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Distribution of microbial biomass and importance of protists in regulating prokaryotic assemblages in three areas close to the Antarctic Peninsula in spring and summer 1995/96

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Abstract

Two cruises were carried out during the Austral spring-summer (November 1995–January 1996: FRUELA 95, and January–February 1996: FRUELA 96), sampling in Bellingshausen Sea, western Bransfield Strait and Gerlache Strait. We investigated whether there were any spatial (among locations) or temporal (between cruises) differences in abundance and biomass of microbial heterotrophic and autotrophic assemblages. Changes in the concentration of chlorophyll *a*, prokaryotes, heterotrophic and phototrophic nanoflagellates abundance and biomass were followed in the above mentioned locations close to the Antarctic Peninsula. Parallel to these measurements we selected seven stations to determine grazing rates on prokaryotes by protists at a depth coincident with the depth of maximum chlorophyll *a* concentration. Measuring the disappearance of fluorescent minicells over 48 h assessed grazing by the protist community. From prokaryotes grazing rates, we estimated how much prokaryotic carbon was channeled to higher trophic levels (protists), and whether this prokaryotic carbon could maintain protists biomass and growth rates. In general higher values were reported for Gerlache Strait than for the other two areas. Differences between cruises were more evident for the oligotrophic areas in Bellingshausen Sea and Bransfield Strait than in Gerlache Strait (eutrophic area). Higher values for phototrophic (at least for chlorophyll *a* concentration) and abundance of all heterotrophic microbial populations were recorded in Bellingshausen Sea and Bransfield Strait during late spring–early summer (FRUELA 95) than in mid-summer (FRUELA 96). However, similar results for these variables were observed in Gerlache Strait as in spring-early summer as well as in mid-summer. Also, we found differences in grazing rates on prokaryotes among stations located in the three areas and between cruises. Thus, during late spring–early summer (FRUELA 95), the prokaryotic biomass consumed from the standing stock was higher in Bellingshausen Sea (26% d^{-1}) and Gerlache Strait (18–26% d^{-1}) than in Bransfield Strait (0.68–14% d^{-1}). During mid-summer (FRUELA 96) a different pattern was observed. The station located in Bellingshausen Sea showed higher values of prokaryotic biomass consumed (11% d^{-1}) than the one located in Gerlache Strait (2.3% d^{-1}). Assuming HNF as the main prokaryotic consumers, we estimated that the prokaryotic carbon consumed by heterotrophic nanoflagellates (HNF) barely covers their carbon requirements for growth. These results suggest that in Antarctic waters, HNF should feed in other carbon sources than prokaryotes.

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1. Introduction

In Antarctic waters the observed concentrations and activity of microbial communities (prokaryotes, nanoflagellates and ciliates) do not differ much from those in lower latitudes (see data in Gasol and Vaqué, 1993, and compare with, e.g., Karl, 1993). However, some variability has been found depending on the hydrographic structures and on the season considered (e.g., Huntley et al., 1991; Berdalet et al., 1997; Becquevort, 1997). Differences in microbial biomass and activities also have been detected between coastal and oceanic Antarctic environments (e.g., Leaky et al., 1996; Pedrós-Alió et al., 1996). During the austral-growing season (spring–summer) is when phytoplankton blooms take place. An increase in DOC released by autotrophs, which is supposed to be used by heterotrophic prokaryotes to grow, can be expected following the phytoplankton bloom, representing the time delay between phytoplankton and prokaryotes blooms (Billen and Becquevort, 1991; Lancelot et al., 1991). Thus, heterotrophic protists (e.g. nanoflagellates) could control prokaryotic assemblages through grazing, converting prokaryotic heterotrophic production (which reach high values in summer, Ducklow and Carlson 1992; Karl, 1993) into larger particles. Those can be used as food by larger protists as ciliates (Verity, 1991) and dinoflagellates (Kuparinen and Bjørnsen, 1992), as well as metazoans (Stoecker and Capuzzo, 1990). Heterotrophic nanoflagellates (HNF) are considered the main consumers of prokaryotes, and grazing can often balance prokaryotic heterotrophic production in temperate waters (Pace, 1988; Berninger et al., 1991). However, in coastal Antarctic waters Leaky et al. (1996) reported that the HNF community appeared to graze substantial prokaryotic heterotrophic production, although grazing never balanced production. Therefore, grazing on prokaryotes by other protists (i.e. ciliates, James et al., 1995) or viral-induced lysis could be relevant alternative sources of prokaryotic mortality (Smith et al., 1992; Steward et al., 1996).

Studies considering the whole protist assemblages (e.g. HNF, ciliates) grazing on prokaryotes in polar waters (coastal and open sea) are scarce. Thus, information to date is based overall on prokaryotic consumption by HNF in coastal or close to the ice edge and their importance in controlling and limiting prokaryotic biomass and production appears to be low (Putt et al., 1991; Leaky et al., 1996; Becquevort, 1997). Hence, there is a need for additional information on prokaryotic losses in different areas other than strictly coastal, as well as in different time periods.

Two cruises were carried out from November 1995 to February 1996 (late spring–mid-summer) at several stations located in three different areas (Bellingshausen Sea, western Bransfield Strait and Gerlache Strait) near the Antarctic Peninsula. We analyzed temporal and spatial changes in microbial plankton biomass as well as prokaryotic carbon flux to protists (HNF, ciliates, dinoflagellates) in these different Antarctic areas. We expected high biomass and activity of phototrophic assemblages during spring–early summer (FRUELA 95), followed by the development of microheterotrophic assemblages during mid-summer (FRUELA 96).

First, we describe the spatial and temporal distribution of chlorophyll *a* concentration, prokaryotes and nanoflagellate abundance and biomass, and determine whether any differences in those microbial assemblages among cruises and areas. Second, we determine how much prokaryotic carbon was channeled to the protistan assemblage (heterotrophic nanoflagellate and ciliates) in seven selected stations representative of the three areas at different periods of time. Finally, we discuss whether protist community controls prokaryotic assemblages top-down and if the ingested carbon suffices protist carbon growth requirements.

2. Material and methods

2.1. Sampling strategy

Two cruises were carried out in the R/V *BIO-Hespérides* from December 1995 to January 1996 (late spring: FRUELA 95) and from January to February 1996 (mid-summer: FRUELA 96). The studied area and sampling sites are shown in

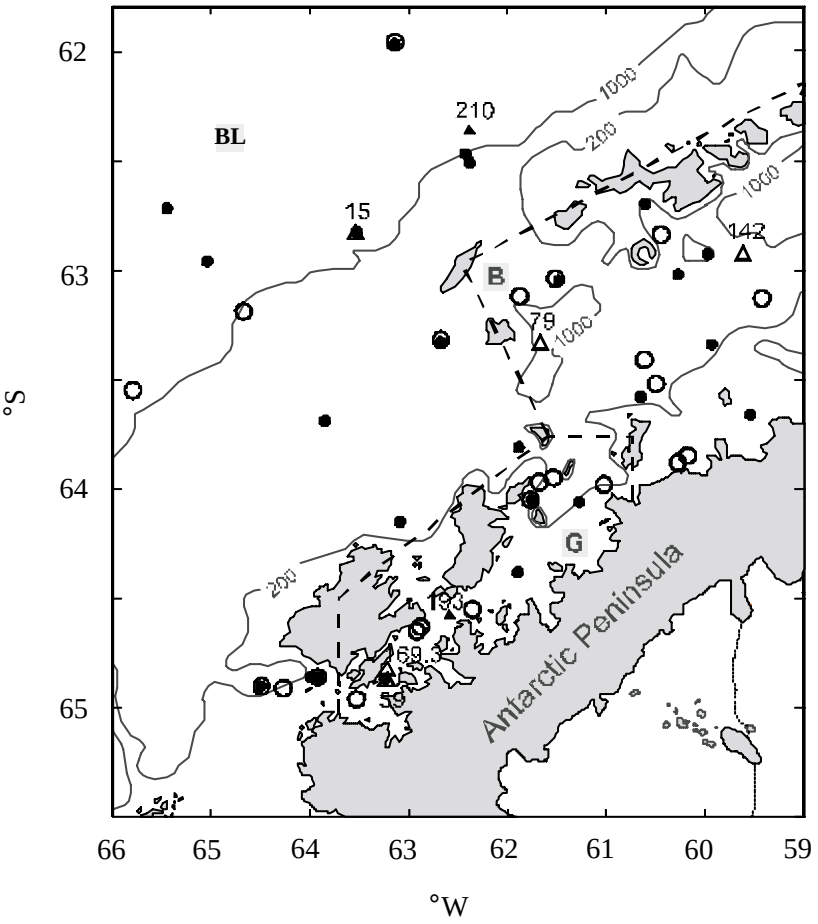


Fig. 1. The study areas (BL: Bellingshausen Sea; G: Gerlache Strait; B: Bransfield Strait) with locations of different station types. Open circles and triangles correspond to the stations sampled during FRUELA 95. Black circles and triangles correspond to the stations sampled during FRUELA 96. (Circles: routine stations; triangles: selected stations for grazing on prokaryotes measurements). 200 and 1000 m isobaths are indicated.

Fig. 1. During both cruises we sampled three representative Antarctic areas. (1) two different deep-water zones (the western basin of Bransfield Strait and the southern Drake Passage: *Bellingshausen Sea*); (2) a frontal zone between the Bellinghausen Sea and Bransfield Strait water masses: *Bransfield Strait*; and (3) the eutrophic and mesotrophic coastal region of *Gerlache Strait* (Fig. 1). Profiles of salinity, temperature, fluorescence and dissolved oxygen were obtained using a CTD EG&G model MkIIIC WOCE between 5 and 1000 m depth. Details on water masses distribution and physico-chemical characteristics as well as water circulation for the studied locations are described in Garcia et al. (2002) and Gomis et al. (2002).

2.2. *Chlorophyll a concentration, prokaryotes and nanoflagellate abundance and biomass*

Samples for chlorophyll *a* were taken from surface to 150 m depth at 10 m intervals with 10 l Niskin bottles attached to a rossette sampler system. Chlorophyll *a* concentration was estimated fluorometrically (Strickland and Parsons, 1972). Samples (100 ml) were collected in 25-mm GF/F glass fiber filters and immediately frozen at -70°C. For more details see Castro et al. (2002).

Six samples of 100 ml (preserved with glutaraldehyde, 1% final concentration) for prokaryotes and nanoflagellates were taken from surface to below the deep chlorophyll maximum (DCM) at 10–20 m intervals at each of the indicated stations (Fig. 1). Water subsamples of 10–20 ml for prokaryotes and 30–50 ml for nanoflagellates were filtered throughout 0.2- and 0.6-μm polycarbonate filters, respectively, and stained with DAPI (4,6-diamidino-2-phenylindole, Porter and Feig, 1980) to a final concentration of 5 μg ml^{-1} (Sieracki et al., 1985). Abundance of these microorganisms was determined by epifluorescence (Nikon Optiphot) microscopy. Nanoflagellate showing red-orange fluorescence and /or plastidic structures were considered phototrophic forms (PNF), while colorless nanoflagellates were counted as heterotrophic (HNF). With this method we could not distinguish mixotrophic nanoflagellates. Prokaryotic size was determined after measurement of approximately 300 cells from two stations from Bransfield Strait and Bellingshausen Sea with an image analysis system attached to the microscope. We custom-modified the software NIH-Image to prokaryotic size. The characteristics of the system, the calibration with latex beads and the choice of filters to process the images are detailed in Massana et al. (1997). Prokaryotic biomass was calculated using the carbon to volume relationship derived by Norland (1993) from the data of Simon and Azam (1989).

$$\text{pg C cell}^{-1} = 0.12 \times (\mu\text{m}^3\ \text{cell}^{-1})^{0.7}.$$

Nanoflagellate size was determined measuring lengths and widths under the epifluorescence microscope, with a calibrated micrometric eyepiece. From 50 to 150 cells (heterotrophic plus phototrophic) were measured per sample. Cell volumes were estimated by assuming the nearest geometrical figure. Carbon content was estimated using a literature volume to carbon factor of 0.22 pg C μm^{-3} (Børsheim and Bratbak, 1987).

2.3. Grazing, prokaryotic heterotrophic production, ciliate and large dinoflagellate biomass

Water samples were collected in representative selected stations of the three considered areas: Bellingshausen Sea, Bransfield and Gerlache Straits. Estimates of grazing on prokaryotes by protists (HNF, ciliates, dinoflagellates,etc.) were determined by disappearance of fluorescent minicells (E. coli strain X-1488, Genetic Stock Center, Yale University), following the Pace et al. (1990) technique. Grazing on prokaryotes was determined at stations 15 and 210 (Bellingshausen Sea), 39, 169.3 and 193 (Gerlache Strait) and 79 and 142 (Bransfield Strait). Stations 15, 39, 169.3, 79 and 142 were occupied in FRUELA 95, and stations 193 and 210 in FRUELA 96 (Fig. 1) at one depth (coinciding with the depth of maximal chlorophyll *a* concentration). In each determination, 4 l samples were taken from the surface (5–20 m), and divided in two parts. 2 l were filtered through 0.8-μm polycarbonate filters (to avoid prokaryotic predators, and used as controls) and the other 2 l through 50-μm net mesh (to eliminate predators larger than 50 μm, e.g., naupliae). Fluorescent minicells were added to the corresponding samples at 20–30% of natural prokaryotic concentrations. Average volume of the used minicells was 0.065 μm^3, rather similar to the average volume of natural prokaryotes (0.054 μm^3). Incubations were run in the dark at in situ temperature, which ranged from −1.19°C to 2.5°C and for 48 h. Minicell, natural prokaryotes, HNF, ciliate, and large dinoflagellate abundance and biomass were determined at the beginning of the experiment and at 48 h by epifluorescence microscopy.

Calculations of consumed prokaryotes ($l^{-1}\,d^{-1}$) were obtained following the mathematical model of Salat and Marrasé (1994):

$$g = -(1/t)\,\text{Ln}\,(\text{Mi}_t/\text{Mi}_0),$$

where g is the grazing rate d^{-1}; t the incubation time; Mi_t the number of minicells at final time and Mi_0 the number of minicells at initial time.

$$a = (1/t)\,\text{Ln}\,(\text{PN}_t/\text{PN}_0),$$

where a is the net growth rate d^{-1}; t the incubation time; PN_t the Prokaryotic number at the end of the experiment, PN_0 the Prokaryotic number at the beginning of the experiment.

$$G = (g/a)(\text{PN}_t - \text{PN}_0),$$

where G is the total grazing (Prokaryotes consumed $l^{-1} d^{-1}$).

Net increase in prokaryotic abundance, here called net prokaryotic heterotrophic production (NPHP, prokaryotes $l^{-1} d^{-1}$), can be obtained by the difference between the number of natural prokaryotes at time t (PN_t, cells l^{-1}) and that of natural prokaryotes at time zero (PN_0, cells l^{-1})

$$NPHP = (1/t)^*(PN_t - PN_0)$$

and gross prokaryotic heterotrphic production (PHP, bacteria $l^{-1} d^{-1}$) was calculated as the sum of total grazing (G) and net prokaryotic heterotrophic production (NPHP)

$$PHP = NPHP + G.$$

These calculations are based on the conservative assumption that all losses of prokaryotes during the incubations are due to grazing by protists.

Ciliate and large dinoflagellate abundance and biomass were examined in single 1 l samples, which were preserved in a 1% final concentration of acidic Lugol solution. A 1 l sample was settled for 48 h, then the supernatant was gently removed until reaching 200 ml. This concentrate was sedimented in 100-ml chambers for at least 48 h before enumeration, at 200 × or 400 × magnification, using an inverted microscope attached to a video camera. Enumeration and sizing were performed from the images recorded in the videotape. Ciliate and dinoflagellate average size was determined after measuring all cells recorded per sample (from 44 to around 400 cells) using the software NIH-Image. Ciliate volume was measured by adjusting each cell to the nearest geometric shape. To avoid the probable underestimation of cell volume due to fixation with Lugol's solution (Leaky et al., 1994a; Stoecker et al., 1994) the average cell volume for each identified group was converted to carbon equivalents using the factor experimentally derived for Lugol's fixed marine oligotrichs, $0.2\,pg\,C\,\mu m^{-3}$ (Putt and Stoecker, 1989). Carbon weight for tintinnids was estimated using the experimentally determined factor of $0.053\,pg\,C\,\mu m^{-3}$ (Verity and Langdon, 1984).

2.4. Data analysis

Data of different variables were depth-averaged for the upper to 80–100 m. These were obtained dividing the integrated values (m^{-2}) by the depth of the water column used as reference (m). The weighted mean obtained has the advantage over an integrated value (m^{-2}) in that it makes the results at stations with different depths of integration comparable.

All variables (chlorophyll a prokaryotes and HNF abundance and biomass) except depth were $\log_{10}$-transformed to equalize variance. The relationships between biological variables and depths were examined by means of Pearson's correlation analysis. Differences in biological variables between cruises and among the three areas were tested by ANOVA. Post hoc Tukey tests were performed when differences between areas were suspected.

3. Results

3.1. Microbial abundance and biomass distribution

The ranges of chlorophyll a, prokaryotes, nanoflagellate (heterotrophic and phototrophic) abundance and biomass at the three sampled zones and for both cruises are shown in Table 1. Average of chlorophyll a concentration and microheterotrophs (prokaryotes and HNF) abundance and biomass showed maximal and minimal values in FRUELA 96 in Gerlache Strait and Bellingshausen Sea, respectively (Table 1). However, PNF abundance presented the highest values in Bellingshausen Sea during FRUELA 95 and lowest in Gerlache Strait during FRUELA 96. HNF were very small, and almost no variations were detected among zones and cruises. Values ranged from $1.39\,\mu m^3\,cell^{-1}$ in Bellingshausen Sea to $8.32\,\mu m^3\,cell^{-1}$ in Bransfield Strait, both minimal and maximal values being detected in FRUELA 96. PNF showed a volume per cell two or three fold higher than HNF. Minimal and maximal values ranged from 5.17 to $16.50\,\mu m^3\,cell^{-1}$ both in Bransfield Strait during FRUELA 96.

Table 1
Number of samples, average, minimum and maximum values of chlorophyll *a* concentration (Chl *a*), prokaryotes (Prok.) and nanoflagellates (heterotrophic: HNF, and autotrophic: PNF) abundance (Ab.) and biomass (Bm), as well as volume (*V*) per nanoflagellate in the different study areas

Variable	Bellingshausen		Bransfield		Gerlache	
	95	96	95	96	95	96
Number of samples	41–42	36–42	47–54	54–66	43–66	36–48
Chl a ($\mu g\,l^{-1}$)						
Average	1.51	0.2	1.01	0.63	2.31	3.53
Range	0.15–4.63	0.04–0.54	0.07–3.97	0.08–1.61	0.11–7.32	0.02–13.62
Prok. Ab. ($\times 10^8$ cells l^{-1})						
Average	3.19	3.19	4.27	3.28	3.83	5.67
Range	1.38–6.81	1.79–6.69	2.10–6.60	1.88–6.52	1.34–7.68	1.99–13.30
Prok. Bm ($\mu g\,C\,l^{-1}$)						
Average	4.96	4.95	6.64	5.11	5.95	8.82
Range	2.15–10.59	2.78–10.41	3.27–10.27	2.92–10.14	2.08–11.95	3.09–20.69
HNF Ab. ($\times 10^6$ cells l^{-1})						
Average	1.47	0.19	0.90	0.34	1.31	1.71
Range	0.30–3.12	0.02–0.36	0.23–1.93	0.06–1.16	0.17–4.72	0.40–5.01
HNF Bm ($\mu g\,C\,l^{-1}$)						
Average	0.99	0.13	0.73	0.28	0.98	1.31
Range	0.17–2.04	0.01–0.38	0.20–1.60	0.04–0.84	0.13–3.27	0.31–3.47
V HNF^{-1} (μm^3 $cell^{-1}$)						
Average	3.05	3.08	3.7	3.78	3.43	3.46
Range	2.48–3.60	1.39–5.56	2.68–4.27	1.90–8.32	2.98–3.78	2.98–3.77
PNF Ab (-10^6 cells l^{-1})						
Average	2.28	1.11	0.83	1.79	1.04	0.33
Range	0.12–7.57	0.09–2.89	0.14–2.35	0.09–5.37	0.12–3.00	0.06–1.56
PNF Bm ($\mu g\,C\,l^{-1}$)						
Average	4.92	2.56	2.11	4.59	2.71	0.78
Range	0.29–19.61	0.14–8.65	0.28–6.17	0.10–16.67	0.21–7.89	0.13–3.79
V PNF^{-1} (μm^3 $cell^{-1}$)						
Average	9.84	9.83	10.95	10.82	10.73	10.47

Vertical distributions of chlorophyll *a* concentration, prokaryotes and nanoflagellate abundance and biomass decreasd between 5 and 100 m in both cruises (Fig. 2; prokaryotes and nanoflagellate biomass are not shown because these variables followed the same trend as abundance). HNF during FRUELA 95, however, did not show any trend with depth. We used a LOWESS (Cleveland, 1979) fit to the data to detect the pattern followed for these variables with depth. Negative correlation between depths and the studied variables were detected (Fig. 2). Distributions of chlorophyll *a*, prokaryotes and nanoflagellate abundance using the integrated values from surface to 80–100 m for each cruise are shown in Figs. 3a–d. Differences among cruises for each integrated variable were investigated by means of ANOVA test. Significant differences were found between FRUELA 95 and

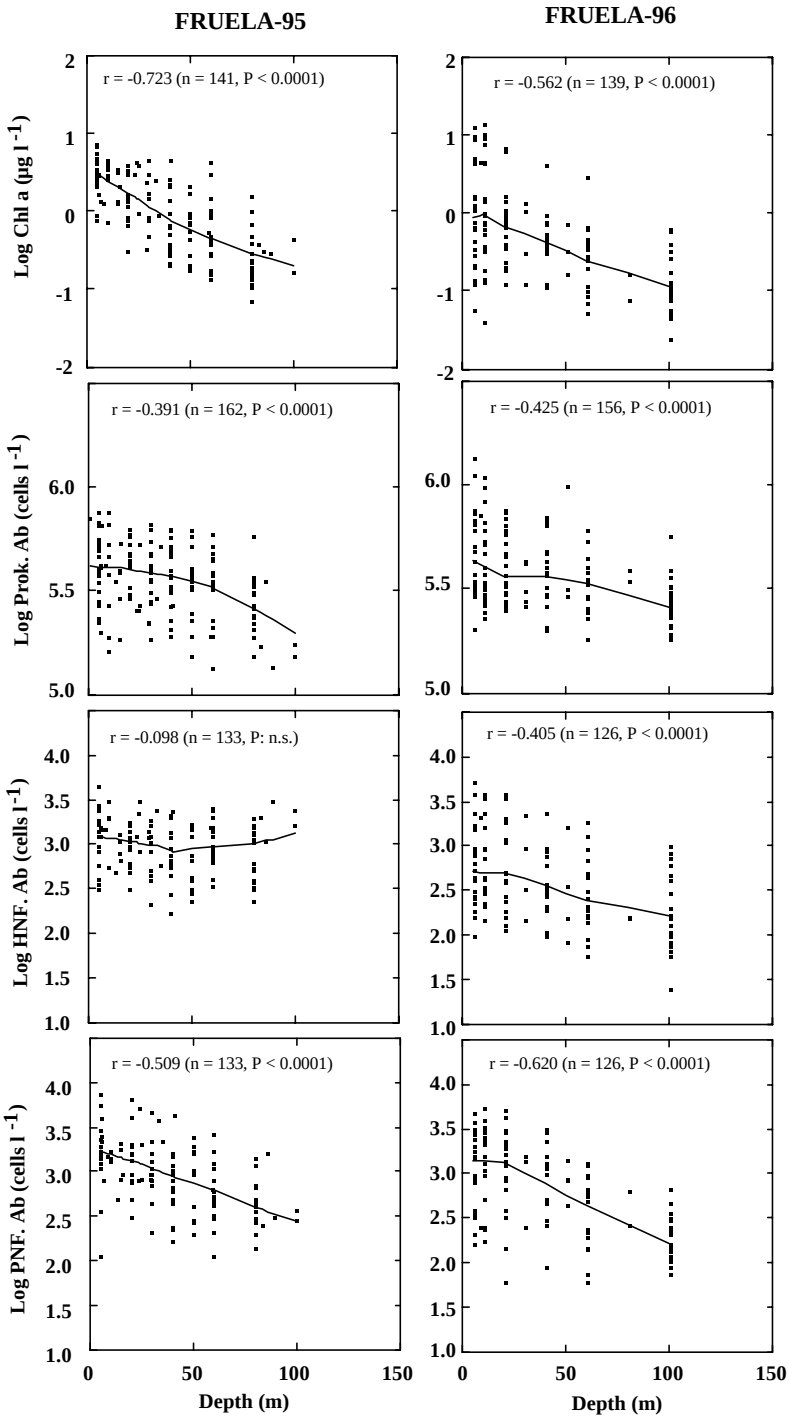
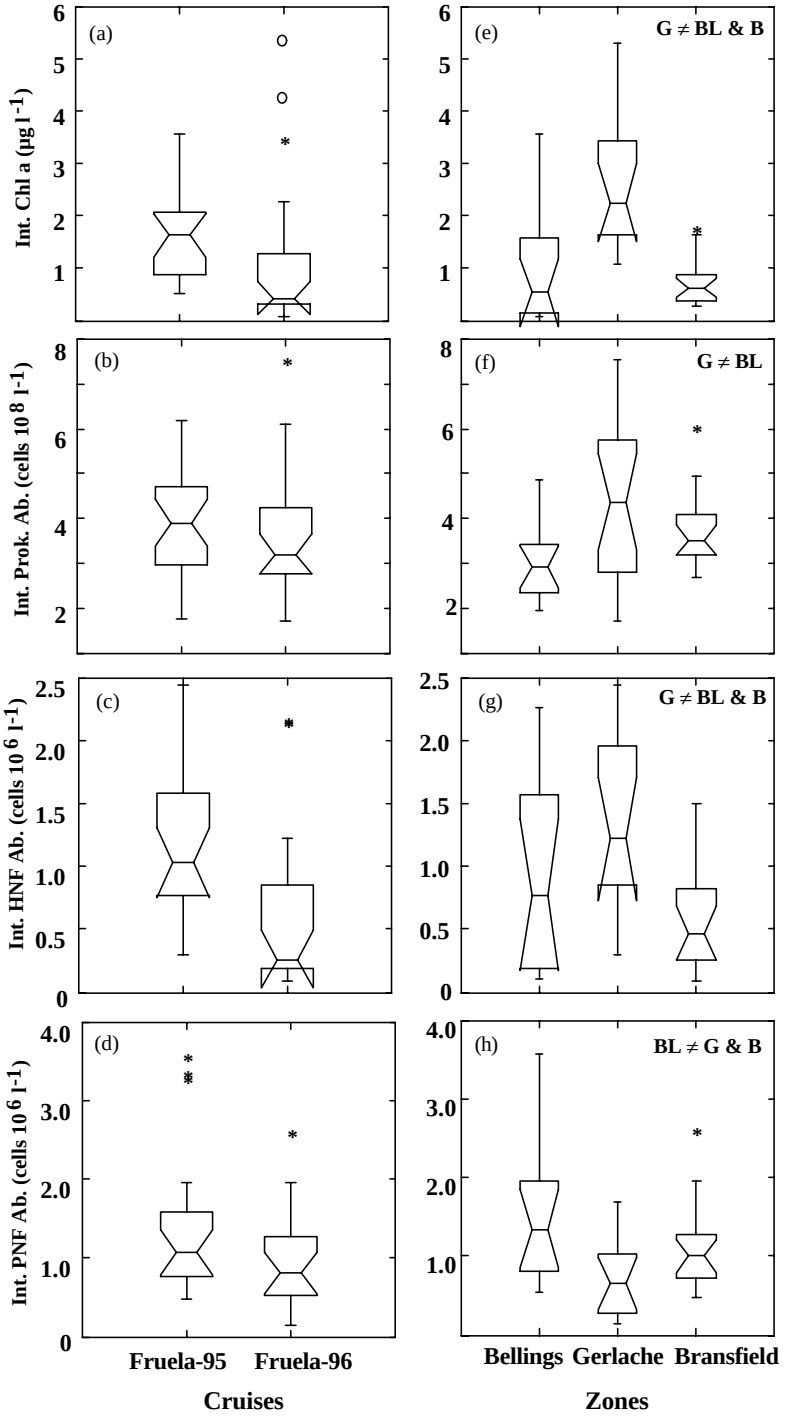


Fig. 2. Deep vertical profiles of pooled log-transformed data of chlorophyll *a* concentration, (Chl *a*), Prokaryotes abundance (Prok. Ab.), heterotrophic nanoflagellate abundance (HNF Ab.), and phototrophic nanoflagellate abundance (PNF Ab.), for each cruise. Correlation coefficients (Pearson) between variables and depth are shown.


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Int. Chl a (µg l-1)
Int. Prok. Ab. (cells 10 8 l-1)
Int. HNF Ab. (cells 10 6 l-1)
Int. PNF Ab. (cells 10 6 l-1)
G ≠ BL & B
G ≠ BL
G ≠ BL & B
BL ≠ G & B
Fruela-95
Fruela-96
Cruises
Bellings
Gerlache
Bransfield
Zones

FRUELA 96 for chlorophyll concentration, HNF abundance ($p<0.05$) and marginally for phototrophic nanoflagellates while no significant differences were found in prokaryote abundances (Table 2). Pooling the integrated data (for each variable) of both cruises, the ANOVA revealed significant differences among the three zones ($p<0.05$ Figs. 3e–h, Table 2). A post hoc Tukey test indicated that the differences were those between Gerlache Strait and the other two areas for chlorophyll *a* and HNF abundance (Figs. 3e and g, Table 2, notice that for HNF, differences between Bellingshausen Sea and Gerlache Strait were marginally significant). For prokaryotic abundance significant differences were found between Bellingshausen Sea and Gerlache Strait (Fig. 3f, Table 2), and PNF abundance showed significant differences between Bellingshausen Sea and the other two areas ($p<0.05$ Fig. 3h, Table 2).

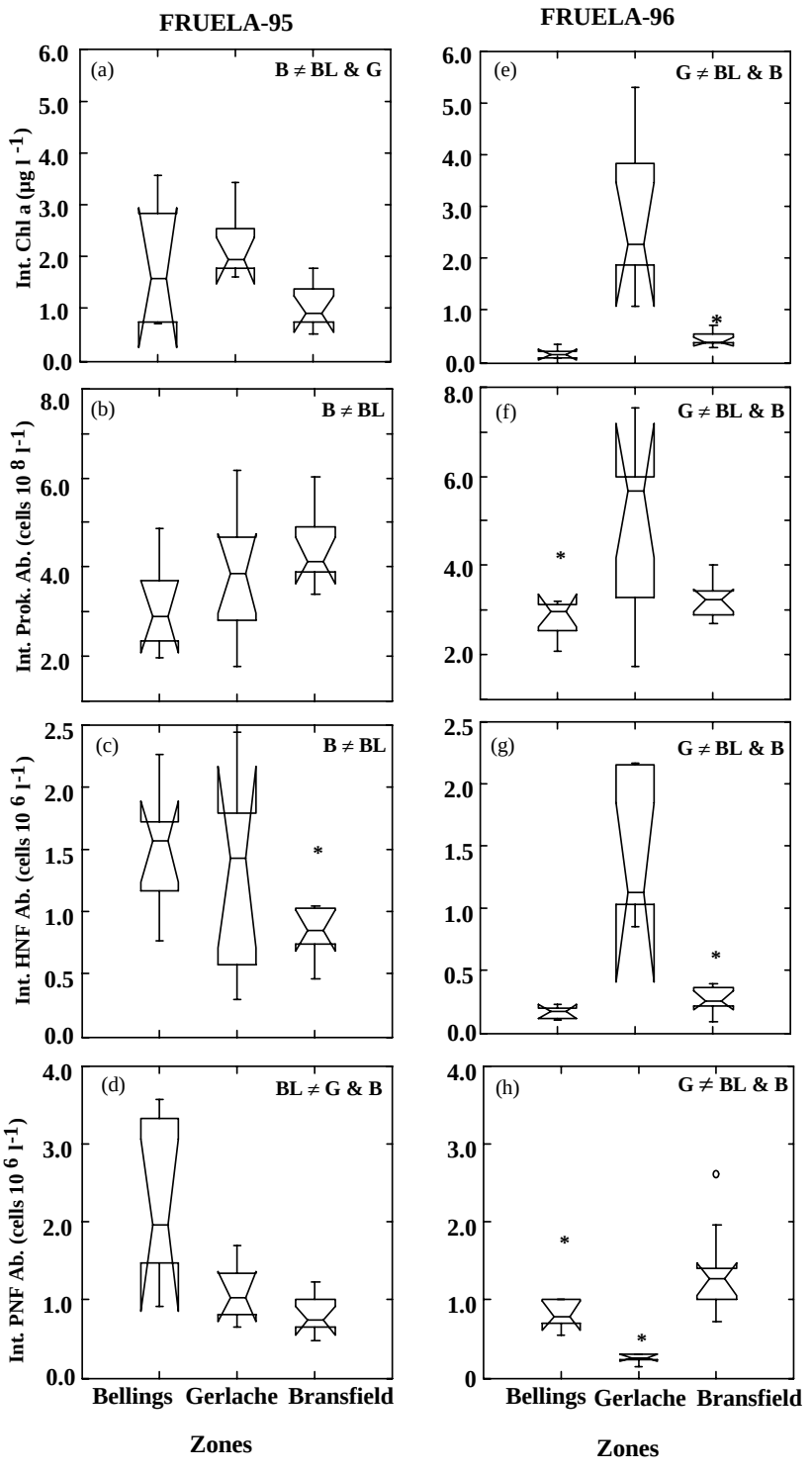
Distribution of the studied variables also was compared among the three areas for each cruise (Figs. 4). During FRUELA 95 differences among areas were observed for chlorophyll *a* concentration and PNF abundance (Figs. 4a and d, Table 2). No differences among areas were observed for prokaryotic abundance or for HNF abundance (Table 2, Figs. 4b–c). A post hoc Tukey test revealed that for FRUELA 95 differences in chlorophyll *a* were significant between Bransfield Strait (achieving the lowest values) and Gerlache Strait and marginally significant with Bellingshausen Sea (Fig. 4a, Table 2). For PNF differences

Table 2
Results of ANOVA test to show differences for each biological variables between cruises and among zones. Differences between zones were performed by Post hoc Tukey test. Values of $p<0.05$, are considered significant.[a]

Cruise & period	Factors	Statistical analysis	Variables											
			Chl *a* conc.			Prok. Ab.			HNF Ab.			PNF Ab.		
			N	*F*	*p*	*n*	*F*	*p*	*n*	*F*	*p*	*n*	*F*	*p*
Fruela 95–96	Cruises	ANOVA	44	5.89	<0.05	53	0.68	0.173	43	11.20	<0.01	43	3.20	0.081
	Zones	ANOVA	42	15.45	<0.001	53	3.81	<0.05	43	5.46	<0.01	43	5.40	<0.01
	BL–G	Post-h.T.	42	15.96	<0.001	53	7.62	<0.01	43	3.56	0.061	43	10.66	<0.01
	BL–B	Post-h.T.	42	0.88	0.355	53	2.67	0.109	43	1.67	0.204	43	4.18	<0.05
	G–B	Post-h.T.	42	29.17	<0.001	53	1.58	0.214	43	10.89	<0.01	43	2.05	0.16
Fruela – 95	Zones	ANOVA	21	4.50	<0.05	27	2.32	0.120	22	1.98	0.166	22	9.85	<0.001
	BL–G	Post-h.T.	21	0.82	0.376	27	1.43	0.243	22	0.46	0.505	22	10.97	<0.01
	BL–B	Post-h.T.	21	3.52	0.075	27	4.63	<0.05	22	3.81	<0.05	22	18.00	<0.001
	G–B	Post-h.T.	21	8.60	<0.01	27	1.26	0.272	22	1.56	0.226	22	0.68	0.421
Fruela – 96	Zones	ANOVA	23	26.35	<0.001	26	6.06	<0.01	21	26.92	<0.001	21	10.40	<0.001
	BL–G	Post-h.T.	23	41.99	<0.001	26	9.61	<0.01	21	42.35	<0.001	21	6.20	<0.05
	BL–B	Post-h.T.	23	0.99	0.332	26	0.22	0.645	21	0.53	0.475	21	3.36	0.081
	G–B	Post-h.T.	23	40.66	<0.001	26	8.80	<0.01	21	40.96	<0.001	21	20.79	<0.001

[a] BL: Bellingshausen Sea, B: Bransfield Strait and G: Gerlache Strait.

Fig. 3. Box and whiskers plots of depth averaged (from the surface to 80–100 m) of chlorophyll *a* concentration (Chl *a*), prokaryotes abundance (Prok. Ab.), heterotrophic nanoflagellate abundance (HNF Ab.) and autotrophic nanoflagellate abundance (PNF Ab.) for each cruise (a–d), and different sampled areas (e–h). Differences between cruises for the study variables are included in the graphs (a–d), and pooled values in each zone (BL: Bellingshausen, G: Gerlache, B: Bransfield) (e–h). The central line of the box is the median of the distribution, and the box limits are the 25% quartiles of the data. The whiskers cover the entire data range, except very extreme observations, which correspond to double of standard deviation (*), or outliers (o).


FRUELA-95
FRUELA-96
(a)
B ≠ BL & G
(e)
G ≠ BL & B
Int. Chl a (µg l -1)
(b)
B ≠ BL
(f)
G ≠ BL & B
Int. Prok. Ab. (cells 10 8 l-1)
(c)
B ≠ BL
(g)
G ≠ BL & B
Int. HNF Ab. (cells 10 6 l-1)
(d)
BL ≠ G & B
(h)
G ≠ BL & B
Int. PNF Ab. (cells 10 6 l-1)
Bellings
Gerlache
Bransfield
Zones

were found between Bellingshausen Sea and the other two areas ($p<0.05$ Fig. 4d Table 2). Differences for prokaryotes and HNF abundance were observed between Bellingshausen Sea and Bransfield Strait ($p\leqslant 0.05$ Figs 4b–c, Table 2). During FRUELA 96 differences among the three areas were detected for all variables ($p<0.05$ Table 2). A post hoc Tukey Test indicated that the significant differences for all variables were those between Gerlache Strait and the other two areas (Figs. 4e–h, Table 2). (Note that data on prokaryotes and nanoflagellate biomass are not shown because we obtained the same differences between cruises and among zones as for abundance.)

3.2. *Microbial assemblages and total grazing rates in seven representative stations*

Temperature varied from −1.19°C in Gerlache Strait (FRUELA 95) to 2.5°C in Bellingshausen Sea (FRUELA 96, Table 3). Changes on phototrophic and heterotrophic microbial biomass assemblages in the stations and depths considered are shown in Table 3. Chlorophyll *a* concentration, prokaryotic, HNF and PNF abundance and biomass followed the same trend as those described in Table 1. Prokaryotic heterotrophic production reached the highest value at the beginning of summer in Gerlache Strait and Bellingshausen Sea (FRUELA 95) coinciding with the maximal values recorded for chlorophyll *a* concentration. However, this is not the case for Gerlache Strait in mid-summer (FRUELA 96) where high chlorophyll *a* concentration did not correspond to high prokaryotic heterotrophic production. Abundance and biomass of ciliates and large dinoflagellate showed the highest values in Gerlache Strait (station 193, Table 4) coinciding with the highest values of prokaryotic abundance and biomass and moderately high nanoflagellate abundance and biomass. The lowest values recorded for these large protists were found in Bransfield Strait (Table 4).

Oligotrichs ciliates were the most abundant group in five of the seven stations sampled. However in stations 142 (Bransfield Strait) and 169.3 (Gerlache Strait) these ciliates represented 27% and 48% of the total ciliate abundance, respectively. Tintinnids were present in Bransfield and Gerlache Straits and showed the highest abundance in station 193 (Gerlache Strait) representing 63% of the total ciliate abundance (Cil l^{-1}) but only 20% of the total ciliate biomass (μg C l^{-1} Figs. 5a and b). Dinoflagellates as large *Gyrodinium* were less abundant than ciliates (Table 4 and Fig. 5a). However, their contribution in biomass to the pool of large protists was remarkable in stations 15 (Bellingshausen Sea), 39 and 193 (Gerlache Strait) (Fig. 5b). Heterotrophic protists therefore were represented by small heterotrophic nanoflagellates, ciliates (naked oligotrichs, small tintinnids and other ciliates) and large dinoflagellates (e. g. *Gyrodinium*). On one hand HNF with linear dimensions smaller than 5 μm dominated the assemblage (>80%) of small protists (Table 5). Only, in stations 15 and 39 (FRUELA 95) and 193 (FRUELA 96) more than 10% of the cells examined were larger than 5 μm and few choanoflagellates were observed. On the other hand, ciliates and dinoflagellate assemblages were dominated by large cells, especially in Gerlache Strait, where cells higher than 20 μm reached more than 80% of the total community. In volume, cells larger than 20 μm reached values up to 10^6 μm^3 cell^{-1} (Table 5).

Measurements of grazing on prokaryotes were determined using long incubation (48 h) and determining the disappearance of minicells (Pace et al., 1990) in water samples previously filtered by 50-μm mesh net. Additionally, we used controls without prokaryotic predators (water filtered through 0.8-μm filters) in which losses of minicells were negligible. During FRUELA 95 net growth rate of prokaryotes and consumption of prokaryotic biomass by protist were higher in the Bellingshausen Sea and Gerlache Strait than in

Fig. 4. Box and whiskers plots of integrated values (from the surface to 80–100 m) of chlorophyll *a* concentration (Chl *a*), prokaryotes abundance (Prok. Ab.), heterotrophic nanoflagellate abundance (HNF Ab.) and autotrophic nanoflagellate abundance (PNF Ab.) for each sampled area in FRUELA 95 (a–d), and FRUELA 96 (e–h). Differences among areas for all study variables (BL: Bellingshausen, G: Gerlache, B: Bransfield) are shown. Explanation of these kind of plots is given in Fig. 3 legend.

Table 3
Date, areas, stations (Stn) and depths (*Z*) where grazing on bacteria was determined, as well as temperature (*T*), chlorophyll *a* concentration (Chl *a*) and the mean (±standard error) of prokaryotes abundance, biomass, production and consumption, and nanoflagellate abundance and biomass (heterotrophic nanoflagellates: HNF and phototrophic nanoflagellates PNF)

Date	Area	Stn	*Z* (m)	*T* (°C)	Chl a ($\mu g\,l^{-1}$)	Prokaryotes				HNF		PNF	
						Abundance ($\times 10^8\,l^{-1}$)	Biomass ($\mu g\,C\,l^{-1}$)	Production ($\mu g\,C\,l^{-1}\,d^{-1}$)	Grazing ($\mu g\,C\,l^{-1}\,d^{-1}$)	Abundance ($\times 10^6\,l^{-1}$)	Biomass ($\mu g\,C\,l^{-1}$)	Abundance ($\times 10^6\,l^{-1}$)	Biomass $\mu g\,C\,l^{-1}$
6-12-95	Bellingshausen	15	20	−0.06	4.43	3.52 (±0.43)	5.61 (±0.68)	4.09 (±0.29)	1.47 (±0.44)	2.17 (±0.21)	1.73 (±0.30)	3.91 (±0.06)	10.12(±0.15)
24-1-96	Bellingshausen	210	30	2.40	0.23	3.48 (±0.40)	5.55 (±0.64)	0.69 (±0.01)	0.76 (±0.00)	0.32 (±0.00)	0.24 (±0.00)	1.35 (±0.36)	2.43 (±0.00)
14-12-95	Bransfield	79	8	0.00	1.34	3.62 (±0.07)	5.78 (±0.12)	0.64 (±0.11)	0.04 (±0.22)	0.87 (±0.07)	0.54 (±0.18)	0.87 (±0.43)	2.34 (±1.10)
18-12-95	Bransfield	142	5	0.17	2.36	6.96 (±0.12)	11.11(±0.19)	0.87 (±0.57)	1.52 (±0.60)	0.52 (±0.04)	0.49 (±0.03)	0.59 (±0.01)	1.58 (±0.31)
10-12-95	Gerlache	39	5	−1.19	3.28	2.48 (±0.00)	3.95 (±0.00)	1.23 (±0.00)	0.99 (±0.02)	0.46 (±0.04)	0.37 (±0.08)	1.27 (±0.02)	3.53 (±0.53)
28-12-95	Gerlache	169.3	5	0.24	6.12	6.01 (±0.66)	9.59 (±1.05)	4.91 (±0.61)	1.77 (±0.25)	0.36 (±0.03)	0.24 (±0.00)	0.74 (±0.03)	2.25 (±0.02)
20-1-96	Gerlache	193	8	0.48	5.92	7.24 (±0.36)	11.55 (±0.56)	0.77 (±0.00)	0.28 (±0.00)	2.07 (±0.00)	1.71 (±0.00)	0.25 (±0.00)	0.57 (±0.00)

Bransfield Strait (Table 3 and Figs 6a and b). However, during FRUELA 96 net growth of prokaryotes and prokaryotic biomass consumption showed a different pattern. The station located in the Bellingshausen Sea showed similar values for net prokaryotic growth and higher prokaryotic biomass consumption than the one located in Gerlache Strait (Table 3, Figs. 6a and b). Comparing both cruises, net prokaryotic growth and prokaryotic consumption were higher in stations sampled during FRUELA 95 than during FRUELA 96. The protistan community, therefore, appeared to consume substantial (up to 26% d^{-1}) or moderately low (down to 0.68% d^{-1}, which was in the detection limit) percentage of prokaryotic biomass, depending on the area as well as on the period considered. The percentage of prokaryotic heterotrophic production (PHP) grazed ranged from 0.93 to 174% d^{-1}, both extreme values occuring in Bransfield Strait during FRUELA 95 (Fig. 6b). Stations with highest percentage of PHP grazed coincided with the lowest values of prokaryotic net growth rates (stations 210 and 142). Net growth rates of HNF did not always show positive values during FRUELA 95 (Fig. 6a). Negative values of HNF net growth rates were detected in Bransfield Strait. No increase in abundance or biomass of ciliates after 48 h. was detected. Probably there was not sufficient time for the ciliates to grow.

4. Discussion

4.1. Temporal and spatial distribution of microbial abundance and biomass

The obtained results show that microbial abundance and biomass distribution can vary spatially (horizontally and vertically) and temporally. Contrary to our expectations, however, similar or higher values for heterotrophic microbes was recorded in late spring–early summer (FRUELA 95) than in mid-summer (FRUELA 96, Table 1). PHP determined in the same cruises by Pedrós-Alió et al. (2002) showed similar patterns as for microbial biomass distribution. Differences of PHP found in both cruises were stronger for

Table 4
Abundance, biovolume and biomass of heterotrophic ciliates and large dinoflagellates present in the selected stations

Area	Stn	Z (m)	Ciliates			Dinoflag		
			Abundance ($\times 10^3$ l^{-1})	Biovolume ($\times 10^8$ µm^3 l^{-1})	Biomass (µg C l^{-1})	Abundance ($\times 10^3$ l^{-1})	Biovolume ($\times 10^8$ µm^3 l^{-1})	Biomass (µg C l^{-1})
Bellingshausen	15	20	6.73	11.11	24.37	1.17	8.17	17.97
Bellingshausen	210	30	2.25	1.73	3.81	0.36	0.41	0.89
Bransfield	79	8	4.85	1.65	3.39	0.36	0.25	0.54
Bransfield	142	5	2.37	0.56	1.23	0.39	0.15	0.33
Gerlache	39	5	4.28	3.02	6.35	0.40	7.11	15.62
Gerlache	169.3	5	5.81	8.64	17.68	0.34	2.46	5.42
Gerlache	193	8	20.91	23.30	43.39	1.24	22.71	49.88

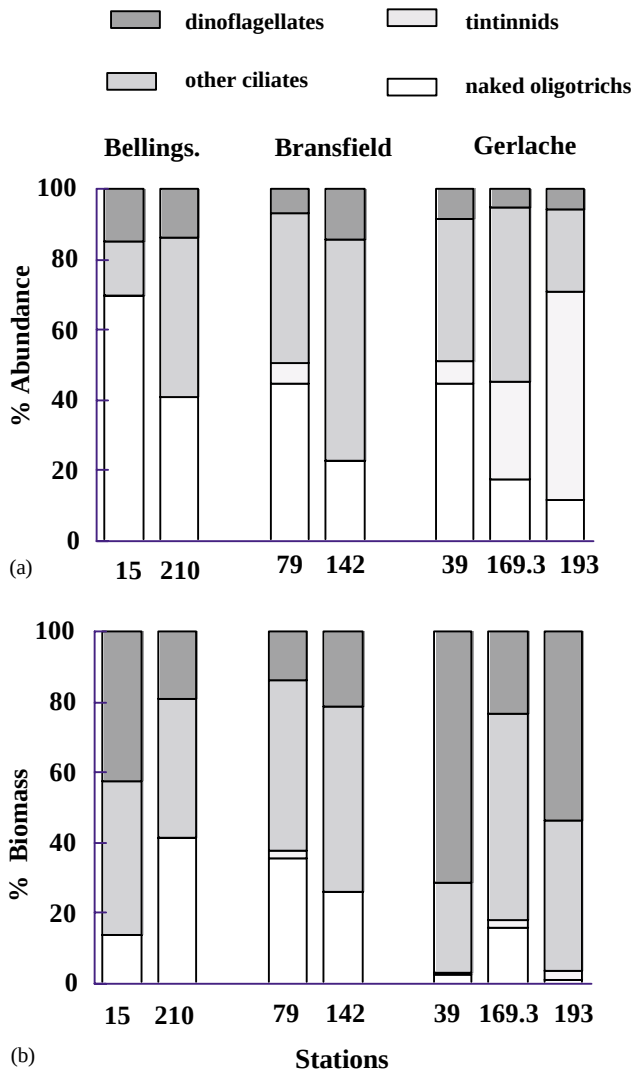


Fig. 5. Contribution of dinoflagellate and ciliate abundance (a) and biomass (b) to the pool of protists larger than 10 µm.

Table 5
Mean cell size and biovolume (with range) and number of measured cells (n) of the heterotrophic nanoflagellates and larger protists (including heterotrophic ciliates plus dinoflagellates) present in samples from selected stations. Percentage of heterotrophic nanoflagellates and other protists smaller and larger than 5 or 20 μm, respectively

Date	Area	Stns	Z (m)	HNF					Ciliates + Dinoflagellates				
				n	Length (μm)	Volume (μm^3)	<5 μm (%)	>5 μm (%)	n	Length (μm)	Volume ($\times 10^3$ μm^3)	<20 μm (%)	>20 μm (%)
6-12-95	Bellingshausen	15	20	40	2.04 (0.80–7.20)	3.60 (0.27–17.16)	90.00	10.00	44	38 (12–96)	37 (0.6–697)	22.00	78.00
24-1-96	Bellingshausen	210	30	10	1.52 (0.80–2.40)	2.60 (0.27–7.24)	100.00	0.00	44	26 (11–78)	8 (0.7–38)	38.60	61.40
14-12-95	Bransfield	79	8	20	1.64 (0.80–4.00)	2.79 (0.27–7.24)	95.00	5.00	44	28 (12–52)	4 (0.5–15)	25.00	75.00
18-12-95	Bransfield	142	5	30	2.00 (0.80–4.80)	4.36 (0.27–7.24)	100.00	0.00	49	29 (8–85)	3 (0.2–8)	34.70	65.30
10-12-95	Gerlache	39	5	40	2.64 (0.80–8.80)	3.62 (0.27–13.27)	80.00	20.00	83	35 (13–139)	21 (0.9–1010)	13.00	87.00
28-12-95	Gerlache	169.3	5	40	1.78 (0.80–8.00)	3.09 (0.27–12.06)	97.50	2.50	108	37 (10–122)	18 (0.5–245)	17.60	82.40
20-1-96	Gerlache	193	8	40	2.21 (0.80–8.80)	3.35 (0.27–13.27)	88.75	11.25	393	49 (10–115)	21 (0.4–3170)	7.90	92.10

Bellingshausen Sea and Bransfield Strait than for Geralche Strait (Pedrós-Alió et al., 2002). Integrated values for chlorophyll *a* concentration, prokaryotes and nanoflagellates generally showed higher values in FRUELA 95 than in FRUELA 96 for Bellingshausen Sea and Bransfield Strait (Fig. 4). However, in Gerlache Strait similar values for those variables were recorded in both cruises (except for phototrophic nanoflagellates).

Differences between Gerlache Strait and the other two areas can be attributed to the more eutrophic status (bloom of diatoms, see Varela et al., 2002) than Bellingshausen Sea and Bransfield Strait (small phytoplankton, Jimenez-Gómez et al., 2002). Comparison of microbial assemblages found in this study with those reported in other Antarctic waters revealed that prokaryotic abundance and biomass were similar, except for the two Maritime Antarctic lakes (Table 6). HNF showed abundances similar to other Antarctic waters, except for Heywood lake (Laybourn-Parry et al., 1996) and Bellingshausen Sea (Pedrós-Alió et al., 1996) characterized by the highest and lowest abundances, respectively. HNF biomass was low in comparison to the biomass found by other authors (Table 6). Small non-collared cells, with a mean linear size lower than 5 μm dominated the main bulk of HNF in these three areas (average: 2.0 μm). Leaky et al. (1996) found in Pridz Bay that small non-collared flagellates (average: 2.5 μm), although fairly abundant throughout the study period, contributed little to the total heterotrophic nanoflagellate biomass. They also found that large non-collared HNF dominated the total assemblage of HNF, comprising between 25% and 95% of the total biomass. Values of prokaryotes and HNF biomass obtained in the present study fall in the low range obtained for other Antarctic waters. Part of the differences in microbial biomass among systems may be attributed to the different ways of cell volume measurements and carbon factors used (see Leaky et al., 1996 and references therein).

4.2. Grazing and production methodologies

Several methods have been used to measure grazing on prokaryotes (see Vaqué et al., 1994,

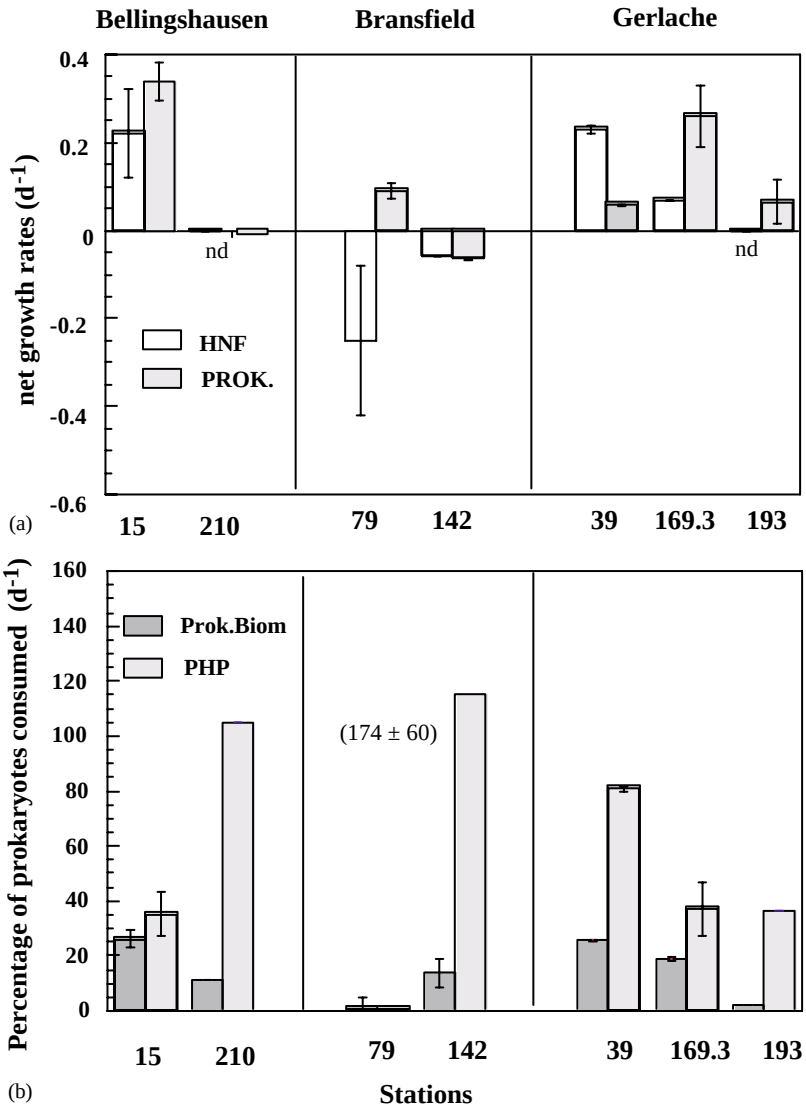


Fig. 6. (a) Net growth rates (d^{-1}) of prokaryotes (Prok.) and HNF measured in the incubations bottles where grazing on prokaryotes was performed, n.d.: not determined. (b) Percentage of consumed prokaryotes d^{-1} from the standing stock (Prok. Biom.) and from the total PHP.

Landry, 1994). The most common method, at least in Antarctic waters, has been the use of fluorescently labeled bacteria (FLB), and determination of the uptake of these tracers by protists (HNF and ciliates) in short term incubations (Putt et al., 1991; Laybourn-Parry et al., 1995, 1996; Becquevort, 1997). In contrast, we used the disappearance of fluorescent tracers (minicells) in long-term incubations (48 h). Both methods has advantages and limitations, but common limitation is the use of heat-killed fluorescent bacteria. There is some evidence that HNF may select living motile prokaryotic cells in preference to FLBs, causing a 50% greater underestimation in grazing rates (Landry et al., 1991; Monger and Landry, 1992; Christoffersen et al., 1997). Direct measurements

Table 6
Abundance and biomass of prokaryotes and heterotrophic nanoflagellate, as well as temperature and grazing on prokaryotes using similar techniques, recorded in different Antarctic environments.[a]

Location and source	Season	Prokaryotes abundance ($\times 10^8$ l^{-1})	Prokaryotes biomass (μg C l^{-1})	HNF abundance ($\times 10^6$ l^{-1})	HNF biomass (μg C l^{-1})	Ingestion (bacteria HNF^{-1} h^{-1})	Prokaryotic biomass grazed (% d^{-1})	Temperature (°C)	Grazing method
Melt Ponds[1] McMurdo Ice shelf	Dec91–Jan92	0.3–3.4	Nd	Nd	Nd	n d	0.0–>10.0[b]	?	BEADS
Crooked lake[2] Ultraoligotrophic Antarctic lake	Dec92–Nov93	1.2–4.5	2.0–10.0	0.0–0.5	0.0–2.4	0.2	n d	2.0–4.0	FLB
Heywood lake[3]	Dec94–Jan95	<10.0–80.0	5.0–450.0	1.0–17.4	2.0–73.0	0.8	n d	2.3–4.8	FLB
Sombre lake Maritime antarctic lake	Dec94–Jan95	<10.0–32.0	2.0–148.0	1.0–4.1	4.0–9.0	0.5	n d	1.3–3.7	FLB
Ice edge[4] McMurdo sound	Nov90–Jan91	0.8–7.0	n.d.	1.0–12.0	n.d.	0.01–2.4	0.5–30.0[c]	−1.0–0.4	BEADS
Drake passage[5]	Jan 94	0.5–7.1	2.7–5.8	0.04–0.4	1.6–2.7	n.d.	0.02–0.05	−1.0–6.0	Estimated
Prydz bay[6]	Dec93–Feb94	2.1–8.3	13.0–64.0	1.6–4.2	7.5–16.0	0.06–8.3	2.8–12.2	−1.4–(−0.4)	FLB
This study	Dec95–Feb96	1.4–13.3	2.1– 20.7	0.02–4.7	0.01–3.5	0.1–13.7	0.7–26.0	−1.2–2.5	MINIS

[a] 1: [20]James et al. (1995); 2: [29]Laybourn-Parry et al. (1995); 3: [30]Laybourn-Parry et al. (1996); 4: [47]Putt et al. (1991); 5: [43]Pedrós-Alió et al. (1996); 6: [33]Leaky et al. (1996); nd: not determined; b: grazing on bacteria by ciliates; c: estimated grazing based in a maximum value of clearence rate.

of feeding rates on prokaryotes avoid bottle effects, and grazing can be ascribed to each kind of protist. However, these measurements are only possible when the abundance of predator and prey are high enough to detect ingestion rates in a short period of time (e.g., lakes of Signy Islands; Laybourn-Parry et al., 1996). James et al. (1995) selected some taxa of prokaryotic consumer ciliates, which were able to ingest a large amount of prokaryotes in a short period of time. Laybourn-Parry et al. (1995) let the natural populations of HNF grow before carrying out grazing measurements, because natural abundance was too low, and Leaky et al. (1996) added large amounts of tracers.

Long-term incubations have the advantage in detecting grazing activity in environments where abundance and production of prey and/ or predator are very low. In this case we are integrating the losses of prokaryotes over 24–48 h. We are certainly aware of bottle effects and those tracers (FLB, minicells,etc.) that are ingested may be assimilated or pass through consumers and egested intact. In the latter case, they likely will be compacted in fecal material as fluorescent particles (Pace and Bailiff, 1987), but some could be redispersed and counted again, thus causing an underestimation of the community grazing rate. It therefore may be, problematic to compare these short-term estimates where only HNF predators are considered to long-term incubations where predators others than HNF also must be considered. Comparison between grazing on prokaryotes determined by short-term and long-term incubations was done in Vaqué et al. (1992, 1994). As expected the later authors found slightly higher grazing values for long-term disappearance experiments than for direct uptake on prokaryotes. Consequently, grazing on prokaryotes in the three study areas must be compared with caution with the values recorded in other Antarctic environments (Table 6).

The most commonly used techniques to estimate PHP are the uptake of ^{3}H-leucine (Kirchman, 1993; Smith and Azam, 1992) and ^{3}H-thymidine (Furhman and Azam, 1982). In the present study, however, PHP was estimated from the increase in prokaryotes after 48 h in the bottles used for

grazing measurements and adding the prokaryotes consumed by grazers for the same period of time. PHP was estimated in this way because it is inappropriate to compare the two activities (grazing and production) obtained with different incubation times and procedures. While estimates of PHP by ^{3}H-leucine or ^{3}H-thymidine is measured within a short time period (4 h, see Pedrós-Alió et al., 2002), grazing determination requires much longer incubations to attain measurable values in these waters. For this reason we prefer to compare the consumed and produced prokaryotes within the same incubation bottles. This estimate of PHP probably is an underestimation because calculations are based on the conservative assumption that all losses of prokaryotes during the incubations were due exclusively to grazing by protists. Guixa-Boixereu et al. (2002) found substantial prokaryotic mortality due to viruses.

4.3. Prokaryotic grazing rates

Grazing rates on prokaryotes presented in this study have to be considered as a rough estimation for each zone and considered time period. We are concerned that the number of stations where grazing rates were measured does not cover by far the large number of stations sampled for each zone throughout FRUELA 95 and FREULA 96. Grazing on prokaryotes was more important in the stations where either PHP or biomass reached the highest values (stations 15, 142, 39 and 169.3, FRUELA 95), with the exception for station 193 (FRUELA 96). At this station prokaryotic and protists biomass reached high values, but PHP and consumption were low, (Table 3). Also, abundance and biovolume of ciliates and dinoflagellates were highest at this status. We could not find any plausible explanation for low prokaryotic consumption in station 193.

Although we expected to find a relationship between total amount of prokaryotes grazed and HNF abundance and growth rate, this was not always evident. Two possible explanations could be given for this lack of relationship. First: the prokaryotic assemblage is not only grazed by HNF, since both ciliates and dinoflagellates also can contribute to prokaryotic consumption (e.g., Lessard, 1991; Sherr and Sherr, 1994), and measured grazing on prokaryotes in these samples corresponds to total protistan community. Second: ciliates and dinoflagellates also could graze HNF, and that would explain the observed moderate abundances of HNF. Indeed, it would be difficult to justify that prokaryotes were the main carbon source for the whole protist community. Prokaryotic abundance in these areas were too low (c.a. 10^8 cells l^{-1}) to maintain populations of bacterivorous ciliates (following the arguments of Fenchel, 1987; Sherr et al. 1989), which showed fairly high biomass in the considered stations. Ciliates, together with heterotrophic dinoflagellates are important grazers of nanoplankton production (Capriulo et al., 1991; Lynn and Montagnes, 1991). It is therefore likely that ciliates and heterotrophic dinoflagellates in the study area were grazing on both nanoflagellates and large phytoplankton, indirectly consuming prokaryotes by grazing on bacterivorous flagellates or by ingesting prokaryotes associated to detrital algal particles (Leaky et al., 1994b; Archer et al., 1996). This would also explain the low nanoflagellate (heterotrophic and phototrophic) biomass and the negative HNF net growth rates in our incubation botttles (Fig. 6a).

The percentage of prokaryotic biomass consumed (0.68–26% d^{-1}) was slightly higher than that observed in other studies, in which only grazing by HNF or ciliates was considered (Table 6). Also, the percentage of PHP consumed was equal to or higher than 100% in the two stations where net prokaryotic growth rate was close to zero or negative (Fig. 6). We were probably overestimating grazing on PHP (calculated as the sum of total grazing and net prokaryotic increase after 24 h), because the PHP removed by viruses was not taken into account. Guixa-Boixereu et al. (2002) found that viruses in stations 15, 79 and 169.3 remove a substantial percentage of PHP. In general low grazing on prokaryotic biomass and production were observed (except for stations 210 and 142, Fig. 6). From these results we infer that grazing by the protist assemblage at many of the stations did not control the prokaryotic communities. Perhaps, if any top-down control on PHP and biomass exists, it could be attributed to other

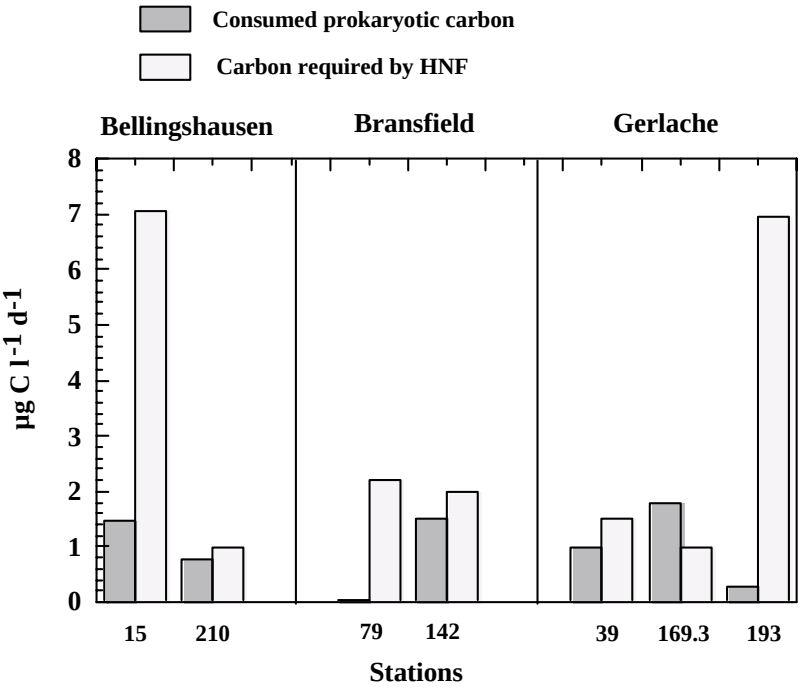


Fig. 7. Ingested prokaryotic carbon and estimated carbon requirements of heterotrophic nanoflagellates for growth.

sources, such as viruses (Guixa-Boixereu et al., 2002).

We estimated prokaryotes ingested per HNF and per hour by dividing the total number of consumed prokaryotes by the abundance of HNF, assuming HNF as main consumers. Six of the seven stations fell in the range (0.1–7.8 prokaryotes $HNF^{-1}\,h^{-1}$) reported by other authors (Table 6). However, ingested prokaryotes per HNF recorded at station 169.3 were slightly higher ($13.7\,HNF^{-1}\,h^{-1}$). Even if HNF ingested all the grazed prokaryotic carbon (Fig. 6), it would barely cover their carbon requirements for growth. To illustrate this, we calculated HNF carbon demand based on the highest net growth rate obtained in the incubation bottles ($0.2\,d^{-1,}$ Fig. 6). The adopted value is similar to that used by Laurion et al. (1995) in Resolute Passage (Canadian Arctic), and assuming a growth efficiency of 30% (Caron and Goldman, 1990). HNF carbon requirement based on net growth rates has to be considered as minimal because HNF mortality is not taken into account. Ingested prokaryotic carbon clearly met HNF carbon demand in one out of seven cases (Fig. 7). Consequently, based in these rough estimates, in Antarctic waters, prokaryotic carbon seems to contribute very little to the HNF biomass (Fig. 7) and even less to that of other protists. Hence, HNF need to feed on carbon sources. They may graze on small algae not much smaller than themselves (Goldman and Caron, 1985) or they may use dissolved organic matter (DOM) in an abbreviated food chain (Sherr, 1988; Marchant and Scott, 1993), a phenomenon already observed in Antarctic waters.

5. Conclusions

Microbial community abundance and biomass distribution presented some differences depending on the study area and sampling time. Opposite to what we expected, higher heterotrophic microbial biomass and production (see Pedrós-Alió et al., 2002) were recorded during the spring–early summer (in the oligotrophic Brllingshausen Sea and Bransfield Strait) than in mid-summer. Differences between spring and summer were not found

for the studied variables in the eutrophic Gerlache Strait. Although grazing on prokaryotes is slightly higher during spring than in summer, protists exerted low control on prokaryotic communities in most of the considered stations, and in any case prokaryotic carbon was not the main carbon source for protists growth.

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