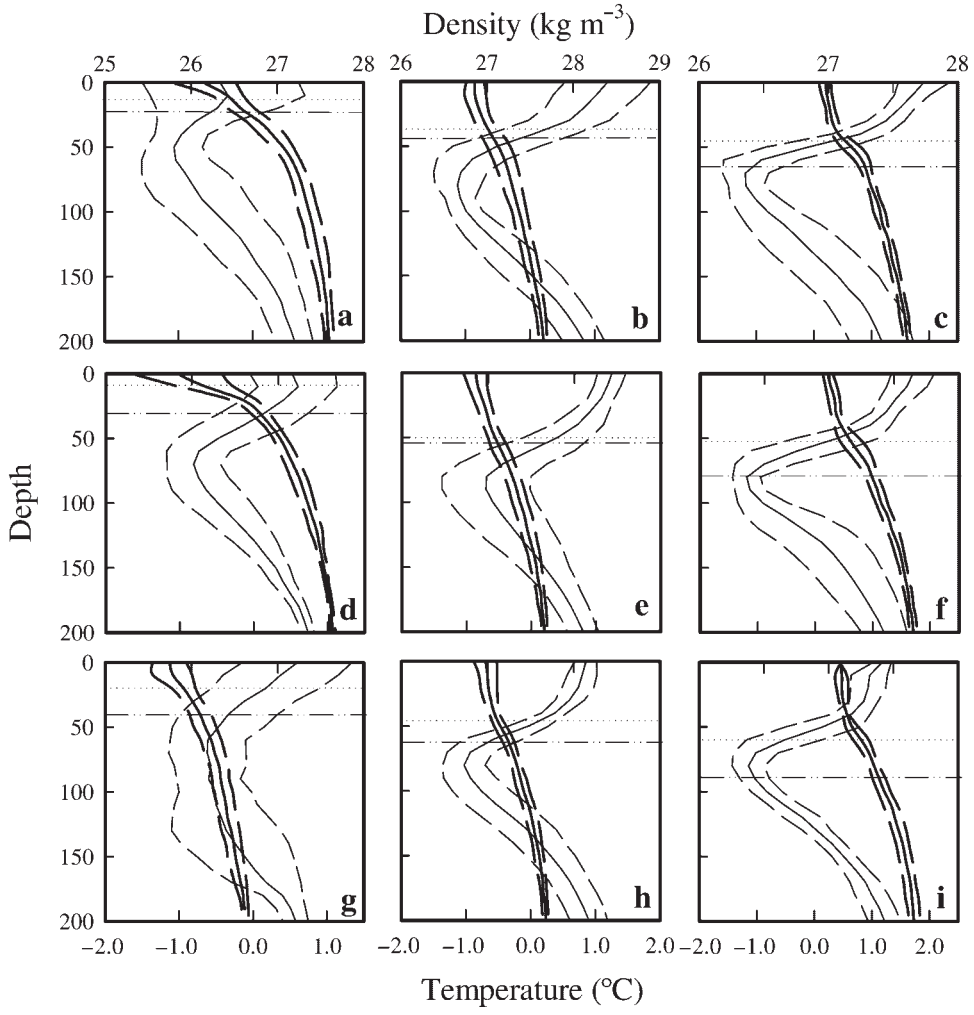


**Fig. 3.** Vertical profiles of water column temperature (thin lines) and sigma-*t* ($\sigma_t$) (thick lines) during (**a**–**c**), Summer 1996; (**d**–**f**) Summer 1997; (**g**–**i**), Summer 1999. Average ± standard deviation in three regions differentiated as in Fig. 7: (**a**), (**d**) and (**g**), coastal region; (**b**), (**e**) and (**h**), mid-shelf region; (**c**), (**f**) and (**i**), oceanic region. Horizontal dotted line, upper mixed layer depth (m$^{-1}$); horizontal dash-dot line, euphotic zone depth (m$^{-1}$). Note differences in scales between plots.

that on/offshore changes in C biomass resulted, at least partially, from changes in cell abundance. In contrast, C biomass and cell abundance distributions did not match for the 1996 summer suggesting that variations in cell size dominated the on/offshore C gradient.

The Chl *a* concentration averaged over the UML also showed an on/offshore gradient (Fig. 5c, f and i), as the one for C biomass. In fact, correlations between Chl *a* and C concentrations were significant ($P < 0.001$) and high ($R^2 = 0.87$, 0.96 and 0.92 for 1996, 1997 and 1999, respectively), indicating a close relationship between these two phytoplankton standing stock estimates. Despite the consistency between C and Chl *a* distribution, the C to Chl *a* ratio showed spatial variability, with open water values twice as high as coastal values (Table II).

Distinct Chl *a* vertical profiles were detected at different stations (Fig. 6), as previously described for the 1997 summer (Garibotti *et al.*, 2003a), evidencing changes in phytoplankton distribution with depth within the area. Based on these differences we delimited three regions named as coastal, mid-shelf and oceanic regions. The coastal region had a surface or near surface Chl *a* maximum and very low concentrations in deeper waters (Fig. 6a, d and g). The mid-shelf region had high Chl *a* concentration in the upper 50 m and a gradual decrease in concentration with depth (Fig. 6b, e and h). The oceanic region had low Chl *a* concentration near surface and higher concentrations between 40 and 100 m depth (Fig. 6c, f and i).

*Table I: Physical and chemical environmental variables during the summer of three different years*

| | Region | Temperature (°C) | Salinity (PSU) | Density (kg $m^{-3}$) | UML depth ($m^{-1}$) | Vertical stability ($10^{-3}$ $m^{-1}$) | Silicate (μM) | Phosphate (μM) | Nitrate plus nitrite (μM) | Ammonium (μM) |
|---|---|---|---|---|---|---|---|---|---|---|
| Summer 1996 | Coastal | −0.41 ± 0.61 | 33.29 ± 0.20 | 26.74 ± 0.14 | 13 ± 11 | 0.55 ± 0.22 | 69.82 ± 12.53 | 1.11 ± 0.53 | 13.86 ± 5.53 | 1.78 ± 0.36 |
| | Mid-shelf | 0.56 ± 0.52 | 33.61 ± 0.16 | 26.95 ± 0.11 | 39 ± 22 | 0.22 ± 0.11 | 64.56 ± 7.64 | 1.63 ± 0.14 | 21.42 ± 1.62 | 2.48 ± 0.96 |
| | Oceanic | 1.21 ± 0.30 | 33.77 ± 0.03 | 27.04 ± 0.04 | 45 ± 4 | 0.15 ± 0.08 | 54.15 ± 11.34 | 1.74 ± 0.15 | 23.63 ± 1.49 | 1.96 ± 0.69 |
| Summer 1997 | Coastal | 0.21 ± 0.48 | 33.14 ± 0.17 | 26.59 ± 0.13 | 10 ± 6 | 0.90 ± 0.41 | 71.51 ± 10.89 | ND | 14.40 ± 7.76 | 2.96 ± 1.28 |
| | Mid-shelf | 0.94 ± 0.23 | 33.64 ± 0.10 | 26.95 ± 0.08 | 49 ± 37 | 0.18 ± 0.12 | 69.96 ± 11.25 | ND | 22.98 ± 3.76 | 2.47 ± 1.09 |
| | Oceanic | 1.25 ± 0.27 | 33.79 ± 0.05 | 27.05 ± 0.04 | 52 ± 9 | 0.12 ± 0.07 | 48.91 ± 11.08 | ND | 25.08 ± 3.08 | 2.04 ± 1.20 |
| Summer 1999 | Coastal | 0.01 ± 0.62 | 33.59 ± 0.16 | 26.97 ± 0.12 | 19 ± 17 | 0.30 ± 0.21 | 55.29 ± 18.16 | 1.39 ± 0.41 | 17.07 ± 7.08 | 2.11 ± 0.92 |
| | Mid-shelf | 0.60 ± 0.20 | 33.73 ± 0.10 | 27.05 ± 0.08 | 46 ± 17 | 0.11 ± 0.07 | 51.08 ± 19.37 | 1.47 ± 0.29 | 19.46 ± 5.42 | 1.92 ± 0.72 |
| | Oceanic | 0.79 ± 0.26 | 33.83 ± 0.03 | 27.12 ± 0.03 | 59 ± 24 | 0.08 ± 0.07 | 40.33 ± 9.92 | 1.51 ± 0.10 | 20.80 ± 2.73 | 1.78 ± 0.41 |

ND, no data; UML, upper mixed layer.

Average ± standard deviation in three regions differentiated within the area according to their vertical distribution of chlorophyll *a* (Chl *a*) as shown in Fig. 7. Values of nutrients are averaged over the upper mixed layer, all other variables are averaged over the upper 50 m of the water column.

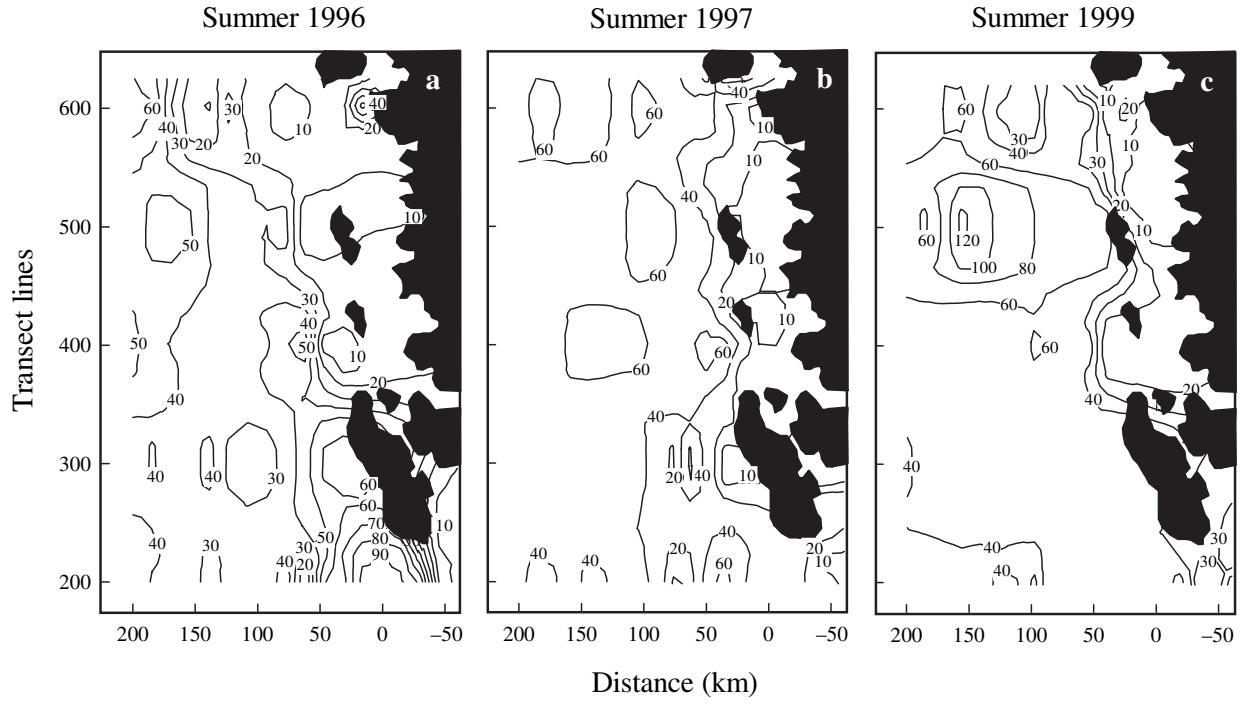


**Fig. 4.** Spatial variability in the upper mixed layer depth ($m^{-1}$) during (**a**) Summer 1996, (**b**) Summer 1997 and (**c**) Summer 1999.

The extents of the coastal, mid-shelf and oceanic regions are shown in Fig. 7. It can be seen that these regions delineate three bands parallel to the coast. The boundary between the coastal and mid-shelf regions was always located near the zone outlined by Anvers, Renaud and Adelaide Islands, whereas the boundary between the mid-shelf and oceanic regions was quite variable from year to year. In fact, the oceanic region comprised the stations located off the continental shelf during 1996 (Fig. 7a), those located on the shelf slope and off the continental shelf during 1997 (Fig. 7b) and those located on the middle portion of the continental shelf, on the shelf slope and off the continental shelf during 1999 (Fig. 7c).

## Phytoplankton characteristics in regions with different Chl *a* vertical profiles

Tables II and III summarize the characteristics of the phytoplankton for each region, delimited according to the Chl *a* vertical profiles. The regions showed differences in phytoplankton biomass concentration (Table II), correlating to the negative on/offshore concentration gradients described previously. In fact, the coastal region accumulated ten times more biomass than the nearby mid-shelf region during the 1996 summer and five times more during the 1997 and 1999 summers. Concentration of phytoplankton biomass in the mid-shelf region was two times higher than in the oceanic region during all three summers. Although in the oceanic region phytoplankton concentrations were low, in comparison to those of the mid-shelf and coastal regions, more than 70% of the integrated water column Chl *a* (0–200 m) was concentrated in the DCM layer (Table IV).

In the coastal region, the high phytoplankton concentration was mostly due to the accumulation of large cells, as evidenced by the high average C and Chl *a* concentration per cell (Table II). Diatoms dominated this region in all three summers, representing more than 69% of total biomass (Table III). The diatoms *Eucampia antarctica* and *Odontella weissflogii* contributed the greater part of the C concentration in this region in 1996 and 1997, representing 47 and 29%, respectively, of diatom C in 1996 and 18 and 55% in 1997 (Appendix 1). Instead, the diatom *Coscinodiscus bouvet* dominated this region during 1999, contributing 62% of diatom C. Also *Chaetoceros socialis* was characteristic of this region, contributing 29, 55 and 62% of diatom abundance during 1996, 1997 and 1999, respectively. However, due to its small biovolume, it contributed a relatively small biomass concentration (less than 17% of diatom C).

In the mid-shelf and oceanic regions, the concentrations of C and Chl *a* per cell were similar, indicating that biomass differences between these regions were mostly

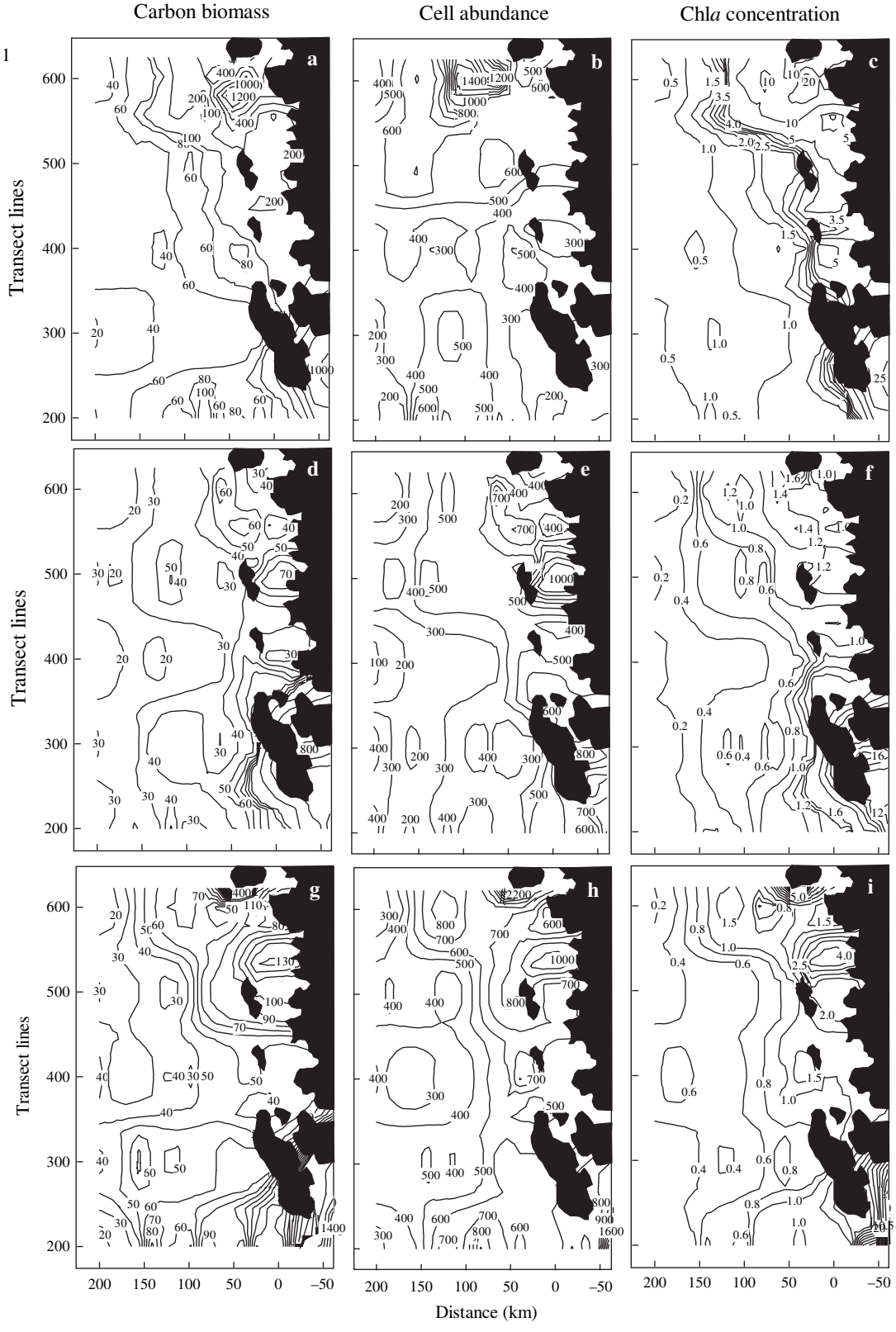


**Fig. 5.** Phytoplankton standing stock distribution during (**a**–**c**), Summer 1996; (**d**–**f**), Summer 1997; (**g**–**i**), Summer 1999. (**a**), (**d**) and (**g**), carbon biomass concentration (μg C $L^{-1}$); (**b**), (**e**) and (**h**), cell abundance ($10^4$ cell $L^{-1}$); (**c**), (**f**) and (**i**), chlorophyll *a* (Chl *a*) concentration averaged over the upper mixed layer (UML) (μg Chl *a* $L^{-1}$).

*Table II: Phytoplankton standing stock in three regions distinguished within the area*

| | Region | Carbon biomass ($\mu g\ C\ L^{-1}$) | Cell abundance ($10^4$ cell $L^{-1}$) | Chlorophyll *a* ($\mu g\ L^{-1}$) | Carbon/ chlorophyll *a* | Carbon per cell ($\mu g\ C\ 10^{-4}$ $cell^{-1}$) | Chlorophyll *a* per cell ($pg\ cell^{-1}$) | Phaeopigment/ total pigment |
|---|---|---|---|---|---|---|---|---|
| Summer 1996 | Coastal | 621 ± 438 | 530 ± 321 | 13.88 ± 7.38 | 43.5 ± 13.9 | 1.61 ± 1.34 | 3.6 ± 3.1 | 6.56 ± 5.18 |
| | Mid-shelf | 62 ± 25 | 458 ± 154 | 1.07 ± 0.48 | 66.5 ± 25.7 | 0.15 ± 0.08 | 0.3 ± 0.2 | 14.69 ± 10.61 |
| | Oceanic | 40 ± 16 | 347 ± 163 | 0.47 ± 0.23 | 90.8 ± 52.2 | 0.14 ± 0.09 | 0.0 ± 0.2 | 12.22 ± 8.87 |
| Summer 1997 | Coastal | 233 ± 296 | 631 ± 225 | 4.38 ± 5.33 | 49.5 ± 20.0 | 0.33 ± 0.37 | 0.7 ± 2.2 | 8.48 ± 4.10 |
| | Mid-shelf | 42 ± 17 | 406 ± 133 | 0.92 ± 0.45 | 51.9 ± 23.8 | 0.10 ± 0.03 | 0.2 ± 0.1 | 8.66 ± 5.06 |
| | Oceanic | 25 ± 11 | 262 ± 121 | 0.22 ± 0.13 | 156.0 ± 120.9 | 0.10 ± 0.04 | 0.1 ± 0.1 | 9.83 ± 7.29 |
| Summer 1999 | Coastal | 334 ± 485 | 979 ± 471 | 5.29 ± 5.87 | 54.1 ± 18.9 | 0.29 ± 0.36 | 0.5 ± 0.4 | 11.54 ± 13.55 |
| | Mid-shelf | 68 ± 27 | 645 ± 131 | 0.94 ± 0.39 | 80.3 ± 30.9 | 0.11 ± 0.04 | 0.1 ± 0.0 | 9.33 ± 4.32 |
| | Oceanic | 34 ± 15 | 371 ± 89 | 0.42 ± 0.17 | 91.5 ± 46.8 | 0.09 ± 0.03 | 0.1 ± 0.1 | 15.29 ± 4.44 |

Regions as in Fig. 7.

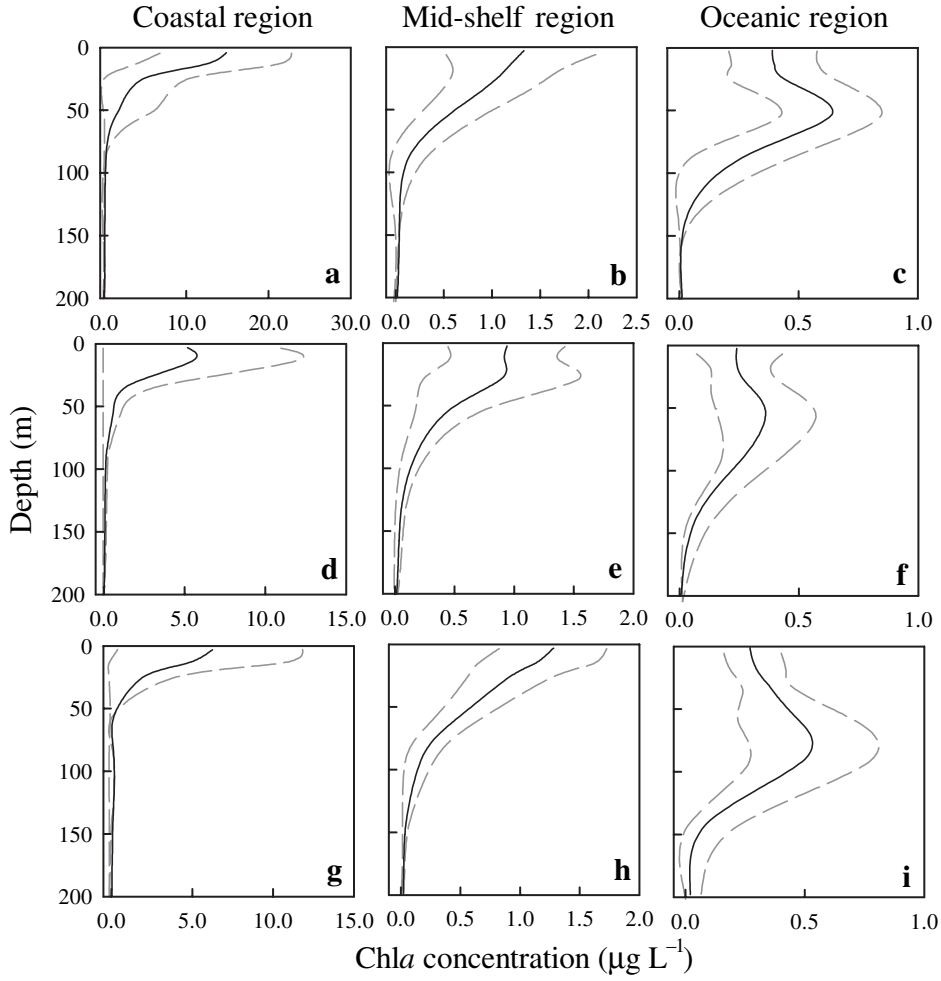


**Fig. 6.** Chlorophyll *a* (Chl *a*) vertical profiles during (**a**–**c**), Summer 1996; (**d**–**f**), Summer 1997; (**g**–**i**), Summer 1999. Average ± standard deviation in three regions differentiated as in Fig. 7: (**a**), (**d**) and (**g**), coastal region; (**b**), (**e**) and (**h**), mid-shelf region; (**c**), (**f**) and (**i**), oceanic region. Note differences in scales between plots.

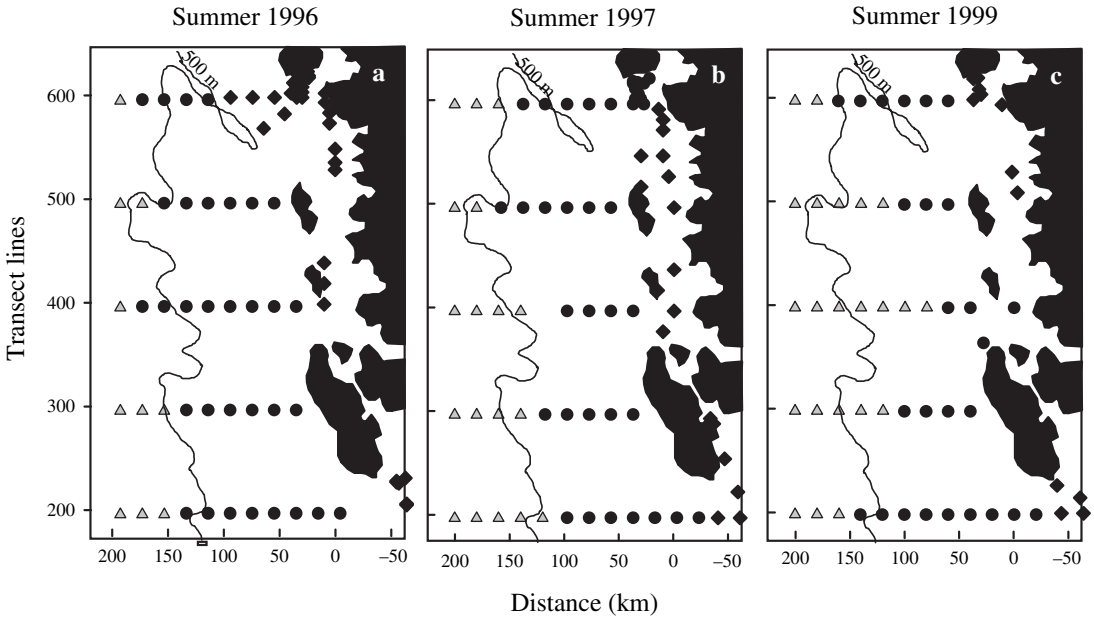


**Fig. 7.** Regions differentiated within the area according to differences in their phytoplankton vertical distribution pattern: ◆, coastal region; •, mid-shelf region; Δ, external region. (**a**) Summer 1996, (**b**) Summer 1997 and (**c**) Summer 1999. The 500-m isobath represents the continental shelf slope.

*Table III: Phytoflagellates and diatoms in three regions distinguished within the area*

| | Region | Phytoflagellate biomass (μg C $L^{-1}$) | Phytoflagellate cells ($10^4$ cell $L^{-1}$) | Diatom biomass (μg C $L^{-1}$) | Diatom cells ($10^4$ cell $L^{-1}$) | % biomass by diatoms | % cells by diatom |
|---|---|---|---|---|---|---|---|
| Summer 1996 | Coastal | 58 ± 65 | 438 ± 329 | 562 ± 461 | 91 ± 49 | 91 | 17 |
| | Mid-shelf | 43 ± 14 | 392 ± 144 | 18 ± 16 | 66 ± 28 | 30 | 14 |
| | Oceanic | 31 ± 14 | 319 ± 156 | 9 ± 5 | 28 ± 12 | 23 | 8 |
| Summer 1997 | Coastal | 53 ± 27 | 571 ± 205 | 179 ± 275 | 60 ± 102 | 77 | 10 |
| | Mid-shelf | 35 ± 14 | 395 ± 131 | 7 ± 7 | 11 ± 14 | 17 | 3 |
| | Oceanic | 19 ± 8 | 248 ± 119 | 6 ± 5 | 14 ± 11 | 25 | 5 |
| Summer 1999 | Coastal | 102 ± 99 | 883 ± 473 | 231 ± 487 | 96 ± 164 | 69 | 10 |
| | Mid-shelf | 52 ± 20 | 583 ± 142 | 16 ± 16 | 63 ± 41 | 23 | 10 |
| | Oceanic | 17 ± 7 | 292 ± 76 | 17 ± 11 | 79 ± 35 | 51 | 21 |

Regions as in Fig. 7.

*Table IV: Phytoplankton characteristics in the deep chlorophyll a (Chl a) maximum layer in the oceanic region*

| | Integrated Chl *a* (mg $m^{-2}$) | % Chl *a* in DCM layer | Maximum Chl *a* (μg $L^{-1}$) | Depth of the Chl *a* maximum ($m^{-1}$) |
|---|---|---|---|---|
| Summer 1996 | 48.65 ± 12.89 | 75 ± 8 | 0.73 ± 0.20 | 54 ± 14 |
| Summer 1997 | 35.06 ± 10.64 | 71 ± 10 | 0.43 ± 0.19 | 69 ± 18 |
| Summer 1999 | 54.33 ± 21.03 | 72 ± 15 | 0.65 ± 0.23 | 72 ± 27 |

DCM layer, deep Chl *a* maximum layer.

due to the reduction of cell number towards offshore (Table II). Phytoplankton abundance and biomass were dominated by phytoflagellates in both regions (Table III). However, during 1997 and 1999 an increase in the relative abundance and biomass of diatoms was found in the oceanic region, in comparison with the lower diatom relative concentrations present in the mid-shelf region (Table III). This higher concentration of diatoms in the oceanic region was mainly the result of the accumulation of small specimens (<10 μm) of three species of the genus *Fragilariopsis*, *F. curta*, *F. pseudonana* and *F. cylindrus* (Appendix 1). These species represented 88% of diatom abundance during both summers and 21 and 51% of the diatom C during 1997 and 1999, respectively. In addition, the microdiatom *Corethron pennatum* contributed a relatively high proportion of C biomass in this region (42 and 11% of diatom C during 1997 and 1999, respectively), although its concentration was lower than in the mid-shelf region (Appendix 1).

## DISCUSSION

### Phytoplankton distribution across the study area

The consideration that the Southern Ocean is a high-nutrient, low-chlorophyll (HNLC) region, with increased phytoplankton biomass associated only to frontal, coastal or ice-edge zones, is now well accepted (Sullivan *et al.*, 1993; Marchant and Murphy, 1994; Rodríguez *et al.*, 2002). Our results for the western Antarctic Peninsula agree with this paradigm. We found relatively low phytoplankton biomass throughout most of the study area, with higher concentrations near the coast, and distinct phytoplankton blooms at Marguerite Bay associated with the ice edge (Fig. 5a, d and g). Thus, the influence of two hydrographic features on phytoplankton distribution can be recognized: proximity to the coast and to the ice edge. These results suggest the combination, within the study area, of two functional zones *sensu* Tréguer and Jacques (Tréguer and Jacques, 1992), the Coastal and Continental Shelf Zone and the Seasonal Ice Zone.

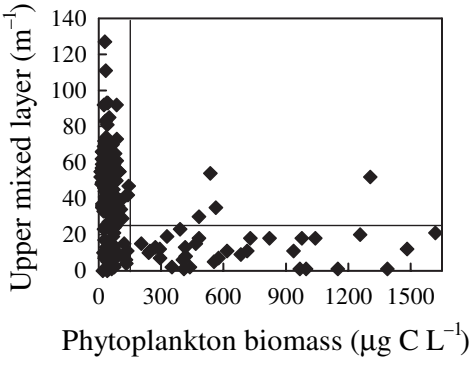


**Fig. 8.** Relationship between phytoplankton carbon biomass and upper mixed layer depth. The horizontal line indicates the 25 m depth and the vertical line the 150 μg C L$^{-1}$.

The spatial distribution of the phytoplankton C biomass consistently showed a conspicuous negative on/offshore gradient, coinciding with a similar gradient in Chl *a* (Fig. 5). This suggests that Chl *a* concentration, which is the manner in which phytoplankton standing stock is usually measured in field studies, is a good estimator of phytoplankton biomass. However, C to Chl *a* ratios varied across the area (Table II), with the high-biomass assemblage (i.e. coastal region) having lower ratios than the low-biomass assemblages (i.e. mid-shelf and oceanic regions). Similar differences between low- and high-biomass assemblages have been determined for other areas of the Southern Ocean (Hewes *et al.*, 1990; Villafañe *et al.*, 1993; Robins *et al.*, 1995), suggesting the generality of this finding for the Antarctic phytoplankton. This result is of utmost importance for studies estimating phytoplankton biomass from ocean colour satellite images.

The highest degree of change in the C on/offshore gradient was found along the boundary between the coastal and mid-shelf regions (Fig. 5a, d and g), indicating major differences between the phytoplankton standing stock in coastal versus open waters of the continental shelf. This boundary was outlined by the Anvers, Renaud and Adelaide Islands, suggesting that their presence generates sheltered conditions onshore, favorable for phytoplankton accumulation. In fact, it has been previously demonstrated for the area that the on/offshore changes in phytoplankton concentration were closely related to the vertical stability of the water column (Garibotti *et al.*, 2003a). Further support to this relationship is provided here since, as shown in Fig. 8, concentrations of phytoplankton higher than 150 μg C L$^{-1}$ accumulated almost exclusively at stations with an UML shallower than 25 m depth, whereas stations with deeper UML presented low C biomass concentrations. Thus, vertical mixing appears as a primary mechanism regulating phytoplankton concentration in surface waters, and the reduction of biomass from the coast towards open ocean can be attributed to the on/offshore gradient in the UML depth (Fig. 4). Frequently, in the Southern Ocean, elevated phytoplankton concentration coincides with a shallow mixed layer (Mitchell and Holm-Hansen, 1991; Helbling *et al.*, 1995; Moline and Prézelin, 1996). This feature has been associated with the fact that restricted vertical mixing may prevent cell sedimentation, allowing cells to remain in the upper water column, under favorable light conditions (Smith

and Sakshaug, 1990; Mitchell and Holm-Hansen, 1991). The same dynamics likely explains the distribution of phytoplankton concentration we found in our area.

The finding of a similar on/offshore gradient of C biomass during all the summers studied demonstrates that the phytoplankton distribution is stable from year to year. This result agrees with the Chl *a* gradients described for ten consecutive summers by Smith *et al.* (Smith *et al.*, 2001). Even when these previous results could suggest that summer phytoplankton remains steady from year to year, our results also showed differences among years in other aspects of the phytoplankton structure (Tables II and III). Particularly different was the 1996 summer, which exhibited the steepest C on/offshore gradient, with 10-fold more C found in the coastal region than in the mid-shelf region (Table II). We determined that accumulation of phytoplankton biomass in the coastal region was due to the presence of large cells (Table II; see the C and Chl *a* concentration per cell) and that these cells were diatoms in a bloom stage (Table III; Appendix 1). In contrast, during 1997 and 1999, the concentration of C found in the coastal region was only 5-fold higher than in the mid-shelf region (Table II), and the on/offshore variations in cell size were less marked, indicating that the biomass gradient was mainly due to cell abundance changes (Table II). Moreover, during these summers the concentration of diatoms in the coastal region was much lower than during 1996 (3 and 2.5 times lower during 1997 and 1999, respectively; Table III). Therefore, we conclude that the interannual variability observed in the magnitude of the C on/offshore gradient was mostly the result of variations in phytoplankton species composition.

Previously, Smith *et al.* (Smith *et al.*, 1998) evidenced that interannual variations in the magnitude of the on/offshore Chl *a* gradient were closely related to variations in the sea-ice extent during the previous winters. Our results agree with this observation given that 1996 was preceded by an extended sea-ice coverage (Fig. 2a), whereas 1997 and 1999 were preceded by a lower sea-ice coverage (Fig. 2b and c). Furthermore, we can conclude that the relationship between the gradient in phytoplankton concentration and the sea ice is due to year-to-year differences in the concentration of diatom blooms.

The relationship between sea ice and phytoplankton composition is explained by the fact that diatom blooms can be associated with the retreating sea ice. In fact, it is known that sea-ice melting releases epontic diatoms to the water column, which may act as inocula of diatom blooms (Garrison and Buck, 1985). Moreover, freshwater input to the water column from sea-ice melting causes stratification of the water column, as seen in the coastal region (Fig. 4), a feature that favours the blooming of diatoms by allowing cells to remain under a propitious light regime. Both effects contribute to explain the concentration of diatoms in the coastal region since, in our area, sea ice retreats progressively from offshore to inshore and consequently had recently disappeared from the coastal region at the period of sampling.

A further question that arises now is how interannual variability in sea ice influences summer phytoplankton, determining the year-to-year variations observed in its structure. An answer can be proposed considering that sea-ice showed year-to-year variations in (i) the maximum extent during the preceding winter and (ii) the timing of retreat from the area (Fig. 2). The possible phytoplankton dynamics associated with these two features is as follows:

(i) As a consequence of the high (low) sea-ice extent during winter, a higher (lower) quantity of freshwater is released to the water column when sea ice melts (Smith and Nelson, 1986; Fischer *et al.*, 2002). Therefore, a stronger (weaker) water column stratification would occur during summer, regulating phytoplankton growth and concentration. However, no significant differences ($P > 0.05$) were found between years in the depth of the UML in the coastal region (Fig. 4 and Table I), suggesting that this is unlikely to be a key factor to explain the observed interannual variability in phytoplankton composition and concentration in this region.

(ii) The late (early) retreat of sea ice during 1996 (1997 and 1999) implies that sea ice had disappeared from the coastal region a relatively short (long) time before the sampling period. This must have favoured the blooming of diatoms in the coastal region at the time of sampling during 1996. Instead, diatom blooming must have started earlier during 1997 and 1999 and must have been on a demise stage or dissipated at the time of sampling, determining the lower concentration of diatoms observed. In fact, the analysis of pha to pigment ratios is consistent with these hypotheses, showing a lower ratio during 1996 than during 1997 and 1999 (Table III). This indicates that the diatom assemblage of the former year was healthier than that of the latter one. Therefore, we conclude that the relationship between interannual variability in sea ice and phytoplankton standing stock was likely associated with year-to-year variations in the timing of the sea-ice retreat.

## Possible impact of the phytoplankton variability observed on the upper trophic levels

The close linkage between interannual sea-ice variability and primary producers is of concern when considering

that a warming trend has been detected in the western Antarctic Peninsula, with a negative impact on sea-ice extent during winter and favouring an earlier sea-ice retreat from the area (Smith and Stammerjohn, 2002). As phytoplankton constitutes the base of the trophic chain in the Southern Ocean, its variability is fundamental for the functioning of the ecosystem. In fact, the observed year-to-year variations in phytoplankton composition and concentration (Tables II and III) can be considered as changes in the quality and quantity of food available for the upper trophic levels. For example, since krill reproduction depends on food availability during the reproductive season (Quetin and Ross, 2001), the higher (lower) autotrophic C concentration found during 1996 (1997 and 1999) must have enhanced (diminished) krill recruitment. Moreover, given that krill feed selectively on large diatoms (Haberman *et al.*, 2003), the higher (lower) concentration of diatoms during 1996 (1997 and 1999) must have been an additional parameter regulating krill recruitment. These hypotheses coincide with the results of Quetin and Ross (Quetin and Ross, 2003) for the study area, who demonstrated that krill recruitment was strong during the 1996 summer and weak during the 1997 and 1999 summers. Therefore, crossing our results with theirs, we establish a further evidence stating that interannual variability in phytoplankton standing stock and composition is closely related to variations in krill reproduction. Since phytoplankton and krill are two of the main components at the base of the food chain, we conclude that sea-ice changes due to global warming will certainly affect the dynamics of the entire trophic web in the Southern Ocean.

## Variability in phytoplankton vertical distribution

A relevant characteristic detected within the study area was the variability in the Chl *a* vertical distribution pattern (Figs 6 and 7). Antarctic phytoplankton is usually described as concentrated in the upper portion of the water column (Holm-Hansen and Mitchell, 1991; Helbling *et al.*, 1995; Smith *et al.*, 1996), coinciding with the Chl *a* distribution profiles we found in the coastal and mid-shelf regions (Fig. 6). However, our data indicate that a DCM layer, between 40 and 100 m depth, is a recurrent feature within the oceanic region (Fig. 6c, f and i). Moreover, in this region, more than 70% of the Chl *a* concentration in the water column was estimated to be in the deep layer (Table IV). This fact allows us to hypothesize that the deep accumulation of phytoplankton may be relevant for the functioning of the pelagic ecosystem. Thus, the question that arises is which is the mechanism that drives the accumulation of phytoplankton in a deep layer? Below we analyse this question considering the variability in environmental conditions throughout the area.

For other marine environments it is generally considered that subsurface Chl *a* maxima are the result of macronutrient exhaustion in the upper layer, which limits phytoplankton growth (Gieskes and Kraay, 1986; Letelier *et al.*, 1993; Barlow *et al.*, 1997; Richardson *et al.*, 2003). However, in our area, macronutrient concentrations were never depleted below 20 μM silicate, 15 μM nitrate plus nitrite, 1 μM phosphate and 1 μM ammonium, values that exceed the concentrations known to be limiting for phytoplankton growth. Thus, macronutrient concentrations could unlikely account for the observed DCM layer. In fact, Antarctic phytoplankton usually do not completely consume the macronutrient stock (Mengesha *et al.*, 1998; Castro *et al.*, 2002). Therefore, we conclude that the occurrence of a DCM layer in the Southern Ocean cannot be ascribed to the same factor that regulates its occurrence in other oceans.

During the last decade some evidence has accumulated to indicate that iron concentration might limit the growth of the Antarctic phytoplankton (Martin *et al.*, 1990; de Baar *et al.*, 1995). At the Drake Passage, Holm-Hansen *et al.* (Holm-Hansen *et al.*, 1994) associated the subsurface Chl *a* maxima with the presence of the WW mass and hypothesized that low concentration of iron limited phytoplankton growth in the upper water column, whereas higher concentration in the WW favoured phytoplankton growth in the deeper layer. In our area, Figs 3 and 6 show that the subsurface Chl *a* maxima were within the WW mass layer. Moreover, they were located in the portion of the WW that can be predicted to be in the euphotic zone, indicating that light was enough for cells to grow at depth. In fact, the relatively low pha to pigment ratio in the oceanic region suggests that the phytoplankton community at the Chl *a* maxima is a healthy one. Thus, we assume that iron concentration might have been also the key factor regulating the occurrence of a DCM layer in the oceanic region, as already reported for January 1997 (Garibotti *et al.*, 2003a).

Microscopic analysis of phytoplankton composition of samples taken at 50% PAR depth showed that, during the 1997 and 1999 summers, the oceanic region was occupied by a phytoplankton assemblage characterized by high diatom concentration (Table III; see the increase in the relative abundance and biomass of diatoms in the oceanic region, in comparison to the mid-shelf region). Although no relative increase in diatom concentration was observed in 1996, it should be noted that the offshore diatom concentration was similar to those found for the other 2 years (Table III). Furthermore, during this summer an increase in diatom concentration in the oceanic region could have been obscured by the high diatom blooms from the coastal

and mid-shelf regions (Table III). In addition, an increased diatom concentration in offshore waters was also detected in our area by Prézelin *et al.* (Prézelin *et al.*, 2000) during the 1993 summer. Their plots showed higher Chl *a* and fucoxanthin (diagnostic pigment of diatoms) at around 50 m depth, indicating that the diatom-enriched assemblage they found was also restricted to the WW mass. All these results strengthen the hypothesis that iron concentration might be controlling the phytoplankton vertical distribution in offshore waters, since it has been previously demonstrated that diatoms show a great increase in biomass with iron supply (Buma *et al.*, 1991; Fitzwater *et al.*, 2000). Thus, it can be expected that an increased concentration of iron in the WW would favour the growth of diatoms over other phytoplankton groups.

Two different mechanisms were previously invoked to explain the possible limitation of iron from the upper mixed layer in the oceanic region (Garibotti *et al.*, 2003a): (i) iron concentration was scarce due to the distance from the continent, a known source of iron and (ii) iron stock was depleted during summer due to phytoplankton consumption during early spring. Although these two mechanisms do not exclude each other, the presence of the DCM layer over the shelf in 1999 (Fig. 7c) suggests that the second one might be more suitable to explain this feature, as analysed below.

In our area, sea ice retreats progressively from north to south and from offshore to inshore (Smith and Stammerjohn, 2001). Consequently, during spring, phytoplankton growth starts earlier in offshore than in inshore waters. Indeed, ocean colour satellite imagery from late 1997 to the present (Smith *et al.*, 2001) is consistent with this interpretation. The occurrence of an early algal bloom associated with the sea-ice edge, and further phytoplankton growth during a long period of time in the oceanic region, may well deplete the iron stock available in the mixed layer, to finally limit phytoplankton growth in the upper mixed layer during summer. As a consequence, summer phytoplankton are restricted to grow in the relatively iron-rich WW. In contrast, summer phytoplankton can even grow at the surface in inshore waters, as observed in the coastal and mid-shelf regions (Fig. 6), given that iron stock might be still high in the mixed layer, due to the shorter length of the growth season.

Our results show that the extent of the oceanic region was highly variable over all three studied years (Fig. 7). If the mechanism we propose is valid, this variability must be related to the length of time during which phytoplankton has been growing in the area. In turn, this is regulated by the timing of sea-ice retreat from the area. For example, the early sea-ice melting during 1999 (Fig. 2c) allowed the initiation of phytoplankton growth during early spring in a large portion of the study area, with the consequent iron depletion near surface, and concentration of phytoplankton in a deeper layer in a large region during summer (Fig. 7c). In contrast, due to the late sea-ice retreat during 1996 (Fig. 2a), phytoplankton had been growing only for a short period of time in most of the area at the moment of sampling, which determined a reduced region with a DCM layer (Fig. 7a).

In the *Introduction* section we have already described that similar subsurface Chl *a* maxima were reported for other areas as well (Yamaguchi *et al.*, 1985; Holm-Hansen *et al.*, 1994, 1997; Berdalet *et al.*, 1997; Fiala *et al.*, 1998; Gilpin *et al.*, 2002; Korb and Whitehouse, 2004), suggesting that this pattern may be widespread in the Southern Ocean. A compilation of these results shows high concordance with ours, as detailed below:

(i) The deep Chl *a* peaks found in other areas of the Southern Ocean were always within the WW layer (Yamaguchi *et al.*, 1985; Fiala *et al.*, 1998; Gilpin *et al.*, 2002) and were also due to a high diatom concentration in the SIZ of the Indian sector of the Southern Ocean (Fiala *et al.*, 1998).

(ii) The deep Chl *a* peaks found in the Indian sector of the Southern Ocean occurred during late summer (Fiala *et al.*, 1998), whereas, during spring, when part of the area was still partially covered by sea ice, Chl *a* was concentrated in the upper portion of the water column (Fiala *et al.*, 2002). Thus, phytoplankton was restricted to deep waters during summer, after having been growing in near surface waters for a long period.

(iii) Earlier data related to iron concentrations at different periods of the year show that iron stock is high in Antarctic surface waters at the beginning of the growing season, and greatly decreased during the spring-summer transition, to be depleted by the end of the summer (de Baar *et al.*, 1995; Measures and Vink, 2001; Moore and Abbott, 2002). These results are concordant and support the hypothesis that phytoplankton growth is limited by the depletion of iron during summer.

We conclude that all these findings for other areas of the Southern Ocean represent a further support to the mechanism we proposed as regulating phytoplankton concentration in a deep layer in offshore waters of our study area. Moreover, the similarity regarding the conditions in which deep Chl *a* peaks were found in our and in other areas allows us to suggest that the mechanism proposed here may be applicable elsewhere in the Southern Ocean.

We consider that this pattern deserves further study. In particular, to validate our hypothesis, future studies should be based on the analysis of the seasonal evolution of phytoplankton on shelf waters and on *in situ* measurements of iron concentration changes during the transition from spring to summer. Moreover, due to the

# Appendix 1

*Composition of diatom communities*

| Coastal region | Cells ($10^2$ cell $L^{-1}$) | Carbon (μg C $L^{-1}$) | Mid-shelf region | Cells ($10^2$ cell $L^{-1}$) | Carbon (μg C $L^{-1}$) | Oceanic region | Cells ($10^2$ cell $L^{-1}$) | Carbon (μg C $L^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| Summer 1996 | | | | | | | | |
| *Chaetoceros neglectum* | 12 ± 49 | 0.2 ± 0.9 | *Actinocyclus actinochilus* | 8 ± 24 | 2.3 ± 6.9 | *Chaetoceros* sp. | 8 ± 24 | 0.0 ± 0.1 |
| *Chaetoceros socialis* | 2662 ± 1054 | 9.9 ± 4.0 | *Cylindroteca closterium* | 110 ± 97 | 0.2 ± 0.1 | *Chaetoceros peruvianus* | 8 ± 24 | 0.1 ± 0.3 |
| *Chaetoceros peruvianus* | 38 ± 105 | 0.5 ± 1.5 | Small *Fragilariopsis* spp.[a] | 6118 ± 2575 | 5.6 ± 2.4 | *Cylindroteca closterium* | 56 ± 42 | 0.0 ± 0.0 |
| *Corethron pennatum* | 19 ± 54 | 2.2 ± 6.1 | *Fragilariopsis curta* | 42 ± 45 | 0.5 ± 0.5 | Small *Fragilariopsis* spp.[a] | 2260 ± 969 | 2.1 ± 0.9 |
| *Coscinodiscus bouvet* | 69 ± 54 | 61.0 ± 47.5 | *Fragilariopsis separanda* | 5 ± 19 | 0.1 ± 0.2 | *Fragilariopsis curta* | 75 ± 70 | 0.9 ± 0.8 |
| *Cylindroteca closterium* | 222 ± 104 | 0.5 ± 0.2 | *Fragilariopsis* sp. | 26 ± 35 | 0.5 ± 0.8 | *Fragilariopsis separanda* | 25 ± 53 | 0.3 ± 0.5 |
| *Eucampia antarctica* | 1438 ± 1524 | 262.7 ± 278.4 | *Nitzschia* sp. | 5 ± 14 | 0.0 ± 0.0 | *Fragilariopsis* sp. | 187 ± 175 | 1.9 ± 1.8 |
| Small *Fragilariopsis* spp.[a] | 2790 ± 2269 | 2.5 ± 2.1 | *Proboscia* sp. | 2 ± 13 | 0.2 ± 1.0 | *Nitzschia* sp. | 60 ± 99 | 0.2 ± 0.4 |
| *Fragilariopsis curta* | 44 ± 47 | 0.9 ± 1.0 | *Thalassiosira* spp. | 172 ± 215 | 6.2 ± 7.8 | *Thalassiosira* spp. | 66 ± 56 | 2.4 ± 2.0 |
| *Fragilariopsis cylindrus* | 14 ± 47 | 0.2 ± 0.6 | Unidentified pennal | 102 ± 67 | 2.9 ± 1.7 | *Thalassiothrix* sp. | 8 ± 24 | 0.6 ± 1.8 |
| *Fragilariopsis separanda* | 6 ± 20 | 0.1 ± 0.2 | | | | Unidentified pennal | 24 ± 37 | 0.6 ± 0.8 |
| *Fragilariopsis* sp. | 318 ± 200 | 7.2 ± 4.5 | | | | | | |
| *Navicula* sp. | 9 ± 39 | 0.1 ± 0.3 | | | | | | |
| *Nitzschia* sp. | 151 ± 161 | 0.4 ± 0.4 | | | | | | |
| *Odontella weisflogii* | 299 ± 378 | 162.6 ± 205.6 | | | | | | |
| *Proboscia* sp. | 75 ± 98 | 5.5 ± 7.2 | | | | | | |
| *Rhizosolenia* sp. | 14 ± 69 | 0.8 ± 3.9 | | | | | | |
| *Thalassiosira* spp. | 756 ± 493 | 41.3 ± 33.0 | | | | | | |
| Unidentified pennal | 179 ± 107 | 3.9 ± 1.8 | | | | | | |
| Summer 1997 | | | | | | | | |
| *Chaetoceros atlanticus* | 65 ± 165 | 1.2 ± 3.0 | *Chaetoceros* sp. | 4 ± 13 | 0.0 ± 0.0 | *Chaetoceros* sp. | 8 ± 24 | 0.0 ± 0.1 |
| *Chaetoceros dichaeta* | 107 ± 277 | 1.9 ± 5.0 | *Coconeis* sp. | 1 ± 9 | 0.0 ± 0.1 | *Corethron pennatum* | 23 ± 42 | 2.7 ± 4.7 |
| *Chaetoceros flexuosum* | 72 ± 185 | 1.0 ± 2.6 | *Corethron pennatum* | 31 ± 54 | 3.5 ± 6.1 | Small *Fragilariopsis* spp.[a] | 1229 ± 1054 | 1.3 ± 1.1 |
| *Chaetoceros socialis* | 3298 ± 2421 | 8.1 ± 6.0 | Small *Fragilariopsis* spp.[a] | 919 ± 1334 | 1.0 ± 1.5 | *Fragilariopsis curta* | 7 ± 19 | 0.1 ± 0.2 |
| *Corethron pennatum* | 28 ± 30 | 3.2 ± 3.4 | *Fragilariopsis curta* | 3 ± 14 | 0.0 ± 0.1 | *Fragilariopsis separanda* | 12 ± 29 | 0.1 ± 0.3 |
| *Eucampia antarctica* | 143 ± 270 | 32.0 ± 60.3 | *Fragilariopsis cylindrus* | 1 ± 9 | 0.0 ± 0.1 | *Fragilariopsis* sp. | 22 ± 66 | 0.2 ± 0.6 |
| Small *Fragilariopsis* spp.[a] | 706 ± 993 | 0.8 ± 1.1 | *Fragilariopsis separanda* | 2 ± 10 | 0.0 ± 0.1 | *Nitzschia* spp. | 77 ± 56 | 0.8 ± 0.6 |
| *Fragilariopsis cylindrus* | 3 ± 12 | 0.0 ± 0.1 | *Fragilariopsis* sp. | 6 ± 35 | 0.1 ± 0.5 | *Thalassiosira* spp. | 15 ± 21 | 1.0 ± 1.4 |
| *Fragilariopsis separanda* | 8 ± 19 | 0.1 ± 0.2 | *Nitzschia* spp. | 99 ± 81 | 1.1 ± 0.8 | Unidentified pennal | 8 ± 17 | 0.0 ± 0.1 |
| *Fragilariopsis* sp. | 464 ± 319 | 6.9 ± 4.9 | *Pseudonitschia* sp. | 19 ± 69 | 0.0 ± 0.1 | | | |
| *Licmophora sp.* | 3 ± 12 | 0.0 ± 0.1 | *Thalassiosira* spp. | 20 ± 21 | 1.0 ± 1.5 | | | |
| *Nitzschia* spp. | 329 ± 192 | 4.7 ± 2.7 | Unidentified pennal | 7 ± 11 | 0.2 ± 0.3 | | | |

*(continued)*

*Continued*

| Coastal region | Cells ($10^2$ cell $L^{-1}$) | Carbon ($\mu g$ C $L^{-1}$) | Mid-shelf region | Cells ($10^2$ cell $L^{-1}$) | Carbon ($\mu g$ C $L^{-1}$) | Oceanic region | Cells ($10^2$ cell $L^{-1}$) | Carbon ($\mu g$ C $L^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| *Odontella weisflogii* | 176 ± 299 | 99.3 ± 168.6 | | | | | | |
| *Proboscia* sp. | 21 ± 37 | 1.1 ± 1.9 | | | | | | |
| *Pseudonitschia* sp. | 477 ± 1137 | 0.8 ± 2.0 | | | | | | |
| *Thalassiosira* spp. | 72 ± 53 | 17.1 ± 14.1 | | | | | | |
| *Trichotoxon* sp. | 2 ± 9 | 0.1 ± 0.6 | | | | | | |
| Unidentified pennal | 63 ± 33 | 0.8 ± 0.4 | | | | | | |
| Summer 1999 | | | | | | | | |
| *Chaetoceros socialis* | 5936 ± 7868 | 39.3 ± 52.1 | *Actinocyclus actinochilus* | 6 ± 20 | 3.7 ± 12.9 | *Chaetoceros dichaeta* | 3 ± 16 | 0.1 ± 0.3 |
| *Coscinodiscus bouvet* | 148 ± 185 | 143.3 ± 179.7 | *Chaetoceros socialis* | 9 ± 33 | 0.1 ± 0.2 | *Chaetoceros neglectus* | 6 ± 27 | 0.0 ± 0.1 |
| *Cylindroteca closterium* | 214 ± 161 | 0.2 ± 0.1 | *Corethron pennatum* | 15 ± 41 | 1.7 ± 4.7 | *Chaetoceros* sp. | 22 ± 75 | 0.0 ± 0.1 |
| *Eucampia antarctica* | 35 ± 102 | 9.3 ± 26.9 | *Cylindroteca closterium* | 300 ± 289 | 0.3 ± 0.3 | *Corethron pennatum* | 17 ± 32 | 1.9 ± 3.6 |
| Small *Fragilariopsis* spp.[a] | 2670 ± 1681 | 3.4 ± 2.1 | Small *Fragilariopsis* spp.[a] | 5686 ± 3696 | 7.2 ± 4.7 | *Cylindroteca closterium* | 258 ± 367 | 0.2 ± 0.3 |
| *Fragilariopsis separanda* | 12 ± 30 | 0.1 ± 0.3 | *Fragilariopsis curta* | 24 ± 70 | 0.2 ± 0.5 | Small *Fragilariopsis* spp.[a] | 6939 ± 3023 | 8.8 ± 3.8 |
| *Fragilariopsis* sp. | 79 ± 106 | 1.7 ± 2.2 | *Fragilariopsis cylindrus* | 5 ± 26 | 0.0 ± 0.1 | *Fragilariopsis curta* | 89 ± 140 | 0.7 ± 1.1 |
| *Nitzschia* spp. | 221 ± 120 | 1.5 ± 1.2 | *Fragilariopsis separanda* | 18 ± 43 | 0.2 ± 0.4 | *Fragilariopsis cylindrus* | 7 ± 32 | 0.0 ± 0.1 |
| *Odontella weisflogii* | 7 ± 25 | 4.1 ± 14.7 | *Fragilariopsis* sp. | 11 ± 38 | 0.1 ± 0.3 | *Fragilariopsis separanda* | 23 ± 47 | 0.2 ± 0.5 |
| *Proboscia truncata* | 19 ± 69 | 0.6 ± 2.1 | *Nitzschia* spp. | 119 ± 110 | 0.3 ± 0.3 | *Fragilariopsis* sp. | 153 ± 185 | 1.1 ± 1.4 |
| *Rhizosolenia* sp. | 5 ± 17 | 0.5 ± 2.0 | *Rhizosolenia* sp. | 6 ± 20 | 0.7 ± 2.4 | *Nitzschia* spp. | 324 ± 203 | 0.8 ± 0.5 |
| *Stellarinma microtidas* | 29 ± 104 | 12.3 ± 44.4 | *Thalassiosira* spp. | 19 ± 28 | 0.5 ± 0.8 | *Rhizosolenia* sp. | 10 ± 27 | 1.2 ± 3.2 |
| *Thalassiosira* spp. | 118 ± 87 | 5.3 ± 4.8 | *Tropidoneis* sp. | 3 ± 14 | 0.7 ± 3.5 | *Thalassiosira* spp. | 10 ± 19 | 0.3 ± 0.5 |
| *Tropidoneis* sp. | 12 ± 35 | 2.9 ± 8.5 | Unidentified pennal | 51 ± 81 | 0.1 ± 0.2 | *Tropidoneis* sp. | 3 ± 15 | 0.8 ± 3.6 |
| Unidentified pennal | 88 ± 104 | 7.0 ± 8.1 | | | | Unidentified pennal | 26 ± 29 | 1.2 ± 1.1 |

Average ± standard deviation in regions delimited within the area, as in Fig. 7.
[a]Including *Fragilariopsis curta*, *Fragilariopsis cylindrus* and *Fragilariopsis pseudonana* (10 μm).




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general low phytoplankton concentration characteristic of the surface waters of pelagic regions, the presence of a DCM layer may be ecologically relevant for the functioning of the ecosystem. Thus, a more comprehensive analysis of this pattern will help to achieve a thorough understanding of the ecology of the Southern Ocean.

## CONCLUSIONS

The analysis of the phytoplankton horizontal spatial variability (alongshore and across-shelf) evidenced that the study area has characteristics which are common for the Southern Ocean. That is, a yearly consistent negative on/offshore gradient in phytoplankton biomass, closely related to variations in the depth of the upper mixed layer. Changes in Chl *a* concentration, usually used as a measurement of phytoplankton standing stock, are shown to be related to changes in phytoplankton C and community composition. Year-to-year variations in the magnitude of the on/offshore phytoplankton biomass gradients were the result of differences in the concentration of diatom blooms. In turn, these variations can be ascribed to variations in the sea-ice dynamics during the previous spring season.

The analysis of Chl *a* vertical profiles showed changes in the phytoplankton vertical distribution in distinct regions within the area. In fact, in coastal and mid-shelf stations, Chl *a* was homogeneously distributed in the upper mixed layer, and stratification of the water column is likely the main factor determining this vertical distribution pattern. In the offshore stations, Chl *a* concentrated in a deep layer, and micronutrient depletion in the upper water column, and higher concentrations in the WW is hypothesized as the control factor of this vertical distribution pattern. We postulate that variations in the vertical Chl *a* distribution were related to the phytoplankton seasonal evolution across the area. In fact, considering that phytoplankton growth progresses from offshore to inshore as sea ice retreats, we conclude that phytoplankton was regulated by the water column stratification at the beginning of the growing season, as found in the coastal and mid-shelf waters, and by iron concentrations later in the season, as found in the offshore waters. A comparative analysis of our results with those reported for other areas of the Southern Ocean allows us to conclude that the dynamics of the phytoplankton here proposed is likely applicable elsewhere.

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