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FEEDING HABITS OF *Engraulis anchoita* LARVAE OFF SOUTHERN BRAZIL

[Hábitos alimentares das larvas de *Engraulis anchoita* no sul do Brasil]

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ABSTRACT

The aim of this work was to investigate the feeding habits of *Engraulis anchoita* larvae off the extreme south of Brazil. Samples were collected using 60 cm Bongo net (300 mm mesh aperture) during the different seasons of the year: spring, summer, autumn and winter (1987-1991). A total of 1231 larvae (2.8-34 mm SL) were analyzed. The smallest larva with gut contents was 3.4 mm long; 40% of the larvae 3.4-4 mm long had at least one item in their guts. A reduction of the feeding incidence in larvae 6-8 mm was observed, suggesting that this could be a critical period for survival. Copepod nauplii, copepod adults, invertebrate eggs and copepodites were the main items identified in the larval diet. Starch grains and fungal spores were also found among gut contents. The structure of the branchial arches suggests that filtration of small particles is not an adequate feeding method for the larvae. High feeding incidences occurred during the night, with items probably ingested through a passive mechanism. Winter is suggested as the most favorable season for larval feeding, with high probability of prey consumption due to shelfbreak upwelling, high vertical stability in the water column, and to high production in the coastal region. The current study on larval feeding habits contributes to a better understanding of the dynamics of this species that dominated the ichthyoplankton and pelagic nektonic community in this region during those periods.

Key words: *Engraulis anchoita*, anchovy, larvae, feeding, Atlantic Ocean, Brazil

RESUMO

Este trabalho teve por objetivo investigar os hábitos alimentares das larvas *de Engraulis anchoita* no extremo sul do Brasil. As amostras foram coletadas na primavera, verão, outono e inverno (1987-1991), utilizando rede Bongo com 60 cm de boca e abertura de malha de 300 mm. Um total de 1231 larvas foram analisadas, com um comprimento padrão (CP) entre 2,8 e 34 mm. A menor larva com conteúdo alimentar tinha 3,4 mm (CP); 40% das larvas no intervalo de 3,4 a 4 mm apresentaram pelo menos um item alimentar em seu trato digestivo. Uma redução da incidência de alimento em larvas de 6-8 mm foi observada, sugerindo que este poderia ser um período crítico. Náuplios de copépode, copépodes adultos, ovos de invertebrados e copepoditos foram os principais componentes da dieta larval. Grãos de amido e esporos de fungo também foram encontrados no trato digestivo. A estrutura dos arcos branquiais sugere que a filtração de pequenas partículas não é o método de alimentação destas larvas. Elevadas incidências de alimento ocorreram durante a noite, relacionando-se à provável ingestão de ítens através de um mecanismo passivo. O inverno é sugerido como a estação mais favorável para a alimentação destas larvas, com elevada probabilidade de consumo de presas relacionada a uma ressurgência de quebra de plataforma, a uma elevada estabilidade vertical da coluna d'água e a águas costeiras com significativa produtividade.

Palavras-chave: *Engraulis anchoita*, larva, alimentação, Oceano Atlântico, Brasil

Introduction

The genus *Engraulis* is widely distributed and *Engraulis anchoita* occurs in the southwestern Atlantic Ocean, from 22° S through 47° S, between the coast and the continental edge (WHITEHEAD; NELSON; WONGRATANA, 1988). During the winter, high biomass of *E. anchoita* is found in the extreme south of Brazil, between 32° and 35° S (MELO, 1978; LIMA and CASTELLO, 1995; CASTELLO, 1997). Despite not being commercially exploited in Brazil, where there have been only trial fishing activities, this species offers an important alternative for fishers.

Engraulis anchoita spawns in the extreme south

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of Brazil virtually all year round, with a peak occurring in winter and spring, when adult biomass reaches very high levels (WEISS and SOUZA, 1977; Lima and CASTELLO, 1995). Egg and larval dispersion to regions of unfavorable abiotic conditions, along with predation and cannibalism upon eggs and larvae, represent part of the mortality suffered by fishes. However, food availability during the initial period of exogenous feeding also may be a major cause of recruitment variability (HJORT, 1914; LASKER, 1981a,b; JOBLING, 1995).

Food availability is conditioned by a combination of enrichment, stability and retention mechanisms (BAKUN, 1996). Even when food is available enough, the larval ability to ingest and digest preys depends on a combination of their functional, anatomical, physiological and behavioral characteristics (KAMLER, 1992). HEATH (1996) links all these aspects and suggests that interactions between dispersal patterns and the dynamics of plankton are of critical importance for larval survival.

Since feeding may be critical in the initial stages of *E. anchoita* larvae, this work was conducted in order to identify the main food items consumed by these larvae in that region, by evaluating the ontogenetic diet variations, examining the daily feeding rhythms, analyzing the relationship between diet and the development of the mouth, gill apparatus and gut, and relating feeding patterns to abiotic and biotic conditions in the region. Understanding the processes that take place during the initial phases of fish development is of fundamental importance in recruitment studies.

Material and Methods

Engraulis anchoita larvae were collected during the cruises of the Project "Avaliação do Ecossistema Pelágico do Extremo Sul do Brasil - ECOPEL" (Pelagic Ecosystem Evaluation in the Extreme South of Brazil): ECOPEL I (Spring of 1987), ECOPEL II (Winter of 1998), ECOPEL III (Summer of 1990) and ECOPEL IV (Autumn of 1991) (Table 1). The sample plan consisted of transects perpendicular to the coast at 15 nautical mile intervals, with samples collected 20 nautical miles apart (Figure 1). Anchovy larvae were collected using Bongo nets with a mouth diameter of 60 cm and a mesh aperture of 300 μm, towed at 2.5 knots in oblique hauls from 5 m above bottom to the surface, with a duration of 15-20 minutes. Larvae were preserved in a 4-5% buffered formalin solution.

A total of sixty-three samples were collected and analyzed. Fifty-six of the samples were taken during the day, between 7 and 19 h (local time), and seven of them at night (Table 2). Larvae identified as *E. anchoita* were measured with a micrometric scale under a stereomicroscope. Standard length (SL) and intestinal length were corrected due to the shrinkage caused by handling and fixation according to THEILACKER (1980).

Table 1. Data for each ECOPEL cruise: Date, percentage of samples collected in each cruise that contained *E. anchoita* larvae (positive samples), and total number of larvae (N) and samples analyzed

Cruise	Date	Positive samples (%)	Number			
			Larvae (N)	Samples	Day samples	Night samples
ECOPEL I (Spring)	OCT/87	79.6	257	20	19	1
ECOPEL II (Winter)	SEP/88	77.4	700	27	21	6
ECOPEL III (Summer)	FEB/90	38.2	55	4	4	0
ECOPEL IV (Autumn)	JUN-JUL/91	59.3	219	12	12	0
Total	-	-	-	63	56	7
N	-	-	1231	-	1042	189

Larvae were stained with Bengal pink for observation of the branchial apparatus and mouth width, measured at the largest transversal section on the ventral side. Mouth width was then related to larval size through a linear regression for each cruise, using the least squares method. An analysis of covariance (ANCOVA) was employed in order to determine if there were significant differences in slopes and intercepts among these regressions, followed by a Tukey test to compare each pair of slopes (ZAR, 1984). The number of gill-rakers and the distance between rakers were determined on the largest *rama* of the first left branchial arch.

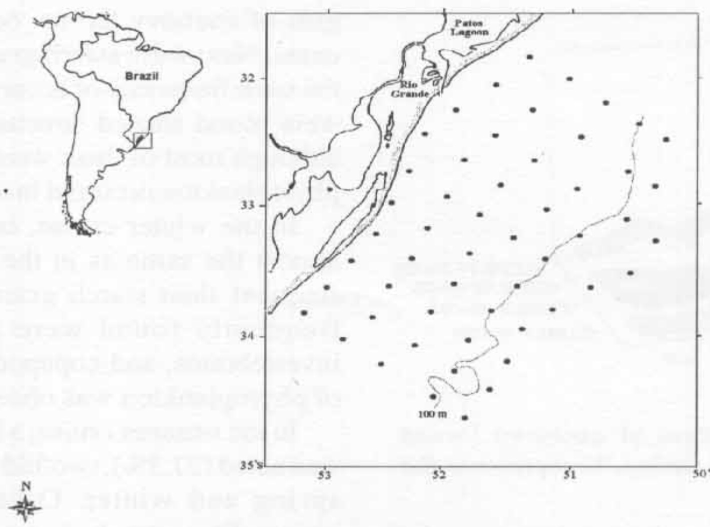

Figure 1. Location of sampling transects for ECOPEL Project. Black circles indicate sampling stations

Table 2. Feeding incidence in percentage for each ECOPEL cruise for day and night samples, pooled and separated. N represents total number of larvae analyzed

CRUISE	Day and Night Incidence (%)		Day Incidence (%)		Night Incidence (%)	
ECOPEL I	36.2	257	37.6	242	20.0	15
ECOPEL II	51.7	700	57.4	526	37.4	174
ECOPEL III	41.8	55	41.8	55	-	0
ECOPEL IV	33.8	219	33.3	219	-	0
Total	44.8	1231	46.9	1042	36.0	189

The hindgut was dissected following Viñas and Ramirez (1996) and Neira; Miskiewicz; Trnski (1998). Gut contents were identified to the lowest possible taxonomic level under a microscope and a stereomicroscope, after being stained with Bengal pink or lugol. The greatest width of the ingested specimens was measured using a micrometric scale and compared to mouth width for each larval size.

Feeding incidence, used as an index of feeding success, was defined as the percentage of the larvae, caught in each cruise, that had food in the gut. Cluster analysis was employed to assess differences among cruises, using Euclidean distance and unweighted pair-group average - UPGMA (Ludwig and Reynolds, 1988). Feeding incidence during the day was determined for two-hour periods, and compared using a chi-square test (Zar, 1984). The Friedman test was employed (Siegel, 1975) to assess differences among larval sizes related to the incidence of each food organism. All statistical tests were carried out using the software STATISTICA (Version 5.0).

Feeding patterns were related to abiotic and biotic conditions in this region, using the ECOPEL Technical Reports.

Results

Length distribution of the analyzed larvae and feeding incidence

A total of 1231 larvae of *Engraulis anchoita* were analyzed from 63 samples taken during the four cruises. Larvae ranged from 2.8 to 34 mm standard length (SL); 93.4% of them were <16 mm long (Figure 2). The four cruises were pooled and 44.8% of the larvae had at least one item in their guts. When only day samples were analyzed (1042 larvae), feeding incidence was 46.9% (Table 3). In night samples (189 larvae), the incidence was 36.0%.

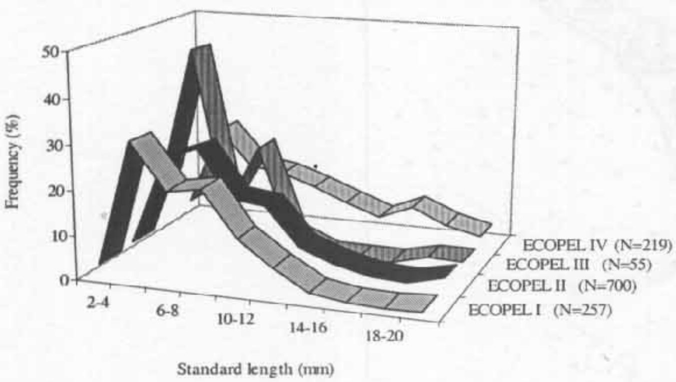

Figure 2. Length distribution of anchovy larvae (*Engraulis anchoita*) in each cruise. N represents the number of larvae analyzed

Food items and the relationship between feeding incidence and larval length

In the spring cruise, the nauplii of copepods presented the highest frequency of occurrence in the guts of anchovy larvae, occurring on 13.2% of the cases. Next were starch grains and copepodites, with the same frequency of occurrence (6.6%). Starch grains were round shaped structures of 5-50 μm diameter, although most of them were 10-20 μm (Figure 3). No phytoplankton occurred in any larvae (Table 3).

In the winter cruise, occurrence of nauplii was almost the same as in the spring (13.9%), but less frequent than starch grains (29.7%). Other items frequently found were fungal spores, eggs of invertebrates, and copepod adults. A low incidence of phytoplankton was observed.

In the summer cruise, a high occurrence of nauplii was noted (27.3%), twofold of the one observed during spring and winter. Other common items were copepodites, starch grains, and copepod adults, but no phytoplankton was found in the diet.

In the autumn cruise, nauplii were the most frequently found item (20.1%), followed by copepodites (9.1%) and copepod adults

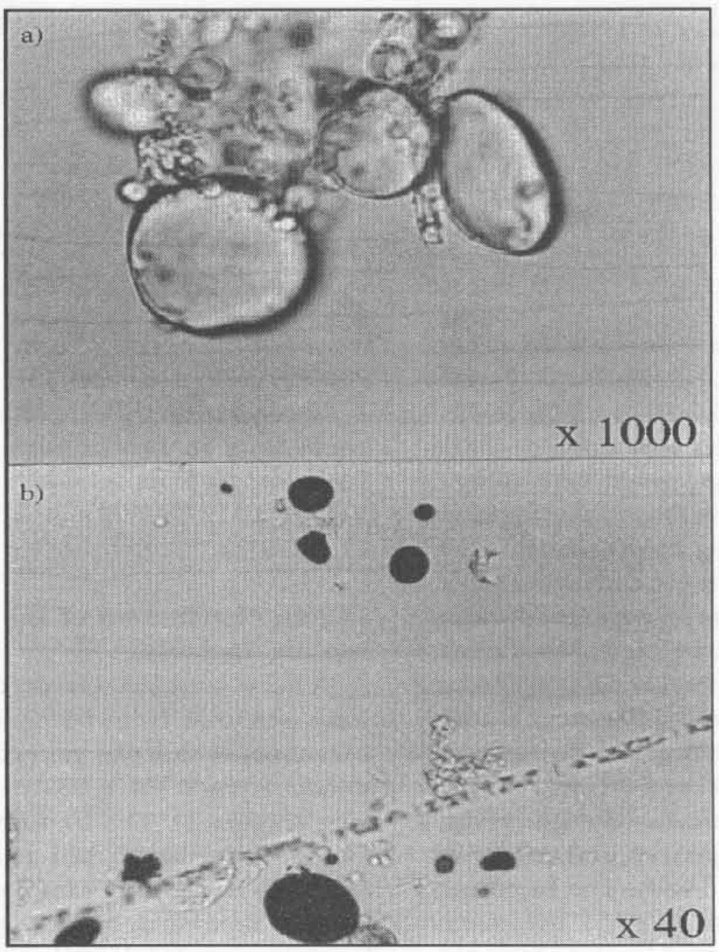

Figure 3. Starch grains: a) Not stained; b) Stained with lugol

Table 3. Percentage of incidence for each food item in gut contents of *E. anchoita* larvae for each cruise

Food item	ECOPEL I (Spring)	ECOPEL II (Winter)	ECOPEL III (Summer)	ECOPEL IV (Autumn)
Nauplii	13.2	13.9	27.3	20.1
Starch grains	6.6	29.7	3.6	1.4
Copepodites	6.6	2	5.4	9.1
Fungal spores	6.2	7.7	3.6	1.8
Eggs of invertebrates	3.1	4.9	1.8	2.7
Copepod adults	2.3	4.6	3.6	4.6
Calanoida	0.8	3.1	0	4.1
Cyclopoida	0.8	0.1	1.8	0.5
Tintinnids	0	1.9	0	0
Phytoplankton	0	0.4	0	2.3
Unidentified crustaceans	0.8	1.4	0	1.4
Unidentified items	3.9	14.3	3.6	4.1
Total number of larvae	257	700	55	219

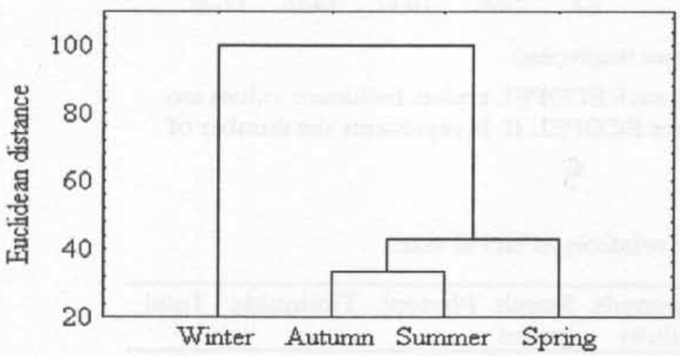

Figure 4. Dendrogram of the clustering of the four cruises (spring, winter, summer and autumn) using Euclidean distance and UPGMA

(4.6%). Observations of Calanoida were more frequent than those of the Cyclopoida, also observed in the winter cruise. Phytoplankton presented the highest frequency in the cruises analyzed (2.3%).

When all cruises were pooled based on the composition of the food items, two main clusters were observed: one that includes autumn, spring and summer, and another one representing just the winter (Figure 4).

Among the copepods, the following species were identified: *Centropages brachiatus, Paracalanus nanus, Paracalanus* spp., *Clausocalanus* spp., *Ctenocalanus vanus*, Pseudocalanidae, Oncaeidae, Oithonidae, *Corycaeus* spp. and *Euterpina acutifrons*. The phytoplankton components were represented by *Prorocentrum* spp., *Ceratium* spp., centric diatoms and flagellates.

A high feeding incidence of 25 to 62% was observed in first-feeding larvae (2-4 mm) on each cruise (Figure 5). Winter feeding incidences were always equal to or higher than 40% for all larval sizes. The smallest larva from the four cruises with at least one food item in its gut was 3.4 mm long. Among larvae of 3.4 to 4 mm SL, 40% had contents that included: nauplii of copepods, tintinnids, fungal spores, starch grains, eggs of invertebrates, centric diatoms and *Prorocentrum* spp.

Nauplii of copepods occurred in all length classes up to 18 mm, with a 10 to 20% incidence (Table 4). Starch grains occurred in all length classes, with the lowest values appearing in classes of 2 to 4 mm and 16 to 18 mm, and the highest values in larvae >20 mm. With increase in larval size, the incidence of copepodites also increased, but the incidence decreased among larvae >14 mm. The incidence of copepod adults showed a continuous increase. Eggs of invertebrates, tintinnids and phytoplankton presented a very reduced incidence.

Relationship between feeding incidence and time of day

Data on feeding incidence and time of day from the four cruises were pooled. Significant differences were observed in the feeding incidence for each time interval ($p<0.05$). For the day period (7-19 h), feeding incidence was always higher than 30% (Figure 6), but unexpected high incidence values were also observed at night.

As the winter cruise was the one with the highest number of analyzed larvae and with the most night samples, an incidence analysis was undertaken separately for each main food group, using only data from this season (Figure 7). The results show that the ingestion of items such as nauplii of copepods, eggs of invertebrates, copepodites, copepod adults and tintinnids occurred exclusively during the day.

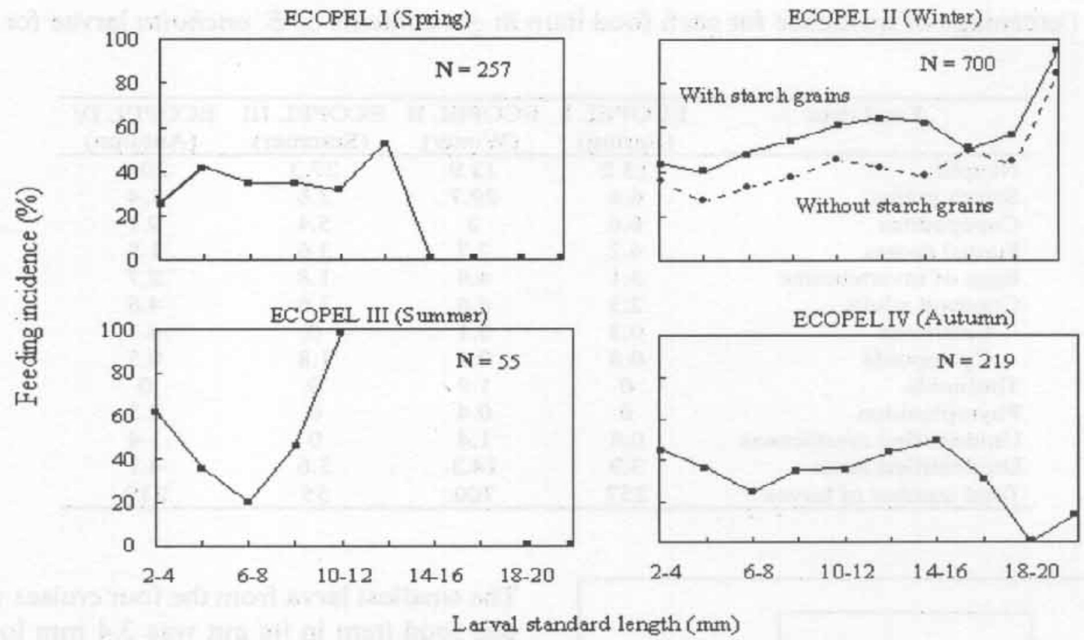

Figure 5. Feeding incidence in each larval size for each ECOPEL cruise. Incidence values are presented including and excluding starch grains for ECOPEL II. N represents the number of larvae analyzed

Table 4. Feeding incidence (%) for all cruises pooled in relation to larval size

Larval size (mm)	Eggs of Invert.	Nauplii	Copepodites	Copepods adults	Starch grains	Phytopl.	Tintinnids	Total
2 - 4	0.04	0.16	0.00	0.00	0.12	0.04	0.06	0.56
4 - 6	0.05	0.27	0.03	0.00	0.33	0.01	0.02	0.94
6 - 8	0.02	0.23	0.04	0.02	0.85	1.60	0.01	3.07
8 -10	0.05	0.26	0.08	0.02	0.55	0.00	0.01	1.32
10 -12	0.04	0.47	0.06	0.07	0.69	0.01	0.00	1.72
12 -14	0.35	0.23	0.25	0.15	1.88	0.01	0.00	3.35
14 -16	0.12	0.34	0.05	0.17	0.32	0.00	0.02	1.20
16 -18	0.16	0.52	0.10	0.35	0.06	0.00	0.00	1.68
18 -20	0.00	0.00	0.00	0.35	0.05	0.00	0.00	0.40
>20	0.87	0.17	0.07	1.63	0.97	0.00	0.00	9.50

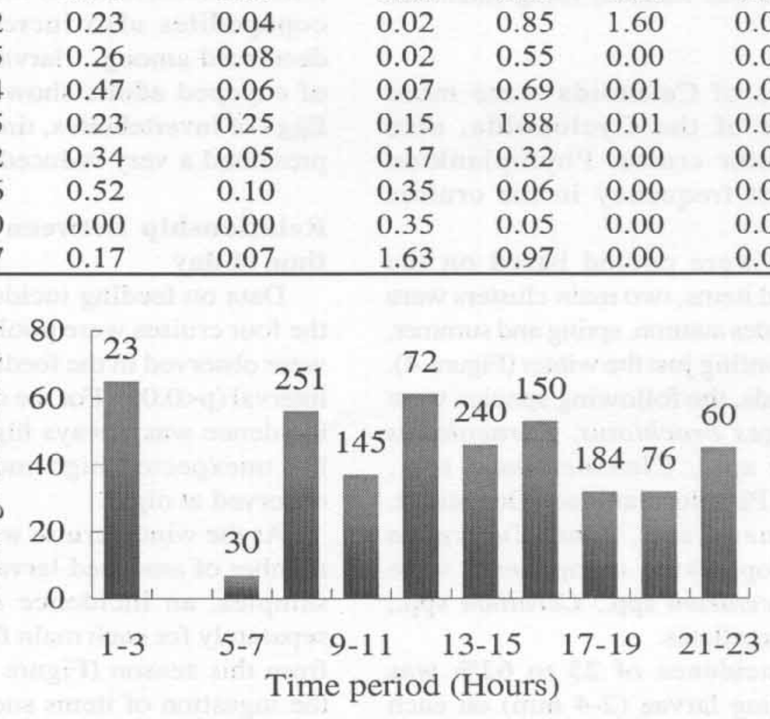

Figure 6. Relationship between feeding incidence and time period. Numbers above columns represent sample size

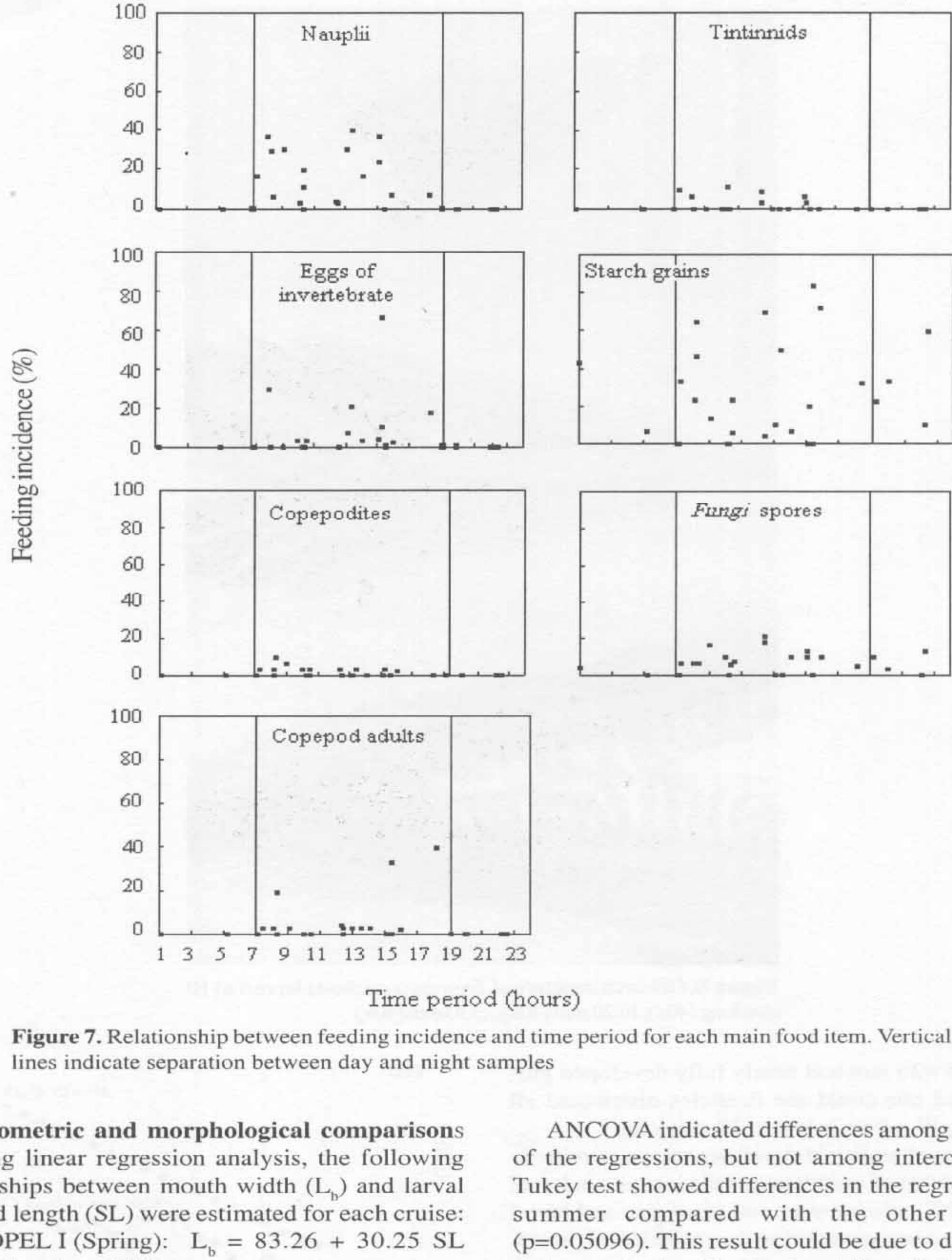

Figure 7. Relationship between feeding incidence and time period for each main food item. Vertical lines indicate separation between day and night samples

Morphometric and morphological comparisons

Using linear regression analysis, the following relationships between mouth width (L_b) and larval standard length (SL) were estimated for each cruise:

ECOPEL I (Spring): $L_b = 83.26 + 30.25$ SL ($r^2 = 0.74$ and n = 200)

ECOPEL II (Winter): $L_b = 110.30 + 26.83$ SL ($r^2 = 0.79$ and n = 550)

ECOPEL III (Summer): $L_b = 22.85 + 40.45$ SL ($r^2 = 0.95$ and n = 44)

ECOPEL IV (Autumn): $L_b = 130.18 + 25.69$ SL ($r^2 = 0.89$ and n = 170)

ANCOVA indicated differences among the slopes of the regressions, but not among intercepts. The Tukey test showed differences in the regression for summer compared with the other seasons (p=0.05096). This result could be due to differences in the sample size. One single relationship is proposed for larval anchovies off Southern Brazil, based on data from all cruises pooled: $L_b = 106.02 + 27.52$ SL (r^2=0.81 and n=964).

The general morphology of gill-rakers is presented in Figure 8. Larvae 12 mm long had rudiments of gill-rakers which first appeared in larvae 8 mm long.

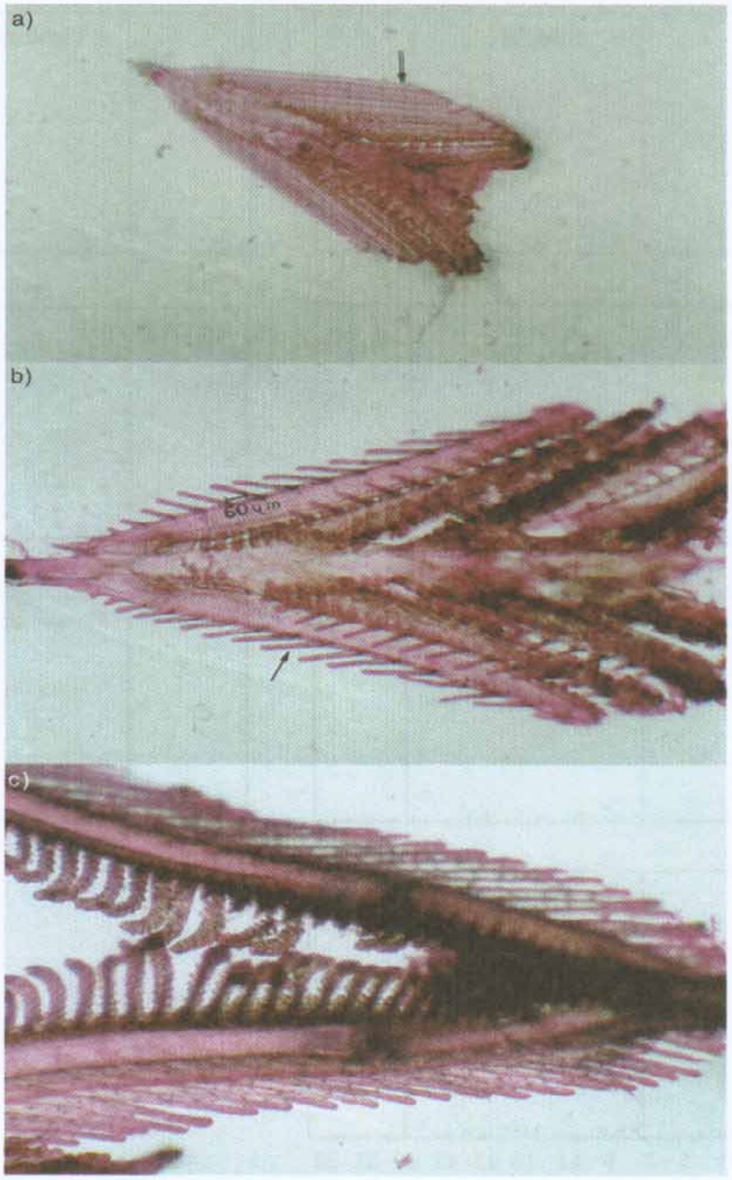

Figure 8. Gill-arch structure of *Engraulis anchoita* larvae: a) 10 mm long (40x); b) 20 mm (40x); c) 30 mm (40x)

Larvae >20 mm had nearly fully developed gill-rakers, and one could see denticles distributed all along the gill-rakers in larvae 30 mm long.

In terms of intestinal development, an increase in size was observed correlating to the increase in larval size. A 50% ratio between intestinal size and larval length was consistent during the entire larval period.

Relationship between food size, mouth width, and larval size

In general, items consumed by *E. anchoita* larvae were from 5 to 400 μm wide. In the winter, some 8 mm larvae fed on items > 300 μm. At this length, a change occurred in the maximum food size ingested,

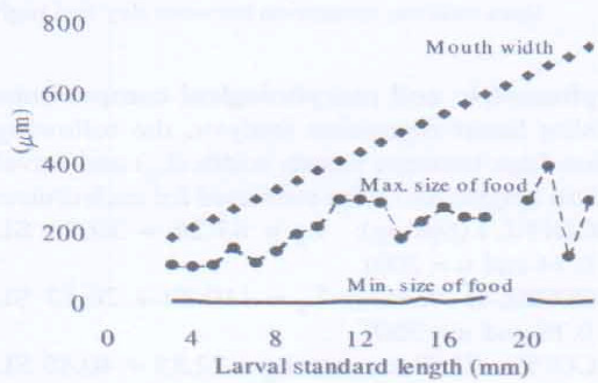

Figure 9. Relationship between mouth width, minimum size and maximum size of prey (μm) and larval standard length for all cruises pooled

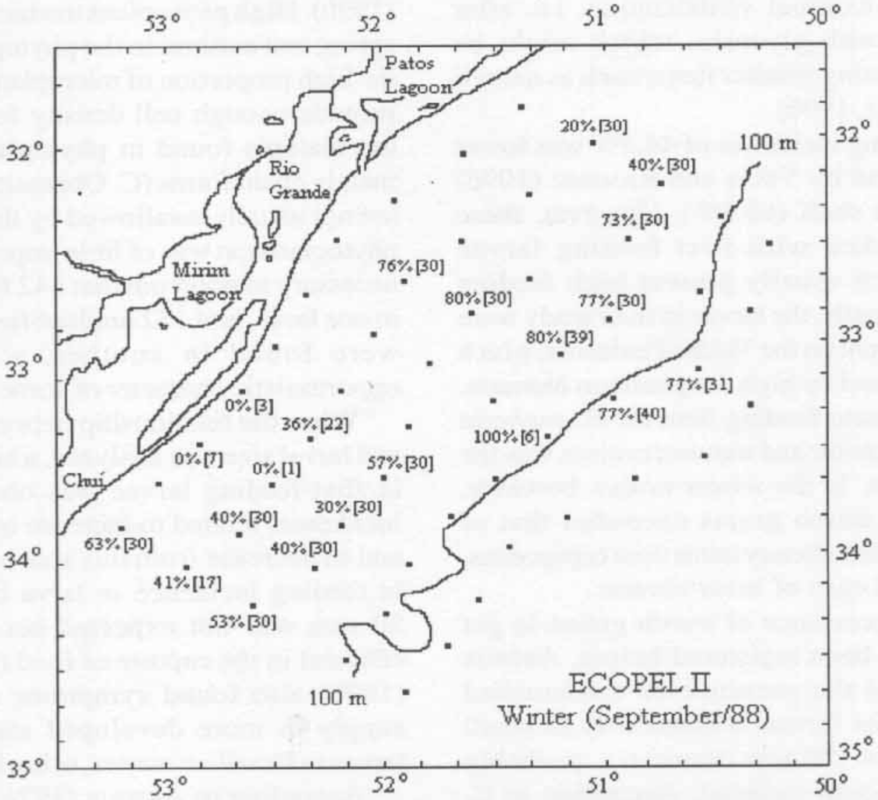

Figure 10. Horizontal distribution of feeding incidence for ECOPEL II (Winter). Percentages represent feeding incidence and numbers in brackets represent number of larvae analyzed

from 150 to 300 μm. The minimum size of ingested items was almost the same in all larval sizes, represented by starch grains, fungal spores and phytoplankton (Figure 9). An increase was observed in the maximum food size consumed by larvae under 12 mm. These, in contrast to larger larvae, fed on items closer to the maximum size allowed by the mouth width.

Horizontal distribution of feeding incidence - ECOPEL II (Winter of 1988)

High feeding incidences were observed in the shelfbreak during the winter, where samples presented incidences of 77 to 100% (Figure 10). Samples from the coastal region in the southern area presented zero incidence (with 7, 1 and 3 larvae analyzed). Further south, incidences of 40 to 63% were found, which characterize the area as favorable with respect to larval feeding. The northern outer shelf region, which lies south of the discharge of Patos Lagoon, had high feeding incidences of 70 to 80%.

Discussion

Engraulis anchoita larvae in the study area represented about 66% of the ichthyoplankton abundance during the spring and 95% during winter (ECOPEL - Technical Reports). In every cruise, more than 30% of *E. anchoita* larvae had contents in their gut. Incidence was 51.7% in the winter cruise, which is a very high value in comparison with the low values generally found in clupeid larvae. ARTHUR (1976) and YAMASHITA (1990) mentioned that low incidences may be caused by defecation during capture. Defecation would be related to the fact that anchovy larval gut is a straight tube in larvae <33 mm (CIECHOMSKI, 1967).

Incidences of larval feeding in this study were also higher than those reported by BERNER (1959) for *Engraulis mordax* off the California coast (1.5%), by SCARLATO (1990) for *E. anchoita* on the continental shelf in the north of Argentina (2.35 to 8.92%) and by SÁNCHEZ and MANAZZA (1994) in the south of Argentina (20%). However, these authors determined food presence by external visualization, i.e. after clearing the gut with glycerin, which might be unsuitable for detecting smaller items such as nauplii (VIÑAS and RAMIREZ, 1996).

The mean feeding incidence of 44.8% was lower than the value found by VIÑAS and RAMIREZ (1996) for the Patagonian shelf (65.3%). However, these authors only worked with first feeding larvae (3 to 5 mm), which usually present high feeding incidences. Additionally, the larvae in their study were collected in a tidal front on the Valdés Peninsula, which is a front characterized by high zooplankton biomass.

The most important feeding item for *E. anchoita* larvae in spring, summer and autumn cruises was the nauplii of copepods. In the winter cruise, however, the occurrence of starch grains exceeded that of nauplii. Other important dietary items were copepodites, copepod adults and eggs of invertebrates.

Although the occurrence of starch grains in gut contents never had been registered before, ARTHUR (1976) pointed out the presence of unidentified spheres in *E. mordax* larvae, defined only as small spherical structures (20 µm diameter), probably originated from vegetal material. According to C. ODEBRECHT (pers.com.), free-floating starch grains also occurred in phytoplankton samples of the ECOPEL Project taken off southern Brazil, possibly discharged into the sea from the ciliate *Mesodinium rubrum*. BURSA (1968) registered starch grains (0.5-36 µm in diameter) free in the sea off Canadian arctic waters, Mediterranean Sea, and Baltic Sea, probably liberated by phytoplankton and benthic algae. It was suggested this could be an important food-source. ALLDREDGE; PASSOW; LOGAN (1993) also discussed about production and liberation of carbohydrates and aminoacids by phytoplankton, which could be assimilated as food by other organisms.

Eggs of invertebrates included those of copepods and echinoderms. Eggs of copepods were almost always attached to the adults. Although they were the fourth most important item, their importance is less than that mentioned by BERNER (1959) for *E. mordax*, CIECHOMSKI (1967) and VIÑAS and RAMIREZ (1996) for *E. anchoita*, and ROJAS DE MENDIOLA and GOMES (1981) for *E. ringens*. The results of this study suggest the possibility that the eggs are not digested, as detected by FLINKMAN; VUORINEN; CHRISTIANSEN (1994), as the eggs found in the gut contents showed no signs of digestion.

Tintinnids and phytoplankton were the least important items in the diet of *E. anchoita* larvae as was also found off Argentina by VIÑAS and RAMIREZ (1996). High phytoplankton biomass found in winter, spring and autumn in the phytoplankton samples and the high proportion of microplankton (>20 µm) would provide enough cell density for feeding. However, the diatoms found in phytoplankton samples were mainly chain forms (C. ODEBRECHT, pers.com.), which are not usually swallowed by these larvae. Although phytoplankton was of little importance in the diet, it is necessary to point out that 442 flagellates were found in one larva, and 152 unidentified spherical structures were found in another, which suggests the opportunistic character of some individuals.

When the relationship between feeding incidence and larval size was analyzed, a high feeding incidence in first-feeding larvae was observed. The feeding incidences tended to increase in larvae up to 14 mm and to decrease from this size onward. The decrease in feeding incidence in larva between 14 mm and 20 mm was not expected because they are more efficient in the capture of food (HUNTER, 1972). SIEG (1998) also found symptoms of insufficient food supply in more developed stages of *E. anchoita* larvae in Brazilian waters, using histological methods.

According to ARTHUR (1976), *Engraulis mordax* adults are zooplankton filters when they feed at night and food selection is based on the size of the available prey. When adults search for favorable feeding conditions, they inadvertently may also select good feeding areas for their larvae. Since adults feed by filtration and also spawn at night, eggs may be released close to adequate food concentrations. Larvae initially grouped in favorable places for feeding would begin to disperse due to water current, and could be dispersed to regions of low food availability, mainly during unfavorable periods of the year. The decrease in feeding incidence, which was observed in 6 to 8 mm larvae in summer and autumn cruises, could be related to this dispersion that occurs after spawning (VASCONCELLOS; FREIRE; CASTELLO, 1998).

The analysis of the daily feeding pattern of *E. anchoita* larvae showed high incidences of some items during the day, which related to the visual detection of prey. Although feeding is fundamentally diurnal, high incidences of gut contents were found in the seven night samples analyzed. These incidences were associated with contents not believed to be captured by active mechanisms of searching and capturing, but were dominated by starch grains and fungal spores, which were probably swallowed by passive way due to their abundance. Such items also may be prevalent in both day and night samples because they are resistant to digestion.

Although the size spectrum of the particles swallowed by *E. anchoita* larvae was wide (5-400 µm), smaller items were predominant. Larvae under 8 mm fed mainly on items under 100 µm, and those >8 mm started swallowing wider items, reaching 400 µm. Changes in the maximum size of the food swallowed by these 8 mm larvae suggest that this is an important period in their development, which could imply a higher intake of energy.

The ingestion of small particles, mainly in the initial phase, could be by filtration using the gill-rakers. However, general observation of the gill-rakers suggests that these structures would not normally permit retention of small food particles because of the shortness of the rakers and denticles, along with the large distance between the rakers (60 µm approximately). Therefore, phytoplankton ingestion could be occasional and associated with the consumption of other items. According to CIECHOMSKI (1967), gill-rakers start being functional at 38 mm, when small phytoplankton items occur in the diet of anchovies.

Intestinal size is another factor related to the feeding habits on phyto or zooplankton. In this study, the small ratio between gut size and standard length found (0.50) is normally related to zooplanktophagous habits.

In an attempt to evaluate which season is the most favorable for *E. anchoita* larvae feeding, the following parameters were used: a) The highest general incidence was observed in the winter cruise; b) 48% of the samples collected during the winter presented an incidence higher than 50%, and 78% had incidences higher than 30%, while in the spring cruise these values were only 20% and 50%, respectively; c) Feeding incidences were always above 40% in the winter cruise in all larval sizes; d) The average number of items consumed by larvae was the highest in the winter, although nauplii, which were the most important items, were found more frequently in the autumn. We suggest that winter could be the most favorable larval feeding period, associated with the spawning peak and with the highest adult biomass, around 1.9 million tonnes (LIMA and CASTELLO, 1995). It has to be pointed out that the seasonal pattern can be disguised by an interannual variation due to the sampling design, in which each season was sampled in a different year.

In the winter cruise, a nucleus of high feeding incidence was observed in the southern area, associated with a region of high water stratification caused by less saline water in the upper layers. High feeding incidences were also observed in larvae collected further away from the coast in a water depth of 100 m, associated with a shelfbreak front (PODESTÁ, 1990; LIMA and CASTELLO, 1995), surprisingly, in an area of low zooplankton biomass (ECOPEL - Technical Reports).

According to KIφRBOE (1993), zooplankton biomass may not be a good indicator of food availability for larvae, and a relationship between the values of zooplankton biomass and feeding incidence is not usually found in areas of upwelling. This phenomenon is due to the intermittent influx of nutrients occurring in short intervals and does not permit the development of the full life cycle of zooplankton organisms. Nevertheless, such regions present high productivity with high concentration of eggs and nauplii of copepods (MANN and LAZIER, 1991). This comparison is limited by technical problems as zooplankton biomass data (ECOPEL – Technical Reports) related to material collected with a WP-2 net with a mesh size of 150 µm. This mesh size is not adequate to sample microzooplankton, the main food-source of *E. anchoita* larvae.

Conclusions

The results indicate that the continental shelf in the extreme south of Brazil is favorable for the feeding of *Engraulis anchoita* larvae, which showed a general feeding incidence of 44.8%. High feeding incidence indicates winter as the most favorable feeding period. In this season, high feeding incidence values in *E. anchoita* larvae were apparently related to shelfbreak upwelling, a high water-column stability, and to an area influenced by coastal waters.

Anchovy larvae in this region are zooplanktophagous, feeding upon nauplii, copepodites, copepod adults, invertebrate eggs and tintinnids. Occasional and sporadic ingestion of high numbers of dinoflagellates and other items demonstrates opportunistic feeding in these larvae.

High incidence of starch grains occurred in the gut contents, mainly in the winter. The possibility of assimilation of these grains as an energy source should be investigated.

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References

ALLDREDGE, A. L.; PASSOW, U.; LOGAN, B. E. 1993 The abundance and significance of the large transparent organic particles in the oceans. *Deep-Sea Res.*, *40*: 1131-1140.

ARTHUR, D. 1976 Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax* and *Trachurus symmetricus*. *Fish. Bull.*, *74*: 517-530.

BAKUN, A. 1996 *Patterns in the ocean. Ocean processes and marine population dynamics*. California Sea Grant/CIB. 323 p.

BERNER JR., L. 1959 The food of the larvae of the northern anchovy *Engraulis mordax*. *ICCAT Bull.*, *4*: 1-22.

BURSA, A. S. 1968 Starch in the oceans. *J. Fish. Res. Can.*, *25*: 1269-1284.

CASTELLO, J. P. 1997 Pelagic teleosts. *In*: SEELIGER, U.; ODEBRECHT, C.; CASTELLO, J. P. (eds.), *Subtropical convergence environments. The coast and the sea in the Southwestern Atlantic*. Spring-Verlag, Berlin: 123-128.

CIECHOMSKI, J. D. 1967 Investigations of food and feeding habits of larvae and juveniles of the argentine anchovy *Engraulis anchoita*. *CalCOFI Rep.*, *11*: 72-81.

FLINKMAN, J.; VUORINEN, I.; CHRISTIANSEN, M. 1994 Calanoid copepod eggs survive passage through fish digestive tracts. *ICES J. Mar. Sci.*, *51*: 127-129.

HEATH, M. R. 1996 The consequences of spawning time and dispersal patterns of larvae for spatial and temporal variability in survival to recruitment. *In*: WATANABE, Y., YAMASHITA, Y., OOZEKI, Y. (eds). *Survival strategies in early life stages of marine resources*, Proc. Int. Workshop, Yokohama, Japan, October/1994, A.A. Balkema, Netherlands: 175-207.

HJORT, J. 1914 Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P-v. Reun. Cons. Perm. Int. Expl. Mer*, *20*: 1-228.

HUNTER, J. R. 1972 Swimming and feeding behavior of larval anchovy *Engraulis mordax*. *Fish. Bull.*, *70*: 821-838.

JOBLING, M. 1995 *Environmental biology of fishes*. Fish and Fisheries Series 16, Chapman & Hall, London. 455 p.

KAMLER, E. 1992 *Early life story of fish: an energetic approach*. Fish and Fisheries Series 4, Chapman & Hall, London. 267 p.

KIØRBOE, T. 1993 Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *In*: BLAXTER, J. H. S., SOUTHWARD, A. J. (eds). *Adv. Mar. Biol.*, *29*: 1-72.

LASKER, R. 1981a Factors contributing to variable recruitment of the northern anchovy (*E. mordax*) in the California Current: contrasting years, 1975 through 1978. *Rapp. P-v. Reun. Cons. Perm. Int. Expl. Mer*, *178*: 375-388.

_____ 1981b *Marine fish larvae. Morphology, ecology, and relation to fisheries*. University of Washington Press, Seattle. 131 p.

LIMA, I. D. and CASTELLO, J. P. 1995 Distribution and abundance of South-west Atlantic anchovy spawners (*Engraulis anchoita*) in relation to oceanographic processes in the southern Brazilian shelf. *Fish. Oceanog.*, *4*: 1-46.

LUDWIG, J. A. and REYNOLDS, J. F. 1988 *Statistical ecology*. John Wiley & Sons, New York. 337 p.

MANN, K. H. and LAZIER, J. R. N. 1991 *Dynamics of marine ecosystems. Biological-physical interactions in the ocean*. Blackwell Scientific Publications, London. 461p.

MELO, M. J. 1978 Estimativa preliminar da biomassa e do potencial pesqueiro de engraulídeos na região sul do Brasil. *Série de Documentos Técnicos, PDP/SUDEPE*, *29*: 6-40.

NEIRA, F. J.; MISKIEWICZ, A. G.; TRNSKI, T. 1998 *Larvae of temperate Australian fishes: laboratory guide for larval fish identification*. University of Western Australia Press, Nedlands. 474 p.

PODESTÁ, G. P. 1990 Migratory pattern of argentine hake *Merluccius hubbsi* and oceanic processes in the Southwestern Atlantic Ocean. *Fish. Bull.*, *88*: 107-177.

ROJAS DE MENDIOLA, B. and GOMEZ, O. 1981 Primera alimentación, sobrevivencia y tiempo de actividad de las larvas de anchoveta (*Engraulis ringens* J.). *Bol. Inst. Peru, Callao, Peru*: 72-79.

SÁNCHEZ, R.P. and MANAZZA, G. O. 1994 Estudios sobre la alimentación de larvas de anchoíta (*Engraulis anchoita*) en relación con los frentes de marea de la región patagónica. *Frente Marítimo 15*: 51-65.

SCARLATO, N. A. 1990 Algunos aspectos de ecologia trofica de larvas de primera alimentación de *Engraulis anchoita* (Hubbs & Marini) (Pisces, Engraulidae) en los distintos ecosistemas marinos de la provincia de Buenos Aires. SEMINARIO DE LICENCIATURA. Universidad Nacional de Mar del Plata, Argentina.

SIEG, A. 1998 A study on the histological classification of the in-situ nutritional condition of larval South-west Atlantic anchovy, *Engraulis anchoita* Hubbsi and Marini, 1935. *Arch. Fish. Mar. Res., 46*: 19-36.

SIEGEL, S. 1975 *Estatística não paramétrica (para as ciências do comportamento)*, McGraw Hill do Brasil, Trad. Alfredo Alves de Farias. 350 p.

THEILACKER, G. H. 1980 Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. *Fish. Bull., 78*: 685-692.

VASCONCELLOS, M. C.; FREIRE, K. F.; CASTELLO, J. P. 1998 Distribution patterns and feeding success of anchovy, *Engraulis anchoita*, larvae off southern Brazil. *Sci. Mar., 62*: 385-392.

VIÑAS, M. D. and RAMIREZ, F. 1996 Gut analysis of first-feeding anchovy larvae from the Patagonian spawning areas in relation to food availability. *Arch. Fish. Mar. Res., 43*: 231-256.

WEISS, G. and SOUZA, J. A. F. 1977 Desova invernal de *Engraulis anchoita* na costa sul do Brasil em 1970 e 1976. *Atlântica, 2*: 5-24.

WHITEHEAD P. J. P.; NELSON, G. J.; WONGRATANA, T. 1988 An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. *FAO Fish. Synop. 7, Part 2*: 305-579.

YAMASHITA, Y. 1990 Defecation of larval Japanese anchovy (*Engraulis japonica*) during net sampling. *Bull.Tohoku Nat. Fish. Res. Inst., 52*: 29-32.

ZAR, J. H. 1984 *Biostatistical analysis*. 2nd ed., Prentice-Hall, New Jersey. 718 p.