



ORIGINAL ARTICLE

Seasonal succession of zooplankton in coastal waters of the Argentine Sea (Southwest Atlantic Ocean): prevalence of classical or microbial food webs

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Abstract

The demographic characteristics of marine zooplankton make it especially suitable for examining the variability of marine ecosystems. The zooplankton annual succession was studied at a permanent coastal station in the Argentine Sea (38°28'S, 57°41'W) in relation to physical conditions and phytoplankton size fractions. Small copepods (<1 mm total length), mainly represented by *Oithona nana* (Cyclopoida) and adults and copepodites of Calanoida, numerically dominated the metazooplankton throughout the year. In summer, small copepods also exceeded large copepods in biomass. Larvaceans (mostly <1 mm total length) were the second most important metazooplankton group, with strong dominance of *Oikopleura dioica*. The zooplankton succession exhibited two main periods throughout the year: (1) a cold winter–spring period characterized by a dominant classical herbivore food web in which the large copepod *Calanoides carinatus* and lamellibranch larvae were associated with the lowest temperatures and highest Chl-*a* and microphytoplankton, and (2) a warm summer period dominated by a microbial food web in which microbial filter-feeders such as *Oithona nana*, *Paracalanus* spp., *Oikopleura dioica* and *Penilia avirostris* predominated and the highest density of picophytoplankton and lowest concentrations of Chl-*a* were recorded. The implications of the present findings for the growth and survival of fish larvae distributed in the study area are discussed.

Key words: mesozooplankton succession, small copepods, larvaceans, phytoplankton fractions, EPEA station, Argentine Sea, Southwest Atlantic Ocean

Introduction

The demographic characteristics of marine mesozooplankton make them especially suitable for examining the variability of marine ecosystems (Mackas & Beaugrand 2010). This is particularly relevant in coastal areas due to ecological, economic and social reasons (Calbet et al. 2001; Lutz et al. 2006). In particular, the coastal waters off Buenos

Aires province in the northern Argentine Sea (Southwest Atlantic) house economically important fish such as anchovy (*Engraulis anchoita*) and jack mackerel (*Scomber japonicus*), mostly during their spawning season (Sánchez & Ciechomski 1995; Perrotta et al. 2001). The coastal area provides not only temperature ranges warmer than the shelf but also adequate zooplanktonic prey (mainly small

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copepods) for first-feeding fish larvae (Perrotta et al. 2001; Viñas et al. 2002).

Small copepods and their developmental stages as well as larvaceans and cladocerans constitute the bulk of the small (<1 mm total length) metazoans in coastal waters and play a key role in the pelagic carbon flux because of their capability of taking energy from the microbial food web and transferring it to higher trophic levels (Calbet et al. 2001; Turner 2004). However, the small zooplankton have been historically understudied worldwide due to the utilization of 200–333- μm meshes in regular zooplankton sampling (Calbet et al. 2001; Di Mauro et al. 2009; Jaspers et al. 2009).

With smaller mesozooplankton generally assumed to have production rates at least equal to or higher than the larger fractions (Hirst & Bunker, 2003), it has become clear it is necessary to obtain more realistic abundance estimates before we can assess their importance to grazing, recycling and vertical flux (Ward et al. 2012).

Traditionally, copepods have been considered the most important metazooplankton group in pelagic food webs (e.g. Verity & Smetacek 1996; Kiørboe 1998). Moreover, larvaceans have been shown to be the second most abundant metazooplankton group when appropriate sampling gear is used (Gorsky & Fenaux 1998). Because of their extraordinary growth rates, their contribution to secondary production can exceed that of copepods, mainly in subtropical and tropical areas (Hopcroft & Roff 1998; Jaspers et al. 2009).

The permanent coastal station EPEA (Estación Permanente de Estudios Ambientales) was established in the coastal waters of the Argentine Sea, 27 nautical miles south from Mar del Plata harbour (38°28'S–57°41'W), in 2000. It is the only permanent station in this large sector of the Southwest Atlantic Ocean where all the plankton components (including bacterioplankton, phytoplankton, zooplankton and ichthyoplankton) are regularly studied in relation to environmental factors (physical and chemical).

Here, we describe, for the first time, the annual cycle of the zooplankton community retained by a 67- μm mesh at the EPEA station, in order to: (1) identify its main components and determine their seasonal succession, (2) analyze its relationship with the physical variables and the size structure of the autotrophic community, and (3) assess the prevalence of classical or microbial food webs in different periods of the year. Also, this investigation will provide useful information concerning the seasonal variation of food availability for the zooplanktivorous fish larvae distributed in the area.

Materials and methods

Study area

The EPEA station is located in the Argentine Sea at 38°28'S–57°41'W (Figure 1). Most of the year it is covered by High Salinity Coastal Waters (HSCW: 33.7–34.2 in salinity) originating from the San Matías Gulf (Lucas et al. 2005). The predominance of these waters agrees with the general circulation (NNE) pattern reported for the Argentine Sea (Martos & Piccolo 1988). The presence of lower salinity Río de la Plata waters and shelf waters has been detected very sporadically at the station (Carreto et al. 1995).

In this coastal system the mixing produced by winds and tides results in a vertically homogeneous water column during the autumn and winter months (Carreto et al. 1995 and references therein). Nutrient concentration, phytoplankton density and chlorophyll-*a* concentration (<2 mg m⁻³), are low during the year (Carreto et al. 1995).

Sample collection and analysis

A total of 19 cruises to the EPEA station (48 m depth) were performed approximately fortnightly between March 2000 and April 2001. In each cruise, conductivity and temperature profiles were obtained with a Seabird SBE1901 CTD.

Water samples for the determination of chlorophyll-*a* concentration (Chl-*a*) and identification of phytoplankton cells were taken from different depths using Niskin bottles. In the laboratory, Chl-*a* was measured from 90% acetone extracts of material collected on glass fibre filters (GF/F size) using the fluorometric method (Holm-Hansen et al. 1965). Water samples (250 ml) were preserved with formaldehyde (0.4% sample final concentration) and phytoplankton cells >5 μm in diameter were identified and quantified by the Utermöhl method (Hasle 1978). For the ultraphytoplankton groups (<5 μm in diameter), an epifluorescence microscope (Verity & Sieracki 1993) was used. In this work, only biomass estimations of micro- (20–200 μm), nano- (2–20 μm) and picophytoplankton (0.2–2 μm ; Sieburth et al. 1978) were analyzed. The carbon biomass of marine diatoms and other protists was calculated using the equations given by Eppley et al. (1970), whereas the biomass of the picophytoplankton components was estimated applying the specific conversion factor of 0.21 pg C cell⁻¹ for *Synechococcus* (Waterbury et al. 1986). Finally, the carbon content of picoeukaryotic algae was estimated using the standard conversion factor of 0.22 pg C μm^{-3} (Booth 1995), from the measurement of cell biovolumes.

Zooplankton samples were obtained with a small bongo net (18 cm diameter, 220- and 67- μm mesh

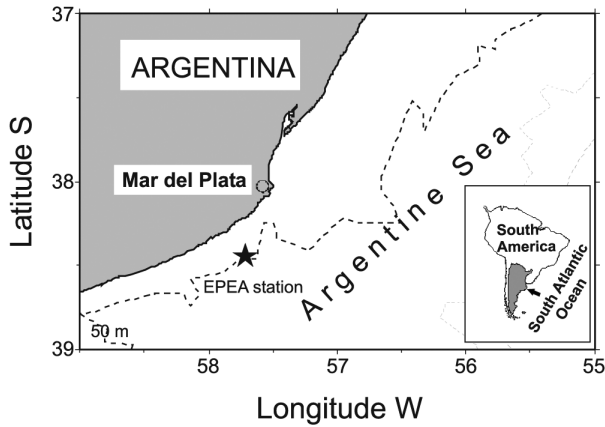


Figure 1. Location of the EPEA station (48 m depth) in the Argentine Sea.

sizes) obliquely trawled from near the bottom (~ 40 m) to the surface. The tows were short (towing time: 2 min; towing rate: 20 m min^{-1}) with the ship moving at 2 knots speed. No clogging of the nets was observed. The volume of filtered water was estimated by means of a mechanical flowmeter in each net mouth. Taking into account the dominance of small mesozooplankton species in the study area (Viñas et al. 2002), only samples obtained with the $67\text{-}\mu\text{m}$ mesh size net were analyzed, which assures the adequate retention of both adults and immature stages (Di Mauro et al. 2009).

Two size categories of zooplankton were considered: mesozooplankton ($>200 \mu\text{m}$) and microzooplankton ($67\text{--}200 \mu\text{m}$). The larger component included copepods (egg sacs, adult and copepodite stages), cladocerans, larvaceans, chaetognaths, meroplanktonic larvae, *Noctiluca scintillans* Kofoid & Swezy, 1921 and hydromedusae, whereas the smaller category referred to free eggs and nauplii of copepods.

Adults and copepodite stages were identified to the lowest possible taxonomic level, using appropriate taxonomic references (Ramírez 1966, 1969; Bradford-Grieve et al. 1999; Ramírez & Sabatini 2000), and then enumerated under a stereomicroscope. For this purpose, subsamples of different volume were obtained in order to include at least 100 adult copepods. Abundance was expressed as individuals per cubic metre (ind m^{-3}). Copepodites of Paracalanidae and Pseudocalanidae were counted together because of the difficulty in discriminating between them at the specific level.

Biomass of the dominant species *Oithona nana* Giesbrecht, 1892, *Calanoides carinatus* (Krøyer, 1849), *Ctenocalanus vanus* Giesbrecht, 1888 and *Paracalanus* spp. was derived from their abundance and mean individual biovolume following Viñas et al. (2010). Biovolumes were converted to wet weight by applying a factor for specific gravity ($1 \text{ ml} = 1 \text{ g}$, Omori & Ikeda 1984). Then, the wet weight was

multiplied first by 0.20 and then by 0.40 to obtain the dry weight and the carbon content, respectively (Postel et al. 2000).

Published abundance data of cladocerans, larvaceans and chaetognaths corresponding to the same annual cycle (Daponte et al. 2004; Viñas et al. 2007; Capitanio et al. 2008) were included in multivariate analyses to have a complete representation of the community.

Data analysis

Seasons were considered to include three consecutive months starting in autumn (April, May and June) at the beginning of the study period.

The vertical distribution of temperature and Chl-*a* were analyzed during this annual cycle. The water masses present at the EPEA station were classified according to the surface salinity ranges, following Guerrero & Piola (1997) and Lucas et al. (2005) into: Low Salinity Coastal Waters (LSCW, <33.3), High Salinity Coastal Waters (HSCW, $33.7\text{--}34.2$), and Mid Shelf Waters (MSW, $33.4\text{--}33.6$). Euphotic-depth-integrated chlorophyll-*a* concentration was also considered.

A multivariate analysis technique of numerical classification was used to define sample groups with distinct biological composition. For that, abundance data of species present in more than 10% of the samples were included in the species matrix. Prior to analysis, data were transformed using $\log(x+1)$. Hierarchical agglomerative clustering was carried out using the Bray–Curtis similarity index (Bray & Curtis 1957) coupled with group average.

A BEST routine was applied to analyze the combination of environmental variables (surface (ST) and bottom (BT) temperature; surface (SS) and bottom (BS) salinity; Chl-*a*; micro-, nano- and picophytoplankton biomass) that best explained the patterns observed in the biological data. The sample groups resulting from the similarity analysis (Euclidean distance index) of the environmental variables selected were ordinated using multidimensional scaling (MDS) analysis.

For the above analyses, the PRIMER v.6 software package (Clarke & Warwick 1994) was used.

Results

Hydrography and phytoplankton biomass

During most of the study period, the EPEA station was covered by HSCW (salinity of $33.7\text{--}34.2$) extending from the surface to the bottom (Figure 2a). The advection of MSW ($33.4\text{--}33.6$) and LSCW

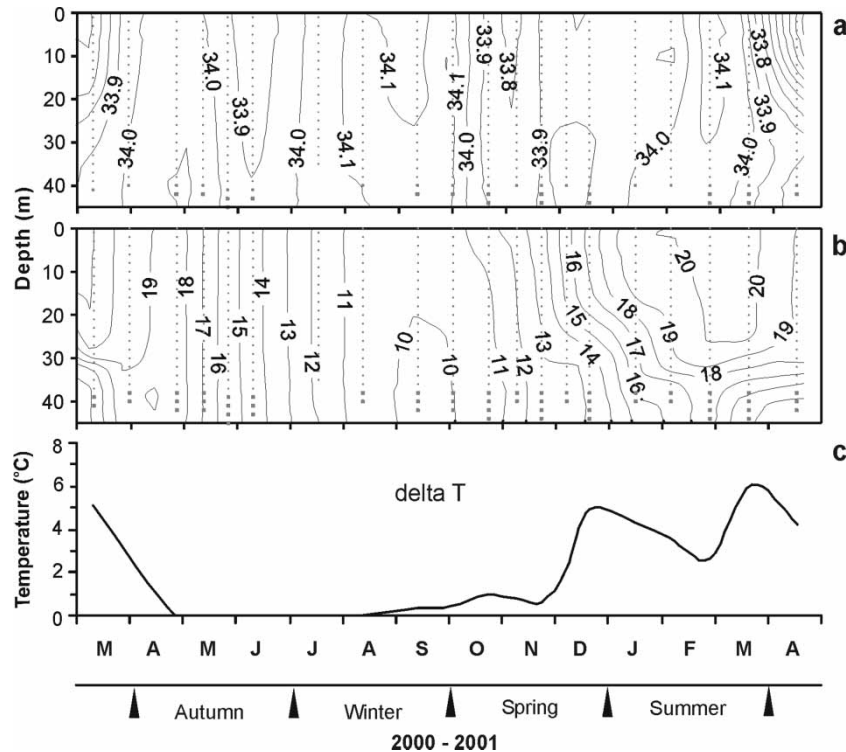


Figure 2. Vertical profiles of (a) salinity and (b) temperature during the study period. The surface-bottom delta T values (c) are also included for each sampling date.

(<33.3) was observed on the surface only in March 2000 and April 2001, respectively (Figure 2a).

The surface temperature fluctuated between 21.1°C in late summer and 10.1°C in winter, whereas the bottom temperature fluctuated between 17.7°C in summer and 9.7°C in winter (Figure 2b). The water column was well-mixed (thermally homogeneous) during autumn and winter, but from the end of winter (September) through the next autumn (April 2001), a temperature gradient was observed between the bottom and surface depths with a maximum delta T of 6°C in late summer (March 2001) (Figure 2c).

Integrated Chl-*a* ranged between a minimum of ~14 mg m⁻² in spring (November) and a maximum of ~70 mg m⁻² in winter (July–August). A secondary seasonal peak (~47 mg m⁻²) was observed in autumn 2000 (April) (Figure 3a).

Phytoplankton biomass fluctuated between 8.9 and 106.7 mgC m⁻³ (November and July 2000, respectively). The contribution of microphytoplankton to the total biomass was most important in early winter, whereas that of nanophytoplankton was highest in late autumn and spring and that of picophytoplankton in summer 2001 (Figure 3b–d).

Zooplankton diversity and abundance

Free eggs and nauplii of copepods dominated the microzooplankton fraction, with the highest abundance in summer (Table I).

Mesozooplankton abundance, excluding *Noctiluca scintillans*, was maximal in summer and minimal in autumn (Table I). Small-size copepods (<1 mm total length), including adults and copepodites of *Oithona nana*, *Paracalanus* spp., *O. helgolandica* and *Euterpina acutifrons*, numerically dominated the mesozooplankton fraction throughout the year, representing 81.1% of its mean annual abundance. Egg sac (corresponding to *Oithona* spp. and *E. acutifrons*) abundance was maximal in spring.

The second most abundant group in the <1 mm mesozooplankton fraction were the larvaceans dominated by *Oikopleura dioica* (Table I), with the highest abundance in summer. Among the cladocerans, *Penilia avirostris* and *Evadne nordmanni* were the most abundant. Hydromedusae were present during winter, spring (when they were most abundant) and summer, but absent in autumn, while *N. scintillans* was strongly dominant during spring and *Sagitta friderici* was more abundant during summer and autumn (Table I). Also within this small-size class, meroplankton, mostly represented by lamellibranch larvae (mean of 80%), exhibited its highest abundance in winter. Other meroplankton components, including mainly the larvae of gastropods, polychaetes and decapods had a maximum of abundance in autumn, with a secondary peak in summer (Table I).

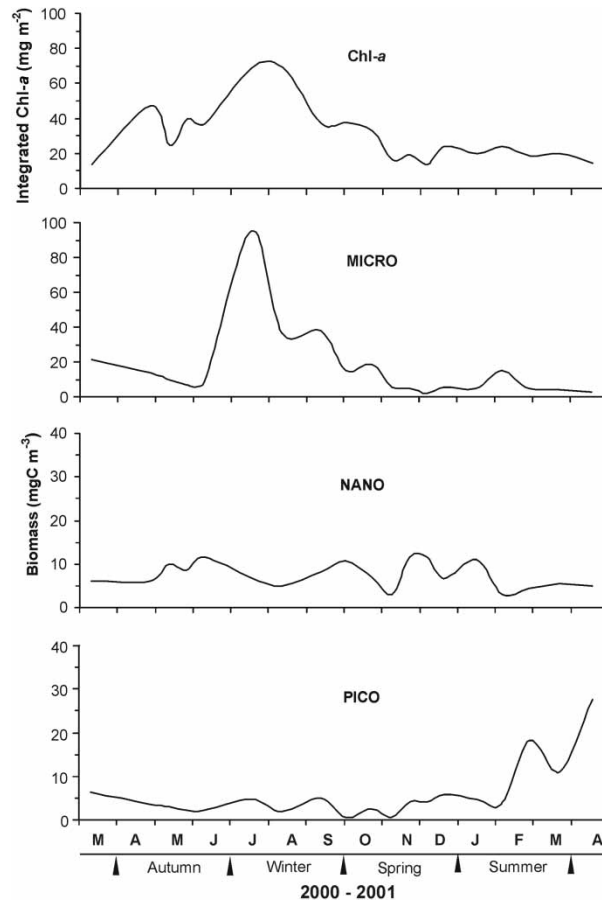


Figure 3. Seasonal variation of (a) integrated water-column chlorophyll-*a* concentration (Chl-*a*); biomass of (b) micro- (MICRO), (c) nano- (NANO) and (d) picophytoplankton (PICO) at the EPEA station.

Seasonal variation of copepod abundance and biomass

The <1 mm sized copepods represented 98% of the total copepod abundance on average, outnumbering the medium (1–2 mm) and large (>2 mm) sized ones by two orders of magnitude. Within the smallest size class, cyclopoids, represented mostly by adults and copepodites of *Oithona nana* and *O. helgolandica*, constituted on average 38% of the total abundance (Figure 4). As observed in Table I, *O. nana* peaked in summer (3,984 ind m⁻³) and had its minimum abundance in autumn. *O. helgolandica* followed a similar trend, but with one order of magnitude lower abundance and minimum records in winter. *Corycaeus amazonicus* occurred almost all year round with its highest abundance in autumn. Calanoids (adults and copepodites of Paracalanidae and copepodites of Pseudocalanidae) averaged 57% of the total abundance. Adult *Paracalanus* spp. occurred all year round but with maximal densities in summer (513 ind m⁻³). Extremely high abundances of copepodites of Paracalanidae and Pseudocalanidae were also observed in summer (>12,000 ind m⁻³ on average). *Euterpina acutifrons* (adults and

copepodites) exhibited an important pulse in autumn and a secondary one in winter.

Among the 1–2 mm size-class copepods, *Ctenocalanus vanus* occurred from late winter through early autumn (Table I), with maximal densities in summer. Adults of *Clausocalanus brevipes* were scarce and present only during winter (Table I).

Within the largest size class (>2 mm), the calanoid *Calanoides carinatus* was present during all seasons with maxima in winter and spring, whereas *Labidocera fluviatilis* occurred in small numbers only in winter (Table I).

In autumn, 79% of the abundance of copepods and 64% of the biomass corresponded to calanoids <1 mm. In winter and early spring, although cyclopoids were the numerically dominant group (54 and 62%, respectively), the biomass was dominated by calanoids >1 mm (74% in winter and 76% in spring). In summer, the situation changed substantially and copepods <1 mm in size (including calanoids, cyclopoids and harpacticoids) dominated the copepod community not only in abundance (99%) but also in biomass (75%) (Figure 5).

Table I. Seasonal variation of the composition and mean abundance (\pm SD) of zooplankton components in the EPEA station (in individuals m^{-3}). A, adults; C, copepodites; TL, total length.

	Autumn	Winter	Spring	Summer
Dinoflagellates				
<i>Noctiluca scintillans</i> (Macartney) Kofoid & Swezy, 1921	43 \pm 87	4,819 \pm 8,219	26,589 \pm 16,808	4,153 \pm 8,204
Microzooplankton				
Copepods nauplii	4,083 \pm 4,370	3,455 \pm 2,312	5,840 \pm 5,981	15,149 \pm 5,052
Copepods eggs	3,053 \pm 5,399	2,068 \pm 1,384	1,796 \pm 1,684	3,753 \pm 3,260
Mesozooplankton				
Copepods (A, C)	2,167 \pm 1,399	3,201 \pm 2,387	5,074 \pm 3,098	18,862 \pm 13,661
Egg sacs	50 \pm 111	479 \pm 652	843 \pm 966	662 \pm 516
<1 mm TL	2,137 \pm 1,394	2,985 \pm 2,163	4,803 \pm 2,664	18,697 \pm 13,561
<i>Oithona helgolandica</i> (Claus, 1863) (A, C)	48 \pm 65	36 \pm 47	83 \pm 114	444 \pm 774
<i>O. nana</i> Giesbrecht, 1892 (A, C)	105 \pm 90	905 \pm 554	2,210 \pm 1,383	3,984 \pm 5,042
<i>Paracalanus</i> spp. (A)	105 \pm 117	19 \pm 10	112 \pm 121	513 \pm 539
<i>Corycaeus amazonicus</i> Dahl, 1894 (A, C)	36 \pm 40	22 \pm 43	0	28 \pm 62
<i>Euterpina acutifrons</i> (Dana, 1847) (A, C)	198 \pm 263	105 \pm 160	23 \pm 40	90 \pm 75
Para-Pseudocalanidae (C)	1,584 \pm 1,316	1,137 \pm 841	1,525 \pm 1,331	12,716 \pm 9,901
1–2 mm TL	27 \pm 23	80 \pm 75	96 \pm 180	124 \pm 88
<i>Clausocalanus brevipipes</i> Frost and Flemiger, 1968 (A)	0	2 \pm 3	0	0
<i>Ctenocalanus vanus</i> Giesbrecht, 1888 (A)	27 \pm 23	78 \pm 75	96 \pm 180	124 \pm 88
> 2 mm TL	3 \pm 8	117 \pm 165	117 \pm 245	38 \pm 77
<i>Labidocera fluviatilis</i> Dahl, 1894 (A, C)	0	3 \pm 6	0	0
<i>Calanoides carinatus</i> (Krøyer, 1849) (A, C)	3 \pm 8	114 \pm 167	117 \pm 245	38 \pm 77
Cladocerans				
<i>Evadne nordmanni</i> Loven, 1836	0	4 \pm 9	130 \pm 75	144 \pm 219
<i>Pseudoevadne tergestina</i> Claus, 1877	0	0	0	6 \pm 11
<i>Pleopis polyphemoides</i> Leuckart, 1859	0	2 \pm 3	13 \pm 29	98 \pm 218
<i>Podon leuckarti</i> (Sars, 1862)	0	0.2 \pm 0.4	29 \pm 52	0
<i>P. intermedius</i> Lilljeborg, 1853	0	0	9 \pm 11	0
<i>Penilia avirostris</i> Dana, 1852	44 \pm 66	0	0	1,089 \pm 1,285
Larvaceans				
<i>Oikopleura dioica</i> Fol, 1872	350 \pm 226	603 \pm 607	610 \pm 406	1,239 \pm 1,783
<i>O. fusiformis</i> Fol, 1872	254 \pm 143	187 \pm 287	487 \pm 406	1,165 \pm 1,802
<i>Fritillaria borealis</i> Lohmann, 1896	5 \pm 8	0	0	35 \pm 79
<i>Appendicularia sicula</i> Fol, 1874	40 \pm 71	415 \pm 405	123 \pm 91	0.9 \pm 1.9
<i>Appendicularia sicula</i> Fol, 1874	51 \pm 39	0.1 \pm 0.3	0	38 \pm 84
Chaetognaths				
<i>Sagitta friderici</i> Ritter-Zahony, 1911	26 \pm 9	13 \pm 11	3 \pm 3	40 \pm 13
Hydromedusae				
	0	0.2 \pm 0.4	39 \pm 80	6 \pm 13
Total meroplankton	808 \pm 985	4,181 \pm 2,978	970 \pm 690	1,527 \pm 1,171
Lamellibranch larvae	487 \pm 615	4,080 \pm 2,920	946 \pm 683	1,383 \pm 1,266

Community structure

Three groups of samples were determined at a 62% level of similarity. Two main assemblages corresponded to winter–spring (*W–S*) and summer (*Su*), while a transition group (*A*) was associated with autumn (Figure 6a). MDS analysis confirmed the assemblages with a stress value of 0.12 (Figure 6b). During winter–spring, surface and bottom temperature were minimal, while Chl-*a* and microphytoplankton presented their highest values. The highest abundance of mostly herbivorous components such as the copepod *Calanoides carinatus* and lamellibranch larvae was recorded during this period. In contrast, picophytoplankton exhibited the lowest values. The summer group was characterized not only by the highest ST and BT values but also by the highest differences between them (see Figure 2c). The minimum of Chl-*a* concentration, the highest proportion of picophytoplankton (Figure

6c) and the dominance of the microbial filter-feeders *Oithona nana*, *Paracalanus* spp., *Oikopleura dioica* and *Penilia avirostris* were also observed during this period (Figure 6c). The transition period was characterized by intermediate values of ST, BT and Chl-*a* and the lowest values of picophytoplankton (Figure 6c).

A combination of two environmental variables (bottom temperature and picophytoplankton biomass) provided the best match (Spearman's rank correlation, $r_s = 0.424$, significance level 0.03, BEST analysis) to the biological patterns observed. Figure 6d shows the MDS ordination resulting from the sample assemblages obtained.

Discussion

The occurrence of high salinity coastal waters (HSCW) during most of the study period is typical

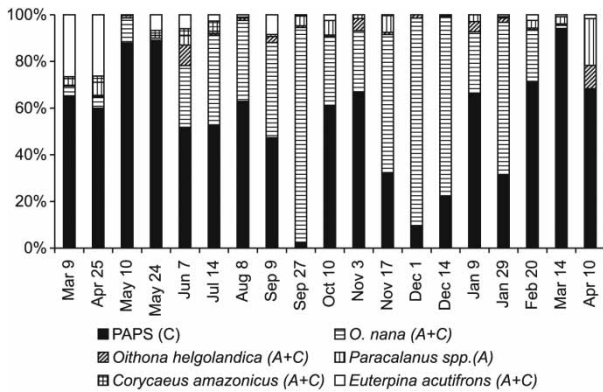


Figure 4. Percentage contribution of different copepod species in the <1 mm size class at the EPEA station. A, adult; C, copepodite; PAPS, Paracalanidae and Pseudocalanidae.

for the area (Temperoni et al. 2011). The advection of cooler waters from the shelf (MSW) and dilute waters from the Río de La Plata river (LSW), observed only during very short periods of time (March 2000 and April 2001, respectively), has been recorded sporadically during the warmer period of the year (Piola et al. 2005). Differences between surface and bottom temperatures observed in spring–summer corresponded to the seasonal stratification of the water column with a well-established thermocline from summer to early autumn followed by the complete mixing of the water column in winter (Lutz et al. 2006). The maximum Chl-*a* concentration recorded in mid-winter (July–August) in this study followed the seasonal input of nutrients at depth through mixing of the water column as it occurs regularly in autumn–winter (Carreto et al. 1998).

Microphytoplankton was the main carbon contributor during the whole study cycle, on average, exhibiting the typical seasonal maximum in winter–spring (Carreto et al. 1995). However, it is worth mentioning that the picophytoplankton had an outstanding contribution (up to 78% of the total

phytoplankton biomass) in summer and early autumn. This result concurs with previous findings by Silva et al. (2009) at the EPEA station, who found that this fraction can reach 50–90% of the total Chl-*a* in summer. Based on the predominant physical (high temperature), optical (high irradiance), chemical (low nitrate concentrations) and biological (low Chl-*a* concentrations) characteristics, Silva et al. (2009) defined this habitat as oligotrophic-like during summer.

Our results showed that a substantial part of the zooplankton community was represented by the <1 mm-sized components, as observed in other regions by using 63 μm mesh nets (Hopcroft et al. 2001; Paffenhöfer & Mazzocchi 2003; Di Mauro et al. 2009). It has been shown that traditional 200 μm mesh nets capture <10% of the mesozooplankton, thus underestimating the biomass by one-third and the secondary production by two-thirds (Gallienne & Robins 2001). Therefore, investigations including the smallest fraction are necessary to understand the functioning of the marine ecosystem (Paffenhöfer 1998).

Small-sized copepods dominated the metazooplankton community at the EPEA station in terms of abundance and biomass, as observed in other temperate and tropical coastal regions (Mazzocchi & Ribera d'Alcalá 1995; Hopcroft et al. 2001; Sata-poomin et al. 2004; Turner 2004; Atienza et al. 2006; Zervoudaki et al. 2007). Moreover, it has been shown that small copepods and their early developmental stages dominate all marine communities (Hopcroft et al. 2001).

The highest abundances of small copepods were recorded in summer in coincidence with minimal concentrations of chlorophyll, which was mainly represented by small-sized (<3 μm) primary producers. It is known that the latter are not grazed efficiently by copepods but are consumed by

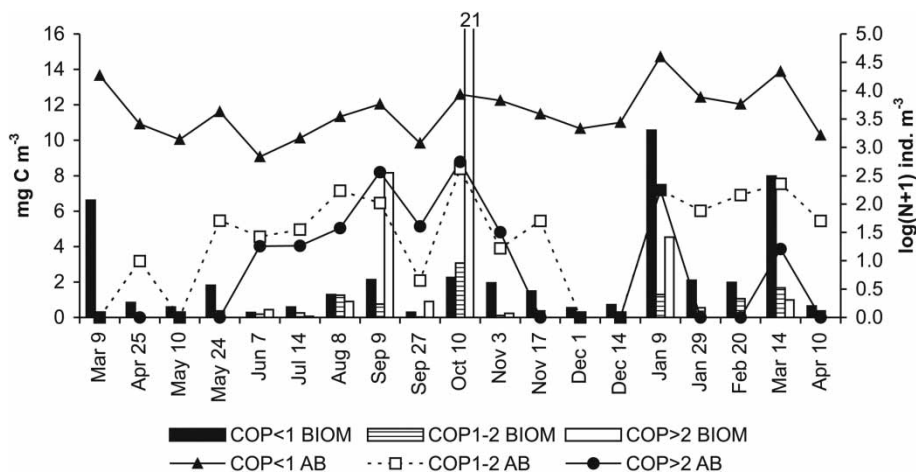


Figure 5. Seasonal variation of abundance (AB) and biomass (BIOM) of copepod size categories at the EPEA station.

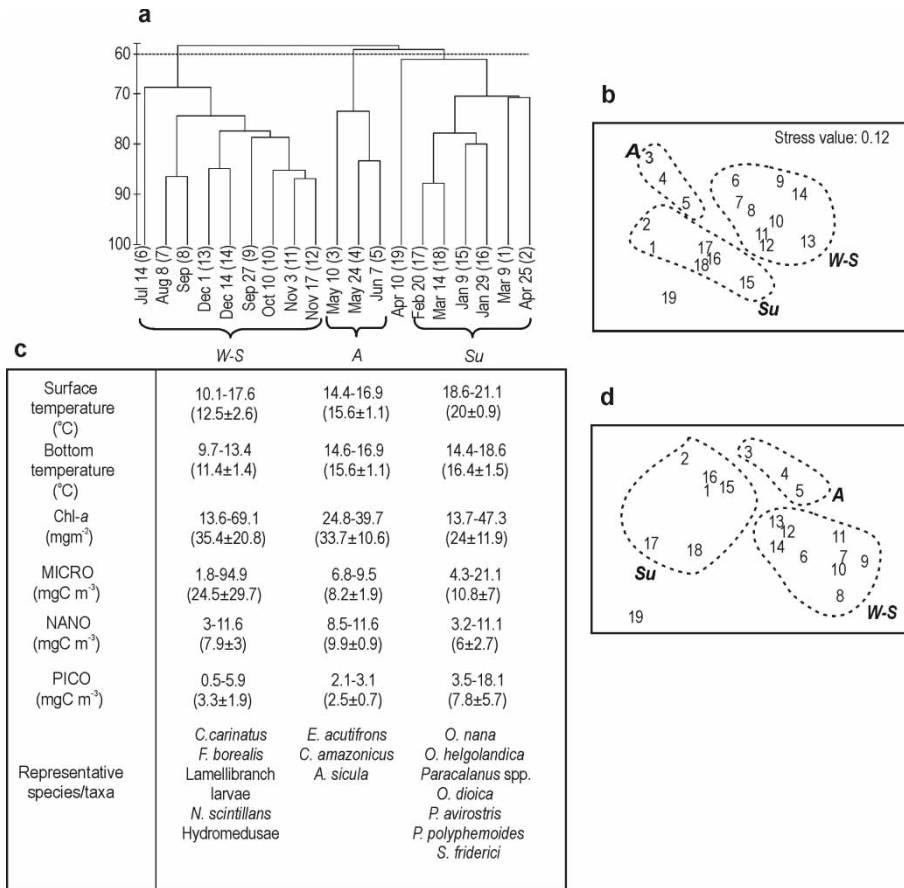


Figure 6. Analysis of similarity among the sampling dates. (a) Cluster analysis and (b) MDS ordination of samples from biological variables (Bray–Curtis index). (c) Range of variability and mean value \pm standard deviation (in parentheses) of the environmental factors (see abbreviations in Figure 2 caption). Each taxon was associated with the season in which it was more abundant. (d) MDS ordination of samples from environmental variables (Euclidean distance index). A, autumn; W–S, winter–spring; Su, summer. Numbers in parentheses in (a) and numbers in (b) and (d) correspond to correlative sample numbers.

nano- and micro-heterotrophs larger than $>3 \mu\text{m}$, which are intensively predated by ciliates. The important role of ciliates in the nutrition of copepods has been highlighted in several studies (Stoecker & Capuzzo 1990; Gifford & Dagg 1991; Zervoudaki et al. 2007). Small copepod species have a greater influence on the efficiency of the trophic coupling between the primary producers, the protozooplankton and higher trophic levels than the larger species (Zervoudaki et al. 2007).

Oithona nana was the dominant small copepod species all year round, which is in line with previous studies (Temperoni et al. 2011) performed at the EPEA station with the same $67 \mu\text{m}$ mesh. It has been demonstrated that the abundance of this species can be underestimated in more than 96% of samples when a $220 \mu\text{m}$ mesh is used (Di Mauro et al. 2009). The permanent occurrence of *O. nana* is probably related to its ability to consume a wide range of food particle sizes from microphytoplankton to microbial heterotrophic components and copepod nauplii (Lampitt 1978; Atienza et al. 2006; Madsen et al.

2008; Böttjer et al. 2010). Therefore, its populations would not be limited by seasonal changes in food availability.

Larvaceans were the second most important components in the <1 mesozooplankton size class, with dominance of *Oikopleura dioica* all year round. It has been recently demonstrated that the abundance of individuals smaller than $1,000 \mu\text{m}$ in length was underestimated by one order of magnitude when a coarse mesh ($220 \mu\text{m}$) was used in comparison with a finer mesh ($67 \mu\text{m}$) (Di Mauro et al. 2009). This is because a substantial part of the larvacean community is within the micro size fraction with only 4% on average represented by adults (Jaspers et al. 2009 and references therein). Consequently, the larvacean community estimates in most of the zooplankton studies are frequently biased given that coarse meshes are typically used in the sampling.

The highest abundances of larvaceans were recorded in summer, coincident with the maximum of picophytoplankton biomass. It is known that *O. dioica* may remove prey ranging in size from fine

colloidal ($<0.2 \mu\text{m}$) to pico- and nanoplankton ($<30 \mu\text{m}$) (Deibel & Lee 1992; Flood et al. 1992; Tönnesson et al. 2005). The high growth rates of larvaceans allow them to respond faster than copepods to favourable conditions of phytoplankton blooms (Troedsson et al. 2002). However, it has been demonstrated that predation by copepods on larvacean eggs and juveniles could limit the larvacean populations (Lopez-Urrutia et al. 2004). The summer population of *O. dioica* at the EPEA station is mainly represented by adult stages and it has been suggested that predation on early stages by copepods could be the main reason for the absence of juvenile larvaceans (Capitanio et al. 2008). During summer, the chaetognath *Sagitta friderici* also exhibited its highest abundance consisting mainly of juveniles from stage 0 and 1 (Daponte et al. 2004). It is well known that only older chaetognaths prey upon appendicularians (Purcell et al. 2004).

Multivariate analysis allowed the identification of two main periods during the study: winter–spring and summer, separated by the transitional autumn season. From the BEST analysis the environmental factors most closely associated with these temporal patterns were mainly the bottom temperature and the picophytoplankton concentrations.

The winter–spring period was characterized by the lowest temperatures in the bottom layer (and also on the surface). This is probably associated with the high nutrient input typical of this mixing period (Carreto et al. 1998), which certainly favour the development of the main phytoplankton bloom of the year. In fact, the highest concentrations of both Chl-*a* and microphytoplankton were recorded during this period. In contrast, picophytoplankton values were low. The occurrence of mostly herbivorous components such as the copepods *Calanoides carinatus* and *Ctenocalanus vanus* and lamellibranch larvae suggests the dominance of a classical food web. Both copepod species are good indicators of highly productive cold waters in frontal and upwelling systems (Santos & Ramírez 1991; Valentín & Monteiro-Ribas 1993; Sabatini & Martos 2002). A strong increase in the abundance of herbivorous lamellibranch larvae was also observed in winter–spring. Although these larvae were not identified to species level, they probably belonged to *Mytilus platensis*, beds of which are distributed in the EPEA area (Bremec & Lasta 1998). A marked synchrony in the emission of gametes with peaks of reproductive activity during September and October (Penchaszadeh 1980) has been reported for *M. platensis* in the study area. *Noctiluca scintillans* was the dominant predator (fish larvae were not included in this study) during this season, in concurrence with high densities of microphytoplankton and copepod eggs,

which are among its main prey (Sato et al. 2010). In September 2000, just before its annual maximum, *N. scintillans* exhibited the lowest mean diameter (Sato et al. 2010), indicating a period of intensive reproduction probably related to high food availability. When food is abundant, *N. scintillans* has a strong tendency to produce the well-known red-tide phenomena with large mass aggregations on the sea surface (Uhlig & Sahling 1990; McLeod et al. 2012).

The warmer summer period was characterized by a strongly stratified water column and the phytoplankton biomass mostly represented by the nano- and picophytoplankton fractions. The latter attains its maximal values in this season. These findings and the concurrent dominance of the microbial filter-feeders *O. nana*, *Paracalanus* spp., *O. dioica* and *Penilia avirostris* suggest the occurrence of a well-developed microbial food web in the warmest period of the year. The contribution of the appendicularian *O. dioica* to the summer group ($>3,000 \text{ ind m}^{-3}$; Capitanio et al. 2008) is almost certainly linked to the high availability of microbial components during this season. As previously mentioned, these tunicates are major pico- and nanoplankton consumers.

The co-dominance of *O. nana* and *P. avirostris* observed in summer at the EPEA station has also been reported in Mediterranean waters (Katechakis et al. 2004) and explained by their different niche allocation. *O. nana* has a narrower prey range, selecting motile organisms such as ciliates and occasionally dinoflagellates, whereas *P. avirostris* grazes mostly on small flagellates, dinoflagellates and diatoms. Both species can also have an enhancing effect on the bacterial community, probably due to the combination of the release of organic matter due to sloppy feeding and to complex trophic cascade effects (Atienza et al. 2006). Accordingly, in our study, the high peaks of *O. nana* and *P. avirostris* recorded in February and January, preceded the annual maximum of picophytoplankton. Members of Paracalanidae, very abundant during this season, are also able to ingest nanoplanktonic organisms at high rates (Calbet et al. 2000). Intensive reproduction of the small copepods *O. nana* and *Paracalanus* spp. took place in summer, as indicated by peaks of their eggs and nauplii. This is probably related to the known reproductive cycle of small copepod species in temperate seas (Pittois et al. 2009), which is positively controlled by temperature (Vidal 1980; Uye & Shibuno 1992). The similarity between the zooplankton succession observed in our study and that observed in other studies from temperate coastal regions is remarkable. The dominance of microbial filter-feeding cladocerans and larvaceans during the warmer season is a common feature in coastal waters of the Mediterranean (Ribera d'Alcalá et al. 2004)

and the Aegean and Black Seas (Siokou-Frangou et al. 2004) as well as in the Northeast Atlantic (Rodríguez et al. 2000). During the cold period, the assemblages are also dominated by cold-water herbivorous copepods (Siokou-Frangou et al. 2004). The occurrence of high densities of lamellibranch larvae has also been reported during late winter–early spring in Mediterranean areas and related to the availability of phytoplankton sinking from the water column after the winter–spring bloom (Ribera d'Alcalá et al. 2004 and references therein).

The incorporation of an adequate mesh size in sampling allowed us to obtain a better understanding of the zooplankton community structure in coastal waters of the Argentine Sea. The outstanding dominance of small components as shown here has been reported for other temperate and cold regions (Zervoudaki et al. 2007; Di Mauro et al. 2009; Pittois et al. 2009; Ward et al. 2012). The important trophic coupling between small mesozooplankton and the microbial components during the warmer season, as suggested in this study, has important implications for higher trophic levels, especially those including small pelagic fishes, e.g. early developmental stages of small copepod species are key prey for first feeding larvae of anchovy (*Engraulis anchoita*) (Viñas & Ramírez 1996). With a biomass fluctuating between one and six million tons (Hansen 2004), *E. anchoita* plays a key role in the marine ecosystem as a main component of the diets of commercially important fish such as hake, as well as of those of marine mammals and sea birds (Leonarduzzi et al. 2010 and references therein).

In a study of the diet of anchovy larvae performed at the EPEA station during the same period, it was observed that the highest feeding incidence occurred in spring (Sato et al. 2011). Most of the larvae, corresponding to first-feeding larvae (<6.9 mm length), preyed mainly (76%) on the early stages of small copepods. Their highest growth rates were also recorded in spring, without a clear relationship to temperature (Leonarduzzi et al. 2010). Other factors such as food availability might influence growth. However, it is rather surprising that the maximal abundance and the highest growth rate of anchovy larvae did not match the highest zooplankton abundances recorded at the EPEA station. Apparently, the mean field values of prey items recorded in spring, in the order of 7,600 early stages of copepods (eggs + nauplii) and 4,800 small copepods (adults + copepodites) per m³, would be adequate to assure maximal growth rates of larvae. Moreover, the spawning spreading over the growing zooplankton season (from spring to summer) in an area of moderate productivity would guarantee a prolonged

period of high food availability favourable to larval growth and survival.

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