

# Spatial patterns of mesozooplankton distribution in the Southwestern Atlantic Ocean (34°–41°S) during austral spring: relationship with the hydrographic conditions

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The mesozooplankton community was analysed in a large region of the Argentine Shelf (34°–41°S) on the main spring spawning ground of the anchovy (*Engraulis anchoita*), and its spatial pattern was related to the hydrographic conditions. Copepods smaller than 1 mm dominated the community. Three faunistic areas were identified by cluster analysis: northern coastal area (NCA), southern coastal area (SCA), and shelf area (SA), each with distinct physical conditions. The NCA, influenced by the Río de la Plata estuary, had relatively high temperature, the lowest salinity, and the highest stratification values. The SCA had the highest salinity and a vertically homogeneous water column. The SA, vertically stratified, was influenced by the Río de la Plata estuary and by Subantarctic shelf waters and had the lowest temperature values and the greatest depths. Canonical correlation analysis was used to analyse the relationship between zooplankton and physical variables and four zooplankton assemblages were identified. Group A included the copepods *Calanus australis*, *C. simillimus*, *Clausocalanus brevipes*, *Centropages brachiatus*, *Drepanopus forcipatus*, *Oithona atlantica*, and *O. helgolandica*, and was preferentially distributed in the SA. Group B, composed of the copepods *Acartia tonsa* and *Corycaeus* spp. and the cladoceran *Pleopis polyphemoides*, showed a strong preference for the NCA. Group C included *Labidocera fluviatilis*, *Ctenocalanus vanus*, *Paracalanus* spp., *Calanoides* cf. *carinatus*, *Euterpina acutifrons*, *Oithona nana*, and the cladoceran *Evadne nordmanni*, and was preferentially distributed in coastal areas (NCA and SCA). Group D only included the cladoceran *Podon intermedius* and was mainly located in high salinity waters of the SCA. Small, omnivorous, fast-reproducing species (groups B, D, and most of C) are better adapted to warmer variable and less productive coastal areas, whereas larger herbivorous species (most of group A) seem to better exploit colder stratified and more productive shelf waters. The mesozooplankton community provides adequate food for *E. anchoita* larvae in coastal areas and for adults in shelf waters.

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## Introduction

In the Argentine Sea, the abundance and distribution of most zooplankton taxa have been studied in relation to the main water masses of the region (see reviews of Boltovskoy, 1981; Boltovskoy, 1999). Among the dominant groups, copepods and cladocerans are the most widely studied (Ramírez, 1966, 1969, 1981; Ramírez and De Vreese, 1974; Ramírez and Pérez Seijas, 1985; Santos and Ramírez,

1991; Fernández Aráoz *et al.*, 1994). Nevertheless, there are few analyses of the zooplankton community as a whole (Fernández Aráoz *et al.*, 1991; Ramírez and Santos, 1994; Viñas *et al.*, 2000, 2002) and its role in pelagic foodwebs.

Fish populations can be affected by variations in the zooplankton community, with important economic consequences (Mann, 1993). This is particularly significant in the case of small pelagic species that are part of short food chains based on zooplankton (Hunter and Alheit, 1995).

*Engraulis anchoita* (Engraulidae), the most abundant pelagic fish in the Argentine Sea, has a wide latitudinal distribution (24°–48°S), from shallow coastal areas to the continental slope. It feeds on zooplankton throughout its entire life cycle (Angelescu, 1982; Viñas and Ramírez, 1996; Pájaro, 1998). South of 34°S, at least two distinct populations occur, separated at approximately 41°S. The northern stock, or Buenos Aires province stock, undergoes annual migrations: during winter it is found in the northern part of its distribution area, in spring it moves to the south along the Buenos Aires province coast where it reproduces, then disperses into outer shelf waters during summer to feed, and returns again to northern waters in winter (Hansen and Madirolas, 1996; Cousseau and Perrotta, 1998).

On the Buenos Aires Shelf, several studies suggest the presence of three productive systems – coastal, shelf, and shelf break or Malvinas – (Ramírez *et al.*, 1973; Carreto *et al.*, 1981, 1986) separated by two semi-permanent fronts: coastal and shelf break. The coastal system has depths of less than 50 m and a vertically homogeneous water column throughout the year. Chlorophyll *a* and nitrate concentrations are generally low. The continental shelf system, under the influence of Subantarctic waters transported by the Malvinas Current, exhibits seasonal vertical stratification and two defined chlorophyll *a* maxima – in spring and fall. The Malvinas system is influenced by the shelf break front and has high phytoplankton densities in summer and fall (Carreto *et al.*, 1995).

Coastal water masses show great variability, as they are modified by the continental discharge of the Río de la Plata, Colorado, and Negro rivers, and by high salinity waters moving from the south (Guerrero and Piola, 1997). North of 38°S, the major hydrographic feature is the Río de la Plata estuary, the second most important estuary in South America, with a mean discharge of 20 000–25 000 m<sup>3</sup> s<sup>-1</sup> (Framiñan and Brown, 1996). The interaction of low salinity waters with oceanic water masses creates a strong front that shows large temporal and spatial variability. The dynamics of upper layer water discharging over the continental shelf are mainly driven by wind stress (Guerrero *et al.*, 1997). High concentrations of ichthyoplankton, zooplankton, and fish have been detected in the estuarine front (Hansen and Madirolas, 1996; Lasta and Acha, 1996; Viñas *et al.*, 2002). This system is characterized by a high primary productivity, driven mainly by the nutrient input from the river and by the high vertical stability of the water column (Carreto *et al.*, 1986). South of 39°S, El Rincón area (39°–40°30'S) is characterized by an external sector influenced by high salinity shelf waters moving northeast from the San Matías Gulf, and a coastal region with dilute waters due to the discharge of the Colorado and Negro rivers (Guerrero and Piola, 1997).

As part of the “*Engraulis anchoita* Assessment Project” of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Argentina, our objective is to describe the mesozooplankton community of the Buenos Aires

province using multivariate techniques, relate the community structure to the hydrographic conditions, and discuss its potential availability for *E. anchoita* during its spring spawning period.

## Materials and methods

The study area included coastal and shelf sectors of the Buenos Aires province between 34°S and 41°S up to a depth of approximately 140 m (Figure 1). Samples were collected on a cruise carried out during 14–23 October 1999 on board RV “Dr. Eduardo Holmberg” using a PaïroVET net (220 µm mesh). Vertical tows were taken at 87 stations (Figure 1) from a depth near the bottom to the surface and filtered water was estimated by means of a mechanical flowmeter. Samples were preserved in 5% formalin (in seawater) for further analyses. Data on temperature, conductivity and pressure of the water were obtained using a CTD (Sea Bird 19). To analyse the stratification of the water column, Simpson’s stability index (Simpson, 1981) was calculated at each station. A value of 40 J m<sup>-3</sup> was selected as the limit between homogeneous and stratified waters (Martos and Sánchez, 1997). Contours of temperature, salinity, and stratification were produced from gridded data using the kriging method.

All mesozooplankton taxa present in the samples were identified and enumerated under a compound microscope. For this purpose, a subsample was obtained from each sample. Its volume was determined according to the density of organisms in the original sample to include at least 100 adult individuals of the dominant copepod. Copepods and cladocerans were identified to the lowest taxonomic level possible (Ramírez, 1966, 1969; Ramírez and De Vreese, 1974; Björnberg, 1981; Boltovskoy, 1981, 1999). Immature copepod stages were grouped as “copepodites”. All copepods (adults and copepodites) in the subsample were measured under magnifier/microscope and classified in three

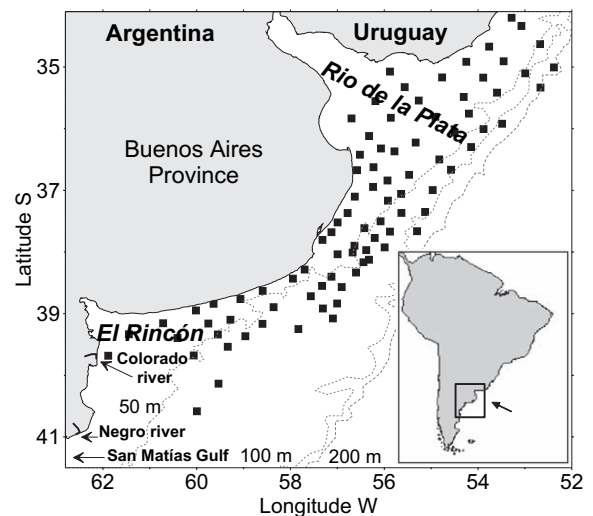


Figure 1. Study area and sampling stations.

size classes of total length: <1 mm, 1–2 mm, and >2 mm. The abundances of the three groups in coastal and shelf waters were compared using the Mann–Whitney non-parametric test.

Biological data were transformed as  $\ln y = \ln(x + 1)$  and cluster and canonical correlation analyses were applied. Species present in less than 10% of the samples and copepodites were excluded from these analyses. Cluster analysis was used to define faunistic areas (groups of stations) using squared Euclidean distance and Ward's linkage method (Johnson and Wichern, 1998). Clusters were represented by means of dendrograms and groups of stations were plotted spatially as faunistic areas (FA).

Canonical correlation analysis (Digby and Kempton, 1989) was used to study the relationship between zooplankton and physical variables (depth, stratification, surface and bottom temperature, and salinity). Stations where both zooplankton and environmental data were collected were selected for this analysis (53 stations). To balance the number of observations and the number of biological variables to be analysed, only taxa identified to the species/genus level were included (copepods and cladocerans). To identify the ecological preferences of the taxa assemblages defined by canonical correlation analysis, the average relative abundances of the species included in the assemblages were calculated for each FA.

Maps of the distribution of eggs, larvae, and adults of *E. anchoita* were produced with data from the same research cruise provided by Pájaro and Hansen.<sup>1</sup> Ichthyoplankton data were obtained from the same PairoVET samples used to estimate zooplankton abundance. All anchovy eggs and larvae present in the samples were enumerated. The abundance of adults of *E. anchoita* was derived from acoustic measurements, as in Hansen and Madirolas (1996). The relationship between zooplankton and *E. anchoita* is discussed.

## Results

Surface temperature ranged between 12°C and 18°C (Figure 2a). Maximum values occurred in the Río de la Plata estuary and El Rincón coastal area. Several thermal fronts occurred associated with the boundary between continental and shelf water masses, and were located between 37°S and 38°S (16–13°C) in the mouth of the estuary (18–15°C) and in the El Rincón area (16–13°C). Bottom temperature varied between 16.5°C and 7°C (Figure 2b), decreasing gradually towards the slope. Warmer waters were restricted to the coast and shelf waters extended further north. Maximum values were observed in the El Rincón area (16.5°C) and in the continental slope at 35°S.

Surface salinity ranged between 16 and 34.2 (Figure 2c). The estuary, where the minimum values occurred, discharged to the south, influencing the continental shelf from 34 to 38°S. The highest salinity values were observed in the El Rincón area (34.2). Bottom values varied between 25 and 35 (Figure 2d), and shelf waters (33.5–33.8) penetrated deeper to the north. High salinity values persisted in El Rincón and another maximum was recognized in the northern part of the area.

The water column was highly stratified in the Río de la Plata estuary and in the northern slope area. The line of  $\Phi = 40$  shows the boundary between homogeneous and stratified waters (Figure 2e). South of 38°S, this line follows the 50-m isobath, defining a broad homogeneous area in El Rincón. The northern part of the study area was stratified both in temperature and salinity, while south of 38°S stratification was only due to temperature gradients (Figure 2f).

A total of 27 species/taxa were identified. Because of their abundance (Table 1) and wide distribution (not shown), eight taxa dominated the mesozooplankton community: the copepods *Calanus australis*, *Ctenocalanus vanus*, *Clausocalanus brevipipes*, *Oithona nana*, *O. helgolandica* (= *similis*), *Paracalanus* spp., the cladoceran *Podon intermedius*, and the appendicularians.

Copepods smaller than 1 mm were numerically dominant throughout the study area, with maximum densities in the Río de la Plata estuary, El Rincón area, and mid-shelf waters (Figure 3). The abundances of the three size classes were significantly different ( $p < 0.001$ ) in coastal and shelf areas. Maximum densities of the three classes were detected in the mid-shelf.

Three groups of stations resulted from the cluster analysis (distance of 30%) (Figure 4a). These groups led to the formation of three clearly separated faunistic areas (Figure 4b): (i) the northern coastal area (NCA) extended between 34°S and 38°S and from the coast to the 50-m isobath, (ii) the southern coastal area (SCA) included the El Rincón area and extended from 38°S to 41°S in coastal areas (<50 m depth), and (iii) the shelf area (SA), from 36°S to 41°S, and from the 50 m isobath towards the slope.

In the canonical correlation analysis, only the first three canonical correlations were significant (Table 2). The first three canonical roots of the physical variables explained 69% of the variance, while the roots corresponding to the combination of biological variables explained 43% of the variance. Table 3 gives the correlations between the original variables (biological and physical) and the first three roots. After selecting the correlations greater than 0.5 (positive or negative values), we can characterize the roots as follows: biological-root1 has information on the copepods *C. australis*, *O. atlantica*, *O. nana*, *O. helgolandica*, *C. similis*, *C. brevipipes*, *C. brachiatus*, *D. forcipatus*, and *E. acutifrons*, while biological-root2 involves *A. tonsa*, *Corycaeus* spp., and *P. intermedius*. Physical-root1 includes depth, surface (ST), and bottom temperature (BT),

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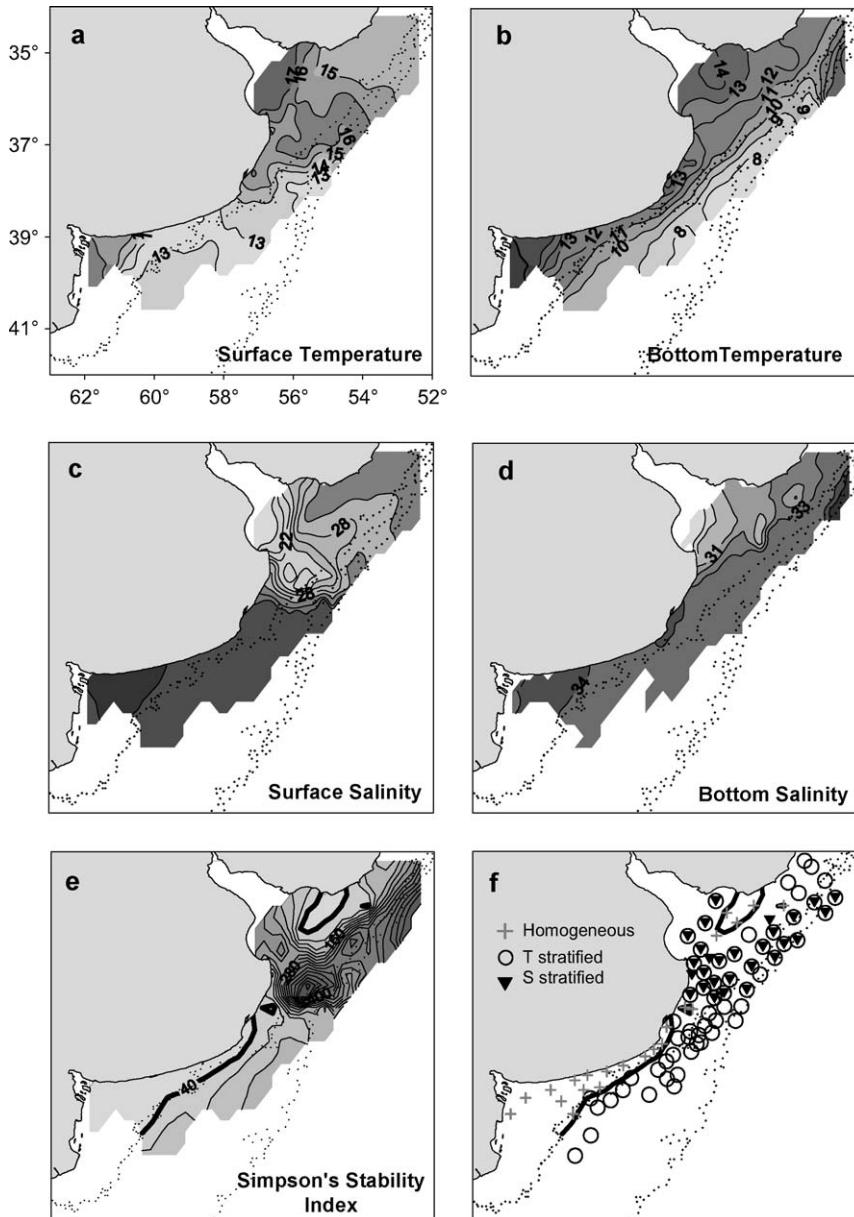


Figure 2. Horizontal distribution of surface and bottom temperature (a and b) and salinity (c and d) in the study area. Distribution of Simpson's parameter (e) and discrimination of the origin of stratification (f).

while physical-root2 has information on surface (SS) and bottom salinity (BS).

When the stations are projected in the plane defined by physical-root1 and physical-root2, the groups originally identified by cluster analysis are again clearly defined (Figure 4c). Taking into account the correlations between the biological and physical roots, and the original variables (Table 3), we can characterize the faunistic areas as follows: the SA can be defined by low temperature values (ST and BT) and the greatest depths. Since there was a strong correlation between physical\_root1 and biologi-

cal\_root1 (Table 2), the SA was also characterized by high densities of the copepods *C. australis*, *O. atlantica*, *O. helgolandica*, *C. simillimus*, *C. brevipes*, *C. brachiatus*, and *D. forcipatus*, and low densities of *E. acutifrons* and *O. nana* (Table 3).

If we consider physical\_root1, the SA showed the characteristics opposite to the NCA and SCA, which were defined by high temperature values (ST and BT), shallower depths, and opposite density trends of the above-mentioned copepod species. Considering physical\_root2, the NCA was opposite to the SCA regarding temperature (ST) and

Table 1. Abundance (individuals m<sup>-3</sup>) of species/taxa in the study area.

Taxa	Mean abundance	Maximum abundance	Standard deviation	% Of stations present
<i>Calanoides</i> cf. <i>carinatus</i> (CCAR)	11.20	196.58	32.33	36.78
<i>Calanus australis</i> (CAUS)	119.28	2 440.68	310.14	65.52
<i>Calanus simillimus</i> (CSIM)	38.57	907.59	129.82	39.08
<i>Labidocera fluviatilis</i> (LFLU)	1.36	30.74	5.14	10.34
<i>Ctenocalanus vanus</i> (CVAN)	140.74	1 852.35	243.64	85.06
<i>Clausocalanus brevipipes</i> (CBRE)	113.56	1 284.25	203.90	64.37
<i>Centropages brachiatus</i> (CBRA)	50.32	1 378.53	173.45	31.03
<i>Drepanopus forcipatus</i> (DFOR)	99.07	1 457.65	232.75	63.22
<i>Acartia tonsa</i> (ATON)	11.66	546.88	62.31	11.49
<i>Paracalanus</i> spp. (PARA)	112.23	1 144.07	191.26	78.16
<i>Corycaeus</i> spp. (CORY)	3.03	37.04	7.25	19.54
<i>Oithona atlantica</i> (OATL)	10.38	117.55	23.83	37.93
<i>Oithona nana</i> (ONAN)	161.77	1 740.74	292.74	83.91
<i>Oithona helgolandica</i> (OHEL)	257.27	3 311.57	465.95	88.51
<i>Euterpina acutifrons</i> (EACU)	6.49	122.96	19.57	27.59
Total copepodites	2 039.77	11 661.02	2 514.40	100
<i>Pleopis polyphemoides</i> (PPOL)	120.92	1 544.91	324.61	34.48
<i>Podon intermedius</i> (PINT)	114.68	761.71	175.77	58.62
<i>Evadne nordmanni</i> (ENOR)	43.33	379.63	73.96	68.97
<i>Podon leuckarti</i>	1.65	64.23	8.02	5.75
Decapod larvae (DLAR)	3.78	27.62	6.15	66.67
Cirripedian larvae (CLAR)	21.05	673.15	90.79	55.17
Bivalve larvae (BLAR)	19.65	280.95	40.45	81.61
Chaetognaths (CHAE)	10.50	161.90	20.65	90.80
Medusae (MEDU)	40.38	405.80	80.39	82.76
Salps (SALP)	0.59	11.30	1.96	18.39
Appendicularians (APPE)	126.61	2 166.67	305.71	96.55
Pteropods (PTER)	16.10	882.84	94.15	71.26

salinity (SS and BS). ST was higher in the NCA, while SS and BS were lower. Concerning the biological variables, in the NCA higher densities of *A. tonsa* and *Corycaeus* spp. and lower values of *P. intermedius* occurred, while in the SCA this trend was the opposite (Table 3).

The physical characteristics detected by the canonical correlation analysis for the SA are related to the presence of typical shelf waters (Figure 2a–d) that have temperature and salinity values ranging between 12.5°C and 14°C and between 33.5 and 33.7, respectively. In this area the water column was stratified both in temperature and salinity north of 38°S and only in temperature south of 38°S. The limit between homogeneous and stratified waters was coincident with the separation of the SA and SCA south of 38°S. The low salinity values detected in the NCA are related to the strong influence of the Río de la Plata river input that generates temperature and salinity fronts. The water column was vertically stratified in temperature and salinity practically throughout this area, where maximum temperature (17°C) and minimum salinity (18) values occurred. In contrast, the SCA was characterized by the presence of thermal fronts, maximum salinity values (34.2), and a vertically mixed water column (Figure 2a–f).

Four groups of taxa/species were identified from the canonical correlation analysis (Figure 5). Group A was composed of the copepods *C. australis*, *C. simillimus*, *C. brevipipes*, *C. brachiatus*, *D. forcipatus*, *O. atlantica*, and *O. helgolandica*, all of which showed a strong preference for the SA (Figure 6).

Group B was composed of the copepods *A. tonsa* and *Corycaeus* spp. and the cladoceran *P. polyphemoides*. In contrast to group A, this group integrated by coastal estuarine species showed a very strong preference for the NCA, as can be seen in Figure 6.

Group C included the copepods *L. fluviatilis*, *C. vanus*, *Paracalanus* spp., *E. acutifrons*, *O. nana*, *C. cf. carinatus*, and the cladoceran *E. nordmanni* (Figure 5). The group consisted of coastal species and was preferentially distributed in areas of wider temperature ranges than group B (Figure 6). The location of *C. vanus* near the origin (Figure 5) indicates its wide distribution. Group D was composed only of the cladoceran *P. intermedius* and was mainly located in high salinity mixed waters of the SCA (Figure 6). Figure 6 also shows the preference of other taxonomic groups for a particular faunistic area. While salps and pteropods preferred the SA, cirripede larvae were almost

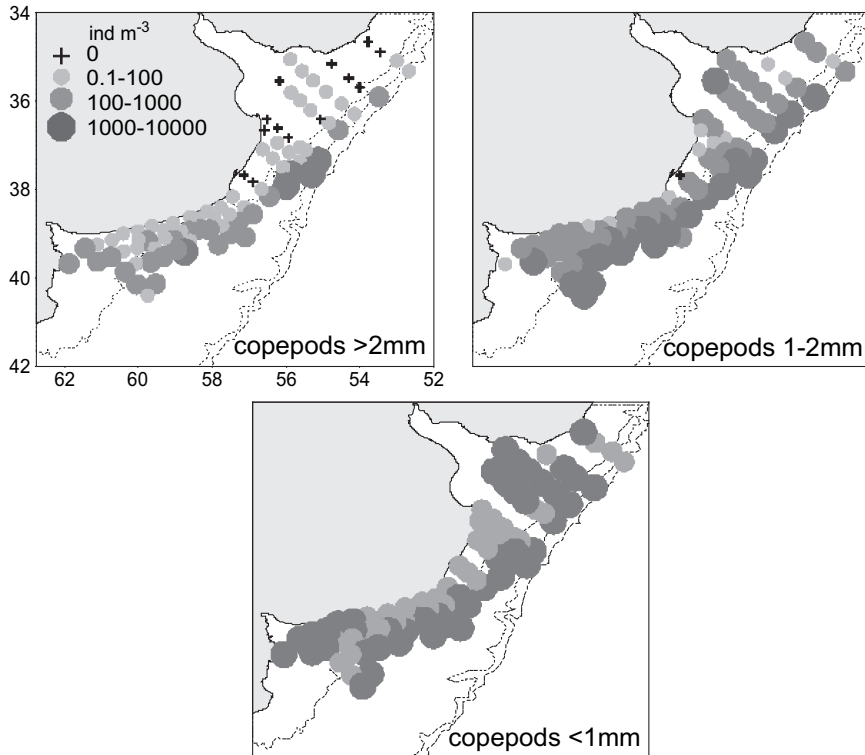


Figure 3. Distribution and abundance (individuals  $m^{-3}$ ) of the three copepod size classes.

exclusively found in the NCA. Other groups (chaetognaths, medusae, decapod larvae, appendicularians, bivalve larvae) showed a strong preference for coastal regions, as they were found in both the NCA and SCA.

*E. anchoita* spawning was concentrated in coastal areas, with the highest densities of eggs and larvae occurring between 36°S and 39°S (Figure 7a, b). In the northern part of the study area, high concentrations were also detected, restricted to salinities greater than 25. Adults were mainly located between 40- and 60-m depth (Figure 7c) within the study area.

## Discussion

### Faunistic areas

A cross-shore zonation was identified in the present study with a shelf system (SA) clearly separated from a coastal one in both the northern (NCA) and southern (SCA) parts of the study area. This concurs with previous studies of the distribution of zooplankton on the Buenos Aires Shelf (Fernández Aráoz *et al.*, 1991, 1994; Santos and Ramírez, 1991; Viñas *et al.*, 2002). When we compare the zooplankton faunistic areas identified in this study with those described by these authors north of 38°S, the shelf area shows a persistent pattern of species distribution and composition. In contrast, in the coastal area the spatial limits and the species present seem to be more variable,

probably due to the higher variability in the physical conditions and nutrient concentrations related to changes in the Río de la Plata river input and wind patterns. This zonation is also coincident in the northern part, with the productive systems described by Carreto *et al.* (1995) based on the distribution of physical variables, nitrate concentrations, and phytoplankton biomass. The zooplankton distribution found in this study is consistent with these productive conditions, as explained further below.

### Dominant taxa, copepod size classes, and community structure

The copepods *C. australis*, *C. vanus*, *C. brevipes*, *O. nana*, *O. helgolandica*, *Paracalanus* spp., and copepodid stages, together with the cladoceran *P. intermedius* and appendicularians dominated the mesozooplankton community. The dominance of these taxa had already been observed in smaller sections of the Buenos Aires province shelf by Ramírez (1981), Ramírez and De Vreese (1974), Esnal (1981), Fernández Aráoz *et al.* (1991, 1994), and Viñas *et al.* (2002). The present study provides the broadest spatial coverage of the Buenos Aires province coastal waters and more detailed information on the abundance and distribution of dominant groups, as well as of numerically less important organisms, thus contributing to a better understanding of the biodiversity of the area.

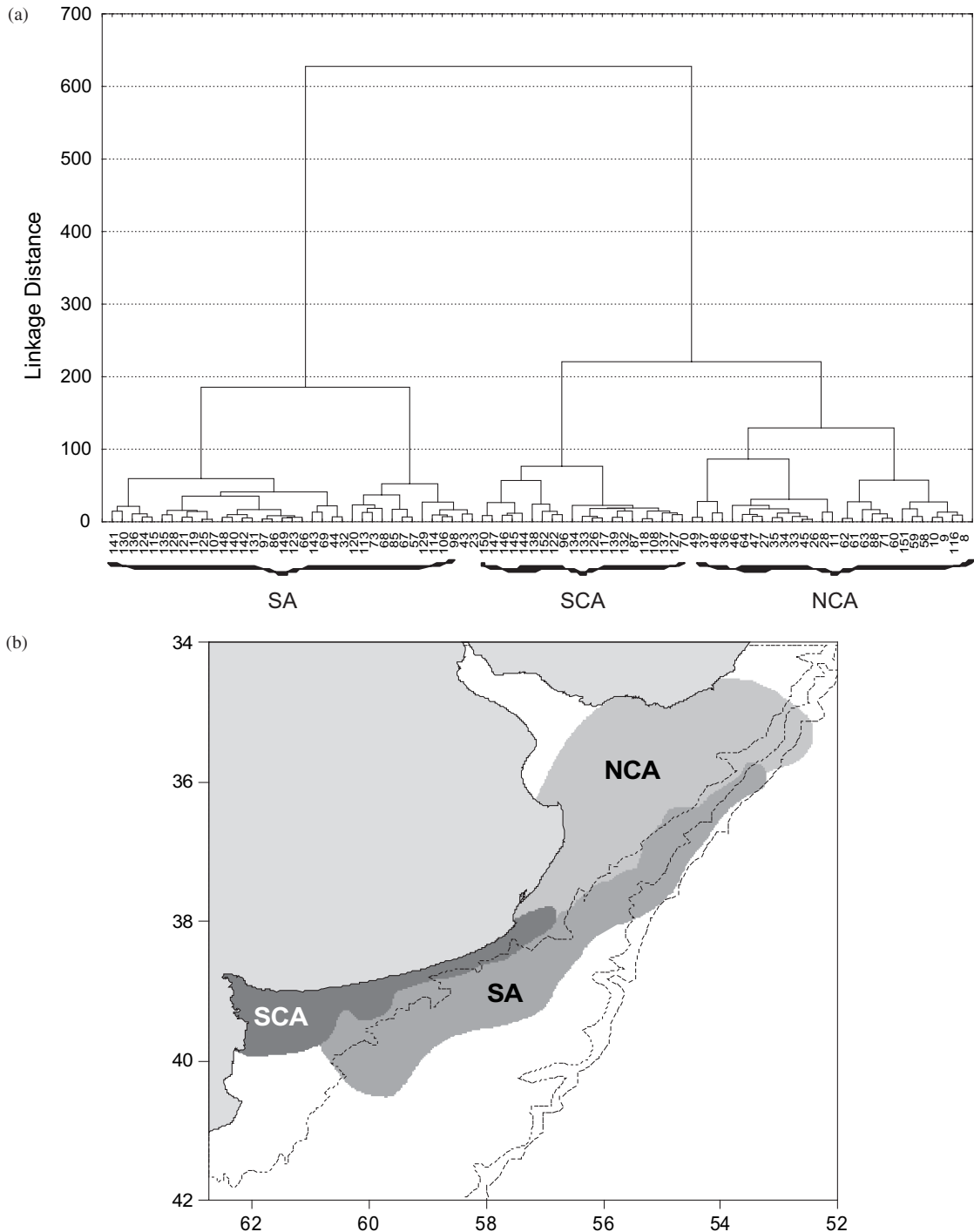


Figure 4. (a) Dendrogram showing station assemblages, (b) geographical location of the faunistic areas identified by cluster analysis, (c) projection of the stations in the first two physical roots. The faunistic areas defined in the cluster analysis are indicated as (SA) shelf area, (SCA) southern coastal area, and (NCA) northern coastal area.

The copepod community was dominated by individuals smaller than 1 mm throughout the study area. Within this size class, *O. helgolandica* was the most widely distributed and abundant copepod, with maximum densities in mid-

shelf waters. This species is probably one of the most abundant copepods in neritic temperate oceans (Sabatini and Kjørboe, 1994). Its wide distribution is explained in terms of its limited specialization. Populations fluctuate

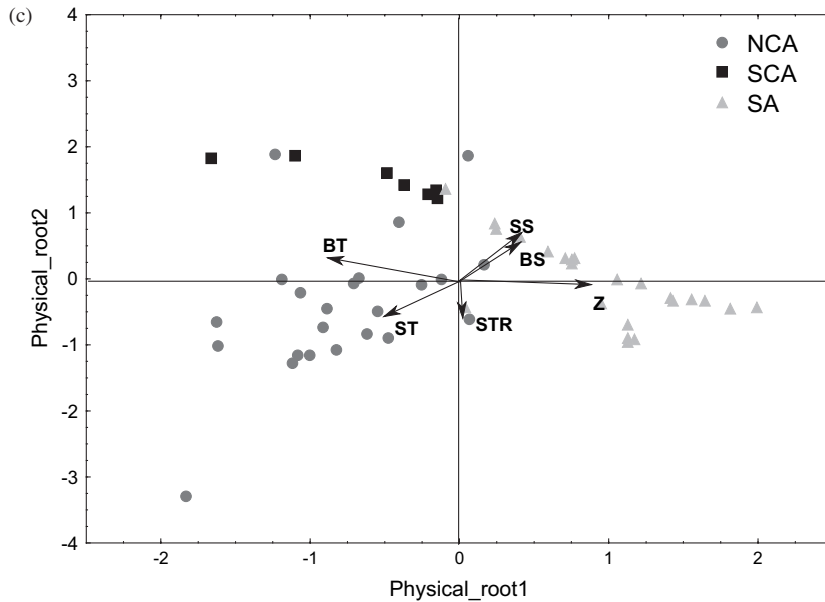


Fig. 4. (continued)

slowly due to the species low feeding, growth, reproductive, and mortality rates. These characteristics, together with the ability to survive under unfavourable conditions, make cyclopoids important stabilizers of planktonic populations (Paffenhöfer, 1993; Sabatini and Kiørboe, 1994).

The highest abundance of the three copepod size classes was observed in stratified mid-shelf waters (> 50 m depth) in areas of high primary productivity (Carreto *et al.*, 1995).

Four zooplankton assemblages were defined in this study. Group A was preferentially located in the SA and was composed mainly of copepods from the Calanidae and Pseudocalanidae families. The dominance of these species in shelf waters has been observed in previous studies (Fernández Aráoz *et al.*, 1991, 1994; Santos and Ramírez, 1991; Viñas *et al.*, 2002) and it is probably due to an affinity for the temperature and salinity ranges, as well as to the high phytoplankton productivity (Carreto *et al.*, 1995). It is known that the distribution of *C. simillimus* and *C. australis* is associated with low temperature and narrow salinity ranges of mid-shelf and outer shelf regions (Ramírez and Sabatini, 2000) and that large herbivorous

species such as these require higher densities of phytoplankton to achieve maximum growth and egg production compared to smaller species (Vidal, 1980; Runge, 1988). Other species in group A from the family Pseudocalanidae (*D. forcipatus*, *C. brevipes*) are also preferentially herbivorous (Mauchline, 1998), thus the SA would be more appropriate than coastal areas for their populations to develop. In contrast, *O. helgolandica* and *O. atlantica* are omnivorous and their inclusion in this group is probably related to their preference for colder stratified shelf waters (Sabatini and Martos, 2002).

Group B was primarily located in the NCA and included the cladoceran *P. polyphemoides* and the copepods *A. tonsa* and *Corycaeus* spp., described as typical of coastal regions (Ramírez, 1969). These species have acquired adaptations to survive in coastal environments. For example, *A. tonsa* has developed an omnivorous diet (Ambler, 1986), high reproductive rates dependent mainly on temperature (Ambler, 1986), and a high tolerance to salinity changes. In addition, *P. polyphemoides* and *A. tonsa* can produce resting eggs under unfavourable conditions (Ramírez and

Table 2. CCA statistics. Physical-root: significant canonical roots of the physical variables, Biological-root: significant canonical roots of the biological variables.

Canonical root	Chi-square tests with successive roots removed				Variance extracted (proportions)	
	Canonical R	$\chi^2$	d.f.	p	Physical-root	Biological-root
1	0.963240	244.2590	114	0.000000	0.374304	0.264158
2	0.850660	141.7380	90	0.000423	0.248807	0.098648
3	0.765308	91.5844	68	0.030058	0.063780	0.071077



Table 3. Root structure. Correlation between biological and physical variables and the first three (significant) canonical roots.

Original variables	Canonical roots		
	1	2	3
<b>Biological</b>			
<i>C. carinatus</i>	-0.237	0.244	-0.540
<i>C. australis</i>	0.804	-0.030	0.106
<i>C. similimus</i>	0.707	-0.202	-0.179
<i>L. fluviatilis</i>	-0.255	0.174	-0.236
<i>C. vanus</i>	-0.150	0.002	-0.125
<i>C. brevipes</i>	0.724	-0.073	-0.220
<i>C. brachiatus</i>	0.645	-0.164	-0.085
<i>D. forcipatus</i>	0.674	-0.128	-0.011
<i>A. tonsa</i>	-0.457	-0.621	0.262
<i>O. atlantica</i>	0.644	-0.230	-0.235
<i>O. nana</i>	-0.549	0.305	0.103
<i>O. helgolandica</i>	0.669	-0.095	-0.326
<i>Paracalanus</i> spp.	-0.309	0.067	-0.437
<i>E. acutifrons</i>	-0.501	0.131	-0.254
<i>Corycaeus</i> spp.	-0.563	-0.599	-0.016
<i>P. polyphemoides</i>	-0.412	-0.436	-0.303
<i>P. intermedius</i>	0.063	0.640	0.408
<i>E. nordmanni</i>	-0.342	-0.063	0.099
<b>Physical</b>			
ST (surface temperature)	-0.522	-0.502	-0.532
SS (surface salinity)	0.488	0.705	-0.157
BT (bottom temperature)	-0.892	0.398	-0.187
BS (bottom salinity)	0.487	0.645	0.059
STR (stratification)	0.006	-0.410	-0.031
Z (depth)	0.838	-0.031	-0.188

De Vreese, 1974; Sabatini, 1990). The high primary productivity (Carreto *et al.*, 1986) and suspended sediment (Framiñan and Brown, 1996) in the Río de la Plata estuary can be exploited by these species.

The highest abundances of the species of group C were found mainly in coastal sectors (NCA and SCA), although they were widely distributed in the study area. This is coincident with previous studies in which most of these species were found in coastal and inner shelf waters (Ramírez, 1981; Fernández Aráoz *et al.*, 1991, 1994; Santos and Ramírez, 1991; Ramírez and Santos, 1994; Viñas *et al.*, 2002). In particular, *C. cf. carinatus* was most abundant in the coastal front between mixed coastal and stratified shelf waters (Carreto *et al.*, 1995), as previously observed by others (Ramírez and Santos, 1994; Ramírez and Sabatini, 2000). However, the species was also abundant in mixed waters of the El Rincón area. Copepods of the genus *Calanoides* are found associated with upwelling regions (Mauchline, 1998), where they have developed migratory behaviour to exploit both stratification and mixing periods. They are also known to inhabit regions of constant mixing, such as coastal areas, where they remain active throughout the year (Mauchline, 1998). The differential distribution of *C. cf. carinatus* in this study would suggest the occurrence of two distinct life strategies, one related to frontal areas with seasonal stratification where the population undergoes diapause in deep waters during unfavourable periods, and another one associated with mixed coastal waters where the species remains active throughout the year. This requires further investigation.

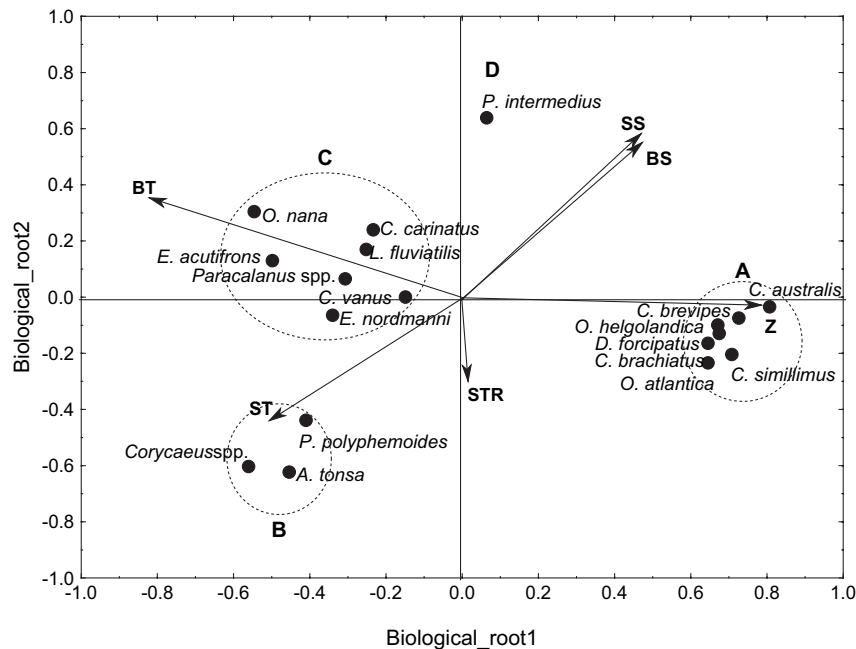


Figure 5. Projection of the species in the first two biological roots.

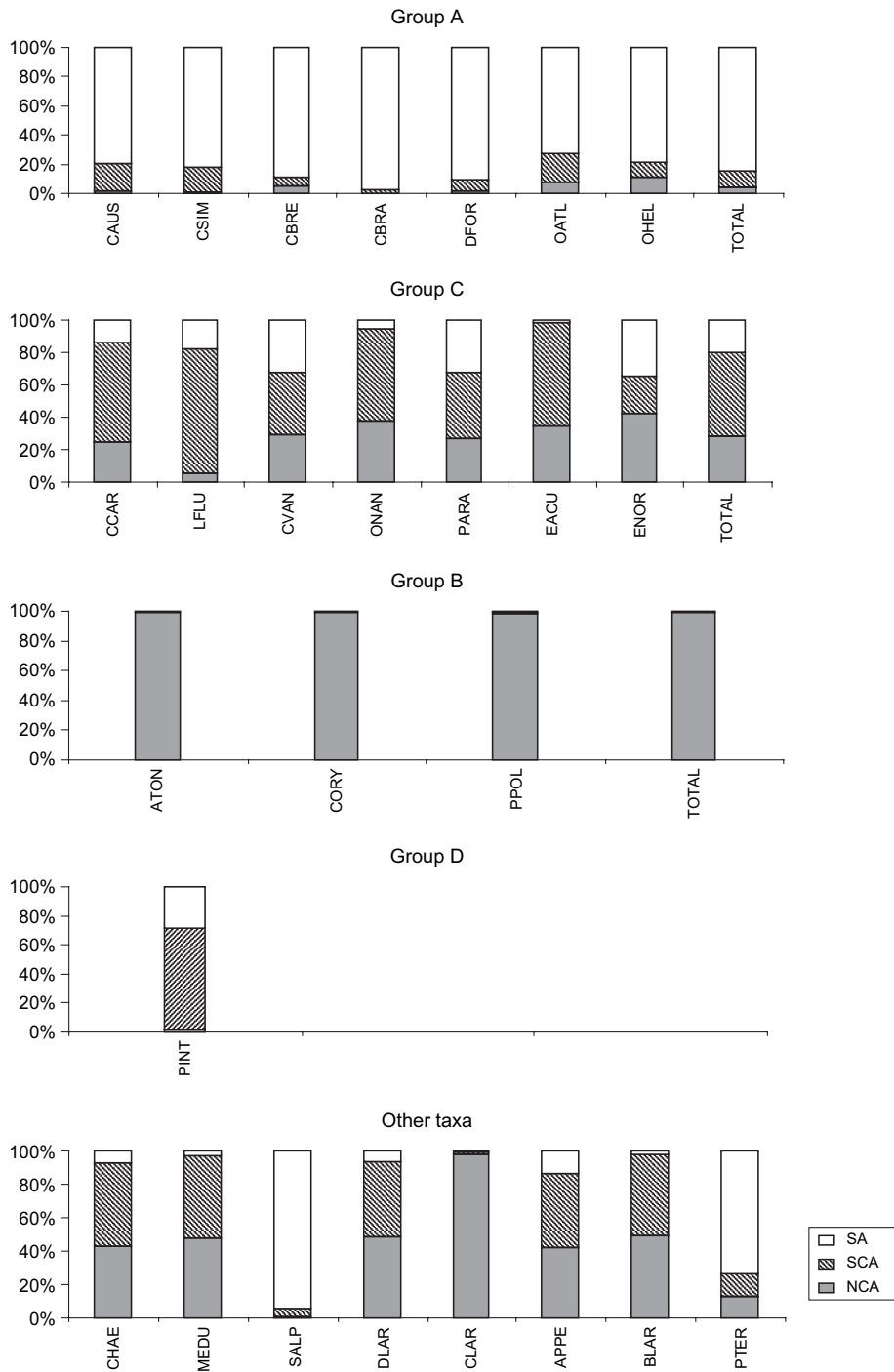


Figure 6. Average relative abundance of the species/taxa of each group (A–D) in each faunistic area (SA, NCA, and SCA) and total percentage for the group. Average relative abundances of other taxa not included in any zooplankton group are also shown (last panel). See Table 1 for abbreviations.

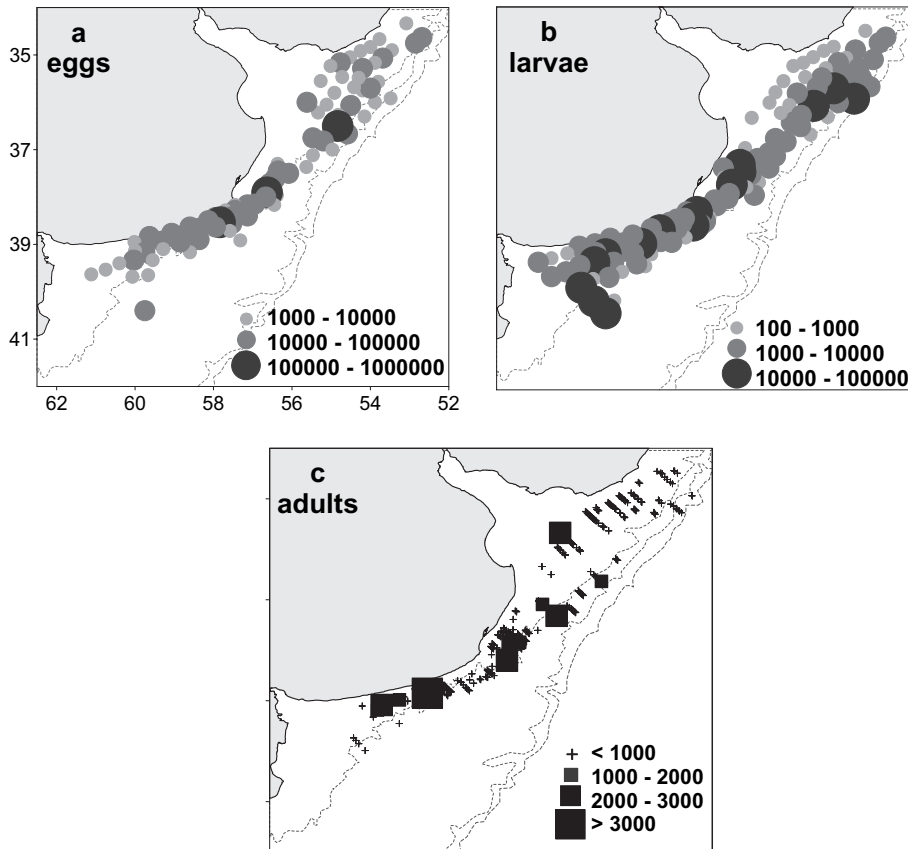


Figure 7. Distribution and abundance of (a) eggs (eggs  $10\text{ m}^{-2}$ ), (b) larvae (larvae  $10\text{ m}^{-2}$ ), and (c) adults (tonnes  $\text{nm}^{-2}$ ) of *E. anchoita*.

Even though Björnberg (1981) characterizes *L. fluviatilis* as a euryhaline species inhabiting waters with salinities lower than 32, in this study it was distributed both in the dilute waters of the Río de la Plata estuary and in the high salinity (>34) area of El Rincón.

Among other taxonomic groups, meroplanktonic larvae and medusae were found in coastal areas consistent with their dependence on benthic phases. The high densities of bivalve larvae identified in the present study can be attributed to the high mussel (*Mytilus edulis platensis*) concentrations near the 50 m isobath along the Buenos Aires province. These organisms reproduce during spring, releasing large densities of larvae (Ciocco *et al.*, 1997).

### Zooplankton—anchovy linkages

Pájaro (1998) proposed that during intense spawning, *E. anchoita* undergoes short migrations towards deep shelf waters to feed and then returns to coastal areas to reproduce. Maximum abundances of anchovy eggs and larvae were detected in coastal areas, where significant densities of small copepods such as *Paracalanus* spp., *O. nana*, *O. helgolandica*, *E. acutifrons*, *Corycaeus* spp., and *A. tonsa* were also recorded. These species reproduce throughout the

year with a constant production of eggs and nauplii, the main prey item of first-feeding larvae of *E. anchoita* (Viñas and Ramírez, 1996). The spatio-temporal co-occurrence of anchovy eggs and larvae and high densities of small copepods have been observed previously in the Río de la Plata estuary (Viñas *et al.*, 2002) and in other coastal areas (Peebles *et al.*, 1996; Coombs *et al.*, 1997; Peebles, 2002).

Biological production may be intensified in areas with physical discontinuities, such as fronts and upwelling processes (Mann, 1993), providing abundant prey for fishes. Kiørboe (1991) suggested that the production of planktivorous fish, as well as the growth and survival of fish larvae, depends primarily on mesozooplankton production at spatio-temporal oceanographic discontinuities. In the NCA, the strong influence of the Río de la Plata estuary results in sharp horizontal and vertical gradients that vary in space and time. Here, the high nutrient supply from the river, together with the vertical stability of the water column, contributes to enhancing primary and secondary production, thus increasing the number of available prey for fish (Carreto *et al.*, 1986; Viñas *et al.*, 2002). It is also likely that prey production is enhanced in warmer coastal waters because of the favourable effect of high temperatures on the reproductive rate of small copepod species (Uye and

Shibuno, 1992; Sautour and Castel, 1995). In addition, Ekman transport towards the coast probably prevents ichthyoplankton from dispersing into less favourable outer areas (Bakun and Parrish, 1991).

The SCA includes the El Rincón area, which is believed to be highly productive due to the occurrence of elevated densities of fish and zooplankton (Macchi and Acha, 1998; Viñas *et al.*, 2000). The circulation in the area is not yet fully understood, but a gyre-like pattern has been detected, which would favour the retention of fish larvae and their prey (Piola and Rivas, 1997).

In summary, the availability of adequate food, the appropriate thermal and saline ranges, the presence of physical discontinuities, and the existence of retention mechanisms make coastal areas in the Buenos Aires province a suitable environment for successful larval fish development. In spring, adult *E. anchoita* feed primarily on calanoid copepods including *C. simillimus*, *C. australis*, and *C. cf. carinatus* (Schwingel and Castello, 1994; Pájaro, 1998). The highest densities of these prey species were located in shelf regions in this study, coincident with adult anchovy distributions. Our results support the hypothesis proposed by Pájaro (1998): during intense spawning, *E. anchoita* undergoes short migrations towards deep shelf waters to feed on larger zooplankton, and then returns to coastal areas to reproduce, where larvae will find appropriate conditions of temperature and food.

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