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Distribution patterns and feeding success of anchovy, *Engraulis anchoita*, larvae off southern Brazil*

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SUMMARY: Feeding success and changes in horizontal patchiness relative to size were studied for anchovy, *Engraulis anchoita*, larvae caught with a Bongo net off southern Brazil. Results show higher feeding success rates during winter, when the combined effect of enrichment, stability and retention mechanisms seems to create optimal conditions for larval feeding. Under optimal feeding conditions larvae of more than 10 mm have higher feeding success rates than smaller size classes. With a simple body structure and low swimming capabilities, larvae of up to 10 mm show a low level of patchiness, low evasion rate of the sampling gear and feeding on small food particles only. Results corroborate the hypothesis of a critical period between two important ontogenic phases: the beginning of exogenous feeding and the onset of active swimming, gas gland buoyancy and school forming behavior.

Key words: *Engraulis anchoita*, larval feeding, distribution, patchiness, critical period.

INTRODUCTION

Anchovy, *Engraulis anchoita*, inhabit the Southwest Atlantic Ocean, between 22° S and 47° S (Whitehead *et al*., 1988), where it is one of the most abundant pelagic fish species. In southern Brazil *E. anchoita* spawns throughout the year, but mainly during the austral winter and spring (Weiss and Souza, 1977) when adult stock biomass may be as high as 1.9 x10^6 tons (Lima and Castello, 1994). Successful anchovy spawning during winter and spring is associated with high biological productivity (Castello *et al*., 1991; Ciotti *et al*., 1995), stable conditions in the water column, and wind induced circulation that retains eggs and larvae on areas over the shelf (Bakun and Parrish, 1991; Lima and Castello, 1995). The combination of enrichment, stability and retention mechanisms is thought to create a suitable habitat for feeding and survival of anchovy larvae on the southern Brazil shelf ecosystem (Lima and Castello, 1995; Bakun, 1996). In this paper we analyze the feeding success of anchovy larvae off southern Brazil to test the hypothesis of improved feeding conditions during austral winter and spring. Feeding success is also compared between larvae size classes with different morphological characteristics and distribution patterns to investigate possible changes in feeding conditions with larval development.

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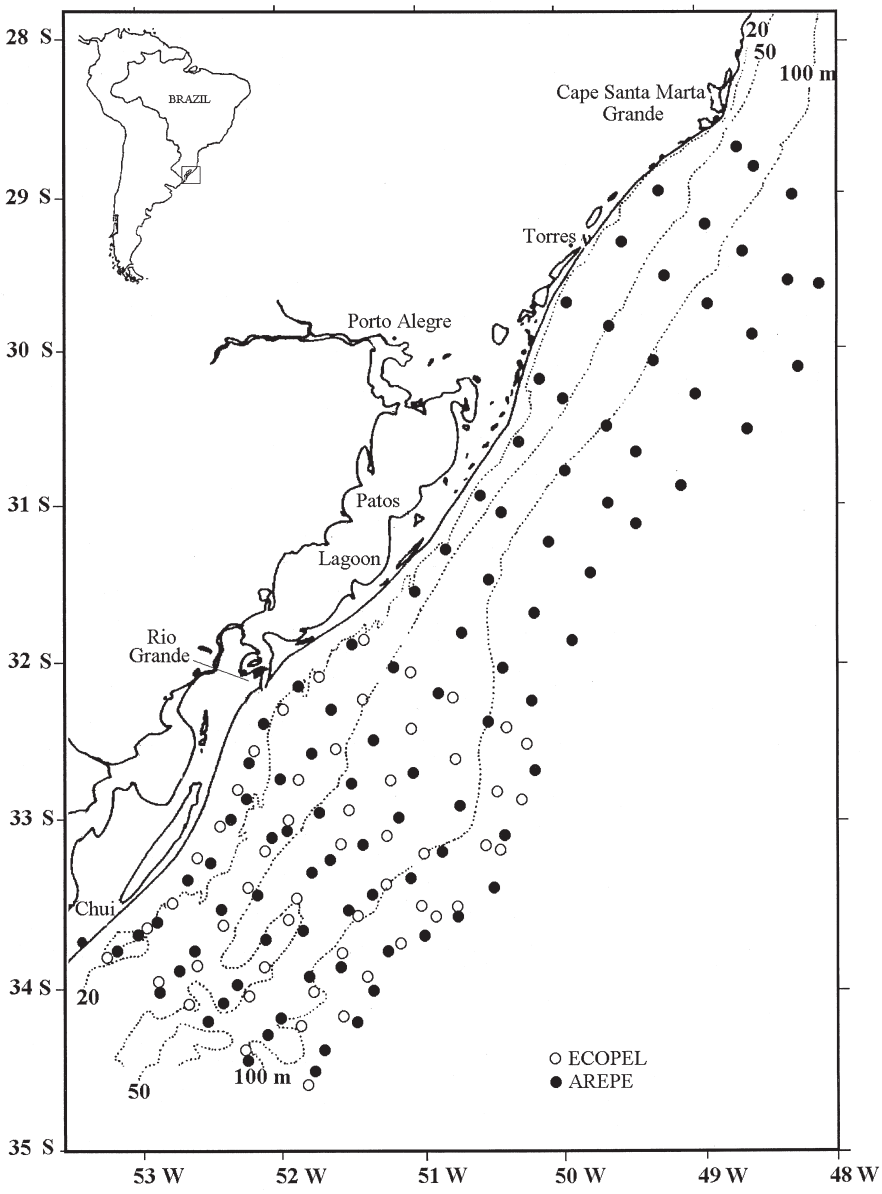

FIG. 1. – Sampled area during ECOPEL and AREPE cruises off southern Brazil.

MATERIALS AND METHODS

Larval samples were collected during eight cruises conducted by the R/V "Atlantico Sul" off southern Brazil between 34°30´ S and 28° 30´ S (AREPE cruises) and between 34° 30´ S and 32° S (ECOPEL cruises) (Table 1; Fig.1). Anchovy larvae were collected with a Bongo net with a mouth diameter of 60 cm and a mesh size of 300 μm. The Bongo net was towed at 2.5 Knots in oblique hauls between the surface and 5 m above the bottom. The water volume filtered was measured by a flow meter attached to the mouth of the net.

Larvae were preserved in a 4% buffered formalin solution, then measured and counted. Standard length (SL, mm) was corrected for shrinkage applying the factor calculated by Theilacker (1980). Feeding and gill raker development were assessed from 1231 larvae between 2.8 and 34 mm SL, collected in 62 hauls from ECOPEL cruises (Table 2). Analysis of larval feeding success was concentrated on samples collected during daylight. Anchovy larvae are thought of as visual feeders, feeding mainly during the day (Sánchez *et al.*, 1991). For food items to be seen in the entire gut, larvae were stained with Bengal Rose and Lugol.

TABLE 1. – Sampling period and total number of ichthyoplankton samples collected during each cruise of R.V. "Atlântico Sul" off southern Brazil.

Cruise	Period	Samples
AREPE I	Autumn 1980	106
AREPE II	Winter 1980	98
AREPE III	Spring 1980	98
AREPE V	Spring 1982	106
ECOPEL I	Spring 1987	53
ECOPEL II	Winter 1988	53
ECOPEL III	Summer 1990	54
ECOPEL IV	Autumn 1991	54

TABLE 2. – Number of samples and number of larvae utilized in the feeding analysis. Larvae -day and -night refer to the total number of larvae analysed from day and night samples respectively.

Cruise	Samples Day	Night	Total	n larvae
Spring 1987	19	1	20	257
Winter 1988	20	6	26	700
Summer 1990	4	-	4	55
Autumn 1991	12	-	12	219
Total	55	7	62	1231
			Larvae-day	1042
			Larvae- night	189

Feeding incidence, used as an index of feeding success, was defined as the percentage of the total larvae caught during daylight with at least one food item in the gut. Differences in feeding incidences among periods and size classes were tested using a Tukey test for proportions (Zar, 1984). Food items were identified to the lowest discernible taxa, being mainly composed by nauplii, copepodites, copepods, eggs of invertebrates and tintinids (Freire, 1995). To evaluate the relationship between particle size, mouth width and larval length, the maximum cross section that the larvae would have to encompass for ingestion was measured. The number of gill rakers in the largest branch of the first left gill arch was counted after staining with Bengal Rose.

The horizontal patchiness and the night/day catch ratio for each length class were analyzed. Larval concentrations were standardized as number caught in 10 m^2 of water surface to correct for differences between water volume filtered at different stations. Patchiness variations with length were analyzed applying the Lloyd patchiness index (Hewitt, 1981). This index is a function of the mean crowding (m*) defined as the mean number of larvae for each length class under a 10 m≤ surface area :

$$m^* = m + m/k$$

where m and k are parameters of the negative binomial distribution, representing the mean density and the degree of patchiness of a population, respectively. Lloyd's patchiness index is calculated as the ratio between mean crowding and mean density:

$$m^*/m = 1 + 1/k$$

and may be considered as a measure of how many times more crowded the larvae are in relation to a randomly distributed population with the same mean density (Hewitt, 1981). This index is frequently applied in the analysis of spatial distribution patterns of fish eggs and larvae due to its independence from population density and the spatial scale of the sampling (McGurk, 1986). The parameter k was estimated by solving iteratively the equation (Krebs, 1989):

$$\log (N/n_0) = k \log(1+x/k)$$

where
N: total number of sampled stations
n_0: number of stations containing zero individuals
x: mean density of a length class
k: negative binomial exponent

The night/day catch ratio for larvae was calculated for each length class in each cruise and used as an index of net evasion.

RESULTS

Feeding success was significantly higher during the winter ($P < 0.001$; Table 3). Feeding incidence was not statistically different for anchovy larvae caught during the spring, autumn and summer cruises. Overall, between 33 and 52% of the larvae caught in any period had food in their gut.

In order to identify possible differences in feeding success due to size, feeding incidence was ana-

TABLE 3. – Feeding incidence of anchovy larvae caught during ECOPEL cruises. Feeding incidence was calculated as the percentage of the total larvae with at least one food item in the gut. (* $p < 0.001$).

Period	Spring 1987	Winter 1988	Autumn 1991	Summer 1990
n	247	521	219	55
Feeding incidence (%)	36.57	52.28*	33.32	41.81

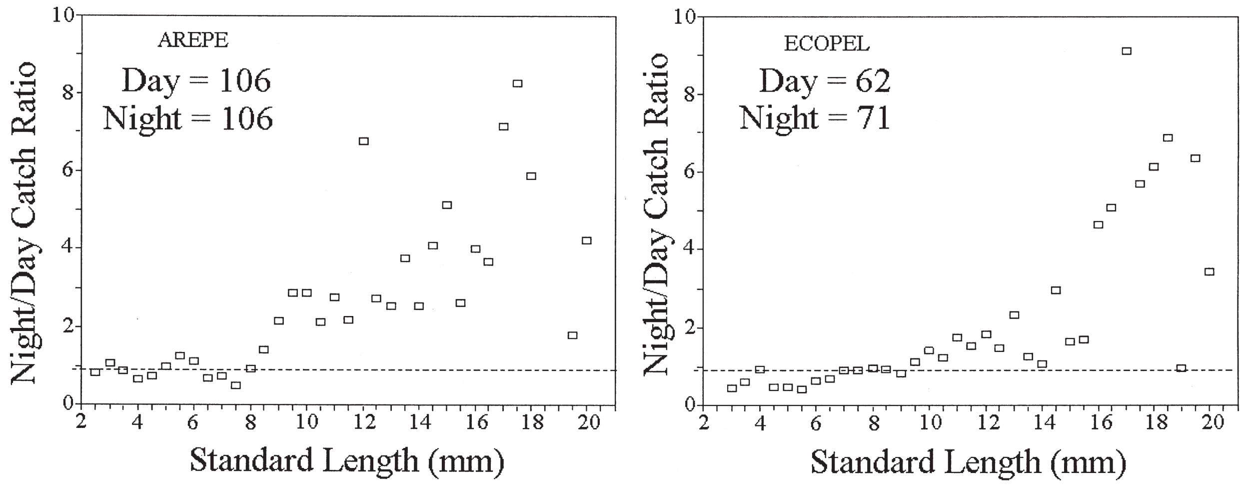

FIG. 2. – Relationship between the night/day catch ratio and larvae standard length. The catch ratio was calculated from the pool of samples obtained in each cruise series (AREPE and ECOPEL). The numbers inside the figures refer to the total number of day and night samples used to calculate the ratios.

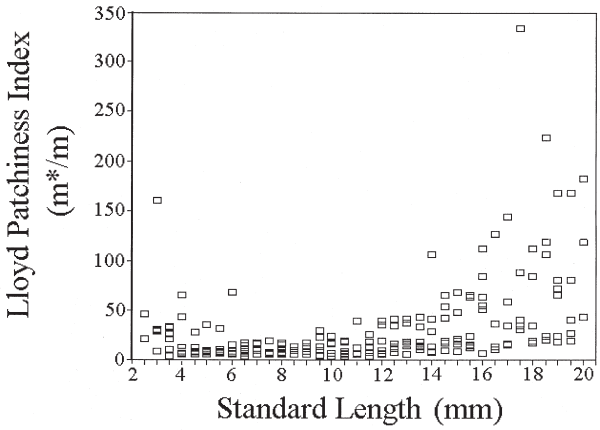

FIG. 3. – Variation of the patchiness degree in larvae distribution, measured by the Lloyd Index (m*/m), in relation to standard length. Each point represents the estimated value of the patchiness index for a given length class durin each cruise (se Table 5 for details of sample size).

lyzed for two length intervals: SL smaller than 10 mm, and SL larger than 10 mm. Larvae with less than 10 mm showed a low evasion rate of the sampling gear (Fig. 2), attained the lowest level of patchiness in their distribution (Fig. 3), possess no developed apparatus for filtration (i.e. gill rakers) (Fig. 4), while feeding mainly on small food particles (Fig. 5). Conversely, larvae with more than 10 mm showed an increasing ability to escape from the sampler during day hauls (higher night/day catch ratio), while attaining higher patchiness and, consequently, lower spatial dispersion in the sampled area. These changes are coincidentally accompanied by the appearance of gill rakers, which increase rapidly in numbers from this length interval, and by the increase in the maximum size of food ingested. Although feeding continued to include large amounts of the more abundant small particles, larvae of more than 10 mm fed on particles that were twice as large as those consumed by smaller size classes (Fig.5). These results indicate substantial changes in larval swimming ability and behavior which could affect both searching for food and feeding success. It was, therefore, hypothesized that under the same conditions of habitat and food availability larvae of more than 10 mm would have a higher feeding success than smaller size classes.

Table 4 shows the values of feeding incidence for each length interval for each period. Difference in feeding success with size was only statistically significant for the winter data, when larvae of more than 10 mm SL had higher feeding success (~64%) than larvae with less than 10 mm (~47 %).

TABLE 4. – Feeding incidence for length interval and period (* denotes a period with difference in feeding success between size classes statistically significant; p< 0.001).

Period	Spring 87		Winter 88*		Autumn 91		Summer 90	
	< 10 mm	> 10 mm	< 10mm	> 10 mm	<10 mm	> 10mm	< 10 mm	> 10 mm
n	189	58	364	157	127	92	51	4
Feeding Incidence (%)	37.68	32.75	47.03	64.45	33.85	32.59	41.18	50.00

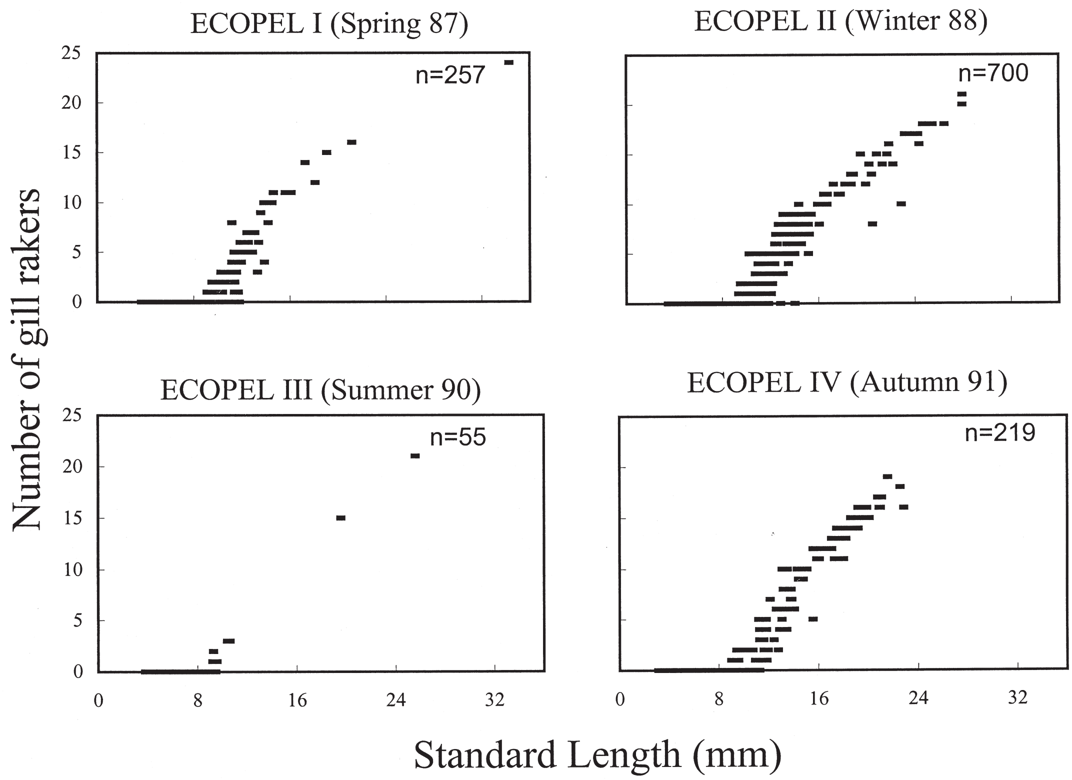

FIG. 4. – Number of gill rakers in the first left-hand gill arch by larval size. Numbers inside the figures represent the number of larvae analysed in each cruise.

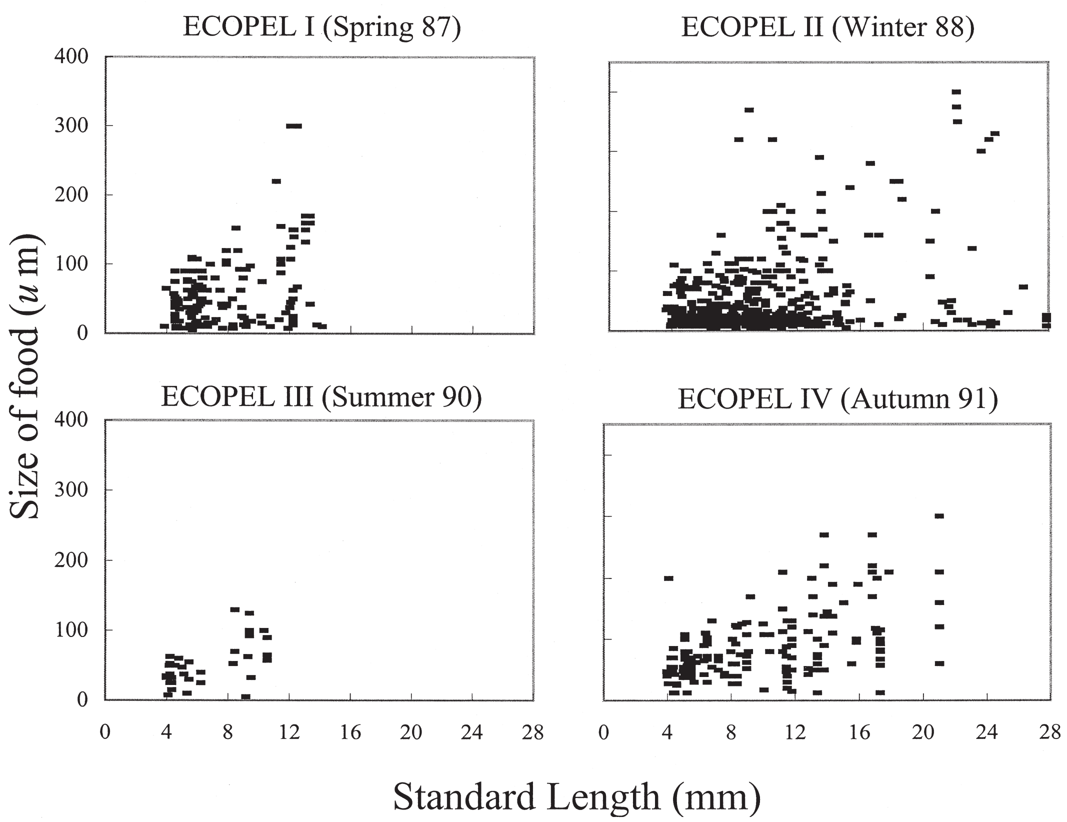

FIG. 5. – Relationship between the size of ingested food and standard length. Each dot represents the size of a food item found in the gut of a given size larvae.

DISCUSSION

Feeding success of anchovy larvae off southern Brazil was higher during austral winter. Higher feeding success rates during the winter are apparently related to the combined effects of freshwater run-off and the flow of cold waters of Subantartic origin, which result in a strong vertical water stability over the shelf (Bakun and Parrish, 1991; Lima and Castello, 1995) and provide conditions which increase primary production (Ciotti *et al.*, 1995) and zooplankton densities (Castello *et al.*, 1991). Surprisingly low feeding incidences were observed in spring data, suggesting below optimal conditions for larval feeding during a highly productive period. Phytoplankton production in the region increases in the early spring with the nutrient influx from continental and southern cold waters (Ciotti *et al.*, 1995). Zooplankton biomass is also high during spring months (up to 98.47 mg C m^{-3}), especially in offshore areas under the influence of Subantartic waters (Montú *et al.*, 1997). Information on zooplankton species composition would be needed to understand the lower feeding incidences encoutered during spring, though feeding success may depend not only on food concentration but also on its specific characteristics, i.e. species and size composition (Lasker, 1975).

Lower feeding success during autumn and summer months were, on the other hand, expected since warm waters dominate the shelf and the amount of rainfall is greatly reduced. As a result, water column stratification is not as strong as in winter and spring (Lima and Castello, 1995), primary production and phytoplankton biomass are considerably lower (Odebrecht and Garcia, 1997) and zooplankton concentrations are frequently associated with gelatinous plankton (Montú *et al.*, 1997).

The analysis of feeding success with size provides important information to better understand the significance of decisive events in anchovy early life history. No ontogenic differences in feeding success were observed in periods with below optimal conditions for feeding (i.e. spring, summer and autumn). Conversely, results indicate that under optimal feeding conditions (winter) larvae with more than 10 mm have higher feeding success than larvae with less than 10 mm. From 7 to 12 mm SL *E. anchoita* larvae pass through a phase of transformations in their body structure marked by fin development and a functional gas gland (Phonlor, 1984) and the appearance of gill rakers (Fig. 4). The development of fins and a gas gland creates better swimming ability and is directly related to the initiation of vertical migration behavior, common among clupeoid species (Sánchez *et al.*, 1991). Similar changes have been noted in the larvae of *E. mordax, E. japonicus* and *E. capensis* (Hunter and Sánchez, 1976; Blaxter and Hunter, 1982). The beginning of vertical migration seems to play an important role in the development of schooling behavior by establishing the concentration of larvae at or near the surface and, therefore, increasing the frequency of visual contacts between individuals (Hunter, 1984). The association between changes in distribution patterns and behavior processes was also shown for *E. mordax* larvae. In this species the onset of schooling behavior begins when larvae are 11 to 12 mm SL and is associated with an increase in patchiness in the sea (Hunter and Coyne, 1982). For *E. anchoita* patchiness increases with size when larvae attain on average ca. 10 mm SL (Fig. 3; Table 5). The increase in patchiness and in the evasion ability of anchovy larvae from the plankton sampler during the day (Fig. 2) denote substantial changes in larval swimming ability which provide improved feeding success and searching capacity for bigger and more motile prey (Fig. 5). This may play an important role in growth and survival of larger larvae. For instance, Hunter (1984) showed that an increase of 2.5 times in copepod size can produce a tenfold increase in dry weight, resulting in a considerable energetic gain for larvae.

The length interval with lower feeding success rates extends over two important ontogenic thresholds (sensu Balon, 1984): the beginning of exogenous feeding and the onset of active swimming, aided by gas gland buoyancy and manifested in school forming behavior. These steps in early development mark important changes in the survival chances of larval anchovy. At the end of yolk absorption, larvae face a very delicate phase when survival depends on food availability in the proper size range and adequate concentration. On the other hand, fin development and a functional gas gland provide anchovy larvae with improved ability for searching for food, preying upon larger organisms and escaping from predators. To evaluate the significance of these events for anchovy larvae survival it is necessary to compare mortality rates throughout larval development. Kitahara and Matsuura (1995) reported higher mortality rates of preflexion anchovy larvae (SL from 3.8 to 12.9 mm) at the particular oceanographic conditions off the

TABLE 5. –Data for the patchiness analysis. N is the total number of sampled stations, n is the number of larvae in a given length class and k is the negative binomial exponent. The Lloyd patchiness index is calculated from the inverse of k (see details in text).

SL (mm)	AREPE II N = 48		AREPE III N = 66		ARERE V N = 84		ECOPEL I N = 43		ECOPEL II N = 41		ECOPEL IV N = 32	
	n	k	n	k	n	k	n	k	n	k	n	k
2.5	0	-	18	0.02	30	0.05	0	-	0	-	2	0.01
3	3	0.01	42	0.03	126	0.13	0	-	25	0.03	0	-
3.5	2	0.03	132	0.11	272	0.33	7	0.03	80	0.05	24	0.01
4	6	0.02	114	0.16	375	0.22	20	0.09	309	0.12	97	0.03
4.5	4	0.04	86	0.21	351	0.21	37	0.09	494	0.13	354	0.03
5	8	0.03	66	0.11	207	0.20	19	0.13	320	0.14	79	0.03
5.5	10	0.03	71	0.11	184	0.18	18	0.14	316	0.19	47	0.04
6	7	0.01	37	0.07	122	0.16	20	0.21	286	0.17	76	0.06
6.5	3	0.07	28	0.06	88	0.11	17	0.14	269	0.19	35	0.09
7	14	0.06	24	0.06	85	0.12	13	0.22	190	0.20	33	0.11
7.5	23	0.15	18	0.05	59	0.15	11	0.25	154	0.20	38	0.08
8	25	0.07	28	0.06	56	0.11	9	0.15	159	0.19	36	0.11
8.5	26	0.12	27	0.08	52	0.08	8	0.20	74	0.23	29	0.10
9	48	0.13	35	0.06	51	0.08	13	0.21	90	0.24	38	0.17
9.5	38	0.08	40	0.04	23	0.05	10	0.12	77	0.34	43	0.13
10	33	0.07	35	0.04	35	0.06	9	0.16	72	0.19	41	0.15
10.5	28	0.14	32	0.06	28	0.05	9	0.20	60	0.17	38	0.25
11	43	0.08	32	0.03	31	0.09	7	0.17	66	0.18	29	0.22
11.5	34	0.08	26	0.04	15	0.06	8	0.09	42	0.15	24	0.14
12	23	0.06	26	0.03	9	0.03	6	0.17	36	0.12	21	0.19
12.5	26	0.08	14	0.03	13	0.03	5	0.10	33	0.06	22	0.16
13	22	0.06	18	0.03	5	0.03	4	0.07	23	0.06	12	0.11
13.5	22	0.08	9	0.03	8	0.02	3	0.10	16	0.06	14	0.16
14	22	0.14	16	0.03	2	0.01	3	0.08	10	0.04	15	0.13
14.5	20	0.06	16	0.02	3	0.02	2	0.06	6	0.02	13	0.11
15	12	0.07	15	0.02	4	0.02	2	0.05	9	0.05	9	0.06
15.5	12	0.07	5	0.02	5	0.02	1	0.07	6	0.04	7	0.04
16	8	0.01	7	0.01	3	0.02	2	0.02	3	0.02	6	0.07
16.5	4	0.08	5	0.03	3	0.01	1	0.03	2	0.03	6	0.11
17	7	0.07	6	0.02	1	-	1	0.03	1	0.01	5	0.03
17.5	6	0.03	3	0.01	2	0.00	2	0.03	0	-	4	0.09
18	3	0.05	9	0.01	0	-	0	0.03	1	0.01	5	0.04
18.5	6	0.05	4	0.00	1	0.01	2	0.01	0	-	2	0.03
19	5	0.02	3	0.01	2	0.01	1	0.04	1	0.01	1	0.03
19.5	1	0.04	0	-	1	0.01	1	0.03	1	0.01	4	0.09
20	5	-	0	-	1	0.01	1	0.01	4	0.02	3	0.02
Total	559		1047		2253		272		3235		1212	

southeastern Brazilian Bight. Larvae of this size range were more abundant in the upper mixed layer (Matsuura and Kitahara, 1995) which is characteristically less productive. As the larger ones start to migrate to deeper water, near the chlorophyll maximum layer, starvation-induced mortality decreases due to enhanced feeding conditions. The analysis of RNA/DNA ratios for anchovy larvae caught in the same area showed that the highest amount of starvation occurred in the length class interval from 4 to 10 mm (Clemmensen *et al.*, in press). These studies, therefore, provide evidence for the importance of vertical migration behavior for larval anchovy feeding and survival. We see these results as a corollary of the hypothesis that the length interval up to 10 mm SL comprises a phase when larval survival chances remain low and thus indicate a decisive or critical period in the species' life history.

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