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Vertical biogenic particle flux during Austral summer in the Antarctic Peninsula area

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Abstract

During both FRUELA cruises, we performed eight circum-diel stations in the Bellingshausen Sea (South of Drake Passage), and the Bransfield and Gerlache straits, where MULTITRAP sediment-traps were deployed for periods of 24 h in order to study carbon (C) and nitrogen (N) export from the photic layer. Two types of regions were visited: High chlorophyll *a* (Chl *a*) areas dominated by large-sized diatoms ($>10\,\mu m$), and low Chl *a* areas dominated by *Cryptomonas* sp. or microflagellates. The vertical fluxes of C, N, and Chl *a*, and the number of fecal pellets (FP) were measured, and the taxonomic composition of the sedimented microplankton was analysed; the results compared to the standing stocks in the water column overlaying the sediment traps. We measured higher carbon export rates in the diatom-dominated regions (Gerlache Strait), than in the stations dominated by small phytoplankton (Bransfield Strait and Bellingshausen Sea). The measured C-fluxes ranged from 115 to 800 mg $C\,m^{-2}\,day^{-1}$. Typical C : N ratio (by atoms) varied from 5.5 to 16.4. Nitrogen export, however, was not directly related to C export and, thus, we measured changes in the C : N ratio with stations having higher abundance of FP or detritus presenting higher C : N ratios. Variations in the vertical C-flux were related to biological variables such as FP number, algal community composition (quantitative counts and qualitative SEM observations), and photosynthetic and prokaryotic activity of the sedimented material. We calculated photic layer loss rates of C, N, Chl *a* (0.53–8.0% day^{-1}) and of the different microplankton taxonomic entities (0.27–9.5% day^{-1}). Some exceptionally high loss values were found for Cryptophyceae during Fruela 96. The obtained results are discussed within the conceptual framework set by the relationships between phytoplankton size and food web structure, and concomitant carbon export from the photic layer.

1. Introduction

Knowledge of the vertical flux of particulate material from the photic zone, as well as its chemical and taxonomic composition, is central

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for the understanding of C cycling in the ocean (Berger et al., 1989; Eppley and Peterson, 1979). The magnitude of the export production is considered to be related to both the trophic organisation of the planktonic food web (Legendre and Le Fèvre, 1989; Peinert et al., 1989) and the rate of primary production (Berger et al., 1989; Hargrave, 1985; Suess, 1980; Wassmann, 1990). The trophic organisation of a given planktonic community lies within a continuum spectrum limited by two extreme configurations: the microbial food web, dominated by small phytoplankters, heterotrophic prokaryotes, ciliates and other protozoa, and the herbivorous food web, characterised by the dominance of large-sized primary producers which have high growth rates during transient periods (see e.g., Goldman, 1988; Legendre and Le Fèvre, 1989).

Legendre and Rassoulzadegan (1996) quantified and modelled the export of biogenic C from distinct oceanic food webs types, and suggested that this rate is under hydrodynamic control. According to this model, high rates of export production are typical of herbivorous food webs, whereas microbial food webs are characterised by rapid recycling of the recently photosynthesised organic matter (Bathmann, 1996; Goldman, 1988; Longhurst et al., 1990). Investigations designed to assess the relationship between vertical carbon flux and food web structure failed to validate empirically Legendre's conceptual model of export production (Rivkin et al., 1996), and concluded that neither food web structure nor new production were able to predict the export of biogenic C from the upper ocean. Moreover, high vertical fluxes of biogenic matter may be due to moderate loss rates of a large suspended biomass, as has been observed in the Barents Sea (Andreassen and Wassmann, 1998).

Two extreme types of planktonic communities have been described in spring phytoplankton blooms in Antarctic waters (Bathmann, 1996). Diatoms and the haptophyte *Phaeocystis* sp. typically prevail close to the ice edge and in shelf and frontal areas. In this community, euphausids or salps are the dominant herbivores. In contrast, photo- and heterotrophic flagellates dominate in low-seasonality environments characterised by high particle retention rates, where the dominant grazers are, typically, ciliates and copepods. These two types of communities have been reported from the Bransfield and Gerlache straits, and the Bellingshausen Sea (Bidigare et al., 1996; Holm-Hansen and Mitchell, 1991), and were also encountered during the macroescale phase of the FRUELA cruises (Rodriguez et al., 2002; Varela et al., 2002).

The development of Antarctic phytoplankton blooms has been largely related with the marginal ice zone and with melting and freezing processes typical of the seasonal cycle (Smith and Sakshaug, 1990; Sullivan et al., 1988). High levels of phytoplankton productivity around the Antarctic Peninsula have been measured whenever algal blooms develop (Holm-Hansen and Mitchell, 1991; Varela et al., 2002). In these situations, high carbon and particle export rates have been reported in the region (Bodungen et al., 1986; Karl et al., 1991; Schnack, 1985). However, most of the studies in the Antarctic Peninsula Area were carried out in the open waters of the Eastern Bransfield Strait and the Scotia Sea, and scarce information is available on export production rates in the Gerlache Strait (Karl and Asper, 1990; Karl et al., 1991; Karl et al., 1996).

The aim of the present study was to determine the vertical flux of carbon and nitrogen from the photic layer in productive and non-productive areas in the vicinity of the Antarctic Peninsula (see (Anadón and Estrada, 2002) and to relate it to the corresponding standing stocks of particulate organic matter in the water column, the quality and auto- and heterotrophic activity of the sinking material and the size structure of phytoplankton assemblages.

2. Materials and methods

Drifting sediment traps were deployed during diel cycles as part of the FRUELA 95 (spring) and FRUELA 96 (summer) cruises. The stations were selected to represent the different phytoplankton communities observed during the macroscale phase (Anadón and Estrada, 2002). Several stations were located in the Gerlache and

Bransfield straits (62°30′S–65°S and 59°40′W–64°W), and one station was occupied in the Bellingshausen Sea, near the Drake Passage (Fig. 1). Two sediment traps deployed in the Gerlache Strait during the first cruise could not be recovered.

2.1. Trap design

The trap array consisted in four individual multitrap baffled and unscreened collectors (60-mm diameter mouth and 640 mm long), similar to the design by Knauer et al. (1979), and used during the RACER cruises (Karl et al., 1991). The traps were placed at depths between 60 and 65 m, and filled with filtered (Whatman GF/F) seawater, supplemented with NaCl ($5\,g\,l^{-1}$) to avoid losses of materials due to turbulence. The salt solution was sterilised after the NaCl addition and filtered through Whatman GF/F filters right before deployement.

Several problems, related to hydrodynamic biases, poor sample preservation or the activity of swimmers, have been argued against the use of this type of traps (Bacon, 1996; Buesseler, 1991) In the present study, swimmers were not removed. Nevertheless, visual observation of the bottom of the traps did not show the presence of meso- or macrozooplanktonic organisms. Preservatives to avoid degradation of sinking materials were not used. The low prokaryotic activity measured in preliminary experiments, together with the short duration (24 h) of the deployments, were not likely to produce a significant change in the amount of C and N, as demonstrated by Taylor et al. (1986). Nodder and Alexander (1999) reported significant underestimates (>60%) of vertical carbon flux when traps were filled with concentrated brine (>50‰), but we used a less concentrated brine (39‰ aprox.) that was not expected to produce significant effects. Some degree of underestimation in the measured fluxes, however, cannot be completely ruled out.

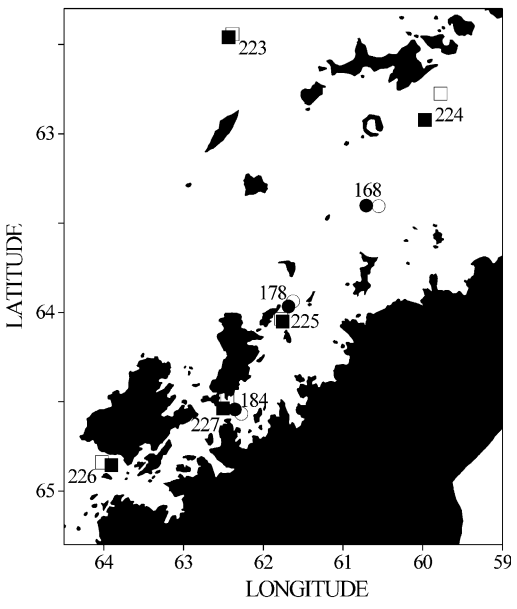


Fig. 1. Map of the studied area. Filled and empty symbols indicate locations where drifting trap arrays were deployed and recovered, respectively. Circles correspond to FRUELA 95 cruise and squares to FRUELA 96 cruise.

2.2. Water column measurements

Samples for the determination of particulate carbon (PC), particulate organic nitrogen (PON) and phytoplankton pigment concentrations, rate of C assimilation and net community production were collected from different depths of the water column down to 60 m. Samples for PC and PON analysis were filtered through Whatman GF/F filters and measured using a Perkin–Elmer 2400 Elemental Analyser (Castro et al., 2002). Carbonate was not removed, but Palanques et al. (2002) showed that the contribution of carbonate to total carbon was less than 2% of the amount of carbon retained by subsurface (500 m) traps located in the Bransfield Strait, during the same period.

Phytoplankton identification and cell counting were performed in 100 ml samples preserved with Lugol's solution. Organisms were identified and counted under an inverted microscope. Size-fractionated Chl *a* (0.2–2 μm; 2–10 μm and >10 μm) was measured after extraction with 90% acetone using a 10.000 R Turner Design fluorometer (Varela et al., 2002). The method used for the size-fractionated C^{14} uptake of water column samples is described in Varela et al. (2002). Water samples were poured into three 300-ml bottles that were incubated in situ for 24 h,

after inoculating each of them with 740 kBq of C^{14} labelled sodium bicarbonate. Following incubation, the samples were sequentially filtered to obtain $>10\,\mu m$, 2–10 μm and 0.2–2 μm fractions (Varela et al., 2002). The filters were placed in scintillation vials and exposed to concentrated HCl fumes for 12 h. The amount of incorporated radiocarbon was determined by liquid scintillation counting.

Zooplankton was sampled (Cabal et al., 2002) by means of vertical net hauls (200 μm mesh size and 40-cm ring diameter). Samples were divided into four size fractions: (200, 500, 1000, and 2000 μm) and filtered on pre-weighted Whatman GF/A fibre filters. The filters were dried at 60°C during 24 h, and zooplankton dry weight obtained by difference. After filter homogenisation (using an agate grinding pot), zooplankton carbon biomass was measured with a Perkin-Elmer 2400 Elemental Analyser.

2.3. Sediment trap measurements

After gently shaking the sample to avoid particulate breakage (fecal pellets (FP) are particularly sensitive), the trapped material was split for different analyses. Half of the volume of each trap was devoted to the analysis of the PC and PON content of the sedimented material, as described above. Subsamples of different volumes were used to determine the concentration of photosynthetic pigments (by fluorescence and HPLC), to perform scanning electron microscopy observations, to identify and count phytoplankton and FP, and to measure carbon incorporation rates by heterotrophic prokaryotes and phytoplankton cells accumulated in the traps. Following Hargrave and Taguchi (1978), results were reported as sedimentation rates (Sd) of PC, PON and Chl *a*, or as daily loss rates (L), $L = \mathrm{Sd} \times 100/\mathrm{Sp}$, where Sd was the sedimentation rate ($mg\,m^{-2}\,day^{-1}$), and Sp the suspended stock ($mg\,m^{-2}$). PC, PON, Chl *a* and phytoplankton abundance data integrated between 0 and 60 m depth were used as "stock" values. The qualitative composition of the trapped particulate matter was studied by microscopic counts of algal species and longer than 100 μm FP, using samples preserved with Lugol's solution (Rodriguez et al., 2002). A cluster analysis of the retained taxa was carried out using the weighted pair-group centroid method, with Euclidean distances. The material retained onto Poretics polycarbonate filters (0.2 μm pore size), after filtration of 100 ml of water, was observed using a Philips XL30 scanning electron microscope.

Pigment extraction was performed in 5 ml of 95% methanol, using a spatula for filter grinding and 5 min sonication at low temperature ($\sim 5°C$). HPLC pigment analysis was performed using a recently developed method based on a C8 column and a pyridine-containing mobile phase (Zapata et al., 2002). Fluorescent emission at 650 nm (excitation wavelength at 420 nm), and UV-Vis absorption spectra obtained by the diode-array detector (350–750 nm, 1.2 nm optical resolution) were used for pigment detection and tentative identification. Pigments were quantified by external standards (pheophorbide *a* and pheophytin *a*) using extinction coefficients compiled by Jeffrey (1997). Chromatograms extracted at 665 nm were employed to estimate the Chl *a* degradation percentage after normalising the peak area for differences in extinction coefficient factors.

The C assimilation of the sedimented phytoplankton cells was measured by the ^{14}C method (see Varela et al., 2002), in short-term incubations (1 h) at saturating light. This measurement was used as an estimate of the viability of the sedimented primary producers. Absolute rates were normalised to total photosynthetic biomass in the traps by dividing them by the trap Chl *a*.

The microbial consumption of the sedimented carbon was measured as the rate of ^{3}H-leucine incorporation (Kirchman et al., 1985) in subsamples of each trap enclosed in Eppendorf vials, as suggested by Smith and Azam (1992). A subsample of the filtered salt solution used to fill the traps before deployment was used as a control for the determination of prokaryotic activity, which was always statistically not different from 0. We did not check for the effect of salt enrichment, but significant changes were not expected given the general resistance of prokaryotes to 10% increases in salt content (Pedrós-Alió et al., 2000). Leucine incorporation was converted to biomass production using the theoretically calculated conversion

Table 1
Depth-integrated (0–60 m) PC and PON (mg m^{-2}), C : N ratio (by atoms), and zooplankton (0–200 m) biomass (mg C m^{-2}) and abundance (ind m^{-2})

Station	PC	PON	C : N	Zooplankton	
			Mean error	Biomass	Abundance
168	6852	1533	6.1±0.08	76	1974
178	5293	1457	4.7±0.15	77	4747
184			6.2±0.15	602	
223	4260	810	7.3±0.16	237	2440
224	3956	830	6.8±0.20	111	1251
225	12648	1818	8.2±0.41	484	3569
226	6284	1280	7.3±0.35	319	3185
227	10174	1876	7.0±0.21	359	5234

factor of 3.1 kg C mol leucine^{-1} (Simon and Azam, 1989) and a prokaryotic growth efficiency [BP/(BP + Resp)] of 33% (Kähler et al., 1997). With the usage of the theoretical conversion factor, and a value of prokaryotic growth efficiency that is in the upper side of those measured in Antarctic waters (see Carlson et al., 1999), our estimates of carbon processing by prokaryotes would have been, if anything, overestimates. The results were expressed as carbon processed per amount of carbon sedimented.

3. Results

3.1. Water column

The termohaline structure and circulation patterns during the FRUELA cruises are described in Garcia et al. (2002) and Gomis et al. (2002). The water column was slightly stratified, with the lowest temperatures located at 100 m, and the lowest salinities in surface waters (Anadón and Estrada, 2002). The mean upper mixed layer (Z_{UML}), as defined by Mitchell and Holm-Hansen (1991), ranged from 12 to 39 m (Castro et al., 2002).

Depth-integrated concentrations of PC and PON (0–60 m), and zooplankton biomass (0–200 m) are shown in Table 1. All these variables were significantly related with photic depth-integrated Chl *a* (Table 2). High PC values were found at st. 184, 225, 226 and 227, in association with the dominance of large (>10 μm) phytoplankton cells, mainly diatoms. In contrast, low PC concentrations were found at st. 168, 178, 223, 224, where small flagellates or *Cryptomonas* formed the bulk of the phytoplankton biomass. The mean C : N ratio (by atom) of the particulate material ranged from 4.7 at stations dominated by *Cryptomonas* to 8.2 at those stations where diatoms were abundant. Size-fractionated Chl *a* concentrations (<2 μm, 2–10 μm, >10 μm) are shown in Fig. 2A. Stations with integrated Chl *a* concentrations greater than 75 mg m^{-2} were characterised by the dominance of >10 μm cells, their relative contribution to total Chl *a* ranging from 54% to 85%; all these stations were located in the Gerlache Strait. Stations with low integrated Chl *a* values were located in the Bransfield Strait and Bellingshausen Sea; in them, large (>10 μm) phytoplankton cells accounted for 8–21% of total Chl *a* (Fig. 2A). The distribution of size-fractionated primary production rates (Fig. 2B) paralleled that of Chl *a*. Integrated Chl *a* and PON were well correlated with PC and primary production (Table 2).

During the FRUELA 95 cruise, the phytoplankton assemblages from "high Chl *a*" areas were dominated by the diatoms *Fragilariopsis cylindrus*, *Eucampia antarctica* and other distinct *Fragilariopsis* species, whereas *Chaetoceros*

Table 2
Linear regression ($Y = a + bX$) between depth-integrated (60 m) variables, with values of, P and r^2

Independent	Dependent	a	b	F	P	r^2
Chl *a*	POC	3794.6	39.6	97.2	0.0002	0.94
Chl *a*	Primary production	0.086	0.013	249.4	0.00001	0.97
Chl *a*	Zooplankton biomass	84.28	2.04	22.7	0.0031	0.79
PON	POC	−1890.9	6.53	15.53	0.011	0.71

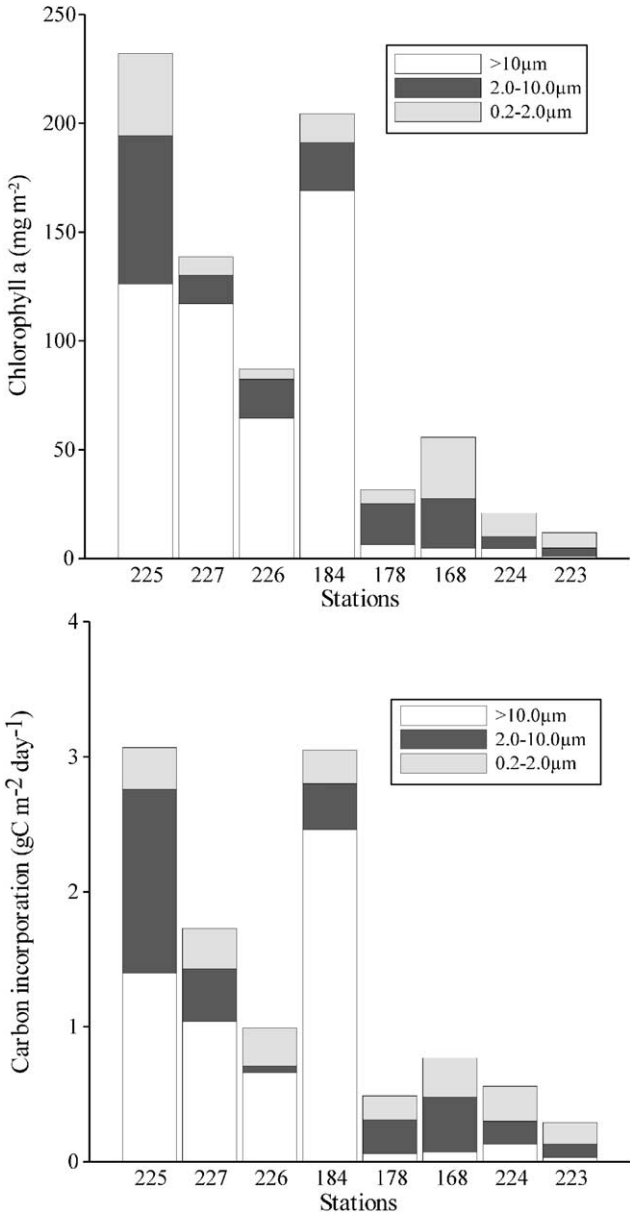
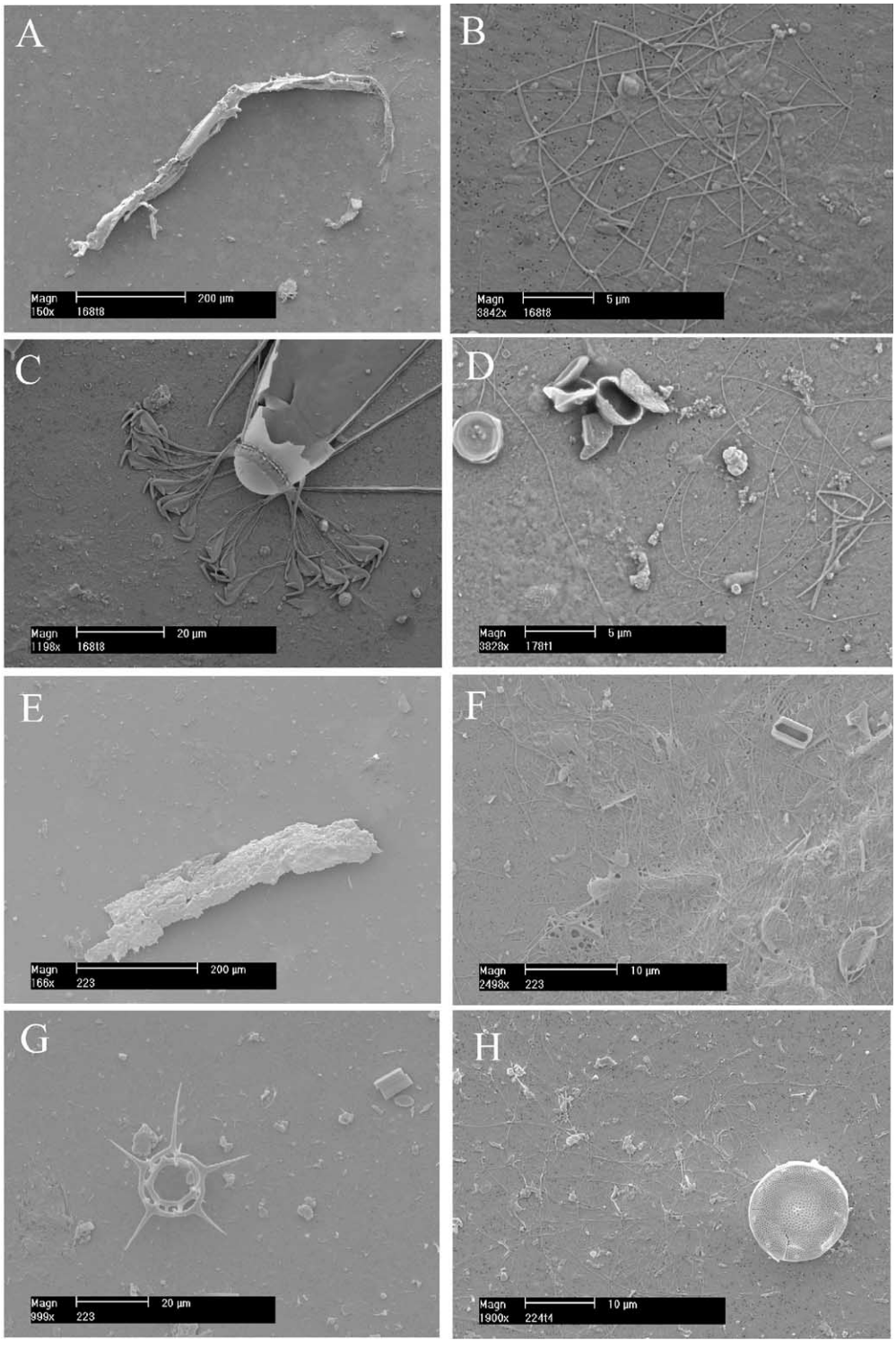


Fig. 2. Size-fractionated depth-integrated Chl *a* (A) and carbon incorporation rates (B) at investigation sites.

Fig. 3. SEM microphotographs of sediment trap material from "Low Chl *a*" stations. In several pictures the filter pores could be observed, indicating a small amount of material. (A) Cuticular exoeskeleton remains of partially degraded crustacea, (B) *Chaetoceros* spp. bristles, (C) spines and projections from the valve margin of the diatom *Corethron criophilum*, (D) diatom remains on a background of unidentified gelatinous material, (E) semidegraded euphausiid FP, (F) aggregates of unidentified thread-like material with some siliceous diatom remains, (G) *Dyctiocha* (*Distephanus*) *speculum* (Silicoflagellate), (H) valve view of the small centric diatom *Thalassiosira sp*.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C
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D
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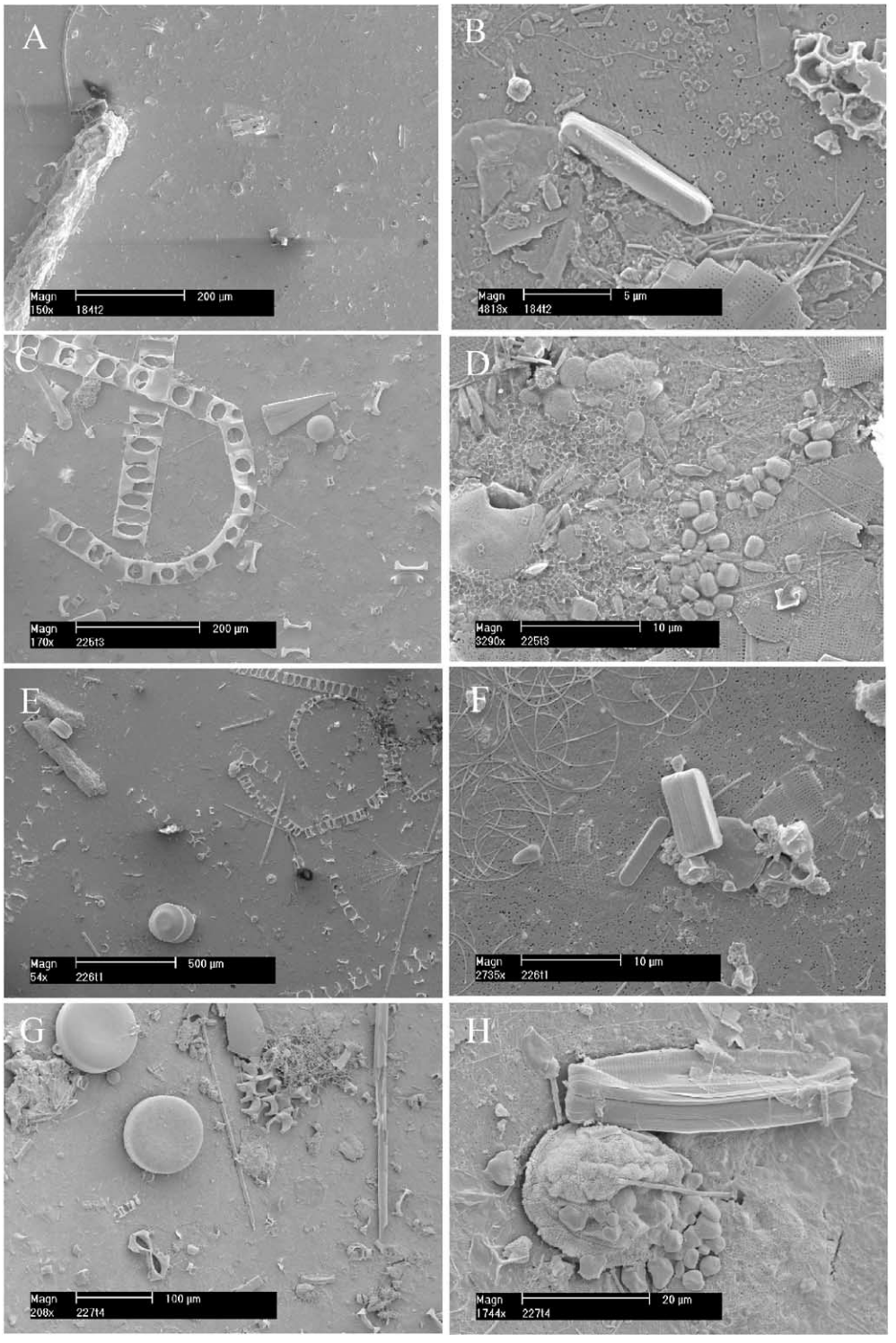
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F
Magn 2735x 226t1 10 µm
G
Magn 208x 227t4 100 µm
H
Magn 1744x 227t4 20 µm

socialis, *Odontella weissflogii, Eucampia antarctica*, and the haptophyte *Phaeocystis* cf. *antarctica* dominated the phytoplankton during the FRUELA 96 cruise. Stations characterised by low Chl *a* concentration were dominated by *Cryptomonas* (st. 168 and 178) and small (3–10 μm) flagellates.

3.2. Sinking material

Scanning electron microscopic analysis of sediment trap materials revealed clear differences between "low Chl *a*" and "high Chl *a*" stations. In general, the first group of stations (Fig. 3) showed unidentified amorphous material scattered on the filter, some euphausid FP, but only a few diatoms. In contrast, samples from "high Chl *a*" stations (Fig. 4) showed recognisable amounts of large and small diatoms, a larger amount of euphausid FP, amorphous or gelatinous material (probably from *Phaeocystis* origin), and aggregates of *Pyramimonas* scales. The amount of diatoms in traps was higher during December and in the Gerlache Strait, and lower in the Bransfiled stations during the two cruises.

We ran a similarity analysis of the phytoplankton taxa retained in the traps to describe the relationship between phytoplankton composition and particle flux at the different stations (Fig. 5). This analysis enabled the definition of two groups of stations. A first group included stations corresponding to the FRUELA 96 cruise, located in the Bellingshausen Sea and in the Bransfield strait (st. 223 and 224). The second group was formed by three subsets of stations: (1) Stations located in the confluence between the Gerlache and Bransfield straits and in the Bransfield Strait during the first cruise (st. 168 and 178); (2) Stations of central Gerlache Strait during FRUELA 95 (st. 184) and the western margin of this strait during FRUELA 96 (st. 226); and (3) Stations of the eastern and central Gerlache Strait (st. 225 and 227) visited during the FRUELA 96 cruise.

This grouping can be combined with that described by Rodriguez et al. (2002) for the water column, to allow the definition of two main subsets of stations: (i) Stations with "low Chl *a*" during the two cruises (st. 168, 178, 223 and 224), dominated by small phytoplankton cells in a "continuum" of taxonomic composition ranging from *Cryptomonas* to small flagellates; (ii) "high Chl a" stations dominated by large phytoplankton cells, including stations of the Gerlache Strait in both cruises (st. 184, 225, 226 and 227).

3.3. Particle fluxes

The vertical fluxes of particulate C and organic N below the photic zone are shown in Fig. 6A, where the stations have been grouped according to the classification described above. Higher vertical C and N fluxes were measured at stations with high PC concentration in the water column, which were dominated by diatoms; the differences were significant between stations ($p<0.05$) and between station type ($p<0.001$) for both C and N, respectively. The C : N ratio (by atoms) of the sinking material ranged from 6.4 at station 178 to a very high value (15.4) at station 184, located in the Central Gerlache Strait (Fig. 6A). The C : N ratio of the sinking particles (Fig. 6) was not correlated to water column C : N ratios (Table 3), the later being higher at all the stations.

The relationship between the relative contribution of large phytoplankton (>10 μm) cells, total Chl *a* and vertical carbon export is shown in Fig. 6B. Vertical carbon flux closely followed total Chl *a* in the water column, but the relationship between PC and >10 μm Chl *a* was less apparent (Fig. 6B, Table 3).

Fig. 4. SEM microphotographs of sediment trap materials from "High Chl *a*" stations. (A) Euphausiid FP, (B) small pennate diatom (*Fragilariopsis* sp.), frustule diatom remains and some box scales of *Pyramimonas* sp., (C) diatoms: *Eucampia antarctica*, *Licmophora* sp. and *Thalassiosira* sp., (D) aggregates of *Pyramimonas* box scales and unidentified material, (E) hard parts of diatoms (*E. antarctica*, *Coccinodiscus* sp., *Rhizosolenia* sp.) and euphausiid FP, (F) valves of a chain of *Fragilariopsis* sp., small dinoflagellates and *Chaetoceros* spp. bristles, (G) valve views of the large centric diatom *Coscinodiscus* sp. and *Rhizosolenia* spp., (H) side view of a small pennate diatom and phytodetrital material.

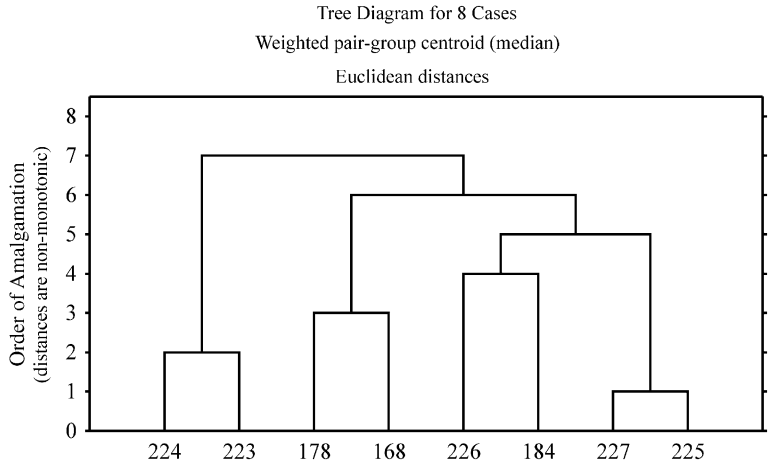

Fig. 5. Similarity dendrogram (Euclidean distances) performed from the abundance of phytoplankton taxa recovered in the traps.

Table 3
Linear regression ($Y = a + bX$) among variables of the sedimented material and of the water column, with values of, P and r^2[a]

Independent	Dependent	a	b	F	P	r^2
Chl*a* wc	Chl*a* sed	−0.727	0.050	40.9	0.0007	0.85
PC wc	PC sed	−162.5	0.07	20.1	0.0065	0.76
C:N wc	C : N sed	0.398	1.409	3.7	0.1109	0.31
Chl*a* > 10 μm wc	PC sed	165.0	2.88	13.1	0.0111	0.63
PP	Chl*a* sed	−1.099	3.863	58.9	0.0003	0.89

[a] wc: water column data; sed: sedimented material.

3.4. Daily loss rate

In all the stations, PC loss rates (% day^{-1}) were higher than PON loss rates (Fig. 7A), which is indicative of a relative retention of N in the water column. Statistically significant differences were not observed between station-type (carbon: $F = 4.253$; $p > 0.05$; nitrogen: $F = 6.062$; $p > 0.05$; $N = 8$), whereas differences were significant between stations (carbon: $F = 12.979$; $p < 0.001$; nitrogen: $F = 22.356$; $p < 0.001$; $N = 8$). These results could be explained by the increase in C : N values in the sinking particles if they are, for example, FP. A lower loss rate than for PC and PON was observed for Chl *a*, although values were close to PON loss rates, or even higher at some station. No significant differences were observed between station type ($F = 2.100$; $p > 0.05$; $N = 8$), although statistically significant differences were found between stations ($F = 18.328$; $p < 0.001$; $N = 8$). The discrepancy observed at st. 184, with a high Chl *a* loss rate but low phytoplankton cell losses, could be due to the large vertical flux of FP, presumably containing Chl *a* (Fig. 8B).

Most phytoplankton groups contributed values of 2–5% (Fig. 7B) of their standing stock to the sedimented material. The five major taxonomic groups found during the two cruises sedimented more during the second cruise at those stations where phytoplankton was dominated by cells > 10 μm, with a very high relative loss at st. 226 for cryptophytes. In contrast, stations where cells < 10 μm dominated during the second cruise showed lower values, except for ciliates in the st. 223.

Similar diatom sinking rates were calculated for stations located in the Gerlache and the Bransfield straits during the FRUELA 96 cruise, and for

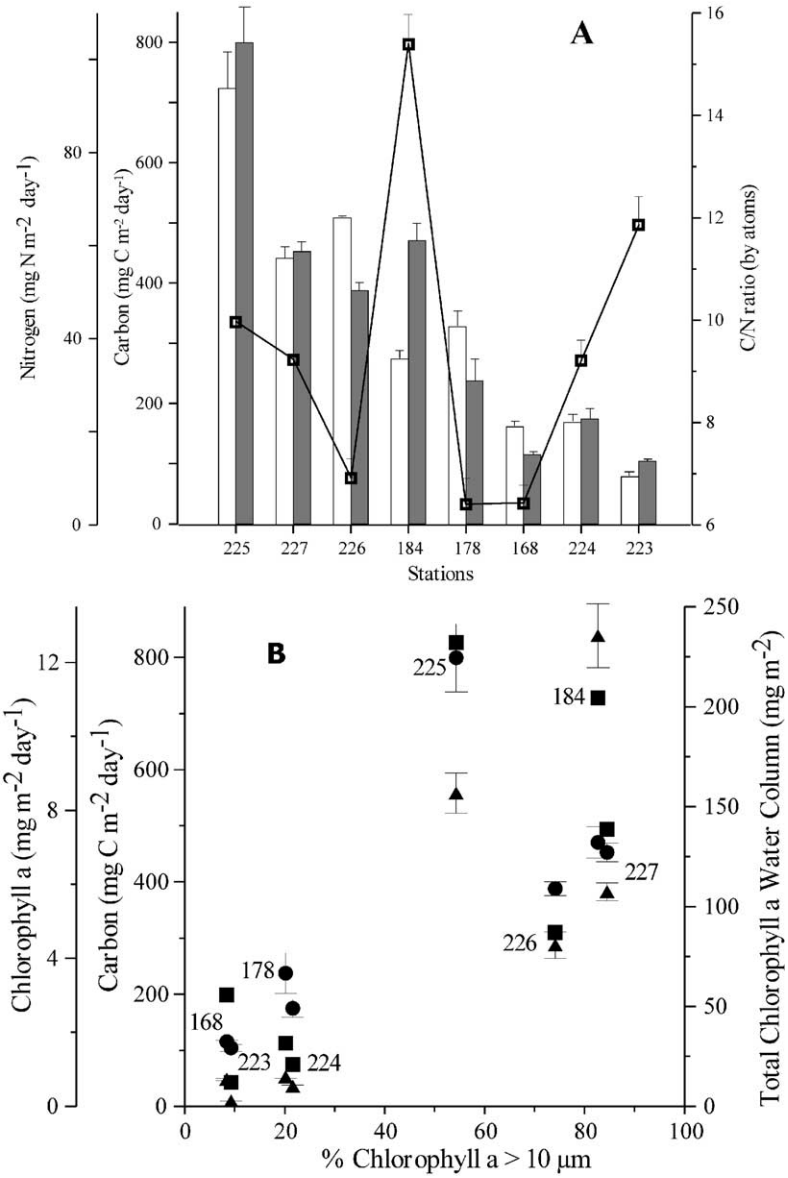

Fig. 6. (A) Vertical fluxes of carbon (■) and nitrogen (□) at the investigation sites. C : N ratio (by atoms) (◘) of sedimented material is also shown. (B) Vertical fluxes of carbon (●) and Chl *a* (▲), as well as total suspended Chl *a* (■) in relation to the percentage of $>10\,\mu m$ suspended Chl *a*.

stations sampled during FRUELA 95 cruise in the boundary of the Gerlache Strait. However, diatom sinking rates were lower in the Bransfield Strait and the Bellingshausen Sea during FRUELA 96 and at central Gerlache Strait during FRUELA 95. The export rate of the diatom *Chaetoceros socialis* was higher (8%) than for other diatom species. The export from the photic zone of motile nano- and microplankton groups such as dinoflagellates, ciliates, small flagellates and cryptophytes were in general low, except for the cryptophytes in the Gerlache Strait stations in January.

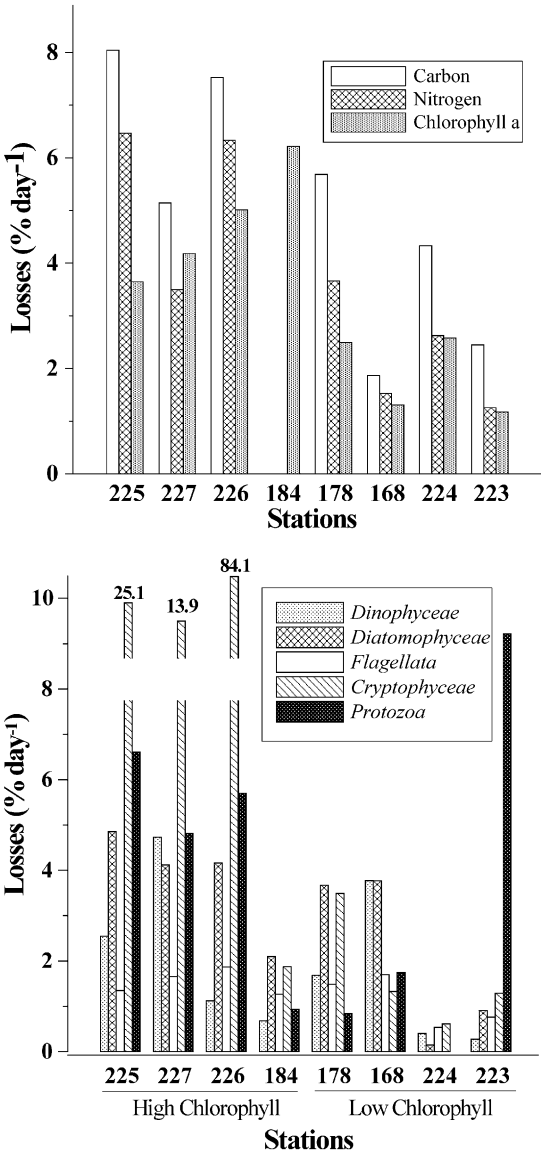

Fig. 7. (A) Losses (related to 60-m water column) of carbon, nitrogen and Chl *a* at the investigation sites. (B) Cells losses of different microbial taxonomic groups at the investigation sites.

3.5. Metabolic activity and degradation of the trapped material

Carbon incorporation rates by phytoplankton cells retained in the traps were considered as an estimate of the physiological activity of the sedimented Chl-*a*-containing particles. Chl-*a*-normalised C incorporation rates at the "high Chl *a*" stations were higher than at the "low Chl *a*" ones during the FRUELA 96 cruise (Fig. 8A). The lowest values were found at two very different stations: st. 184 (central Gerlache Strait during FRUELA 95 cruise) which showed the highest flux of Chl *a* for all data set, and st. 223 (Eastern Bellingshausen Sea, close to the Drake Passage, during the FRUELA 96 cruise). The reason for these low values could be the high amount of FP in the case of st. 184 (Fig. 8B). The presence of degraded particles, originated during the phytoplankton bloom observed during the FRUELA 95 cruise in the slope area (Rodriguez et al., 2002), could explain the low values found at st. 223. Stations located in Bransfield Strait displayed very low C incorporation rates during the two cruises.

Red fluorescent Chl *a* degradation products included the dephytylated chlorophyllide *a* and several Mg-deficient derivatives, such as pheophorbide-*a*-like pigments eluting at different retention time, and two non-polar major peaks with a pheophytin-*a*-like spectrum. The contribution of Chl *a* degradation products to the whole pool of pigments absorbing at 665 nm is shown in Fig. 8A. The distribution pattern was related to the phytoplankton type as well as to the Chl *a* concentration in the water column (see Rodriguez et al., 2002).

The rates of heterotrophic prokaryotic activity of the material retained in the traps (Fig. 8B) indicate that less than 1% of the sedimented material was degraded per day. The heterotrophic prokaryotic activity in the traps (Fig. 8B) was much higher than the activity at the depth of the water column where the traps were located (data not shown), except at st. 227. In general, "low Chl *a*" stations showed higher trap prokaryotic activity (Fig. 8B) than the "high Chl *a*" ones, in spite of higher fluxes and the dominance of $>10\,\mu m$ phytoplankton at these stations. Prokaryotic activity could be related both to the C : N ratio of particulate matter caught in traps and to the FP flux, as demonstrated by the multiple linear regression model: BA $= -7.75$ $(\pm 0.79) + $ C : N 1.068 $(\pm 0.026) -$ FP 3.69E$-$06 $(\pm 1.07$E$-$06); (r^2:

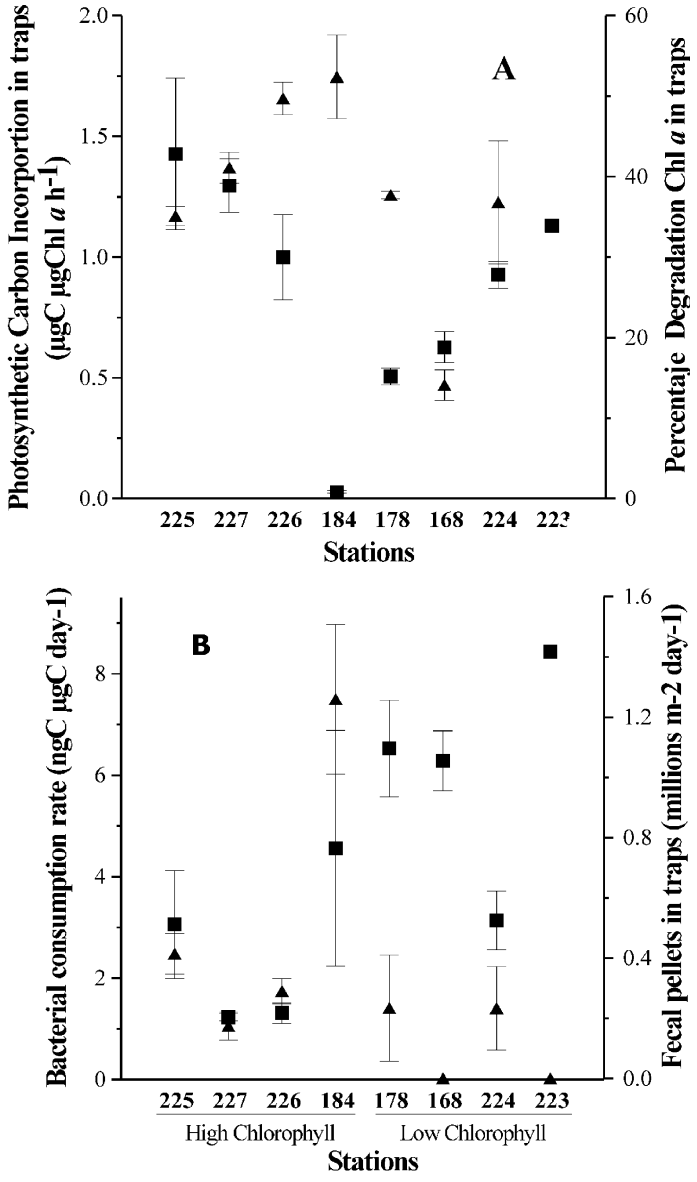

Fig. 8. (A) Photosynthetic carbon incorporation rate of the sedimented material normalised to the Chl *a* of the traps (■) and percentage of Chl *a* degraded products of the sedimented material (▲). (B) Prokaryotic consumption rate normalised to the carbon content in the traps (■) and vertical flux of FP (▲). "High Chl *a*" st.: 184, 225, 226 and 227. "Low Chl *a*" st.: 168, 178, 223 and 224.

0.98; $F = 852.3$; $p < 0.0000$; $N = 23$). The standard errors are given in brackets.

The sedimentation rate of FP longer than 100 µm exceeded 0.2×10^6 FP m^{-2} day^{-1} (Fig. 8B), except for st. 168 and 223, suggesting a relative low impact of the meso- and macrozooplankton community in these stations. At st. 184, a high FP sedimentation rate was detected (with many euphausids FP), linked with a low photosynthetic activity of the sedimented material.

4. Discussion

Although it is difficult to compare data obtained using different methods and deployment depths, the PC fluxes measured during this study appear to be among the highest compiled for Antarctic waters by Karl et al. (1991). Only the rates reported by Bodungen et al. (1986) in a coastal area of the Eastern Bransfield Strait exceed those reported here for the productive areas of the Gerlache Strait.

The vertical flux measured at st. 223 in January (115 mg $C\,m^{-2}\,day^{-1}$) is quite similar to that obtained by (Karl et al., 1991) for their st. 39. Similarly, the C fluxes at st. 168 (115 mg $C\,m^{-2}\,day^{-1)}$ and 224 (175 mg $C\,m^{-2}\,day^{-1}$) of the western Bransfield Basin are close to the rates reported by Karl et al. (1991) for their st. 48. A small increase in the C flux was observed between December (FRUELA 95) and January (FRUELA 96), in agreement with the results of Karl et al. (1991). This increase was not related to higher total primary production rates neither in RACER nor in FRUELA (Varela et al., 2002). However, in our case, a small increase in the production of >10-μm cells was detected (Varela et al., 2002). Export of C in Gerlache was well above the rates obtained by Karl et al. (1991) in their st. 43, located in the transition between the Gerlache and Bransfield straits, possibly as a result of the higher phytoplankton standing stock observed during FRUELA with respect to RACER cruises: our C export values were also well above the mass flux data obtained at 100 m depth with moored traps by Karl and Asper (1990) in the same area. The Gerlache Strait, with sedimentation rates similar to those measured in the confluence between the East Bransfield and the Weddell Sea (Bodungen et al., 1986), appears to be an area of high summer sedimentation, as compared to other Antarctic areas. Carbon flux measurements carried out with moored sediment traps, at 500 m depth in the Western Bransfield Strait (Palanques et al., 2002), accounted only for 2.2% and 4.2% of the measured carbon flux in our traps at the end of December 95 (st. 168) and January 96 (st. 224), respectively.

Wefer et al. (1988), who used deep traps (494 and 1588 m), showed that the flux of biogenic particles in the Bransfield Strait was limited to the December–February period. Our results for the Gerlache Strait show that high biogenic particle flux occurs also at the beginning of February, suggesting a longer productive season in Gerlache, although the observed differences also could be due to the high interannual variability in primary production characteristic of the region (Smith et al., 1988). The fact that the Gerlache Strait is a relatively enclosed area as compared to neighbouring zones, together with the stabilising effect of the melting of glaciers in the coast, could help to maintain a relatively shallow mixed layer, thus enhancing phytoplankton growth during a longer period of time (Varela et al., 2002).

The temporal variation of PC and PON export of N out the photic zone was different among stations; in the Bransfield Strait, the rates were similar during both cruises, whereas in the boundary of the Gerlache Strait, the rates obtained during the second cruise were twice as high (carbon export was three times higher) compared to those measured in FRUELA 95. In the central Gerlache Strait N-export was lower in relation to C for both cruises, probably due to the amount of FP on samples. In general, figures for the vertical N-flux during FRUELA were higher than the rates reported in the RACER study. However, this discrepancy could be due to a simple methodological difference, since sediment traps during RACER and FRUELA were located at 100 and 60 m depth, respectively, and the N-flux decreases rapidly with depth (Karl et al., 1991).

The higher C : N ratios (by atoms) of the material collected by the traps, as compared to the ratios of the particulate material in the water column above the traps reflect a faster mineralisation of nitrogen with respect to carbon. This was also observed by Karl et al. (1991) during the RACER cruises, but not by Bodungen et al. (1986). The highest C : N ratio observed during FRUELA appeared in the Gerlache Strait, at st. 184, where most FP were encountered in the traps, although it did not correspond to a high C : N ratio in the water column (Table 1). The C : N ratio was also high at st. 223 (East of Bellingshausen

Sea), characterised by a low vertical flux, probably related to aged material derived from the Chl *a* maximum detected a month before in the shelf break zone (Castro et al., 2002; Varela et al., 2002).

4.1. Zooplancton and prokaryotic influence in vertical fluxes

FP are known to represent on some occasions a significant amount of the carbon exported from the photic layer (i.e. Andreassen et al., 1996; Bathmann et al., 1987; Gonzalez et al., 1994; Small et al., 1987). The fluxes due to FP can be related with low heterotrophic prokaryotic activities in trap material, as has been previously reported by Karl et al. (1988), as well as with a higher C : N ratio. Low autotrophic C incorporation rates by the sedimented material and presence of degraded pigments derived from zooplankton grazing were measured in association with high vertical fluxes of FP.

The lowest percentage of sedimented cells was measured at stations where FP were abundant and >10-μm cells dominated (st. 184), supporting the idea of the important role of zooplankton in fluxes between photic and deeper waters. However, FP can be grazed and effectively degraded (coprophagy and coprohexy) by meso- and macrozooplankton (Gonzalez and Smetacek, 1994; Noji et al., 1991), representing part of the losses of particulate organic material occurring between 60 and 500 m, as discussed above. These considerations would be valid for most of the stations, where an important amount of FP was observed, but could be of minor relevance for st. 223, where FP were a negligible fraction of the sedimented material.

The amount of carbon processed by prokaryotes in the traps was very low, ranging from 0.01% to 1.8% of the carbon retained during a 24-h period. This was not originated by prokaryotic inhibition, because the prokaryotic activity measured in the traps was 400% higher than the prokaryotic activity at the depth where the traps had been placed. The role of attached prokaryotes converting large, rapidly sinking particles, into non-sinking particles of 0.3–0.6 μm was proposed by Cho and Azam (1988). However, even if prokaryotic activity is relevant in the conversion between POC and DOC, sinking particles appear to be a poor habitat for prokaryotic growth (Karl et al., 1988; Simon and Azam, 1992). FP, in particular, are known to be poorly degradable by prokaryotes (Andrews et al., 1984). The low prokaryotic production rates correlate well with the low respiratory activity measured in the water column at the same stations (Varela et al., 2002) during the FRUELA cruises. We calculated that the time needed to degrade all the sedimented PC would vary between 50 and 2700 days, suggesting that a significant fraction of the exported carbon could reach the sediment without major prokaryotic transformations. These values fit well with the 1500 days estimated by Karl et al. (1988).

4.2. Sinking of nano- and microplankton cells

Sedimentation of phytoplankton (and other small plankton) cells is a complex process, generally related to the sinking of individual cells, but also to the formation of aggregates with marine snow, or with other cells or chains. In this case, both cell stickiness and the formation of transparent exopolimeric particles (TEP) could be relevant processes (Kiørboe et al., 1996).

The methodological approach adopted in this study does not allow to test the possible role of TEP, as splitting of the material intercepted by the traps would produce a disaggregation phenomenon. The daily loss rates obtained for the taxa considered were similar to the rates of C and N export, and of the same magnitude than those obtained by Andreassen et al. (1996) and Andreassen and Wassmann (1998) in Arctic waters. According to our results, the residence time of the cells in the euphotic zone was ca. 20 days. Only in the case of Cryptophyceae a very high significant flux of cells was observed, mainly at the end of January or February (FRUELA 96 cruise), representing a residence time in the photic layer of 1–5 days.

As found here for *Chaetoceros socialis*, the export rate of *Chaetoceros* spp. was shown (Leventer, 1991) to be the major component of the diatoms sedimented during the RACER cruise,

reflecting their high daily loss rate, as well as their abundance in the water column. The importance of *Chaetoceros* spp. and *Chaetoceros socialis* has also been reported for Arctic waters (Andreassen et al., 1996; Andreassen and Wassmann, 1998).

4.3. Phytoplankton size and sedimentation rates

Generally, models explaining the export of particles from the photic layer invoke the effect of phytoplankton size as a principal explanatory variable (Legendre and Demers, 1984; Legendre and Le Fèvre, 1989; Legendre and Rassoulzadegan, 1996). Rivkin et al. (1996) analysed the role of contrasting pelagic food web structures on biogenic carbon export in the Gulf of St. Lawrence, and concluded that the vertical flux of C was independent of trophic structure. The conceptual model of particle export developed by Bathmann (1996) for the Southern Ocean also relates sedimentation to the size structure of the community and to phytoplankton succession patterns, characteristic of the transition from ice melting waters to ocean open waters. This model assumes that productive seasons are characterised by diatom-dominated phytoplankton with higher sedimentation rates, whereas flagellate-dominated communities occur during post-bloom or even during more oligotrophic seasons. We failed to demonstrate significant differences in daily loss rates between "high Chl *a*" stations dominated by large phytoplankton cells $>10\,\mu m$ and "low Chl *a*" stations dominated by small sized phytoplankton cells, although export rates were in general lower for stations in which small cells were dominant, at the end of productive season. These observations support the idea of Rivkin et al. (1996) that sedimentation processes are independent of the main trophic mode and are not related to the dominance of herbivorous or microbial trophic pathways (Legendre and Rassoulzadegan, 1996)

To assess the relative importance of different particles-size classes in vertical fluxes, a produc-

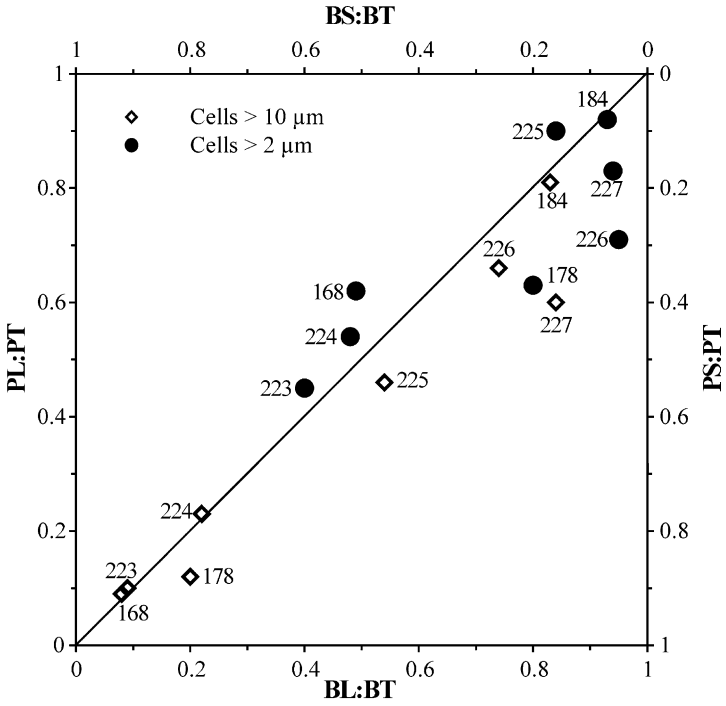

Fig. 9. Relationship between the relative contribution of $>10\,\mu m$ primary production rate, $>10\,\mu m$ Chl *a*, as in Tremblay and Legendre (1994) for the studied stations. PL and PS: production of large and small cells; PT: total production; BL and BS: Chl *a* in large and small cells; BT: total chlorophyll. "High Chl *a*" st.: 184, 225, 226, 227. "Low Chl *a*" st.: 168, 178, 223, 224.

tion–biomass (P–B) diagram (Tremblay and Legendre, 1994) was built using water-column integrated data (Fig. 9). According to this model, data close to the diagonal line represent stations where the relative contribution of large particles to biomass and production is similar, i.e. where production and export are balanced. During FRUELA, we observed significant departures from the diagonal line for stations where the biomass was dominated both by large ("high Chl *a*" stations) and small cells ("low Chl *a*" stations, Fig. 9). At these stations, large phytoplankton seemed to accumulate in the water column, suggesting that patterns in the export rates of phytoplankton in Antarctic waters are more complex than predicted from simple models.

A considerable amount of the biomass stock is exported to deep waters. We estimated a mean daily PC export from the euphotic zone of $294 \pm 89\,\mathrm{mg\ C\,m^{-2}\,day^{-1}}$ for the surveyed area ($7 \times 10^{10}\,\mathrm{m^2}$) and the whole period (52 days). This gives a total amount of 1.1 Mt C exported for the whole area and period, which represents 25.6% of the primary production (4.2 Mt C estimated from data of Varela et al., 2002) and 720% of the estimated air–sea CO_2 flux (0.15 Mt C, derived from data of Álvarez et al., 2002). A comparison of C export with C burial rates is only possible for the Western Bransfield Strait ($0.11 \times 10^{10}\,\mathrm{m^2}$). In this area, C export from the photic layer during the study period was 0.12 Mt C, whereas the estimated mean yearly C burial (only for the area below 1000 m depth) was $0.33\,\mathrm{Mt\ C\,yr^{-1}}$ ($5.6\,\mathrm{g\ C\,m^{-2}\,yr^{-1}}$, Masqué et al., 2002); therefore, the exported C represented only 37% of the carbon accumulated yearly in sediments.

The above calculations indicate that considerable amount of organic carbon must be exported at the beginning of the productive season or alternatively during the unproductive season, unless other mechanisms, such as advection from shelf waters or transport by zooplankton migrating across the photic layer, are taking place. We conclude that the Antarctic Peninsula area plays an important role as a carbon sink, although special attention must be paid in the future to imbalances between C export and CO_2 exchange with the atmosphere or C burial as have been detected during the present survey.

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