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Interannual fluctuations in copepod abundance and contribution of small forms in the Drake Passage during austral summer

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Abstract The relative importance of small forms of copepods has been historically underestimated by the traditional use of 200–300-μm mesh nets. This work quantified the distribution and abundance of copepods, considering two size fractions (<300 μm and >300 μm), in superficial waters (9 m deep) of the Drake Passage and contributed to the knowledge of their interannual fluctuations among three summers. Four types of nauplii and eleven species of copepods at copepodite and adult stages were identified, with abundance values of up to 13 ind L^{-1} and 28,300 μg C m^{-3}. The <300-μm fraction, composed of *Oithona similis*, small cyclopoids and nauplii, dominated the copepod communities in the 3 years; it accounted for more than 77% of the total number and for between 40 and 63% of the total biomass. Changes in density and biomass values among the three cruises differed according to copepod size fraction and water mass; the >300-μm fraction showed no changes among the 3 years, both in Antarctic (density and biomass) and in Subantarctic waters (density), whereas the <300-μm fraction showed higher (density and biomass) values in 2001 both in Subantarctic and in Antarctic waters. Sea surface temperature and its anomaly accounted for the largest proportion of variability in copepod density and biomass, particularly for the <300-μm fraction.

Introduction

Historically, studies on the quantification of mesozooplankton (200–2000 μm) have underestimated the abundance of small marine copepods (namely nauplii, copepodite stages and adults of some species) due to the use of nets with mesh sizes between 200–333 μm. This is also the case for the current major large-scale monitoring programme, which uses the Continuous Plankton Recorder (CPR) for mapping zooplankton distribution in order to evaluate the impact of future changes on climate (Mc Leod et al. 2010). The lack of information on the smaller-sized fraction of the community (nauplii, copepodite developmental stages and adults of some small species) prevents obtaining an adequate estimate of its importance in the oceanic carbon cycle (López et al. 2007). Recent studies using 100-μm mesh nets indicated that smaller copepods were more abundant and had a higher biomass than larger ones (Metz 1996; Atkinson and Sinclair 2000; Gallienne and Robins 2001; Dubischar et al. 2002; Turner 2004b). In the Atlantic Sector of the Southern Ocean, the most accurate and detailed estimates of copepods (using <100-μm mesh nets that allow collecting nauplii and small species) have been reported from the eastern and southern area (East portion of the Scotia Sea, Weddell Sea and their Confluence; Mizdalski 1988; Fransz and Gonzalez 1997; Dubischar et al. 2002; Ward et al. 2004, 2006). The level of

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spatial detail in the western area of the Atlantic sector (namely, the Drake Passage and nearby the Scotia Sea) has been limited by the spatial coverage of observations. However, when a good spatial coverage was available, copepods have been underestimated (Fig. 1a and references therein).

The Drake Passage is unique in that it provides a direct link between marine organisms of the Pacific and Atlantic Oceans, and it is where the Antarctic Circumpolar Current (ACC) is constricted to its narrowest extent (Nowlin et al. 1977). The ACC in the Drake Passage is characterised by a series of relatively narrow eastward flowing jets, separated by broader bands of flow (Nowlin et al. 1977). The strongest flow and transport is associated with the Polar Front (Sprintall 2003; Lenn et al. 2007), which separates the cold Antarctic surface water mass from the warmer Subantarctic surface water mass to the north.

As far as we know, no studies have been carried out on the density and biomass of small planktonic copepods from the Subantarctic and Antarctic waters of the Drake Passage

and on their interannual fluctuations. Accurate information on the number and biomass of copepod communities in general, and of nauplii and small copepod species in particular, is critical for understanding their role in the dynamics of carbon flux and in the food webs of the Southern Ocean.

The purposes of this work were (i) to quantify the distribution and abundance of copepods classified into two size fractions, <300 μm and >300 μm, in the superficial waters (9 m deep) of the Drake Passage and to assess potential changes among three summers; and (ii) to relate the composition and abundance (density and biomass) of each copepod size fraction to hydrological conditions considering three summers.

Materials and Methods

Zooplankton samples and environmental data were collected at 56 oceanographic stations in Subantarctic and Antarctic waters of the Atlantic Sector of the Southern Ocean (the Drake Passage and the Scotia Sea; 55–63°S between 40 and 70°W, Fig. 1b) during three austral summers: 2000 (CAV2000-Spanish initials for Summer Antarctic Cruise 2000, January-February), 2001 (CAV2001—February) and 2003 (CAV2003, February). At each oceanographic station, samples for studies of copepods and chlorophyll *a* were taken with a centrifugal pump at 9 m depth on board the icebreaker 'Almirante Irizar', during navigation.

For chlorophyll *a* analysis, seawater samples of between 0.5–2 L were filtered through 2-μm-mesh-size filters at each sampling station, during the summers of 2001 and 2003. Filters were stored dried and frozen prior to extraction with 90% acetone and analysis by fluorometric techniques in the laboratory (Evans and O'Reilly 1983). Concentrations were calculated following Strickland and Parsons (1972).

For the 3 years of interest, information on environmental conditions was obtained by two ways: (1) in situ continuous measurements of temperature and salinity at the same depth as that of the samples, data provided by the ARGAU project (http://dataipsl.ipsl.jussieu.fr/ARGAU/argau.htm); (2) data derived from satellite imagery, i.e., AVHRR Oceans Pathfinder Sea Surface Temperature (SST) and Sea Surface Temperature Anomaly (SSTa) data, obtained from the Physical Oceanography Distributed Active Archive Center (PO.DAAC) Ocean ESIP Tool (POET) at the NASA Jet Propulsion Laboratory, Pasadena, CA. (http://podaac.jpl.nasa.gov/poetthe); and chlorophyll *a* concentration data, provided by the SeaWIFS Project at NASA Goddard Space Flight Center (http://oceancolor.gsfc.nasa.gov).
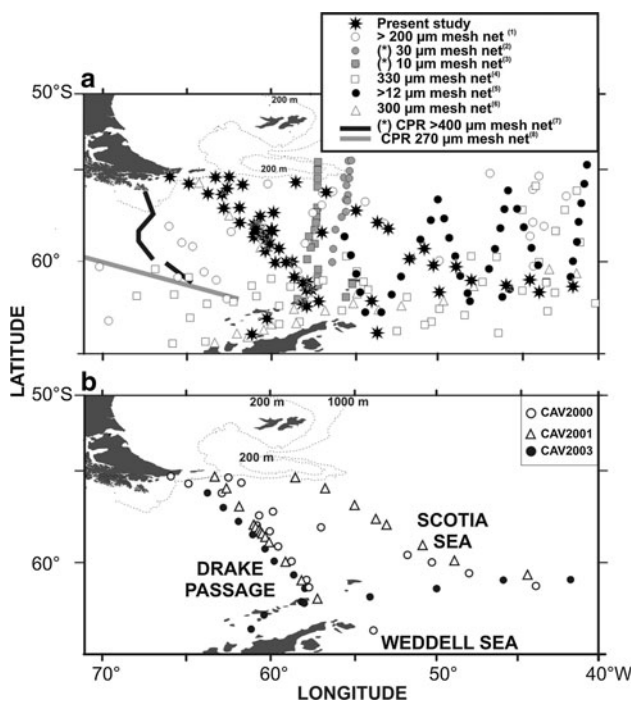

Fig. 1 **a** Distribution of ocean samples of copepods in the study area [1] net samples collected during the discovery expeditions (Atkinson and Sinclair 2000); [2] TABIA I–III samples (Thompson 2001); [3] PRONTAR XI samples (Fernandes and Brandini 1999); [4] CCAMLR 2000 survey (Ward et al. 2004); [5] Jr82 cruise (Ward et al. 2006); [6] Oceantar I, (Ramirez and Dinofrio 1976); [7] Discovery Expedition 1927 (Hardy 1936); [8] SO-CPR Survey Tow 68/70 (Takahashi et al. 2010); [*] Only total copepods were reported. **b** Geographic location of the stations in summer 2000 (CAV 2000), 2001 (CAV 2001) and 2003 (CAV 2003)

Samples for the study of copepods, obtained mainly with a spatial resolution of 3.5–6.5 nautical miles, were collected from 500 to 3,000 L (CAV 2000, 19 samples), 400–600 L (CAV 2001, 21 samples) and 80–200 L (CAV 2003, 16 samples) of seawater filtered through a 20-μm mesh and fixed in 3% formol solution. To detect fluctuations in the flux of seawater, amount of water filtered was estimated at the beginning and at the end of each station. Prior to laboratory analyses, each plankton sample was separated into two fractions using a 300-μm-pore-size mesh, which is traditionally used to collect copepods. Copepods were identified according to the classification systems of Bjornberg (1972), Ramirez and Dinofrio (1976), Björnberg et al. (1994) and Bradford-Grieve et al. (1999). Nauplii of calanoid and cyclopoid copepods were assigned to a single category because of the difficulty in identifying species and developmental stages. Community structure and abundances of nauplii and some species of copepods in the fraction <300 μm were estimated under an inverted microscope at 200x magnification. When samples were large, counts were made over 3 subsamples of each sample. Otherwise, the entire sample was counted. Copepods in the fraction >300 μm (i.e. nauplii, copepodite stages I–V and adult males and females)were identified under stereoscopic microscope at 40x magnification and the entire sample was examined. A total of 2,604 (cruise CAV2000), 7,794 (cruise CAV2001) and 1,636 (cruise CAV2003) specimens were collected, most from Subantarctic waters (2,429, 3,088 and 610 specimens, respectively).

Copepod biomass was estimated from body measurements of each specimen (nauplii, copepodite or adult). The wet weight (WW in μg) of nauplii was calculated according to Gradinger et al. (1999) as $WW = 360 \times LT \times W^2$, where 360 is a conversion factor ($\mu g \, mm^{-3}$), LT is the length (mm), and W is the width (mm). A factor of 30% was used to correct for weight lost due to preservation in formaldehyde (Böttger-Schnack 1985). Dry weight was estimated as 22.5% of corrected wet weight (Gradinger et al. 1999) and carbon concentration was assumed to be 40% of the dry weight (Feller and Warwick 1988). Adult and copepodite wet weight (WW in μg) was calculated according to Gradinger et al. (1999) and Nozais et al. (2001) as $WW = 0.9 \times 1.13 \times LT \times W^2 \times C$, where 0.9 is a dimensionless conversion factor, 1.13 is the specific gravity ($\mu g \, nL^{-1}$), LT is the total length (mm), W is the width (mm), and C is a conversion factor depending on body shape (C: 560 for semi-cylindrical shape or C: 400 for pyriform shape). Dry weight and organic carbon content were calculated as for nauplii.

A two-way ANOVA design was used to detect significant changes in copepod density and biomass among the three cruises and between Subantarctic and Antarctic waters (Zar 1999). The analyses were carried out for each copepod size fraction separately and for the sum of the two fractions. The factors were year (2000, 2001 and 2003) and site (Subantarctic and Antarctic stations) as fixed factors. Significant differences in density or biomass between years for each site were assessed using a posteriori Tukey's HSD multiple comparison test (Zar 1999).

Stepwise multiple linear regression analyses with forward selection were performed to determine the most important independent environmental factors (in situ: seawater temperature and salinity and satellite-derived: SST, SSTa, SeaWIFS chlorophyll a), accounting for the variability of the dependent variables: density or biomass for each copepod size fraction separately and together. No colinearity was found between the environmental factors, as all pairwise correlations were below 0.90. Spearman's rank order correlation test was used to determine correlations between density or biomass of copepods and in situ chlorophyll a (not recorded in 2000).

To analyse the degree of spatial and temporal similarity among copepod associations, a similarity matrix (fourth root transformed data of density, Bray Curtis Index) was constructed considering nauplii and copepodite stages and sex (adults) for each sampling station with presence of copepods (46 stations), and hierarchical analyses were performed (unweighted pair-group method using arithmetic averages; Romesburg 1984).

Results

Environmental setting

A southward decrease in seawater temperature and salinity was observed in the three summers (2000: 6.5–1.7°C, 34.44–33.82 psu; 2001: 7.5–2.0°C, 34.18–33.62 psu; and 2003: 7.8–2.4°C, 34.32–33.28 psu). Chlorophyll a values were below 1.0 mg L^{-1}, and a single peak (4.1 mg L^{-1}) was registered in Antarctic waters during 2003.

A latitudinal comparison of satellite-imagery-derived data (SST, SSTa and SeaWIFS Chl a) between the three summers is shown in Fig. 2. Summer 2003 was characterised by higher SST values and a warm SSTa (average: 1.25°C), whereas summer 2000 had lower SST values (average difference with summer 2003: 1.25°C) and a cold SSTa (average: −0.50°C). The Polar Front, identified by a sharp decrease in SST, was located farther north in summer 2001 than in summer 2000 and 2003 (Fig. 2). Summer 2001 was characterised by intermediate values of SST and lower values of SSTa (average: −0.20°C). SeaWIFS chlorophyll a profiles were similar during the three summers, with low values to the north of 62°S and different increasing levels to the south of this latitude (Fig. 2).

Fig. 2 Sea surface temperature profile, sea surface temperature anomaly, and SeaWIFS chlorophyll *a* data for summer 2000, summer 2001 and summer 2003, along a transect at 62.5°W. PF2000: Polar Front summer 2000; PF2001: Polar Front summer 2001; PF2003: Polar Front 2003
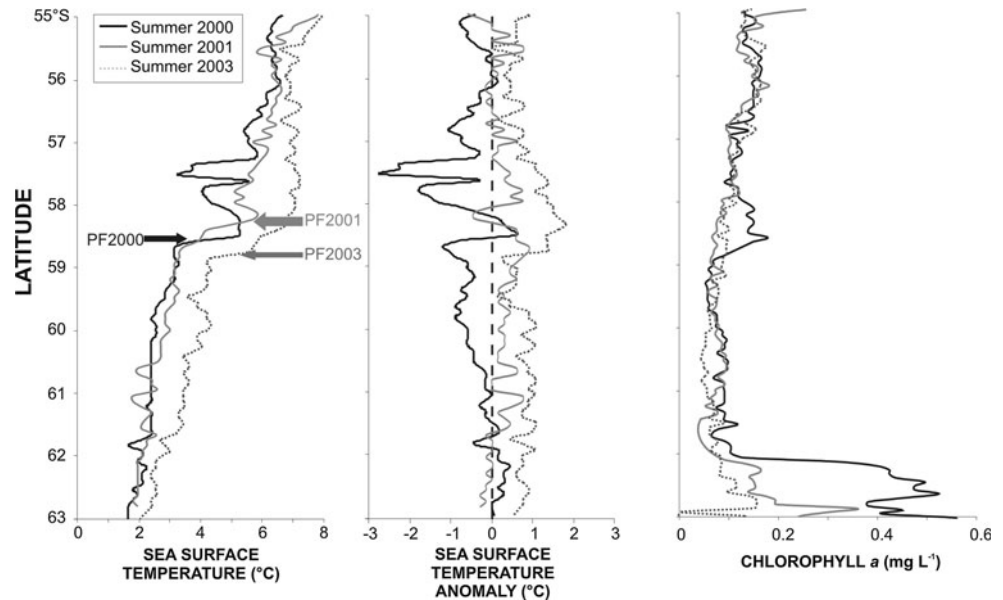
Copepods

Copepods were found in 95, 80 and 60% of the samples collected during summers 2001, 2000 and 2003, respectively. Four types of nauplii and 11 species of copepods at copepodite and adult stages were identified. The <300-μm fraction was represented by the cyclopoids *Oithona similis* (Oithonidae) and *Oncaea curvata* (Oncaeidae), nauplii of calanoid and cyclopoid copepods and the harpacticoid *Microsetella norvegica* (nauplii included). The >300-μm fraction was characterised by the presence of calanoids, nauplii of *Rhincalanus gigas* (Rhincalanidae) and copepodites and adults of *Calanus simillimus* (Calanidae), *Calanoides acutus* (Calanidae), *Metridia gerlachei* (Metridinidae), *Subeucalanus longiceps* (Eucalanidae), *Clausocalanus laticeps* (Clausocalanidae), *Ctenocalanus citer* and *Paraeuchaeta antarctica* (Clausocalanidae) and *Sapphirina* sp. (Sapphirinidae).

Density and biomass values of copepods differed between the three cruises (Table 1), with values always being significantly higher in Subantarctic than in Antarctic waters for each size fraction, both separately and together (Fig. 3, Tables 2, 3, 4).

In terms of numbers, the following results were obtained during the three cruises: (*i*) the <300-μm fraction prevailed mainly in Subantarctic waters (over 77%, Tables 1, 2), with nauplii being the dominant developmental stage (Table 2, Fig. 3b); (*ii*) when considering copepodites and adults, the most frequent specimens belonged to *Calanus simillimus, Calanoides acutus* and *Oithona similis*, showing higher densities during summer 2001 (Table 2). Of these, *O. similis*, together with nauplii, was recorded both in Subantarctic and in Antarctic waters during the three

Table 1 Average and maximum value (in parenthesis) of density and biomass for each copepod size fraction and relative contribution of each copepod size fraction to total density and biomass in each summer cruise

	2000	2001	2003
Density (ind L^{-1})			
<300-μm fraction	0.402 (2.04)	2.499 (9.71)	1.047 (6.88)
>300-μm fraction	0.096 (1.00)	0.319 (2.99)	0.013 (0.06)
All	0.498 (3.04)	2.818 (12.70)	1.060 (6.93)
Relative contribution			
<300-μm fraction	77%	92%	80%
>300-μm fraction	22%	8%	20%
Biomass (μg C m^{-3})			
<300-μm fraction	58 (227)	443 (4,659)	84 (438)
>300-μm fraction	786 (5,242)	4,046 (27,540)	238 (3,294)
All	667 (5,291)	4,490 (28,300)	322 (3,409)
Relative contribution			
<300-μm fraction	40%	63%	54%
>300-μm fraction	60%	36%	46%

cruises (Fig. 4a, b), whereas the other species were observed only in Subantarctic waters during the three summers (Table 2); (*iii*) specimens of *Microsetella norvegica, Oncaea curvata, Metridia gerlachei, Subeucalanus longiceps, Ctenocalanus citer, Clausocalanus laticeps, Paraeuchaeta antarctica* and *Sapphirina* sp. were occasionally observed, generally at densities below 0.1 ind L^{-1} (Table 2).

Peaks of biomass were registered at the Polar Front and at the northern stations near the continental shelf break (Fig. 3c), which were attributed to copepodites IV–V and adults of *C. acutus, C. simillimus* (2000 and 2001) and

Fig. 3 a Density and **b** relative contribution of each copepod fraction (>300 and <300 μm) to total density. **c** Biomass and **d** relative contribution of each copepod fraction (>300 and <300 μm) to total biomass of copepods for summer 2000, 2001 and 2003. Circle size is proportional to the absolute values of density and biomass. The *central black dot* indicates the location of the stations in summer 2003
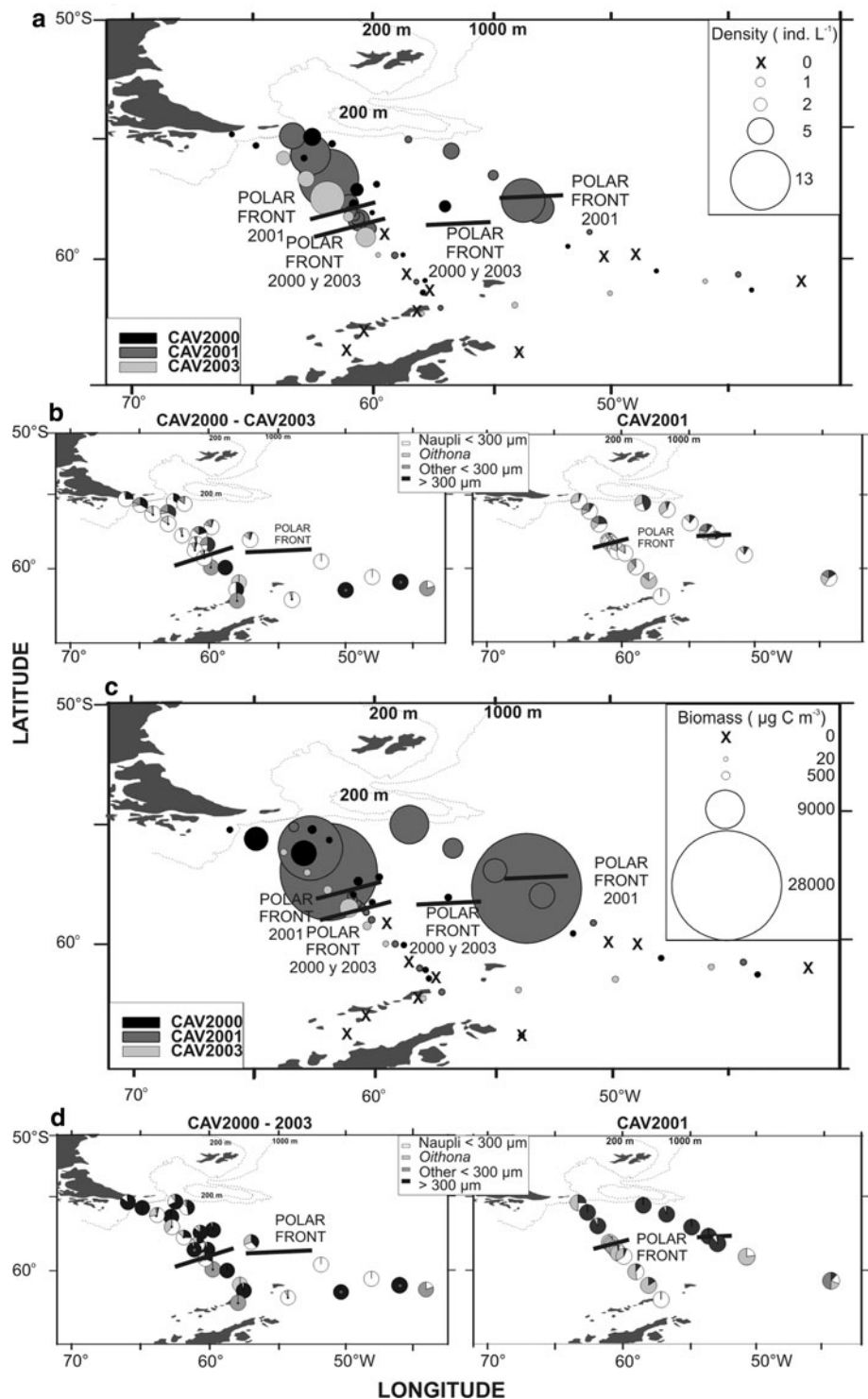
M. gerlachei (2000). In comparison, values of biomass were lower during summer 2003 at all the stations (Table 3). The contribution of the <300-μm fraction was variable (40–63%, Table 1); this fraction accounted for the largest proportion of biomass in some areas, most of which were located in the vicinity of the Polar Front and the Antarctic Peninsula (Fig. 3d). In regard to the dominant

components of this fraction, nauplii represented 28% of the total biomass with a maximum of 63%, whereas *O. similis* represented 22% of the total biomass with a maximum of 84% (Fig. 4c, d).

The density and biomass of copepods differed between the three cruises according to the size fraction and water mass (Table 4). No significant differences in copepod

Table 2 Average and maximum value (in parenthesis) of density for both copepod size fractions and their relative contribution to total density during summer in Subantarctic (Subant.), Antarctic (Antar.) waters and Polar Front

	Summer 2000		Summer 2001			Summer 2003	
	Subant. waters (n: 10)	Antar. waters (n: 9)	Subant. waters (n: 6)	Polar Front (n: 4)	Antar. waters (n: 11)	Subant. waters (n: 4)	Antar. waters (n: 12)
Density (ind L^{-1})							
<300-μm fraction	0.715 (2.04)	0.019 (0.14)	4.239 (9.71)	4.375 (8.054)	0.868 (3.82)	2.740 (6.88)	0.031 (0.29)
>300-μm fraction	0.170 (1.00)	0.006 (0.05)	0.741 (2.99)	0.557 (1.098)	0.002 (0.02)	0.026 (0.06)	0.006 (0.04)
All	0.885 (3.04)	0.024 (0.19)	4.980 (12.7)	4.931 (8.991)	0.870 (3.82)	2.766 (6.93)	0.036 (0.29)
Relative contribution							
<300-μm fraction	79%	75%	83%	91%	97%	99%	50%
>300-μm fraction	21%	25%	17%	9%	3%	1%	50%
Density (ind L^{-1})							
Nauplii	0.65 (2.04)	0.01 (0.09)	2.61 (4.98)	3.13 (5.12)	0.76 (3.20)	2.39 (6.38)	0.03 (0.28)
Oithona similis	0.08 (0.27)	0.001 (0.01)	0.97 (2.46)	0.76 (1.23)	0.18 (0.61)	0.25 (0.46)	0.001 (0.01)
Microsetella norvegica	0.03 (0.09)	0.001 (0.01)	0.01 (0.03)	0.06 (0.20)	–	0.07 (0.15)	–
Oncaea curvata	0.01 (0.02)	–	–	–	0.004 (0.04)	–	–
Rhincalanus gigas	0.002 (0.01)	–	–	–	–	–	–
Calanus simillimus	0.07 (0.20)	–	0.71 (3.94)	0.51 (1.05)	0.001 (0.004)	0.01 (0.04)	–
Calanoides acutus	0.01 (0.07)	0.001 (0.004)	0.62 (2.07)	0.40 (1.41)	0.001 (0.004)	0.01 (0.06)	–
Ctenocalanus citer	0.002 (0.01)	–	–	–	–	–	0.003 (0.02)
Metridia gerlachei	0.01 (0.05)	–	0.03 (0.08)	0.04 (0.16)	–	0.01 (0.05)	–
Clausocalanus laticeps	1E−04 (0.01)	–	–	–	–	–	–
Sapphirina sp	–	–	0.001(0.004)	–	–	–	–
Paraeuchaeta antartica	–	–	–	0.003 (0.012)	–	–	–
Subeucalanus longiceps	0.001 (0.01)	–	–	–	–	–	–

All the species recorded are shown

density were observed between years for Antarctic or Subantarctic waters when considering the >300-μm fraction (Table 4). However, when analysing the <300-μm fraction and both size fractions together, density values were significantly higher in 2001 than in 2000 for Subantarctic waters (Tukey HSD; P: 0.047) and in 2001 than in 2000 and 2003 for Antarctic waters (Tukey HSD; P: 0.021 and P: 0.048, respectively). The main components of the <300-μm fraction followed the same overall trend: nauplii and *O. similis* showed densities up to 5.0 and 2.5 ind L^{-1}, respectively, during summer 2001 and below 2.0 and 0.3 ind L^{-1}, respectively, during summer 2000 (Table 2, Fig. 4a, b). Biomass analysis revealed no significant differences between the three years for the >300-μm fraction in Antarctic waters (Tukey HSD, P > 0.901), whereas the biomass of the <300-μm fraction in Antarctic waters was significantly higher in 2001 than in 2000 and 2003 (Tukey HSD; P: 0.001 and P: 0.007, respectively). As a result, there was a marginal significant difference between these years (Tukey HSD, P: 0.059 and P: 0.007, respectively) when considered both fractions together. The biomass of the >300-μm fraction showed for Subantarctic waters

higher values in 2001 than in 2003 (Tukey HSD, P: 0.035 and P: 0.047, respectively), whereas the biomass of the <300-μm fraction shown no significant difference between the three years. As a result, there was no difference between these years in Subantarctic waters. These results provide evidence of the importance of the <300-μm fraction in terms of numbers and biomass and particularly of its main components: *O. similis* and nauplii (Fig. 4).

Stepwise multiple regression analysis showed that SST and SSTa were the primary predictors of copepod biomass and density at the Drake Passage during summer (Table 5). The density and biomass of nauplii, *O. similis,* and each size fraction separately and together increased significantly with increasing SST and decreasing SSTa. However, the biomass and density values of the <300-μm fraction explained the largest proportion of variability (R^2: 0.72 and 0.36, respectively, Table 5). An increase in the density and biomass of copepods and a peak of in situ chlorophyll a was observed in the Polar Front in 2001, but these variables were not significantly correlated (P > 0.110).

Hierarchical analysis showed four distinct groups of stations (Fig. 5): two of the groups corresponded to

Table 3 Average and maximum value (in parenthesis) of biomass for both copepod size fractions and their relative contribution to total biomass during summer in Subantarctic (Subant.), Antarctic (Antar.) waters and Polar Front

	Summer 2000		Summer 2001			Summer 2003	
	Subant. waters	Antar. waters	Subant. waters	Polar Front	Antar. waters	Subant. waters	Antar. waters
Biomass (µg C m^{-3})							
<300-µm fraction	87 (227)	0.2 (0.5)	1,098 (4,659)	464 (758)	79 (291)	222 (438)	1.7 (16)
>300-µm fraction	1,179 (5,242)	2 (9.8)	8,778 (20,244)	8,068 (27,542)	2.2 (8.5)	618 (3,293)	10 (82)
All	1,151 (5,291)	1.5 (10)	9,877 (24,903)	8,531(28,300)	81 (291)	840 (3,409)	12 (82)
Relative contribution							
<300-µm fraction	30%	61%	18%	53%	96%	67%	50%
>300-µm fraction	70%	39%	82%	47%	4%	33%	50%
Biomass (µg C m^{-3})							
Nauplii	9 (90)	0.01 (0.06)	77 (937)	76 (488)	9 (123)	137 (344)	1.5 (15)
Oithona similis	42 (127)	0.08 (0.49)	787 (3,545)	150 (322)	40 (136)	81 (196)	0.2 (1.7)
Microsetella norvegica	4 (15)	0.12 (1)	2.2 (12)	9 (24)	–	4 (12)	–
Oncaea curvata	1 (4)	–	–	–	1 (10)	–	–
Rhincalanus gigas	2 (16)	–	–	–	–	–	–
Calanus simillimus	1,042 (5,041)	–	1,372 (7,847)	810 (2131)	–	34 (204)	–
Calanoides acutus	41 (154)	1.2 (9.7)	7,276 (14,550)	6,600 (23,855)	0.9 (8)	549 (3,294)	–
Ctenocalanus citer	0.4 (2)	–	–	–	–	–	4 (27)
Metridia gerlachei	51 (234)	–	124 (415)	134 (508)	–	30 (182)	–
Clausocalanus laticeps	4 (37)	–	–	–	–	–	–
Sapphirina	–	–	4 (27)	–	–	–	–
Paraeuchaeta antartica	–	–	–	517 (2,068)	–	–	–
Subeucalanus longiceps	1 (11)	–	–	–	–	–	–

All the species recorded are shown

Table 4 Summary of two-way ANOVA with fixed factors (year and site) for the analysis of copepod density and biomass considering each copepod size fraction and their sum

	All			>300 µm fraction			<300 µm fraction		
	df	F-ratio	P	df	F-ratio	P	df	F-ratio	P
Factor—DENSITY DATA									
Site (SA, A)	1.46	39.86	**<0.001**	1.46	17.15	**<0.001**	1.46	25.86	**<0.001**
Year (2000, 2001 & 2003)	2.46	8.72	**<0.001**	2.46	1.57	0.217	2.46	7.52	**0.001**
Site × Year	2.46	1.56	0.22	2.46	1.51	0.230	2.46	0.86	0.429
Factor—BIOMASS DATA									
Site (SA, A)	1.46	110.01	**<0.001**	1.46	99.07	**<0.001**	1.46	64.32	**<0.001**
Year (2000, 2001 & 2003)	2.46	12.50	**<0.001**	2.46	5.80	**0.005**	2.46	11.44	**<0.001**
Site × Year	2.46	0.30	0.741	2.46	7.12	**0.002**	2.46	1.62	0.207

SA samples from Subantarctic waters (*N*: 20), *A* samples from Antarctic waters (*N*: 32), *df* degrees of freedom, significant *P* values are indicated in bold

Subantarctic waters, one including the stations surveyed in 2000 and 2001, and the other the stations surveyed in 2003. These groups showed almost the same species composition but differed in species abundance and occurrence of co-pepodite stages. The third group, which was related to the

Polar Front (2001), corresponded to a heterogeneous habitat which varied depending on its location in the Drake Passage-Scotia Sea region. Around 60–61°W, the copepod community was characterised by the occurrence of different developmental stages of *O. similis* and absence of a
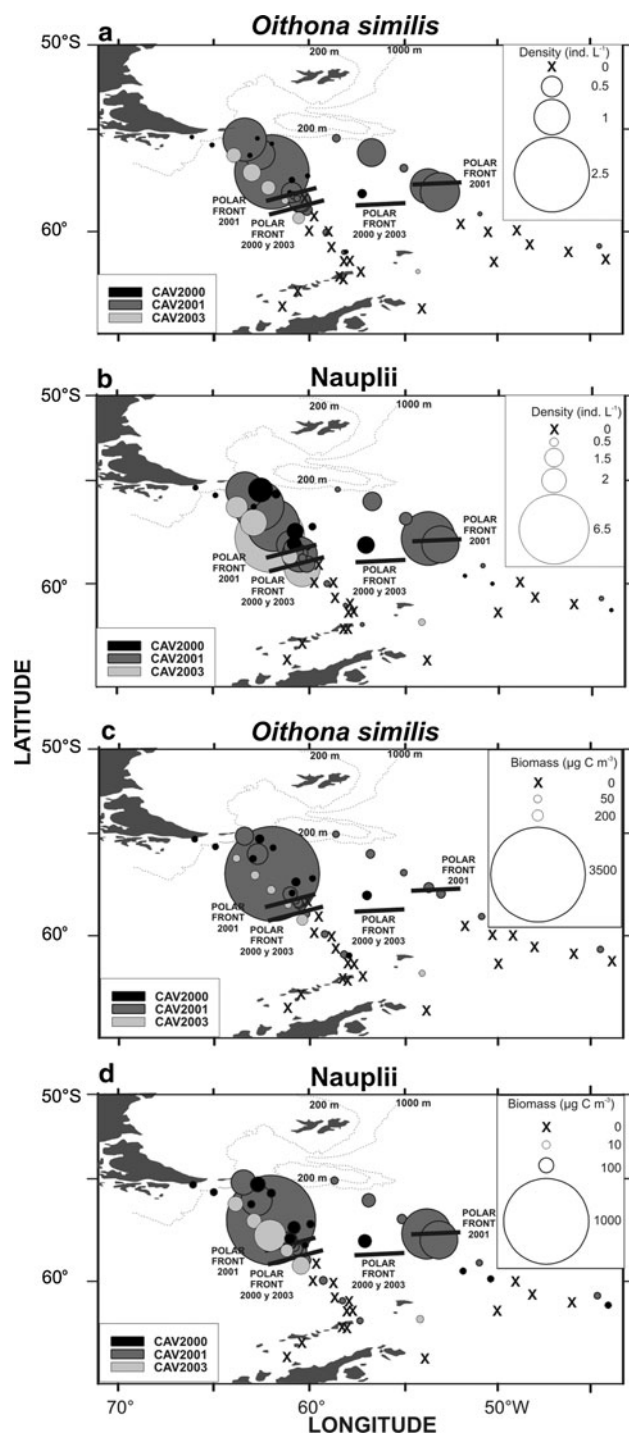
Fig. 4 Density and biomass of *Oithona similis* (**a**, **c**) and nauplii (**b**, **d**) for summer 2000, 2001 and 2003. Circle size is proportional to the absolute values of density and biomass

peak of copepod abundance or chlorophyll *a* concentration. Around 53–54°W, all the copepodite stages (I–V) showed a peak of biomass, adults of *Calanoides acutus*, *Microsetella norvegica*, *Oithona similis*, *Calanus simillimus* and *Metridia gerlachei* were recorded, and chlorophyll *a*

concentration reached maximum values. The fourth group was located in Antarctic waters, most of the species were absent, and the few species present showed low densities (Table 2, Fig. 5).

Discussion

Copepod abundance, distribution and species composition

Results differed depending on whether the <300-μm copepod size fraction was considered or not, both for Subantarctic and Antarctic waters. *Oithona similis*, together with small cyclopoids and nauplii, accounted for the largest percentage of the total number of copepods in the community and for the highest biomass value (63% of total copepod biomass). This acquires particular relevance when considering that zooplankton biomass in the Southern Ocean is usually dominated by copepods (Atkinson 1991; Ward et al. 2004).

Densities recorded in this study (mean: 0.5–2.8 ind L^{-1}, maximum: 3–13 ind L^{-1}, Table 1) were comparable only with those previously reported for similar depths at point positions using Niskin bottle samplers (6–22 L), followed by filtration through a sieve of 15–20-μm mesh (up to 7 ind L^{-1}; Boltovskoy and Alder 1992; Alder and Boltovskoy 1993; Thompson and Alder 2005). The similarity in density values may indicate that copepods display a similar response of active avoidance to the pump sampler and to bottle samplers. A likely explanation to this result is that the turbulence created by the ship would reduce the escape reaction of zooplankton (Singarajah 1975). Both methodologies, the pump-net system used in this study and the bottle sampler, may help to solve the problem of collecting small-sized stages of development and small species. Moreover, the former, like net and continuous plankton recorder samplers, has the advantage of filtering large seawater volumes required for biogeographic studies and monitoring programmes.

In this study, the species identified, including their respective nauplii and copepodite stages, allowed us to discriminate between the hydrological zones under consideration (Subantarctic and Antarctic) and to detect the presence of the Polar Front. The hierarchical analysis performed here revealed changes in the composition of the copepod community and a sharp drop in density values from Subantarctic to Antarctic waters. The geographic distribution of the copepods indicated that *C. acutus* and *R. gigas* are the only species endemic to the Southern Ocean *sensu lato* (from 45° S to ice edge, Razouls et al. 2000), which also occur in the Atlantic, Pacific and Indian Oceans. *C. simillimus*, *C. laticeps*, *C. citer*, *P. antarctica*,

Table 5 Results of stepwise multiple regression analyses for the dependent variables copepod density or biomass considering each copepod size fraction and their sum (log transform data) and the independent environmental variables (AVHRR-SST, AVHRR-SSTa, SeaWIFS Chl a, seawater temperature, salinity) during the three cruises

| Dependent variable	Statistically significant independent variable	B	SE B	P-value	R^2
Biomass					
<300-μm fraction	SST	0.588	0.081	<0.001	0.72
	SSTa	−0.366	0.084		
Total	SST	0.634	0.082	<0.001	0.69
	SSTa	−0.376	0.084		
Oithona similis	SST	0.567	0.085	<0.001	0.68
	SSTa	−0.355	0.089		
Nauplii	SST	0.557	0.090	<0.001	0.64
	SSTa	−0.379	0.093		
>300-μm fraction	SST	0.532	0.115	<0.001	0.40
	SSTa	−0.289	0.119		
Density					
Total	SSTa	−0.387	0.118	<0.001	0.39
	SST	0.412	0.111		
< 300 μm fraction	SSTa	−0.403	0.121	<0.001	0.36
	SST	0.341	0.113		
Nauplii	SST	0.399	0.113	<0.001	0.36
	SSTa	−0.329	0.121		
Oithona similis	SSTa	−0.363	0.124	0.002	0.22
	SST	0.275	0.124		
>300-μm fraction	SST	0.329	0.127	0.011	0.20
	SSTa	−0.309	0.135		

Only significant relationships are shown

SST AVHRR sea surface temperature, *SSTa* AVHRR sea surface temperature anomaly, *Chl a*: SeaWIFS chlorophyll a, *B* (beta) is the standardized regression coefficient or the slope of the least squares line. *SE B* is the standard error of beta

S. longiceps, M. gerlachei and *O. curvata* are cosmopolitan species originating in the Subantarctic sector (off Brazil–Argentina, central South Atlantic Ocean, east and west of South Africa; Razouls et al. 2000), and *O. similis* is a cosmopolitan species of wide distribution in subtropical, temperate and polar waters (Pinkerton et al. 2010). *M. norvegica* and the genus *Sapphirina* are endemic to subtropical and tropical waters (Bradford-Grieve et al. 1999). *M. norvegica* is referred to as a cosmopolitan species, but no reports have hitherto been published on its occurrence in Subantarctic waters of the Atlantic Ocean, whereas records of *Sapphirina* in these waters are doubtful (Razouls et al. 2000; Razouls et al. 2005–2010).

The sampling depth and navigation speed used in this study (9 m depth and 10–14 knots) are similar to those used in continuous plankton recorder (CPR) surveys (6.7 ± 1,3 m depth; 9–17 knots, Batten et al. 2003). The sampling distance of each station (mainly 3.5–6.5 nautical miles) is similar to that used to determine the length of each CPR silk segment for further analysis (5 nautical miles, Hunt and Hosie 2003; Takahashi et al. 2010). Moreover, the 20-μm-mesh net increases the efficiency of collecting small copepods, but these pass through the 270-μm-mesh of the CPR silk; the latter, in contrast to the pump-net methodology, does not prevent clogging. On this basis and given the size range of copepods, the pump-net methodology is proposed as a good complement to CPR sampling. This can be exemplified with *O. similis* and nauplii. *O. similis*, which is one of the most abundant species in CPR samples (Takahashi et al. 2010; McLeod et al. 2010), showed a sharp decrease in absolute density to the south of the Polar Front but contributed highly to some Antarctic samples. Moreover, although data from CPR sampling indicate that *O. similis* is abundant in Antarctic and Subantarctic waters, it cannot be quantified because the efficiency of retention (mean: 30%) changes with copepod length (Batten et al. 2003; Pinkerton et al. 2010). On the other hand, nauplii comprised an average of 70% (range 26–95%) of the total copepods in this study and less than 1% in CPR studies (Takahashi et al. 2010).

Fig. 5 Biogeographic zones in Drake Passage, as defined by cluster analysis (fourth root transformed density data, Bray Curtis Index, UPGMA clustering method) using 2000, 2001 and 2003 data sets
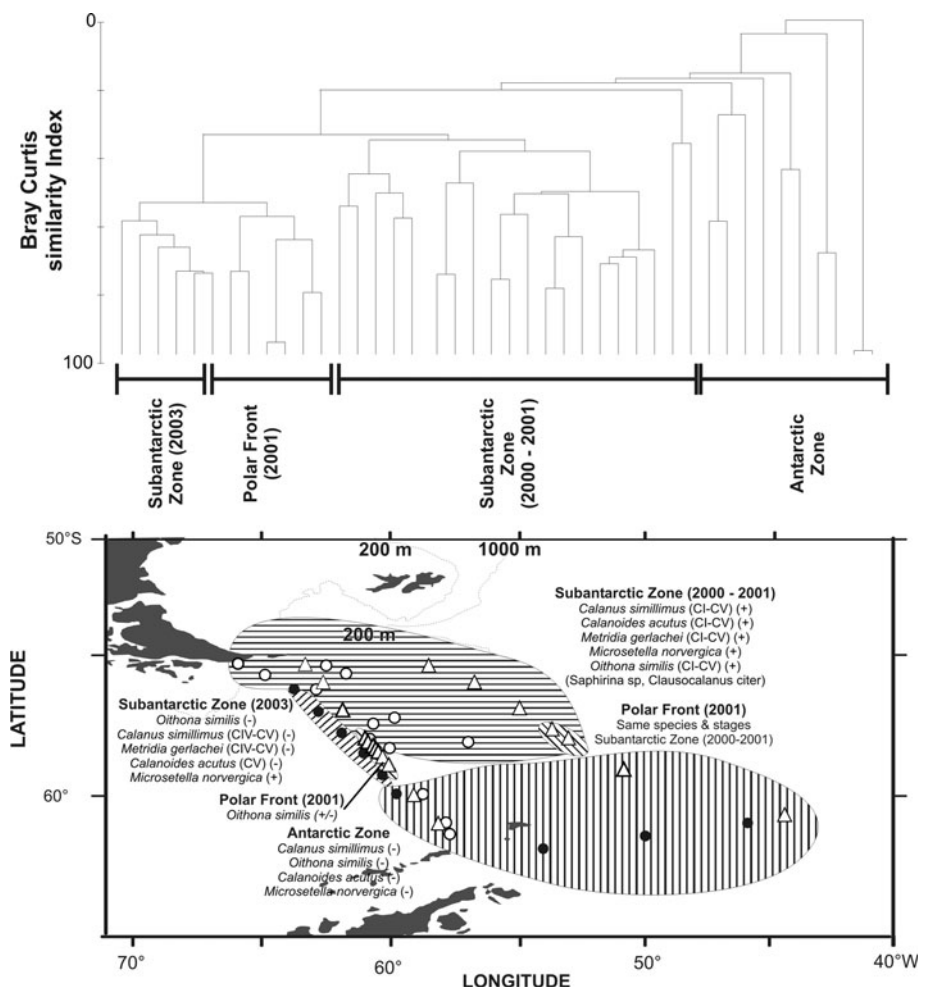
Interannual fluctuations of copepods and hydrological conditions

Higher density/biomass of copepods seemed to be related to less anomalous sea surface temperatures (2001), whereas more anomalous temperature conditions, particularly warmer temperatures (2003), were unlikely to increase copepod abundance. The lack of correlation between copepod abundances and chlorophyll *a* values could be related to the fact that at high latitudes, the phytoplankton bloom is often uncoupled from zooplankton production (Frost 1987; Paul et al. 1991).

The life cycle strategies of calanoids and cyclopoids (which showed the highest proportions in the >300- and <300-μm fraction, respectively) may account for the differences observed between the summers under consideration. Large calanoid species have been characterised as seasonal migrants (Vervoort 1965; Atkinson and Sinclair 2000). Calanoids and late copepodite stages overwinter at the same depth, spawning is associated with their ascent in spring, and the new generation grows within the surface layers in summer. Afterwards, later copepodites

progressively and gradually descend**.** In regard to the most frequent calanoid species *Calanus simillimus* and *Calanoides acutus,* adults were found in superficial waters during 2001, in agreement with the pattern previously described. During the cooler summer (2000), however, the proportion of adults was lower and that of copepodite stages was higher, revealing a population structure typical of later spring and earlier summer generations. This explained the significantly lower biomass values of the >300-μm fraction during 2000, despite the similar density values between 2000 and 2001. On the other hand, the larger number of calanoid nauplii suggests the occurrence of spawning during the warmer summer (2003), when calanoid copepodites and adults were occasionally observed, and a significant decrease in biomass was recorded. Atkinson (1991) suggested that *C. simillimus* and *C. acutus* experience developmental delay under cold-water conditions and hence that their spawning is temperature dependent. In this study, the change in population structure in relation to variations in SST among years and the somewhat significant prediction values of SST and SSTa for the density and biomass of the >300-μm fraction supports Atkinson's results.

The life cycle strategy of the cyclopoid *Oithona similis* differs substantially from that of calanoids; it is considered an epipelagic non-seasonal migrant (Atkinson and Sinclair, 2000), with nauplii and copepodite stages occurring throughout the year (Atkinson 1990; Metz 1995, 1996), even in low chlorophyll *a* environments (Fransz 1988). In addition, population structure obtained in this study differed from that reported for calanoids species, with later copepodite stages (IV–V) and adults being more numerous during the cooler 2000 than in 2001 and 2003. This may explain the limited prediction value of SST and SSTa for *O. similis* density and biomass.

The results obtained here suggest that planktonic copepods of the Southern Ocean may be considered as good indicators of changes in local oceanographic conditions during summer at a large spatial scale. This information is important 1) for designing the Southern Ocean CPR monitoring programme aimed at evaluating the future impact of climate change and 2) in long-term studies of the effects of the 'El Niño-Southern Oscillation' (ENSO) on pelagic ecosystems in the Southern Ocean and coastal Antarctic regions. The ENSO has a profound effect on the weather and oceanic conditions in tropical and in mid-latitude areas and its teleconnections (statistically significant relationships between ENSO and climatic parameters in remote locations). The effect is particularly strong at high southern latitudes in the South Pacific Ocean, off the coast of Antarctica and in the vicinity of the Drake Passage (Turner 2004a).

In summary, the present results showed the quantitative importance of small copepods and the advantages of using the pump-net methodology in regular sampling and as a complement of CPR studies; to obtain an accurate estimation of copepod abundance in the Drake Passage, both methods should be performed simultaneously for a yearly cycle. This will allow a better understanding of the role played by this group in the ecosystem and in the transfer of energy through the food web. In addition, the different effect of temperature variations in the life cycle of the three dominant copepod species may explain the different predictive value of SST and SSTa for the abundance of each copepod size fraction. This information highlights the importance of considering the < 300-µm copepod size fraction in future studies in the Drake Passage to improve the knowledge of this particular system.

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