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Structure, abundance and biomass size spectra of copepods and other zooplankton communities in upper waters of the Southwestern Atlantic Ocean during summer

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Little attention has been paid to small copepods and other zooplankton inhabiting pelagic ecosystems of the Southwestern Atlantic Ocean under the influence of the Antarctic Circumpolar Current circulation, despite their important role in the trophic chain and fisheries. This study gives a synoptic view (January 2001) of the micro and mesoplankton size fractions and normalized biomass size spectra (NBSS) in upper waters of five different ecological domains (shelf and oceanic Subantarctic and Antarctic waters) including the Brazil–Malvinas confluence (BMC). Copepods were always the main component of the zooplankton; the <300- μm fraction represented between 70 and 99% in terms of numbers and from 20 to 88% in terms of biomass. Other zooplankton contributed with <40% to total zooplankton densities, though showing some biomass peaks (>50%). Chlorophyll *a*, sea surface temperature and salinity were the environmental variables that best explained the distribution trend of zooplankton, mainly that of the <300- μm fraction. For all the domains, NBSS revealed flat slopes (–0.6 to –1), suggesting a higher proportion of large organisms than expected at equilibrium.

A dome-shape feature was detected in the BMC. Total biomass and trophic levels of the system were related to the composition of the community and the hydrological conditions of the domains covered.

KEYWORDS: size structure; copepods; zooplankton; Southwestern Atlantic; normalized biomass size spectra

INTRODUCTION

The size structure of planktonic communities has the potential to indicate the transfer of energy up the trophic web and can influence the pathways of carbon export and sequestration (Legendre and Le Fèvre, 1991; San Martín *et al.*, 2006). The abundance-size spectrum (the relative abundance of organisms of different sizes) is a highly effective approach to summarize the size structure of plankton communities (Cottingham, 1999; Cózar *et al.*, 2003), predict fish stocks (Sprules *et al.*, 1983), reflect changes in the upper ocean carbon flux and describe rates of material transfer in the upper ocean of different regions (San Martín, 2005).

Theoretical models of the size structure of pelagic ecosystems have been developed during the last 40 years, starting with the work by Sheldon *et al.* (Sheldon *et al.*, 1972). Platt and Denman (Platt and Denman, 1978) proposed an empirical model to calculate the biomass distribution as a function of organism size (biomass spectrum) in the pelagic ecosystem of the open ocean. In this model, the flux of biomass produced at a steady state mostly by individual growth within a weight class is equal to the respiration loss of the system (Silvert and Platt, 1978). Based on a function of individual body weight, Heath (Heath, 1995) proposed an energy balance between growth and mortality. Through their population dynamics theory of plankton, Zhou and Huntley (Zhou and Huntley, 1997) suggested that the governing equations deduced by them represent the mass balance between the biomass flux from small to large sizes due to individual growth and the sum of sources and sinks such as birth, natural death and predation. Their theory was based on the distribution of abundances as a function of individual body weight and growth rate and the law of conservation of mass.

The slope of a plankton biomass spectrum is a means of measuring the relationship between growth, mortality and respiration of a community (Zhou *et al.*, 2004 and references therein) and represents the ratio of specific population mortality to specific individual and population body mass growth rates (Heath, 1995; Zhou and Huntley, 1997). The metabolic rate is the primary or physiological scaling of body mass of individual

organisms (Platt, 1985; Dickie *et al.*, 1987); a secondary scaling of body mass, the secondary specific production, reflects the effect of the distribution and interactions of groups of organisms as part of populations (Dickie *et al.*, 1987).

Using normalized biomass size spectra (NBSS), their slopes and zooplankton species information from *in situ* samples can be an effective approach for the study of biomass flow, community changes and trophic interactions (Zhou *et al.*, 2009). Trophic levels (TL) within a plankton community can be estimated based on a normalized biomass size spectrum. The number of trophic interactions can vary over short-time scales, with lower and higher TLs during periods of higher and lower phytoplankton concentrations, respectively, as mesozooplankton species change from a more herbivorous to a more omnivorous diet (Basedow *et al.*, 2010).

Empirical data regarding planktonic size structure in offshore areas are scarce (Quiñones *et al.*, 2003). Transects from the North to the South Atlantic (67°N to 39°S) revealed the importance of small copepods and naupliar stages (over 53 μm) during spring (48°N to 39°S; López and Anadón, 2008), and latitudinal variations in plankton size spectra (over 10 μm) during autumn and spring (67°N to 49°S; San Martín *et al.*, 2006). López and Anadón (López and Anadón, 2008) found that copepods were the major grazers of phytoplankton and that small copepods and nauplii account for a higher amount of total chlorophyll ingestion than larger copepods, even in oligotrophic areas where these were relatively more abundant. San Martín *et al.* (San Martín *et al.*, 2006) found a relatively flat average slope (-1.07) across the Atlantic, compared with the theoretical prediction of -1.22 and with observed mean values for the North Atlantic (-1.16) and the North Pacific (-1.15) (Platt and Denman, 1978; Rodríguez and Mullin, 1986a; Quiñones *et al.*, 2003). Relatively flat slopes reflect a higher proportion of large organisms and an increase in biomass with size. These authors suggested a change in the trophic transfer efficiency (and coupling between phytoplankton and mesozooplankton) due to spatial variations in ecosystem productivity (shallower slopes in productive upwelling areas,

steeper slopes in oligotrophic convergence regions) and seasonal input of biomass.

Apart from this, relatively little attention has been paid to the planktonic community structure of the Southwestern Atlantic Ocean (SAO) (Angel, 1979; Berasategui *et al.*, 2005), although its relevance in the life history of many commercially exploitable species is recognized (Rodhouse *et al.*, 1992; Mauchline, 1998). The SAO is a hydrologically complex region with several frontal systems delimiting distinct water masses and ecological domains (Fig. 1, Orsi *et al.*, 1995; Matano *et al.*, 2010; Piola *et al.*, 2010), and under the influence of the Antarctic Circumpolar Current (ACC) circulation. Large-scale studies on zooplankton from the SAO have covered mainly copepods and macrozooplankton over 200 μm in size (Tarling *et al.*, 1995; Gallienne and Robins 1998; Bradford-Grieve *et al.*, 1999; Woodd-Walker *et al.*, 2002; Berasategui *et al.*, 2005), total crustacean larvae over 30 μm in relation to other protozoans (Thompson *et al.*, 1999, 2001; Thompson, 2001) and planktonic diatoms (Olguín *et al.*, 2006; Olguín and Alder, 2011).

In this context, the aim of the present study was to investigate the spatial distribution of the composition, density and biomass of copepods and the contribution of other micro- and smaller meso-zooplankton during summer, from 37°S in the Continental Shelf Waters of the northern Argentine shelf (CSW) to the South Orkney Islands (ORK) throughout the oceanic domain of the Brazil–Malvinas confluence (BMC) to Subantarctic (SAW) and Antarctic Surface Waters (AW) up to 61°S. A secondary goal of the study was to test the hypothesis that environmental differences among the SAO ecological domains (see below) are reflected in the NBSS and the trophic structure of the zooplankton community when applying the model of Platt and Denman (Platt and Denman, 1978).

Within the Southwestern Atlantic, the BMC is an extensive region where subantarctic waters (Malvinas Current), subtropical waters (Brazil Current) and waters of the South Atlantic Drift mix both horizontally and vertically creating a region of strong mesoscale variability (Chelton *et al.*, 1990; Goni and Wainer, 2001). The limit between the BMC and the SAW is the Subantarctic Front (48–50°S, Fig. 1). SAW are cold, fresh (<10°C at the surface in summer) and nutrient-rich waters carried by the Malvinas Current, a northbound branch of the ACC running along the western edge of the Argentine Basin up to about 38°S (Piola and Gordon, 1989; Peterson, 1992; Matano *et al.*, 2010). Their southern limit is the Antarctic Convergence or Polar Front (55–60°S, Fig. 1), which can be described as a surface front with a strong

temperature gradient (1.7°C in 47 km; Moore *et al.*, 1997). The AW is represented by the colder and nutrient-rich waters (Smith, 1991) of the ACC, which extends with rather uniform properties from the Polar Front to the Southern Boundary (SBACC; Fig. 1) (Orsi *et al.*, 1995).

Waters from the Argentine shelf (CSW) result from the mixing of the continental runoff, the western branch of the Malvinas Current (which runs north-eastward over the continental shelf) and the eastern branch previously described. The shelf break front separates CSW from SAW (Franco *et al.*, 2008) with a NW–SE orientation in summer (Saraceno *et al.*, 2004; Barré *et al.*, 2006). Slope water intrusions onto the continental shelf near 41°S contribute to the development of phytoplankton blooms over the outer continental shelf (Piola *et al.*, 2010). South Orkney Shelf Waters (ORK) are located in the Weddell–Scotia Confluence between the SBACC and the Weddell Front, and are characterized by both high nutrient concentrations and high productivity with complete ice cover (Holm-Hansen *et al.*, 2004a,b).

METHOD

Field sampling

Subsurface (9 m depth) plankton samples and environmental data were collected over a transect performed on board the icebreaker “Almirante Irizar” in the SAO (37–61°S, 44–56°W, Fig. 1) during austral summer (4–9 January 2001). At each oceanographic station, samples were taken with a pumping system (specially designed to filter a constant volume of water and to operate while the ship was underway) at a spatial resolution of 3.5–5 nautical miles. The flow rate was checked using a flowmeter. A total of 24 samples were collected by filtering 460–670 L of seawater through a 20- μm mesh, and samples were subsequently fixed with 3% formalin solution. Data on environmental conditions were obtained from *in situ* measurements and satellite images. *In situ* measurements of seawater temperature, salinity, size-fractionated chlorophyll *a* (GF/F and 10 μm) and chlorophyll fluorescence were taken at the same depths as the plankton samples (9 m). These data were provided by the ARGAU project (<http://dataipsl.ipsl.jussieu.fr/ARGAU/argau.htm>).

Eight-day-composite satellite images were derived from the AVHRR Oceans Pathfinder Sea for Surface Temperature (SST), and from SeaWiFS for sea surface chlorophyll *a* concentration. AVHRR data were provided by the Physical Oceanography Distributed Active

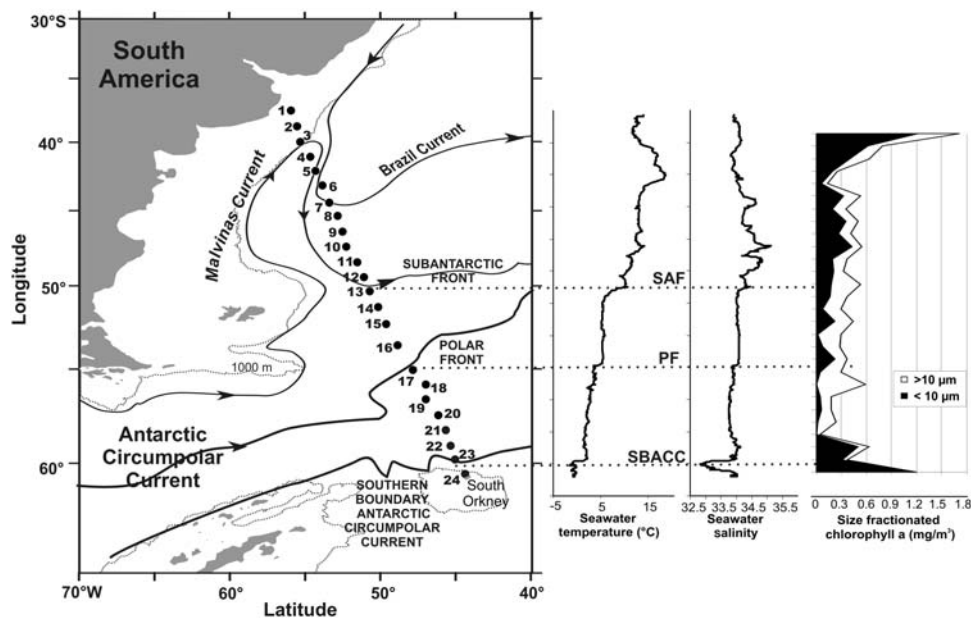


Fig. 1. A geographic location of the stations, fronts and general circulation pattern. The latitudinal profile of *in situ* seawater temperature, seawater salinity and size fractionated chlorophyll *a* is shown.

Archive Center (PO.DAAC) Ocean ESIP Tool (POET) at the NASA Jet Propulsion Laboratory, Pasadena, CA, USA (<http://poet.jpl.nasa.gov>), and SeaWiFS data by the SeaWiFS Project at NASA Goddard Space Flight Center, USA (<http://oceancolor.gsfc.nasa.gov>).

Sample analyses

Prior to laboratory analyses, each plankton sample was separated into two fractions using a 300- μm mesh. From the entire $>300\text{-}\mu\text{m}$ fraction, copepods and larger zooplankton were identified under a stereomicroscope at $40\times$ magnification. From the $<300\text{-}\mu\text{m}$ fraction, community structure and abundance of microplankton ($>20\ \mu\text{m}$), copepods and other zooplankton were estimated using an inverted microscope (at $200\times$ magnification) on Utermöhl settling chambers, after samples had settled for at least 24 h. Three subsamples of 10 mL were counted when abundances were high (>500 ind. per sample); otherwise the entire sample was analyzed. Protists were enumerated from the whole sample except for diatoms and dinoflagellates, for which at least 50 fields were scanned from two chambers and 500 cells were counted (variations among counts were $<15\%$).

Copepods were identified to species level according to Bradford-Grieve *et al.* (Bradford-Grieve *et al.*, 1999), other zooplankton to order or family level according to Boltovskoy (Boltovskoy, 1999). Nauplii of calanoid and cyclopoid copepods were assigned to a single category

because of the difficulty in identifying species and developmental stages. Unicellular microplankton was split into two categories: microzooplankton (tintinids, foraminifera and radiolarians) and other unicellular microplankton (total dinoflagellates, diatoms and silicoflagellates).

Biomass was estimated from body measurements of each copepod and other zooplankton groups (n : 14 106) by using previously established conversion factors of volume to (wet or dry weight) biomass [naupliar forms (Gradinger *et al.*, 1999), pteropods (Comeau *et al.*, 2010), amphipods (Watts and Tarling, 2012), euphausiids (Daly, 2004), polychaetes (Hansen *et al.*, 1999), copepods (Gradinger *et al.*, 1999; Nozais *et al.*, 2001) and microzooplankton (Verity and Langdon, 1984; Caron *et al.*, 1995)]. Wet weight (ww) and dry weight (dw) values were converted to carbon (C) using Wiebe's relationship (Wiebe, 1988). One advantage of this method is the nearly linear relations between weights and body carbon; the regression equations used were $\log_{10}(\text{ww})$: $-1.537 + 0.852 \cdot \log_{10}(\text{C})$ (r^2 : 0.92, $P < 0.001$) and $\log_{10}(\text{dw})$: $0.499 + 0.991 \cdot \log_{10}(\text{C})$, (r^2 : 0.97, $P < 0.001$) where ww, dw and C were expressed in g m^{-3} , mg m^{-3} and mg C m^{-3} , respectively. Since biomass estimations based on body volume and published conversion factors are subject to errors, confidence limits for each sample were calculated for carbon concentration values in accordance with Wiebe *et al.* (Wiebe *et al.*, 1975) and Zar (Zar, 1999). The 95% lower and upper confidence limits of zooplankton body biomass were $\sim 0.44\text{--}2.20$ times the mean value, respectively. The total density

and biomass of zooplankton, and the relative contribution of each size fraction were determined for each station.

Statistical analyses

To test for violation of independence in the data (spatial autocorrelation), Moran's I value was used. This index evaluates whether the pattern of distribution of density and biomass values (for each relevant copepod species, and for copepod and non-copepod zooplankton size fractions) was clustered, dispersed or random. A Moran's I value near 1 indicates clustering and positive spatial autocorrelation, whereas a value near -1 indicates dispersion. Values near zero indicate an absence of spatial autocorrelation. The Moran's I function calculates a z -score value that indicates whether the spatial patterns (e.g. clustering or dispersion) could be the result of random chance or are statistically significant (SAM v4.0, Rangel *et al.*, 2010).

The Clarke and Ainsworth (Clarke and Ainsworth, 1993) routine for linking multivariate community structures to environment variables (Bio-Env) was used to estimate which set of environmental variables best explained the density or biomass values of zooplankton considering both size fractions either together or independently. The environmental variables used were latitude, longitude, local depth, *in situ* seawater salinity, size-fractioned chlorophyll a and chlorophyll fluorescence, sea surface temperature and SeaWiFS chlorophyll a . The Bio-Env analysis is based on determining Spearman's rank correlation between the environmental and biological similarity matrices. The high rank similarity indicates the environmental variable that better explains the biological data. Then different combinations of environmental variables were compared to determine which combination shows the highest correlation with the biological data. The environmental and biological similarity matrices were constructed using the Euclidean distance and Bray-Curtis Index, respectively. When pairwise correlations between environmental variables were >0.90 , co-linearity was assumed, and one of these variables was not considered for the analyses (correlation occurred between SST and *in situ* seawater temperature and so only the former was analyzed).

The influence of independent abiotic and biotic variables on the density and biomass of each relevant copepod species and zooplankton taxa was analyzed by multiple linear regression analyses (Myers, 1990).

As our samples were collected at a fixed depth, the size frequency distribution of total copepods and other zooplankton (20–4000 μm) was analyzed at each station in order to detect possible variations between

day- and night-samples within each ecological domain and to determine which size ranges may have been affected by the diel vertical migration of the organisms, thus influencing further analyses.

Biomass spectra analyses

Biomass size spectra of copepods and other zooplankton were organized in a maximum of 25 fixed size classes, ranging from 0.0001 to 1000 $\mu\text{g C ind}^{-1}$, which represent a range of eight orders of magnitude, from microzooplankton to smaller mesozooplankton (range: 20–4000 μm total length). Daytime and nighttime stations within each ecological domain were analyzed separately. For individual stations, and for daytime or nighttime groups of stations, the zooplankton biomass size-spectrum was normalized (weight interval on an octave scale) and plotted on a log–log scale (NBSS) according to Platt and Denman (Platt and Denman, 1978). The NBSS has the advantage of setting up the conservation equations and being integrated over the size range analyzed. The area under the NBSS is equal to the total biomass. Extreme sizes (<0.0001 and $>1000 \mu\text{g C ind}^{-1}$, respectively) were not included in the analyses, as they could cause potential errors in the calculation of the slope and intercept.

To compare the NBSS, slopes and intercept were computed by fitting a linear regression line to the data. In those cases where a linear regression analysis proved inappropriate to model the biomass size spectrum of a station (i.e. no significant fit was obtained), the slope and intercept of the line were not estimated. Prior to the comparison of regression lines, the assumption of homogeneity of variance was tested using Bartlett's test. Within each ecological domain, daytime samples were compared with nighttime samples on the basis of the slopes using Student's t test. In those cases where slopes did not differ, daytime and nighttime samples were pooled together and a common slope and intercept were estimated for the domain. All resulting slopes were then compared using the F test for multiple comparisons, and this procedure was followed by applying Tukey's multiple comparison tests to detect differences within each pair of slopes. This analysis allowed pooling domains (or their divisions) in groups with similar slopes. In each of these groups, the intercept of the NBSS has been suggested as an indicator of the total biomass in the system provided that the slopes are similar (Sprules and Munawar, 1986; Gasol *et al.*, 1991; Quiñones *et al.*, 2003) and so F -test and t -test were used to test for differences in the elevations of the NBSS (Zar, 1999).

The number of TLs was calculated on the basis of the slope of the NBSS and the mean community assimilation efficiency of zooplankton $\{Zhou, 2006: TL = (1 + \eta_n)/[\eta_n(\delta \ln b/\delta \ln w)]\}$. Community assimilation efficiency was held constant to a mean of 70%, a value commonly used for copepods (Zhou, 2006; Basedow *et al.*, 2010). The number of TLs within the whole zooplankton community (20–4000 μm) was estimated for each ecological domain or, when appropriated, for its daytime and nighttime groups of stations. It should be noted that the estimated TLs do not represent exact TLs, but the variations in TL represent the differences in trophic structure between zooplankton communities (Basedow *et al.*, 2010).

RESULTS

Environmental conditions

Environmental conditions assessed either through *in situ* measurements or satellite data were clearly different between the ecological domains studied (Fig. 1 and Table I). Seawater temperature showed a southward decrease, with strong gradients indicating the location of the Shelf Break Front, Subantarctic Front, the Polar Front and the Southern Boundary of the ACC (Fig. 1). Strong salinity gradients also indicated the location of these fronts. Shelf domains (CSW and ORK) showed higher values of chlorophyll (fluorescence and SeaWIFS data) than the oceanic domains (BMC, SAW, AW), while Antarctic waters showed a southern decrease in SeaWIFS values. The <10- μm chl *a* fraction showed its highest contribution in shelf domains (CSW and ORK), BMC and southern stations of AW (Fig. 1), while the contribution of the >10- μm chl *a* fraction was higher in SAW and northern stations of AW (Fig. 1).

Structure and abundance of copepods, other zooplankton and protists

In terms of density and biomass, copepods were the main component of the zooplankton. Mean density and biomass contributions to total zooplankton in all ecological domains were over 77 and 75%, respectively (Figs 2 and 3; Tables II and III). Highest copepod densities were recorded for Argentine Continental Shelf Waters (CSW; up to 259 ind. L^{-1}), followed by oceanic Subantarctic Waters (SAW; up to 18 ind. L^{-1}). In contrast, highest copepod biomass values were recorded at the northern sector of the area investigated: a major peak was detected in the BMC (up to 170 mg C m^{-3}) followed by a secondary increase in CSW (up to 81 mg C m^{-3}).

The density of the <300- μm copepod fraction represented, on average, 70–99% of total copepods recorded (Fig. 2, Table II). This fraction comprised mainly nauplii, specimens of the genus *Oithona*, several small calanoids (*Calocalanus tenius*, *Eucalanus* sp., *Labidocera* sp. and copepodite stages of *Clausocalanus* spp.) and harpacticoids (*Euchirella rostrata*, *Euterpina* sp., *Microsetella norvegica*, *Tachidius* sp. and *Tegastidae* sp.) (Table II). The >300- μm copepod fraction was represented by 19 species belonging to 10 genera of calanoids. The most abundant genera were *Calanoides*, *Calanus*, *Clausocalanus*, *Ctenocalanus*, *Neocalanus* and *Paracalanus*, all with densities <7 ind. L^{-1} (Table II). The genera *Drepanopus*, *Metridia*, *Rhincalanus*, and *Subeucalanus* were observed occasionally with densities <0.06 ind. L^{-1} .

The <300- μm fraction represented an important contribution to biomass at several stations near and south of the Subantarctic Front (Stations 12, 13, 16–18, 24 and Fig. 3), with mean values between 61 and 88% for SAW, AW and ORK (Fig. 3 and Table III). The mean contribution of copepod nauplii and *Oithona* over

Table I: Summary of environmental information for each domain covered in the SAO during 2001

Stations	CSW 1–3	BMC 4–12	SAW 13–16	AW 17–23	ORK 24
<i>In situ</i> seawater temperature (°C)	12.55–21.5	11.4–17.2	5.4–10.2	–0.84–3.54	–0.62
<i>In situ</i> seawater salinity (PSU)	33.89 ^a	33.10–34.71	34.00–34.27	33.06–34.12	33.94
Chlorophyll fluorescence (a.u.)	2.8 ^a	0.9–1.3	1.4–1.7	1.0–1.3	4.4
Chl <i>a</i> size fraction (mg m^{-3})					
<10 μm	1.22 ^a	0.20–0.52	0.06–0.22	0–0.52	0.25
>10 μm	0.48 ^a	0.06–0.22	0.15–0.35	0.05–0.58	0.12
SeaWIFS chlorophyll (mg m^{-3})	1.6–5.5	0.6–1.5	0.2–1.0	0.1–0.6	2.8
AVHRR-SST (°C)	16.5–20.4	11.1–15.9	4.9–7.5	(–1.5)–3.75	–0.9
Ice cover	No	No	No	No	Yes
Local depth (m)	25–180	>3000	>1500	>3000	48

CSW, Continental Shelf Waters; BMC, Brazil-Malvinas confluence; SAW, Subantarctic Waters; AW, Antarctic Surface Waters; ORK, South Orkney Shelf Waters.

^aData not available for stations 1 and 2.

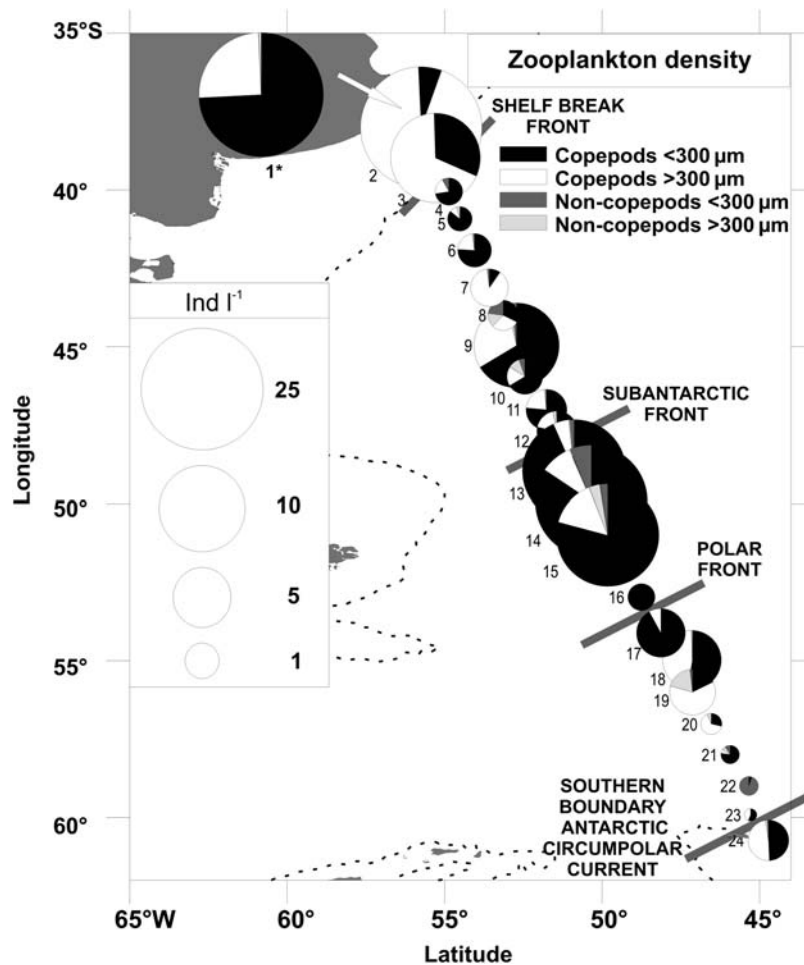


Fig. 2. The density and relative contribution of each fraction (>300 and <300 μm) of copepods and non-copepod zooplankton to total density. The circle size is proportional to the absolute values of density, except for station 1* (259 ind. L^{-1}).

the entire study area was *ca.* 21 and 17%, respectively. Additionally, *Oithona* showed increased relative importance in oceanic waters, with contributions up to 73% of total biomass (Table III). The highest values of copepod biomass within the >300 - μm fraction were recorded in the BMC and CSW, with contributions decreasing southward (Fig. 3 and Table III). Copepodite stage V and males of *Neocalanus tonsus* represented over 98% of the peak found in the BMC, while the main contribution to biomass in Argentine CSW was provided by later copepodite stages and adults of *Calanus simillimus*, *Clausocalanus breviceps*, *Paracalanus* spp. and *Neocalanus tonsus* (Table III). *Calanus simillimus* showed some increments in SAW and WA (stations 15 and 19: 11.5 and 3.6 mg C m^{-3} , respectively), while the rest of the calanoids reached, on the whole, values below 1 mg C m^{-3} (Table III).

Non-copepod zooplankton represented $<23\%$ of total zooplankton densities, with some peaks in AW

(station 22 Fig. 2). The main groups in the >300 - μm fraction were euphausiids, cephalopod larvae, large polychaetes, ostracods, amphipods and limacine pteropods, while the <300 - μm fraction was represented by small limacine pteropods, small cephalopod larvae, non-copepod nauplii larvae and small polychaetes. Individual groups from both fractions showed densities <1.3 ind. L^{-1} (Table IV), and were observed mainly during nighttime. Pteropods (in BMC and SAW, up to 1.25 ind. L^{-1}), euphausiids (in BMC, SAW and AW up to 0.2 ind. L^{-1}) and cephalopod larvae (in the five domains, up to 0.12 ind. L^{-1}), were the more frequent groups (over 40% of the samples). In terms of biomass, highest values of non-copepod zooplankton were found in the BMC (stations 10–11) and in AW (stations 19–22), where the >300 - μm fraction dominated the zooplankton community and represented up to six times the total biomass of copepods (Fig. 3). Contrary to the trend found for copepods, the contribution in density

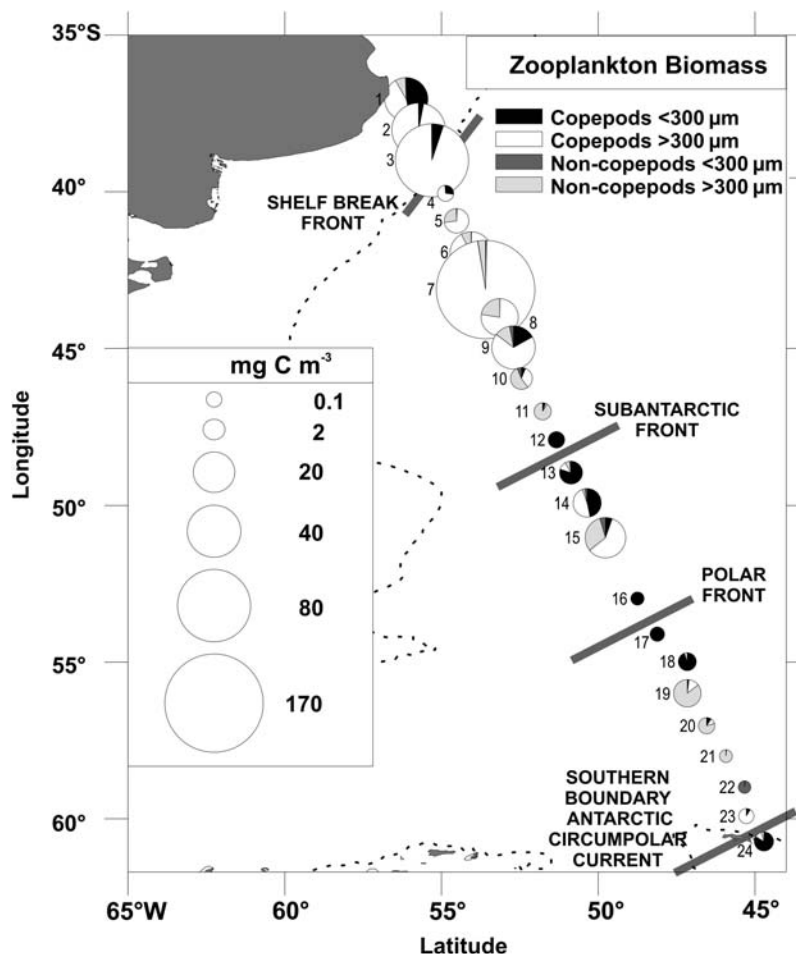


Fig. 3. The Biomass and relative contribution of each fraction (>300 and <300 μm) of copepods and non-copepod zooplankton to total biomass. The circle size is proportional to the absolute values of biomass.

and biomass of the >300-μm fraction of non-copepod zooplankton was higher than that of the <300-μm fraction in each of the ecological domains, except of in SAW (Table IV).

The highest contribution of unicellular microzooplankton (tintinnids, radiolarians and foraminifera) was found in the BMC and near the Subantarctic Front (Fig. 4 and Table IV). Other microplanktonic protists (dinoflagellates, diatoms and silicoflagellates) showed higher densities in shelf waters (CSW and ORK; stations 1 and 24) and in oceanic waters (AW; stations 19–21; Fig. 4; Table IV).

No significant spatial autocorrelation was detected for any variable (all Moran’s *I* between -0.22 and 0.14 , *z*-score between -0.35 and 0.25 , $P > 0.09$). Chlorophyll *a*, SST and salinity were identified by the Bio-Env analyses as the environmental variables that best explained the spatial distribution of both total zooplankton and its <300-μm fraction, while only SST

and salinity explained the distribution of its >300-μm fraction (Table V). Results of the multiple regression analyses on each taxon that had a significant relationship with independent abiotic and biotic variables are shown in Table VI. SST and chlorophyll *a* explained over 60% of the variability in the distribution of density and biomass of copepod nauplii, *Oithona* spp. and the harpacticoid *Microsetella norvegica*. All variables showed a positive correlation with the above-mentioned taxa (Table VI).

Figure 5 illustrates the body length distribution of copepods and other zooplankton at daytime and nighttime stations within each ecological domain. Specimens with a total length from 750 to 4000 μm had a higher contribution at nighttime stations when compared with daytime stations. The increase in the nighttime contribution was different in each of the domains due to the presence of the following species: (i) *Metridia lucens*, *Subeucalanus* spp. and other large calanoids (found in

Table II: The average and maximum value (in parenthesis) of density for both copepod size fractions and their relative contribution to total density during summer 2001

Stations	CSW 1–3	BMC 4–12	SAW 13–16	AW 17–23	ORK 24
Copepods					
Density (ind. L ⁻¹)					
>300 µm fraction	4.6 (8)	0.3 (1.3)	0.2 (0.5)	0.1 (0.5)	0.1
<300 µm fraction	91.2 (258)	1.7 (9)	12.4 (18)	1.2 (4)	1.6
All	95.7 (259)	2 (10)	12.6 (18)	1.3 (4)	1.7
Relative contribution (%)					
>300 µm fraction	30	22	1	9	5
<300 µm fraction	70	78	99	91	95
Density (ind. L ⁻¹)					
Naupli stages	78 (231)	0.9 (4)	10 (15)	0.8 (3)	0.4
<i>Oithona</i> spp.	5.2 (13)	0.7 (4)	1.8 (3)	0.5 (2)	0.1
Harpacticoids	0.38 (0.87)	0.01 (0.05)	0.13 (0.3)	0.01 (0.03)	0.8
Small calanoids	7.4 (14)	0.1 (0.8)	0.15 (0.4)	0.001 (0.006)	0.2
<i>Calanoide</i> spp.	—	—	0.01 (0.03)	0.001 (0.004)	—
<i>Calanus</i> spp.	0.8 (1.9)	0.03 (0.25)	0.06 (0.22)	0.01 (0.06)	0.01
<i>Clausocalanus</i> spp.	1.8 (3)	0.12 (1)	0.14 (0.3)	0.001 (0.007)	0.02
<i>Ctenocalanus citer</i>	—	0.002 (0.15)	—	0.05 (0.36)	—
<i>Neocalanus tonsus</i>	1.7 (5)	0.18 (1.2)	—	—	—
<i>Calocalanus tenuis</i>	—	0.01 (0.05)	0.10 (0.40)	—	—
<i>Paracalanus</i> spp.	3.8 (7)	—	—	—	—

CSW, Continental Shelf Waters; BMC, Brazil-Malvinas confluence; SAW, Subantarctic Waters; AW, Antarctic Surface Waters; ORK, South Orkney Shelf Waters. Only copepods with >2% of total numerical abundance on any occasion included.

Table III: The average and maximum value (in parenthesis) of biomass for both copepod size fractions and their relative contribution to total biomass during summer 2001

Stations	CSW 1–3	BMC 4–12	SAW 13–16	AW 17–23	ORK 24
Biomass (mg C m ⁻³)					
>300 µm	47.4 (77)	25.4 (170)	5.4 (18)	0.7 (4.7)	0.12
<300 µm	5.6 (11)	0.6 (4.5)	1.7 (2.7)	0.24 (0.73)	0.86
All	47.4 (81)	26 (170.1)	7 (20)	0.95 (5.4)	0.98
Relative contribution (%)					
>300 µm	80	75	39	33	12
<300 µm	20	25	61	67	88
Biomass (mg C m ⁻³)					
Naupli stages	0.8 (2.1)	0.05 (0.26)	0.45 (0.8)	0.045 (0.2)	0.065
<i>Oithona</i> spp.	2.5 (6)	0.45 (3.3)	1.1 (2)	0.2 (0.7)	0.076
Harpacticoids	0.01 (0.23)	0.004 (0.02)	0.015 (0.02)	0.001 (0.007)	0.59
Small calanoids	2.2 (2.9)	0.12 (0.9)	0.12 (0.26)	0.001 (0.003)	0.1
<i>Calanoide</i> spp.	—	—	0.3 (1.2)	0.015 (0.1)	—
<i>Calanus</i> spp.	17 (50)	1.5 (11.7)	3.1 (11.9)	0.5 (3.6)	0.007
<i>Clausocalanus</i> spp.	5.4 (15)	0.7 (6)	1 (2.1)	0.009 (0.06)	0.025
<i>Ctenocalanus citer</i>	—	0.008 (0.07)	—	0.16 (1)	—
<i>Neocalanus tonsus</i>	15 (32)	23 (170)	—	—	—
<i>Calocalanus tenuis</i>	—	0.005 (0.05)	0.066 (0.26)	—	—
<i>Paracalanus</i> spp.	3.9 (8.9)	—	—	—	—

CSW, Continental Shelf Waters; BMC, Brazil-Malvinas confluence; SAW, Subantarctic Waters; AW, Antarctic Surface Waters; ORK, South Orkney Shelf Waters. Only copepods with >2% of total numerical abundance on any occasion included.

lower densities during daytime) in the BMC; (ii) *Neocalanus tonsus*, *Clausocalanus breviceps* and *Calanus similimus* in CSW; (iii) *Calanoide* spp., *Rhincalanus gigas*, *Metridia lucens* and *Subeucalanus* spp in SAW and (iv) *Eucalanus* sp.

and *Ctenocalanus citer* in AW. With the exception of *Eucalanus* sp. (600–700 µm), these calanoids reached body lengths over 1000 µm (mostly belonging to the >300-µm fraction considering the ellipsoid shape of

Table IV: The average and maximum value (in parenthesis) of density and biomass for other zooplankton for both size fractions and their relative contribution during summer 2001

Stations	CSW 1–3	BMC 4–12	SAW 13–16	AW 17–23	ORK 24
Non-copepod mesozooplankton					
Density (ind. L ⁻¹)					
>300 μm	0.45 (1.32)	0.06 (0.19)	0.18 (0.60)	0.07 (0.46)	0.03
<300 μm	0.07 (0.17)	0.06 (0.23)	0.48 (1.24)	0.03 (0.14)	0.02
All	0.52 (1.49)	0.12 (0.42)	0.66 (1.30)	0.10 (0.51)	0.05
Relative contribution (%)					
>300 μm	63	55	26	66	62
<300 μm	37	45	74	34	38
Biomass (mg C m ⁻³)					
>300 μm	0.63 (1.9)	2.6 (6.5)	2.5 (9.8)	4.9 (33)	0.043
<300 μm	0.06 (0.20)	0.13 (0.80)	0.40 (1.4)	0.009 (0.05)	0.003
All	0.68 (2)	2.8 (6.5)	3 (11)	5 (33)	0.046
Relative contribution (%)					
>300 μm	64	81	70	80	94
<300 μm	36	19	30	20	6
Microzooplankton (ind. L ⁻¹)	1.05 (1.60)	90 (300)	200 (650)	36 (124)	16
Microzooplankton (μg C m ⁻³)	5 (5.1)	201 (380)	380 (780)	270 (580)	160
Other unicellular microp. (ind. L ⁻¹)	2300 (6700)	620 (1800)	1500 (2900)	4000 (17 500)	60 000

Microzooplankton: tintinids, foraminifera and radiolarians. Other unicellular microp.: Other unicellular microplankton (dinoflagellates, diatoms and silicoflagellates). CSW, Continental Shelf Waters; BMC, Brazil-Malvinas confluence; SAW, Subantarctic Waters; AW, Antarctic Surface Waters; ORK, South Orkney Shelf Waters.

copepods and their published length to width ratio between 2 and 3, Hays *et al.*, 1994). Smaller specimens (total length <750 μm) dominated at some stations of CSW, BMC and AW, and in most of the stations of SAW, both during the day and night. Density and biomass of *Oithona* was higher during nighttime (ANOVA $F_{14,3} > 8.45$, $P < 0.01$) due to the fact that the specimens found were larger than during daytime (Fig. 6). Copepod nauplii showed similar concentrations (ANOVA $F_{14,3}$: 0.03, P : 0.85) with similar contributions in length for daytime and nighttime samples (Fig. 6).

Biomass size spectra

Highly significant regressions of log biomass on log individual weight were determined for 18 of the 24 stations. The slopes varied from -0.20 to -0.90 (except stations 16: -1.73), thus indicating an increase in biomass towards the larger weight classes (Fig. 7A). The NBSS showed a strong nonlinearity in stations 2, 3, 6, 7, 20 and 24, which accounts for the relative dominance of certain size classes and so their slopes were not estimated (see Method).

At the spatial level, the slopes of NBSS for daytime and nighttime stations from BMC were not significantly different from one another (Student's $t_{0.05,34} < 1.2$, $P > 0.5$), while in SAW and AW they were more negative during daytime (Student's $t_{0.05,35} > 6.4$, $P < 0.02$). The increase in biomass during nighttime was due to the

higher contribution of larger organisms, which results in flatter slopes. According to this, only within SAW and AW were the NBSS considered separately. Differences in daytime and nighttime NBS slopes were not tested for shelf waters (CSW and ORK) because of the non-linearity of the spectra estimated at stations 2, 3 and 24, respectively.

The mean normalized biomass spectra and their 95% confidence intervals for each ecological domain (or, when appropriate, for its daytime/nighttime differentiation) and the regression parameters are shown in Fig. 7B. Regressions were highly significant and residual variations were low ($r^2 > 0.81$) except for BMC, where a dome-like feature was observed (on the log₂ scale, between -8 and 5 μg C ind⁻¹, Fig. 7B), as also occurred at station 24, located in the ORK (data not show). In the latter case, the low number of micro- and mesozooplankton found in the sample (n : 128) precludes making generalizations. For each ecological domain, the 95% confidence intervals showed more increases at small than at large biomass size range, without a clear pattern across each spectrum.

Multiple comparison of NBSS slopes revealed significant differences among the ecological domains defined ($F_{5,96}$: 5.31, $P < 0.001$). Two groups were defined according to slope similarity: Group 1, encompassing CSW, BMC and nighttime samples from AW and SAW, and Group 2, with slopes significantly more negative and comprising daytime samples from AW and SAW (Tukey's

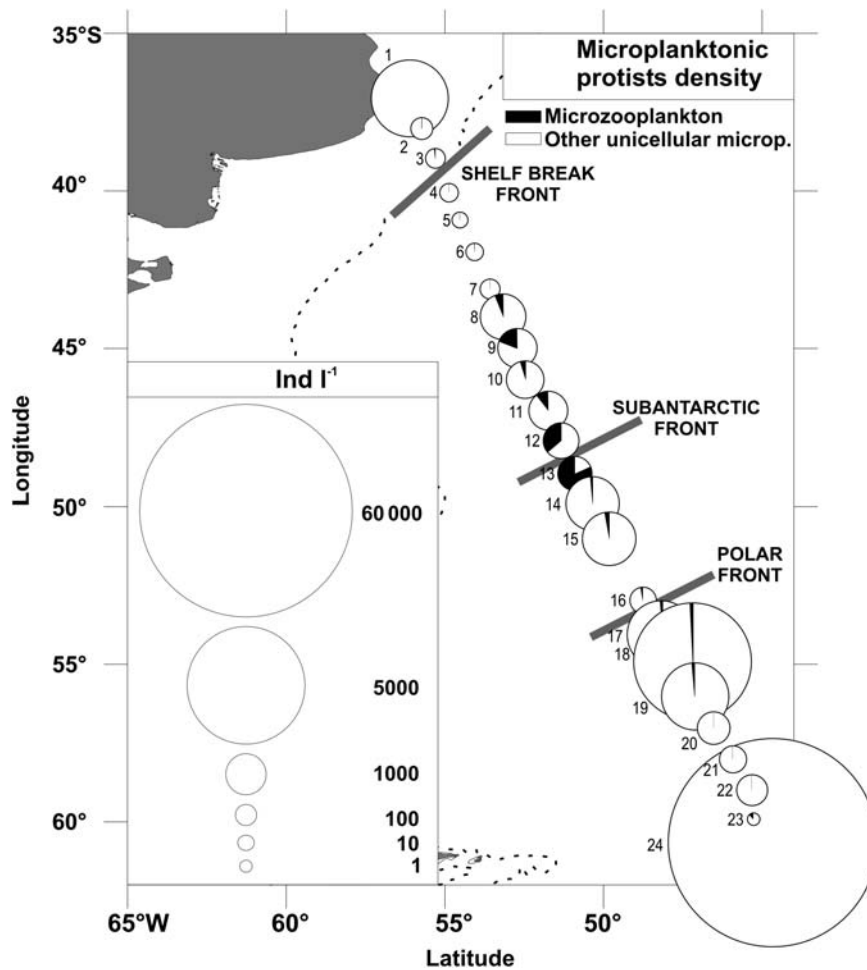


Fig. 4. The density and relative contribution of microzooplankton (tintinids, foraminifera and radiolarians) and other unicellular microplankton (dinoflagellates, diatoms and silicoflagellates) to the density of microplanktonic protists. The circle size is proportional to the absolute values of density. Other unicellular microp.: Other unicellular microplankton.

HSD, $q_{0.05,100,6} > 5$, $P < 0.05$, Fig. 7B). When considering these two groups of NBSS, intercept comparison inside each group showed significant differences among ecological domains (Group 1: $F_{3,72}$: 16.61, $P < 0.001$; Group 2: $t_{0.05(2),26}$: 2.04, P : 0.017). Total biomass was significantly higher in CSW and decreased to the south, with lower values in nighttime AW (Group 1). In addition, daytime SAW showed higher biomass than daytime AW (Group 2; Fig. 7B). These results suggest that both the slope and the intercept of NBSS within each ecological domain (including daytime/nighttime divisions) reflect environmental differences among domains.

TL estimations of zooplankton communities were higher for the stations of Group 1, with estimated values of 5.9 for BMC and, 4.7 for AW at night, 4.2 for CSW and 3.6 for SAW at night. Group 2 showed

similar, lower values of TLs for both AW and SAW daytime stations (2.9 and 2.7, respectively).

DISCUSSION

Hydrological conditions and plankton community structure

This was the first large mesoscale survey covering, in a single transect, five ecological domains within the SAO during summer. Previous large mesoscale surveys ($> 2 \times 10^3$ km) on zooplankton abundance in the South Atlantic Ocean have been mostly carried out up to 49°S during Atlantic Meridional Transect cruises (Gallienne and Robins, 1998; Woodd-Walker *et al.*, 2002; Robinson *et al.*, 2006; San Martin *et al.*, 2006).

Table V: Summary of results from the Bio-Env method based on Spearman's rank correlations (r_s) between both zooplankton size fractions separate and together and environmental variables

Fraction	Number of variables	Correlation (r_s)	Variable selections
Density			
All	2	0.499	SST, Chl. Fl.
	3	0.499	SST, Chl. Fl., Salinity
<300- μ m size fraction	2	0.483	SST, Chl. Fl.
	3	0.483	SST, Chl. Fl., salinity
>300- μ m size fraction	2	0.240	SST, salinity
Biomass			
All	2	0.470	SST, Chl. Fl.
	3	0.470	SST, Chl. Fl., Salinity
<300- μ m size fraction	2	0.464	SST, Chl. Fl.
	3	0.464	SST, Chl. Fl., Salinity
>300- μ m size fraction	2	0.255	SST, salinity

Only the results for best possible solutions are presented. SST, sea surface temperature; Chl. Fl, chlorophyll fluorescence.

Table VI: Results of stepwise multiple regression analyses for the dependent variables [copepod species and associated zooplankton taxa, density or biomass (log-transformed data)] and the independent environmental variables (SST, AVHRR-SST; SW Chl a, SeaWiFS Chl a)

Dependent variable	Statistically significant independent variable	B	SE B	P-value	R ²
Density					
Copepod nauplii	SST	1.145	0.285	0.002	0.82
	SW Chl a	1.809	0.421	0.001	
<i>Oithona</i> spp.	SW Chl a	2.320	0.754	0.015	0.69
<i>Microsetella norvegica</i>	SST	0.890	0.320	0.021	0.73
Biomass					
Copepod nauplii	SST	1.001	0.310	0.007	0.78
	SW Chl a	1.542	0.458	0.007	
<i>Oithona</i> spp.	SW Chl a	2.153	0.769	0.023	0.67
<i>Microsetella norvegica</i>	SST	0.944	0.347	0.024	0.68

Only significant relationships are shown.

The present study corroborates previous findings indicating that variations in zooplankton abundance and community size structure are significantly related to the

presence of frontal systems defining community boundaries (Tables II–IV). Differences in copepod composition and densities have been reported north and south of the Subantarctic Front (Woodd-Walker *et al.*, 2002; Berasategui *et al.*, 2005) and between Continental Shelf Waters and the BMC (Berasategui *et al.*, 2006). On the other hand, similarities in copepod composition but differences in their density and biomass were reported north and south of the Polar Front (Thompson *et al.*, 2012). Probably as a result of the use of a 20- μ m mesh net, the present study also detected differences in the body length distribution of copepods and other zooplankton among ecological domains (Fig. 5), together with differences between daytime and nighttime distributions in the upper water column mainly from the SAW and AW domains.

The predictive values of environmental variables in the spatial distribution of the <300- μ m fraction and their main components (nauplii larvae, *Oithona similis*, and the harpacticoid *Microsetella norvegica*) complemented previous results in this respect (Tables V and VI). SST accounted for the largest proportion of variability in abundance and biomass of this size fraction in the Drake Passage waters during summer (Thompson *et al.*, 2012). Studies based on mesh sizes >330 μ m showed that SST and salinity were important predictors of copepods composition in the SAO (Berasategui *et al.*, 2005), while others have suggested that SST is more important than chlorophyll *a* in defining plankton assemblages in the Southern Ocean (Chiba *et al.*, 2001; Ward *et al.*, 2012). The fact that chlorophyll *a* is a good predictor of density and biomass of the <300- μ m fraction but not for the >300- μ m fraction suggests a higher dependence of the former fraction on phytoplankton as a food source (Table V). López and Anadón (López and Anadón, 2008) concluded that small copepods and nauplii accounted for a higher amount of total chlorophyll ingestion than larger copepods. The use of finer mesh nets has revealed the numerical relevance of these organisms in the SAO (Thompson, 2001) and, more recently, in Argentine Continental Shelf Waters (Di Mauro *et al.*, 2009), in Antarctic Waters of the Atlantic Sector (Ward *et al.*, 2012) and in the Drake Passage (Thompson *et al.*, 2012).

The ratios of heterotrophic/autotrophic biomass estimated from zooplankton biomass data (Fig. 3), chlorophyll *a* biomass (Fig. 1) and the C:Chl *a* latitudinal relationship (Taylor *et al.*, 1997) showed averaged values over 1 for each domain (CSW: 1.5; BMC: 3.3; SAW: 1.7 and AW: 2.1) except for ORK (0.33). Although it cannot be discounted that the ratios found were attributable to an artifact introduced by the spatial (depth) and temporal data bias (see below), these results

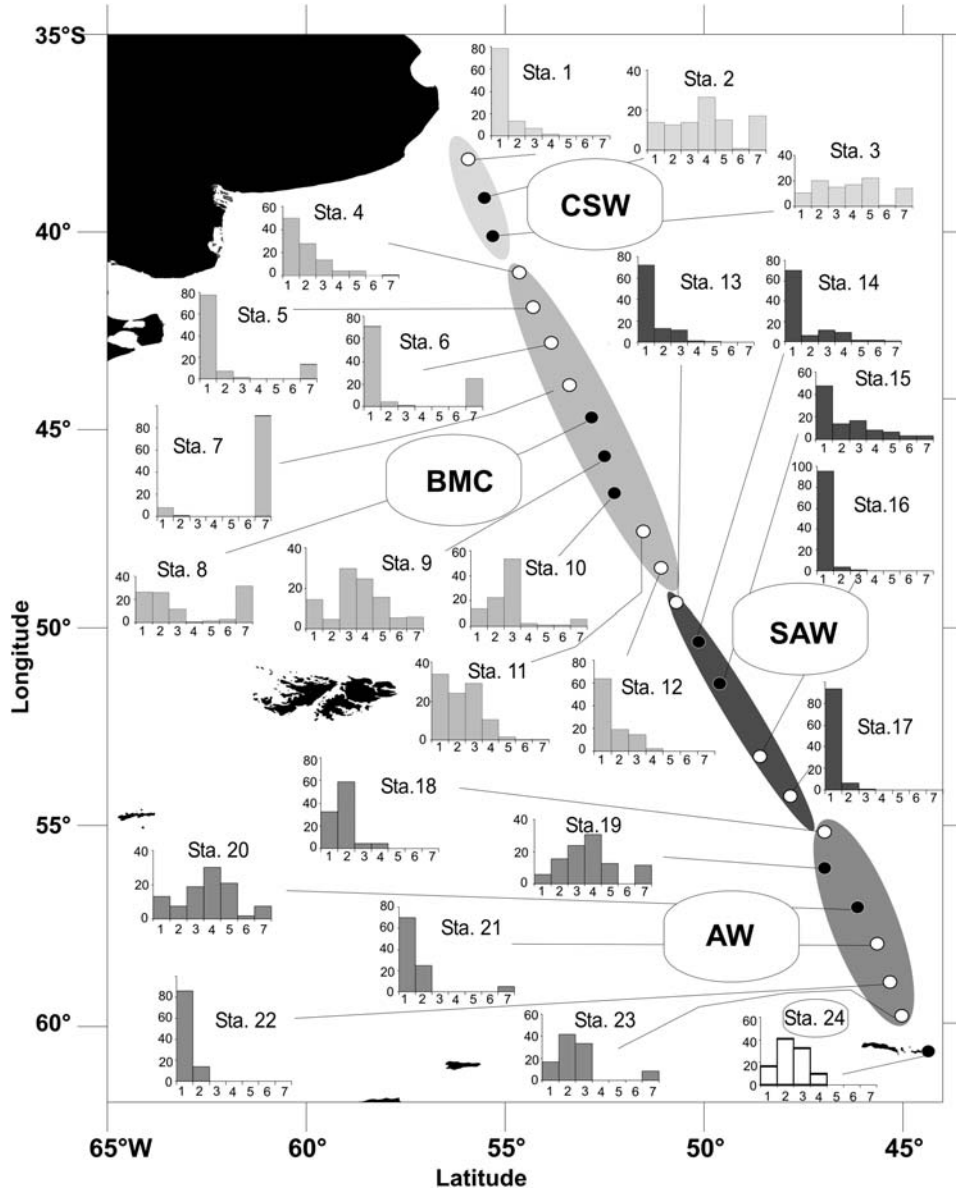


Fig. 5. The relative contribution of different sized copepods and other zooplankton for each station (1, <250 μm ; 2, 250–500 μm ; 3, 500–750 μm ; 4, 750–1000 μm ; 5, 1000–1500 μm ; 6, 1500–2000 μm ; 7, 2000–4000 μm total length). White dots indicate daylight samples. Black dots indicate night samples. CSW, continental shelf waters; BMC, Brazil-Malvinas confluence; SAW, Subantarctic waters; AW, Antarctic Surface Waters.

suggested a dominance of heterotrophic over autotrophic biomass, which corresponds to an inverted biomass pyramid (IBPs; Gómez-Canchong *et al.*, 2013). IBPs have been observed in both coastal waters and the upper layer of open oceans (Gasol *et al.*, 1997). Del Giorgio *et al.* (Del Giorgio *et al.*, 1999) hypothesized that a high growth rate of prey and a low death rate of predators lead to an IBP. In this sense, the higher contribution of nanophytoplankton (with a high growth rate) to total chlorophyll *a* biomass, and the higher contribution

of nauplii and cyclopid copepods (with a low death rate; Paffenhöfer, 1993; Gallienne and Robins, 2001) to total zooplankton in the study area, gives support to the existence of IBPs during the study season.

Methodological considerations of the NBSS

Some possible methodological limitations of the present study should be recognized in view of their potential influence on the NBSS:

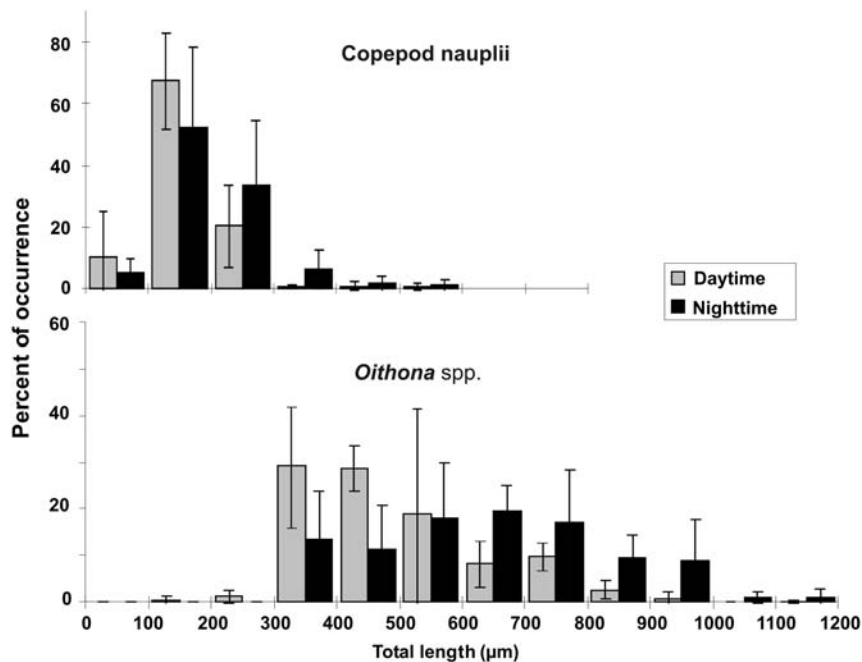


Fig. 6. The size (mean \pm standard deviation) frequency distribution of copepod nauplii and *Oithona* spp. considering daytime and nighttime samples.

- (i) The analysis of the zooplankton community is restricted to microzooplankton and mesozooplankton smaller than 4000 μm . The comparison of zooplankton counts from an in-line pump system and the further filtering onto a 200- μm mesh gauze against those obtained from the simultaneous use of a standard 200- μm WP2 net yielded similar results (Gallienne and Robins, 1998). Based on these authors' assertion that the pump might undersample only zooplankton $>8000 \mu\text{m}$ we consider that the counts performed for the present study (organisms with sizes up to half this value) are acceptably accurate.
- (ii) Sampling at a fixed depth of 9 m results in missing part of the plankton community and leads to bias in the interpretation of NBSS results. Accurate spectra of a pelagic system should be obtained from a representative part of the water column; therefore a fixed depth could bias interpretation of results. Previous studies showed that NBSS slope was less negative (flattened slope) with increasing depth, which indicates an increase in the relative importance of larger microplankton from the surface to the bottom of the euphotic zone (Rodriguez and Mullin, 1986a). The fixed depth also restricts the results, thus reflecting only partially the signal derived from zooplankton vertical migration. However, at least part of the zooplankton

diel migration has been detected at 9 m, according to changes in the NBSS slope between daytime and nighttime. The latter was characterized by a significantly higher contribution of larger zooplankton (body length $>750 \mu\text{m}$, Fig. 5), which supports previous findings by Mullin *et al.* (Mullin *et al.*, 1975) and corroborates the suggestion that the spectrum in the euphotic zone can be altered by nocturnal immigration of larger organisms (Rodriguez and Mullin, 1986b). It is likely that slope differences between daytime and nighttime would have been greater if larger organisms (4–8 mm) or a representative portion of the water column were considered. Rodriguez and Mullin (Rodriguez and Mullin, 1986b) found an increase in biomass in the upper 100 m at night during summer mainly due to the increase of this size range.

- (iii) No small gelatinous zooplankton (e.g. salps, siphonophores, medusae, ctenophores, etc.) were collected in this study, indicating that these fragile organisms were destroyed by the pumping system. Destruction of fragile organisms is a well-known problem also when sampling with nets (Remsen *et al.*, 2004), and it can introduce bias in the size structure estimate. Gelatinous zooplankton can dominate the zooplankton biomass in bays and enclosed seas, but their distribution and abundance

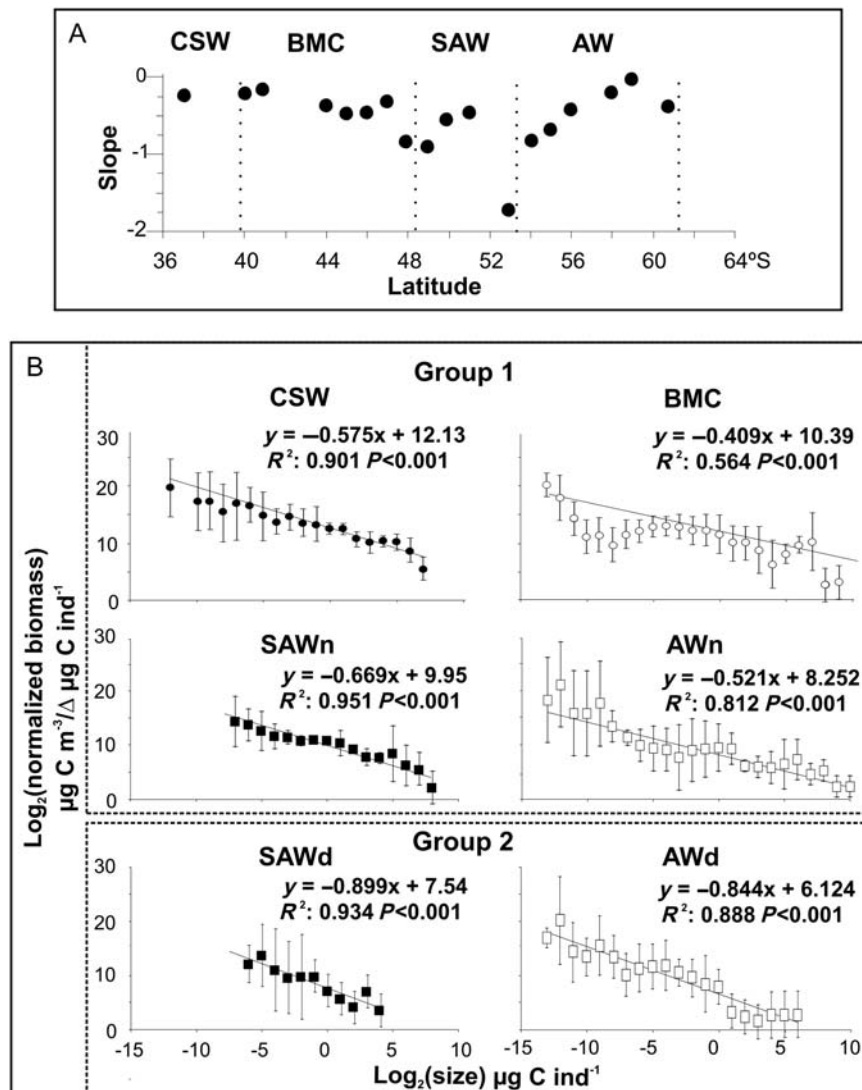


Fig. 7. (A) A spatial distribution of NBSS slopes of plankton; only stations with significant slopes are plotted. (B) NBSS in carbon units of plankton for each ecological domain. Straight lines are the least-square regressions fitted to the data. Error bars indicate the 95% confidence intervals. CSW, Argentine continental shelf waters; BMC, Brazil-Malvinas confluence; SAW, Subantarctic waters; AW, Antarctic Surface Waters; d, daytime; n, nighttime. Group 1 and Group 2 defined from Tukey's multiple comparison tests of slopes.

patterns in the ocean are poorly known (Mianzan *et al.*, 2001). Vinogradov (Vinogradov, 1997) determined a carbon contribution for gelatinous zooplankton between 25 and 40% of the plankton in the Pacific Ocean. If the fragile organisms were underestimated, then some of the larger size classes considered in our analyses would be underestimated, implying that the slope should be more positive (flattened slope) than that determined (Quiñones *et al.*, 2003).

- (iv) Level of precision of biomass values estimated from published conversion factors. The sources of error and uncertainty have been estimated as

overall biomass confidence limits. Most of the existing methods for estimating zooplankton biomass from net samples are not completely satisfactory. Unfortunately, up to now this is the only way of estimating planktonic biomass without the interference of detrital particles, since automatic or semiautomatic methods based on the Coulter principle (counting and sizing of "particles") cannot discriminate between organisms and detritus (Alcaraz *et al.*, 2003). In spite of this uncertainty, biomass values obtained in the present study for the $>300\text{-}\mu\text{m}$ fraction were comparable to the zooplankton biomass conversion of OPC counts

for the 0.25–2 mm equivalent spherical diameter (lengths between 0.5 and 4 mm) range for BMC (Gallienne and Robins, 1998) and for AW (Pollard *et al.*, 2002). We found up to 21 mg C m⁻³ (except for stations 7: 170 mg C m⁻³) for BMC and an average of 5.6 mg C m⁻³ for AW (Fig. 3, Tables III and IV), while OPC counts estimated, respectively, from 14 to 36 mg C m⁻³ and between 4 and 10 mg C m⁻³. Furthermore, the validity of slopes of NBSS was corroborated by the estimation of biovolume spectra (data not shown). Biovolume estimates were not subject to the same uncertainty as carbon estimates, as the accuracy of the former do not depend on differences in the plankton community composition. NBSS slopes in biovolume units were somewhat more positive (flatter) than in carbon units, which agrees with previous findings (Quiñones *et al.*, 2003).

NBSS slopes and dome-like feature

Caution must be applied in using the size spectrum as a zooplankton descriptor by keeping in mind data bias due to the methodological problems previously described. These limitations suggest that slope values (NBSS slopes less negative than -1; Fig. 7A and B) should be interpreted carefully. Flat slope values were in agreement with (and complement) previous findings for the Atlantic Ocean. San Martin *et al.* (San Martin *et al.*, 2006) found flat slopes (i.e. less negative than the theoretical prediction of -1.22) for the BMC and SAW domains (means of -1.10 and -1.13, respectively, integrated data from 0 to 50 m depth) and for the Atlantic Ocean (49°N-49°S). NBSS and their flat slopes suggested for summer (this study), autumn and spring (San Martin *et al.*, 2006) seasons a higher proportion of large organisms in relation to the smaller ones in the zooplankton communities of the SAO. As stated previously, if deeper waters had been included in our analyses, the contribution of larger organism to NBSS would have been higher (Rodríguez and Mullin, 1986a). A higher proportion of large organisms than expected at equilibrium suggested that more biomass was transferred up the spectrum (high efficiency) and more carbon was available to higher TLs (San Martin *et al.*, 2006).

Latitudinal change in NBSS slope values observed in oceanic waters (Fig. 7A) also have been reported for large-scale studies in the Atlantic (San Martin *et al.*, 2006) and North Pacific (Fukuda *et al.*, 2012) Oceans. Slope changes in our study might have been related to modifications in zooplankton structure among different

domains, due to variations in copepod and non-copepod composition, abundance and biomass values (Tables II–IV), which were correlated with variations in environmental factors, such as chlorophyll *a* and SST (Table V). San Martin *et al.* (San Martin *et al.*, 2006) suggested that changes in NBSS slopes were related to possible modifications in trophic coupling between primary and secondary producers due to latitudinal increase in seasonality. On the other hand, Fukuda *et al.* (Fukuda *et al.*, 2012) suggested that differences in the presence of large predators affected the NBSS slopes; however, these authors did not quantified micro-sized (<335 μm) taxa.

One particular feature of the NBSS was the dome-like feature of biomass, such as the one observed in the BMC (Fig. 7B). Domes are generated within a single trophic position (secondary specific production; Dickie *et al.*, 1987) and are the result of the interaction of opposing energetic processes: gross production, grazing efficiency and the ratio of body size between predator and prey (Boudreau *et al.*, 1991). Although it cannot be completely ruled out that in our study the dome could be an artifact introduced by the bias of data, the BMC had some properties that support the presence of a dome; the BMC showed the most complex trophic interactions (high TL), and the highest value of total biomass (NBS intercept, Fig. 7B) for the oceanic domains covered in this study. The BMC is also a transition zone in which most species found together have their distribution centers elsewhere (Boltovskoy, 1986; Tarling *et al.*, 1995). The highest TL might be due to the presence of carnivorous zooplankton like the copepods *Neocalanus tonsus*, *Labidocera* sp. and *Metridia lucens* (Haq, 1967; Ohman, 1987; Doi *et al.*, 2010) or euphausiids (Meyer *et al.*, 2002) ingesting copepods that could have derived their energy from omnivorous diets, like *Oithona* sp., *Ctenocalanus* sp. and *Calanus simillimus* (Kleppel *et al.*, 1988; Zeldis *et al.*, 2002; Schmidt *et al.*, 2003; Pond and Ward 2011) or like naupliar forms, which can act as a trophic link between the microbial and classical food webs (Turner and Roff, 1993; López *et al.*, 2007). These groups, together with herbivorous (pteropods and *Clausocalanus* sp.; Lalli and Gilmer, 1989; Pasternak *et al.*, 2005) and detritivorous (harpacticoid copepods; Bradford-Grieve *et al.*, 1999) specimens, showed the complexity of trophic interactions. According to this, we suggest that the dome-shaped curve obtained might be a manifestation of the effect of the temporal pulses of production (Boudreau *et al.*, 1991; Brandini *et al.*, 2000; Barré *et al.*, 2006) due to the interactions between the Brazil and Malvinas currents (Barré *et al.*, 2006) during the period of study.

NBSS: trophic interactions

Higher trophic values, related to a flatter NBSS slope, reflect stronger trophic coupling (Zhou, 2006; Basedow *et al.*, 2010); however, bias of the data could affect the accuracy of TL estimates. Considering this, dissimilar TLs were used as an indicator of the trophic coupling between phytoplankton and zooplankton. The spatial and temporal fluctuation of zooplankton feeding forms in each domain or, when appropriate, in daytime and nighttime groups of stations were reflected in dissimilar values of TLs. Carnivorous zooplankton like *Rhincalanus gigas*, *Neocalanus tonsus*, *Metridia lucens* and euphausiids were mostly observed during nighttime, resulting in increases of TLs at SAW and AW. Changes in the composition of the phytoplankton community were also reflected in changes in TLs. High microphytoplankton (>10 µm chl *a*) concentrations, registered in SAW, were related to high contribution of herbivorous (i.e. *Calocalanus tenius*, *Clausocalanus* sp.; Table III) zooplankton, a weak trophic coupling and a decrease of TLs, while low concentrations of microphytoplankton (BMC and AW) were linked to high contribution of omnivorous (i.e. *Ctenocalanus* sp., *Calanus* sp. and *Oithona* sp.; Table III) zooplankton and implied a strong trophic link and an increase of TLs, which agrees with previous finding at an Arctic polar front (Basedow *et al.*, 2010).

In conclusion, this mesoscale study of the SAO reveals the importance of small zooplankton in structuring the biomass of the community, in spite of the acknowledged methodological limitations. The <300-µm fraction was dominant in terms of abundance in the five domains CSW, BMC, SAW, AW, ORK and in terms of biomass in SAW, AW and ORK. Chlorophyll *a* was found to be a good predictor for abundance and biomass values within this fraction. The heterotrophic/autotrophic ratios suggested the existence of IBPs in the study area. Dissimilarities in the contribution of chlorophyll *a* size fractions, jointly with the dissimilarities in the complexity and dominance of feeding forms of copepods and other zooplankton among ecological domains provide support to the IBPs. We propose that environmental differences between water masses in the SAO during summer are reflected in the NBSS, slopes and trophic structure of the plankton community. Despite some factors that may have influenced NBSS estimations (see above), trends in biomass spectra in relation to dissimilar hydrological conditions represent a first approach and are thought to deserve further investigation which should include depth integrated and season-based evaluations of plankton size structure in the SAO.

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REFERENCES

- Alcaraz, M., Saiz, E., Calbet, A. *et al.* (2003) Estimating zooplankton biomass through image analysis. *Marine Biology*, **143**, 307–315.
- Angel, M. V. (1979) Zoogeography of the Atlantic. In Van der Spoel, S. and Pierrot-Bults, A. C. (eds), *Zoogeography and Diversity of Plankton*. Edwards Arnold, London, pp. 160–190.
- Barré, N., Provost, C. and Saraceno, M. (2006) Spatial and temporal scales of the Brazil-Malvinas confluence documented by simultaneous MODIS Aqua 1.1-km resolution SST and color images. *Adv. Space Res.*, **37**, 770–786.
- Basedow, S. L., Tande, K. S. and Zhou, M. (2010) Biovolume spectrum theories applied: spatial patterns of trophic levels within a mesozooplankton community at the polar front. *J. Plankton Res.*, **32**, 1105–1119.
- Berasategui, A. D., Menu Marque, S., Gomez Erache, M. *et al.* (2006) Copepod assemblages in a highly complex hydrographic region. *Estuarine, Coastal Shelf Sci.*, **66**, 483–492.
- Berasategui, A. D., Ramirez, F. C. and Schiariti, A. (2005) Patterns in diversity and community structure of epipelagic copepods from the Brazil-Malvinas confluence area, South-western Atlantic. *J. Mar. Systems*, **56**, 309–316.
- Boltovskoy, D. (1986) Biogeography of the south-western Atlantic: current problems and prospects. In: Pierrot-Bults, A. C., Zahuranec, B. J. and Johnson, A. C. (eds), *Proceedings of the International Conference on Pelagic Biogeography*. UNESCO, Paris, pp. 14–24.
- Boltovskoy, D. (ed.) (1999). *South Atlantic Zooplankton*. Backhuys, Leiden.
- Boudreau, P. R., Dickie, L. M. and Kerr, S. R. (1991) Body-size spectra of production and biomass as system-level indicators of ecological dynamics. *J. Theor. Biol.*, **152**, 329–339.
- Bradford-Grieve, J. M., Markhaseva, E. L., Rocha, C. E. F. *et al.* (1999) Copepoda. In Boltovskoy, D. (ed.), *South Atlantic Zooplankton*,

- Vol. 2. Backhuys Publishers, Leiden, The Netherlands, pp. 869–1098.
- Brandini, F. P., Boltovskoy, D., Piola, A. R. *et al.* (2000) Multiannual trends in fronts and distribution of nutrients and chlorophyll in the southwestern Atlantic (30–62°S). *Deep-Sea Res. I*, **47**, 1015–1033.
- Caron, D. A., Dam, H. G., Kremer, P. *et al.* (1995) The contribution of microorganisms to particulate carbon and nitrogen in surface waters of the Sargasso Sea near Bermuda. *Deep-Sea Res.*, **42**, 943–972.
- Chelton, D. B., Schlax, M. G., Witter, D. L. *et al.* (1990) Geosat altimeter observations of the surface circulation of the Southern Ocean. *J. Geophys. Res.*, **95**, 17877–17903.
- Chiba, S., Ishimaru, T., Hosie, G. W. *et al.* (2001) Spatio-temporal variability of zooplankton community structure off east Antarctica (90–1601E). *Mar. Ecol. Prog. Ser.*, **216**, 95–108.
- Clarke, K. R. and Ainsworth, M. (1993) A method of linking multivariate community structure to environmental variables. *Mar. Ecol. Prog. Ser.*, **92**, 205–219.
- Comeau, S., Jeffree, R., Teyssie, J. L. *et al.* (2010) Response of the Arctic Pteropod *Limacina helicina* to projected future environmental conditions. *PLoS One*, **5**, E11362.
- Cottingham, K. L. (1999) Nutrients and zooplankton as multiple stressors of phytoplankton communities: evidence from size structure. *Limnol. Oceanogr.*, **44**, 810–827.
- Cózar, A., García, C. M. and Gálvez, J. A. (2003) Analysis of plankton size spectra irregularities in two subtropical shallow lakes (Esteros del Iberá, Argentina). *Can. J. Fish. Aquat. Sci.*, **60**, 411–420.
- Daly, K. L. (2004) Overwintering growth and development of larval *Euphausia superba*: an interannual comparison under varying environmental conditions west of the Antarctic Peninsula. *Deep-Sea Res. II*, **51**, 2139–2168.
- Del Giorgio, P. A., Cole, J. J., Caraco, N. F. *et al.* (1999) Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. *Ecology*, **80**, 1422–1431.
- Dickie, L. M., Kerr, S. R. and Boudreau, P. R. (1987) Size-dependent processes underlying regularities in ecosystem structure. *Ecol. Monogram*, **57**, 233–250.
- Di Mauro, R., Capitanio, F. and Viñas, M. D. (2009) Capture efficiency for small dominant mesozooplankters (Copepoda, Appendicularia) off Buenos Aires Province (34°S–41°S), Argentine Sea, using two plankton mesh sizes. *Braz. J. Oceanogr.*, **57**, 205–214.
- Doi, H., Kobari, T., Fukumori, K. *et al.* (2010) Trophic niche breadth variability differs among three *Neocalanus* species in the subarctic Pacific Ocean. *J. Plankton Res.*, **32**, 1733–1737.
- Franco, B. C., Piola, A. R., Rivas, A. L. *et al.* (2008) Multiple thermal fronts near the Patagonian shelf break. *Geophys. Res. Lett.*, **35**, L02607.
- Fukuda, J., Yamaguchi, A., Matsuno, K. *et al.* (2012) Interannual and latitudinal changes in zooplankton abundance, biomass and size composition along a central North Pacific transect during summer: analyses with an Optical Plankton Counter. *Plankton Benthos Res.*, **7**, 64–74.
- Gallienne, C. P. and Robins, D. B. (1998) Trans-oceanic characterization of zooplankton community size structure using an optical plankton counter. *Fish. Oceanogr.*, **7**, 147–158.
- Gallienne, C. P. and Robins, D. B. (2001) Is *Oithona* the most important copepod in the world's oceans? *J. Plankton Res.*, **23**, 1421–1432.
- Gasol, J. M., del Giorgio, P. A. and Duarte, C. M. (1997) Biomass distribution in marine planktonic communities. *Limnol. Oceanogr.*, **42**, 1353–1363.
- Gasol, J. M., Guerrero, R. and Pedrós-Alió, C. (1991) Seasonal variations in size structure and prokaryotic dominance in sulfureous. *Lake Ciso. Limnol. Oceanogr.*, **36**, 860–872.
- Gómez-Canchong, P., Quiñones, R. A. and Brose, U. (2013) Robustness of size-structure across ecological networks in pelagic systems. *Theor. Ecol.*, **6**, 45–56.
- Goni, G. and Wainer, I. (2001) Investigation of the Brazil current front variability from altimeter data. *J. Geophys. Res.*, **116**, 31117–31128.
- Gradinger, R., Friedrich, C. and Spindler, M. (1999) Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice. *Deep-Sea Res.*, **46**, 1457–1472.
- Hansen, B. W., Nielsen, T. G. and Levinsen, H. (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation: III. Mesozooplankton. *Aquat. Microb. Ecol.*, **16**, 233–249.
- Haq, S. M. (1967) Nutritional physiology of *Metridia lucens* and *M. longa* from the Gulf of Maine. *Limnol. Oceanogr.*, **12**, 40–51.
- Hays, G. C., Proctor, C. A., John, W. G. *et al.* (1994) Interspecific differences in the diel vertical migration of marine copepods: the implications of size, color and morphology. *Limnol. Oceanogr.*, **39**, 1621–1629.
- Heath, M. R. (1995) Size spectrum dynamics and the planktonic ecosystem of Loch Linnhe. *ICES J. Mar. Sci.*, **52**, 627–642.
- Holm-Hansen, O., Kahru, M., Hewes, C. D. *et al.* (2004b) Temporal and spatial distribution of chlorophyll-a in surface waters of the Scotia Sea as determined by both shipboard measurements and satellite data. *Deep-Sea Res. II*, **51**, 1323–1331.
- Holm-Hansen, O., Naganobu, M., Kawaguchi, S. *et al.* (2004a) Factors influencing the distribution, biomass, and productivity of phytoplankton in the Scotia Sea and adjoining waters. *Deep-Sea Res. II*, **51**, 1333–1350.
- Kleppel, G. S., Frazel, D., Pieper, R. E. *et al.* (1988) Natural diets of zooplankton off southern California. *Mar. Ecol. Prog. Ser.*, **49**, 231–241.
- Lalli, C. M. and Gilmer, R. W. (eds.) (1989) *Pelagic Snails: The Biology of Holoplanktonic Gastropod Mollusks*. Stanford University Press, Stanford.
- Legendre, L. and Le Fèvre, J. (1991) From individual plankton cells to pelagic marine ecosystems and to global biogeochemical cycles. In Demers, S. (ed.), *Particle Analysis in Oceanography*. Springer-Verlag, Berlin, Heidelberg, pp. 261–300.
- López, E. and Anadón, R. (2008) Copepod communities along an Atlantic Meridional transect: abundance, size structure, and grazing rates. *Deep-Sea Res. I*, **55**, 1375–1391.
- López, E., Viesca, L. and Anadón, R. (2007) Seasonal variation in abundance and feeding rates of the first stages of copepods in a temperate sea. *Mar. Ecol. Prog. Ser.*, **352**, 161–175.
- Matano, R. P., Palma, E. D. and Piola, A. R. (2010) The influence of the Brazil and Malvinas currents on the Southwestern Atlantic Shelf circulation. *Ocean Sci.*, **6**, 983–995.
- Mauchline, J. (1998) *The biology of calanoid copepods*. In Blaxter, J. H. S., Southward, A. J. and Tyler, P. A. (eds), *Adv. Mar. Biol.* Academic Press, London.
- Meyer, B., Atkinson, A., Stubing, D. *et al.* (2002) Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter—I. Furcilia III larvae. *Mar. Biol.*, **47**, 943–952.
- Mianzan, H., Pájaro, M., Alvarez Colombo, G. *et al.* (2001) Feeding on survival-food: gelatinous plankton as a source of food for anchovies. *Hydrobiologia*, **451**, 45–53.

- Moore, J. K., Abbott, M. R. and Richman, J. G. (1997) Variability in the location of the Antarctic Polar Front (90°–20°W) from satellite sea surface temperature data. *J. Geophys. Res.*, **102**, 825–833.
- Mullin, M. M., Perry, M. J., Renger, E. H. *et al.* (1975) Nutrient regeneration by oceanic zooplankton a comparison of methods. *Mar. Sci. Commun.*, **1**, 1–13.
- Myers, R. H. (1990) *Classical and Modern Regression with Applications*, 2nd edn. Duxbury, Boston, MA.
- Nozais, C., Gosselin, M., Michel, C. *et al.* (2001) Abundance, biomass, composition and grazing impact of sea-ice meiofauna in the North Water, northern Baffin Bay. *Mar. Ecol. Prog. Ser.*, **217**, 235–250.
- Ohman, M. D. (1987) Energy sources for recruitment of the subantarctic copepod *Neocalanus tonsus*. *Limnol. Oceanogr.*, **32**, 1317–1330.
- Olguín, H. and Alder, V. (2011) Species composition and biogeography of diatoms in antarctic and subantarctic (Argentine shelf) waters (37–76°S). *Deep-Sea Res. II*, **58**, 139–152.
- Olguín, H., Boltovskoy, D., Lange, C. *et al.* (2006) Distribution of spring microphytoplankton (mainly diatoms) in the upper 50 m of the Southwestern Atlantic Ocean (30° to 61°S). *J. Plankton Res.*, **28**, 1–22.
- Orsi, A. H., Whitworth, T. III and Nowlin, W. D. Jr. (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Res.*, **42**, 641–673.
- Paffenhöfer, G. A. (1993) On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). *J. Plankton Res.*, **15**, 37–55.
- Pasternak, A., Wassman, P. and Riser, C. W. (2005) Does mesozooplankton respond to episodic P inputs in the Eastern Mediterranean? *Deep-Sea Res. Pt. II*, **52**, 2975–2989.
- Peterson, R. G. (1992) The boundary currents in the western Argentine Basin. *Deep-Sea Res.*, **39**, 623–644.
- Piola, A. R. and Gordon, A. L. (1989) Intermediate waters in the southwest South Atlantic. *Deep-Sea Res.*, **36**, 1–16.
- Piola, A. R., Martínez Avellaneda, N., Guerrero, R. A. *et al.* (2010) Malvinas-slope water intrusions on the northern Patagonia continental shelf. *Ocean Sci.*, **6**, 345–359.
- Platt, T. (1985) Structure of the marine ecosystem: its allo-metric basis. *Can. Bull. Fish. Aquat. Sci.*, **213**, 55–64.
- Platt, T. and Denman, K. (1978) The structure of pelagic marine ecosystems. *Rapports et Proces-verbaux des Reunions. Conseil International pour l'Exploration de la Mer*, **173**, 60–65.
- Pollard, R. T., Bathmann, U., Dubischar, C. *et al.* (2002) Zooplankton distribution and behaviour in the Southern Ocean from surveys with a towed Optical Plankton Counter. *Deep-Sea Res. II*, **49**, 3889–3915.
- Pond, D. W. and Ward, P. (2011) Importance of diatoms for *Oithona* in Antarctic waters. *J. Plankton Res.*, **33**, 105–118.
- Quiñones, R. A., Platt, T. and Rodríguez, J. (2003) Patterns of biomass-size spectra from oligotrophic waters of the Northwest Atlantic. *Prog. Oceanogr.*, **57**, 405–427.
- Rangel, T. E., Diniz-Filho, J. A. F. and Bini, L. M. (2010) SAM: a comprehensive application for spatial analysis in Macroecology. *Ecography*, **33**, 46–50.
- Remsen, A., Samson, S. and Hopkins, T. (2004) What you see is not what you catch: a comparison of concurrently collected net, optical plankton counter, and SIPPER data from the northeast Gulf of Mexico. *Deep Sea Res.*, **51**, 129–151.
- Robinson, C., Poulton, A. J., Holligan, P. M. *et al.* (2006) The Atlantic Meridional Transect (AMT) Programme: a contextual view 1995–2005. *Deep-Sea Res. II*, **53**, 1485–1515.
- Rodhouse, P. G., Symon, C. and Hatfield, E. M. C. (1992) Early life cycle of cephalopods in relation to the major oceanographic features of the Southwestern Atlantic Ocean. *Mar. Ecol. Prog. Ser.*, **89**, 183–195.
- Rodríguez, J. and Mullin, M. M. (1986a) Relation between biomass and body weight of plankton in a steady-state oceanic ecosystem. *Limnol. Oceanogr.*, **31**, 361–370.
- Rodríguez, J. and Mullin, M. M. (1986b) Diel and interannual variation of size-distribution of oceanic zooplanktonic biomass. *Ecology*, **67**, 215–222.
- San Martín, E. (2005) Latitudinal variation in plankton size spectra along the Atlantic Ocean. Ph.D. Thesis. University of Southampton.
- San Martín, E., Harris, R. P. and Irigoien, X. (2006) Latitudinal variation in plankton size spectra in the Atlantic Ocean. *Deep-Sea Res. II*, **53**, 1560–1572.
- Saraceno, M., Provost, C., Piola, A. R. *et al.* (2004) Brazil Malvinas Frontal System as seen from 9 years of advanced very high resolution radiometer data. *J. Geophys. Res.*, **109**, C05027.
- Schmidt, K., Atkinson, A., Stübing, D. *et al.* (2003) Trophic relationships among Southern Ocean copepods and krill: some uses and limitations of a stable isotope approach. *Limnol. Oceanogr.*, **48**, 277–289.
- Sheldon, R. W., Prakash, A. and Sutcliffe, W. H. Jr. (1972) The size distribution of particles in the ocean. *Limnol. Oceanogr.*, **17**, 327–340.
- Silvert, W. and Platt, T. (1978) Energy flux in the pelagic ecosystem: a time-dependent equation. *Limnol. Oceanogr.*, **23**, 813–816.
- Smith, W. O. Jr. (1991) Nutrient distributions and new production in polar regions: parallels and contrasts between the Arctic and Antarctic. *Marine Chem.*, **35**, 245–257.
- Sprules, G. W., Casselman, J. M. and Shuter, B. J. (1983) Size distribution of pelagic particles in lakes. *Can. J. Fish. Aquat. Sci.*, **40**, 1761–1769.
- Sprules, W. G. and Munawar, M. (1986) Plankton size spectra in relation to ecosystem productivity, size, and perturbation. *Can. J. Fish. Aquat. Sci.*, **43**, 1789–1794.
- Tarling, G. A., Ward, P., Shearer, M. *et al.* (1995) Distribution patterns of macrozooplankton assemblages in the southwestern Atlantic. *Mar. Ecol. Prog. Ser.*, **120**, 29–40.
- Taylor, A. H., Geider, R. J. and Glibert, F. J. H. (1997) Seasonal and latitudinal dependencies of phytoplankton carbon-to-chlorophyll a ratios: results of a modelling study. *Mar. Ecol. Prog. Ser.*, **152**, 51–66.
- Thompson, G. A. (2001) Distribución y abundancia del microzooplankton en el Atlántico Sudoccidental, con especial énfasis en la biogeografía de Tintinnina (Protozoa: Ciliata). Ph.D. thesis. Universidad Buenos Aires, Buenos Aires.
- Thompson, G. A., Alder, V. A. and Boltovskoy, D. (2001) Tintinnids (Ciliophora) and other net microzooplankton (>30 µm) in Southwestern Atlantic shelf break waters. *PS.Z.N.: Mar. Ecol.*, **22**, 343–355.
- Thompson, G. A., Alder, V. A., Boltovskoy, D. *et al.* (1999) Abundance and biogeography of Tintinnids (Ciliophora) and associated microzooplankton in the Southwestern Atlantic Ocean. *J. Plankton Res.*, **21**, 1265–1298.

- Thompson, G. A., Dinofrio, E. O. and Alder, V. A. (2012) Interannual fluctuations in copepod abundance and contribution of small forms in the Drake Passage during austral summer. *Helgoland Mar. Res.*, **66**, 127–138.
- Turner, J. T. and Roff, J. C. (1993) Trophic levels and trophospecies in marine plankton: lessons from the microbial food web. *Mar. Microb. Food Webs*, **7**, 225–248.
- Verity, P. G. and Langdon, C. (1984) Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. *J. Plankton Res.*, **6**, 859–868.
- Vinogradov, M. E. (1997) Some problems of vertical distribution of meso- and macroplankton in the ocean. *Adv. Mar. Biol.*, **32**, 1–92.
- Ward, P., Atkinson, A. and Tarling, G. (2012) Mesozooplankton community structure and variability in the Scotia Sea: a seasonal comparison. *Deep-Sea Res. II*, **59**, 253–266.
- Watts, J. and Tarling, G. A. (2012) Population dynamics and production of *Themisto gaudichaudii* (Amphipoda, Hyperiididae) at South Georgia, Antarctica. *Deep-Sea Res. II*, **59–60**, 117–129.
- Wiebe, P. H. (1988) Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction. *Fish. Bull.*, **86**, 833–835.
- Wiebe, P. H., Boyd, S. and Cox, J. L. (1975) Relationships between zooplankton displacement volume, wet weight, dry weight and carbon. *Fish. Bull.*, **73**, 777–786.
- Woodd-Walker, R. S., Ward, P. and Clarke, A. (2002) Large-scale patterns in diversity and community structure of surface water copepods from the Atlantic Ocean. *Mar. Ecol. Prog. Ser.*, **236**, 189–203.
- Zar, J. (1999) *Biostatistical Analysis*. Prentice-Hall Inc., Englewood Cliffs, NJ.
- Zeldis, J., James, M. R., Grieve, J. *et al.* (2002) Omnivory by copepods in the New Zealand Subtropical Frontal Zone. *J. Plankton Res.*, **24**, 9–23.
- Zhou, M. (2006) What determines the slope of a plankton biomass spectrum. *J. Plankton Res.*, **28**, 437–448.
- Zhou, M. and Huntley, M. E. (1997) Population dynamics theory of plankton based on biomass spectra. *Mar. Ecol. Prog. Ser.*, **157**, 61–73.
- Zhou, M., Tande, K. S., Zhu, Y. *et al.* (2009) Productivity, trophic levels and size spectra of zooplankton in northern Norwegian shelf regions. *Deep-Sea Res. II*, **56**, 1934–1944.
- Zhou, M., Zhu, Y. and Peterson, J. O. (2004) Growth and mortality of mesozooplankton during the austral winter in Marguerite Bay and its vicinity. *Deep-Sea Res. II*, **51**, 2099–2118.