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Size-fractionated phytoplankton biomass and primary production in the Gerlache and south Bransfield Straits (Antarctic Peninsula) in Austral summer 1995–1996

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Abstract

From the beginning of December 1995 to the beginning of February of 1996, 29 stations were visited in the area of Bransfield and Gerlache Straits, and Bellingshausen Sea. Size-fractionated chlorophyll and primary production rates (0.2–2, 2–10 and $>10\,\mu m$), as well as phytoplankton species composition were determined. Primary production experiments were carried out following JGOFS protocols and samples incubated from dawn during 24 h.

The study area was divided into three main regions:

A—*Large diatoms region*, Gerlache Strait on both cruises, and shelf break of Bellingshausen Sea area during the cruise FRUELA 95, with high values of primary production and predominance of large ($>10\,\mu m$) phytosynthetic phytoplankters. Primary production and chlorophyll *a* (Chl *a*) concentration averaged, respectively, $2.1\,g\,C\,m^{-2}\,d^{-1}$ and $165\,mg\,Chl\,a\,m^{-2}$. Eighty percent of Chl *a* and 70% of primary production corresponded to cells larger than 10 μm, such as big chain-forming diatoms, the large flagellate *Pyramimonas*, and colonies of *Phaeocystis*.

B—*Cryptophycean region*, Bransfield Strait and confluence with Gerlache Strait. Characterised by moderate values of primary production of small size organisms. Mean primary production values were ca. $1.0\,g\,C\,m^{-2}\,d^{-1}$ and $62\,mg\,Chl\,a\,m^{-2}$, and the phytoplankton community was formed essentially by *Cryptomonas* species. Approximately 80% of Chl *a* and primary production corresponded to less than 10-μm cells. Within this region, a subarea could be distinguished in the central zone of Bransfield Strait, with low phytoplankton biomass (around $20\,mg\,Chl\,a\,m^{-2}$) and primary production (ca $0.6\,gC\,m^{-2}\,d^{-1}$). In this subarea, the phytoplankton community was dominated by free cells of *Phaeocystis* and *Cryptomonas*; Sixty-five percent of the Chl *a* and 80% of primary production corresponded to smaller fractions.

C—*Region of very low phytoplankton biomass*, all Bellingshausen Sea during the FRUELA 96 cruise. Primary production was around $0.2\,g\,C\,m^{-2}\,d^{-1}$ and Chl *a* about $10\,mg\,m^{-2}$. Phytoplankton was dominated by microflagellates ($<10\,\mu m$), small dinoflagellates ($<20\,\mu m$), and very small ($<10\,\mu m$) diatoms. More than 70% of the primary production and Chl *a* corresponded to the smaller than 10-μm fraction.

No statistical relationship was found between phytoplankton distribution and hydrography and/or concentrations of dissolved inorganic nutrients for the different regions. The upper mixed layer was always within the photic zone, and levels of nutrients were always high enough to be non-limiting for phytoplankton growth. Grazing pressure as well as

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sedimentation and respiration losses, in combination with shallow mixed layers, specially in some and very high productive stations of Region A, might be the main factors controlling the phytoplankton distribution in this area of the Antarctic Peninsula.

1. Introduction

Two distinct areas can be differentiated in the Southern Ocean, according to the studies carried out during the last two decades: Open-ocean waters, with low levels of production in spite of high levels of nutrients (El-Sayed, 1978, 1987; Jacques, 1989; Priddle et al., 1986; Holm-Hansen et al., 1977), and Shelf waters where levels of phytoplankton biomass are usually very high during spring and summer (Alexander and Niebauer, 1981; El-Sayed and Taguchi, 1981; Jennings et al., 1984; Smith and Nelson, 1986; Holm-Hansen and Mitchell, 1991). In oceanic waters, some factors as mixed-layer depth, advection caused by strong winds and storms, and limiting micronutrients such as iron have been invoked to explain low phytoplankton biomass (Hart, 1934; Bidigare et al., 1986; Lipski and Rakusa-Suszczewski, 1990; Priddle et al., 1994). On the other hand size-fractionated chlorophyll typically shows a predominance of nanoplankton ($<20\,\mu m$) and even picoplankton ($<2\,\mu m$) (Fay, 1973; El-Sayed et al., 1979; Bröckel, 1981, 1985; Kosaki et al., 1985; Weber and El-Sayed, 1987). In coastal shelf waters, however, iron is not likely to be a limiting micronutrient for primary production, due to runoff from land (Holm-Hansen et al., 1989). In addition, in protected coastal areas such as those of the Antarctic Peninsula, specially in the Gerlache and Bransfield Straits, meteorological events such as wind and storms, are less important and therefore deepening of upper mixed layer (UML) and advection processes are minimized (Holm-Hansen and Mitchell, 1991), allowing the development of important phytoplankton blooms. In addition, melting of ice in these areas, results in increased stability of the upper water column (UWC), enhancing phytoplankton growth (Gran, 1931; Marshall, 1957; Smith and Nelson, 1986; Smith et al., 1987, 1996; Lancelot et al., 1993), mainly of large chain-forming diatoms (Holm-Hansen et al., 1989). In shelf waters, size-fractionated biomass distribution is much the same as that in temperate waters and, even though studies of size classes distribution are scarce, there is evidence that microplankton (>10–$20\,\mu m$) dominates the phytoplankton community during blooms (Holm-Hansen et al., 1989).

The main objective of the FRUELA Program was to quantify the carbon cycle during the Austral summer when phytoplankton blooms occur in the west region of the Antarctic Peninsula. In this paper, we present the study of size-fractionated phytoplankton chlorophyll and primary production in the Gerlache and Bransfield Straits and NE Bellingshausen Sea (see Estrada and Anadón, 2002). The main objectives of this work were to quantify the size class distribution of primary production and chlorophyll *a*, to determine the phytoplankton composition in the area of study, and to study the temporal changes of these variables during the summer. Size-fractionation studies have been carried out in the Antarctic for many years (Fay, 1973; Bröckel, 1985; Weber and El-Sayed, 1987; Holm-Hansen et al., 1989), as the distribution of cell size of phytoplankters plays an important role in the trophic organization and community structure of pelagic ecosystems. However, little information on size class distribution is available in the region of Gerlache and Bransfield straits, and no information exists on fractionated primary production in the area (Bidigare et al., 1996). On the other hand, studies on temporal changes in phytoplankton community structure changes are very scarce in this zone (Smith et al., 1996).

The aim of this paper is to provide a database to document variability during the phytoplanbkton growth season in the area of the Bransfield–Gerlache Straits and Bellingshausen Sea, as well as to allow a comparison with other environments of the Antarctic. The data provided here, along with other information shown in this volume

(Anadón et al., 2002), allow us to test the hypothesis that phytoplankton size influences sedimentation rates, which are supposed to be higher in areas of high production with a community dominated by large phytoplankters.

2. Material and methods

2.1. Study site and sample collection

Phytoplankton chlorophyll and primary production studies were carried out during two cruises, FRUELA 95 (December 1995), and FRUELA 96 (January 1996), in the northeastern area of Bellingshausen Sea and the Bransfield and Gerlache Straits (Fig. 1). Samples were collected at 29 stations (16 in FRUELA 95 and 13 in FRUELA 96), occupied by R.V. *Hesperides* between 3 December 1995 and 5 February 1996. Samples were obtained with PVC Niskin bottles in a CTD rossete system (no trace metal clean) at depths of 100, 50, 25, 10 and 1% of surface PAR. Detailed descriptions of the survey strategies carried out on these cruises can be found in Estrada and Anadón (2002).

2.2. Physical variables

Temperature, salinity and in situ fluorescence profiles were recorded with a Mark IIIC probe. CTD profiles were used to delimit the depth of the

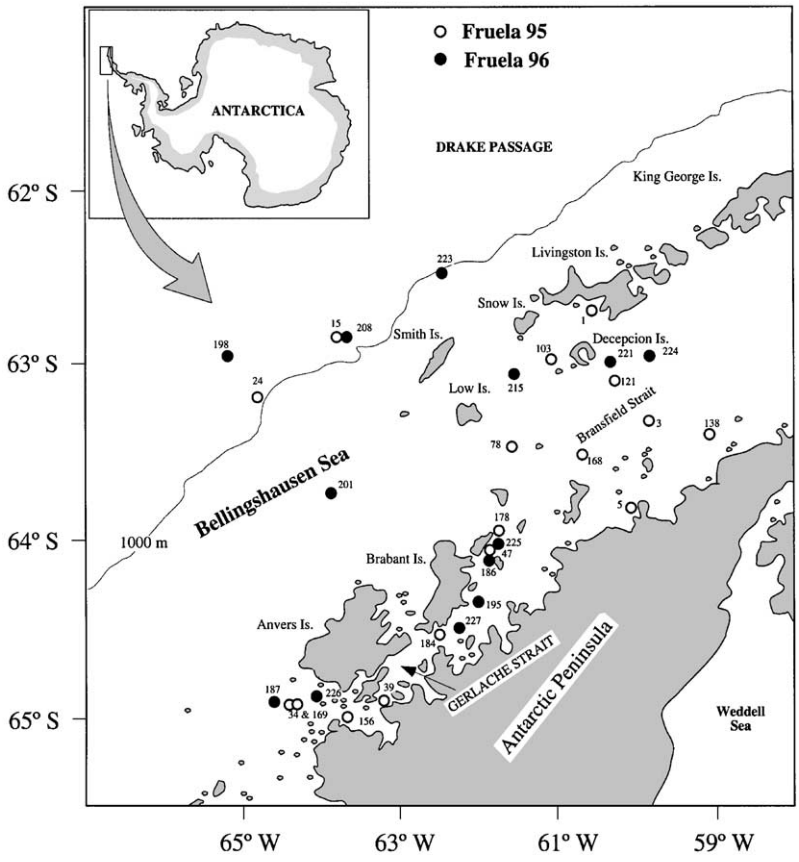

Fig. 1. Map of the study area showing the sampling stations for both cruises and shelf break of Bellinghausen Sea. The stations 15 and 24 near the 1000 m isobath, mark the position of SbyACC front during the FRUELA 95 cruise.

upper mixed layer (UML). A change of $\sigma t > 0.05$ over 5 m depth interval was the criterion to establish the depths of UML (Z_{UML}, see Castro et al., 2002).

Irradiance profiles were measured at noon, using a LICOR irradiance sensor and total irradiance was measured on board (Figueroa, 2002)

2.3. Chlorophyll

Samples for chlorophyll fractionation were obtained from 29 stations (Fig. 1). Particulate material was concentrated by filtration of 100–250 ml of seawater, and pigments were extracted in 90% acetone (Parsons et al., 1984) for 24 h in dark at 4°C. Chlorophyll *a* concentration was measured fluorimetrically on board, using a Turner Designs fluorometer (Yentsch and Menzel, 1963; Castro et al., 2002). No sonication or destruction of filters was carried out. Besides the samples taken for chlorophyll fractionation (Fig. 1), additional samples (see Castro et al., 2002) obtained at most of the stations, and chlorophyll estimates derived from CTD fluorescence data were used to depict a more precise distribution of total integrated chlorophyll over the photic zone.

2.4. Primary production

The method followed for the ^{14}C uptake experiments was based on that described in the JGOFS protocols (UNESCO, 1994). Water samples from each sampled depth were poured into three clear 300-ml polycarbonate bottles. In addition, a dark bottle was used for the 100%, 25% and 1% levels. Each bottle was inoculated with 20 μCi (740 kBq) of ^{14}C labelled sodium bicarbonate and incubated for 24 h in a deck incubator refrigerated with surface water. The different light regimes of the sampling depths were simulated using neutral density filters. For some stations, two sets of data were obtained, one from on deck incubations and the other from in situ incubations. As the correlation between the two data sets was very good ($n = 25$; $r^2 = 0.98$; $p < 0.0001$), we used both of them for a wider spatial coverage of the study area. Following incubation, samples were sequentially filtered (see next section) and the filters were placed into scintillation vials and exposed to concentrated HCl fumes for 12 h. The incorporated radiocarbon was determined using a Beckman Liquid Scintillation Counter.

2.5. Size fractionation

Samples for chlorophyll and primary production (after incubation) measurements were size-fractionated by sequential filtration through Nucleopore 10 μm, Nucleopore 2 μm, and Whatman GF/F filters, under vacuum pressures lower than 250 mm Hg. The working definitions for these size fractions were as follows: *microplankton*: the plankton retained on a 10-μm filter; *nanoplankton*: the plankton passing through 10 μm but retained by 2 μm; and *picoplankton*: the material which passed through 2-μm Nucleopore but was retained on a Whatman GF/F filter.

2.6. Dissolved oxygen and net community production

A 250-ml gravimetrically calibrated, borosilicate bottle was carefully filled from every Niskin bottle by means of a silicone tube. Fixing and storage procedures, reagents and standardisation followed the recommendations by Grasshoff et al. (1983). Dissolved oxygen concentration was measured through automated precision Winkler titration performed with a Metrohm 716 DMS Titrino, using a potentiometric end point (Oudot et al., 1988; Pomeroy et al., 1994). Aliquots of fixed samples were delivered by a 50-ml overflow pipette. Rates of O_2 production and consumption by the planktonic community were determined by in vitro changes of seawater O_2 concentration in transparent (“light”) and dark bottles incubated in situ during 24 h. Sampling and incubation were carried out at the same depths of ^{14}C experiments. Twelve 250-ml, gravimetrically calibrated, borosilicate bottles were carefully filled from every Niskin bottle by means of a silicone tube, overflowing more than 500 ml. Filled bottles were immediately closed and kept, in darkness, in a deck incubator refrigerated with surface water.

This procedure minimised temperature changes until the whole set of bottles was filled and the buoy, carrying the in situ incubation device, was ready for deployment. An initial set of four dark bottles was fixed at once, the remaining (four dark, covered with aluminium foil, and four transparent or "light" bottles) were attached to the buoy at the depths of origin of the sampled water. Dissolved oxygen concentration was determined following the method described above. Data were available only for four stations of the FRUELA 95 cruise, two in the Gerlache Strait and two in the Bransfield Strait.

2.7. Phytoplankton counting

Aliquots of 125 ml were preserved with Lugol's solution (Margalef, 1974). Samples were taken at the same stations and depths as the samples for fractionated chlorophyll and primary production, and kept dark and cool (4°C) until counting. A total of 145 samples were studied using an inverted microscope Nikon TMD, following Utermöhl's technique. Detailed information on counting procedures can be seen in Rodríguez et al. (2002b).

3. Results

3.1. Summary description of oceanographic features for the area of study

The most important hydrographic feature (García et al., 2002) was frontal zone of the Southern Boundary of the Antarctic Circumpolar Current (SbyACC), developed in the shelf break of the Bellingshausen Sea during the FRUELA 95 cruise (Fig 1). This front was not apparent during FRUELA 96. The other relevant feature was the marked hydrographic front at the NE mouth of Gerlache Strait, in the confluence with Bransfield. This front separated the cooler, more saline and vertically more homogeneus waters of the Bransfield Strait from the waters of central Gerlache Strait, stabilised after freshwater inputs from glacier melting (see Garcia et al., 2002, for a detailed description of water masses).

The distributions of physico-chemical variables have been presented and discussed by Castro et al. (2002), García et al. (2002) and Rodríguez et al. (2002a).

3.2. Spatial and temporal distribution of chlorophyll a and primary production in the photic zone

During FRUELA 95 (December 1995), a large part of the study area showed high chlorophyll *a* (Chl *a*) concentrations, exceeding 100 mg Chl *a* m^{-2} (Fig. 2). Higher values were recorded in the Gerlache Strait and the confluence Gerlache–Bellingshausen Sea, with concentrations ranging from 150 to more than 200 mg Chl *a* m^{-2}. Slightly lower values were found in the northern area over the shelf break (Fig. 1), but with values close to 200 mg Chl *a* m^{-2} in the SBACC frontal zone. Lower values were observed north of Brabant and Anvers Islands, with Chl *a* concentrations well below 50 mg Chl *a* m^{-2}.

During FRUELA 96 (January 1996), phytoplankton biomass was markedly lower (Fig. 2). Only the area restricted to Gerlache Strait showed comparable values to those of FRUELA 95, even though in January 1996, the higher Chl *a* concentrations were limited to the NE part of the Strait in the confluence with the Bransfield Strait, where values exceeded 200 mg Chl *a* m^{-2}. The rest of the study area was characterized by low values of Chl *a* (10–50 mg Chl *a* m^{-2}). On the shelf break, where high phytoplankton biomass was observed during FRUELA 95, the chlorophyll concentration had decreased sharply and values had dropped below 10 mg Chl *a* m^{-2}.

Technical problems prevented obtaining a spatial coverage for primary production as complete as that of chlorophyll, specially on the FRUELA 95 cruise. Higher production levels were found in the Gerlache Strait and in the shelf break area during FRUELA 95, although, unlike Chl *a*, higher primary production was recorded in the middle strait area with values exceeding 3 g C m^{-2} d^{-1}. Values in the shelf break area were well over 1 g C m^{-2} d^{-1}, and close to 2 g C m^{-2} d^{-1} near Deception Island (Fig. 2). In the Bransfield Strait, primary production rates ranged between

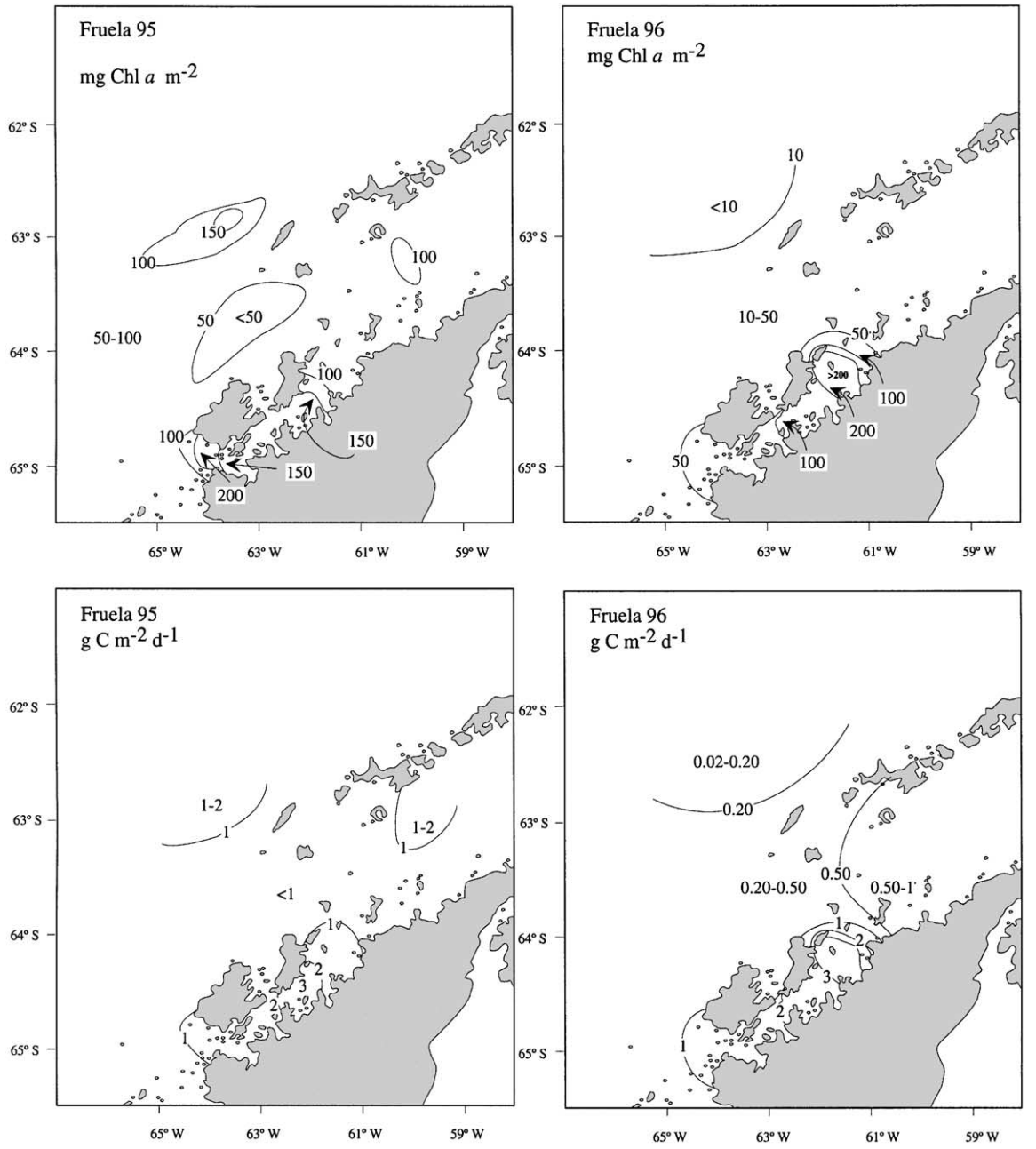

Fig. 2. Depth-integrated values of chlorophyll and primary production for FRUELA 95 and FRUELA 96 cruises. Complementary stations were used besides those for fractionation experiments (see Castro et al., 2002).

0.5 and 1 g C m^{-2} d^{-1}, and in the rest of the area, between Brabant-Anvers Islands and the shelf-break, values were lower than 0.5 g C m^{-2} d^{-1}, but always exceeding 0.4 g C m^{-2} d^{-1}.

The spatial pattern in FRUELA 96, as in the case of chlorophyll, was quite different. Except for the Gerlache Strait, where primary production rates were similar to those of FRUELA 95, or even

higher (maximum rates exceeding $4\,g\,C\,m^{-2}\,d^{-1}$ at station 225), in the rest of the area primary production was remarkably lower than in the FRUELA 95 cruise. The Bransfield Strait zone showed values ranging between 0.5 and $0.8\,g\,C\,m^{-2}\,d^{-1}$, and the rest of the study area presented values well below $0.5\,g\,C\,m^{-2}\,d^{-1}$. In the shelf break region, where high phytoplankton biomass was found during FRUELA 95, productivity rates dropped below $0.15\,g\,C\,m^{-2}\,d^{-1}$, and at station 198, production reached only $0.02\,g\,C\,m^{-2}\,d^{-1}$.

3.3. Phytoplankton assemblages

Numerically, nanoflagellates (2–10 μm) largely dominated the phytoplankton community. Considering larger phytoplankters (>10 μm), phytoplankton species composition showed a great variability, both in space and time. During FRUELA 95, larger phytoplankton was dominated by chain-forming diatoms in areas of high productivity and/or biomass: shelf-break at Bellingshausen Sea and Gerlache Strait. In the Bransfield Strait and in the confluence of Gerlache with both the Bellingshausen Sea and the Bransfield Strait, moderate values of biomass and primary production were found, and phytoplankton was mainly constituted by *Cryptomonas*. In both, high and moderate phytoplankton biomass areas, *Phaeocystis* cf. *antarctica* was also a characteristic species. The large flagellate *Pyramimonas* (>20 μm mean spherical diameter), accounted for 80–85% of the microphytoplankton (>10 μm) abundance in the most productive stations of the Gerlache Strait in both cruises (stations exceeding $20\,mg\,Chl\,a\,m^{-3}$).

During FRUELA 96, well formed colonies of *Phaeocystis* were not detected in microscopic counts and diatoms increased their numbers significantly. *Phaeocystis* remained in isolated stations in the center of Bransfield, but colonies showed a high degree of degradation, and most cells could be observed as free individuals. On the other hand, the diatom-dominated phytoplankton community observed at the shelf break during FRUELA 95 (satations 15 and 24) had been substituted (stations 203 and 223) by a nanoplankton-dominated community with small flagellates (<10 μm), dinoflagellates (10–15 μm), and very small diatoms (<10 μm) as the most representative phytoplankters.

In summary, during FRUELA 96, phytoplankton blooms were restricted to the Gerlache Strait, the importance of *Phaeocystis* decreased, and diatoms became more dominant, except for those stations of very high phytoplankton biomass where *Pyramimonas* accounted for a very important percentage of phytoplankton biomass. The area of the cryptophycean-dominated community was limited to the confluence of Gerlache with Bransfield and, to a lesser extent, with the Bellingshausen Sea.

3.4. Productivity zones

According to chlorophyll values, primary production and phytoplankton species composition, and considering both cruises jointly, the area of study can be divided into three regions (Fig. 3):

Zone A: Large diatoms region, corresponds to most of the Gerlache Strait (southwest of the frontal zone located in the confluence with Bransfield) in both cruises and the shelf-break area in FRUELA 95. It was characterized by high values of primary production and the predominance of large (>10 μm) photosynthetic phytoplankters (Table 1). Primary production ranged between 0.87 and $4.54\,g\,C\,m^{-2}\,d^{-1}$, and chlorophyll *a* between 90 and 270 mg Chl *a* m^{-2}. Microplankton (>10 μm) clearly dominated in the areas of high biomass, accounting for about 80% of total chlorophyll, whereas nanoplankton (2–10 μm) and picoplankton (0.2–2 μm) represented 7% and 15%, respectively, in the upper 50 m. (Table 1). A similar pattern was found for size-fractionated primary production, with microplankton representing almost 70% of fractionated primary production, and picoplankton and nanoplankton accounting for 12% and 21%, respectively. Phytoplankton was dominated by large chain-forming diatoms, the big flagellate *Pyramimonas*, and colonies of *Phaeocystis* (Table 1). The vertical distribution of gross O_2 production (GP) matched perfectly that of C incorporation at every sampled station (GP = 2.067*C incorporation

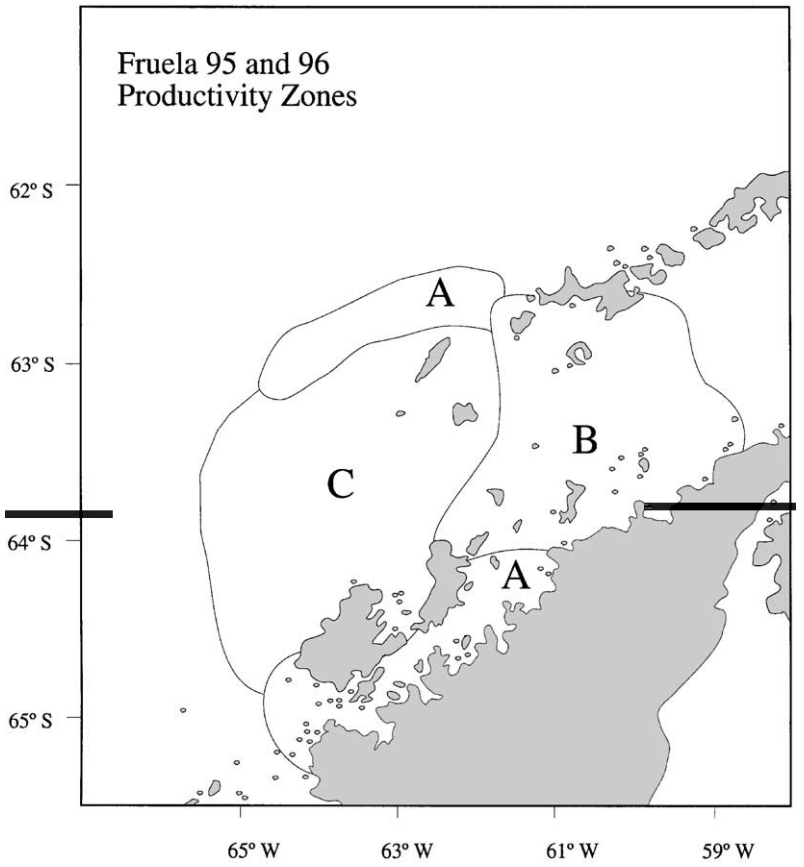

Fig. 3. Distribution of productivity zones considering both cruises. Areas were established according to phytoplankton biomass, primary production, and species composition. Region A, at the shelf-break of Bellinghausen Sea was only observed during FRUELA 95 cruise.

$+1.082$; $r^2 = 0.97$; $p<0.001$). The molar ratio of oxygen gross production to C incorporation was clearly higher than 1.4, the value estimated for new production (Laws, 1991), suggesting that C incorporation was closer to net production than to gross production, as could be expected from 24 h incubations. Dark respiration rates represented a very small percentage of gross production at all depths, suggesting that production predominates over respiration.

Zone B: Cryptomonas region, confluence of Gerlache–Bransfield Straits and Gerlache–Bellingshausen as well as Southwest of Bransfield. Primary production ranged between 0.5 and 1.5 g C m^{-2} d^{-1}. Chlorophyll ranged between 20 and 100 mg Chl *a* m^{-2}. Most phytoplankton biomass and primary production was concentrated in the smaller sizes, especially in the nanoplankton fraction, which accounted, for respectively, 48% and 47% of the chlorophyll and primary production. Total phytoplankton biomass was similar in both cruises; however, during FRUELA 96, a shift of phytoplankton to larger sizes was observed. The phytoplankton community was formed essentially by *Cryptomonas* species (Table 1). As in the case of zone A, C incorporation was close to net production and the molar ratio of oxygen gross production was even higher than in zone A, suggesting the importance of primary production over respiration. Respiration rates showed important differences among stations of this zone. While in the confluence Gerlache–Bransfield (st 178)

Table 1
Mean values of different variables, integrated for the photic zone, measured and characteristic phytoplankton species in each productivity zone during *FRUELA* cruises[a]

Parameter	Zone A	Zone B	Zone C
Z_{UML}	13.2±4.7	17.4±5.7	23.1±6.5
Chlorophyll *a* ($mg\,m^{-2}$)	165.2±21.2	42.7±6.9	10.4±2.5
Primary production ($g\,C\,m^{-2}\,d^{-1}$)	2.1±0.4	0.8±0.2	0.21±0.07
Net community production ($g\,C\,m^{-2}\,d^{-1}$)	2.0±1.2	0.9±0.2	—
Phytoplankton species			
Dinoflagellate > 30 μm	1.9±0.3	0.9±0.2	0.5±0.1
Dinoflagellate < 30 μm	35.9±4.3	81.2±11.5	37.1±5.3
Chaetoceros socialis	43.5±10.1	1.8±1.1	0.14±0.11
Eucampia antarctica	25.5±6.3	3.5±2.7	0.03±0.02
Odontella weissflogii	10.3±2.6	1.2±0.7	0.87±0.84
Proboscia alata	3.8±0.6	0.4±0.2	0.3±0.08
Thalassiosira gravida	14.0±2.2	2.8±1.6	0.3±0.2
Pseudonitzschia heimii	5.3±0.7	5.1±2.1	1.6±0.3
Pyramimonas sp	173.2±67.6	4.3±1.9	0.08±0.08
Phaeocystis antarctica	1167±190	382±89	6.2±3.1
Cryptomonas sp	81.8±45.3	1135±268	27±14
Monads 8–10 μm	80.6±13.9	179.5±23.2	86.2±14.5
Monads 5–8 μm	337.5±61.3	340.5±45.1	242.3±34.2
Monads 3–5 μm	2898±449	2782±287	874.5±81.8
Monads < 3 μm	1260±123	1072±105	380.2±34.9
Flagellate/diatoms index	58.1±10.9	305±60	139±28
% of chlorophyll fractions			
Picoplankton	7±1.4	33±6.1	42±5.3
Nanoplankton	15±3.2	38±5.7	35±4.2
Microplankton	78±4.2	27±6.1	23±3.5
% of primary production fractions			
Picoplankton	12±1.1	40±4.2	44±7.5
Nanoplankton	16±3.9	46±6.1	25±4.4
Microplankton	72±3.9	21±9.8	31±10.7

[a] Mean ± standard error. Z_{UML}: depth of the upper mixed layer. Flagellate/diatom index was calculated from number of cell/ml. Only flagellates > 3 μm considered. Phytoplankton species in cell/ml. Microplankton: > 10 μm, nanoplankton: 2–10 μm, picoplankton: 0.2–2 μm.

Zone A: Gerlache Strait and Shelf Break of Bellingshausen Sea only in *FRUELA 95*.

Zone B: Bransfield Strait.

Zone C: Bellingshausen Sea.

dark respiration was high in surface waters (600 and 876 $mg\,C\,m^{-2}\,d^{-1}$ at 20 and 50 m, respectively), in the rest of the area respiration showed lower values (156 and 252 $mg\,C\,m^{-2}\,d^{-1}$ at 35 and 50 m, respectively), despite nano and picoplankton-dominated communites. Comparing zones A and B, we found higher values of dark respiration in the former, 957±286 versus 471±165, than in the latter.

In zone B, we can distinguish a subregion in the central part of Bransfield (sts 221 and 224 during FRUELA 96). Primary production was low (ca 0.6 $g\,C\,m^{-2}\,d^{-1}$) and mainly generated by small-sized organisms. Chl *a* concentration was around 30 $mg\,m^{-2}$. Pico and nanoplankton chlorophyll accounted for 60% of total phytoplankton biomass, whereas contribution of these fractions to total primary production was higher than 80%.

There was an increase of the relative importance of picoplankton and nanoplankton during FRUELA 96. Besides microflagellates, degraded colonies of *Phaeocystis* and *Cryptomonas* formed the bulk of phytoplankton (Table 1).

Zone C: Region of very low phytoplankton biomass, including the shelf-break area during FRUELA 96 and most of NE Bellingshausen Sea, especially during FRUELA 96. Primary production rates were around $0.2\,g\,C\,m^{-2}\,d^{-1}$ and Chl *a* about $10\,mg\,m^{-2}$. We found similar contributions of pico and nanoplankton for both chlorophyll and primary production, 50% and 30%, respectively. No differences were observed between cruises with respect to chlorophyll fractions (Table 2). Phytoplankton was dominated by microflagellates ($<10\,\mu m$), small dinoflagellates ($<20\,\mu m$), and very small ($<10\,\mu m$) diatoms (Table 1). No data on respiration were available for this zone.

3.5. Vertical distribution of phytoplankton chlorophyll and primary production

Figs. 4 and 5 show the vertical distribution of average values for chlorophyll and primary production as well as the relative contribution of each microplankton size fraction. The vertical distribution of phytoplankton biomass was quite variable in the area of study, according to the level of phytoplankton biomass. In zones A and B, most of the biomass accumulated in the upper 30 m. Station 225 (Gerlache Strait, zone A) presented the highest values measured during both cruises (ca. $25\,mg\,Chl\ \underline{a}\ m^{-3}$ in the surface). At this station chlorophyll *a* decreased from 5 to 20 m by one order of magnitude. In zones C and D, with low phytoplankton biomass, a more homogeneous vertical distribution of chlorophyll was observed.

As expected, primary production decreased with depth. However, this decrease was more evident in zones A and B (Figs. 4 and 5), where the shadow effect of high phytoplankton biomass resulted in very low values of production below 20 m depth. The more productive stations (184 and 225, both in zone A, Gerlache Strait) showed very low values of primary production below 10 m depth. In contrast, the decrease in primary production values with depth occurred more steadily in zones B and C. As figures clearly show, the depth of the upper mixed layer (Z_{UML}) was always within the photic zone (1% of surface PAR)

4. Discussion

The results presented in this paper, together with those reported in the literature, suggest that phytoplankton blooms occur consistently in the studied area from year to year. Levels of chlorophyll and primary production measured in Gerlache were similar to those reported for other protected regions in the vicinity of the Antarctic Peninsula, such as Arthur Harbor (Krebs, 1983; Holm-Hansen et al., 1989; Smith et al., 1996). At station 184, values higher than $20\,mg\,m^{-3}$ were reached, whereas at station 225 chlorophyll concentrations exceeded $25\,mg\,m^{-3}$. These values were probably close to an upper limit for Antarctic phytoplankton in absence of grazing (Holm-Hansen et al., 1989). In some stations, values of Chl *a* were in the range of the potential phytoplankton standing stock for Southern Ocean waters ($25–50\,\mu g\,l^{-1}$) before nutrients become limiting (Sakshaugh and Holm-Hansen, 1986; Spies, 1987). However, our data of integrated chlorophyll over the photic zone (Table 1) are far lower than those of Holm-Hansen and Mitchell (1991), who reported values higher than $700\,mg\,Chl\ a\ m^{-2}$. On the other hand, the values of primary production we measured are in the range reported by these authors.

Relationships between integrated chlorophyll *a* over the photic zone and surface chlorophyll *a* measurements are interesting for interpretation of remote sensing or mooring data. These estimations are especially useful in oceanographic studies where ship time is limited and it is not possible to obtain a vertical profile of phytoplankton biomass in the upper water column (UWC). Our data (Fig. 6) show a good correlation between surface Chl *a* and Chl *a* integrated over the photic layer (0–50 m). This finding is in agreement with those previously reported by Comiso et al. (1990) and Holm-Hansen and Mitchell (1991) in the same area, suggesting that chlorophyll measurements in

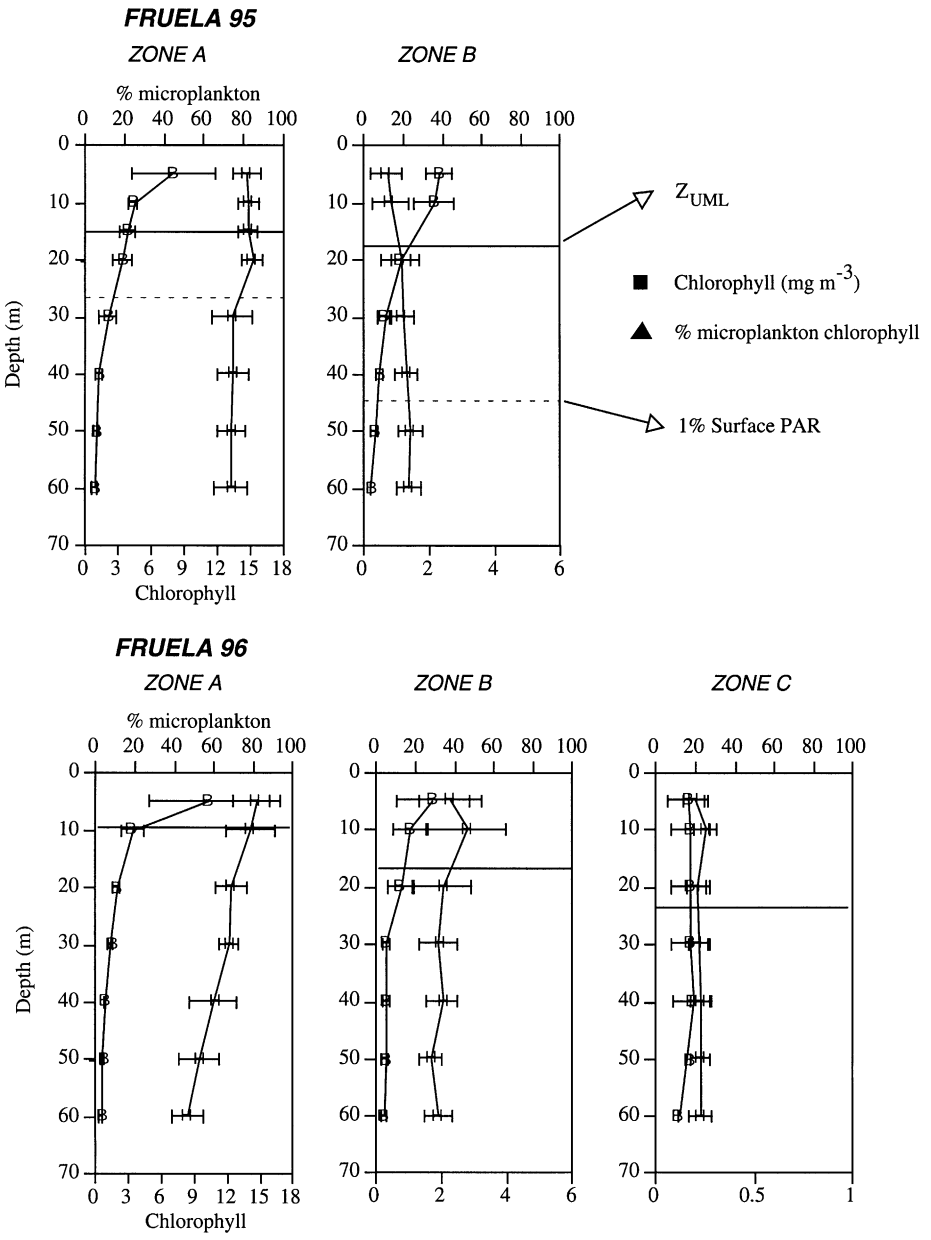

Fig. 4. Vertical profiles of chlorophyll and respective percentage of microplankton (>10 μm). Mean values±standard error. Z_{UML} (depth of upper mixed layer) is always above the 1% of surface PAR.

surface waters of the Antarctic Peninsula can be used for a reliable estimation of phytoplankton biomass in the photic layer. In addition, Fig. 6 also shows that surface Chl *a* can be used as a good estimator of the integrated primary production of the water column.

The first papers published on cell size distribution in the Southern Ocean pointed out the predominance of nanoplankton as compared to microplankton (Fay, 1973; Bröckel, 1981). Since then, many investigators have found that these results are applicable to most Antarctic waters

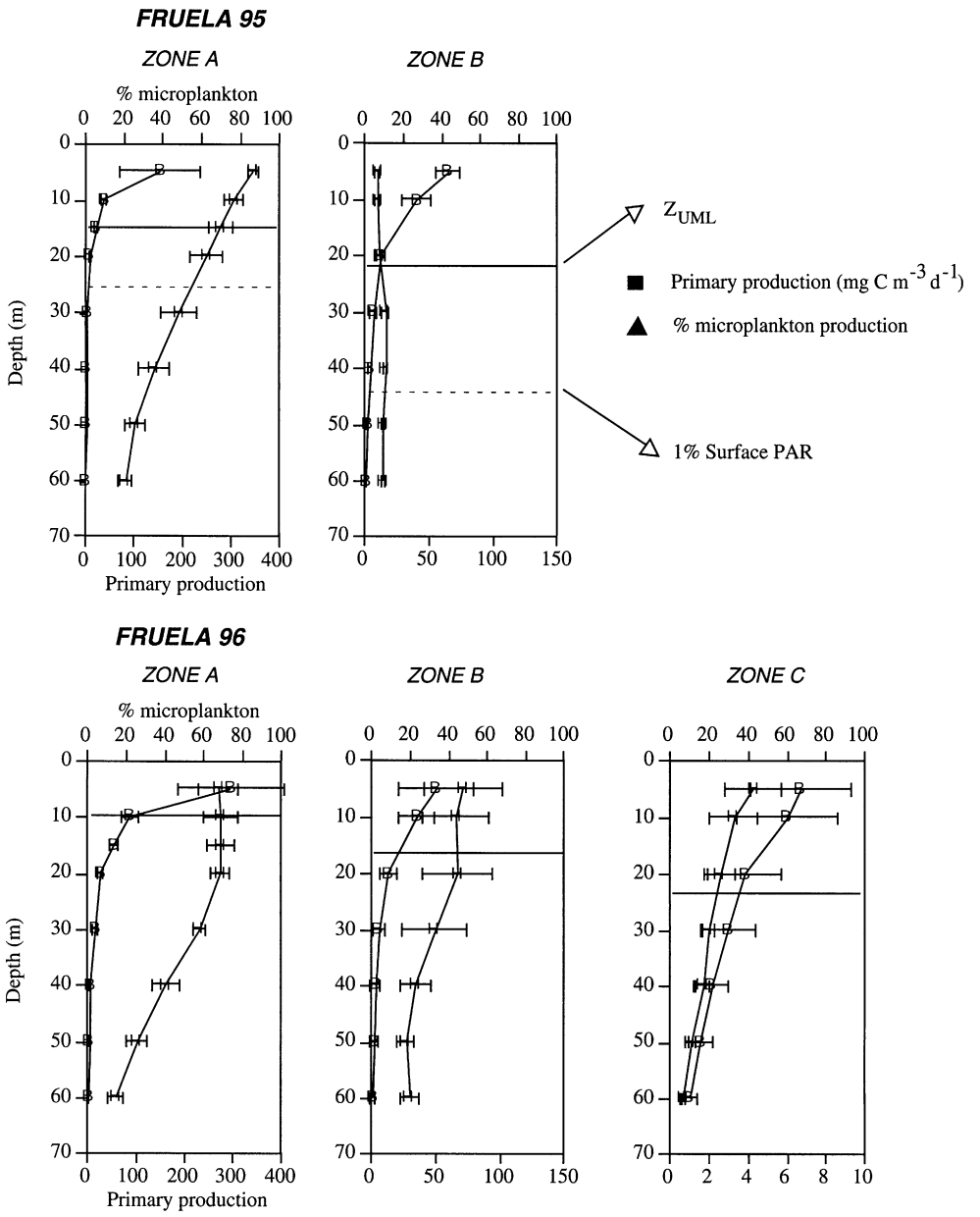

Fig. 5. Vertical profiles of primary production and respective percentage of microplankton (>10 μm). Mean values ± standard error. As in Fig. 4.

(Hewes et al., 1985; El-Sayed, 1988; Weber and El-Sayed, 1987). However, this seems to be a feature of open-ocean waters. Holm-Hansen et al. (1989), suggested that microplankton was an important component of total biomass in Palmer Station. We found that in the areas of higher biomass (Chl $a > 20\,mg\,m^{-3}$) and production, phytoplankton was dominated by microplankton, including *Phaeocystis* colonies, some species of large diatoms (*Eucampia antarctica*, *Odontella weissflogii*), and

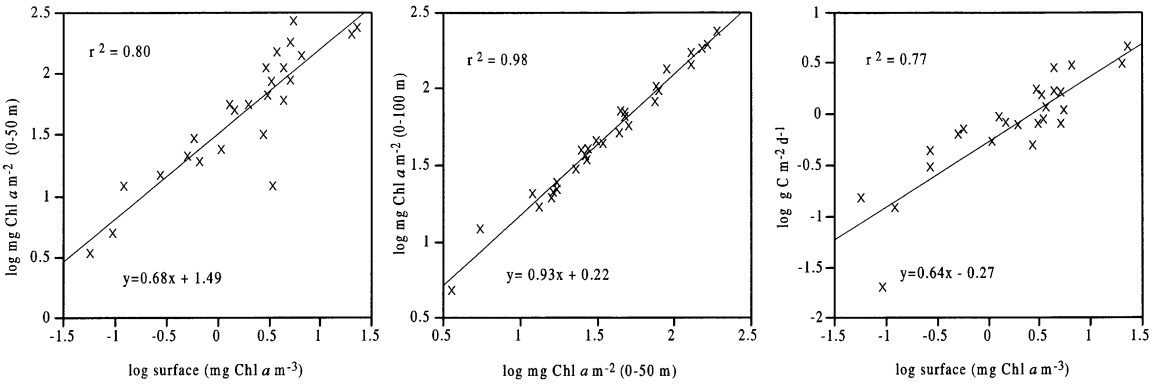

Fig. 6. Relationships between surface chlorophyll, integrated chlorophyll (photic zone; and 0–100 m water column) and integrated productivity considering all available data obtained during the study.

the large Prasinophyte *Pyramimonas* (Table 1). However, as biomass decreased, the importance of nano and picoplankton increased (Table 1; Figs. 4 and 5). Our findings on the relation between total phytoplankton biomass and size fractions differ from those reported by Weber and El-Sayed (1987) for different areas of the Southern Ocean. These authors did not find a relation between phytoplankton biomass (as measured by Chl *a* concentration) ant the relative importance of phytoplankton fractions. However, in our study, the correlation coefficients (r^2) between the microplankton fraction ($>10\,\mu m$) and total Chl *a* and primary production were 0.87 and 0.76, respectively, in agreement with the conclusions drawn from temperate to tropical waters (Malone, 1980). Thus, the relative contribution of microplankton was clearly a function of the total phytoplankton stock, as pointed out by different authors (Malone, 1980; Kosaki et al., 1985), and is the fraction dominating during blooms.

Our data confirm previous studies about seasonality in the area, at least in the Gerlache Strait. During the FRUELA cruises, maximum values for chlorophyll *a* were found in December. However, integrated primary production in Gerlache was higher in January. These findings are in agreement with data reported by Smith et al. (1996) on phytoplankton biomass and primary production distribution in the area of the western Antarctic Peninsula. *Phaeocystis*, typical of spring blooms in receding ice zones, was especially abundant in FRUELA 95 in Gerlache Strait. However, its abundance markedly decreased during FRUELA 96. The scarce colonies found were degraded, indicating a more advanced stage of succession. In Bransfield Strait, the seasonal change was less intense, with slightly higher values found in December.

Most of the taxa found in this work had been previously cited as common components of the Antarctic flora (Hendey, 1937; Kang and Fryxell, 1993, and references therein). *Phaeocystis* cf. *antarctica* was the main component of phytoplankton blooms in our study, being abundant in Gerlache and the frontal zone at the shelf break during FRUELA 95. The presence of *Phaeocystis* associated to ice has been documented by Fryxell and Kendrick (1988), Scharek et al. (1994), and Bidigare et al. (1996), among others. These authors found that *Phaeocystis* was dominant or codominant under the ice. This suggests the importance of ice populations as contributors to phytoplankton biomass in the area of Gerlache Strait. *Phaeocystis* was also found in open waters, together with diatoms, associated to a shelf-break front SBACC in the Bellingshausen Sea. This presence of *Phaeocystis* dominating in frontal zones of polar and other marine regions has been noted by several authors (Hayes et al., 1984; Estrada and Delgado, 1990; Iverson et al., 1979; El-Sayed et al., 1983; Veldhuis et al., 1986). Fryxell and Kendrick

(1988) reported a covariation of *Phaeocystis* and diatoms while other studies did not indicate such a relationship (Palmisano et al., 1986). In our case *Phaeocystis* colonies as well as free *Phaeocystis* cells were always found associated to diatoms (Table 1).

Pyramimonas sp was dominant in areas of extremely high phytoplankton biomass. A previous citation on this phytoplankter was made by Bird and Karl (1992) for northern Gerlache in 1986–1987, associated to levels of chlorophyll reaching 25 mg m^{-3}. In our case, *Pyramomonas* had densities well over 1000 cells ml^{-1} in stations exceeding 20 mg Chl *a* m^{-3} in middle (St 184, FRUELA 95) and northern (St 225, FRUELA 96) Gerlache Strait.

Phytoplankton blooms in Gerlache Strait and shelf break seemed to be low-light adapted. This situation was found in previous studies in Bransfield Strait (Arbones, 1999; Figueiras and Arbones, 1999) and demonstrated for our area of study during FRUELA 95 cruise (Lorenzo et al., 2002). Assimilation numbers (Table 2) fell in the range of 0.7–1.2 mg C mg Chl a^{-1} h^{-1} for picoplankton, 0.3–1 mg C mg Chl a^{-1} h^{-1} for nanoplankton and 0.32–0.63 mg C mg Chl a^{-1} h^{-1} for microplankton, respectively. For total phytoplankton in all areas, this ratio was quite constant, 1.1 ± 0.2 mg C mg Chl a^{-1} h^{-1}. Values found in this study were comparable to those found in previous studies in the Bransfield and Gerlache Straits (Tilzer et al., 1985; Mandelli and Burkholder, 1961; Bodungen, 1986), but slightly lower than those reported by Arbones (1999) and Figueiras and Arbones, 1999, probably because of our larger incubation times (24 h compared to 2–3 h of these authors), and also because our values are integrated for the photic zone. However, a great variability must exist, since Sakshaugh and Holm-Hansen (1986) reported values ranging between 0.75 and 4.4 for Antarctic waters. If phytoplankton during the FRUELA cruises was low-light adapted, then differences in light intensities among different areas would not explain differences in phytoplankton biomass distribution, and therefore light would not be a main factor controlling phytoplankton growth in the zone of study.

Vertical profiles of Chl *a* at some stations, like 184 and 225, showed that phytoplankton concentrations decreased dramatically from surface maxima of >20 mg m^{-3} to around 3 mg m^{-3} at 10 m depth. This decrease was probably caused by shadow effects of the surface biomass on the lower levels of water column. This same effect also was observed at other stations, such as 226, 178 and 138, with lower biomass levels. At all these stations, the accumulation of phytoplankton biomass in surface layers was related to the lowest values of Z_{UML} for all stations (average $Z_{UML} < 2$ m). In contrast, other profiles showed a more homogeneous distribution of Chl *a* through the water column, probably due to high wind stress, which could have evenly distributed the phytoplankton biomass through the UML. For these stations, the average Z_{UML} was around 25 m. Accordingly, the vertical profile of primary production decreased more steadily for these deep Z_{UML} stations than for the former ones.

As expected, macronutrients appeared not to be limiting in the studied area (Castro et al., 2002). Low levels of iron have been suggested as one of the main factors limiting phytoplankton development in the Antarctic. However, controversy still exists on this issue, and the results are not conclusive (Buma et al., 1991; de Baar et al., 1995). In any case it seems that iron limitation does not affect phytoplankton growth in the shelf and coastal waters because levels of this metal are always high due to coastal runoff (Holm-Hansen et al., 1989).

The Gerlache Strait is always a region of high biomass as compared to other neighboring zones, which are also representative of shelf environments (as Trinity, Livingstone and Deception Islands). Previous studies (Balech et al., 1968; Holm-Hansen et al., 1989; Holm-Hansen and Mitchell, 1991) indicate the existence of high primary production in the Gerlache Strait and the confluence Gerlache–Bransfield. The Gerlache Strait is a well-protected area compared with neighbouring zones. This fact, along with the presence of melting water from floes and glaciers along the shore line, favors the development of a sharp vertical density gradient, giving rise to very low UML depths. Both factors could account for the

development of phytoplankton blooms during this study. It can be postulated that Gerlache acts as a marginal ice zone (MIZ) and therefore constitutes an area of enhanced phytoplankton growth (Smith and Nelson, 1986; Wilson et al., 1986; Nelson et al., 1987; Smith et al., 1996). On the other hand, ice microalgae could account for an important fraction of the phytoplankton abundance (Wilson et al., 1986; Heywood and Whitaker, 1984). In our case, *Phaeocystis* cf. *antarctica*, which is considered as a typical ice algal-bloom producer (Scharek et al., 1994; Fryxell and Kendrick, 1988; Heywood and Whitaker, 1984), was very abundant in Gerlache. Furthermore, most of species found in this area (Table 1) were typical of ice-edge zones of the Antarctic Peninsula (Bidigare et al., 1996; Fryxell and Prasad, 1990).

The depth of the upper mixed layer (Z_{UML}), which depends on mixing intensity and controls the permanence of phytoplankton in the photic layer, often has been invoked as a main factor influencing phytoplankton growth (Holm-Hansen et al., 1989; Holm-Hansen and Mitchell, 1991; Berdalet et al., 1996) in some Antarctic waters. However, statistical analyses often show no or very weak correlation between integrated chlorophyll *a* or abundance of phytoplankton, and the UML depth (Paden et al., 1981; Holm-Hansen et al., 1989). In this study we did not find a significant relationship between UML depth and both integrated primary production and chlorophyll *a* ($r^2 = 0.067$, $p = 0.23$ and $r^2 = 0.004$, $p = 0.76$, respectively). In addition, we failed to find significant differences between the different productivity zones (A, B, and C) for UML (ANOVA factorial, $p = 0.67$). In both FRUELA cruises, the photic zone (1% of surface PAR) was above 40–50 m throughout the area; therefore UML depth (Table 1) was always included within the photic layer and was not expected to be the main factor in controlling phytoplankton blooms during our study. However, the lack of significant statistical relationships between UML depth and phytoplankton biomass or production does not mean that hydrography does not play a role in phytoplankton growth; the lack of temporal resolution in the evolution of UML and phytoplankton growth may mask any existing relationships. The shallow UML would explain the presence of low levels of phytoplankton chlorophyll below the photic zone. Most of chlorophyll *a* was present in the upper 50 m of water column. Integrated (100 m) values of Chl *a* were much the same as those relative to 50 m of water column (Fig. 6). This means that there were no physical mechanisms of transport of phytoplankton biomass to deep layers of the upper water column as reported by Holm-Hansen and Mitchell (1991) for RACER cruises, where approximately 50% of total chlorophyll was detected below 50 m.

Nutrient distribution (see Castro et al., 2002) and differences in Z_{UML} (see Table 1) do not explain by themselves the high differences found in phytoplankton biomass between the Gerlache and Bransfield areas. Krill also has been considered as one of the main biological factors controlling phytoplankton biomass distribution in Antarctic waters (Bidigare et al., 1986, 1988; Jacques, 1989; Jacques and Panouse, 1991; Ross and Quentin, 1991; Price, 1989). However, data provided by Cabal et al. (2002) do not support the hypothesis of krill (and zooplankton as a whole) grazing controlling phytoplankton development in all areas for both cruises. The grazing pressure by krill estimated by these authors was always low, accounting for less than 5% of primary production in most cases. On the other hand, mesozooplankton grazed in average only 0.1% of the Chl *a* standing stock and 10% of primary production. Nevertheless, the importance of grazing by large size phytoplankton (krill and salps) cannot be discarded. Cabal et al. (2002) points out that data on this plankton component should be considered with caution because of potential net avoidance by the animals or extremely aggregated distributions. On the other hand, the same authors indicate that Actinopoda and Foraminifera were not taken into account in their study, in spite of their high densities, because the sampling method was not adequate for those groups. Cabal et al. (2002) also point out that grazing can account for up to 50% of primary production when salps and euphasiids were dominant. Therefore, grazing cannot be completely discarded as one of the factors controlling phytoplankton blooms. There are many lines of evidence pointing to the importance

of grazing, especially in the Bransfield area. The Bransfield Strait is considered to be one of the main breeding grounds for krill (Marr, 1962; Capella et al., 1992), and krill grazing in this area might be expected to be intense. In fact, values of chlorophyll *a*, and particulate organic matter in the Bransfield Strait are usually lower than in nearby areas (Burkholder and Sieburth, 1961; Lipski, 1982; Kopczynska and Ligowski, 1982; Holm-Hansen and Mitchell, 1991; Villafañe et al., 1995) of the Western Antarctic Peninsula, and our own data support this idea. On the other hand, grazing experiments have shown that krill consume particles over a large size range, and that the nanoplankter *Cryptomonas* is often the main phytoplankter remaining at the end of the experiments (Jacques and Panouse, 1991). *Cryptomonas* dominated the phytoplankton community in he Bransfield Strait (zone B) during FRUELA 96. This dominance has been also reported by several authors (Kang and Lee, 1995; Ferrario and Sar, 1992; Vernet, 1992) for the same area and the same season, and, as pointed out above, is probably the consequence of krill grazing (Jacques and Panouse, 1991; Smith et al., 1996).

The hypothesis of grazing is also supported by the predominance of flagellates over diatoms. According to Kopczynska (1992), areas of high grazing pressure show a higher flagellates/diatom ratio. In our case, this ratio was of around 58 in Gerlache Strait, but increased up to around 305 in Bransfield. The dominance of *Cryptomonas* in the Bransfield Strait during both FRUELA cruises supports the idea of heavy krill grazing pressure in this area, which could prevent developing of extensive blooms. The opposite occurs in Gerlache Strait, where adults of *Euphasia superba* were not found at any time during 1989 and 1991 (Brinton, 1993). Phytoplankton biomass in zone B was lower than in zone A, but specific growth rate was higher in the former (Serret, pers.com.), suggesting active phytoplankton growth. Probably this growth did not result in high biomass values because of probable high grazing pressure in zone B. Other processes that could account for this lower biomass are sedimentation of phytoplankton cells (see Anadón et al., 2002) and even phytoplankton respiration (Serret pers com.). Both, sedimentation and respiration rates were significantly higher in the cryptophycean-dominated area of Bransfield, especially in the confluence with Gerlache. In addition, other factors such as the influence of different circulation patterns and physico-chemical characteristics associated with different water masses cannot be discarded. The disappearance of the phytoplankton bloom observed during FRUELA 95 cruise in the shelf break (SPF/CWP) of the Bellingshausen Sea could be due, to a great extent, to advection of water masses, wiping out the populations. During FRUELA 96, the shelf break area showed a layer of relatively high temperature and low salinity of southern and probably near-ice origin (Gomis et al., 2002), with extremely low phytoplankton biomass. The important decrease of phytoplankton biomass observed in the NE Gerlache Strait from FRUELA 95 to FRUELA 96 could be the result of combined grazing pressure and alterations of hydrography caused by meteorology. Weather was usually calm during FRUELA 95 while force 6–7 NW winds were common during FRUELA 96 (Cabal et al., 2002), causing advection of surface layers, disappearance of the front and dispersion of the phytoplankton populations.

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