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First report on the contribution of small-sized species to the copepod community structure of the southern Patagonian shelf (Argentina, 47-55°S)

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Summary: The copepod community structure, with special emphasis on small-sized species, was studied over the southern Patagonian shelf in late summer 2004, applying the first plankton sampling in the region with a fine-mesh (66 μm) net. The key role of the copepods *Drepanopus forcipatus* and *Calanus australis* was confirmed, but also the high abundance and frequency of occurrence of the microcopepods *Oithona helgolandica* and *Microsetella norvegica* and of the medium-sized copepod *Ctenocalanus vanus* were revealed. Copepod community structure was nearly homogenous over the entire study area. *Drepanopus forcipatus, O. helgolandica* and *M. norvegica* were identified as the typical species of the region, although secondarily *C. australis* and *Oithona atlantica* also contributed significantly to community similarity across the area. The study of interspecific relationships of dominant copepods indicated that *D. forcipatus* and *C. australis* were associated positively with *O. helgolandica*, while *C. vanus*, and *M. norvegica* constituted a separate assemblage with *Clausocalanus brevipes* and *O. atlantica*. The importance of fine-mesh-size nets for collecting the smaller size fractions of mesozooplankton and for accurately portraying the mesozooplankton assemblage structure in the area is stressed by this study.

Keywords: mesozooplankton; microcopepods; southern Patagonian shelf; size spectra; *Oithona helgolandica*; *Micosetella norvegica*; *Drepanopus forcipatus*.

Primer informe sobre la contribución de microcopépodos a la estructura de la comunidad mesozooplanctónica de la plataforma patagónica austral (Argentina, 47-55°S)

Resumen: La estructura de la comunidad de copépodos, con especial énfasis en las especies de pequeño tamaño, se estudió en la plataforma patagónica austral durante el verano tardío de 2004, a partir del primer muestreo de plancton en la región con una red de malla fina (66 μm). Se confirmó el rol clave de las especies *Drepanopus forcipatus* y *Calanus australis*, pero al mismo tiempo se evidenció la gran abundancia y frecuencia de ocurrencia de los microcopépodos *Oithona helgolandica* y *Microsetella norvegica* y del copépodo de tamaño medio *Ctenocalanus vanus*. La estructura de la comunidad de copépodos fue aproximadamente homogénea en toda el área de estudio. *Drepanopus forcipatus, O. helgolandica* y *M. norvegica* resultaron las especies típicas de la región y, aunque secundariamente, *C. australis* y *Oithona atlantica* también contribuyeron significativamente a la similitud en el área. El estudio de las interrelaciones entre las especies dominantes indicó que *D. forcipatus* y *C. australis* estuvieron positivamente asociados con *O. helgolandica*, mientras que *C. vanus* y *M. norvegica* conformaron otra asociación con *Clausocalanus brevipes* y *O. atlantica*. A partir de este estudio se enfatiza la importancia de las redes de malla fina para colectar las fracciones de tamaño más pequeñas del mesozooplancton y para describir correctamente la estructura de la comunidad mesozooplanctónica en el área.

Palabras clave: mesozooplancton; microcopépodos; plataforma patagónica austral; rango de tamaños; *Oithona helgolandica*; *Micosetella norvegica*; *Drepanopus forcipatus*.

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INTRODUCTION

Quantitative assessment of planktonic organisms is a key issue in determining food web structure and material cycling in pelagic ecosystems. In particular, reliable data on the mesozooplankton (0.2-20 mm), an important size class of the zooplankton community that links primary producers with higher trophic levels, are essential in order to accurately interpret the structure of marine pelagic ecosystems. The widespread use of coarse plankton nets with standard mesh sizes of 200-330 μm to collect mesozooplankton has led researchers to focus primarily on large copepod species, and to substantially underestimate the abundance of smaller organisms. However, as a result of the increasing use of fine plankton nets, microcopepods (i.e. species with a total body length between 0.2 and 1.0 mm in the adult and early copepodite stages) are currently recognized as essential contributors to the mesozooplankton community (e.g. Hopcroft et al. 1998, Di Mauro et al. 2009) and to the secondary production of marine ecosystems (e.g. Turner 2004, Gallienne and Robins 2001, Zervoudaki et al. 2007, Narcy 2010).

Mesozooplankton communities of the southern Patagonian shelf have been well studied over the last 40 years. However, most of the information on the taxonomic composition (Ramírez 1970a, 1971, 1981), biomass patterns (Sabatini and Álvarez Colombo 2001, Sabatini et al. 2004, Sabatini 2008a), population traits and life strategies (Sabatini 2008b) of the zooplankton was obtained from samples collected with nets with a mesh size of 200 μm (or larger). Therefore, the structure and function of the mesozooplankton community have been analysed in the region primarily for the larger, most abundant and most frequently occurring species captured by those standard nets. The smallest taxa, which are commonly undersampled and missed by coarse mesh sizes (e.g. Vanucci 1968, Evans and Sell 1985, Paffenhöfer 1998, Hwang et al. 2007, Pitois et al. 2009, Di Mauro et al. 2009) have been largely overlooked. Therefore, despite its importance, the overall structure of the zooplankton community of the Patagonian shelf has not been studied in detail, and species diversity patterns are poorly described.

As a result of sampling with coarse nets, two copepod species, the medium-sized clausocalanid *Drepanopus forcipatus* and the large calanid *Calanus australis* (mean prosome lengths are 983 and 2544 μm, respectively, Sabatini 2008b) are currently recognized as dominant components of the mesozooplankton biomass in the southern Patagonian shelf and are considered key species in the local planktonic food web. More recently, a study comparing the catching efficiency of plankton nets of 66 and 150 μm mesh has revealed that smaller species and early developmental stages of copepods have been significantly underestimated, and community and population structures have been severely biased by the coarse net (Antacli et al. 2010). Specifically, abundances of the first copepodite stage (C1) of *D. forcipatus*, all copepodite stages of the small-sized cycolopoid *Oithona helgolandica* including their detached egg-sacs, and pooled nauplii of all species are undersampled by the coarse net. Although not statistically treated, Antacli et al. (2010) also showed the underestimation of the small harpacticoid *Microsetella norvegica*.

Especially in oligotrophic waters where the microbial trophic food web prevails, microcopepods are considered important connectors between the classical and microbial food webs (Turner 2004). The southern Patagonian shelf (SW Atlantic, 47-55°S) is a cold-temperate ecosystem characterized by seasonal variation in biological production, following marked changes in abiotic conditions. During late summer and early autumn, primary production is low and the phytoplankton and protozoan zooplankton communities are dominated by ultraplanktonic cells (Alder and Franzosi 2003, 2005, Almandoz et al. 2007, Antacli 2011, Silva unpublished data), while abundances of larger nanoplankton and microplankton are low (Olguín et al. 2005, Santoferrara and Alder 2009a,b, Cefarelli et al. 2010, Antacli 2011, Akselman unpublished data). This size structure indicates the dominance of a microbial trophic web sustained by pico- and nanoeukariotes and bacterioplankton in the inner area of the Patagonian shelf during late summer (Antacli 2011, Antacli et al. submitted). Taking those previous observations into account, the smaller and less studied copepod taxa may have important roles in the local planktonic food web. Their relative contributions to the copepod community and to trophic transfers, along with those of *D. forcipatus* and *C. australis,* deserve revision on the basis of sampling with fine-mesh nets.

The overall objective of this study was to examine the structure of the copepod community, with particular reference to small-sized species, by sampling plankton for the first time over the southern Patagonian shelf in late summer with a fine-mesh (66 μm) net. We specifically tested the hypothesis that microcopepods are major contributors to the copepod community in the region during summer. We report here (i) the specific composition, abundance and spatial distribution of the copepod community, (ii) the spatial distributions of distinctive copepod assemblages and (iii) the interspecific relationships of dominant copepods.

MATERIALS AND METHODS

Sampling

The study area extended over the continental shelf off southern Patagonia (~47-55°S/61-69°W). Mesozooplankton was collected in late summer (March/April 2004) on a cruise aboard RV *Dr. E. L. Holmberg* at 32 stations along four latitudinal transects (Fig. 1). A small, vertically retrieved Bongo sampler (mouth opening 20 cm, nets of 66 and 150 μm mesh size) was used to collect samples from just above the bottom or from a maximum depth of about 100 m. A weight of 18 kg was attached to the center of the frame to overcome the drag of the sampler. Wire angles were thus maintained close to vertical and the nets were retrieved at a wire speed of 10 m per minute. Filtered volumes were estimated with digital flowmeters (Hydro-Bios) positioned

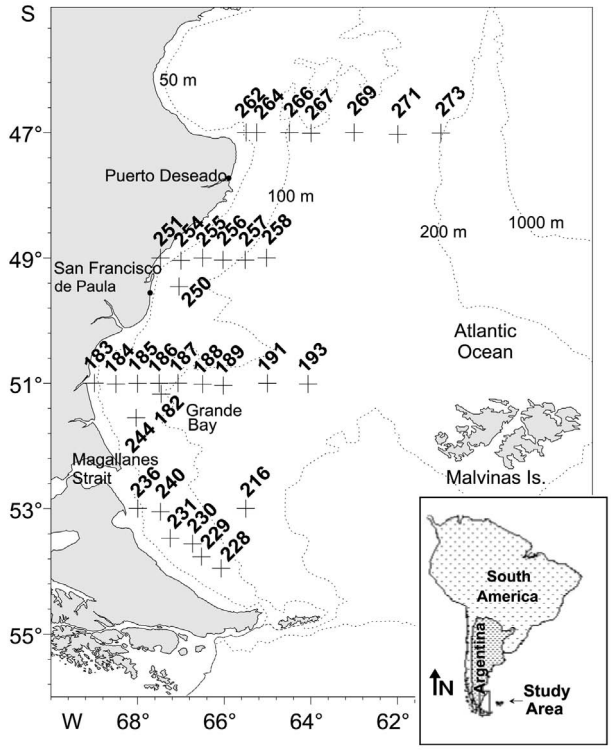

Fig. 1. – Mesozooplankton sampling stations (crosses) over the southern Patagonian shelf during the cruise EH-03/04 (INIDEP) carried out in late summer March/April, 2004 onboard RV *Dr. E.L Holmberg*.

in the mouths of the nets (on average 4.6±2.6 m^3 and 5.1±2.7 m^3 for the 66 and 150 μm nets, respectively). Samples were preserved in 4% buffered-formaldehyde for later analysis in the laboratory. The time of zooplankton collection depended on the arrival at stations after the general course of the cruise (17 stations were sampled during daylight hours and 15 at night). However, this contingency should not be a drawback because zooplankton samples were representative of the whole water column. In contrast, we are aware that larger and faster-swimming zooplankton (mainly euphausiids, amphipods and chaetognats which did occur in the samples) were most likely undersampled by the small Bongo due to the low retrieving speed and small-sized mouth of the sampler. Therefore, those groups were excluded from analysis.

Copepod species and abundance

Identification of copepods was accomplished after Grandori (1912), Ramírez (1970b, 1971, 1981), Heron and Bowman (1971), Björnberg (1981), Bradford et al. (1988), Sabatini (1990), Hulsemann (1991), Bradford-Grieve (1999) and Ramírez and Sabatini (2000).

On the basis of previous results regarding mesh selection effects in the study area (Antacli et al. 2010), quantitative data were estimated from the samples collected with the fine 66-μm net. Individuals were counted under a stereomicroscope (Leica M8). Separate subsamples were used for quantifying each species/taxon because of their different abundances in the samples. That is, samples were split into a series of successive aliquots accordingly to the relative abundances of taxa. The aim was to count at least 200 individuals of the most abundant stage in each sample (Postel et al. 2000). On the other hand, the entire sample was analysed when copepods were few. Nauplii were not identified to species or stage but pooled for counting.

Counting results were organized into three groups according to organism size: (i) adult (C6) and copepodite stages (C1-C5) of large copepods (e.g. Calanidae, Eucalanidae, Rhincalanidae), (ii) C1-C6 of small and medium-sized copepods (e.g. Clausocalanidae, Harpacticoida, Cyclopoida), and (iii) other small-sized items (e.g. naupliar stages, egg-sacs of *Oithona* spp. and fecal pellets). The relative abundance, RA%

$$RA_i = 100(\sum_{j=1}^{S} x_{ij} \,/\, \sum_{i=1}^{I}\sum_{j=1}^{S} x_{ij}) \,,$$

i.e. the average contribution of each taxon i to the total abundance, I being the total number of taxa and S the total number of samples] and the frequency of occurrence, $FO\%$ [FO_i=100(n_{ji}/S), i.e. the number of samples j in which a given taxon i occurs in relation to the total number of samples (S)] were then calculated.

Statistical analyses

Copepod community structure

Multivariate statistics were used to examine the copepod community structure in general, and specifically to identify the typical species within the copepod community and to analyse the spatial distribution of copepod assemblages. Analyses were performed with the PRIMER software package (Clarke and Warwick 1994) version 5.2.9 (Primer-E). We used an initial matrix composed of 23 copepod species/taxa and 32 samples. The analyses included all the species, even the rare taxa (i.e. those with low relative abundance and low frequency of occurrence) (Clarke and Warwick 1994). The abundance data, x_i, for each species, i, were transformed to $x'_i = \ln(x_i+1)$ to reduce the influence of the most abundant species.

A similarity matrix was produced from the natural logarithms of the abundance data by calculating the Bray-Curtis similarity measure. Then, a one-way analysis of similarity (ANOSIM, Clarke and Warwick 1994) was used to test whether the copepod community structure showed significant differences among four latitudinal sections (47, 49, 51, and 53°S) or between two bathymetric areas: inner shelf and mid-shelf. Those regions were defined a priori because we assumed the existence of variations in the copepod distribution patterns as functions of latitude and longitude. Data from the bathymetric areas were grouped according to station depth, for comparison of inner shelf (≤50-100 m) and mid-shelf (≥100-200 m) communities. ANOSIM is analogous to one-way ANOVA and based on the statistic R, which quantifies the distinctions among the groups. R values near to 1 indicate large differences among groups; R values near to 0 indicate small differences; negative R values

indicate that differences within groups are larger than between groups. *R* values >0.75 represent well separated groups, *R* values >0.5 indicate overlapping but clearly different groups and *R* values <0.25 suggest barely separable groups (Clarke and Warwick 1994, Clarke and Gorley 2001).

A similarity percentage routine (SIMPER, Clarke and Warwick 1994) was applied to the ln-transformed abundance values (x'_i) in order to identify the copepod taxa contributing the most to average similarity across the entire study area. SIMPER examines how much each species contributes to the average similarity, $\overline{S}_i$, within a group of samples (the more abundant the species the more it contributes). It is considered that a species typifies a group if it is found at a consistent abundance throughout. In that case, the standard deviation of its contribution to similarity, $sd(S_i)$, will be low, and the ratio $\overline{S}_i/sd(S_i)$ will be high (Clarke and Warwick 1994). In this study the species contributing to similarity with $\overline{S}_i$ values ≥10% were considered typical species (Bulleri et al. 2005).

Copepod assemblages

To portray the spatial association between dominant copepod species, a principal component analysis (PCA) based on the correlation matrix was performed (STATISTICA v.7). This is a simple, graphical way to examine the relationships among species. In such analyses the variables (species) are represented on the ordination space of the first two components by their correlation values, all of which will be included within the *correlation circle*. Those falling close to one other within the correlation circle are positively correlated, while those placed in opposite quadrants are negatively correlated (Borouche and Saporta 1983). An index of importance, *I*, was calculated for each species/taxon, *i*, as the average of the relative abundance and the frequency of occurrence, in order to identify the dominant species (after Morales et al. 2010). Then, only the species with *I* values ≥20% were considered important and included in the PCA. This procedure excluded the rare species from the analysis and, thereby, reduced the noise level. Abundance values were standardized and ln-transformed before the PCA.

RESULTS

Abundance and distribution of copepod species

A total of 23 copepod taxa were identified over the study area (Table 1). *Drepanopus forcipatus* was the most numerous species at all stations, accounting for 79% of total copepod numerical abundance. *Oithona helgolandica* was next with 15%. *Ctenocalanus vanus*, *Calanus australis* and *Microsetella norvegica* contributed much less to total numbers, accounting for 1 to 2% each. The least abundant copepod taxa accounted for <0.1% and are all listed in Table 1 (see also Fig. 2A).

Drepanopus forcipatus and *O. helgolandica* occurred at all stations (*FO*=100%). *Microsetella norvegica, C. australis, C. vanus, Oithona atlantica* and *Clausocalanus brevipes* were frequent taxa, being present at 59 to 88% of the sampled sites. Less frequent copepods were *Acartia tonsa, Neocalanus tonsus, Rhincalanus nasutus, Calanus simillimus, Calanoides* cf. *patagoniensis, Metridia lucens* and Siphonostomatoida sp. (*FO*=15-25%), while all other taxa occurred occasionally (*FO*<15%) (Table 1, Fig. 2B).

Table 1. – List of copepod species/taxa collected with a 66-µm mesh net (small Bongo sampler) over the southern Patagonian shelf in March/April 2004. Taxonomic classification after Boxshall and Halsey (2004). *RA*, relative abundance; *FO*, frequency of occurrence; *I*, index of importance (average between *RA* and *FO*). Important or dominant species are in bold (*I*≥20%).

ORDER Family	Species/taxa	Abundance range (ind m^{-3})	*RA* (%)	*FO* (%)	*I*
CALANOIDA					
Augaptilidae	*Euaugaptilus* sp.	0-3	0.001	3	1.50
Metridinidae	*Metridia lucens*	0-14	0.01	16	8.01
Clausocalanidae	***Drepanopus forcipatus***	8-79732	79.4	100	**89.7**
	Clausocalanus brevipes	0-431	0.26	59	**29.63**
	Ctenocalanus vanus	0-3417	1.57	69	**35.29**
Calanidae	***Calanus australis***	0-1898	1.45	84	**42.73**
	Calanus simillimus	0-115	0.03	16	8.02
	Neocalanus tonsus	0-232	0.08	19	9.54
	Calanoides cf. *patagoniensis*	0-2	0.001	16	8.00
Paracalanidae	*Paracalanus parvus*	0-464	0.12	13	6.56
	Calocalanus sp.	0-8	0.003	9	4.50
Acartiidae	*Acartia tonsa*	0-1540	0.59	25	12.80
Centropagidae	*Centropages* sp.	0-9	0.002	6	3.00
Eucalanidae	*Eucalanus* sp.	0-0.2	0.0001	3	1.50
Rhincalanidae	*Rhincalanus nasutus*	0-1	0.001	16	8.00
CYCLOPOIDA					
Oithonidae	***Oithona helgolandica***	9-11603	15.1	100	**57.55**
	Oithona nana	0-132	0.1	13	6.55
	Oithona atlantica	0-197	0.14	69	**34.57**
	Oithona cf. *plumifera*	0-3	0.001	3	1.50
HARPACTICOIDA					
Ectinosomidae	***Microsetella norvegica***	0-917	1.11	88	**44.56**
	Euterpina acutifrons	0-5	0.001	3	1.50
Clytemnestridae	*Clytemnestra rostrata*	0-0.3	0.0001	3	1.50
SIPHONOSTOMATOIDA	Siphonostomatoida sp.	0-6	0.002	16	8.00

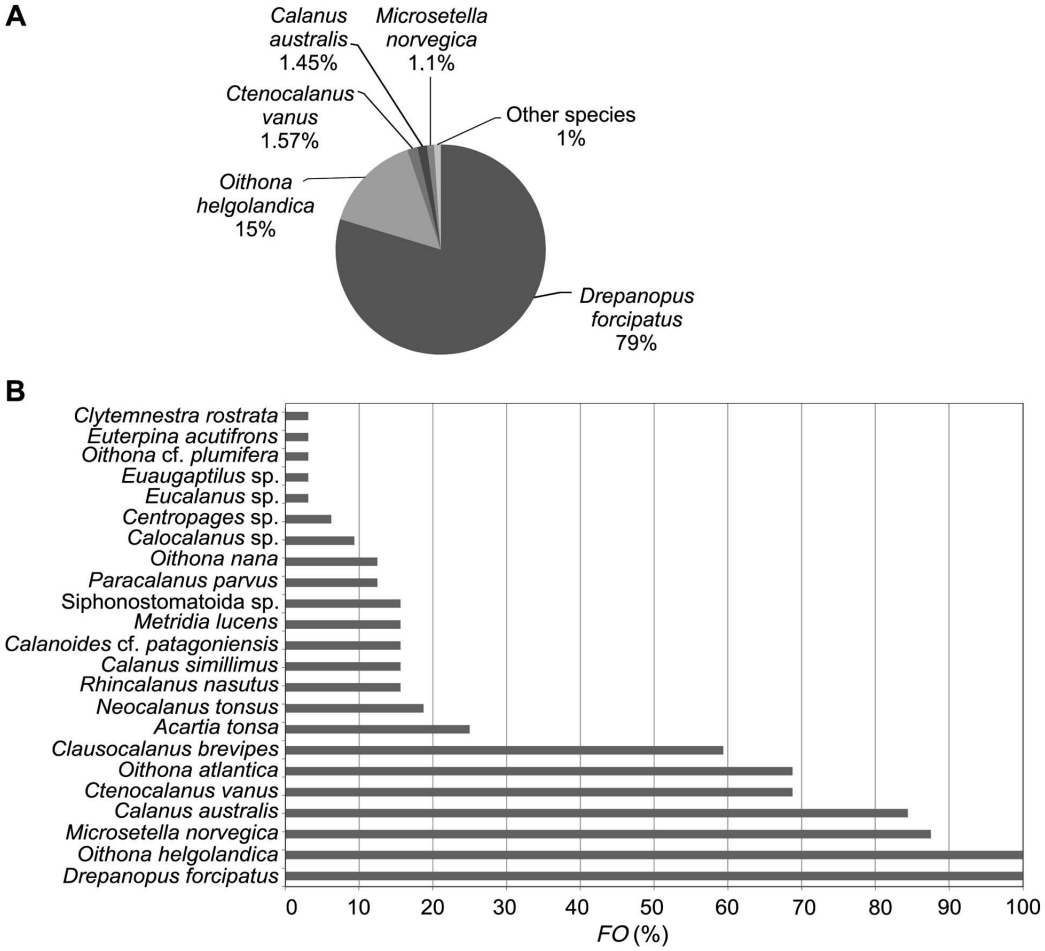

Fig. 2. – Relative abundance (A) and frequency of occurrence (B) of copepod taxa. In (A), Other species includes the rest of the copepod taxa with low relative abundance and frequency of occurrence listed in Table 1.

The distributions of all copepod taxa within the surveyed region are shown in Figure 3A-E. Among large calanids, *C. australis* dominated with abundances up to ca. 2000 ind m^{-3} at 49°S and ca. 700 ind m^{-3} at 51°S. This species was distributed over the entire area, mainly in inner shelf waters, diminishing in the offshore direction. Other calanid species were present occasionally and in very low numbers: *Calanus simillimus* was recorded mostly at the outermost stations (max. 115 ind m^{-3} at 47°S), *N. tonsus* (only C5) was found exclusively in the Grande Bay area at stations offshore (max. *ca*. 115-200 ind m^{-3}), and C4 and C5 of *Calanoides* sp. (likely *C. patagoniensis*) were present at 51 and 53°S (max. 2 ind m^{-3}) (Fig. 3A).

The medium-sized clausocalanid species were distributed over the entire shelf. They were represented by the dominant *D. forcipatus*, along with *C. vanus* and *C. brevipes*. Higher numbers of *D. forcipatus* were recorded over the inner shelf area of Grande Bay at 51°S (max. ca. 80000 ind m^{-3}). Abundances of *C. vanus* were higher at two locations in mid-shelf waters (St. 273 at 47°S and St. 191 at 51°S, 2500-3500 ind m^{-3}). Much less abundant, *C. brevipes* was relatively better represented in stations at 47°S, mostly in the offshore area (max. *ca*. 450 ind m^{-3}), decreasing gradually towards the south (Fig. 3B).

The smallest size range in the copepod community was represented by cyclopoid and harpacticoid species. The former group was dominated by *O. helgolandica*, distributed mainly in the northern area, with higher abundances over the inner shelf waters at 49°S (7000 and 11600 ind m^{-3}). Other less abundant cyclopoids were *Oithona nana*, distributed in coastal and inner shelf waters at 51°S (max. 100 ind m^{-3}), and *O. atlantica*, present over the entire shelf with higher abundances offshore at 47 and 51°S (max. 200 ind m^{-3}). Specimens of *Oithona* (possibly *O. plumifera*) were found in very low numbers (max. 3 ind m^{-3}) offshore at 51°S (Fig. 3C). Among harpacticoids, *M. norvegica* dominated with 950 ind m^{-3} at 51°S, increasing gradually in the offshore direction; *Euterpina acutifrons* (max. 5 ind m^{-3}) and *Clytemnestra rostrata* (max. 0.3 ind m^{-3}) were present occasionally in very low numbers (Fig. 3D).

Acartia tonsa (max. 1500 ind m^{-3}) and *Paracalanus parvus* (max. *ca*. 500 ind m^{-3}) were less abundant and less frequent species. Adult females and C5 of *Metridia lucens*, adult females of *Calocalanus* sp. and of *R. nasutus*, adult females and C5 of *Centropages* sp., C5 of *Eucalanus* sp., adult females of *Euaugaptilus* and one unidentified siphonostomatoid species were the least abundant copepod taxa (<15 ind m^{-3}) (Fig. 3E).

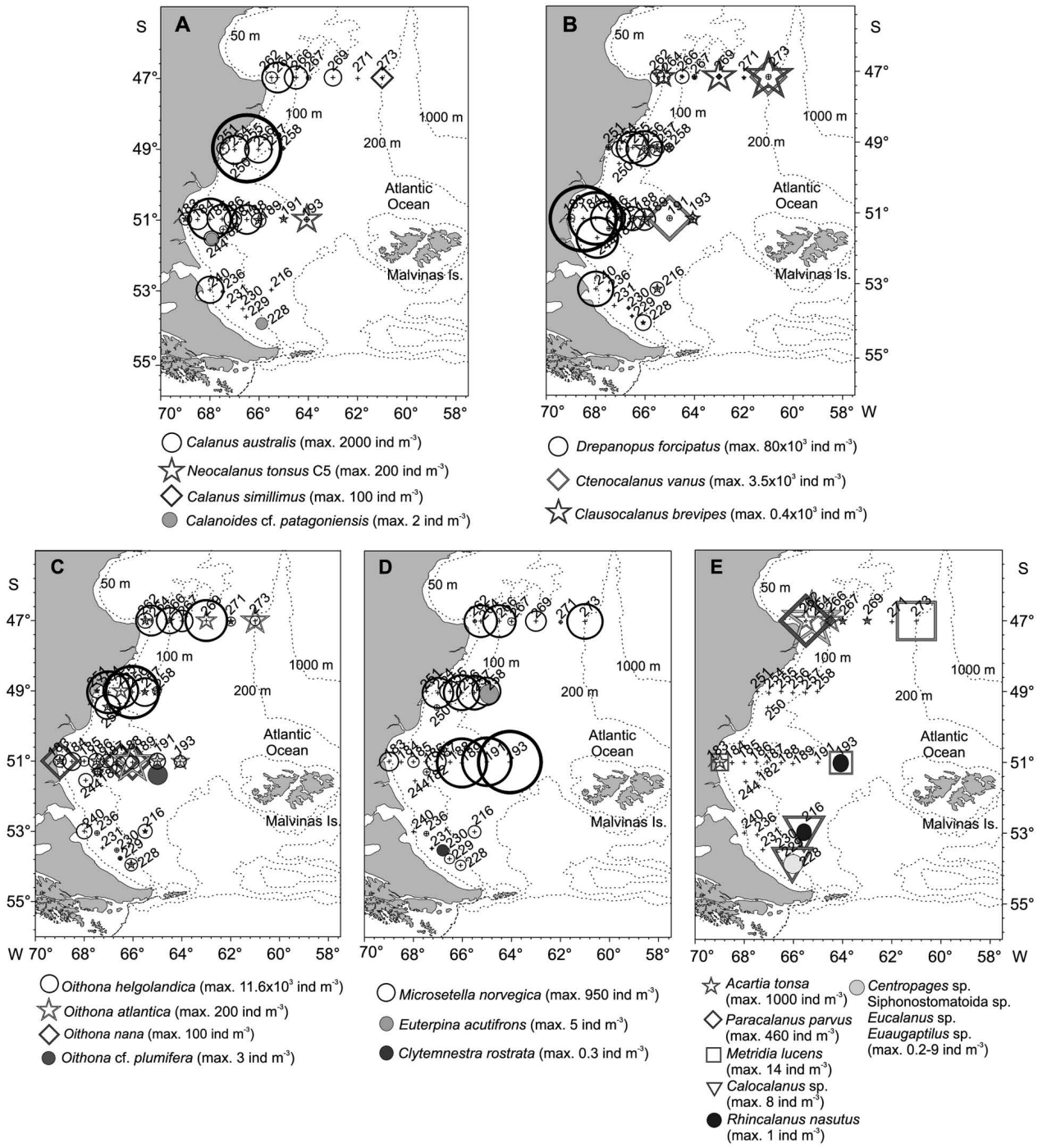

Fig. 3. – Spatial distribution and abundance of (A) large-sized calanid copepods (B) medium-sized clausocalanid copepods, (C) small-sized cyclopoid copepods, (D) small-sized harpacticoid copepods and (E) other less abundant and less frequent copepod taxa.

Community structure

Results from the one-way analysis of similarity performed on the station groups considered a priori as potentially different (ANOSIM, Table 2) indicated that there were no significant differences in the copepod assemblage among the four latitudinal sections (i.e. 47, 49, 51 and 53°S) or across the shelf (i.e. inner shelf versus mid-shelf). The results showed a relatively homogeneous community throughout the study area. Low values of the statistic *R* (in general <0.25) indicated small differences between groups, and that latitudinal section and bathymetric area per se were not significant factors in the ordination of stations. Negative values of the statistic *R* showed that differences within groups were greater than those between groups (e.g. 47 versus 49°S).

According to the SIMPER analysis, the typical species that contributed most to similarity in the area were *D. forcipatus, O. helgolandica* and *M. norvegica*. These species were the three most frequent and among the five most abundant taxa in the entire area. Although at lesser levels, *C. australis* (fourth in abundance and

Table 2. – Analysis of similarity (ANOSIM test) performed to test for significant differences in the copepod community structure among latitudinal sections and shelf areas. For detailed derivation of groups see Materials and Methods. All values of *R* in the pairwise tests are significant at P=0.05%.

Factors	Global *R*	*R* statistic pairwise test	Significance level P (%)
Latitudinal sections	0.185		0.3
47-49°S		–0.022	53.7
47-51°S		0.245	2.1
47-53°S		0.251	2.8
49-51°S		0.084	16.9
49-53°S		0.208	6.2
51-53°S		0.299	1.0
Across shelf areas			
Inner shelf-Mid-shelf	0.051		17.8

Table 3. – SIMPER analysis. List of copepod species with major contributions to similarity over the southern Patagonian shelf. The percentage contributed by each species to similarity and the ratio between its average similarity value and the standard deviation of its contribution are indicated. Average between sample similarity in the entire area ($\overline{S}_i$) was 59%. Taxa were ranked in order of decreasing average contribution to similarity. Typical species are in bold (see Materials and Methods for details).

Species	Contribution to similarity (%)	$\overline{S}_i/sd(S_i)$
Drepanopus forcipatus	**34.14**	**3.05**
Oithona helgolandica	**33.52**	**3.96**
Microsetella norvegica	**10.82**	**1.29**
Calanus australis	8.76	0.78
Oithona atlantica	3.63	0.67

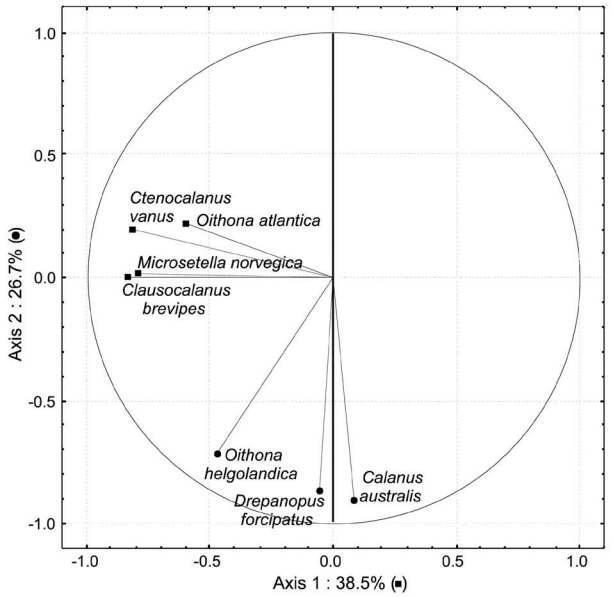

Fig. 4. – Principal component analysis (PCA) based on the correlation matrix. Representations on the ordination space of the correlations of species (variables) with the Axes 1 and 2 (circle of correlation).

occurrence) and *O. atlantica* (fifth in occurrence but low in abundance) also contributed significantly to similarity in the area (Table 3).

Copepod assemblages

According to the index of importance, *I*, only 7 copepod species (out of 23) were important and included in the PCA ($I_i \geq 20\%$, Table 1). In decreasing order of importance, those species were *D. forcipatus, O. helgolandica, M. norvegica, C. australis, C. vanus, O. atlantica* and *C. brevipes*.

Table 4. – PCA ordination of dominant copepod species. Entries are eigenvalues of the correlation matrix between the ln-transformed abundance values of dominant copepod species and the PCA Axes 1 and 2. Species contributing most to axis placement and consequent ordination are in bold.

Species/taxon	PCA Axis 1	PCA Axis 2
Eigenvalues	3.0815	2.1362
% Total variance	38.5	65.2
Drepanopus forcipatus	–0.0574	**–0.8578**
Clausocalanus brevipes	**–0.7785**	0.0148
Ctenocalanus vanus	**–0.8090**	0.1941
Calanus australis	0.0893	**–0.9048**
Oithona helgolandica	–0.4665	**–0.7038**
Oithona atlantica	**–0.5894**	0.2202
Microsetella norvegica	**–0.8249**	–0.0030

Results from the PCA indicated that all species included in the analysis were well represented by the two first axes, C1 and C2, which together explained 65.2% of the total variation in the distribution of copepod abundance. Axis 1 explained 38.5% of variance, and Axis 2 explained 26.7%. The correlations of species (variables) with both axes are listed in Table 4, and their representations on the ordination space are shown in Figure 4. A clear and positive association of *D. forcipatus, C. australis* and *O. helgolandica* is evident from their joint and close relation to Axis 2. On the other hand, *C. brevipes, C. vanus, O. atlantica* and *M. norvegica* together as a separate assemblage correlated mostly with Axis 1. As indicated by their orthogonal position, the two species assemblages are uncorrelated with each other.

DISCUSSION

The species composition and the relative abundances and distribution patterns of the copepod community were similar to those described from preceding studies. The copepod *D. forcipatus* was the most conspicuous component (because of its relative abundance and frequency of occurrence) of the mesozooplankton community, in keeping with previous surveys. Along with *C. australis*, this species has been repeatedly recognized as dominant in terms of biomass in the local mesozooplankton community (e.g. Sabatini et al. 2001, Sabatini 2008b). Furthermore, the distribution patterns of *D. forcipatus* and *C. australis* were mostly concentrated in the inner shelf waters of the Grande Bay area and northwards, coinciding with earlier studies in the region (e.g. Sabatini et al. 2000, Sabatini 2008b). Abundances of both species were significantly greater in the present study, especially in the case of *D. forcipatus*; this difference may be due to the use of a fine-mesh net (66 μm versus ≥150 μm). It is likely that the coarser nets used in previous studies undersampled the early copepodites (C1 in particular) of *D. forcipatus* (see Antacli et al. 2010).

The most notable differences in species composition and relative abundance between previous studies in the area and this study are twofold and most likely

related to the use of a 66 μm mesh net. First, the contribution of the smaller and less studied components to the mesozooplankton community was better established from our results. For example, *Oithona helgolandica* and *M. norvegica* were among those species, and their significant contributions to the community structure in terms of abundance and occurrence were, until now, completely unknown for the southern Patagonian shelf. *Oithona helgolandica* occupied the second place in the community after *D. forcipatus* in terms of abundance and occurrence; this species was distributed over the entire shelf and more abundantly to the north (47-49°S). *Microsetella norvegica* showed a high frequency of occurrence over the entire shelf, had its highest abundances in mid-shelf waters at 51°S and in the northern area (47-49°S), and was rather scarce in the coastal area of Grande Bay and at 53°S. Second, the importance of *C. australis* in the community in comparison with previous studies was minor. Until this study, *C. australis* was considered the second species in relative abundance after *D. forcipatus*. Here, *C. australis* was the fourth most numerous species in the mesozooplankton community after *D. forcipatus, O. helgolandica* and *C. vanus*. Despite its comparatively low abundance (mean of 178 ind m^{-3}, relative abundance 1.45%), *C. australis* was among the four most frequent (*FO*=84%) and important (*I*=42.73%) species in the region, following *D. forcipatus, O. helgolandica* and *M. norvegica*. It is important to consider, nonetheless, that the slowly towed Bongo system that we used may have conversely resulted in underestimating the abundance of large-sized copepods. When the suitability of the system was evaluated, the fine 66-μm net appeared to be more efficient than the coarser 150-μm net in sampling small-sized taxa, without biasing the catchability of the older and larger copepodites of *Calanus australis* (Antacli et al., 2010). However, we cannot rule out completely the possibility that large-sized copepods may have avoided the 20 cm opening of the small Bongo sampler because of a greater escape response (Anderson and Warren 1991). To be caught efficiently, some large-sized species may also require higher towing speeds than those recommended for vertical hauls such as those performed in this study.

Beyond our present findings highlighting the relative significance of small-sized species, it is worth noting that *D. forcipatus* stays as the most abundant key copepod over the southern Patagonian shelf, as is clearly shown in Figure 2. Current understanding of this species is not, however, in consonance with its presumed importance for the trophodynamics of the region, and its biology and ecology certainly deserve further research.

Strengthening the simple listing of counting results, the SIMPER analysis recognized *O. helgolandica* and *M. norvegica,* together with *D. forcipatus*, as typical species over the southern Patagonian shelf and, although to lesser extents, *C. australis* and *O. atlantica* contributed significantly to average similarity. Marine planktonic communities are often dominated by a few species, which develop key roles in energy transfer through their trophic web (Verity and Smetaceck 1996). This seems to be the case for the southern Patagonian shelf ecosystem, where a few copepod species dominated the mesozooplankton community in late summer 2004. Likely, *O. helgolandica* and *M. norvegica* play important roles in the regional trophic web. *Oithona helgolandica* may act as a key link between the microbial and the classical trophic webs (Turner 2004), similarly to closely related *Oithona* species occurring in other cold-temperate ecosystems (e.g. Gallienne and Robbins 2001, Narcy 2010). The pelagic harpacticoid *M. norvegica*, which often represents a large proportion of the total copepod abundance (e.g. Fish 1955, Yamazi 1956, Hirota 1964, Hirota and Hara 1975, Dugas and Koslow 1984, Uye et al. 2002) and mostly depends on food attached to surfaces (Koski et al. 2005), may play important roles as a secondary producer and in the degradation of aggregates, such as marine snow, during late summer in the region.

Despite its relatively low abundance (*RA*=1.57%), *C. vanus* showed a relatively high frequency of occurrence (*FO*=69%) and index of importance (*I*=35.29). So, although not detected by the SIMPER as a typical species, its role in the ecosystem of the southern Patagonian shelf should be taken into account. This species could have a strong impact on phytoplankton biomass of the southern Patagonian shelf region, as has been suggested for sub-Antarctic and Antarctic ecosystems (e.g. Bernard and Froneman 2002, 2003, 2005).

The distribution patterns of the rest of the copepod taxa found in this study were broadly in agreement with previous records in the area (e.g. Ramírez 1970b, 1981, Ramírez and Sabatini 2000, Sabatini 2008a). *Paracalanus parvus* and *O. nana* were more abundant in inner waters, while *C. brevipes, C. simillimus, R. nasutus, M. lucens, O. atlantica* and C5s of *N. tonsus* were better represented in the offshore direction. *Ctenocalanus vanus*, recognized typically as a coastal species (Ramírez 1970b) was, however, mostly concentrated in offshore waters in this study. Although in very low abundance, the harpacticoid *Clytemnestra rostrata* was present in cold high-latitude waters at 53°S, an unusual result because it is typically associated with warm subtropical waters (Ramírez 1970a). The concentration of *A. tonsa* over inner waters near to the coast at 47°S must be related to the presence of waters of low salinity coming mainly from the discharge of the Río Deseado. This is in agreement with the characteristic distribution reported for this species mainly in shallow coastal waters (Ramírez 1970a).

The homogeneity of the copepod community structure with both latitude and bathymetry over the southern Patagonian shelf in late summer 2004 was shown by the ANOSIM analysis. Similarly, Sabatini et al. (2012) found few differences in the copepod community structure in spring between the inner and mid-shelf sectors.

Concluding remarks

This is the first comprehensive study on the copepod community structure in the southern Patagonian shelf ecosystem based on sampling with a fine-mesh

(66 μm) net, as opposed to the standard coarser nets (≥150 μm) utilized historically in the region to sample mesozooplankton.

Our results support the initial hypothesis that small-sized copepods are key components of the local mesozooplankton community over the southern Patagonian shelf in summer. From the deployment of a fine-mesh net, four major conclusions can be drawn from this study: (1) the microcopepods *O. helgolandica* and *M. norvegica* and the medium-sized *C. vanus* are significant components of the summer mesozooplankton community on the southern Patagonian shelf and they deserve special attention in future studies; (2) medium-sized *D. forcipatus* remains as the most important copepod in the region; (3) the relative importance of *C. australis* in the mesozooplankton community of the region may be less than previously recognized; and (4) the copepod community structure was nearly homogenous over the entire study area, both among latitudinal sections and across the shelf. All of these conclusions strongly support the importance of fine-mesh nets for collecting the smallest size fractions of the mesozooplankton in order to better assess the food web structure of the southern Patagonian shelf.

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