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Mesozooplankton distribution and grazing during the productive season in the Northwest Antarctic Peninsula (FRUELA cruises)

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Abstract

Mesozooplankton distribution and community structure in the Bellinghausen-Bransfield sector of the Antarctic Ocean were investigated during the FRUELA cruises (December 1995–February 1996). Total mesozooplankton biomass ranged between 0.015 and 1.43 g C m^{-2}. Biomass was higher in the Southern boundary of the Antarctic Circumpolar Current (SbyACC) area and in coastal waters of the Antarctic Peninsula. Total mesozooplankton abundance ranged from 0.4×10^3 to 1.3×10^5 individuals m^{-2}, of which 41.6–99.5% corresponded to copepods, mainly families Oithonidae, Oncaeidae, Pseudocalanidae, Calanidae and Metrididae. There was no evidence of coupling between mesoscale physical features and biomass or community structure. While coastal stations mainly at the Gerlache Strait remained in a highly productive state through the spring–summer, oceanic stations experienced a marked shift from a productive condition during FRUELA 95 to a low biomass, pteropod-dominated situation during FRUELA 96, possibly due to changing weather conditions. The median ingestion rates of herbivorous crustaceans during the FRUELA cruises were 0.7 mg Chl *a* m^{-2} day^{-1}. Measured ingestion rates represented only 0.1% of the chlorophyll standing stock or 10% of the daily primary production. Thus, crustacean mesozooplankton had little control on the development of phytoplankton blooms in the area.

1. Introduction

An important objective of the FRUELA project was to quantify of the downward flux of photosynthetically fixed CO_2 as phytoplankton aggregates and zooplankton fecal pellets in an area of elevated productivity in the Antarctic Ocean: the East Bellinghausen Sea and the Bransfield and Gerlache Straits. The magnitude of carbon fluxes associated with sinking fecal pellets depends not only on the amount of carbon ingested by zooplankton but also on the taxonomic structure of zooplankton populations (Fortier et al., 1994). In the Bellinghausen-Bransfield sector of the Antarctic Ocean, studies have focused on the distribution of groups of selected species (Marin and Schnack-Schiel, 1993) or macrozooplankton

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assemblages (Witek et al., 1985; Pakhomov et al., 1994), but seldom on mesozooplankton assemblages (e.g., Hopkins, 1985). In the 80s and 90s, the RACER cruise paid attention to the dynamics of particular species such as *Calanoides acutus* or *Metridia gerlachei* (Huntley and Escritor, 1991; Lopez and Huntley, 1995), while the STERNA cruise focused on the response of mesozooplankton to the spring phytoplankton bloom (Robins et al., 1995; Atkinson and Shreeve, 1995). The FRUELA project's goal of understanding the temporal and spatial variability of the biological pump in the Bellinghausen and Bransfield Straits required a mixed approach involving quantification of fluxes and assessment of taxonomic structure over broad spatial scales. In this context, the first aim of the present study was to quantify the mesozooplankton species composition and biomass as well as their relationship with environmental and biological parameters. A secondary aim was to quantify the carbon flux through the crustacean herbivorous community using the gut pigment technique.

2. Materials and methods

Sampling was conducted aboard R/V BIO Hespérides during the FRUELA 95 (December 1995 to January 1996, spring) and FRUELA 96 (January to February 1996, summer) cruises (Anadón and Estrada, 2002; see Fig. 1 for station map). Both cruises included an initial macroscale survey, with several transects in the Brandsfield Strait and neighbouring Bellingshausen Sea areas, a further sampling of several stations at the

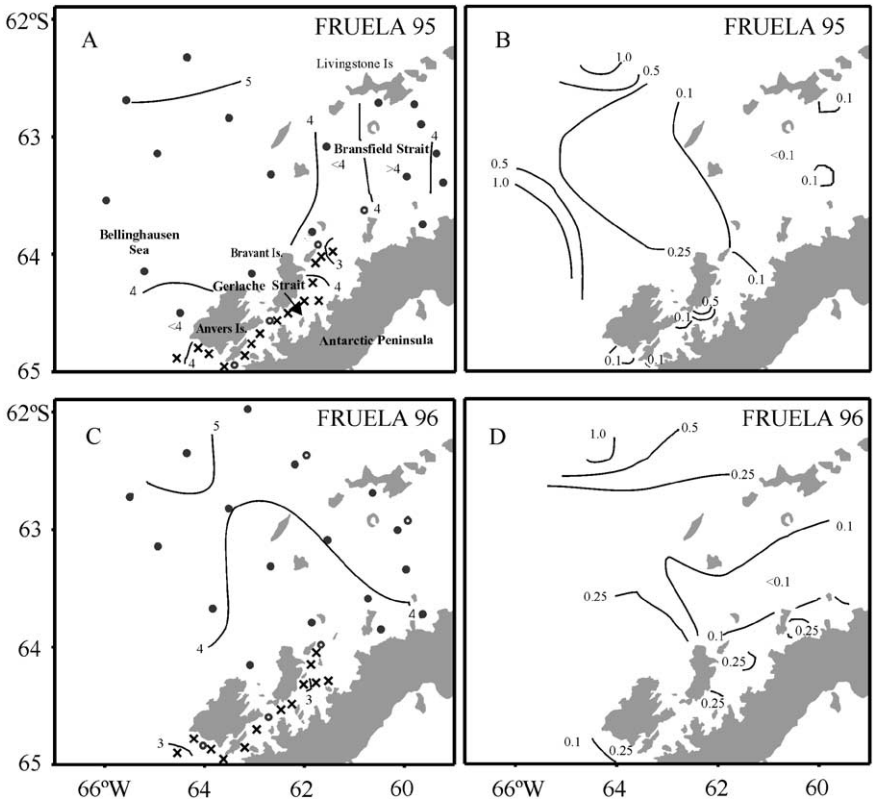

Fig. 1. Abundance and biomass. A: Stations map and zooplankton abundance [$\log_{10}$(individuals) m^{-2}] in FRUELA 95. B: Zooplankton biomass ($g\,C\,m^{-2}$) in FRUELA 95. C: Stations map and zooplankton abundance (log indv. m^{-2}) in FRUELA 96. B: Zooplankton biomass ($g\,C\,m^{-2}$) in FRUELA 96. Legend: ●, macroscale stations; ○, daily cycle sts.; ×, Gerlache Strait sts.

Gerlache Strait, and a last section comprising 30-h stations with diel cycle sampling every 6 h, at positions determined by a drifting buoy. Sampling procedures for physical and chemical variables can be found in Gomis et al. (2002) and García et al. (2002), and for chlorophyll concentration and primary productivity in Varela et al. (2002).

Zooplankton samples for taxonomy analysis, CNH biomass determination and gut pigment content analysis were collected by 200–0 m vertical tows of a modified triple-ring WP2 net with 0.125-m^2 mouth area and 200-μm mesh size. Cod end contents were immediately fractionated into three size fractions, 200–500 (small), 500–1000 (medium), and >1000 μm (large), using sieve cups equipped with Nitex screens. Samples for taxonomic analysis were preserved in 2–4% sodium borate-buffered formalin, and later examined under a stereomicroscope to assess the species composition and abundance. We did not include Actinopoda and Foraminifera in our taxonomic analysis, in spite of their high densities at some stations, because our sampling method was not adequate for these groups. Similarly, the abundance data of large size zooplankton (Euphausiids and Salps) must be considered with caution because of potential net avoidance or extremely aggregated distributions. Samples for biomass analysis were rinsed with 0.2-μm filtered seawater, filtered onto pre-combusted (450°C, 24 h), preweighed Whatman GF/A filters and dried at 60°C for 24 h; their dry weight was measured with a Sartorius microbalance. After grinding each sample in a mortar, the CNH content of a subsample was measured with a Perkin Elmer CNH 2400-II analyzer.

We used the gut pigment technique (Mackas and Bohrer, 1976) to measure grazing rates of herbivorous crustacean zooplankton. For the analysis of gut pigment contents, zooplankton from the different size fractions was rinsed by immersion in filtered (0.2 μm) seawater, filtered onto 45-mm diameter sharkskin filters (Head, 1986), and stored at −60°C in the dark. The entire procedure was completed in less than 5 min. Animals for gut evacuation experiments were collected using a WP2 net equipped with closed, soft plastic cod ends. Cod-end contents were size fractionated as above and introduced in a cooler filled with filtered seawater from the same station. Subsamples were filtered and stored (as above) during 45 min for copepods and 3 h for euphausiids. Sampling interval was 5 min during the first 30 min for both groups, with additional sampling at 45 min for copepods and at 45, 60, 90, 120 and 180 min for euphausiids.

Animals were picked from the frozen filters, within 1 year of collection, under a dim light stereomicroscope. The number of copepods picked varied between 1 and 50, and was typically greater than 10. When the number was large enough, duplicate samples were taken. Euphausiids were analysed independently, except for a few small animals that were pooled in groups. No attention was paid to species or development stage, but carnivorous species were avoided. Animals were placed in 25-ml glass vials with 5 ml of 90% acetone and pigments were extracted overnight, in the dark, at 4°C. Fluorescence was measured in a Turner Designs II fluorometer before and after acidification (Mackas and Bohrer, 1976). Pigment concentration was estimated as chlorophyll *a* equivalents (Chl *a*). No correction for background fluorescence or pigment destruction was applied. Individual ingestion rate was calculated as

$$I = \mathrm{GPC}\, k,$$

where I is ingestion rate (ng Chl *a* $\mathrm{ind}^{-1}\,\mathrm{day}^{-1}$), GPC is individual gut pigment content (ng Chl *a* ind^{-1}), and k (d^{-1}) is the gut evacuation rate, represented by the slope of the exponential decay in gut contents with time obtained in the gut evacuation experiments (Mackas and Bohrer, 1976). Population grazing rates of each zooplankton category were calculated as individual ingestion (calculated by equation above) times population densities. Chlorophyll a values were converted into C using a C : Chl factor of 60.

The variance structure of the mesozooplankton abundance data was summarized by principal component analysis (PCA) of the correlation matrix between abundances of species. Rare taxa that appeared in less than 10% of the samples were excluded from the analysis. For PCA, raw abundance data were transformed as $\log_{10}$ (species abundance + 1) to normalize distributions and

stabilize variances (as tested by Kolgomorov-Smirnov and Barlett tests). Cluster analysis (Ward's method) was performed on the station component scores to separate stations in groups. ANOVA and a posteriori Student-Newman-Keuls were used to test the differences between cluster groups. SPSS + PC + and STATISTICA packages were used for all data analyses.

3. Results

3.1. Abundance and biomass

Mesozooplankton abundance within the top 200-m layer varied between 0.4×10^3 and 1.3×10^5 indv. m^{-2}. It was higher in the offshore stations and reached minima in some isolated stations close to coastal areas (Fig. 1). Copepods comprised between 41.6% and 99.5% of the total zooplankton by numbers.

Mesozooplankton biomass ranged between 0.01 and 1.5 g C m^{-2} during FRUELA 95, and averaged ($\pm$SD) 0.158 ± 0.230 for the large, 0.065 ± 0.135 for the small and 0.021 ± 0.030 g C m^{-2} for the medium size fractions, although the latter comprised more than 90% of the total biomass in some coastal stations. Maximum values occurred in the area of the SbyACC, near the continental slope, and minimum values in the Bransfield Strait; low or intermediate values were found in the Gerlache Strait (Fig. 1). A similar distribution was found in FRUELA 96, with maximum values in the Bellinghausen Sea, offshore of the continental slope (Fig. 1). Average mesozooplankton biomass at the Gerlache Strait was higher during FRUELA 96 than during FRUELA 95 (t-test, $p < 0.001$), and increased from the southern to the northernmost stations.

3.2. Species composition

A total of 76 mesozooplankton taxa were found in the FRUELA cruises. In FRUELA 95, a total of 62 mesozooplankton taxa were identified, of which 36 were copepods. 48 mesozooplankton taxa were identified in FRUELA 96, including 28 copepod species. The numerically dominant taxa were species of the families Oithonidae (*Oithona similis*, *Oithona frigida*), Oncaeidae (*Oncaea curvata*, *Oncaea antarctica*) and Pseudocalanidae (*Ctenocalanus citer*, *Microcalanus pygmaeus*). Cyclopoid (*Oithona* spp.) and Poecilostomatoid (*Oncaea* spp.) copepods often dominated the copepod assemblage and accounted for 40–80% of total numbers of the mesozooplankton community. The most abundant species of Calanoid copepods were *Ctenocalanus citer, Metridia gerlachei*, *Microcalanus pygmaeus*, *Rhincalanus gigas*, *Calanoides acutus, Calanus propinquus* and *Calanus simillimus*.

3.3. Community structure

To summarize the spatial and temporal patterns of variation in the structure of the mesozooplankton community, we performed a Principal Component Analysis (PCA) on the matrix of correlation between the log-transformed abundances of 58 taxa that appeared in more than 20% of the samples (Fig. 2). In addition, we applied a cluster routine on the samples according to their scores on each of the principal components; this procedure allowed us to discriminate four distinct groups of samples: 1, 2, 3 and 4 (Fig. 2).

The first three principal components of the PCA accounted for 44% of the total variance. The first principal component (PC I), which explained 17% of the total variance, had a high positive contribution from the subantarctic species *C. simillimus*, *Oithona similis* and *Limacina helicina*, and moderate negative contribution of *Oncaea curvata, M. gerlachei* as well as nauplius and eggs of *Euphausia superba* (Fig. 2). This component showed moderate, negative correlations with the average water column chlorophyll and salinity, and separated group 3 from the rest of groups (Fig. 2). Group 3 samples are thus characterized by high values of component 1 and are associated with low chlorophyll concentrations and low salinity (Fig. 2; Table 1). These samples were collected at the oligotrophic, open waters of the Bellinghausen Sea and Bransfield Strait during FRUELA 96 (Fig. 3), and representative species like *Calanus simillimus* (Table 1) are distributed accordingly (Fig. 4).

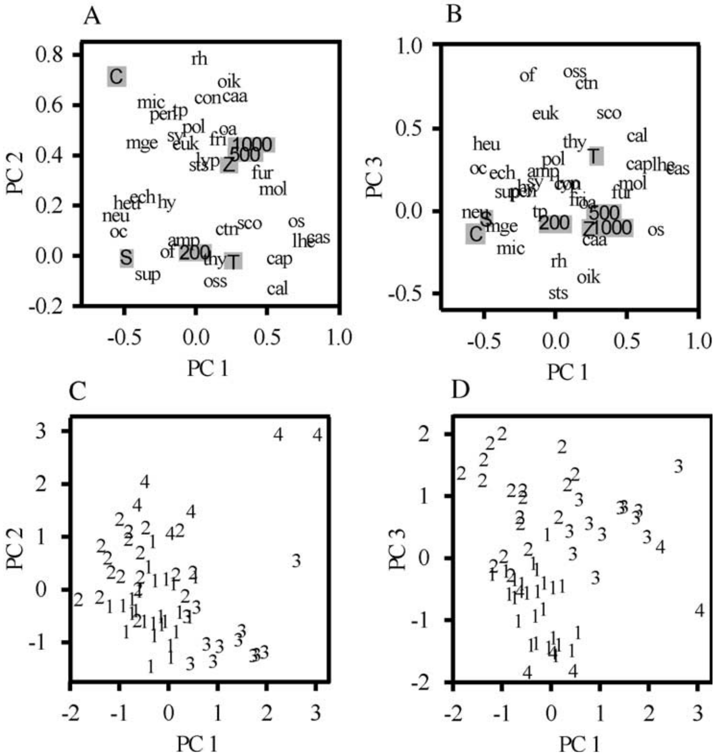

Fig. 2. Result of the Principal Components Analysis (PCA) performed on the species abundances vs. sampling station matrix. (a) Plot of the factor loadings of each taxa on principal components 1 and 2. amp: Hyperiid amphipoda; caa: *Calanoides acutus*; cal: *Calanus spp*. juveniles; cap: *Calanus propinquus*; cas: *Calanus similimus*; cli: *Clio pyramidata*; con: *Conchoecia spp*; ctn: *Ctenocalanus citer*; ech: echinodermata larvae; euk: *Eukrohnia hamata*; fri: *Fritillaria antarctica*; heu: euphausiid egg; hy: hidrozoa; lhe: *Limacina helicina*; lyp: calyptopis; fur: furcilias; mge: *Metridia gerlachei*; mic: *Microcalanus pigmaeus*; mol: molusca larvae; neu: euphausiid nauplii; oa: *Oncaea antarctica*; oc: *Oncaea curvata*; of: *Oithona frigida*; oik: *Oikopleura gaussi*; os: *Oithona similis*; oss: *Oithona spp*.; pen: *Paraeuchaeta antarctica*; pol: polychaeta larvae; rh: *Rhincalanus gigas*; sco: *Scolecithricella minor*; sts: *Sagitta spp*.; sup: *Euphausia superba*; sy: siphonophora; tad: unidentified tadpole-like larvae; thy: *Thysanoesa macrura*; tp: *Tomopteris carpenteri*. The shaded squares represent other environmental and zooplankton biomass variables, not included in the PCA but which are plotted according to their correlation with the principal components. (b) Same as (a) above, but for principal components 1 and 3. (c) Plot of the scores of each sample on principal components 1 and 2. Numbers represents groups of stations as defined by cluster analysis on the species abundance vs sampling station matrix. (d) Same as (c), but for principal components 1 and 3.

The second principal component (PC2) accounted for 15% of the total variance. Most of the species, but especially *Rhincalanus gigas*, *Microcalanus pigmaeus* and the appendicularian *Oikopleura* sp., showed positive loading coefficients on this component (Fig. 2). PC2 was strongly correlated with the average water column chlorophyll, and moderately correlated with the biomass in the 500–1000 and >1000 mesozooplankton size fractions, but not with the 200–500 size fraction (Fig. 2), indicating an association with chlorophyll-rich areas in which large zooplankton was abundant. PC2 separated group 4 samples from those of the rest of groups. Group 4 samples were collected during FRUELA 1995 in the Bellingshausen Sea (Fig. 3), which was characterized by a dense phytoplankton bloom associated with the shelf break. However, many of the species characteristic of group 4, like *Rhincalanus gigas* (see Table 1), also appeared with moderate densities in the Gerlache Strait (Fig. 4).

Table 1
Mean (±SE) values of environmental variables, zooplankton biomass, abundance of dominant mesozooplankton species, and comparison of variable values between cluster groups according to a multiple range SNK test[a]

	Group 1	Group 2	Group 3	Group 4	SNK Test
Number of stations	25	18	12	6	
Surface temperature (°C)	0.38±0.17	0.85±0.34	1.43±0.18	0.09±0.09	3>1
Mean temperature (°C)	−0.19±0.09	−0.01±0.08	0.48±0.08	−0.12±0.17	3>4=2>1
Surface salinity	33.24±1.04	32.61±1.25	25.08±3.25	33.84±0.02	4=1=2>3
Mean salinity	34.18±0.02	34.19±0.02	34.03±0.05	34.07±0.02	1=2>3
Chlorophyll *a* (mg m^{-2})	112±14	84±13	31±6	137±35	4=1=2>3
Zooplankton biomass (mg C m^{-2})					
>200 μm	84±38	37±10	61±30	119±46	n.s.
>500 μm	12±2	27±7	12±4	105±49	4>1=2=3
>1000 μm	100±24	115±25	249±102	603±252	4>1=2=3
Total	178±42	180±35	323±108	828±348	4>1=2=3
Zooplankton abundance (indv. m^{-2})					
Siphonophora	6±2	19±7	0±0	15±6	4=2>3
Tomopteris carpenteri	1±1	6±2	1±1	62±51	4>1=3
Polychaete larvae	13±6	142±49	26±17	180±105	4=2>1=3
Limacina helicina	2±1	3±2	62±23	114±72	4=2>1=3
Mollusca larvae	3±2	11±6	593±556	157±101	4=3>1
Sagitta spp.	39±10	18±11	22±18	572±270	4>1>2=3
Eukrohnia hamata	5±4	55±15	17±16	89±89	2>1=3
Calanus spp. (juveniles)	4±2	45±20	91±25	119±119	3>1=2=4
Calanus propinquus	5±3	8±3	34±12	278±278	3>1
Calanus simillinus	0±0	3±3	77±36	258±170	4=3>1=2
Calanoides acutus	31±9	33±8	465±452	1611±644	4>1=2=3
Rhincalanus gigas	16±5	19±6	0±0	4480±3812	4>2=1>3
Microcalanus pygmaeus	548±153	1069±355	4±3	1650±373	4=2=1>3
Ctenocalanus citer	199±59	1746±417	2340±1531	3000±1797	2=3>1
Paraeuchaeta antartica	66±30	165±58	25±18	172±111	2>1=3
Scolecithricella minor	11±6	88±36	120±80	131±109	3=2>1
Metridia gerlachei	561±191	676±149	140±101	1655±735	4>2>1>3
Oithona similis	4474±1048	3869±1521	15831±4221	19512±6093	4=3>2=1
Oithona frigida	65±38	5151±1048	675±373	0±0	2>3>1=4
Oithona spp.	26±23	1541±369	1873±919	0±0	2=3>1=4
Oncaea antartica	138±69	383±127	142±100	749±333	4>1
Oncaea curvata	13±5	350±164	0±0	0±0	2>3
Conchoecia spp.	2±1	27±16	3±3	383±318	4>1=2
Euphausiid eggs	41±26	752±297	1±1	97±97	2>1=3=4
Euphausiid nauplii	96±50	194±82	1±1	557±420	2>3
Euphausiid calyptopis larvae	49±30	288±87	143±50	2481±1231	4=3=2>1
Euphausia superba	6±3	4±1	1±1	4±4	4=3=2>1
Thysanoessa macrura	1±1	8±4	9±5	1±1	4=3=2>1
Fritillaria antartica	19±11	250±211	10±8	592±512	4>1
Oikopleura gaussi	13±9	11±9	0±0	964±370	4>2=1=3
Total	7206±1386	17514±2653	22933±8328	86088±47212	4>3=2=1

[a] Note: >, significant ($P<0.05$) difference; =, non-significant ($P>0.05$) difference.

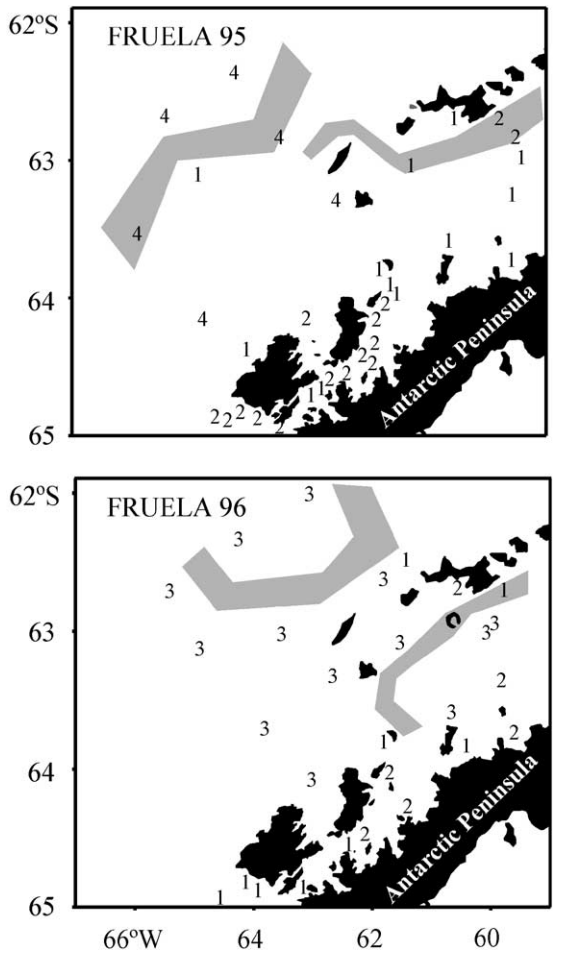

Fig. 3. Geographical distribution of station groups defined by cluster analysis. SbyACC and Bransfield fronts (according to García et al., 2002) are shown by dashed lines.

The third component (PC3) explained 12% of the total variance and showed high contributions from *Oithona similis*, *Oithona frigida* and *C. citer* (Fig. 2). This component separated samples belonging to group 1 from these belonging to group 2 (Fig. 2), both of them collected at coastal stations. We do not have a clear interpretation for PC3, which was weakly correlated with temperature (Fig. 2). Both groups, 1 and 2, showed similarly, high chlorophyll concentrations ($>83\,mg\,m^{-3}$) and low mesozooplankton biomass ($<181\,mg\,C\,m^{-2}$) (Table 1), although small-sized animals were more abundant in group 2 stations, according to the total number of animals and the total biomass (Table 3). Samples belonging to groups 1 and 2 occupied the Gerlache and Bellingshausen straits during FRUELA 95, but only areas sheltered by islands during FRUELA 96 (Fig. 3).

To summarize, the spatial distribution of cluster groups did not reveal a strong coupling between mesoscale physical features (continental water boundary fronts) and mesozooplankton distributions (Fig. 3). There were two coastal (1 and 2) and two open-water (3 and 4) groups. During FRUELA 95, groups 1 and 2 were distributed over the Gerlache and Bransfield straits, while group 4 occupied the Bellingshausen Sea (Fig. 3). During FRUELA 96, groups 1 and 2 were restricted to the Gerlache Strait, except for several stations in the vicinity of the South Shetland Islands, while group 3 occupied the rest of the study area (Fig. 3).

3.4. Diel variations

Differences in total mesozooplankton abundance between day and night were significant during the summer FRUELA 96 cruise (i.e. 4-fold; *t*-test, $P<0.001$), but not during the spring FRUELA 95 cruise (Fig. 5). These variations were often due to a night-time increase in the abundance of *M. gerlachei* and *Oithona similis*, and ocassionally of euphausiids and other groups of zooplankton (Fig. 5). However, we did not observe strong variations in composition, but mainly a change in the relative abundance of these species.

3.5. Community grazing rates

Table 2 summarizes copepod and euphausiid abundance, gut contents, and community ingestion in the different groups of stations. Data from both FRUELA 95 and FRUELA 96 cruises are considered together. Gut contents increased with body size, reaching maximum values of 7.8×10^{3} ng Chl *a* ind^{-1} for euphausiids in group 2 stations. Of the fractions considered, higher gut contents were found in group 2, especially in the medium and large copepod size fractions and in euphausiids.

Gut evacuation experiments were conducted with medium and large copepods, and with

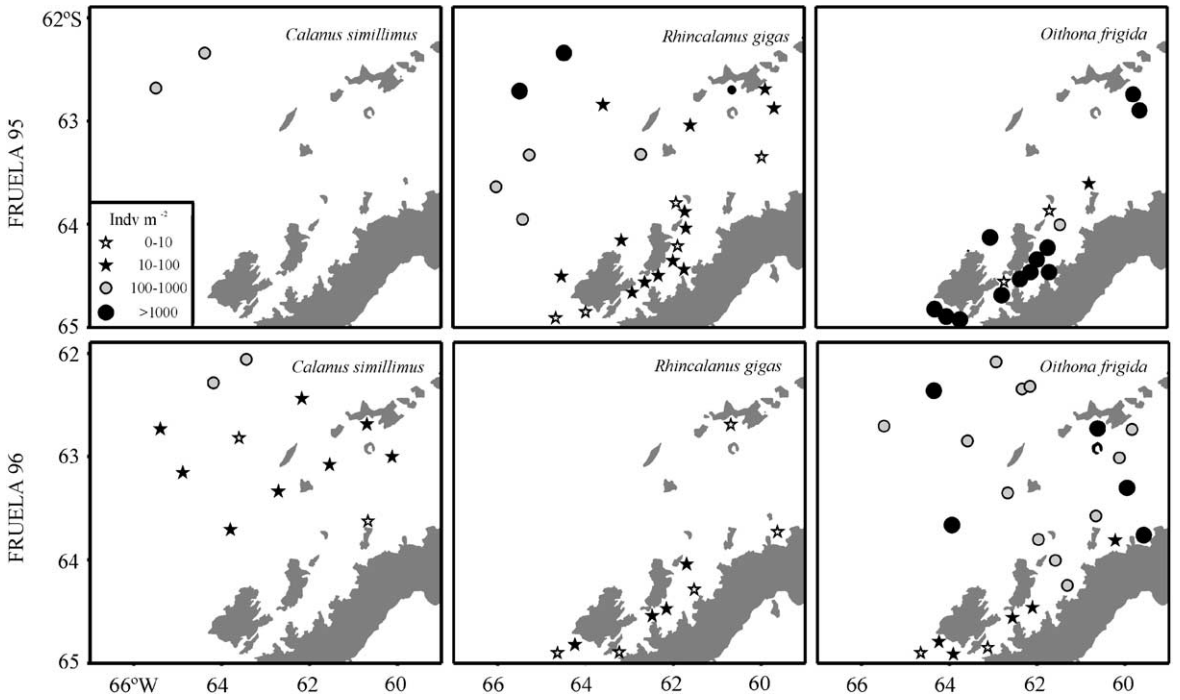

Fig. 4. Spatial distribution of some representative species.

euphausiids. Average values of the gut evacuation constant for each taxonomic group ($0.022\,\mathrm{min}^{-1}$ for medium copepods, $0.005\,\mathrm{min}^{-1}$ for large ones, and $0.016\,\mathrm{min}^{-1}$ for euphausiids) were used for further calculation of ingestion rates. Analysis of covariance did not show significant differences in the slopes of the six curves obtained for the large copepod fraction ($p > 0.1$). We had no success in experiments with small copepods because of contamination by phytoplankton (i.e. high chlorophyll: pheopigment ratios); therefore, for this fraction we used a value of $0.06\,\mathrm{min}^{-1}$, derived from the empirical relationship between gut evacuation rate and average temperature by Dam and Peterson (1988).

Due to low population densities, chlorophyll *a* ingestion rates for the total community were also very low. The highest medians of the ingestion rate values were found in group 2 for copepods (102 and 40 μg Chl $a\,\mathrm{m}^{-2}\,\mathrm{day}^{-1}$ for the medium and large fraction, respectively) and in group 1 for euphausiids (ca. 7 μg Chl $a\,\mathrm{m}^{-2}\,\mathrm{day}^{-1}$). Daily ingestion by each of the fractions considered represented very low percentages of the chlorophyll standing stock (Table 3), with values lower than 0.1% in the stations where data from all the fractions were available. With respect to primary production, values increased to an average of 10% ingested daily, although an extremely high value of 676% of the production was ingested in one station from group 1. No statistical differences between cruises (*t*-test; $p > 0.05$) were found in gut contents, abundance or pigment ingestion in group 1, although some differences were found in group 2. In this group, gut contents in the euphausiid and large copepod fraction and total pigment ingestion in all the fractions were higher during FRUELA 95.

4. Discussion

4.1. Standing stock

During the FRUELA cruises, small copepods like *Oithona similis*, *O. frigida, Oncaea antarctica*, *Ctenocalanus citer* and *Microcalanus pygmaeus*

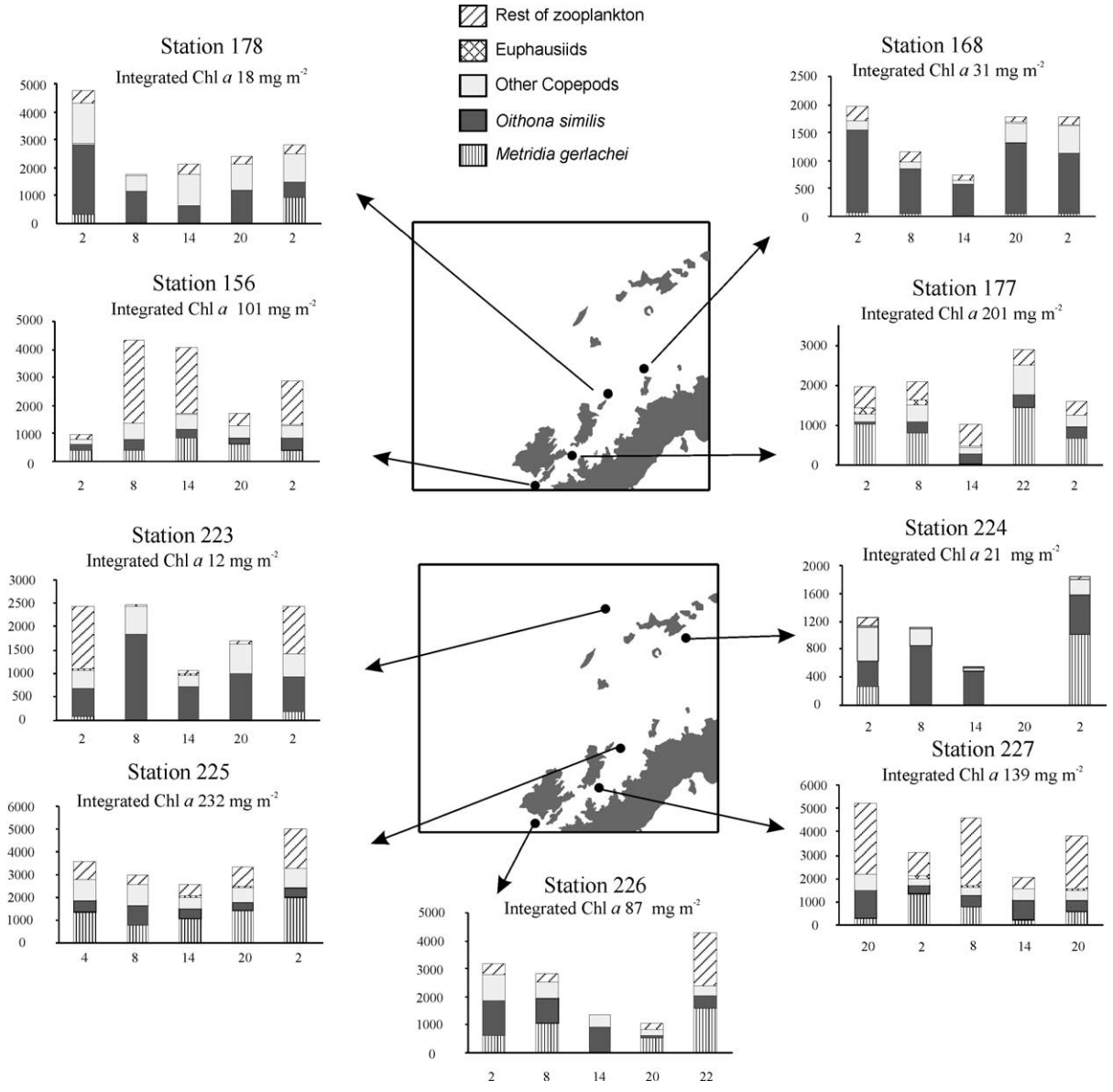

Fig. 5. Diel variation in the abundance of zooplankton during the FRUELA 95 and 96 cruises. *Y*-axes: zooplankton abundance (indv. m^{-2}). *X*-axes: time of the day.

showed relatively high population densities, against the typical background of large antarctic species like *Rhincalanus gigas*, *Calanus propinquus*, *C. simillimus*, *Calanoides acutus* and *Metridia gerlachei*; this observation is consistent with other investigations in the Southern Ocean (Fransz and Gonzalez, 1997 and references therein). Zooplankton standing stock in the Bransfield-Bellinsghausen region has been found to be comparable to that of other adjacent areas (Hopkins, 1985; Hopkins and Torres, 1988) and lower latitudes. In this study, mesozooplankton biomass values

Table 2
Summary data for small (200), medium (500) and large (1000) copepods and euphausiid (Euf) gut contents (GC), abundance (Ab) and pigment ingestion (PING) at each of the groups of stations (Fruela 95 and Fruela 96 pooled) except group 4 (no data available)[a]

Group	200	500	1000	Euf
GC (ng Chl *a* $indv^{-1}$)				
1	0.10	0.4	2.2	9
	[0–0.25]	[0.03–31.5]	[0.18–34.6]	[1.5–3.9×10^3]
	{10}	{18}	{17}	{10}
2	0.13	6.2	9.2	16
	[0–2.6]	[0.01–16.4]	[0.9–20.6]	[2–7.8×10^3]
	{4}	{12}	{12}	{5}
3	0.03	0.2	1.9	5
	[0–0.13]	[0.01–2.9]	[1.6–2.25]	[1.5–6.75]
	{7}	{5}	{2}	{6}
Ab ($indv\,m^{-2}$)				
1	335	462	366	28
	[0–9.4×10^3]	[8–1.7×10^3]	[7–1.1×10^3]	[8–87]
	{11}	{19}	{18}	{10}
2	9.7×10^3	303	462	8
	[0–11.6×10^3]	[8–2.1×10^3]	[8–1.2×10^3]	[8–15]
	{4}	{11}	{12}	{5}
3	5.5×10^3	263	143	28
	[0–31.4×10^3]	[8–804]	[56–230]	[8–191]
	{7}	{5}	{2}	{6}
PING (ng Chl $a\,m^{-2}\,day^{-1}$)				
1	603	1.4×10^4	6.2×10^3	6.9×10^3
	[0–9.7×10^3]	[49–4.2×10^5]	[224–1.0×10^5]	[300–4.2×10^6]
	{11}	{18}	{17}	{10}
2	3.2×10^4	1.0×10^5	4.0×10^4	2889
	[0–3.5×10^5]	[1.1×10^3–3.7×10^5]	[146–1.7×10^5]	[383–2.9×10^6]
	{4}	{11}	{13}	{5}
3	5990	748	1.7×10^3	3482
	[0–3.2×10^4]	[254–1.9×10^3]	[889–2.5×10^3]	[541–2.7×10^4]
	{7}	{5}	{2}	{6}

[a] Note: Data represent medians, range [] and number of observations {}.

were similar to those previously reported by other authors for the same area, but lower than those of other areas of the Antarctic (Boysen-Ennen et al., 1991). Our data are also consistent with the general increase in mesozooplankton biomass in association with Antarctic frontal systems, which has been reported in previous regional studies (Pakhomov et al., 1994). During the FRUELA cruises, temporal variations of biomass were more important in the oceanic area, with a sharp decrease in the oceanic stations from spring to summer; in the coastal areas, however, high values of biomass were maintained throughout the spring and summer.

In our study area, high zooplankton biomass usually has been associated with swarms of salps or euphausiids (Hopkins, 1985; Huntley and Escritor, 1991); however, during FRUELA, copepods represented an important part of the zooplankton. Several authors have indicated that copepod biomass may be equal or higher than krill biomass (Voronina, 1968, Conover and Huntley, 1991), and our results show that small (200–500 μm) copepods were an important fraction of the total mesozooplankton biomass (Table 1). Although the dry weight of small-sized copepods was only between 5.9 and 9.4 μg (Fransz and

Table 3
Summary data for small (200), medium (500) and large (1000) copepod size fraction and euphausiid (Euf) daily percentage of chlorophyll standing stock (Chl *a*) and primary production (PP) grazed at each of the groups of stations (Fruela 95 and Fruela 96 pooled) excepting group 4 (no data available)[a]

Group	Chl *a* ($mg\,m^{-2}$)	PP ($mgC\,m^{-2}\,day^{-1}$)	% Chl *a*				% PP			
			200	500	1000	Euf	200	500	1000	Euf
1	52	35	0.001	0.01	0.010	0.004	0.10	4.8	0.9	19.5
	[24–328]	[7.2–98]	[0–0.02]	[0–0.12]	[0–0.02]	[0.002–0.2]	[0–0.4]	[0.1–25]	[0.3–6.3]	[0.3–676]
	{12}	{6}	{9}	{9}	{8}	{5}	{3}	{5}	{4}	{3}
2	91	176	0.06	0.05	0.003	0.004	—	3.8	0.8	0.2
	[26–446]	[141–271]	[0–0.1]	[0.001–0.12]	[0.001–0.04]	[0.001–0.01]	—	[0.7–3.7]	[0.1–2.3]	[0.04–0.3]
	{8}	{3}	{3}	{7}	{7}	{4}	—	{3}	{3}	{2}
3	29	14	0.02	0.002	0.01	0.01	6.2	6.6	16.7	3.77
	[9.5–58]	[0.9–26]	[0–0.1]	[0–0.01]	[0.001–0.01]	[0.001–0.2]	[1.9–10.5]	[0.1–13]		[2–5.5]
	{10}	{4}	{7}	{5}	{2}	{6}	{2}	{2}	{1}	{2}

[a]Note: Data represent medians, range [] and number of observations {}. Chl *a* and PP data obtained from Varela et al., (2002).

Gonzalez, 1997), their high numbers suggest their importance in the dynamics of polar marine systems, as consumers of debris and small flagellates (Hopkins, 1985), which are often very abundant (see Rodríguez et al., 2002; Smetacek et al., 1990).

4.2. Community structure

We found no spatial coherence between the structure of the zooplankton community and the horizontal distribution of physical features (i.e. the Bransfield Current and the SbyACC); Fig. 3). Both phyto- (Varela et al., 2002) and zooplankton distributions (groups 1 and 2 in Fig. 3) were consistent in that neither showed marked temporal changes at the Gerlache Strait, where a nearly steady state diatom bloom community persisted throughout the summer. The diatom-copepod/euphausiid food chain present in this zone has been interpreted by Varela et al. (2002) as analogous to that from a receding ice-edge ecosystem. Moreover, in the shelf break of the Bellingshausen Sea, both zoo- and phytoplankton assemblages exhibited a marked seasonal shift from a diatom-copepod/euphausiid bloom community during FRUELA 95 (Varela et al., 2002; Fig. 3), to an impoverished community based on very small cells and pteropod/euphausiid consumers during FRUELA 96. Since this shift was not accompanied by a comparable change in macronutrient distributions (see Castro et al., 2002) and hydrographic characteristics, Varela et al. (2002) ruled out the effects of macronutrient limitation or physical water-column properties. According to these authors, grazing pressure by krill could explain the absence of a phytoplankton bloom in the Bellingshausen Strait during FRUELA 96, because this area serves as a breeding ground for krill and because krill were nearly absent from the Gerlache Strait during the RACER study. Moreover, the dominance of small cryptomonads in the phytoplankton communities of parts of the Bransfield Strait, during FRUELA 96, was interpreted by Varela et al. (2002) as a consequence of the selective pressure of krill on large phytoplankton, which tends to favour smaller organisms (Jacques and Panouse, 1991; Smith et al., 1996).

In spite of the methodological limitations inherent to sampling krill by vertical tows with a relatively small net, our data do not support the hypothesis of phytoplankton control by krill grazing. First, krill abundance was similar in the Bransfield Strait during FRUELA 96, where a phytoplankton bloom did not develop, and in Gerlache during FRUELAs 95–96 and Bransfield Strait during FRUELA 95, where large blooms did develop (Table 1). Second, grazing pressure by krill was moderate both in absolute (i.e. less than 5% of primary production in most cases; Table 3), and relative terms (i.e. less than any other zooplankton fraction; Table 2). In search for alternative causes for the absence of offshore blooms during FRUELA 96, we tend to favor horizontal advection of water masses associated with strong wind conditions. During FRUELA 96, the water column in offshore stations was capped with a layer of higher temperature and lower salinity water, which was not apparent during FRUELA 95. While weather was usually calm during FRUELA 95, force 6–7 NW winds were the norm during the first half of FRUELA 96, which could have caused an advection of the surface water layers in the direction of the prevailing winds. This interpretation is further supported by the changes in the taxonomic composition of the zooplankton assemblages. A rich zooplankton community with a significant contribution from coastal meroplankton similar to that found in the Gerlache Strait (i.e. groups 1 and 2 of our cluster analysis) characterized most of the Bransfield Strait during FRUELA 95 (Fig. 3). This same area was occupied by a poor, oceanic community (group 3) characterized by the presence of the copepod *Calanus similimus* and the pteropod *Limacina helicina* during FRUELA 96 (Fig. 3), although some areas located leeward of the South Shetlands still retained coastal groups 1–2 communities (Fig. 3). These observations clearly suggest that coastal communities widely distributed during FRUELA 95 were wiped out by advected water masses, and remained only in highly protected coastal areas (i.e. Gerlache Strait) or at the wind protected side of the islands. These advected water masses contained relatively long-lived pteropods and copepods, which were nearly absent only 20 days before, during FRUELA 95, thus ruling out a local origin.

4.3. Community grazing

In our study area, the mesozooplankton community grazed in average only 0.1% of the chlorophyll standing stock, or 10% of the primary production (Table 3). Gut pigment and clearance rate studies in the Southern Ocean and Bellinghausen Sea suggest that less than 1% of the primary production is grazed by copepod-dominated zooplankton communities (e.g., Dubischar and Bathmann, 1997; Atkinson, 1995), while this figure rises to more than 50% when dense salp and euphausiid swarms are dominant. We have not considered the gelatinous zooplankton in our community grazing measurements, but higher community grazing rates when euphausiids are abundant seem to confirm this pattern. In general, our findings suggest low grazing by the crustacean community, relative to the chlorophyll standing stock and primary production; therefore, we must seek for alternative mechanisms (i.e. mixing by the severe winds which prevailed during most of the FRUELA 96 cruise or the southern, probably ice-covered origin of the water at offshore stations; Gomis et al., 2002) to explain the low phytoplankton biomass found in oceanic areas during FRUELA 96. Figures up to 30% of the primary production consumed at inshore stations could be raised if a significant chlorophyll degradation was occurring within the guts of these grazers. However, pigment degradation is known to decrease as the ingestion rate increses (Head, 1988, 1992), and there is strong evidence that feeding by copepods at copepod-dominated, inshore areas during the FRUELA cruises was saturated (see Calbet and Irigoien, 1997). Dam and Peterson (1988) proposed an average value of 33% of pigment destruction for copepods. Assuming this factor, calculated ingestion rates would underestimate actual rates by a factor of 1.4, which does not change our general conclusions. At the more productive, coastal stations, low relative grazing and a feeding preference of the dominant copepod *Metridia gerlachei* for particles $<10\,\mu m$ in size (Calbet and Irigoien, 1997) suggest that the bloom

of large chains of diatoms, which accounted for most of the production, could sink ungrazed to deep layers. In fact, contents of sediment traps at these stations showed high numbers of large, chain-forming diatoms, some euphausiid fecal pellets and a very small number of copepod fecal pellets (Anadón et al., 2002).

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