

Research Article

Importance of the Río de la Plata estuarine front (southwestern Atlantic Ocean) in the feeding ecology of Argentine anchovy, *Engraulis anchoita* (Clupeiformes, Clupeidae)

Luciano N. Padovani^{1,2,3}, María D. Viñas^{1,2,3} & Marcelo Pájaro¹

¹Instituto Nacional de Investigación y Desarrollo Pesquero, P.O. Box 175, B7602HSA
Mar del Plata, Argentina

²Consejo Nacional de Investigaciones Científicas y Técnicas, P.O. Box 175, B7602HSA, Argentina

³Universidad Nacional de Mar del Plata, P.O. Box 175, B7602HSA, Argentina

ABSTRACT. The feeding of *Engraulis anchoita* was studied in the coastal reproductive habitat of the northern population during the spawning period. Stomach contents of anchovy adults and plankton samples taken during a research cruise were examined. The highest stomach fullness values were found in the Río de la Plata estuary, particularly at stations close to the surface salinity front. Copepods, particularly those < 1 mm total length, represented by *Paracalanus* spp. and *Oithona* spp., were the most abundant prey. The dominance of small copepods in the Argentine anchovy diet is noted for the first time. Ecological implications of this fact are discussed. Other abundant preys were appendicularians, cladocerans, and fish eggs. The species composition of the zooplankton samples coincided roughly with that found in the stomach contents. However, selective feeding was observed on preys > 1 mm total length. This might be explained by a low gill rakers efficiency of adult anchovies to retain small prey. In the Río de la Plata front, both the reported large biomasses of zooplankton and the observed intense anchovy feeding revealed the ecological significance of this front, especially when compared with the contiguous “poor in food” coastal areas.

Keywords: *Engraulis anchoita*, feeding, stomach content, estuarine front, copepods, southwestern Atlantic, Argentina.

Importancia del frente estuarial del Río de la Plata (Océano Atlántico sudoccidental) en la ecología trófica de la anchoíta argentina, *Engraulis anchoita* (Clupeiformes, Clupeidae)

RESUMEN. Se estudió la alimentación de la población norteña de *Engraulis anchoita* en el hábitat reproductivo costero durante su periodo de desove. Se analizaron los contenidos estomacales de adultos de anchoíta y muestras de zooplancton tomados durante un crucero de investigación. Los mayores valores de repleción estomacal se encontraron en el estuario del Río de la Plata, particularmente en estaciones cercanas al frente salino de superficie. Los copépodos fueron las presas más abundantes, particularmente especímenes < 1 mm de longitud total, representados por *Paracalanus* spp. y *Oithona* spp. Este dominio de pequeños copépodos en la dieta de la anchoíta argentina se destaca por primera vez. Se discutieron las implicancias ecológicas de este hecho. Otras presas abundantes fueron: apendicularias, cladóceros y huevos de peces. La composición de especies en las muestras de zooplancton coincidió a grandes rasgos con las encontradas en los contenidos estomacales. Sin embargo, se observó selección sobre presas > 1 mm de longitud total. Esto se puede explicar por la baja eficiencia del aparato branquial de anchoítas adultas para retener pequeñas presas. En el frente del Río de la Plata, las altas biomásas de zooplancton reportadas y la intensa alimentación observada, evidencian su significancia ecológica, especialmente cuando se compara con aguas costeras adyacentes pobres en alimento.

Palabras clave: *Engraulis anchoita*, alimentación, contenido estomacal, frente estuarial, copépodos, Atlántico sudoccidental, Argentina.

INTRODUCTION

Engraulis anchoita is the most abundant and widespread pelagic fish in the southwest Atlantic. It plays a key role in the pelagic ecosystem of the Argentine Sea, being an important component in the diet of commercial species such as hake, squid and mackerel (Angelescu, 1982). Two distinct populations are recognized south of 34°S: the northern stock, between 34° and 41°S; and the Patagonian stock between 41° and 48°S (Hansen *et al.*, 1984). The northern stock, object of this study, performs seasonal migrations between coastal and shelf waters. In spring and early summer the schools migrate into the coastal reproductive habitat (hereafter CRH) off the Buenos Aires Province (< 50 m depth), where massive spawning takes place (Sánchez & Ciechomski, 1995). Larvae and juveniles remain in coastal waters during their growing period. After spawning, in summer and early autumn, schools disperse into outer shelf waters to feed, accumulating a large amount of energy for the next reproductive cycle (Angelescu, 1982; Hansen & Madirolas, 1996).

E. anchoita adults are opportunistic predators on meso and macrozooplankton. They exhibit, like other engraulids, two different feeding mechanisms: filtration for smaller prey, and capture or biting for larger ones (Leong & O'Connell, 1969; Angelescu, 1982).

Previous studies indicate that anchovy feeding in the CRH was negligible when compared with the intense feeding occurring in shelf waters (Angelescu & Anganuzzi, 1981; Angelescu, 1982; Schwingel & Castello, 1994; Capitano *et al.*, 1997; Pájaro, 2002). In the former, individuals feed almost exclusively on small zooplankters (e.g. small copepods species, appendicularians and cladocerans) while in shelf waters large zooplankters constitute their food (e.g. Calanidae copepods, euphausiids and hyperiid amphipods). This feeding pattern seems to reflect the food availability found in zooplankton studies with lower biomass in the CRH than in shelf waters (Pájaro, 2002; Viñas *et al.*, 2002; Marrari *et al.*, 2004). However, in northern sector of the CRH high zooplankton biomasses have been reported (Viñas *et al.*, 2002; Marrari *et al.*, 2004). This sector is strongly influenced by the Rio de la Plata (RdP), the second most important river of South America. Its estuarine front plays a central role in the biological production, and zooplankton aggregations are a recurrent feature in this area probably because of retention and accumulation process (Madirolas *et al.*, 1997; Acha *et al.*, 2008).

The presence of zooplankton aggregations together with the fact that high densities of anchovy schools occur frequently in RdP front (Hansen & Madirolas, 1996; Martos *et al.*, 2005) suggest that this may be a

potential anchovy feeding area into the CRH. This is not surprising since other estuarine fronts in the world have been related to important anchovy spawning and feeding grounds (Palomera, 1992; Motos *et al.*, 1996; Peebles, 2002). However, previous studies in the CRH have not been addressed to this question. Moreover, the characterization of anchovy diet (e.g. taxonomic identification and quantification of ingested prey items) was inaccurate in these studies, especially regarding small prey.

In this work, anchovy stomach contents were analysed in order to assess differences in the feeding activity between RdP front and the rest of the CRH. Characterization of anchovy diet in the CRH was carried out and prey composition in stomach contents was compared with the prey availability in the field.

MATERIALS AND METHODS

Study site

Subantarctic coastal waters of the Buenos Aires Province (< 50 m depth) are vertically homogeneous all over the year because they are mixed by winds and tides. They are poorer in nitrate and less productive than subantarctic shelf waters (> 50 m depth) which are stratified during the warmer season. Both are separated by a semi-permanent temperature front (Carreto *et al.*, 1995). North of 38°S the coastal waters are modified by the RdP estuary (Fig. 1). This estuarine front shows a high primary productivity, driven by the nutrient input from the river and by the vertical stability of the water column (Carreto *et al.*, 1986). It is characterized by a salt wedge structure and strong horizontal salinity gradients. More saline and dense marine waters penetrate into the estuary on the bottom, whereas more dilute and less dense river waters flows toward the sea at the surface (Guerrero *et al.*, 1997). The estuarine dynamics and the strong pycnoclines of the salt wedge would favor the accumulation and retention of plankton (Acha *et al.*, 2008).

Sample collection, treatment and data analysis

The material used in this study was obtained on board the R/V "Oca Balda" on a cruise performed in coastal areas of the Buenos Aires Province between 34° and 41°S (Fig. 1). The sampling period (16 October-2 November 2004) was coincident with the peak of anchovy spawning in the study area (Sánchez & Ciechomski, 1995).

Oceanographic data were obtained in 70 stations with a CTD system (Kiel Multisonde Compact System, ME Meerestechnik Elektronik, Kiel, Germany). The salinity CTD data were calibrated by salinometer

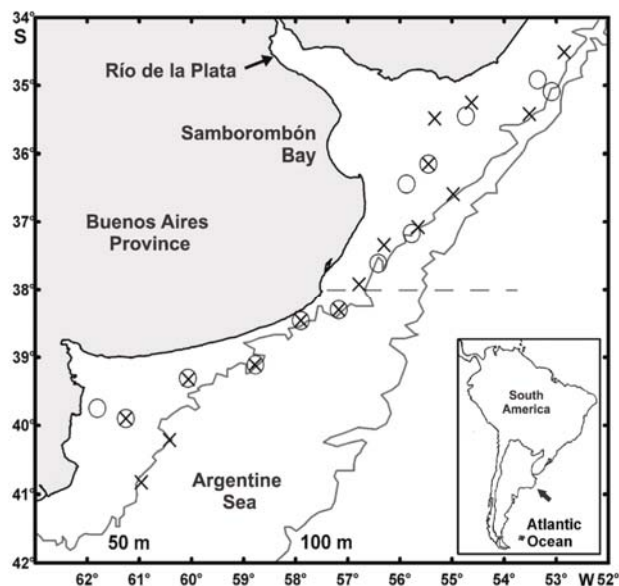


Figure 1. Study area and location of the sampling stations. (X) trawls, (O) zooplankton. Dashed line divides northern and southern sectors of study area (38°S).

Figura 1. Área de estudio y ubicación de las estaciones de muestreo. (X) lances de pesca, (O) zooplancton. La línea de guiones divide los sectores norte y sur del área de estudio (38°S).

measurements of discrete water samples. Surface salinity distribution was drawn to locate the RdP estuarine front.

Anchovies were collected using a Nichimo midwater trawl net with a 10 mm mesh size and immediately fixed in 10% formaldehyde. Stomach contents of 240 adult fishes of both sexes (110 to 194 mm total length) randomly selected from sixteen trawl stations ($n = 15$ per trawl) were examined (Fig. 1). Tows were performed both during the day and night (Table 1). Each stomach was weighed with and without food content in order to determine the weight of the ingested prey, expressed as the difference between both weights. To assess the feeding activity, mean "Stomach Fullness Index" (mSFI) was calculated for each trawl as the ratio between ingested prey and whole animal weights. According to Angelescu (1982), this index indicates the stage of satiety and ranges from empty stomach ($< 0.5\%$ of anchovy total weight) to full stomach ($> 6\%$ of anchovy total weight).

Anchovies and stomachs were weighed using a digital balance to nearest 0.01 g. No correction was applied to the weight values for fixation effect on the individuals. The dilated stomachs found empty for regurgitation during trawling, were discarded.

Zooplankton samples ($n = 13$) were collected with a 200 μm meshed 61 cm diameter Bongo net, using oblique tows in the whole water column (Fig. 1). The samples were fixed in 4% formaldehyde.

In the laboratory, both zooplankton and stomach content samples were sub-sampled into aliquots in order to quantify the zooplankters. The individuals were identified to the lowest possible taxonomic level and their total length (TL) was measured. They were placed in three size classes, < 1 and $1\text{--}2$ mm TL for the mesozooplankton and > 2 mm TL for the macrozooplankton.

Anchovy feeding selectivity in relation to food availability was calculated as the alpha selectivity index (α_i) of Chesson (1978), using the formula:

$$\alpha_i = r_i/p_i \left(\sum_{i=1}^n r_i/p_i \right)^{-1}; i = 1, \dots, n \quad \sum_{i=1}^n \alpha_i = 1$$

where; r_i = the percentage of food item i in the stomach content; p_i = the percentage of the same item in zooplankton; n = the total number of food items assessed.

RESULTS

Hydrography

Surface salinity values in the study area were ranged between 19.5 and 33.9 (Fig. 2). The lowest values corresponded to the RdP estuary. The isohaline of 30, considered the boundary of estuarine waters (Guerero, 1998), showed a south-eastward extension indicating a river discharge in this direction whose influence reaches $37^{\circ}50'S$. A well-defined frontal zone was observed with highest salinity gradients south of Samborombón Bay. In the rest of the study area, out of the river influence, the salinity values were above 33.

Feeding index

Mean Stomach Fullness Index (mSFI) of anchovy in the CRH showed a well-defined pattern with the four highest values located in RdP frontal area (Fig. 2).

This highest values were observed in specimens collected from trawl stations close to the surface salinity front, (away from the 30 isohaline): station N°4 (mSFI: 2.49), N°5 (mSFI: 2.01), N°7 (mSFI: 1.34) and N°8 (mSFI: 1.33). Some individuals reached SFI values about 6, which mean a full stomach. In the remaining stations, the mSFI were smaller than 1.00 indicating empty or partially empty stomachs.

Prey composition

The total bulk of anchovy diet was made up of zooplankton (Table 1). Mesozooplankton < 1 mm TL fol

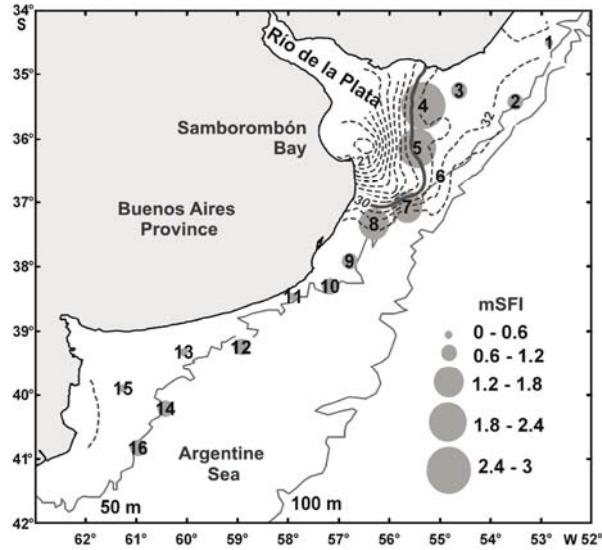


Figure 2. Mean Stomach Fullness Index (mSFI) of *Engraulis anchoita* adults at each trawling position in relationship with surface salinity distribution. Isohaline 30 is shown thicker.

Figura 2. Índice de Repleción Estomacal promedio (IREp) de adultos de *Engraulis anchoita* para cada lance de pesca en relación con la distribución de salinidad superficial. La isohalina de 30 se muestra engrosada.

lowed by the 1-2 mm TL fraction were dominant. Copepods were the most important group reaching almost 50% of prey items (PI). Other important groups were appendicularians (22.1% PI), cladocerans (14.7% PI), represented by *Evadne nordmanni* and *Podon* spp., and fish eggs (12.6% PI), including unidentified fish eggs and anchovy eggs. To a lesser extent veliger stages of lamellibranchs, unidentified nauplii, decapod larvae and amphipods were found.

The more abundant copepods in stomachs belonged to the < 1 mm TL fraction (*Paracalanus* spp. + Calanoida copepodites and *Oithona* spp.). Copepods size class 1-2 mm TL (*Ctenocalanus vanus*, *Clausocalanus brevipipes*, *Centropages brachiatus* + Calanoida copepodites) was less abundant and individuals > 2 mm TL (*Calanoides carinatus*) were fairly rare.

Zooplankton composition and food selectivity

Mesozooplankton < 1 mm TL fraction was the most abundant in study area (Table 2). Copepods (*Paracalanus* spp. + Calanoida copepodites and *Oithona* spp.) constituted the bulk of this fraction followed by cladocerans (*Evadne nordmanni* and *Podon* spp). The 1-2 mm TL size class was represented by copepods (*Ctenocalanus vanus*, *Clausocalanus brevipipes*, *Centropages brachiatus* +

Calanoida copepodites) and to a lesser extent by appendicularians. Anchovy eggs and unidentified fish eggs were less numerous. The least abundant macrozooplankton > 2 mm was dominated by decapod larvae and the *Calanoides carinatus* copepod.

From the application of the feeding selectivity index to different prey size classes, high selectivity was observed for mesozooplankton 1-2 mm TL and macrozooplankton > 2 mm TL at the expense of mesozooplankton < 1 mm (Fig. 3a). Furthermore, unidentified fish eggs showed high index in the northern sector of the study area (north of 38°S) while the appendicularians were in the southern part (south of 38°S) (Fig. 3b); what happened due to the high number of specimens found in stomach from stations 4 and 12 for unidentified fish eggs and appendicularians respectively (Table 1).

DISCUSSION

High feeding activity was detected in anchovies from the proximity of RdP surface salinity front, in contrast with a lower activity recorded in the rest of the CRH. Moreover, it is worth mentioning that during the cruise high anchovy biomasses were recorded in

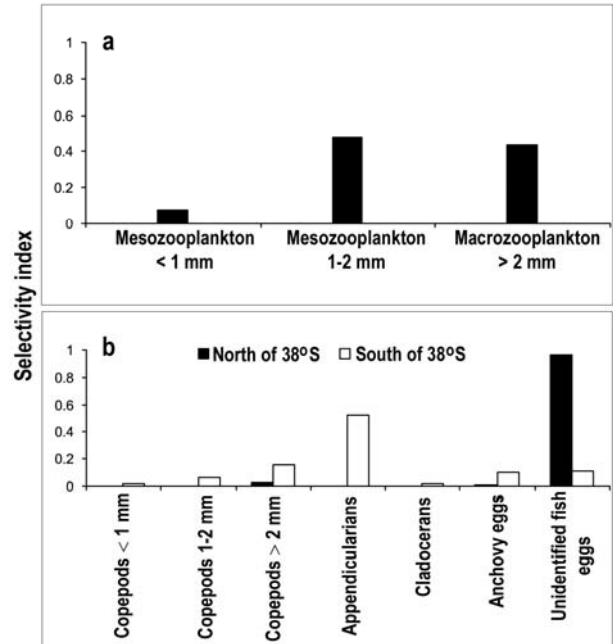


Figure 3. Feeding selectivity index values according to Chesson (1978). a) prey size classes; b) main anchovy prey items (north and south of 38°S).

Figura 3. Valores del índice de selectividad de Chesson (1978). a) por clases de tamaño de presa; b) por principales ítems presa (al norte y sur de 38°S).

Table 1. Stomach contents of *Engraulis anchoita* adults in its coastal reproductive habitat (CRH). Average number of specimens of each prey item from each trawl is indicated. (n: number of anchovies examined). * *Ctenocalanus brevipes*, *Ctenocalanus vanus*, *Clausocalanus vanus*, *Ctenocalanus brevipes*, *Centropages brachiatus* and *Calanoida* copepodites.**Table 1.** Contenido estomacal de adultos de *Engraulis anchoita* en su hábitat reproductivo costero (HRC). Se indica el número promedio de especímenes de cada ítem presa para cada lance. (n: número de anchoítas analizadas) * *Ctenocalanus vanus*, *Clausocalanus vanus*, *Ctenocalanus brevipes*, *Centropages brachiatus* y copepoditos de *Calanoida*.

Trawl	1 (n=15)	2 (n=15)	3 (n=15)	4 (n=15)	5 (n=15)	6 (n=15)	7 (n=15)	8 (n=15)	9 (n=15)	10 (n=15)	11 (n=15)	12 (n=15)	13 (n=15)	14 (n=15)	15 (n=15)	16 (n=15)	Total
Time	10:57	10:35	20:14	23:55	8:34	20:51	22:53	20:44	0:27	16:35	16:16	18:47	10:19	20:57	10:40	18:08	
Mesozooplankton (< 1 mm)	49.50	242.71	108.75	199.24	1259.24	112.03	179.29	87.65	143.16	55.22	136.33	1020.11	61.50	1813.81	87.89	606.67	6163.08
Copepods	44.05	206.43	99.75	159.41	1083.24	29.92	149.18	53.62	80.77	45.11	81.66	805.91	38.83	775.16	86.82	536.33	4276.20
<i>Euterpina acutifrons</i>	13.85	0.89	2.01	1.06	14.26	0	5.92	0	0.83	0.91	3.19	0.07	0.67	0	0	1.12	44.80
<i>Oithona</i> spp.	8.50	92.38	19.71	117.03	733.14	12.91	48.70	29.68	38.78	9.94	29.23	155.20	6.17	422.77	68.67	71.86	1864.66
<i>Paracalanus</i> spp. + Calanoida copepodites	21.70	113.15	78.03	41.31	335.84	17.02	94.56	23.94	41.16	34.26	49.24	650.63	32.00	352.40	18.15	463.35	2366.73
Unidentified nauplii	0	1.89	0.33	10.17	0	0.22	1.33	0.33	1.33	0.56	0.50	0	0.50	0	0	0	17.16
Cladocerans	0.95	28.20	1.67	27.33	120.33	78.67	14.78	30.72	50.33	7.17	52.83	214.20	21.50	1038.64	1.07	70.33	1758.72
<i>Evadne nordmanni</i>	0	17.00	0.56	16.17	65.89	55.83	4.83	11.79	37.51	2.33	13.54	180.93	0.35	531.89	0	9.07	947.69
<i>Podon</i> spp.	0.95	11.20	1.11	11.16	54.44	22.84	9.95	18.93	12.82	4.84	39.29	33.27	21.15	506.75	1.07	61.26	811.03
Veliger stages of Lamellibranchs	4.50	6.20	7.00	2.33	55.67	3.22	14.00	2.97	10.72	2.39	1.33	0	0.67	0	0	0	111.00
Mesozooplankton (1-2 mm)	3.50	133.74	24.85	1202.98	253.76	31.30	141.41	93.40	51.34	35.53	36.29	3114.25	19.00	280.82	26.64	46.98	5495.77
Copepods*	2.05	7.99	20.51	9.65	77.76	1.41	35.07	27.96	11.90	3.80	16.12	980.58	3.00	131.33	0.71	33.31	1363.16
Fish eggs	0.50	2.73	2.33	1192.17	24.67	10.11	7.11	43.05	5.94	0.33	19.17	0	15.67	142.82	24.60	7.33	1498.54
Anchovy eggs	0	1.93	0.67	132.33	24.67	10.11	7.11	41.76	5.94	0.33	19.17	0	15.33	142.82	17.46	7.33	426.97
Unidentified fish eggs	0.50	0.8	1.66	1059.84	0	0	0	1.29	0	0	0	0	0.34	0	7.14	0	1071.57
Appendicularians	0.95	123.01	2.00	1.17	151.33	19.78	99.22	22.39	33.50	31.39	1.00	2133.67	0.33	6.67	1.33	6.33	2634.07
Macrozooplankton (> 2 mm)	0	0	1	1.55	0	0	3	235	0	0	1	20	0	9	0	1	272.42
Copepods	0	0	0.40	0.21	0	0	2.96	234.00	0	0	0.93	20.37	0	2.59	0	0.22	261.69
<i>Calanoides carinatus</i>	0	0	0.40	0.21	0	0	2.96	234.00	0	0	0.93	20.37	0	2.59	0	0.22	261.69
Decapod larvae	0	0.47	0.33	1.33	0	0.33	0.22	0.44	0	0	0	0	0	6.67	0	0.80	10.60
Amphipods	0	0	0	0	0	0	0	0.07	0.07	0	0	0	0	0	0	0	0.13
Total	53.00	376.92	134.33	1403.77	1513.00	143.66	323.88	415.56	194.56	90.74	173.54	4154.73	80.50	2103.88	114.53	654.67	11931.28
Copepods (%)	86.98	56.89	89.83	12.06	76.73	21.81	57.80	75.94	47.63	53.90	56.88	43.49	51.97	43.21	76.43	87.05	49.46
Appendicularians (%)	1.79	32.64	1.49	0.08	10.00	13.77	30.63	5.39	17.22	34.59	0.58	51.36	0.41	0.32	1.16	0.97	22.08
Cladocerans (%)	1.79	7.48	1.24	1.95	7.95	54.76	4.56	7.39	25.87	7.90	30.44	5.16	26.71	49.37	0.93	10.74	14.74
Fish eggs (%)	0.94	0.73	1.74	84.93	1.63	7.04	2.20	10.36	3.06	0.37	11.04	0	19.46	6.79	21.48	1.12	12.56

Table 2. Taxonomic composition and abundance (ind m⁻³) of zooplankton in coastal reproductive habitat (CRH) of anchovy. (SD: standard deviation). **Ctenocalanus vanus*, *Clausocalanus brevipes*, *Centropages brachiatus* and Calanoida copepodites.

Tabla 2. Composición taxonómica y abundancia (ind m⁻³) de zooplancton en el hábitat reproductivo costero (HRC) de la anchoíta (SD: desviación estándar). **Ctenocalanus vanus*, *Clausocalanus brevipes*, *Centropages brachiatus* and Calanoida copepodites.

Taxa	Mean	SD	Abundance range
Mesozooplankton < 1 mm	988.92	1233.54	134.23 - 4546.16
Copepods	736.61	1164.65	61.13 - 4408.57
<i>Euterpina acutifrons</i>	10.38	34.42	0 - 124.77
<i>Oithona</i> spp.	156.10	154.92	13.37 - 518.67
<i>Paracalanus</i> spp. + Calanoida copepodites	570.13	1107.14	46.98 - 4173.52
Unidentified nauplii	27.20	68.94	0 - 254.44
Cladocerans	212.08	324.92	2.44 - 1206.41
<i>Evadne nordmanni</i>	130.83	235.38	0 - 820.55
<i>Podon</i> spp.	81.25	115.03	0 - 385.86
Veliger stages of Lamellibranchs	13.03	22.74	0 - 74.52
Mesozooplankton 1-2 mm	144.42	116.86	25.84 - 396.03
Copepods*	76.92	86.97	3.25 - 286.64
Fish eggs	9.88	11.50	0 - 33.76
Anchovy eggs	9.59	11.05	0 - 31.93
Unidentified fish eggs	0.29	0.56	0 - 1.83
Appendicularians	57.63	87.41	0 - 327.77
Macrozooplankton > 2 mm	7.81	13.36	0.58 - 50.31
Copepods	1.52	2.83	0 - 10.7
<i>Calanoides carinatus</i>	1.52	2.83	0 - 10.7
Decapod larvae	1.97	5.69	0 - 20.80
Amphipods	0.04	0.09	0 - 0.27
Chaetognaths	3.30	4.91	0 - 16.88
Pteropods	0.97	3.39	0 - 12.23

this area (Hansen, 2004), which agrees with the cited preference of this species for salinity frontal regions (Martos *et al.*, 2005).

Although the low number of samples does not allow to be conclusive, these results support the hypotheses that this area could be a preferred site of intense food intake by anchovy within less productive coastal waters.

The different time of the day when samples were collected might reduce the significance of this finding, taking into account that a diel feeding cycle has been described for *E. anchoita* (Angelescu, 1982). However, this cycle was observed mainly in shelf waters where two periods of feeding activity at sunset and sunrise were reported. On the contrary, in the CRH this pattern was weak probably due to lower food availability. Under these conditions of limited food availability an extended feeding period has been

observed in *E. anchoita* and several other anchovy species (Angelescu, 1982; Tudela & Palomera, 1997; Pájaro, 2002).

In this study, most of items ingested by anchovies belonged to < 1 mm and 1-2 mm TL mesozooplankton fractions. According to Angelescu (1982), these prey size (< 2 mm) would correspond to a filtration feeding mechanism in Argentine anchovy. The prey spectrum found is in accordance with the taxonomic groups mentioned by other authors in the CRH where the copepods were the main prey of anchovy followed by appendicularians and cladocerans (Capitanio *et al.*, 1997; Mianzan *et al.*, 2001; Pájaro *et al.*, 2007).

However, the large incidence of small copepods (< 1 mm TL) in Argentine anchovy diet is highlighted in this work because they were, for the first time, accurately identified and quantified. These results agree with those frequently reported for European

anchovy (Tudela & Palomera, 1997; Plounevez & Champalbert, 1999, 2000; Borme *et al.*, 2009).

The main small copepod species found in stomach content were *Paracalanus* spp., *Oithona* spp. and copepodite stages of Calanoida. It is known that these copepods form dense aggregations associated with saline discontinuities of the estuarine front (Viñas *et al.*, 2002; Marrari *et al.*, 2004).

Small copepods are important links in marine food webs, acting not only as major grazers of small phytoplankton but also preying upon heterotrophic protists which are components of the microbial loop (Turner, 2004). Thus, they might play a significant role in the energy transfer to anchovy by an alternative pathway to the traditional herbivorous food web of shelf waters: spring diatom bloom-herbivorous calanoid copepods-fish.

The species composition and relative abundance observed in zooplankton samples coincided roughly with the stomach contents. However, despite of the large abundance of small copepods in anchovy diet, a clear selectivity for prey greater than 1 mm TL was observed in this work. This might be explained by a decrease in retention efficiency of small prey by the filtering apparatus of larger fishes. In fact, an increase in gill-raker spacing with anchovy size has been previously shown (Angelescu, 1981).

Intensive predation on patches of unidentified fish eggs and appendicularians was observed in two specific hauls in northern and southern sectors of the study area respectively. Fish eggs aggregations are frequently found in the RdP estuary, belonging of about twenty fish species including anchovy that spawn pelagic eggs there (Madirolas *et al.*, 1997; Berasategui *et al.*, 2004). On the other hand, appendicularians are known to form dense breeding patches near the surface water during the sexual maturity period (Fenau, 1985; Capitanio *et al.*, 1997). Anchovy predation on these occasional prey patches confirms its opportunistic feeding habits.

Some authors suggest that the planktivorous fishes spawn in zooplankton-rich locations, which is reasonable due to the high energetic cost of reproduction (Hunter & Leong, 1981; Peebles *et al.*, 1996; Peebles, 2002). In fact, Patagonian anchovy stock spawns in a frontal area where high biomass of copepods has been detected (Ramírez *et al.*, 1990). However, in the CRH of the northern stock it has been widely mentioned that feeding conditions are unfavourable for anchovy adults (Angelescu, 1982; Ciechowski & Sánchez, 1983; Pájaro, 2002; Pájaro *et al.*, 2007). Pájaro (2002) proposed that favourable conditions for the adults might not be the same for

eggs and larvae, due to the fact that greatest amounts of large zooplankton also mean higher amounts of potential predators. According to this, the strategy of the fishes could consist in feeding in shelf waters, which is dominated by high concentrations of large zooplankton, and subsequently migrate into the CRH where dominant small zooplankton is suitable for feeding larvae (Pájaro, 2002).

The present findings, although based on few samples, would suggest that in RdP front, the above mentioned strategy should be revised since intense feeding occurs in this sector of the CRH. The coincidence of both feeding and spawning grounds could have important implications. It might be expected an increased reproductive potential of *E. anchoita* in the estuarine front as it was reported for other anchovy species spawning in food rich areas (Peebles *et al.*, 1996). Further studies are required to confirm this observation.

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REFERENCES

- Acha, M.E., H. Mianzan, R. Guerrero, J. Carreto, D. Giberto, N. Montoya & M. Carignan. 2008. An overview of physical and ecological processes in the Río de la Plata Estuary. *Cont. Shelf Res.*, 28: 1579-1588.
- Angelescu, V. 1981. Ecología trófica de la anchoíta del Mar Argentino (Engraulidae, *Engraulis anchoita*). Parte I. Morfología del sistema digestivo en relación con la alimentación. *Acta VIII Congreso Latinoamericano de Zoología, Mérida*, pp. 1317-1350.
- Angelescu, V. 1982. Ecología trófica de la anchoíta del Mar Argentino (Engraulidae, *Engraulis anchoita*). Parte II. Alimentación, comportamiento y relaciones tróficas en el ecosistema. *Ser. Contrib. Inst. Nac. Invest. Des. Pesq.*, 409: 83.
- Angelescu, V. & A. Anganuzzi. 1981. Ecología trófica de la anchoíta del Mar Argentino (Engraulidae, *Engraulis anchoita*) en el área explorada por el B/I "Shinkai Maru" durante las campañas VI y VIII en el Mar Argentino. *Ser. Contrib. Inst. Nac. Invest. Des. Pesq.*, 383: 281-298.

- Berasategui, A.D., E.M. Acha & N.C. Fernández-Araoz. 2004. Spatial patterns of ichthyoplankton assemblages in the Río de la Plata estuary (Argentina, Uruguay). *Estuar. Coast. Shelf Sci.*, 60: 599-610.
- Borme, D., V. Tirelli, S.B. Brandt, S. Fonda Umani & E. Arneri. 2009. Diet of *Engraulis encrasicolus* in the northern Adriatic Sea (Mediterranean): ontogenetic changes and feeding selectivity. *Mar. Ecol. Prog. Ser.*, 392: 193-209.
- Capitaino, F.L., M. Pájaro & G.B. Esnal. 1997. Appendicularians (Chordata, Tunicata) in the diet of anchovy (*Engraulis anchoita*) in the Argentine Sea. *Sci. Mar.*, 61: 9-15.
- Carreto, J.I., R.M. Negri & H.R. Benavides. 1986. Algunas características del florecimiento del fitoplancton en el Frente del Río de la Plata. Parte 1: Los sistemas nutritivos. *Rev. Invest. Des. Pesq.*, 5: 7-29.
- Carreto, J.I., V. Lutz, M. Carignan, A.D. Cucchi Coleoni & S. De Marco. 1995. Hydrography and chlorophyll *a* in a transect from the coast to the shelf-break in the Argentine Sea. *Cont. Shelf Res.*, 15(2/3): 315-336.
- Ciechomski, J.D. & R.P. Sánchez. 1983. Relationship between ichthyoplankton abundance and associated zooplankton biomass in shelf waters of Argentina. *Biol. Oceanogr.*, 3: 77-101.
- Chesson, J. 1978. Measuring preference in selective predation. *Ecology*, 59: 211-215.
- Fenaux, R. 1985. Rhythm of secretion of Oikopleurid houses. *Bull. Mar. Sci.*, 37: 498-503.
- Guerrero, R.A. 1998. Oceanografía física del estuario del Río de la Plata y el sistema costero de El Rincón. Noviembre 1994. INIDEP, Informes Técnicos, 21: 29-54.
- Guerrero, R.A., E.M. Acha, M.B. Framiñán & C.A. Lasta. 1997. Physical oceanography of the Río de la Plata estuary, Argentina. *Cont. Shelf Res.*, 17: 727-742.
- Hansen, J.E. 2004. Evaluación de anchoíta bonaerense en la primavera del año 2004. Plan e informe de campaña. INIDEP, Mar del Plata (MS): 43 pp.
- Hansen, J.E., M.B. Cousseau & D.L. Gru. 1984. Características poblacionales de la anchoíta (*Engraulis anchoita*) del Mar Argentino. Parte I. El largo medio al primer año de vida, crecimiento y mortalidad. *Rev. Invest. Des. Pesq.*, 4: 21-48.
- Hansen, J.E. & A. Madirolas. 1996. Distribución, evaluación acústica y estructura poblacional de la anchoíta. Resultados de las campañas del año 1993. *Rev. Invest. Des. Pesq.*, 10: 5-21.
- Hunter, J.R. & R. Leong. 1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. *Fish. Bull. U.S.*, 79(2): 215-230.
- Leong, R.J.H. & C.P. O'Connell. 1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). *J. Fish. Res. Board Can.*, 26: 557-582.
- Madirolas, A., E.M. Acha, R. Guerrero & C. Lasta. 1997. Sources of acoustic scattering near a halocline in an estuarine frontal system. *Sci. Mar.*, 61(4): 431-438.
- Marrari, M., M.D. Viñas, P. Martos & D. Hernández. 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., J.E. Hansen, R.M. Negri & A. Madirolas. 2005. Factores oceanográficos relacionados con la abundancia relativa de anchoíta sobre la plataforma bonaerense (34°S-41°S) durante la primavera. *Rev. Invest. Des. Pesq.*, 17: 5-33.
- Mianzan, H., M. Pájaro, G. Alvarez Colombo & A. Madirolas. 2001. Feeding on survival-food: gelatinous plankton as a source of food for anchovies. *Hydrobiology*, 451: 45-53.
- Motos, L., A. Uriarte & V. Valencia. 1996. The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus* L.). *Sci. Mar.*, 60 (Suppl. 2): 117-140.
- Pájaro, M. 2002. Alimentación de la anchoíta argentina (*Engraulis anchoita* Hubbs y Marini, 1935) (Pisces: Clupeiformes) durante la época reproductiva. *Rev. Invest. Des. Pesq.*, 15: 111-125.
- Pájaro, M., J. Curelovich & G.J. Macchi. 2007. Egg cannibalism in the northern population of the Argentine anchovy, *Engraulis anchoita* (Clupeidae). *Fish. Res.*, 83: 253-262.
- Palomera, I. 1992. Spawning of anchovy *Engraulis encrasicolus* in the northwestern Mediterranean relative to hydrographic features in the region. *Mar. Ecol. Prog. Ser.*, 79: 215-223.
- Peebles, E.B. 2002. Temporal resolution of biological & physical influences on bay anchovy *Anchoa mitchilli* egg abundance near a river-plume frontal zone. *Mar. Ecol. Prog. Ser.*, 237: 257-269.
- Peebles, E.B., J.R. Hall & S.G. Tolley. 1996. Egg production by the bay anchovy *Anchoa mitchilli* in relation to adult and larval prey fields. *Mar. Ecol. Prog. Ser.*, 131: 61-73.
- Plounevez, S. & G. Champalbert. 1999. Feeding behaviour and trophic environment of *Engraulis*

- encrasicolus* (L.) in the Bay of Biscay. Estuar. Coast. Shelf Sci., 49: 177-191.
- Plounevez, S. & G. Champalbert. 2000. Diet, feeding behaviour and trophic activity of *Engraulis encrasicolus* (L.) in the Gulf of Lions (Mediterranean Sea). Oceanol. Acta, 23: 175-192.
- Ramírez, F.C., H. Mianzan, B. Santos & M.D. Viñas. 1990. Synopsis on the reproductive biology and early life of *Engraulis anchoita*, and related environmental conditions in Argentine waters. Zooplankton. IOC Workshop Rep. 65(V): 4-6.
- Sánchez, R.P. & J.D. Ciechomski. 1995. Spawning and nursery grounds of pelagic fish species in the sea-shelf off Argentina and adjacent areas. Sci. Mar., 59(3/4): 455-478.
- Schwingel, R.P. & J.P. Castello. 1994. Alimentación de la anchoíta (*Engraulis anchoita*) en el sur de Brasil. Frente Marítimo, 15(A): 67-86.
- Tudela, S. & I. Palomera. 1997. Trophic ecology of the European anchovy *Engraulis encrasicolus* in the Catalan Sea (northwest Mediterranean). Mar. Ecol. Prog. Ser., 160: 121-134.
- Turner, J.T. 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool. Stud., 43(2): 255-266.
- Viñas, M.D., R.M. Negri, F.C. Ramírez & D. Hernández. 2002. Zooplankton assemblages and hydrography in the spawning area of anchovy (*Engraulis anchoita*) off Río de la Plata estuary (Argentine, Uruguay). Mar. Freshw. Res., 53(6): 1031-1043.

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