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Diet and ontogenetic shift in habitat use by *Rhinosardinia bahiensis* in a tropical semi-arid estuary, north-eastern Brazil

FERNANDO JOSÉ KÖNIG CLARK AND ANDRÉ LUIZ MACHADO PESSANHA

Laboratório de Biologia Marinha, Universidade Estadual da Paraíba, Avenida das Baraúnas, 351, 58429-500 Campina Grande, PB, Brazil

*The feeding biology of bahia sprat (*Rhinosardinia bahiensis*) was studied in two habitats of a tropical semi-arid estuary, on the north-eastern Brazilian coast. Samplings were collected on a monthly basis (January 2010–February 2011), and fish were caught during the day using an 8 m beach seine. Habitat use was size-dependent, with tidal mudflat occupied by higher size-classes than tidal creeks, which were occupied by smaller conspecifics. The diet analysis of different size-classes revealed that all sizes of fish consumed similar taxa (Calanoida, Cyclopoida and Decapoda larvae), and that the relative proportion of taxa consumed reflected fish size. Dietary differences between the two nursery areas mainly reflected prey availability. Although high diet overlap was only found between some size-classes in tidal mudflat, these results seem to demonstrate a strategy for efficient use of space potential; intraspecific competition was probably minimized by a differential habitat use patterns.*

Keywords: trophic ecology, tidal creeks, mudflat, ontogeny, Clupeidae

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INTRODUCTION

Semi-arid tropical estuaries are those located in coastal wetlands, but the conditions of their interior basins are intermittent (Barletta & Costa, 2009), and house a large number of fish species (Barletta *et al.*, 2010). In this environment we can find two distinct shallow habitats: tidal flats and mangrove creeks. Each one has great value to many species, including larval and juvenile fish, due to their provision of optimal conditions for feeding, growth and protection from predators (Allen & Barker, 1990). Aerial root systems create a productive and structurally complex environment that can be used as a place of refuge and feeding, whereas tidal mudflats are structurally less complex, but they provide a great abundance of a variety of phytoplankton and zooplankton, including copepods, gastropods, plant detritus and sediments which are particularly important nursery habitats for juvenile fish (Tse *et al.*, 2008).

Representatives of the family Clupeidae illustrate the concept of a marine estuarine opportunist strategy, with many of these species abundant in estuaries, particularly as juveniles (Thiel & Potter, 2001). One of these representatives, *Rhinorsardinia bahiensis* (Steindachner, 1879), has neotropical zoogeographical distribution in estuaries of South America, from the mouth of the River Orinoco to the north-east of Brazil (Whitehead, 1985); they are considered important components in terms of their contribution to biomass, and they represent an important link in the food chain and energy flow by acting as a carrier of matter and energy between the estuarine ecosystems and inner continental shelf (Boehlert & Morgan, 1985; Barletta & Blaber, 2007). Despite the wide distribution of this species, there is a need for better knowledge about the trophic relationships in the environments considered as their nursery areas.

During the development of the fish, several processes contribute to changing aspects of their lifestyle that end up reflected in their diet. Such changes can be attributed to interactions with external (e.g. habitat, food availability and predation risk) and internal factors (e.g. anatomical structures and physiological demands) (Luczkoviche *et al.*, 1995; Hart, 1997; Wooton, 1999). Local hydrological conditions associated with transport processes and spawning patterns are identified as factors responsible for differences in the distribution of the early life stages of the fish (Arshad *et al.*, 2003). Some studies indicate that habitat selection is made primarily on the basis of salinity and temperature (Ramos *et al.*, 2006), but characteristics associated with food resources and low density of competitors and predators also increase the value of shallow areas as a nursery (Akin *et al.*, 2003).

The observed dietary changes in some species of Clupeidae in temperate and tropical areas are associated with changes in the exploitation of different estuarine environments (Bailey *et al.*, 1975; Godin, 1981), allowing better exploitation of resources between individuals and between different sizes. Different diets within the same species are often found through the stages of development, due to differences in energy demand and morphological constraints, which implies different diets during development (Kaiser & Hughes, 1993). This issue is critical to their survival; it results in an increase in growth rate and reduction in

Corresponding author:
A.L.M. Pessanha
Email: andrepessanhauepb@gmail.com

susceptibility to predation, which was considered by Cowan *et al.* (1997) as the most likely cause of larval mortality.

The Clupeidae family shows significant habitat association by size (Barko *et al.*, 2004). Clupeid size distribution may support the theory that fish utilize different portions of their habitat as they develop, even in early life stage fish. Understanding the processes that determine the occurrence and timing of niche changes is important for a proper evaluation of the size of the local population. This study aims to examine spatial variability in the dietary habits of *Rhinosardinia bahiensis* by comparing the composition of the diet of juvenile fish between two micro-habitats located along a salinity gradient and structure among vegetated (mangrove tidal creek) and shallow non-vegetated (mudflat) areas, as well as aspects related to their life cycle in a semi-arid tropical estuary.

MATERIALS AND METHODS

Study area

The River Mamanguape estuary is located on the north coast of the Paraíba State and extends for 25 km in the east–west direction and for 5 km in the north–south direction. It is part of the Environmental Protection Area (Área de Proteção Ambiental—APA) of Barra de Mamanguape (Figure 1). The regional climate is classified by Köppen as As-type (hot and humid). The rainy season begins in February and lasts until July, with maximum rainfalls occurring from April to June, whereas the dry season occurs in August–January, with the lowest rainfalls occurring between October and December (Pereira & Alves, 2006). The average rainfall recorded in the area is between 1750 and 2000 mm annually, and the average temperature is approximately 24–26°C. There is a well-preserved mangrove in the area, composed of *Avicennia germinans*, *Avicennia schaweriana*, *Conocarpus erectus*, *Laguncularia racemosa* and *Rhizophora mangle*, which grows around the primary channel and tidal creeks and extends to 600 ha, in addition to Atlantic Forest remnants (Rocha *et al.*, 2008). Endangered species, such as the seahorse, *Hippocampus reidi*, and the West Indian manatee, *Trichechus manatus*, are also found in this estuary (Mourão & Nordi, 2003; Castro *et al.*, 2008).

The study was conducted in two intertidal habitats in the River Mamanguape estuary that display a mesotidal semi-diurnal tidal regime (range 2.2 m), regularly exposed and submerged twice a day. The tidal mud flat (6°46′27″S 34°55′20″W), located 2.3 km from the estuary mouth, is 1200 m long and has very calm waters because of the diminished influence of waves (Figure 1). The mudflat is greatly influenced by the entrance of ocean waters, where marine sediments are regularly exposed and submerged by tidal, and has a maximum depth of 4 m. The tidal mudflat (6°46′27″S 34°55′20″W) examined is a non-vegetated area with a gentle slope and fine muddy sediment in the intertidal zone; in the subtidal zone, seagrass, sessile invertebrates, macroalgae, mangrove leaves, and fallen branches form the benthic cover (Xavier *et al.*, 2012). The tidal creeks (6°47′03.15″S 34°57′10.75″W) consist of a mangrove canal located in the most central part of the estuary, bordered along its entire extension (1.4 km) with well-preserved mangrove, besides more deep and muddy sediment, resulting from the deposition of silt and mud (Figure 1).

Data collection

Samples were collected in both the rainy season (February–July 2011) and the dry season (August 2011–January 2012) to sample the ichthyofauna of the tidal mudflat more completely and efficiently during the local hydrological regime.

To collect fish during daylight, a beach seine (10 m long and 1.5 m height, with a stretched mesh size of 5 mm) was hauled parallel to an extension of approximately 30 m and to a maximum depth of 1.5 m. Temperature, salinity, and water transparency were measured, using a thermometer, an optical refractometer and a Secchi disc, respectively. The sampling unit was standardized with five replicates in

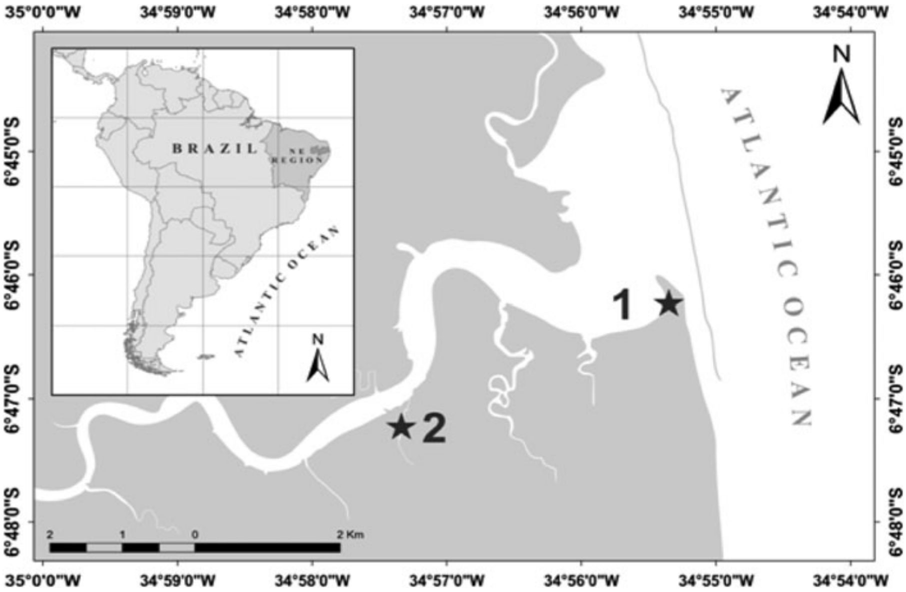

Fig. 1. River Mamanguape estuary, north-eastern Brazil, with indications of the sampling sites: 1, tidal mudflat; 2, tidal creeks.

an effort to capture individuals that use the area for feeding. The collected fish were fixed in 10% formalin for later identification in the laboratory, according to Araújo *et al.* (2004). The total length (TL, mm) and body weight (*g*) were measured for each individual.

The morphological measurements used were related to feeding apparatus: mouth height (M_H) is the height of the gape when the mouth fully open; mouth width (M_w) is the width of the gape when the mouth fully open. The mouth area (M_A) (assuming an elliptical shape) is described by:

$$M_A = 0.25\pi(M_H M_w) \quad \text{(Karpouzi \& Stergiou, 2003).}$$

Statistical analysis

Two-way analysis of variance (ANOVA) ($P < 0.05$) was used to compare fish abundance and biomass and environmental variables among seasons and habitats. Data were examined for normality and homoscedasticity by the Shapiro–Wilk test and Cochran's test, respectively, and data were transformed by $\log_{10}(x + 1)$ where necessary prior to analysis. A *post hoc* Tukey HSD test followed ANOVA procedures every time that the null hypothesis was rejected at $\alpha = 0.05$ (Zar, 2009).

To analyse each diet, the frequency of occurrence (%F), the percentage number (%N) and the volume (%V) of different food items were calculated (Hyslop, 1980), and the index of relative importance (IRI) was subsequently applied (Pinkas *et al.*, 1971). For items that could not be counted, a value of 0.1 was given for their number (%N) when they were present in the diet to offset distortions in the index (Abdurahiman *et al.*, 2010).

In order to determine the number of open intervals of length, classes were defined by Sturges's rule (Triola, 2005):

$$K = 1 + 3.3 \times \log(n)$$

where: K = number of classes, and n = number of cases. Size of captured individuals ranged from 43 to 106 TL mm. For the ontogenetic variations, individuals were separated into eight size-classes: I = <50 mm TL; II = 51–58 mm TL; III = 59–66 mm TL; IV = 67–74 mm TL; V = 75–82 mm TL; VI = 83–90 mm TL; VII = 91–98 mm TL; and VIII = >99 mm. For subsequent analyses involving fish size, the latter three size-classes were combined, since insufficient fish of the largest size-class were collected.

A non-metric multidimensional scaling (nMDS) ordination was applied to obtain a graphical representation of the trophic groups, using the volume of food items. The Bray–Curtis coefficient was calculated for each size-class after a fourth-root transformation. One-way analysis of similarity (ANOSIM) was performed on the similarity matrix to test whether the composition of the diet differed significantly amongst the size-classes. Similarity percentages (SIMPER) were used to determine which dietary items contributed most to similarity between the samples for different size-classes.

Volumetric data of feeding items were used to calculate the Shannon–Wiener diversity index, as a proxy of the niche breadth. The simplified Morisita overlap index (Krebs, 1989) was used to assess niche overlap among sites and size-classes. Those values that exceeded 0.60 (Labropoulou & Eleftheriou, 1997) were considered biologically significant. The simplified Morisita index was also calculated based on the numerical data for the feeding items.

RESULTS

Environmental variables

The only environmental variable that showed significant differences between the study points was salinity, with higher values observed on the tidal mudflat (Table 1). Temporally, such differences were stronger, with higher values of transparency and salinity registered within the dry season. For temperature, no patterns were found, while for salinity and transparency, such differences were significant by ANOVA; the interaction term was also significant for salinity (F = 5.6; P = 0.01) (Table 1).

Spatial and temporal variation in abundance

The spatial variation showed the same pattern for both fish abundance (CPUE) and for biomass, with higher values registered on the tidal mudflat (Figure 2); although no significant differences were observed between CPUE (F = 0.51; P = 0.47) and biomass (F = 0.93; P = 0.33).

The temporal analysis of abundance showed a gradual increase at the end of the rainy season through to the dry season (October), while lesser abundance occurred mostly during the rainy season (Figure 2). Biomass had a continuous increase from November to January, with the latter showing higher values of biomass (Figure 2). Such temporal differences were not significant for abundance (F = 2.20; P = 0.14) or for biomass (F = 3.103; P = 0.080); the interaction term was also not significant for abundance (F = 1.36; P = 0.24) or biomass (F = 0.78; P = 0.37). The larger individuals (>60 mm) were more frequent in the mudflat, while the smallest were more frequent in the tidal creeks (Figure 3).

Table 1. Mean values (±standard error) and results for analysis of variation for comparisons among environmental factors of sites and the hydrological regime on the River Mamanguape estuary, Paraiba, Brazil.

Environmental parameters	Mudflat		Tidal creeks		Habitat (H)	Season (S)	Interaction ($H\times S$)
	Rainy	Dry	Rainy	Dry			
Temperature (°C)	28.95 ± 0.67	30.14 ± 036	29.08 ± 0.30	29.48 ± 0.33	0.49^{ns}	0.04^{ns}	2.41^{ns}
Salinity	25.5 ± 1.44	34.46 ± 0.86	15.64 ± 1.76	17.96 ± 1.37	65.05^{ns}	10.04^{ns}	5.68^{ns}
Transparency (cm)	34.60 ± 2.47	48.33 ± 2.71	40.68 ± 4.47	42.00 ± 2.84	0.318^{ns}	14.87^{ns}	0.54^{ns}

ns, not significant.

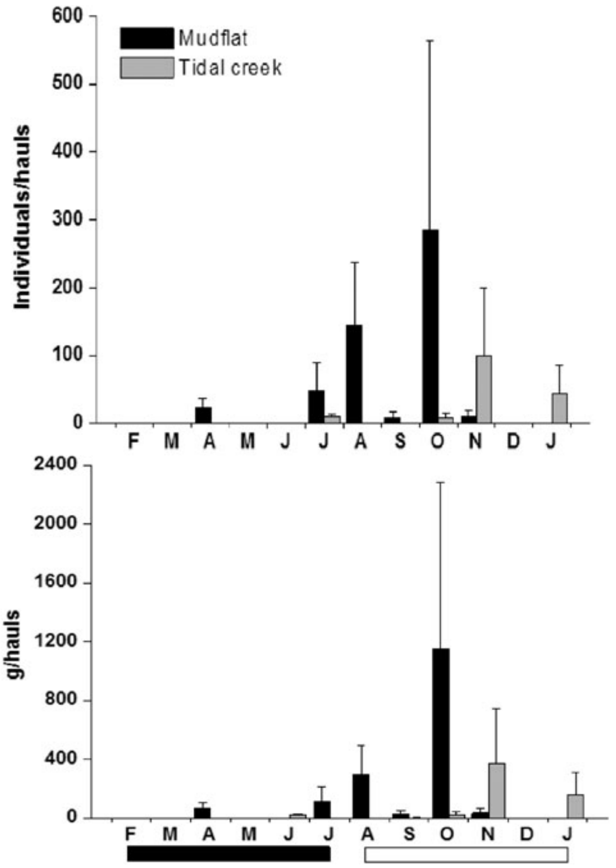

Fig. 2. Means (±standard error) for abundance (CPUE) and biomass of the *Rhinosardinia bahiensis* in the River Mamanguape estuary.

Table 2. Frequency of occurrence (%F), and percentage contribution by number (%N) and volume (%V) of the dietary items in the stomach contents of *Rhinosardinia bahiensis* in the mudflat and tidal creeks of the River Mamanguape estuary. Dietary items that contributed most in the index of relative importance are in bold. ni, not identified.

	Mudflat (N = 313)			**Tidal creeks (N = 99)**		
Dietary category	**%F**	**%N**	**%V**	**%F**	**%N**	**%V**
Diatoms	39.93	0.02	0.28	**61.11**	**0.14**	**1.21**
Foraminifera	6.07	0.08	0.40	1.01	0.02	0.19
Tintinnid	0.32	0.08	0.02	–	–	–
Trematoda	0.32	<0.01	0.02	–	–	–
Nematoda	10.54	0.49	1.07	–	–	–
Sipuncula	5.43	0.05	0.38	–	–	–
Polychaeta larvae	0.95	<0.01	0.06	1.00	0.04	0.20
Crustacea ni	0.32	<0.01	0.04	–	–	–
Decapoda larvae	**43.45**	**3.52**	**10.31**	**5.01**	**93.27**	**74.34**
Decapoda	2.23	0.04	0.25	–	–	–
Tanaidacea	0.95	<0.01	0.25	1.09	0.02	0.38
Isopoda	4.15	0.03	0.29	5.05	0.30	0.96
Amphipoda	0.95	<0.01	0.12	–	–	–
Caprella	0.31	0.02	0.15	–	–	–
Copepoda ni	9.58	5.08	1.75	–	–	–
Calanoida	**43.13**	**43.46**	**30.83**	**10.00**	**1.44**	**2.50**
Cyclopoida	**50.79**	**40.84**	**40.78**	**19.01**	**1.91**	**7.33**
Harpacticoida	0.32	<0.01	0.02	–	–	–
Ostracoda	**42.81**	**0.58**	**3.25**	**43.01**	**2.05**	**9.07**
Mollusca ni	0.31	<0.01	0.04	–	–	–
Gastropoda larvae	**31.94**	**3.57**	**4.34**	3.00	0.11	0.38
Bivalvia larvae	**27.79**	**1.59**	**2.68**	**10.00**	**0.56**	**2.31**
Invertebrate eggs	5.11	0.22	0.47	–	–	–
Scale	1.59	<0.01	0.27	–	–	–
Fish eggs	8.30	0.10	0.66	–	–	–
Fish	0.32	<0.01	0.04	–	–	–
Plant Material	5.75	<0.01	0.48	7.07	0.01	0.83
Algae	0.31	<0.01	0.02	–	–	–

Overall dietary composition

A total of 412 stomachs were analysed and the dominant prey was zooplanktonic and some infauna items (Table 2). On the tidal mudflat, 313 stomachs were analysed and the most contributive items were: Cyclopoida (IRI = 46.39%), Calanoida (IRI = 37.47%) and Decapoda larvae (IRI = 7.66%), while in the tidal creeks 99 stomachs were analysed

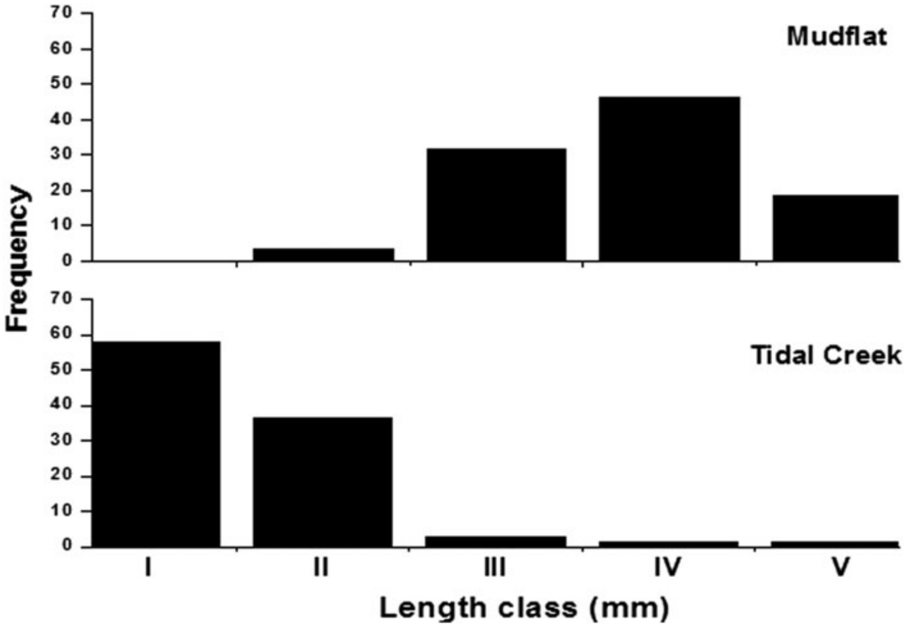

Fig. 3. Length–frequency distribution for *Rhinosardinia bahiensis* in tidal mudflat and tidal creeks in the River Mamanguape estuary.

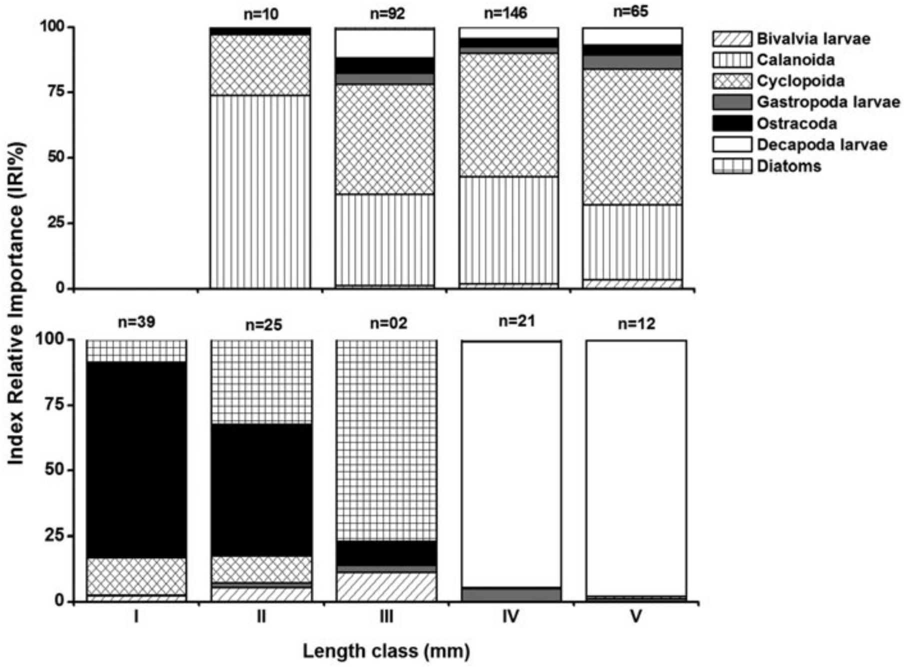

Fig. 4. Index of relative importance (%IRI) of the principal dietary items of the stomach contents of sequential total length-class of *Rhinosardinia bahiensis* in mudflat (A) and tidal creeks (B), from the River Mamanguape estuary. Sample sizes are given above each histogram.

and items were mainly: Cyclopoida (IRI = 15.84%), Ostracoda (IRI = 42.23%) and Decapoda larvae (IRI = 30.84%) (Table 2).

The diet analysis for different size-classes showed differences for each site (Figure 4). In tidal mudflat there was a progressive increase in the use of Cyclopoida with the ingestion of other preys, such as Bivalvia and Gastropoda larvae. In tidal creeks it was observed that within the smaller classes (I and II) there was a greater intake of Ostracoda, which was replaced by planktonic organisms, like copepods and Decapoda larvae (Figure 4).

Following nMDS of the data for dietary samples of all size-classes of *R. bahiensis*, the samples from small size-class in the tidal creek lay to the upper right the ordination plot, while the samples from other size-classes the tidal mudflat and tidal creek tended to be widely distributed throughout the plot and thus did not form discrete groups (Figure 5). ANOSIM demonstrated that, the dietary composition was significantly different between size-classes (Gobal $R = 0.604$; $P = 0.029$). SIMPER showed that small sizes of *R. bahiensis* consumed relatively greater volumes of diatoms, Bivalvia and Gastropoda larvae, whereas the Calanoida, Cyclopida,

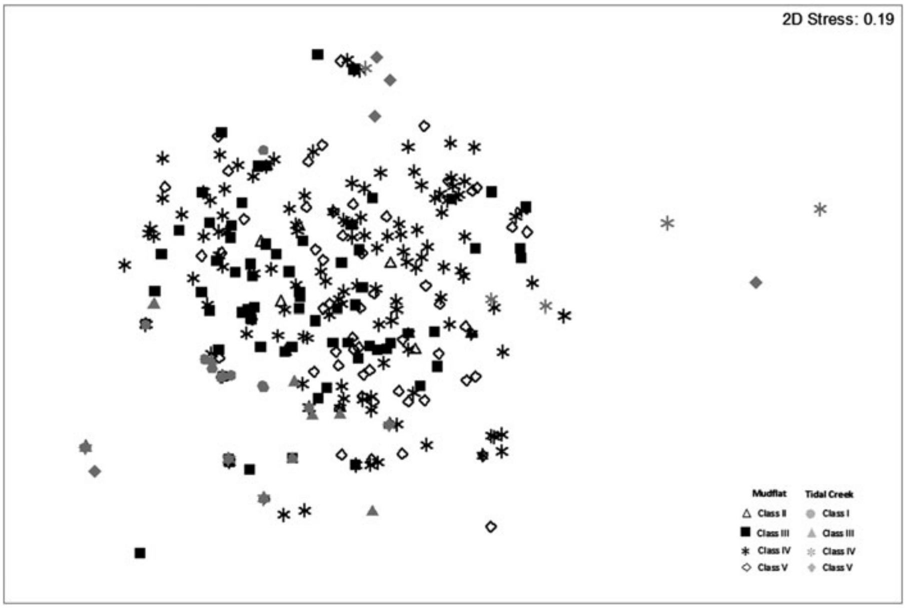

Fig. 5. Non-metric multidimensional scaling ordination of the percentage volumetric contributions of the various dietary items in each fish size-class of *Rhinosardinia bahiensis* in the River Mamanguape estuary, Brazil.

Table 3. Discriminating dietary items for size-classes in the mudflat and tidal creek determined by SIMPER analysis. Dia, diatoms; For, Foraminifera; Cal, Calanoida; Cycl, Cyclopoida; Dec, Decapoda larvae; Ost, Ostracoda; Biv, Bivalvia larvae; Gas, Gastropoda larvae.

		Average abundance								Average similarity	Contribution cumulative (%)
		Dia	**For**	**Cal**	**Cyc**	**Dec**	**Ostr**	**Biv**	**Gas**		
Mudflat	I	–	–	–	–		–	–	–	–	–
	II		1.10	0.95						47.97	94.67
	III		0.34	0.51	0.75	0.50	0.57			35.54	95.25
	IV			0.84	0.73	0.61	0.35		0.40	30.31	86.11
	V			0.81	0.56	0.57	0.53	0.56	0.59	38.24	94.05
Tidal creek	I	0.47							0.68	53.93	93.70
	II	0.44			0.30		0.57			42.09	95.11
	IV	0.38		0.23			0.31			24.98	100.00
	V	0.35				0.39				27.56	94.39

Ostracoda, Decapoda larvae were relatively greater contribution in latter sizes (Table 3).

Niche breadth showed an increase in these values as individuals increased in size ($F = 13.43$; $P < 0.001$) (Table 4). Niche overlap was observed among all size-classes within tidal mudflat, mainly due to the use of Calanoida and Cyclopoida among such individuals; in tidal creek, the greatest amount of intraspecific overlap (>0.6) was found for the smallest and largest size-classes (Table 5).

When we analysed the mouth area of different size-classes, it was observed that smaller individuals (Class I and Class II) presented lower ranges, while in the bigger sizes larger ranges were recorded (Figures 5 and 6).

DISCUSSION

The study population *Rhinosardinia bahiensis* exhibited strong and distinct habitat selection within the estuary. Factors contributing to variation in recruitment are often manifested in patterns of habitat selection by fish: (1) microhabitat selectivity by species increases their survival rate (the predator avoidance behaviour); (2) it provides more food (because the species is generalist it can widen its food range at a certain stage of development); and (3) the species, as an estuarine-resident, is well adapted to fluctuating salinity.

Microhabitat selection has a strong influence on the success of the population because of the abundance and accessibility of resources, which are discontinuous in natural environments, and the exposure of individuals to density-dependent processes such as predation (Scharf *et al.*, 2000; Krivan & Sirot, 2002). Such attributes may have influenced the pattern observed in this study, with larger individuals being recorded in an environment with little structural complexity, while the smallest were recorded in the tidal creeks where there is protection provided by mangrove roots and a great availability of food resources. The high abundance of juveniles in the turbid and calm waters of the tidal creeks can be explained by the high concentration of particulate matter that increases visual contrast for encountering prey and greater protection from predators (Blaber & Blaber, 1980; Boehlert & Morgan, 1985). Also, the non-selective filter-feeding of food items can be used by herring when the prey concentration is higher in tidal creeks (Yako *et al.*, 2002). Predation pressure and protection are important features for determining the use of space, which is particularly true for recruits (McCormick, 1998). Predation risk is high in non-vegetated areas, especially in estuaries, and small fish may select shallow water to avoid large natant predators (Rozas & Zimmerman, 2000).

The results of spatial diet showed that the items were very similar in the two areas analysed, due to resource utilization of zooplankton. Predation on zooplankton has been recorded in other tropical and temperate estuaries for Clupeidae (Höfling *et al.*, 2000; Yako *et al.*, 2002). The largest number of items recorded in the tidal mudflat, was due to the influence of the tides; this strongly affected mixing and circulation patterns at the entrance to estuary. A higher frequency and volume of Bivalvia and Decapoda larvae were observed in tidal creeks, given the requirement by juveniles of zooplankton in a size range appropriate for ingestion (Möllmann *et al.*, 2004).

Table 4. Niche breadth values (Shannon–Wiener diversity index) for length-class of *Rhinosardinia bahiensis* in mudflat and tidal creeks in the River Mamanguape estuary.

Length-class	Habitat mudflat	Tidal creeks
I	–	0.18 ± 0.03
II	0.22 ± 0.09	0.21 ± 0.04
III	0.31 ± 0.02	0.33 ± 0.01
IV	0.33 ± 0.01	–
V	0.44 ± 0.03	–

Table 5. Simplified Morisita index based on the numerical percentage for length-class of *Rhinosardinia bahiensis* in mudflat and tidal creeks in the River Mamanguape estuary. Values ≥0.6 in bold.

Habitat/class	I	II	III	IV	V
Mudflat					
I		–	–	–	–
II		–	–	–	–
III		**0.84**	–	–	–
IV		**0.88**	**0.98**	–	–
V		**0.85**	**0.97**	**0.99**	–
Tidal creeks					
I	–	–	–	–	–
II	**0.98**	–	–	–	–
III	0.46	0.53	–	–	–
IV	0.01	0.01	0.00	–	–
V	0.00	0.00	0.00	**0.99**	–

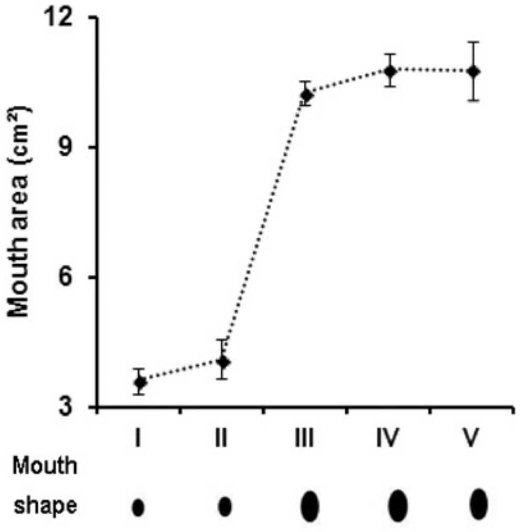

Fig. 6. Mouth area values and mouth shapes for length-class of *Rhinosardinia bahiensis* from the River Mamanguape estuary.

Studies also suggest that an increase in density of larvae occurs during periods of low rainfall, when it is registered in the recruitment of tidal creeks (Cavalcanti *et al.*, 2008). In this case, the habitat selection may indeed be lead by size segregation in different parts of the environmental, as is observed when comparing the results.

Fish distribution in the present study may be responding to differences in structural complexity between habitats, which are reflected in diet. Probably the capacity of adaptation for microhabitats and mangrove structure seems to be important for *Rhinosardinia bahiensis* development, and may ensure rapid rates of growth due to the reduction of mortality of larvae and juveniles. The presence of mangroves and submerged vegetation in estuarine areas has a large influence on the diet and feeding strategy of Clupeiformes (Chaves & Vendel, 2008).

In the present study we observed the prevalence of Ostracoda in the first and second size-classes, while in the third size-class it is interesting to note that there was a greater 'equitable' distribution of items, or even varying of diet to include more items. This may be related to the spawning period, when trying to get protein from various resources available in the environment, with an increase in the volume of larvae of Bivalvia, Gastropoda and Decapoda. In the fourth size-class (TL = 67–74 mm) diet remained relatively varied, and in the last size-class (TL > 75 mm) there were the largest quantities of Foraminifera, Decapoda larvae, and diatoms; more than half of their diet consisted of Cyclopoida and Calanoida. An increasing proportion of individuals started to mix their feeding methods from biting only, through combinations of biting, gulping and filtering (mixed feeders), to filtering only. It is important to emphasize that the spatial separation between sizes as a strategy for habitat use at different stages of the life cycle, forms an important process to avoid overlapping between different size-classes.

The main feature of the estuarine fish was their opportunistic feeding habits, given the high productivity of food resources produced at these sites (Bennemann *et al.*, 2006; Paiva *et al.*, 2008). Other studies indicate the sharing of common resources and the flexibility to explore the prey population (Ley *et al.*, 1999). A clear expansion of the variety of food items during fish ontogenetic development was observed, the main diet of smaller fish composed of Ostracoda. From that point, there was an inversion and the dominance of Cyclopoida and Calanoida in other classes until adulthood where a wide range of items were observed. This process and the reasons why it occurs are not yet clear (Choat & Clements, 1993), but it is supported by studies conducted by Jones (1984) and McCormick (1998) who both attest to the same process of decline among the reasons of food items, as *Rhinosardinia bahiensis* at the same time decreasing the amount of certain items equalizes in numbers (Decapoda larvae, Foraminifera, Cyclopoida and Calanoida).

Morphological characteristics, especially those related to the capture and ingestion of prey, have evolved to maximize the performance of feeding, and have been strongly correlated with diet (Wainwright & Richard, 1995; Ward-Campbell *et al.*, 2005). In *Rhinosardinia bahiensis*, increased mouth area directly influenced the filtering as well as the aspect of the overlay. Smaller individuals presented lower values for the mouth area, determining the capture of a high volume of prey, such as diatoms, Decapoda and Bivalvia larvae in the tidal creek, while larger individuals ingested larger quantities of Calanoida and Cyclopoida in the tidal mudflat; this is a further trend towards segregation of their feeding niches by consuming significantly different prey quantities. As pointed out by Maes & Ollevier (2002), rates of filtration in herring vary according to fish size (mouth area), swimming capacity and concentration of prey. This intraspecific partition by different sizes occurs in other species of Clupeidae (Casini *et al.*, 2004).

According to Brown (1985), juveniles tend to be more vulnerable to predators than adults, but in addition, they have high energy requirements. Thus, populations in different size-classes must 'harmonize' their susceptibility to predation with the need to obtain food for survival. This fact explains in part the relative abundance and small biomass presented in the tidal creeks (possibly a protection factor). Since these individuals exist in regions above the estuary, the low salinity affects the ability of other species to predate *Rhinosardinia bahiensis* there, promoting a physiological 'barrier' for those predators.

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Correspondence should be addressed to:

A.L.M. Pessanha
Laboratório de Biologia Marinha, Universidade Estadual da Paraíba, Avenida das Baraúnas, 351, 58429-500, Campina Grande, PB, Brazil
email: andrepessanhauepb@gmail.com