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The nursery function of sandy beaches in a Brazilian tropical bay for 0-group anchovies (Teleostei: Engraulidae): diel, seasonal and spatial patterns

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The role of sandy beaches as nursery areas for 0-group anchovies (Teleostei: Engraulidae) was investigated in a tropical bay, south-eastern Brazil. Spatial and temporal (diel and seasonal) changes in fish abundance and environmental influences at two beaches were assessed, one located in the outer zone, and the other in the inner zone of Sepetiba Bay. The two sites were sampled quarterly at the same time (0800, 1100, 1400, 1700, 2000, 2300, 0200 and 0500 hours) over a 24 h cycle by beach seine with three replicates, between winter 1998 and autumn 1999. Environmental variables of water temperature, salinity, and transparency (as % depth) were taken at each fish-sampling occasion. Five species in three genera (*Anchoa tricolor, A. januaria, A. lyolepis, Cetengraulis edentulus*, and *Lycengraulis grossidens*) were identified. *Anchoa tricolor* and *A. januaria* were the most abundant species and indications of spatial separation were detected, with *A. tricolor* being more abundant in the outer bay (higher salinity and lower temperature), while *A. januaria*, in the inner bay (lower salinity and higher temperature). Overall, young-of-the-year Engraulidae peaked during the day, perhaps an adaptation to avoid competition with other abundant species which peak at night. Maximum densities of anchovies due to 0-group influxes were found in spring and paucity in summer. Spatial segregation to optimize resource uses and daily habits adapted to take advantage of the rich planktonic bay waters seems to be the strategy developed by these closely related species to use the area during early life cycle. Their high abundances suggest the suitability of the sandy beaches as nursery areas.

INTRODUCTION

Engraulidae fish are believed to be the major trophic link in bay food chains through their role in converting planktonic biomass into forage for piscivorous fish, because they are the largest zooplankton consumers among the fish (Baird & Ulanowicz, 1989). Overall, 0-group recruits in large numbers at the sandy beaches where they spend their early life cycle. In Sepetiba Bay, a semi-closed 450 km^2 area in south-eastern Brazil (22°54′/23°04′S 43°34′/44°10′W), Engraulidae rank among the most abundant fish both as juvenile recruits in the sandy beaches, and as adults occupying different deeper areas in the inner and outer bay zones. The Engraulidae family contributed up to 35% of the total number of individuals in experimental beach seines (Pessanha et al., 2003). Strategies of resource uses must be developed by closely related species to allow coexistence and to avoid competitive exclusion. Spatial overlap of closely related species is possible if they separate on the basis of time, diet, or foraging techniques. Infrequently, closely related species segregate by occupying the same space at different times of day or period of the year. Differential habitat selection is one of the principal relationships which permit species to coexist (Rosenweig, 1981). Preliminary studies on spatial distribution for the most abundant Engraulidae species were performed by Silva & Araújo (2000) explaining coexistence as a result of the use of different resources supplied by different areas in Sepetiba Bay. Sergipense et al. (1999) found that *Anchoa januaria* and *Cetengraulis edentulus*, common in the inner Sepetiba Bay area, present a different feeding strategy, with the first species feeding predominantly on zooplankton and the latter, on phytoplankton.

Environmental variables could also be influencing the period that these fish migrate from the bay to open areas in the inner continental shelf and vice-versa. Heavy rainfall seasons seem to increase plankton availability, due to a large amount of nutrients brought by rivers, favouring the development of planktivorous fish. *Anchoa marinii* movements from coastal areas to the Patos Lagoon estuary were associated with intrusion of high salinity deep waters, while *Lycengraulis grossidens* was associated with areas of low salinity (Weiss & Krug, 1977). In Sepetiba Bay, Silva & Araújo (2000) found that young-of-the-year of *A. januaria* occur in sites more influenced by continental drainages. *Cetengraulis edentulus* is reported to occur near to muddy substrates (Sergipense & Sazima, 1995). The goal of this paper is to examine, using beach seine, the distribution of juveniles of Engraulidae species in Sepetiba Bay, by investigating their spatial, diel and seasonal occurrence, and to assess eventual influences of the environmental variables.

MATERIALS AND METHODS

Study area

Sepetiba Bay (Figure 1) was originated by an extensive process of sand deposition that formed a sandbank at its

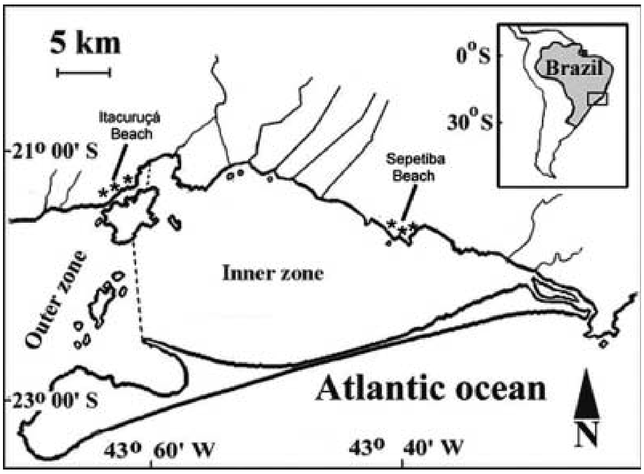

Figure 1. Study area, Sepetiba Bay, with indications of the two sandy beaches.

southern extremity. It has a wide communication with the Atlantic Ocean at its westbound extremity. The bay has a mean depth of 8.6 m, a maximum depth of 30 m, and its drainage area is ~2700 km^2. Waters are predominantly polyhaline (salinity average=30). The annual rainfall is between 1000 mm and 2100 mm (Araújo et al., 2002) but this does not influence the bay salinity due to the existence of only small tributaries. Most of the substrate is silt and mud. The tidal range is approximately 1 m and predominantly 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. The outer zone has a sandy and gravel bottom and was close to the sea limit (highest salinity, transparency, depth and lowest temperature); 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

The surveys were carried out in August 1998, November 1998, February 1999 and June 1999 to ensure that samples were obtained in each season, e.g. winter, spring, summer, and autumn. Fish were sampled using a beach seine net (10×2.5 m; 7-mm mesh size). Seine hauls were 30 m long, parallel to and close to shore, and were taken out to approximately 1 m depth. This procedure was replicated three times at each 3-h interval throughout the 24-h period. Samples were taken simultaneously at the two sites, Itacuruçá (outer bay) and Sepetiba (inner bay) beaches, in the following period: 0800, 1100, 1400 and 1700 hours (day period); and 2000, 2300, 0200 and 0500 hours (night period). This design resulted in a total of 192 samples: 2 sites, 8 h-period, 3 replicates, and 4 seasons. Water temperature, salinity and transparency were taken at every sampling occasion at approximately 0.5 m below surface water. Temperature and salinity were measured with a Horiba U-10 internally recording temperature–salinity recorder. A Sechi disc was used to measure water transparency which was calculated as per cent of the depth. Fish were fixed in 10% formalin, identified to species, counted, measured (total length in mm) and weighed in grams.

Data analysis

The relative abundances (in number) were estimated from the sampling capture-per-unit-effort (CPUE, number/sample). A parametric analysis of variance (ANOVA) and '*a posteriori*' Student–Newman–Keuls (SNK) test ($\alpha=0.05$) were used to test for differences in relative abundance of Engraulidae and environmental variables among locations, season and day vs night hours. Both biotic and environmental raw data were previously Log$_{10}$ transformed to address ANOVA assumptions of normality and homoscedasticity. Influences of environmental variables on fish occurrence were assessed by grouping fish numbers in intervals of temperature in degrees Celcius (1: $\leqslant$24; 2: 24.1–28; 3: 28–32; 4: >32), salinity (1: <24; 2: 24–28; 3: 28–32; 4: >32) and transparency in % of depth (1: <25; 2: 25–50; 3: 50–75; 4: >75). Relationships between fish occurrence and environmental variables were assessed through a canonical correspondence analysis.

RESULTS

Composition and relative abundance

A total of 16,868 Engraulidae fish were collected. *Anchoa tricolor* was the most abundant species, amounting to 97.28% of the total number of Engraulidae, followed by *A. januaria* 2.50%, *A. lyolepis* 0.15%, *Cetengraulis edentulus* 0.06% and *Lycengraulis grossidens* 0.01%. All fish were juveniles, mainly young-of-the-year ranging from 18 to 60 mm total length.

Anchoa tricolor (Table 1), was more abundant in the outer zone when compared with the inner zone ($P<0.05$). *Anchoa januaria* did not show significant differences in densities between the two sites, although there was a trend for higher abundance in the inner zone. The remaining species were too rare for a spatial pattern to be detected.

Seasonally, significant differences ($P<0.05$) were shown for *A. tricolor* and *A. januaria*. *Anchoa tricolor* was more

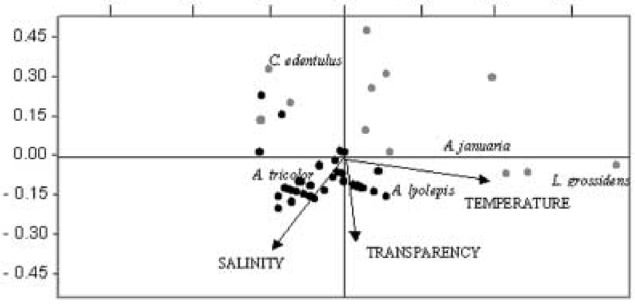

Figure 2. Ordination diagram of the two first axes from canonical correspondence analyses on fish abundance and environmental variables in Sepetiba Bay, 1998/1999. ●, Itacuruçá (outer zone); ●, Sepetiba (inner zone) beaches.

Table 1. *Significant F-values and differences in densities of anchovies among sites, seasons diel and environmental intervals in Sepetiba Bay, 1998/1999. Average values (capture-per-unit-effort=number/sample unit) in parentheses. *, P<0.05; **, P<0.01. Environmental intervals as describe in Materials and Methods.*

Species	Factors	F-values	Student–Newman–Keuls test		
A. tricolor	Site	10.7**	Itacuruçá (outer zone) (163.7)	>	Sepetiba (inner zone) (7.1)
	Season	19.0**	Winter > spring (244.3) (96.2)	>	Summer, autumn (0.0–1.2)
	Diel	41.2**	Day (164.9)	>	Night (10.7)
	Temperature	5.14**	1, 2 (95.4–178.5)	>	3, 4 (0.5–0.9)
	Salinity	30.2**	4 (359.45)	>	1, 2, 3 (0.1–20.5)
	Transparency	7.56**	2, 4 (291.5–331.25)	>	1, 3 (16.1–24.7)
A. januaria	Season	2.0*	Spring (8.2)	>	Summer, autumn, winter (0.0–0.5)
	Temperature	8.57**	4 (23.6)	>	1, 2, 3 (0.26–4.13)
C. edentulus	Temperature	2.67*	4 (0.33)	>	1, 2, 3 (0.0–0.13)

Table 2. *Summary of the canonical correspondence analysis performed on the abundance of anchovies. Significant factors were selected by a stepwise procedure analogous to forward elimination in multiple regression analysis. Highest correlation between environmental variables and axes in bold.*

Axes	1	2	3	4
Correlation of environmental variables				
Salinity	**−0.2952**	**−0.3521**	0.0083	0.0000
Temperature	**0.5904**	−0.0658	−0.0036	0.0000
Transparency	0.0001	**−0.2919**	−0.0513	0.0000
Summary statistics for ordination axes				
Eigenvalues	0.255	0.034	0.001	0.525
Species-environment correlations	0.598	0.407	0.074	0.000
Cumulative percentage of variance				
of species data	18.8	21.3	21.4	60.2
of species-environment correlations	88.0	99.6	100.0	0.0
Sum of all unconstrained eigenvalues				1.355
Sum of all canonical eigenvalues				0.290

abundant in winter/spring while *A. januaria* was more abundant in spring. Daily, *A. tricolor* presented higher abundance during the day when compared with the night period (Table 1).

Influence of environmental variables

Anchoa tricolor and *A. januaria* showed significant differences in abundances among the ranges of temperature, while the former also showed differences among ranges of salinity (Table 1). *Anchoa januaria* peaked at the highest temperature (>32°C), while *A. tricolor* was more abundant in the lowest temperature (<28°C), and highest salinity (>32). Despite being recorded at low densities, *A. lyolepis* and *C. edentulus* showed a defined pattern for transparency, with the former being more abundant in the highest transparency, while the latter in the lowest transparency.

Canonical correspondence analysis showed for the first two axes eigenvalues of 0.255 and 0.034, respectively, explaining 88.0% and 11.6% of the total variance (Table 2). The species−environmental correlation was 0.598 for the axis 1 and 0.407 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 temperature gradient, with lower weight for the transparency, while axis 2 represents the salinity and transparency gradient. A marked shift in the Engraulidae populations from the inner to the outer zone, along axis 2, coincided with spatial gradient of transparency and salinity. The ordination diagram of the first two axes separates at the upper part samples from the inner zone, characterized by the lowest salinity and transparency, in opposition to samples from the outer zone at the lower part, which are characterized by the highest transparency and salinity (Figure 2).

DISCUSSION

Spatial segregation was detected for the two most abundant members of the Engraulidae family in Sepetiba Bay, during their early life cycle at the sand beaches. The dominant *Anchoa tricolor* occurred mainly at Itacuruçá beach in the outer bay zone, while *A. januaria* showed peaks at Sepetiba beach in the inner bay zone. This pattern is probably part of an adaptive process that these closely related species underwent in order to explore the available resources and to avoid competition. It closely agrees with the hypothesis that each species is distributed according to its own genetic, physiological, and population characteristics and has its own way of relating to environmental factors; hence no two species are distributed alike (Levins, 1968). The recruitment in large numbers, mainly of *A. tricolor* and *A. januaria* at the sandy beaches in Sepetiba Bay could be linked to this spatial segregation, optimizing the uses of the available resources.

Young-of-the-year of *A. tricolor* recruits mainly at the outer zone with higher influence of seawater. Young-of-the-year of *A. januaria*, on the other hand, recruited mostly in a more confined area in the inner bay; this species is the only anchovy to occur in restricted estuarine areas such as lower river reaches or its confluences with the bay (Silva & Araújo, 2000). Sergipense & Sazima (1995) also found *A. januaria* in higher abundances at sites in the inner zone between 1983 and 1985. The principle of competitive exclusion states that in a stable community, no two species can be limited by the same factor. Species respond in differing ways to factors that vary within communities in space and time, and it is the differences in response patterns to these spatiotemporal differences that determine which species can coexist. This principle 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 their fundamental habitat preferences (Rosenzweig, 1981). On the other hand, the rare *Cetengraulis edentulus*, *A. lyolepis* and *Lycengraulis grossidens* rarely occurred in the beach seines, suggesting that they use a different area for recruitment purposes other than the shallow sandy beaches of Sepetiba Bay.

Seasonal changes in photoperiod and temperature are relatively narrow in the tropics, when compared with temperate areas; furthermore, seasonal changes in winds and rainfall are common causes for seasonal changes in many tropical ecosystems. Such changes are prone to affect habitats, mainly via qualitative and quantitative changes in food availability. Additionally, species match their spawning periods to maximize larvae and juvenile survival rate in most periods of favourable and abundant food availability.

Spatial and temporal distribution of the Engraulidae family in Sepetiba Bay could also be due to influences of environmental variables, with each species showing a differentiated adaptive history to exploit different conditions and habitats. The outer bay zone suffers a greater influence of marine waters, presenting higher salinity and transparency, while the inner zone showed the other way around, with a higher influence of natural and artificial continental drainage and increased temperature. Differences in sediment type have also been reported by Araújo et al. (2002), with the inner and central zone being mainly muddy, while the outer zone presents a coarse and sand–muddy bottom.

Temperature was probably the main environmental parameter to contribute for spatial separation of the most abundant Engraulidae species in Sepetiba Bay, with *A. tricolor* being more abundant at the lowest temperatures, which coincide with the peaks in spawning period in late winter/early spring (Silva & Araújo, 2000). *Anchoa januaria* and *Cetengraulis edentulus* peaked in the highest temperatures in the inner zone. *Anchoa tricolor* is more abundant in higher salinity, mainly in the area that suffers the highest seawater influence.

An increase in *A. tricolor* abundance was recorded during the day and the same pattern occurred to a lesser extent to *A. januaria*. Pessanha et al. (2003) found that the closely related *Harengula clupeola*, another abundant clupeoid in Sepetiba Bay, uses the outer sandy beaches during the night. The day activity of anchovies in the area could be an adaptation to avoid competition with *H. clupeola*, therefore optimizing the available resource use.

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