Potential zooplankton preys (Copepoda and Appendicularia) for *Engraulis anchoita* in relation to early larval and spawning distributions in the Patagonian frontal system (SW Atlantic Ocean)

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SUMMARY: We investigated the spatial distribution of the abundance, biomass and size of zooplankton (nauplii, calanoids, cyclopoids and appendicularians) in relation to the distribution of first-feeding larvae and eggs of *Engraulis anchoita* across the frontal system of Peninsula Valdés. Twelve samples of zooplankton and ichthyoplankton were taken with small Bongo (67 μm) and Pairovet (200 μm) nets during the spring of 2004 along two transects. The total abundance of zooplankton and the chlorophyll *a* concentration were higher in homogeneous waters, while total biomasses were higher in stratified waters. Temperature was negatively correlated with biological variables and was the main factor affecting the zooplankton distribution. In both transects, abundance peaks of first-feeding larvae were detected at coastal stations along with the smallest fraction of zooplankton (<500 μm), while the largest fraction was dominant at the external stations, coinciding with the highest egg abundance. The physical structure of this front generates different levels of food availability for first-feeding larvae. Calanoids (southern transect) and cyclopoids (northern transect) are predominant followed by nauplii and appendicularians. The biomass of zooplankton preys contributes to the carbon transfer to the upper trophic levels and is probably important for the survival and growth of anchovy larvae in this frontal system.

Keywords: southwestern Atlantic Ocean, North Patagonian frontal system, copepods, appendicularians, zooplankton-anchovy linkage.

RESUMEN: Potenciales presas zooplanctónicas (Copepoda y Appendicularia) para *Engraulis anchoita* en relación con las distribuciones de larvas tempranas y de desove en la región frontal patagónica (océano Atlántico sudoccidental). – Se investigó la distribución espacial de la abundancia, biomasa y las tallas del zooplancton (nauplii, calanoideos, ciclopoideos y apendicularias) en relación con la distribución de las larvas en estadio de primera alimentación y los huevos de *Engraulis anchoita* en el sistema frontal de Península Valdés. Se tomaron 12 muestras de zooplancton e ictioplancton durante la primavera de 2004 a lo largo de dos transectos, mediante una red Minibongo (67 μm) y una Pairovet (200 μm) respectivamente. La abundancia total del zooplancton y la concentración de clorofila fue mayor en aguas homogéneas, mientras que la biomasa fue mayor en aguas estratificadas. La temperatura se correlacionó negativamente con las variables biológicas siendo ésta el principal factor que afectó la distribución del zooplancton. En las estaciones costeras de ambos transectos, se encontró la mayor abundancia de larvas en coincidencia con la fracción más pequeña de zooplancton (<500 μm), mientras que la fracción más grande fue dominante en las estaciones externas, en coincidencia con la mayor abundancia de huevos. La estructura física de este frente genera diferente disponibilidad de alimento para las larvas siendo los calanoideos (transecto sur) y los ciclopoideos (transecto norte) predominantes, seguidos por nauplii y apendicularias. La biomasa de dicho alimento zooplanctónico podría contribuir a la transferencia de carbono a los niveles tróficos superiores y esto sería importante para la supervivencia y crecimiento de la anchoita en este sistema frontal.

Palabras clave: océano Atlántico sudoccidental, sistema frontal norpatagónico, copépodos, apendicularias, relación zooplancton-anchoita.

INTRODUCTION

Copepods are considered the most abundant meso-zooplankton group in many pelagic environments (Kiørboe 1998), and along with appendicularians, they are the most important secondary producers (Gorsky and Fenaux 1998, Hopcroft and Roff 1998, Sato *et al.* 2008). Both groups play an important role as consumers of both the phytoplankton and microbial components of food webs. Moreover, they are also preyed on by several pelagic ichthyoplankters (Berggreen *et al.* 1988, Deibel and Lee 1992, Flood *et al.* 1992; Stibor *et al.* 2004, Castro *et al.* 2010). Fish reproduction is linked to plankton production cycles, and larvae, juveniles and adults generally coincide with peaks in zooplankton biomass (Kiørboe 1991, Bollens *et al.* 1992, Hunter and Alheit 1995, Cushing *et al.* 1996). Various factors affect the survival of young fish, and predation and starvation are the main sources of mortality. Hjort (1914) suggested that larval survival might be affected by lack of food during the early stages of external feeding. Various copepod stages are the main component of the diet of many pelagic fish during their ontogenetic development (Last 1980). Therefore, the availability of prey for fish larvae will partially depend on the transference rate of primary producers through copepods.

In frontal areas, biological production may be intensified (Mann and Lazier 1993). The circulation in frontal systems is usually associated with a density difference between two water masses that generates a convergence at the surface or bottom boundary and makes the front an abrupt transition (Largier 1993). The most conspicuous feature in the Patagonian coastal area is the development during spring and summer of a tidal front that extends from 42° to 45°S, north from Peninsula Valdés to Camarones Bay. Its middle position is oriented NE-SW, closely following the isobaths of 75-80 m (Sabatini and Martos 2002). High tidal dissipation rates generate strong vertical mixing in near shore waters that can homogenize the entire water column. Wind stress on the surface layer also contributes to forming and maintaining the homogeneity of the front. This feature, combined with the stratification of shelf waters induced by seasonal surface warming, results in the highly mixed coastal waters being separated from the stratified offshore waters. This structure is maintained until autumn when stratification breaks down (Carreto *et al.* 1986, Glorioso 1987, Acha *et al.* 2004).

Several authors have studied the horizontal and vertical distributions of zooplankton in this front (e.g. Santos and Ramirez 1995, Capitanio and Esnal 1998, Sabatini and Martos 2002). They highlight the high productivity of this system, which supports several commercial target species, such as hake, mackerel and anchovy, among others (Sánchez *et al.* 1997, Bezzi 2000). Anchovy (*Engraulis anchoita*) is the main pelagic species in the Argentine Sea and its range extends from southern Brazil (22°S) to Patagonia (48°S). South of 34°S, at least two populations of *E. anchoita*

occur separately at approximately 41ºS: the northern population and the southern population (Patagonian stock) (Hansen *et al.* 1984). The Patagonian stock spawns during late spring and summer in association with tidal frontal systems, and the spawning area varies between 39063 and 78440 km^2. Whether there are anchovy eggs off Patagonia depends on the formation of these systems, and eggs can reach densities from 425 to 1023 eggs m^{-2} y^{-1} (Sánchez and Ciechomski 1995, Pájaro *et al.* 2009a). However, the annual anchovy larval density, mostly first-feeding larvae, ranges from 84 to 833 larvae m^{-2} (Pájaro *et al.* 2009b). Anchovy is a zooplanktivorous species throughout its life cycle, and therefore its population could play an important role in shaping pelagic food webs (Pájaro 1998). Viñas and Ramirez (1996) and Capitanio *et al.* (1997) studied the stomach contents of first feeding larvae of Patagonian anchovy, and found that appendicularians, nauplii, copepod eggs and small copepods such as *Paracalanus parvus*, *Oithona* spp, *Microsetella norvergica* and *Euterpina acutifrons* were the main food items. Although the spatial distribution of *E. anchoita* populations in the external area of Río de la Plata estuary has been associated with the densities of small zooplankters, such as copepods, cladocerans and appendicularians (Viñas *et al.* 2002, Marrari *et al.* 2004, Capitanio *et al.* 2005), there are still very few studies on the Patagonian anchovy. We investigated the spatial distribution of the abundance, size spectra and biomass of dominant zooplankton (nauplii, calanoids, cyclopoids and appendicularians) in relation to the distribution of anchovy first-feeding larvae and spawners (determined according to egg distributions) in the Peninsula Valdés tidal front. We tested the hypothesis that the zooplankton distribution is influenced by temperature and we analyzed the distribution patterns of some of the potential food preys available for *E. anchoita* in the homogeneous and stratified waters of this front.

MATERIALS AND METHODS

Twelve zooplankton samples were taken during the spring (December) of 2004 along two transects (Fig. 1a) by the Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina. The zooplankton samples were collected with a small Bongo net with a 0.2 m diameter (67 μm) operated at 1 to 1.2 m s^{-1}. A Pairovet net with a mouth diameter of 0.225 m and 220 μm mesh size was used for the anchovy larvae. Small Bongo and Pairovet nets were operated from the bottom to the surface with vertical and oblique tows respectively. A mechanical flowmeter (Hydrobios) was used to measure the volume of filtered water and all samples were fixed on board with 2% formaldehyde. In the frontal area (41°-45°S) vertical continuous conductivity-temperature-depth (CTD) profiles were recorded with a Searbid 19. In order to quantify the stratification at the front, the f parameter of stability (Simpson, 1981) in J m^{-3} was used as a measure of the energy needed to mix the water column. The parameter
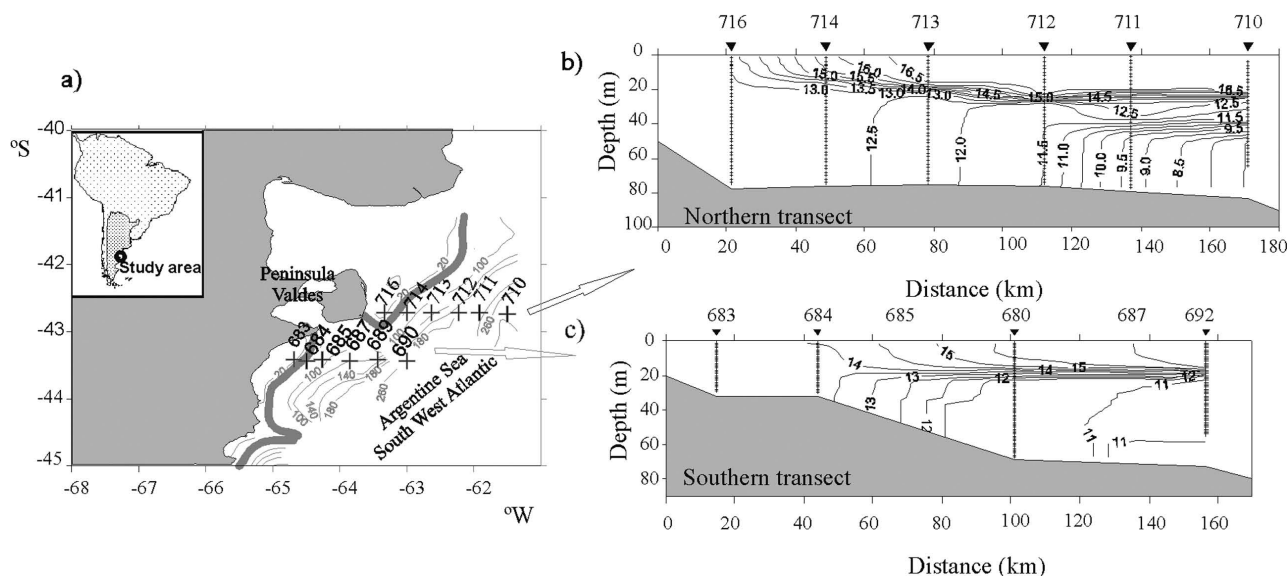
Fig. 1. – a) Location of the sampling stations and distribution of the Simpson Index (Φ). Line represents Φ = 40 J m^{-3}. b) and c) profiles of temperature (°C) in the northern and southern transects respectively.

is defined as follows: $\Phi = g.h - h.\int^{\circ}(\rho - \rho0).Z.dz$ where g is the acceleration of gravity, h is the total depth, ρ is the density of sea water, $\rho0$ is the average density of the water column and z is the depth. These calculations were made with MatLab Software, and a critical value of 40 J m^{-3} was used to separate mixed and stratified waters according to Martos and Sánchez (1997). Temperature profiles were analyzed at each station of the two transects. The surface chlorophyll *a* concentration was estimated from satellite images corresponding to the sampling dates (14 to 17 December 2004), provided by ANTARES and processed according to Buono and Cucchi Colleoni (2009). The appendicularians and copepods (calanoids, cyclopoids and nauplii) present in all plankton samples were separated in the laboratory using a stereoscopic microscope. In addition, those samples that had more than 200 specimens were fractionated. Anchovy eggs and first-feeding larvae were also identified and counted under a binocular-dissecting microscope. Density was calculated for each group and determined for all stations and species by microscopic inspection of subsamples. Between 30 and 50 organisms of each group were measured using an ocular micrometer in order to analyze the size structure of the different groups in each zooplankton sample. In these subsamples, the trunk length (appendicularians), prosome length (calanoids and cyclopoids) and cephalothorax length (nauplii) were measured and extrapolated to the total sample. Using these sizes, the biomass (μg C m^{-3}) of each individual was estimated using the relationships described in Sabatini and Kiørboe (1994), Capitanio *et al.* (2008) and Jasper *et al.* (2009), and then extrapolated to the biomass of each group.

Georeferenced maps showing the position of the front, and temperature profiles were drawn using the Golden Software's Surfer program 8.0. The abundances for each group (cyclopoids, calanoids, nauplii and appendicularians) were compared in the two transects whit a Mann-Whitney nonparametric test. A principal component analysis (PCA) was applied to establish the relationship between biological (total zooplankton, nauplii, cyclopoids, calanoids and appendicularians densities), and standardized environmental (temperature and Simpson index) variables. Statistica 6.0 and InfoStat packages were used for data analysis.

RESULTS

Relationships between zooplankton (copepods and appendicularians) and the environment

The stratified and homogeneous waters of the front were separated according to a critical value of 40 J m^{-3}, taking into account the distribution of the Simpson index (Fig. 1a). In the northern transect, only the coastal station (station 716) was homogeneous (<40 J m^{-3}), and the surface signal of the front was detected at 26 km from the coast with a gradient of 0.25°C/10 km. In contrast, the bottom signal was located at 140 km from the coast (stations 712 and 711) with a gradient of 0.75°C/10 km. In the southern transect, two coastal stations (stations 683 and 684) were homogeneous and both the surface and the bottom signals of the front were recorded at a distance of 70 km, with a gradient of 0.29°C/10 km and 0.54°C/10 km respectively. The temperature of homogeneous waters varied between 13°C and 14°C for both transects, while in stratified waters the temperature varied from 16.5 to 7.5°C and from 16.5 to 11°C (surface to bottom layers) in the northern and southern transects respectively (Fig. 1b, c). The maximum surface (satellite) chlorophyll *a* concentrations (3.5-5.0 mg m^{-3}) were found in homogeneous and transitional waters, mainly in the southern transect. However, stratified waters showed consider-
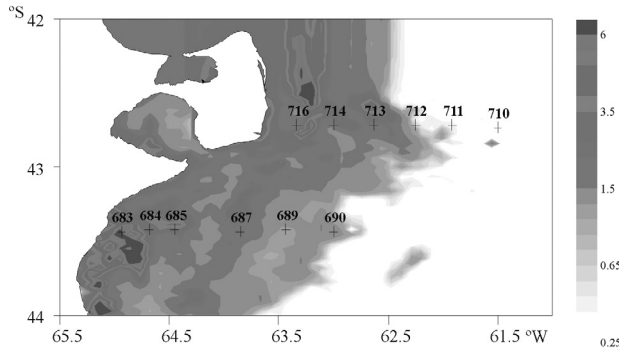
Fig. 2. – Spatial distribution of satellite chlorophyll *a* concentration in the frontal system of Peninsula Valdés. Data provided by ANTARES network (www.antares.ws).
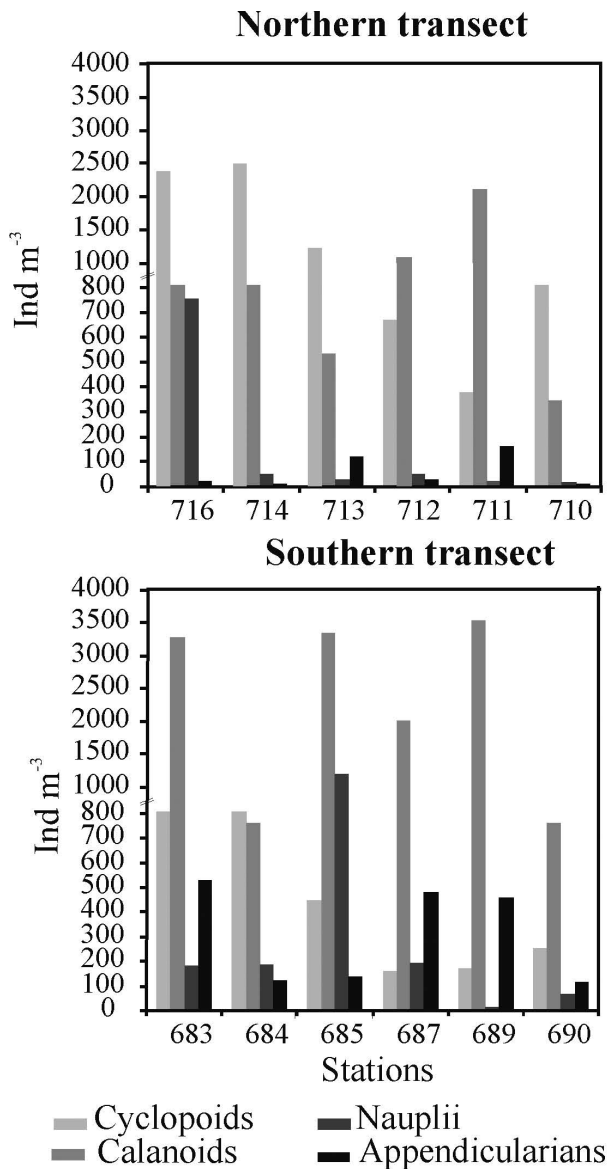

Fig. 3. – Density of cyclopoids, calanoids, nauplii and appendicularians in the northern and southern transects of the frontal system of Peninsula Valdés.

ably lower values, 1.5 mg m^{-3} and 0.3 mg m^{-3} for the southern and northern transects respectively (Fig. 2).

The distribution of calanoids, cyclopoids, nauplii and appendicularians was analyzed in relation to the frontal area. We found two species of cyclopoids, *Oithona helgolandica* and *Oithona nana*, and several calanoid species, *Acartia tonsa*, *Calanoides carinatus*, *Paracalanus parvus*, *Ctenocalanus vanus*, *Centropages brachiatus* and *Drepanopus forcipatus*. Moreover, *Oithona* spp., *C. carinatus*, *C. vanus*, *A. tonsa* and *P. parvus* were present at every station (homogeneous and stratified) in both transects, while *D. forcipatus* and *C. branquiatus* were present only at stratified stations. *Oikopleura dioica* was the only appendicularian species registered. The densities calculated for copepods and appendicularians are shown in Figure 3. The abundances of cyclopoids and calanoids differ between transects (Mann-Whitney test, U=5 and U=6 respectively, p<0.05), and cyclopoids are more abundant (2622 ind. m^{-3}) in the northern transect and calanoids (3554 ind. m^{-3}) in the southern transect. No differences in abundances between transects were observed for nauplii (Mann-Whitney test, U=9, p>0.05), which reached densities of 1358 ind. m^{-3}. The highest densities of *O. dioica* appendicularians were recorded in the southern transect with values between 400 and 526 ind. m^{-3} (Mann-Whitney test, U=5, p<0.05).

The principal component analysis showed that components 1 and 2 explained 48.5% and 30.8% of the total variability respectively (Fig. 4). The Simpson index, temperature, total zooplankton and nauplii densities were mainly correlated with the first component. Both environmental variables were inversely correlated with the biological variables as higher zooplankton and nauplii abundances were found in homogeneous waters where a lower Simpson index and temperature were detected. Cyclopoids and appendicularians showed an
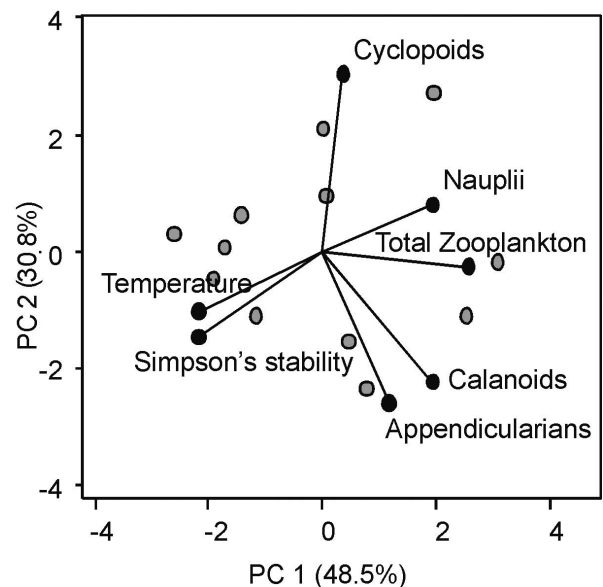

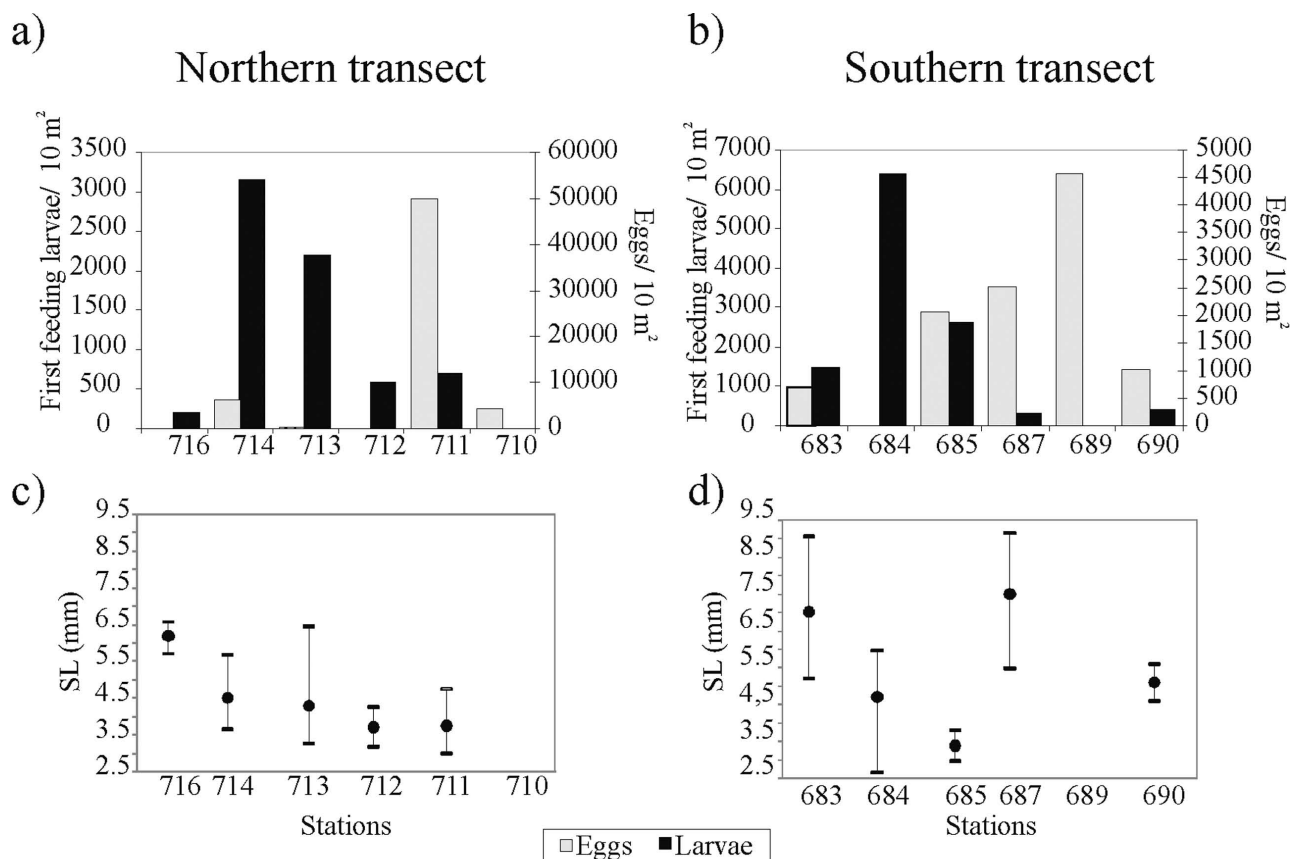Fig. 4. – Scatterplot of PC 2 on PC 1 (See Table 1).

Fig. 5. – Density of first-feeding larvae and eggs of *E. anchoita* in the northern (a) and southern (b) transects. Standard length (SL, mm) of first-feeding larvae in the northern (c) and southern (d) transects. The mean and range in each station are indicated.

TABLE 1. – Results of the PCA analysis, eigenvectors (Evc), eigenvalues, percent of the variance explained by the original data set (r^2), and correlation (r) of the original variables with the first two principal components.

	PC1		PC2	
	r	evc	r	evc
Temperature	-0.80	-0.43	-0.30	-0.20
Nauplii	0.71	0.39	0.23	0.16
Calanoids	0.71	0.38	-0.66	-0.45
Cyclopoids	0.13	0.07	0.89	0.61
Appendicularians	0.44	0.24	-0.76	-0.52
Total zooplankton	0.94	0.51	-0.07	-0.05
Simpson's stability	-0.81	-0.44	-0.44	-0.30
Eigenvalue		3.39		2.16
r^2		48.5		30.8

inverse relationship and were mainly associated with component 2 (Table 1).

Small-sized zooplankters as potential prey of *E. anchoita* in the frontal system

Engraulis anchoita larval abundance was highest at coastal stations (stations 714, 713 and 684), mainly in the southern transect (max. 6000 larvae/10 m²), in contrast to egg abundance, which was higher at the outside stations (station 711 and 689) of both transects

(max. 50000 eggs/10 m²) (Fig. 5). The standard lengths of first-feeding larvae ranged from 2.6 mm to 9 mm, and the largest larvae were found in the southern transect. Zooplankton sizes in the different stations were also analyzed (Fig. 6). The smallest sizes (mainly <500 μm) were predominant in homogenous coastal waters, while larger organisms (>500 μm) dominated in the external stratified waters. Nauplii ranged from 50 to 500 μm and were larger in the southern transect. The largest calanoids were found mainly at the external stations and the largest appendicularians, *O. dioica* (>1000 μm), were found at the coastal stations of the southern transect. In the northern transect the sizes of this last species were much smaller. The cyclopoids were predominant in the northern transect, and small individuals under 500 μm prevailed at coastal stations. In general, it was observed that the dominance of the smallest sizes of zooplankton at the coastal stations coincided with the highest larval abundances, while the dominance of the largest fractions at outside stations coincided with the highest egg abundances. In terms of biomass (Fig. 7), the main carbon contributions were found at the external stations (stations 711 and 689) of the northern and southern transects (12384 μg C m⁻³ and 40777 μg C m⁻³ respectively). The largest values corresponded to calanoids (40000 μg C m⁻³)
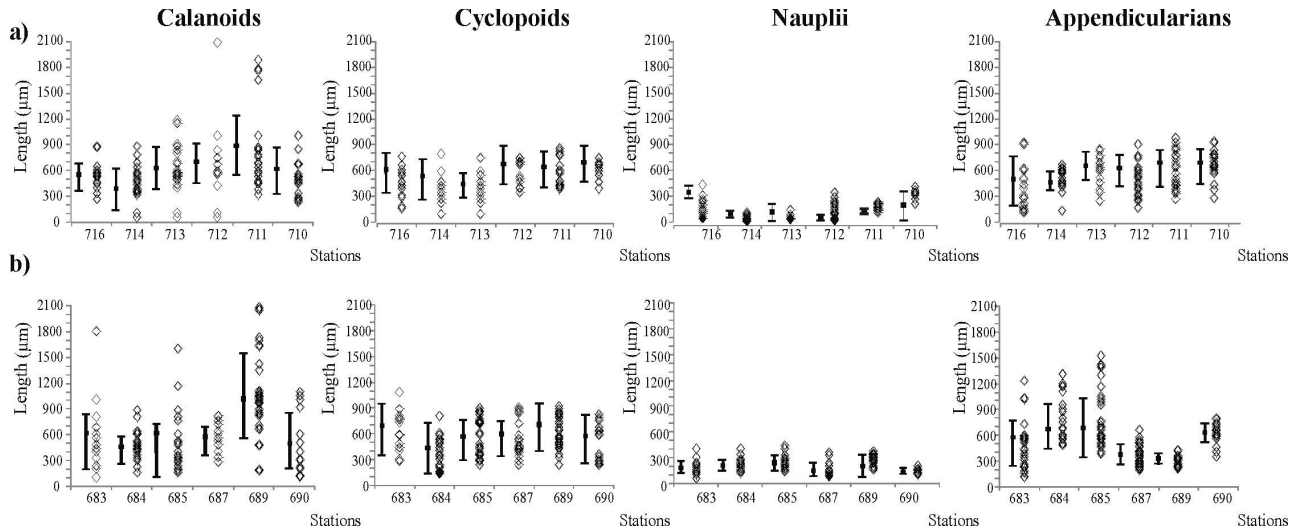
Fig. 6. – Size structures (μm) of calanoids, cyclopoids, appendicularian *O. dioica* and nauplii in the northern (a) and southern (b) transects across the front. The mean and standard deviation at each station are indicated.
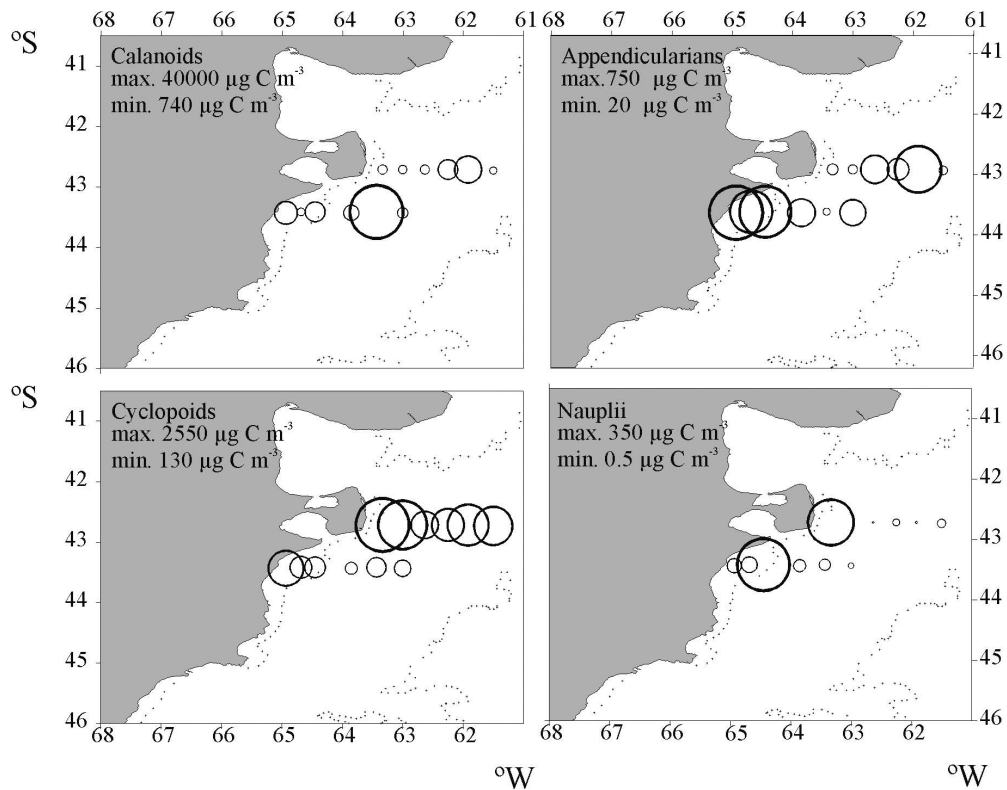

Fig. 7. – Biomasses (μg C m^{-3}) of calanoids, cyclopoids, appendicularians and nauplii in the frontal system of Peninsula Valdés. Maximum and minimum values for each group are also indicated.

followed by cyclopoids (2550 μg C m^{-3}), appendicularians (750 μg C m^{-3}) and nauplii (350 μg C m^{-3}). At stations 716, 714 and 710 of the northern transect, cyclopoid biomasses were two times higher than calanoid biomasses. In general, cyclopoid, nauplii and *O. dioica* appendicularian biomasses were higher in homogeneous coastal waters, while calanoid biomasses were higher in the external stratified waters.

DISCUSSION

The physical structure of the North Patagonian frontal system shows latitudinal differences that may be related to changes in the relative importance of meteorological forces, such as tides and winds. The marked thermal gradient observed along the two transects, both in distance from the shore and depth,

resulted in different zooplankton compositions and distribution patterns. Cyclopoids were dominant (ca. 70%, with few exceptions) in the northern transect and calanoids (average 80%) were dominant in the southern transect. *P. parvus* and *C. vanus* were dominant in homogeneous waters and *D. forcipatus* and *C. branchiatus* in stratified waters. It is known that cyclopoids are associated with microbial production processes (Franz and Gonzalez 1995, Nielsen and Sabatini 1996), which could explain the observed dominance of cyclopoids over calanoids because a low chlorophyll *a* concentration was found in the northern transect. The same pattern of the latitudinal distribution of zooplankton was observed in the spring of 1995 and 1998 (Sabatini and Martos 2002). However, in relation to stratification and water mixing, higher densities were found in stratified waters in 1995, and in homogeneous waters in 1998, which could be related to the physical conditions of the front (the temperature was higher in 1998 throughout the entire frontal system compared to 1995). In our study, the surface temperature in homogeneous waters of the northern transect was similar to that of 1998 and higher than that of 1995. However, when the stratified waters were compared, the temperature observed was higher than in 1995 and 1998, and there was a very pronounced thermocline ($\Delta T= 9°C$). As the southern transect in Sabatini and Martos (2002) was located further south, we did not compare it with our southern transect. In addition, in our study, temperature was negatively correlated with all biological variables, and the differences in zooplankton abundances in homogeneous and stratified waters corresponded to fluctuations in their physical structure. Temperature was the main factor affecting the zooplankton distributionThe abundance and biomass of calanoids and cyclopoids were significantly higher than those of appendicularians, mainly in homogeneous and transitional waters. There were higher densities of copepods and *O. dioica* appendicularians in the transitional waters of the front, coinciding with a higher chlorophyll *a* concentration (Viñas and Ramirez 1996, Capitanio and Esnal 1998). Although both the biomass and abundance of copepods were higher than those of appendicularians, the latter had significantly higher production rates (Sato *et al.* 2008, Jaspers *et al.* 2009). While several experimental studies have shown an indirect interaction between calanoids and appendicularians, no studies have been carried out on the interactions between cyclopoids and appendicularians. In the coastal waters of the Japan Sea and Baltic Sea, blooms of *O. dioica* occur after the calanoid abundances decline or whenever they are low (Behrends 1996, Nakamura 1998, Sommer *et al.* 2000, 2003, Stibor *et al.* 2004). In addition, Tönnesson *et al.* (2005) suggested that there is predation pressure by calanoids on appendicularian eggs, which would thus influence their population dynamics. Moreover, in our southern transect, the largest calanoids were observed with the smallest *O. dioica* appendicularians at the external stations, while the smallest calanoids were

found with the largest *O. dioica* appendicularians at the coastal stations. However, the negative relationship between the total abundance of cyclopoids (mainly small *Oithona* spp.) and *O. dioica* appendicularian suggests there is competition for food.

The distribution of first-feeding larvae of *E. anchoita* in this frontal system was related to the small sized copepods (mainly <500 μm). The peaks of larvae at coastal stations (mean larval standard length: 4.6 mm, St. 684) coincided with the highest abundances of these small zooplankton sizes, mainly calanoids and cyclopoids. In this front Sabatini and Martos (2002) registered low densities of nauplii in relation to the low fecundity of copepod females found experimentally. During our sampling period (14-17 December), nauplii densities were also low (they reached 1358 ind. m^{-3} only at St. 685 of the southern transect), which indicates that the study was probably conducted out of the reproductive period of most copepods or that their fecundity was low. In terms of the carbon contribution of these four groups to the mixed waters of the front, 60% and 50% of the total biomasses corresponded to cyclopoids and calanoids in the northern and southern transects respectively. Moreover, Diaz *et al.* (2009) found highly propitious nutritional conditions for the anchovy larvae collected in this frontal system, including the first-feeding larvae. Viñas and Ramirez (1996) analyzed the stomach contents of anchovy larvae (2.5 to 5.5 mm standard length), and found that nauplii, eggs and small copepods (<500 μm) were the main food items. In our study, the small copepods *P. parvus* and *Oithona* spp. were registered at all plankton stations of the front, and were thus available as the main food source for anchovy larvae. The diets of other clupeid larvae, such as *Sardinella aurita*, are based on different copepod stages, and a higher preference for nauplii in larvae <8 mm has been detected (Morote *et al.* 2008). In addition, Morote *et al.* (2010) observed prey selectivity in the feeding ecology of *E. encrasicolus* larvae (2.7 to 14.5 mm), which begin feeding on prey items >150 μm length. On the Algerian coast, copepods are found in 98% of the stomach contents of adults of this species, and during its first year of life, anchovy feed almost exclusively on copepods (mainly small and medium sized preys). As the anchovy grow, copepods are gradually substituted by large crustaceans, such as decapods and amphipods (Bacha and Amara 2009).

It is known that before the spring-summer spawning season, schools of the Patagonian stock of *E. anchoita* feed on the larger zooplankton available in deep shelf waters and then migrate to coastal areas, such as the frontal system of Peninsula Valdés, to reproduce (Pájaro 1998). Wind mixing, and its associated turbulence, influence plankton populations in different ways, with either beneficial or detrimental consequences depending on their role within pelagic food webs. In particular, homogeneous waters enhance encounter rates between zooplankton preys and icthyoplankton predators (Rothschild and Osborn 1988). The complex ecological

interactions among the vast numbers of zooplankton organisms can result in positive, negative or random relationships, which can be related to physical and biological environmental conditions. Moreover, these relationships are not fixed over time and can vary according to the type of interactions between organisms. In this study, we detected a positive relationship between the small zooplankton fraction and the first-feeding larvae of *E. anchoita*. According to Sanvicente-Añorve *et al.* (2006), this type of relationship may be due to the absence or low abundance of the main predators of the icthyoplankton, and the high food availability for fish larvae; however, in this study no data on predators of anchovy larvae were available.

In the Patagonian area, the onset of anchovy spawning and the distribution of anchovy eggs depend on the formation of tidal frontal systems. Sánchez *et al.* (1996) observed larger concentrations of eggs in the transition and stratified waters, which was also observed in our study. The high densities of anchovy eggs at external stations in coincidence with larger calanoids (>1000 μm) could be indicative of the presence of spawning groups of anchovies feeding on them. Furthermore, the higher biomass (mainly calanoids) in these stratified waters would contribute to the carbon transfer to the upper trophic levels and anchovy adults would be benefited. During winter, Castro *et al.* (2009, 2010) reported that variations in the biochemical composition of *Engraulis ringens* eggs in the upwelling system off the Chile coast were beneficial for young larvae. These authors found a negative relationship between egg size and food availability for larvae: smaller-sized copepods (presumably more prone to being captured by the youngest larvae) were most abundant when eggs were smaller because larvae would not need much lipid reserves to survive due to the abundance of small food sources in the sea. In other areas, such as on the Catalan coast (NW Mediterranean), high larval densities of both *E. encrasicolus* and *Sardinella aurita* suggest that the high abundance of zooplankton in surface layers forms a favourable habitat for the nutrition and survival of these larvae. Accordingly, high correlations between both larvae and the trophic variables (i.e. sea surface fluorescence) were detected (Olivar *et al.* 2010). In our study, in the Peninsula Valdés front, similar results were found because high chlorophyll *a* concentrations were recorded together with high abundances of small zooplankton and larvae in the homogenous waters. Although other fish larvae (e.g. *Merluccius hubbsi*) are usually spawned on the Patagonian coast (Macchi *et al.* 2007), no interaction between larvae of the different species is possible due to their different temporal distribution patterns.

It is therefore evident that frontal zones play a key role in ecological processes of the ocean (Acha *et al.* 2004), allowing an exceptionally large primary production (Carreto *et al.* 1986), offering adequate feeding and reproductive habitats for planktivorous species and acting as retention areas for larvae. In the Peninsula Valdés frontal system, homogeneous and transitional waters constitute a suitable environment for the small fraction of zooplankton, and the abundances of these prey foods would be important for the survival and growth of first-feeding larvae. Therefore, more studies on the links between zooplankton and anchovy are still necessary.

ACKNOWLEDGEMENTS

REFRENCES

Acha E.M., Mianzan H., Guerrero R., Favero M., Bava J. 2004. Marine fronts at the continental shelves of austral South America. Physical and ecological processes. *J. Mar. Sci.* 44: 83-105.
Bacha M., Amara R. 2009. Spatial temporal and ontogenetic variation in diet of anchovy (*Engraulis encrasicolus*) on the Algerian coast (SW Mediterranean). *Estuar. Coast. Shelf Sci.* 85: 257-264.
Behrends G. 1996. Long term investigations of seasonal mesozooplankton dynamics in Kiel Bight, Germany. Proceedings of the 13th. Baltic Marine Biology Symposium, Jurmala, Latvia, *Inst. Aquat. Ecol., Univer. Latvia, Riga, Latvia,* 93-98.
Berggreen U., Hansen B., Kiørboe T. 1988. Food size spectra ingestion and growth of the copepod *Acartia tonsa* during development. Implications for determination of copepod production. *Mar. Biol.* 99: 341-352.
Bezzi S. 2000. Síntesis de las evaluaciones y sugerencias de manejo efectuadas sobre el recurso merluza (*Merluccius hubbsi*) entre el año 1986 y mayo de 1997. INIDEP *Inf. Téc.* 30. INIDEP, Argentina, pp 1-16.
Bollens S.M., Frost B.W., Thoreson D.S., Watts S. 1992. Diel vertical migration in zooplankton: a field test of the predator avoidance hypothesis. *Hydrobiologia.* 234: 33-39.
Buono J., Cucchi Colleoni D. 2009. Proceso de imágenes satelitales de clorofila. INIDEP *Inf. Técnico* 19. INIDEP, Argentina, pp 11-20.
Capitanio F.L., Pájaro M., Esnal, G.B. 1997. Appendicularians in the diet of anchovy *Engraulis anchoita* in the Argentine Sea. *Sci. Mar.* 61: 9-15.
Capitanio F.L., Esnal G.B. 1998. Vertical distribution of the maturity stages of *Oikopleura dioica* (Tunicata, Appendicularia) in the frontal system off Valdés Peninsula, Argentina. *Bul. Mar. Sci.* 63: 531-539.
Capitanio F., Pájaro M., Esnal G. 2005. Appendicularians: an important food supply for the Argentine anchovy *Engraulis anchoita* in coastal waters. *J. Appd. Ich.* 21: 414-419.
Capitanio F.L., Curelovich J., Tresguerres M., Negri R., Viñas M.D., Esnal G. 2008. Seasonal cycle of appendicularians at a coastal station (38º28′S, 57º41′W) of the SW Atlantic Ocean. *Bul. Mar. Sci.* 82: 171-184.
Carreto J.I., Benavides H.R., Negri R.M., Glorioso P.D. 1986. Toxic red tide in the Argentine sea. Phytoplankton distribution and survival of the toxic dinoflagellate *Gonyaulax excavata* in a frontal area. *J. Plankton Res.* 8: 15-28.
Castro L.R., Claramunt G., Krautz M.C., Llanos-Rivera A., Moreno P. 2009. Egg trait variation in anchoveta *Engraulis ringens*: a maternal response to changing environmental conditions in contrasting spawning habitats. *Mar. Ecol. Prog. Ser.* 381: 237-248
Castro L.R., Claramunt G., González H.E., Krautz M.C., Llanos-Rivera A. Méndez J., Schneider W., Soto S. 2010. Fatty acids in eggs of anchoveta *Engraulis ringens* during two contrasting

winter spawning seasons. *Mar. Eco. Prog. Ser.* 420: 193-205.

Cushing J., Dennis M.B., Desharnais R.A., Costantino R.F. 1996. An interdisciplinary approach to understanding nonlinear ecological dynamics. *Ecol. Model.* 92: 111-119.

Deibel D., Lee S.H. 1992. Retention efficiency of submicrometer particles by the pharyngeal filter of the pelagic tunicate *Oikopleura vanhoenffeni*. *Mar. Ecol. Prog. Ser.* 81: 25-30.

Diaz M.V., Pájaro M., Sánchez R.P. 2009. Employment of morphometric variables to assess nutritional condition of Argentine anchovy larvae *Engraulis anchoita* (Hubbs and Marini, 1935). *Rev. Biol. Mar. Oceanogr.* 44: 539-549.

Flood P.R., Deibel D., Morris C. 1992. Filtration of colloidal melanin from seawater by planktonic tunicates. *Nature* 355: 630-632.

Franz H.G., Gonzalez S.R. 1995. The reproduction of *Oithona similis* (Copepoda: Cyclopoida) in the Southern Ocean. *ICES J. Mar. Sci.* 52: 549-555.

Glorioso P. 1987. Temperature distribution related to shelf-sea fronts on the Patagonian shelf. *Cont. Shelf Res.* 7: 27-34.

Gorsky G., Fenaux F. 1998. The role of Appendicularians in marine food webs. In: Bone Q. (ed.). *The biology of Pelagic Tunicates.* Oxford University Press, pp. 161-169.

Hansen J.E., Cousseau M.B., Gru D.L. 1984. Características poblacionales de la anchoíta (*Engraulis anchoita*) del Mar Argentino. Parte I. El largo medio al primer año de vida, crecimiento y mortalidad. *Revista de Investigación y Desarrollo Pesquero.* 4: 21-48.

Hjort J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological researches. *Rapp. p-v Réu., Con. int. Expl. Mer* 20: 1-128.

Hopcroft R.R., Roff J.C. 1998. Production of tropical larvaceans in Kingston Harbour, Jamaica: are we ignoring an important secondary producer? *J. Plankton Res.* 20: 557-569.

Hunter J.R., Alheit J. 1995. International GLOBEC Small Pelagic Fishes and Climate Change program. Report of the First Planning Meeting. GLOBEC Report No. 8, México.

Jaspers C., Nielsen T.G., Garstensen J., Hopcroft R.R., Møller E.F. 2009. Metazooplankton distribution across the Southern Indian Ocean with emphasis on the role of Larvaceans. *J. Plankton Res.* 31: 525-540.

Kiørboe T. 1991. Pelagic fisheries and spatio-temporal variability in zooplankton productivity. In: Proceedings of the Fourth International Conference on Copepoda. *Bull. Plankton Soc. Jpn. Sp. Vol.* 229-249.

Kiørboe T. 1998. Population regulation and role of mesozooplankton in shaping marine pelagic food webs. *Hydrobiologia* 363: 13-27.

Largier J.L. 1993. Estuarine fronts: how important are they? *Estuaries* 16: 1-11.

Last J.M. 1980. The food of twenty species of fish larva e in the west-central North Sea. *Fish. Res. Tech. Rep.* 60: 1-44.

Macchi G.J. Pájaro M., Dato C. 2007. Spatial variations of the Argentine hake (*Merluccius hubbsi* Marini, 1993) spawning shoals in the Patagonian area during a reproductive season. *Rev. Biol. Mar. Ocea.* 42: 345-356.

Mann K.H., Lazier J.R.N. 1993. Dynamics of Marine Ecosystems. Biological Physical Interactions. In: Blackwell (ed.) *The Oceans, 2nd.* Cambridge, USA. 480 pp.

Marrari M., Viñas M.D., Martos P., Hernández D. 2004. Spatial patterns of mesozooplankton distribution in the Southwestern Atlantic Ocean (34-41°S) during austral spring: Relationship with the hydrographic conditions. *ICES J. Mar. Sci.* 61: 667-679.

Martos P., Sánchez R.P. 1997. Caracterización oceanográfica de regiones frontales en la plataforma Patagónica en relación con áreas de desove y cría de la anchoita (*Engraulis anchoita*). In: Coloquio Argentino de Oceanografía, IAPSO-IADO (Conicet), Bahía Blanca, Argentina.

Morote E., Olivar R.P., Villate F., Uriarte I. 2008. Diet of round sardinella, *Sardinella aurita*, larvae in relation to plankton availability in the NW Mediterranean. *J. Plankton Res.* 7: 807-816.

Morote E., Olivar M.P., Villate F., Uriarte I. 2010. A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the Northwest Mediterranean: influence of prey availability and ontogeny. *ICES J. Mar. Sci.* 5: 897-908.

Nakamura Y. 1998. Blooms of tunicates *Oikopleura* spp. and *Dolioletta gegenbauri* in the Seto Inland Sea, Japan, during summer. *Hydrobiologia* 385: 183-192.

Nielsen T.G., Sabatini M. 1996. Role of cyclopoid copepods *Oithona* spp. in North Sea plankton communities. *Mar. Ecol. Prog. Ser.* 139: 79-93.

Olivar M.P., Emelianov M., Villate F., Uriarte I., Maynou F., Alvarez I., Morote E. 2010. The role of oceanographic conditions and plankton availabilityin larval fish assemblages off the Catalan coast (NW Mediterranean). *Fish. Oceanogr.* 19: 209-229.

Pájaro M. 1998. *El canibalismo como mecanismo regulador denso-dependiente de mortalidad natural en la anchoíta argentina (*Engraulis anchoita*). Su relación con las estrategias reproductivas de la especie.* PhD Thesis, Univ. Nacional de Mar del Plata, Argentina, 297 pp.

Pájaro M., Macchi G., Leonarduzzi E., Hansen J.E. 2009a. Spawning biomass of Argentine anchovy (*Engraulis anchoita)* from 1996 to 2004 using the daily egg production method. *J. Mar. Biol. Assoc. U.K.* 89: 829-837.

Pájaro M., Martos P., Leonarduzzi E., Díaz M.V., Di Mauro R., Sabatini M. 2009b. Estrategia de puesta de la anchoíta argentina (*Engraulis anchoita*) en relación con áreas frontales. I Simposio Iberoamericano de "Ecología Reproductiva, Reclutamiento Pesquerías", Vigo, España.

Rothschild B.J., Osborn T.R. 1988. Small-scale turbulence and plankton contact rates. *J. Plankton Res.* 10: 465-474.

Sabatini M., Kiørboe T. 1994. Egg production, growth and development of the cyclopoid copepod *Oithona similis*. *J. Plankton Res.* 16: 1329-1351.

Sabatini M., Martos P. 2002. Mesozooplankton features in a frontal area off northern Patagonia (Argentina). *Sci. Mar.* 66: 215-232.

Sánchez R.P., Ciechomski J.D. 1995. Spawning and nursery grounds of pelagic fish species in the sea-shelf off Argentina and adjacent areas. *Sci. Mar.* 59: 455-478.

Sánchez R.P., Pájaro M., Macchi G.J. 1996. The application of the daily egg production method to the assessment of the SW Atlantic anchovy, (*Engraulis anchoita*), spawning biomass off Argentina. *Inter. Council Expl. Sea.* 1-29.

Sánchez R., Madirolas A., Reta R., Ehrlich M.D., Álvarez Colombo G., Macchi G. 1997. The reproductive biology of the patagonian sprat (*Sprattus fuegensis*): several facts and still some speculations. *ICES Ann. Sci. Conf.* 10 pp.

Santos B.A., Ramírez F.C. 1995. Distribución y abundancia de copépodos en el sistema frontal de Península Valdés, durante florecimientos fitoplanctónicos. *Thalassas* 11: 133-142.

Sanvicente-Añorve L., Soto L.A., Espinosa-Fuentes M.L., Flores-Coto C. 2006. Relationship patterns between ichthyoplankton and zooplankton: a conceptual model. *Hydrobiologia* 559: 11-22.

Sato R., Ishibashi Y., Tanaka Y., Ishimaru T., Dagg M.J. 2008. Productivity and grazing impact of *Oikopleura dioica* (Tunicata, Appendicularia) in Tokio Bay. *J. Plankton Res.* 30: 299-309.

Simpson J.H. 1981. The shelf-sea fronts: implications of their existence and behaviour. *Phil. Trans. Roy. Soc. London* 302: 531-546.

Sommer F., Stibor H., Sommer U., Velimirov B. 2000. Grazing by mesozooplankton from Kiel Bight, Baltic Sea, on different sized algae and natural seston size fractions. *Mar. Ecol. Progr. Ser.* 199: 43-53.

Sommer F., Hansen T., Feuchtmayr H., Santer B., Tokle N., Sommer U. 2003. Do calanoids copepods suppress appendicularians in the coastal ocean? *J. Plankton Res.* 27: 869-871.

Stibor H., Vadstein O., Lippert B., Roederer W., Olsen Y.R. 2004. Calanoid copepods and nutrient enrichment determine population dynamics of the appendicularian *Oikopleura dioica*: a mesocosm experiment. *Mar. Ecol. Progr. Ser.* 270: 209-215.

Tönnesson K., Maar M., Vargas C., Friis Moller E., Satapoomin S., Zervoudaki S., Christou E., Giannarkourou A., Sell A., Kjerulf P.J., Nielsen T.G., Tiselius P. 2005. Grazing impact of *Oikopleura dioica* and copepods on an autumn plankton community. *Mar. Biol. Res.* 1: 365-373.

Viñas M.D., Ramírez F.C. 1996. Gut analysis of first-feeding anchovy larvae from Patagonian spawning area in relation to food availability. *Arch. Fish. Mar. Res.* 43: 231-256.

Viñas M.D., Negri R.M., Ramírez F.C., Hernández D. 2002. Zooplankton assemblages and hydrography in the spawning area of anchovy (*Engraulis anchoita*) off Río de la Plata estuary (Argentina, Uruguay). *Mar. Freshwater Res.* 53: 1031-1043.