Habitat selection by anchovies (Clupeiformes: Engraulidae) in a tropical bay at Southeastern Brazil

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Distribution of anchovies (Clupeiformes, Engraulidae) was described in the Sepetiba Bay, a coastal area of Southeastern Brazil, to assess eventual mechanisms of habitat selection. Two fish sampling programmes were accomplished; one using beach seine (1998/2000) to catch juveniles in sandy beaches, and the other, using seines (1999/2000) to catch adults in deeper bay areas. Six species representing 4 genera were recorded: *Anchoa tricolor, Anchoa januaria, Anchoa lyolepis*, *Cetengraulis edentulus*, *Engraulis anchoita* and *Lycengraulis grossidens*. *Anchoa tricolor* and *A. januaria* were the most abundant species, with the former peaking in the outer bay, while the latter peaking in the inner bay. Adults *A. tricolor* are target of heavy commercial fisheries in the bay during Spring-Summer, while *E. anchoita*, an abundant species in the continental shelf, was occasionally caught in large numbers during the Autumn. The habitat selection, by using two different bay areas, was developed by the two most abundant species, a probable mechanism to enable their coexistence.

A distribuição de manjubas (Clupeiformes, Engraulidae) foi descrita na Baía de Sepetiba, uma área costeira do Sudeste do Brasil, para determinar eventuais mecanismos de seleção de habitat. Dois programas de amostragem foram realizados; um usando arrasto de praia (1998/2000) para captura de juvenis, e outro, usando arrasto de fundo (1999/2000) para captura de adultos. Seis espécies representadas por quatro gêneros foram capturadas: *Anchoa tricolor, Anchoa januaria, Anchoa lyolepis*, *Cetengraulis edentulus*, *Engraulis anchoita* e *Lycengraulis grossidens*. *Anchoa tricolor* e *A. januaria* foram as espécies mais abundantes, com a primeira ocorrendo principalmente na zona externa da baía, enquanto a segunda com maior abundância na zona interna. Adultos *A. tricolor* são alvo de intensas pescarias comercial na baía durante a Primavera-Verão, enquanto *E. anchoita*, uma abundante espécie na plataforma continental, foi ocasionalmente capturada em grande numero durante o Outono. A seleção de hábitat, através do uso de diferentes áreas da baía, foi desenvolvida pelas duas espécies mais abundantes, um provável mecanismo para permitir a coexistência.

Key words: Fish distribution, Sandy beach, Anchovy, Sepetiba bay.

Introduction

Fishes of the Engraulidae family, known as anchovies, are widely distributed in tropical and sub-tropical waters (Mcgowan & Berry, 1983). In Sepetiba Bay, a 450 km² embayment of Brazilian Southeastern coast, they rank among the most abundant species either as juveniles recruits in the sandy beaches, and as adults, occupying different areas in the inner and outer bay zones. Most anchovies spawn in open coastal areas in the inner continental shelf. Recruitment occurs in protected, shallow areas that offer food and shelter against predators (Coto *et al*., 1988). Adults have been demonstrated to move on seasonal and diel timescales between open coastal areas and bays (Macgregor & Houde, 1996), where they form large aggregations that are targeted by important fisheries. Engraulidae fishes are believed to be a major trophic link in bay food chains through their role in converting planktonic

biomass into forage for piscivorous fishes (Hildebrand, 1963).

Sepetiba Bay (Fig. 1) is located in the State of Rio de Janeiro, Southeastern Brazil. Several marine fishes enter and leave the bay for nursery, reproductive and feeding purposes (Araújo *et al*., 2002). There is a trend of decreasing water quality in the bay. Recent enhancement of the Sepetiba Bay Port included dredging of the access channel to 20 m depth, which will enable it to receive ships up to 150,000 ton of capacity.

Three species of the Engraulidae family: *Anchoa januaria* (Steindachner, 1879)*, Anchoa tricolor* (Spix & Agassiz, 1829) and *Cetengraulis edentulus* (Cuvier, 1829) rank among the most abundant fishes in the Sepetiba Bay (Pessanha *et al*., 2003) although their coexistence mechanisms and population biology are poorly known. High diversity and abundance of Engraulidae in the Sepetiba Bay suggest that some mechanisms of the resources and habitat partition occur in order to avoid competition (Silva & Araújo, 2000); they justified coexistence

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as result of use of different resources supplied by different areas in the bay. Species that share the same area use different strategies to explore the available food resources. Sergipense *et al.* (1999) found that *A. januaria* and *C. edentulus*, common in the inner Sepetiba Bay area, have a different feeding strategy, with the first species feeding predominantly on zooplankton and the latter feeding on phytoplankton. Heavy rainfall seasons seem to increase plankton availability, due to great amount of nutrients brought by rivers, favoring the development of planktofagous fish (Macgregor & Houde, 1996).

Environmental variables could also influence the period that these fishes migrate from the bay to open areas in the inner continental shelf and vice-versa. *Anchoa marinii* Hildebrand, 1943 movement from coastal areas to the Patos Lagoon estuary was associated to intrusion of high salinity deep waters, while *Lycengraulis grossidens* Agassiz, 1829 was associated to areas of low salinity (Weiss & Krug, 1977). In the Sepetiba Bay, Silva *et al.* (2004) found that young-of-the-year of *A. januaria* occur in shallow and transparent waters, while Sergipense & Sazima (1995) found this species mostly in sites with more influence of continental drainages. *Cetengraulis edentulus* occurs mainly near to muddy substrate (Gay *et al.*, 2000).

The present work aims to assess mechanisms of habitat selection by species of Engraulidae in the Sepetiba Bay, by investigating their spatial and seasonal distribution, and to verify the influences of the environmental variables. Specifically, the use of select habitats (inner bay and outer bay) was evaluated by indices of anchovies abundance, as determined from seine and beach seine surveys. In an effort to better understand the mechanisms underlying habitat selection, anchovies abundances were correlated with several abiotic parameters measured at the sampling sites.

Material and Methods

Study area

Sepetiba Bay (Fig. 1) is a sedimentary embayment in the coast of Rio de Janeiro State (Lat. 22º54'-23º04'S; Long. 43º34'-44º10'W) in southeastern Brazil. It originated by an extensive process of sand deposition, which formed a barrier beach at its southern end. It has a wide communication with the Atlantic Ocean at its western end. The bay has a surface area of approximately 450 km², a mean depth of 8.6 m, a maximum depth of 30 m, and is within a drainage area of 2700 km2. Waters are predominantly polyhaline (salinity average = 30). The annual rainfall is between 1000 mm and 2100 mm (Barbieri & Kronemberger, 1994) but this does not influence the bay salinity much due the existence of only small tributaries. Most of the substrate is silt and mud. The tidal range is approximately 1 m. Predominant north-easterly and south-westerly winds activate thermal currents between the bay and the ocean.

Two bay zones were arbitrarily defined to maximize variation in habitat characteristics, defined according to depth, salinity, transparency, temperature and influences of human activities (Fig. 1). The outer zone has a sandy and gravel bot-
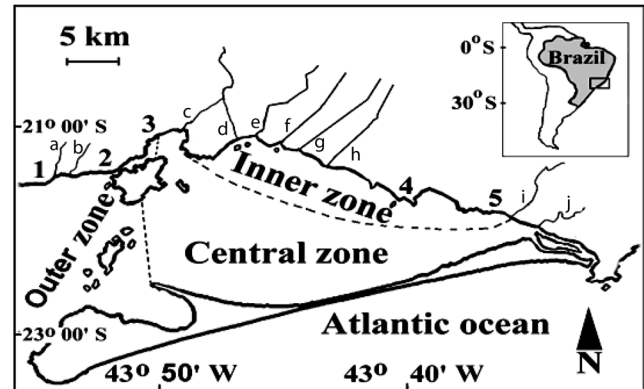
Fig. 1. Study area, Sepetiba Bay, Brazil, with indication of the beach seine sampling sites (1-5). a - rio Prata; b - rio Corumbi; c - rio Cação; d - rio Mazomba; e - rio Guarda; f - canal São Francisco; g - canal Guandu; h - canal Itá; i - rio Piraquê; j - rio Piracão.

tom and was close to the sea limit (highest salinity, transparency, depth and lowest temperature); and the inner zone, with opposite oceanographic conditions, has a heavy mud bottom and was located within a protected area of the bay, near to anthropogenic influences from urban-industrial wastes.

Sampling. Two fish sampling programmes were accomplished, one using beach seine nets to caught early juveniles, and other using seines to catch adults in deeper bay areas. Beach seines were performed monthly, from September 1998 to August 2000, at five sites, during the day. A 10 m long, 2 m deep beach seine with 7 mm mesh was used. The net was pulled through the water parallel and close to the shore for a distance of 30 m at approximately, 1.5 m depth, and then onto the shore. Three replicates seines were performed at each site. Monthly samples were carried out at sites 1, 2 and 3 (outer zone), and sites 4 and 5 (inner zone) (Fig. 1).

Seines in deep areas were carried out using a 15 m long boat provided with an acoustics echosounder Royal RV400 equipment to monitor fishing procedure. The net was 240 m long, 27 m deep and size mesh of 8 mm in the upper part and 10 mm in de lower part. Samplings were performed preferably near to central bay islands (Fig. 1). The net was released with the help of a small auxiliary boat used to anchor the net, while the fishing boat encircled the schooling, closing the net.

Water temperature and salinity were taken at every sampling occasion at approximately 0.5m below surface water. A Sechi disc was used to measure water transparency which was calculated as percent of the depth (beach seines), which was determined with a weighted line marked in 10-cm intervals. Transparency was expressed in cm for the seine programme (adults). Fish were fixed in 10% formalin, identified to species, counted, measured (total length in mm) and weighed in grams. Sub-samples from very abundant catches were taken. After 2 days they were drained, soaked in fresh water for 2 hours and transferred to 70% ethanol for storage. Voucher specimens were deposited in the ichthyological collection of

the Fish Ecology Laboratory, Universidade Federal Rural do Rio de Janeiro (LEP-UFRRJ).

Data analysis. The relative abundances (in number) were estimated from the sampling catch-per-unit-effort (CPUE, number / sample). A parametric three-way analysis of variance (ANOVA) and a Student-Newman-Keuls-SNK test (a = 0.05) were used to test for differences in numerical abundance of Engraulidae among sites, seasons and years for juveniles (beach seine). One-way ANOVA was used to compare number of individuals among season for adults (seine) and to compare number of individuals of both juveniles and adults among the ranges of environmental variables. Both biotic and environmental raw data were previously Log_{10} (x + 1) transformed to address ANOVA assumptions of normality and homocedasticity (Sokal & Rohlf, 1981). Influences of environmental variables on fish occurrence were assessed by grouping fishes numbers in four intervals of temperature in degree Celsius (1: ≤ 24.1; 2: 24.1-28.0; 3: 28.1-32.0; 4: ≥ 32.0), salinity (1: ≤20.1; 2: 20.1-25.0; 3: 25.1-30.0; 4: ≥ 30.0), and transparency in % of depth (1:≤25.1; 2: 25-50.0; 3: 50.1-75.0; 4: ≥ 75.0) for beach seine samples (juveniles), and in three intervals of temperature in degree Celsius (1: < 23.1; 2: 23.1–26.0; 3: > 26.0), salinity (1: < 25.1; 2) 25.1–30.0; 3: > 30.0) and transparency in cm (1: < 180.0; 2: 180.1–290.0; 3: > 290.0). Patterns between fish occurrence and environmental variables were assessed through a Canonical Correspondence Analysis-CCA (Teer Braak, 1986). This is one of the best methods for direct gradient analysis in community ecology (Rodriguez & Lewis, 1997; Araújo *et al.*, 2002) and is widely used to assess environmental influences on fish occurrence.

Results

Composition and relative abundance

Juveniles. A total of 20430 Engraulidae fishes were collected in beach seine, mainly young-of-the-year, being 67 % in the 1998/99 and 33 % in 1999/00. *Anchoa tricolor* was the most abundant species, amounting to 77.45 % of the total number of Engraulidae, followed by *A. januaria* (20.02 %), *A. lyolepis* (2.49 %) and *C. edentulus* (0.03 %). Only two individuals of *L. grossidens* were caught, therefore this species was not included in the analyses.

Spatial separation was shown for juveniles of different species (Fig. 2, Table 1). *Anchoa tricolor*, *A. januaria*, *A. lyolepis* and *C. edentulus* showed significant differences in numerical abundance (p < 0.05) among sites (Table 1). *Anchoa tricolor* and *A. lyolepis* were more abundant in the outer zone , while *A. januaria* and *C. edentulus*, in the inner zone . *Anchoa tricolor* predominated at site 2, *A. januaria* at site 4, and *A. lyolepis* at site 1. Despite of low abundance, *C. edentulus* presented significant differences among sites, being more abundant at site 4 (Table 2). Factor interactions were mainly non-significant or with low significant F-values, except for season *versus* year interactions for *A. tricolor* and *A. lyolepis* (Table 1)*.* These

significant interactions were due to the highest abundance of *A. tricolor* to be recorded in Spring in 1998/1999 (overall average = 212.0 individuals per sample), and in Winter (49.9 individuals per sample) in 1999/2000, while *A. lyolepis* had the highest CPUE in Autumn (overall average = 8.2 individuals per sample) in 1998/1999, and in Spring (overall average = 6.2 individuals per sample) in 1999/2000.

Seasonally, significant differences (p < 0.05) were shown for *A. tricolor, A lyolepis* and *C. edentulus* (Tables 1 and 2). *Anchoa tricolor* and *A. lyolepis* were more abundant in Winter/Spring, and *C. edentulus* in Spring. Significant difference between the two-year period was found only for *A. januaria* that was more abundant in 1998/1999 than in 1999/2000.

Adults. Adults of *A. tricolor* and *Engraulis anchoita* caught by seines showed significant temporal variation in their densities in number of individuals, with *A. tricolor* being more

Table 1. F-Values and significance from three-way ANOVA for comparisons of number of juveniles individuals of each species from Engraulidae family among sites, season e years. ** higly significant (p < 0.01); * significant (p < 0.05); ns = non significant.

Main Effects	df	*A. tricolor*	*A. januaria*	*A. lyolepis*	*C. edentulus*
Site	4	8.71*	4.36*	14.40*	3.62*
Season	3	8.99*	0.29ns	5.86*	3.02*
Year	1	2.80ns	4.18*	0.38ns	2.59ns
Site x Season	12	2.84*	1.72ns	4.38*	1.82*
Site x Year	4	1.58ns	2.14ns	2.91*	1.49ns
Season x Year	3	7.68*	3.47*	8.31*	1.1ns
Site x Season x Year	12	1.02ns	2.39*	6.44*	0.62ns

Table 2. Significant differences (p < 0.05) in number of individuals for both juveniles and adults of each species from Engraulidae family, among sites and seasons, according to Student-Newman-Keuls (SNK) test. Mean values (number of individuals / sample) in brackets.

		Juveniles		
A. tricolor	Sites	2 (134.1)	>	1, 3, 4, 5 (0.02-32.1)
	Sites	1, 4, 5 (23.7-32.1)	>	3 (0.02)
	Season	Spring, Winter (41.6-115.9)	>	Summer, Autumn (8.5-9.6)
A. januaria	Sites	4 (12.7)	>	1, 2, 3, 5 (0.02-35.4)
	Year	1998/1999 (22.1)	>	1999/2000 ((3.7)
A. lyolepis	Sites	1 (7.1)	>	2, 3, 4, 5 (0.0-0.53)
	Season	Spring, Winter (1.4 -4.1)	>	Summer, Autumn (0.0-0.12)
C. edentulus	Sites	4 (0.02)	>	1, 2, 3, 5 (0.0-0.004)
	Season	Spring (0.05)	>	Summer, Autumn, Winter (0.0-0.02)
		Adults		
A. tricolor	Season	Spring, Summer (138.5-171.1)	>	Autumn, Winter (15.2-33.5)
E. anchoita	Season	Autumn (70.0)	>	Spring, Summer, Winter (0.0-1.2)
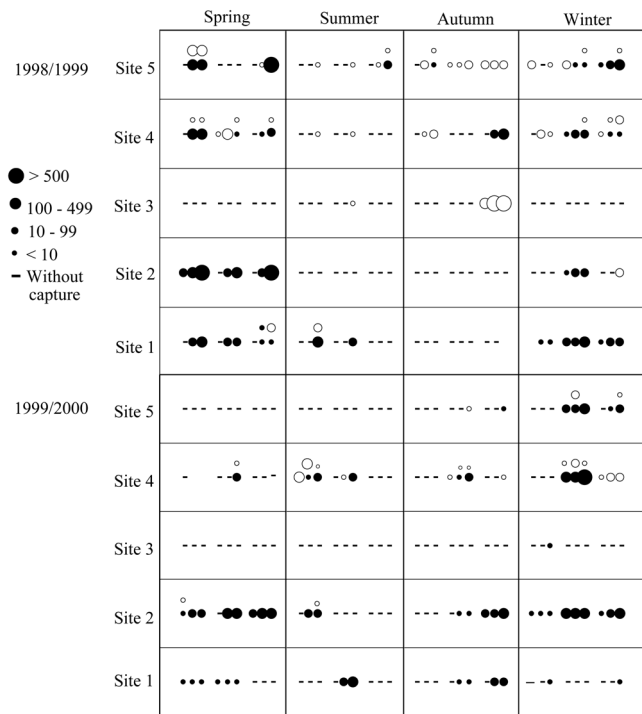
Fig. 2. Spatial and seasonal densities of juveniles *A. januaria* (○) and *A. tricolor* (●) in the Sepetiba Bay, 1998/2000. Each sample (mark in the graphic) represents the total number of fish.

abundant in Spring and Summer, while *E. anchoita* was more abundant in Autumn (Table 2). Adults Engraulidae amounted to 3145 kg, 86 % comprised by *A. tricolor*, 9 % *E. anchoita*, 4 % *A. januaria* and 1 % *C. edentulus*.
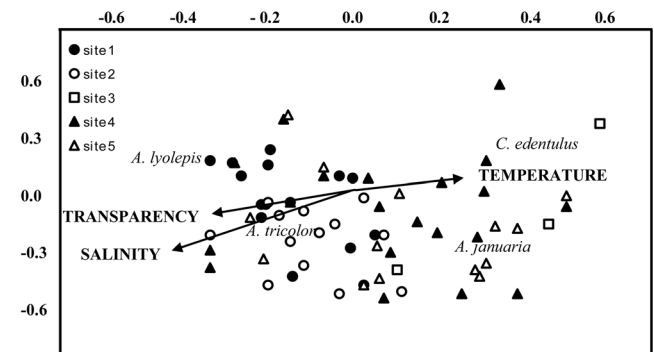
Influence of environmental variables

Juveniles. *Anchoa tricolor* and *A. lyolepis* showed significant differences in numerical abundance among the ranges of temperature, while *A. tricolor* and *A. januaria* showed differences among the ranges of salinity and transparency (Table 3 and 4). *Anchoa tricolor* peaked at temperature < 28°C, while *A. januaria* showed no defined preference for a given range of temperature. *Anchoa tricolor* and *A. lyolepis* were more abundant in the highest salinity (> 25), while *A. januaria* and *C. edentulous* peaked in the lowest salinity (< 25) (Table 4). *Anchoa tricolor* and *A. januaria* were more abundant in intermediary range of transparency.

Canonical correspondence analysis showed for the first two axes eigenvalues of 0.212 and 0.027, respectively, explaining 82.1% and 10.7% of the total variance (Table 5). The species-environmental correlation was 0.611 for the axis 1 and 0.269 for the axis 2. Correlation coefficients between the environmental variables and the two first ordination axes reflect the relative importance of each environmental variable in the species composition. Axis 1 corresponded to salinity and transparency gradient, with lower weight for the temperature, while axis 2 represents the salinity gradient. The main source

of variation of the model is marked shift in the Engraulidae populations from the inner to the outer zone, along axis 1, coinciding with spatial gradient of transparency and salinity. The ordination diagram of the first two axes separates on the left side samples from outer zone, characterized by higher transparency and salinity, in opposition to samples from inner zone on the right side, which are characterized by higher temperature and lower transparency and salinity (Fig. 3).

Adults. Significant differences (p<0.05) were detected in abundance (in numbers) among the ranges of temperature for *A. tricolor* and *A. januaria*, and among the ranges of salinity for *A. januaria* (Table 4). *A. tricolor* showed significant (p<0.01) higher abundance in temperature higher than 23.1°C, while *A. januaria* peaked in the lowest salinity range (<25).

Canonical correspondence analysis showed for the first and second axes, eigenvalues of 0.633 and 0.204, respectively, explaining 74.8 % and 24.0 % of the total variation (Table 6). The species-environmental correlation was 0.869 for axis 1 and 0.732 for axis 2. Axis 1 corresponded to salinity and transparency gradient, while axis 2 represents the seasonal temperature variation (Fig. 4). The main source of variation of the model is a marked shift in the Engraulidae populations from Winter to Spring/Summer, with Autumn presenting an intermediary condition.

Fig. 3. Canonical correspondence analysis ordination diagram of juvenile Engraulidae abundance data, with environmental variables. Bay Zones: Sites 1, 2 and 3 (outer); 4 and 5 (inner).
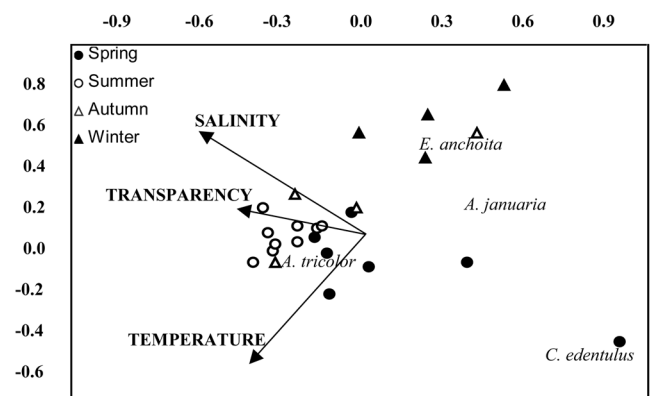
Fig. 4. Canonical correspondence analysis ordination diagram of adults Engraulidae abundance data, with environmental variables. Samples coded by seasons.

Table 3. Means and standard deviation of number of individuals for ranges of enviromental variables.

	A. tricolor	A. januaria	A. lyolepis	C. edentulus	E. anchoita
			Juveniles		
Salinity					
1) < 20.1	1.12 ± 4.9	65.69 ± 268	0	0.02 ± 0.1	0
2) 20.1 – 25.0	12.06 ± 54.1	14.10 ± 54.1	0.22 ± 1.5	0.06 ± 0.3	0
3) 25.1 – 30.0	58.62 ± 392	3.87 ± 24.7	2.38 ± 18.9	0.01 ± 0.1	0
4) > 30.0	46.98 ± 130	0.89 ± 3.81	0.15 ± 1.3	0	0
Temperature (°C)					
1) < 24. 1	38.6 ± 109	25 ± 163	4.4 ± 25.8	0	0
2) 24.1 – 28.0	89.9 ± 535	7 ± 34.9	0.009 ± 0.09	0.009 ± 0.09	0
3) 28.1 – 32.0	20.0 ± 63.7	6.5 ± 36.7	0.26 ± 1.48	0.06 ± 0.28	0
4) > 32.0	0.3 ± 2.0	0.06 ± 0.2	0	0	0
Transparency (%depth)					
1) < 25.1	11.07 ± 34.4	1.57 ± 8.7	0.34 ± 2.38	0.01 ± 0.10	0
2) 25.1 – 50.0	109 ± 656	46.4 ± 210	0.16 ± 1.35	0	0
3) 50.1 – 75.0	79.9 ± 230	4.47 ± 19.8	0	0.02 ± 0.14	0
4) > 75.0	28.1 ± 108	1.25 ± 9.51	0.83 ± 7.47	0	0
			Adults		
Salinity					
1) < 25.1	25 ± 35.3	40 ± 56.5	0	10 ± 14.14	0
2) 25.1 – 30.0	141 ± 147.7	0	0	0	17.8 ± 52.5
3) > 30.0	66.5 ± 64.1	9.1 ± 14.9	0	0	0
Temperature (°C)					
1) < 23.1	27 ± 42.6	11 ± 15.9	0	0	17 ± 35.2
2) 23.1 – 26.0	65 ± 42.7	0	0	0	40 ± 89.4
3) > 26.0	160.3 ± 150	5.7 ± 21.3	0	1.42 ± 5.34	0
Transparency (cm)					
1) < 180.0	91.7 ± 107.9	12.5 ± 28.1	0	2.5 ± 7.07	10 ± 28.2
2) 180.1 – 290.0	90.7 ± 68.5	2.5 ± 9.3	0	0	14.6 ± 53.3
3) > 290.0	350 ± 353	0	0	0	0

The diagram separates the Spring/Summer samples on the left side, that is characterized by higher salinity and transparency, in opposition to the Winter samples, on the right side, that is characterized by lower salinity and transparency. The Autumn samples showed a wide distribution in the diagram, reflecting an intermediary condition and a wide variation of these environmental variables, with a slight trend to be closer to Spring/Summer samples. Axis 2 can be interpreted as temperature gradient in opposition to the salinity, with the Spring/Summer samples concentrated on the lower part of the diagram, characterized by higher temperature and lower salinity, while the winter samples were distributed on the upper part, characterized by lower temperature and higher salinity.

Discussion

The most abundant members of the Engraulidae family in the Sepetiba Bay showed spatial separation during their early life cycle at the sandy beaches. *Anchoa tricolor* dominated in the outer bay zone, while *A. januaria* peaked in the inner bay zone. This agrees with May & MacArthur (1972)

Table 4. Significant differences (p < 0.05) in number of individuals for each species from Engraulidae family, among ranges of environmental variables, according to Student-Newman-Keuls (SNK) test. Mean values in brackets. Environmental ranges according to Table 3.

	Juveniles		
Temperature			
Anchoa tricolor	1, 2, 3 (20.0-89.9)	>	4 (0.2)
Anchoa lyolepis	1 (5.9)	>	2, 4 (0.0-0.09)
Salinity			
Anchoa tricolor	3, 4 (46.9-58.6)	>	1, 2 (1.1-12.0)
Anchoa januaria	1 (65.6)	>	2, 3, 4 (0.8-14.1)
Transparency			
Anchoa tricolor	3 (79.9)	>	1, 4 (11.0-28.1)
Anchoa januaria	2 (46.4)	>	1, 4 (1.2-1.5)
	Adults		
Temperature			
Anchoa tricolor	2, 3 (65.0-160.3)	>	1 (27.0)
Anchoa januaria	1 (11.0)	>	2, 3 (0.0-5.7)
Salinity			
Anchoa januaria	1 (40.0)	>	2, 3 (0.0-9.1)

Table 5. Summary of the CCA performed on the abundance of juveniles species of Engraulidae family. Significant environmental variables were selected by a stepwise procedure analogous to forward elimination in multiple regression analysis. Significant values (p < 0.05) in bold.

AXES	1	2	3	4
Correlation of Environmental Variables				
Salinity	**-0.4089**	**-0.1255**	-0.0048	0.0000
Temperature	0.2533	0.0221	0.0573	0.0000
Transparency	**-0.3276**	-0.0545	-0.0704	0.0000
Summary Statistics for Ordination Axes				
Eigenvalues	0.212	0.027	0.019	0.394
Species-environment correlations	0.611	0.269	0.231	0.000
Cumulative Percentage of Variance				
of species data	16.3	18.4	19.9	50.2
of species-environment correlations	82.1	92.8	100.0	0.0
Sum of al Unconstrained Eigenvalues		1.298		
Sum of all Canonical Eigenvalues		0.258		

statement which predicted on theoretical grounds that species segregating along a single niche dimension in a fluctuating environment must maintain a certain minimum niche difference. The distributional boundaries of each species reflect its relationship with the environment, including physiological responses to physical characteristics and various interactions with other species, including predators, prey and pathogens (Ricklefs & Schluter, 1993). The successful recruitment and high abundance of these fishes in the sandy beaches in Sepetiba Bay (Silva *et al*., 2004) would be directly linked to this strategy and it was confirmed in the present work.

These two most abundant species have different areas of recruitment in the Bay. Young-of-the-year of *A. tricolor* recruits mainly in the outer bay zone. This area is located in a protected part of the bay due to its proximity to the largest isle, which enable recruitment in relatively calm and transparent waters. Juveniles of *A. lyolepis* were captured basically in the outermost site in the bay (site 1), where the influence of the sea is the highest. *Anchoa tricolor* and *A. lyolepis* may have different strategies as they coexist in the outer zone. There is also a conspicuous morphological difference between these two species, with the former showing a fairly short and blunt snout, while the latter, a prominent and pointed snout. Differences in morphological features between species have been used as indices of differences in resource use (Strong, 1984). Coexistence of morphologically or physiologically different phenotypes, as well as the behavioral or microgeographic diversity mentioned above, would be useful on both individual and population levels for exploitation of a diversified niche, and it is therefore probable that under the above conditions the population would be more variable than if it occupied a narrower niche (Van Valen, 1965). Furthermore, some arguments have been raised against this hypothesis because there are important interspecific habitat differences in sibling species which do not differ morphologically (Storch & Frynta, 2000).

Juveniles of *A. januaria* recruit mostly in the inner bay zone, which suffer more influence of continental drainage and effluent discharges from urban-industrial areas. *Anchoa januaria* showed indications of preference for estuarine areas such as lower rivers reaches (Araújo *et al*., 2002). Sergipense & Sazima (1995) also found *A. januaria* in higher abundance in sites in the inner zone between 1983 and 1985. Santos *et al*. (2007) reported that *A. januaria* in Sepetiba Bay shows movements between feeding areas (sandy beaches in the inner Bay) and spawning areas (lower rivers reaches), another evidence that this species use low salinity waters in the bay.

Juveniles of *Cetengraulis edentulus* rarely occurred in the beach seines, suggesting a different recruitment area other than the shallow sandy beaches of the Sepetiba Bay. Its recruitment probably takes place in deeper bay zones, where the sediment is mainly muddy, or outside the bay. Gay *et al*. (2000) reported that the distribution of this species in Itaipu lagoon, a coastal lagoon in the Rio de Janeiro State, is associated to muddy substrate.

Engraulis anchoita did not spend early life period in the Sepetiba Bay, since no young-of-the-year was recorded in the

Table 6. Summary of the CCA performed on the abundance of adults species of Engraulidae family. Significant environmental variables were selected by a stepwise procedure analogous to forward elimination in multiple regression analysis. Significant values (p<0.05) in bold.

AXES	1	2	3	4
Correlation of environmental variables				
Salinity	**-0.6003**	**0.5273**	-0.0022	0.0000
Temperature	**-0.4254**	**-0.6106**	0.0346	0.0000
Transparency	**-0.4651**	0.1470	-0.0591	0.0000
Summary statistics for ordination axes				
Eigenvalues	0.633	0.204	0.010	0.621
Species-environment correlations	0.869	0.732	0.144	0.000
Cumulative percentage of variance				
of species data	37.0	48.9	49.5	85.7
of species-environment correlations	74.8	98.8	100.0	0.0
Sum of al unconstrained eigenvalues	1.713			
Sum of all canonical eigenvalues	0.847			

beaches. Only a few juveniles were occasionally captured in a sand beach outside the bay. It is understood that this species distribution area is farther south, ranging from Latitude 23° to 33°S in open areas on the continental shelf, where it is target of large fisheries (Nakatani, 1982). Figueiredo & Menezes (1978) reported that *E. anchoita* is the only species of Engraulidae family to be found in deeper coastal waters in the continental shelf.

Adaptative strategies developed by species, mainly linked to spawning periods, allow the larvae and juveniles to increase survival rate in most favorable food availability, allowing fast growth and more efficient predator avoidance. In the Sepetiba Bay there is no available information on this seasonality, but some example in other areas could be mentioned. According to Macgregor & Houde (1996) seasonal abundance of eggs and larvae of *A. mitchilli* in Chesapeake are linked to seasonal food availability trigged by nutrient from seasonal rainfall.

Adults of *A. tricolor* penetrate into Sepetiba Bay mainly during late Winter, staying in the area until late Summer. *Anchoa lyolepis*, *A. januaria* and *C. edentulus* showed highest abundance in Spring. Spring is also considered as the season which favors high abundance of anchovies in other similar environments (Rakocinski *et al*., 1992; Sans *et al*., 1992; Paiva-Filho *et al*., 1986; Dorsey *et al*., 1996; Zastrow *et al*., 1991; Luo & Musick, 1991). *Engraulis anchoita* adults, on the other hand, presented significant seasonal variations with the highest abundance in the Autumn, probably due to a very differentiated life cycle from the others Engraulidae. Few numbers of this species penetrate in the Sepetiba Bay during late Autumn and move away during late Winter. In late Spring this species forms "patches" in dense schoolings on the continental shelf (Sanchez, 1986).

Relationship between fish occurrence and environmental variables were assessed although statistical associations between fishes and measured environmental factors (salinity, temperature, etc.) do not necessarily prove cause and effect. Juveniles of *A. tricolor* were related to lowest temperatures, which coincide with the spawning peaks during late Winter/ early Spring (Silva *et al*., 2004). In Spring 1999/2000 tem-

peratures were relatively higher and juvenile occurrences were lowest when compared to the previous year, and this could be an indication of suitability of lowest temperature for the recruitment success. Adults did not follow the same occurrence pattern in relation to temperature, since their highest captures occur in higher temperatures in the Summer. *Anchoa januaria* showed a wider occurrence in the ranges of examined temperature. *Cetengraulis edentulus* presented higher abundance in the highest temperatures, and this is also due to its highest occurrence in the inner zone. Salinity was probably the main environmental parameter to contribute for spatial separation of the most abundant Engraulidae species in the Sepetiba Bay. Juveniles and adults of *A. tricolor* were more abundant in higher salinity, while *A. januaria* and *C. edentulus* in lower salinity; these two latter species occur mainly in the area that receives the highest contribution of continental drainage. May & MacArthur (1972) reported that the relationship between environmental variability and niche overlap implies that several species compete on a one-dimensional continuum of resources. The location of the peak gives the optimal environment for that phenotype, the height of the peak is the measure of the best performance in the optimal environment, and the breadth of the curve is a measure of the tolerance for non-optimal environments (Levins, 1968). Each species is distributed according to its own genetic, physiological, and population characteristics and its own way of relating to environmental factors; hence no two species are distributed alike. Species respond in differing ways to factors that vary within communities in space and time, and such differences determine which species can coexist (Whittaker & Levin, 1975). This principle of competitive exclusion is not the only response for coexistence mechanisms. Patterns of species occupancy of habitats depend on the densities of the interacting species, the competitive hierarchy among them, the presence of detectable intra-type variation in patch quality, and on their fundamental habitat preferences (Rosenzweig, 1981, 1991). Allen *et al.* (1995) found that the entrance of *Anchoa mitchilli* (Valenciennes, 1848), during the Spring in estuaries of Carolina of the South (USA), causes a redistribution of other planktivorous species, with predominant *A. mitchilli* occurring in the deep part of the water column, while *Anchoa hepsetus* (Linnaeus, 1758) and *Menidia menidia* (Linnaeus, 1766) that were distributed in whole water column, concentrate in the upper parts near to the surface.

Overall, spatial partition is the main mechanism developed by the most abundant Engraulidae species to coexist in the Sepetiba Bay, with *A. tricolor* using the outer zone, while *A. januaria*, the inner zone. This two abundant species probably evolved in a differentiate way to adapt at different environmental conditions, avoiding competition. The assumption that former competition is the general cause of species differences in communities has been satirically termed "the ghost of competition past" (Connell, 1980). This also could be an acceptable hypothesis for the coexistence in high abundance of this closed related group of fishes in the Sepetiba Bay. Significant interespecif differences in habitat selection requirements are strongly species-specific, with some overlap in the distribution among the species probably due to the preferred features of habitat are not exclusive.

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