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DIETARY OVERLAP AND FOOD RESOURCE PARTITIONING AMONG FISH SPECIES OF A TROPICAL ESTUARY IN NORTHEASTERN BRAZIL

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ABSTRACT – The current work investigates dietary overlap and food partitioning among nine abundant carnivorous fishes caught in the shallow waters of the Paraíba do Norte river estuary, Paraíba State, Brazil. Fishes were sampled with a beach seine net between January and December 2008 and a total of 958 specimens had their stomach content analyzed. Crustacea was the dominant food resource for *Lutjanus alexandrei*, *L. jocu* and *Bathygobius soporator*, whereas Telostei were consumed mainly by *Centropomus undecimalis* and *C. parallelus*. In contrast, Polychaeta were preyed upon mainly by *Diapterus rhombeus*, *Eucinostomus argenteus*, *Sciades herzbergii* and *S. parkeri*. Although most species consumed similar food items, they did that in varying proportions and amounts. Overall, the niche overlap among species was low (< 0.60), but there were several cases where pair of species had their feeding niche highly overlapped (between 0.72 and 0.97). These findings corroborate the hypothesis that food resource partitioning determines species coexistence in estuarine tropical environments.

KEY WORDS: JUVENILE FISH, TROPHIC ECOLOGY, CARNIVOROUS, SHALLOW WATERS, PARAÍBA DO NORTE RIVER ESTUARY.

SOBREPOSIÇÃO ALIMENTAR E PARTIÇÃO DE RECURSOS ALIMENTARES ENTRE ESPÉCIES DE PEIXES DE UM ESTUÁRIO TROPICAL NO NORDESTE DO BRASIL

RESUMO – Foram estudadas a sobreposição alimentar e a partilha de recursos entre nove espécies de peixes carnívoros capturados em águas rasas do estuário do rio Paraíba do Norte, Paraíba, Brasil. Os peixes foram amostrados com rede de arrasto de praia, entre janeiro e dezembro de 2008. Ao todo, foram analisados 958 estômagos. Crustacea foi o recurso alimentar dominante para *Lutjanus alexandrei*, *L. jocu* e *Bathygobius soporator*, enquanto Telostei foram consumidos principalmente por *Centropomus undecimalis* e *C. parallelus*. Em contraste, Polychaeta foram predados principalmente por *Diapterus rhombeus*, *Eucinostomus argenteus*, *Sciades herzbergii* e *S. parkeri*. Embora a maioria das espécies faça uso de itens alimentares semelhantes, elas o fazem em diferentes proporções e quantidades. No geral, a sobreposição de nicho entre as espécies foi baixa (< 0,60), mas houve casos em que duas espécies tiveram nicho alimentar altamente sobreposto (entre 0,72 e 0,97). Estes resultados corroboram a hipótese de que a partilha de recursos alimentares determina a coexistência de espécies em ambientes tropicais estuarinos

PALAVRAS-CHAVE: JUVENIS, ECOLOGIA TRÓFICA, CARNÍVOROS, ÁGUAS RASAS, ESTUÁRIO DO RIO PARAÍBA DO NORTE.

LA SOBREPOSICIÓN ALIMENTARIA Y PARTICIONAMIENTO DE RECURSOS ALIMENTARES ENTRE ESPECIES DE PECES EN ESTUARINE AMBIENTES, NORESTE DE BRASIL

RESUMEN – La sobreposición alimentaria y la división del alimento fueron estudiados entre nueve especies de peces carnívoros capturados en aguas someras del río Paraíba do Norte, Paraíba, Brasil. Los peces fueron colectados con red de arrastre de playa entre enero y diciembre del 2008. En total, fueron analizados 958 estômagos. Crustacea fue el recurso alimentario dominante para *Lutjanus alexandrei*, *L. jocu* y *Bathygobius soporator*, mientras que Telostei fue consumido principalmente por *Centropomus undecimalis* y *C. parallelus*. En contraste, Polychaeta fue predado principalmente por *Diapterus rhombeus*, *Eucinostomus argenteus*, *Sciades herzbergii* y *S. parkeri*. A pesar de que la mayoría de las especies consume ítems alimentarios similares, éstos son consumidos en proporciones y cantidades diferentes. En general, la sobreposición del nicho entre las especies fue baja (< 0.60), sin embargo, se observó sobreposición de nicho alimentario para dos especies en varios casos (entre 0.72 y 0.97). Estos resultados corroboran la hipótesis de que el particionamiento de recursos alimentares determina la coexistencia de especies en ambientes tropicales estuarinos.

PALABRAS CLAVE: JUVENILES, ECOLOGÍA TRÓFICA, CARNÍVOROS, AGUAS SOMERAS, ESTUÁRIO DE RIO PARAÍBA DO NORTE.

INTRODUCTION

Feeding habits constitute a clear example of how fishes are closely associated with its environment and are essential information towards a complete understanding of a fish's life cycle (Gerking 1994). The diet of individuals depends on variables intrinsic to each species, such as trophic morphology (Fugi et al. 2001), nutritional requirements and capability to detect and to capture prey, and they can also vary within the same stage of life according to local availability of food resources (Kennish 1990). Understanding the species' diet comprising a fish assemblage is crucial in order to identify different trophic guilds, the energy transfer within a system, mechanisms behind ecosystem stability (Gerking 1994) and to explain the inter relationships among the components of that community (Pasquaud et al. 2010). Prior studies based on the traditional method of stomach content analysis had revealed that fish play a major ecological role in the functioning of ecosystems (Windell and Bowen 1978; Winemiller 1990; Oumarou and Abe, 2009).

The coastal areas represent highly productive and valuable ecosystems, which provide numerous habitats for fish and support fundamental ecological links with other environments (Vasconcelos et al. 2010). Estuaries are essential for the life cycles of many fish species since they provide shelter and refuge from large fish predators (Scharf et al. 2000; Paterson and Whitfield 2000) and abundant food resources (Lugendo et al. 2006). Not surprisingly, these environments are considered important nursery grounds for juvenile fishes (e.g. Laegdsgaard and Johnson 1995; Blaber, 2000), harboring a highly abundant and diverse fish fauna (Day et al. 2012).

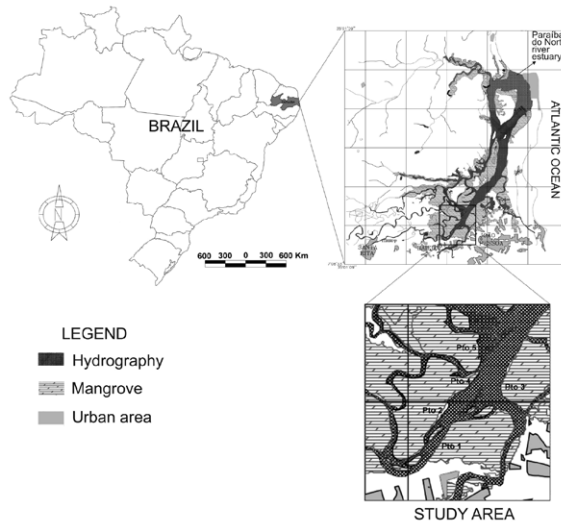
Overall, fish species exhibit different diets and feeding behaviors that help them to minimize niche overlap and interspecific competition for food estuarine resources (Alanara et al. 2001; Dantas et al. 2012). In estuaries, in particular, prior studies have shown that fish species commonly explore distinct food resources (Kanou et al. 2004; Dolbeth et al. 2008). These feeding patterns are usually view as adaptations that minimize niche overlap and, therefore, favor higher abundance and diversity (Wootton 1999). In this study, we investigate dietary overlap and food resources use in nine carnivorous fishes commonly found in a Brazilian tropical estuary, based on the working hypothesis that food partitioning determines species coexistence in estuarine tropical environments.

MATERIAL AND METHODS

Study area

The study was carried out in the Paraíba do Norte river estuary, Northeastern Brazil (07°05'57"S, 34°53'41"W and 07°06'43"S, 34°54'13"W) (Fig. 1). This estuary is situated in the municipalities of Santa Rita, Bayeux, João Pessoa, Lucena and Cabedelo, so the largest portion of the estuary is located in urban areas and this mangrove area has been strongly impacted by anthropogenic projects. Geomorphologically, this estuary is part of the classical model of plain estuary coastal flooding. It has meander sand several islands in their upper portions, but the Restinga and Stuart are the greatest ones.

Figure 1 - Map of the study area showing the sampling locations of the Paraíba do Norte river estuary, Brazil.



Sampling

Samples were collected monthly from January to December 2008 in five locations of the Paraíba do Norte river estuary (Fig. 1) using a beach seine net (15 m long, 1.2 m high and with 16 mm mesh size). A total of two hauls were carried out at each site monthly, during daylight hours even at low tide. Each beach seine haul lasted for five minutes and were conducted in waters less than 1.2 m deep. Fish caught were immediately stored on ice and transported to the laboratory, where each individual was placed in buffered formalin, identified and measured in total length (mm) and weight (0.1g). To describe the hydrological conditions during field samplings, monthly values were determined for the following variables at each sampling site: water temperature, salinity and water transparency (Secchi disk). Samples were performed with the authorization of the environmental agency (ICMBio n° 18623-1).

Data analysis

In laboratory, stomachs were removed and fixed in 10% buffered formalin. They were later examined and each dietary item identified to the lowest possible taxonomic level, depending on the digestion level of each food item. Empty stomachs and unidentifiable material were excluded from the analysis. For each identified item, were estimated Frequency of Occurrence (%FO), the number of stomachs analyzed where a food item is found in relation the total number of non-empty stomachs analyzed and the Points Method (P), the proportion of points occupied by a food item spread over a grid paper in relation to the total number of points in the grid occupied by the entire food content (Hyslop 1980). These parameters were combined in the Index of Preponderance (IP), which described the relative contribution of food items in the diet (Natarajan and Jhingran 1961). Diet overlap was calculated using simplified Morisita's Index (Krebs 1989), where overlap is

generally considered to be biologically significant when the value exceeds 0.60 (Labropoulou and Eleftheriou 1997), also diet overlap was estimated using the IP of each prey found in the stomachs.

The IP values were square root transformed and converted into a triangular matrix of similarities among all samples using the Bray-Curtis similarity (Schafer et al. 2002). This similarity measure was used due to low number of samples and because the influence of the dominant species/feeding items in diet patterns (Krebs 1989). A non-metric multidimensional scaling (nMDS) procedure was employed to assess variation among the nine species. The Bray-Curtis matrix was also used to construct the clustering dendrogram, which used the group average method to identify species clusters. The nMDS and Cluster analysis procedures were performed with the PRIMER v.6 software package (Clarke and Gorley 2006).

RESULTS

Salinity and water transparency showed greater variation along the study than water temperature. Salinity values varied from 0 to 30 with an average value of 8.71 (± 6.39 SD) and water transparency ranged from 5 to 95 and had an average value of 36.29 (± 21.38 SD), whereas temperature ranged from 25.9 to 33.0°C and showed an average value of 29.31 (± 1.88 SD).

A total of 1,665 fish representing 27 families and 55 species were recorded in Paraíba do Norte river estuary during this study. Among them, 958 individuals of nine species had their stomach content analyzed: *Sciades herzbergii*, *Sciades parkeri*, *Centropomus parallelus*, *Centropomus undecimalis*, *Lutjanus alexandrei*, *Lutjanus jocu*, *Diapterus rhombeus*, *Eucinostomus argenteus* and *Bathygobius saporator* (Table 2). These species constituted nearly 60% of the fishes caught in shallow waters during the study period.

Overall, these fish species were carnivorous feeding mainly on benthic invertebrates or Teleostei. Crustacea was the main food category in the diet of *L. jocu*, *L. alexandrei* and *B. saporator*, being found in more than 85% of their stomachs, followed by Polychaeta (16%), Teleostei (17%) and Algae (19%). However, the Index of Preponderance (IP) showed contributions values different to Crustacea item: *L. jocu* (Brachyura crabs = 81.28%; Penaeid shrimps = 11.68%); *L. alexandrei* (Brachyura crabs = 97.06%; Penaeid shrimps = 0.79%) and *B. saporator* (Brachyura crabs = 85.82%; Penaeid shrimps = 0.80%) (Table 1; Fig. 2). In *C. parallelus* and *C. undecimalis*, Teleostei was the main food category in the diet, contributing with over 80% the stomachs analyzed. Crustacea made appreciable contributions with high IP values: in *C. undecimalis* was Brachyura crabs (IP= 7.50%), whereas *C. parallelus* was Penaeid shrimps (IP= 7.29%) (Table 1; Fig. 2).

The dominant prey category in Ariidae and Gerreidae was Polychaeta. This item was the most commonly food category in the *S. parkeri* (IP= 88.57%), *D. rhombeus* (IP= 78.29%), *S. herzbergii* (IP= 57.42%) and *E. argenteus* (IP= 53.0%). The next mostly consumed food category was Teleostei (IP= 15.20%) and Brachyura crabs (IP= 15.51%) to *S. herzbergii*; Teleostei to *S. parkeri* (IP= 2.59%); and Nematoda (IP= 13.05; 3.16%) to *E. argenteus* and *D. rhombeus*, respectively (Table 1; Fig. 2). The number of items in *S. herzbergii* (12) was much higher than in the other species (e.g., 5 in *D. rhombeus* and *E. argenteus*) (Table 1). The *B. saporator* was the only species that consumed Rhodophyta (*Caloglossa leprieurii*, *C. ogasawaraensis*, *Bostrychia elegans*) and Ochrophyta algae (*Ectocarpus* sp.).

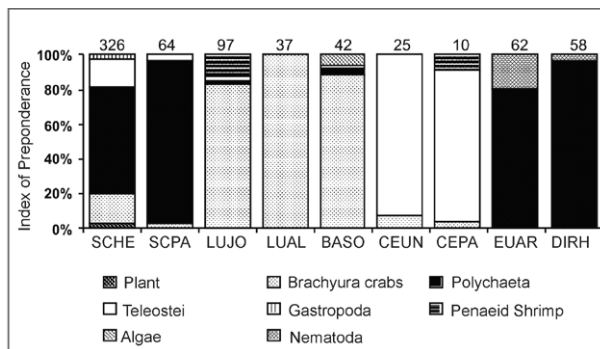
Table 1 - Frequency of Occurrence (%FO) and Points Method (P) of the stomach contents for nine abundant species collected in Paraíba do Norte river estuary.

Species	<i>Sciades herzbergii</i>		<i>Sciades parkeri</i>		<i>Centropomus parallelus</i>		<i>Centropomus undecimalis</i>		<i>Lutjanus alexandrei</i>		<i>Lutjanus jocu</i>		<i>Diapterus rhombeus</i>		<i>Eucinostomus argenteus</i>		<i>Bathygobius soporator</i>			
	FO	P	FO	P	FO	P	FO	P	FO	P	FO	P	FO	P	FO	P	FO	P		
Nematoda	5.3	3.5	1.6	1.0									8.6	12.2	46.8	17.8				
Polychaeta	48.9	34.3	64.1	60.3			12.0	3.1	13.5	1.8	29.9	2.3	53.4	48.6	85.5	39.6	16.7	9.3		
Bivalve	1.2	< 0.1											1.7	0.6						
Gastropoda	2.4	4.5	1.6	0.2																
Copepoda					10.0	1.0			2.7	0.3	13.4	3.1								
Isopoda	4.6	2.4			10.0	1.0			18.9	2.6	12.4	1.2								
Caprellidea	12.3	2.1	3.1	2.0					10.8	1.9	1.0	< 0.1								
Gammaridea	0.2	< 0.1							8.1	3.2	2.1	0.1								
Brachyura crabs	32.0	14.2	15.6	6.7	20.0	4.9	4.0	13.3	83.3	81.2	76.6	60.9					66.7	56.6		
Penaeid shrimps	1.5	0.5			20.0	11.6	24.0	1.2	10.8	5.2	45.4	14.6			4.8	1.9	9.5	3.7		
Insecta	8.0	1.2	4.7	0.5			4.0	0.3	2.7		2.1	0.2			6.5	0.8	4.8	0.8		
Teleostei	23.0	19.3	9.4	12.1	40.0	62.2	48.0	81.1	5.4	1.3	17.5	9.7					9.5	8.0		
Algae																		19.0	13.8	
Plant material	21.8	3.9	10.9	4.4					13.5	1.5	15.5	1.0	1.7	0.3				2.4	0.3	
Sediment	15.0	0.2	17.2	7.1									1.0	< 0.1	8.6	1.5	1.6	0.1	2.4	1.3
N° stomachs		413		65		12		29		42		121		92		107			77	
Empty stomachs		87		01		02		04		05		24		34		45			35	

Table 2 - Numerical abundance (n), biomass (g) and size range (minimum and maximum total length, mm) of nine fish species who had their stomach contents analyzed in the Paraíba do Norte river estuary from January to December 2008.

Family	Taxon	Abundance (n)	Biomass (g)	Size range (mm)
Ariidae	<i>Sciades herzbergii</i> (Bloch, 1794)	413	2126.1	46 – 305
	<i>Sciades parkeri</i> (Traill, 1832)	65	278.6	41 – 285
Centropomidae	<i>Centropomus parallelus</i> Poey, 1860	12	120.5	47 – 145
	<i>Centropomus undecimalis</i> (Bloch, 1792)	29	324.9	80 – 186
Lutjanidae	<i>Lutjanus alexandrei</i> Moura & Lindeman, 2007	42	2306.3	40 – 115
	<i>Lutjanus jocu</i> (Bloch & Schneider, 1801)	121	1128.8	35 – 185
Gerreidae	<i>Diapterus rhombeus</i> (Cuvier, 1829)	107	581.2	20 – 124
	<i>Eucinostomus argenteus</i> Baird & Girard, 1855	92	703.8	25 – 244
Gobiidae	<i>Bathygobius soporator</i> (Valenciennes, 1837)	77	560.4	50 – 103
Total		958	8,130.6	

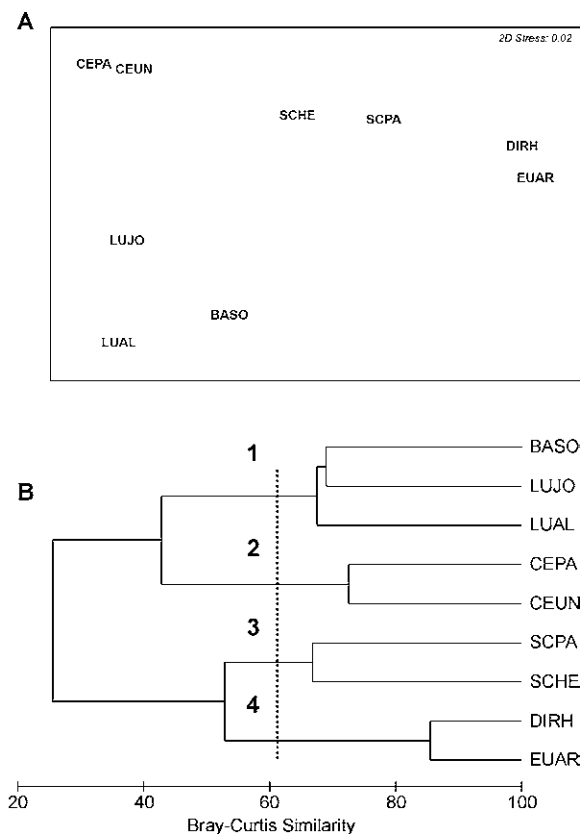
Figure 2 - Index of Preponderance (IP) values for nine abundant fish species collected in Paraíba do Norte river estuary. Numbers above the columns indicate number of non-empty stomachs examined. (SCHE = *Sciades herzbergii*; SCPA = *Sciades parkeri*; CEPA = *Centropomus parallelus*; CEUN = *Centropomus undecimalis*; LUJO = *Lutjanus jocu*; LUAL = *Lutjanus alexandrei*; DIRH = *Diapterus rhombeus*; EUAR = *Eucinostomus argenteus* and BASO = *Bathygobius soporator*).



MDS analysis based on the Index of Preponderance revealed marked differences in the diet of the studied species (Fig. 3A). In general, individuals of the nine abundant species were segregated in four groups: samples of *D. rhombeus* and *E. argenteus* located on the right side of the diagram, samples of *S. herzbergii* and *S. parkeri* were located in center of the diagram, *L. alexandrei*, *L. jocu* pooled in the left side, and *B. soporator* in the lower and *C. parallelus* and *C. undecimalis*

in the upper portion of the diagram (Fig. 3 A). Similarly, cluster analysis based on the Index of Preponderance also showed the formation of four groups of species with similar diet (Fig. 3B): group 1 formed by *L. alexandrei*, *B. soporator* and *L. jocu*, which consumed mainly Crustacea (Table 1, Fig. 2); group 2 composed by *C. undecimalis* and *C. parallelus*, which had a diet based mainly on Teleostei; group 3 comprised of the catfish *S. herzbergii* and *S. parkeri*, which had a diet comparatively more diverse in number of main food items like Polychaeta and Decapoda and group 4 formed by *E. argenteus* and *D. rhombeus*, which had diet based mainly on Polychaeta and Nematoda (Table 1, Fig. 2).

Figure 3 - n-MDS (A) and cluster dendrogram (B) plots showing similarities in the diet (based on Index of Preponderance, IP) of the nine abundant fish species collected in Paraíba do Norte river estuary, PB. See Figure 2 for species abbreviations.



Dietary overlap values among fish species were, in general, low (<0.60), but some pair of species showed high (> 0.60) dietary overlap in their diet (Table 3). As expected, the greatest values (> 0.90) in diet overlap were observed between pair of species belonging to the same group revealed by the cluster analysis, such as *B. soporator*, *Lutjanus jocu* and *L. alexandrei* (group 1), *Centropomus undecimalis* x *C. parallelus* (group 2) and *Eucinostomus argenteus* x *Diapterus rhombeus* (group 4) (Table 3).

Table 3 - Simplified Morisita's index of dietary overlap for the nine abundant species collected in Paraíba do Norte river estuary, PB. See Fig. 2 for species abbreviations.

Species	SCHE	SCPA	LUJO	LUAL	BASO	CEUN	CEPA	EUAR
SCPA	0.85	-						
LUJO	0.85	0.76	-					
LUAL	0.29	0.12	0.94	-				
BASO	0.48	0.29	0.94	0.90	-			
CEUN	0.43	0.23	0.29	0.17	0.27	-		
CEPA	0.48	0.24	0.28	0.20	0.23	0.92	-	
EUAR	0.72	0.76	0.09	0.02	0.17	0.03	1.19	-
DIRH	0.76	0.86	0.08	0.02	0.17	0.03	0.15	0.97

DISCUSSION

The dominance of carnivores in this estuary was evident and items such as Brachyura crabs, Penaeid shrimps, Polychaeta and Teleostei were commonly found in most stomachs. The higher consumption of such preys is presumably related to their availability in the estuary and often within the mangrove canopy. The dominance of carnivorous over other groups has been reported in estuaries in temperate latitudes (Sá et al. 2006), in Caribbean mangroves (McDonald et al. 2009) and in demersal fish assemblages of coastal areas (Abdurahiman et al. 2010).

Prior studies have shown that differences in composition and feeding activity can occur among fish species, which reduces overlap in the supposed partitioning of resources and promotes co-existence and use of their habitats (Zahorcsak et al. 2000; Denadai et al. 2012). The results obtained in the present study demonstrated that dietary compositions of the species within the same family were particularly similar. The proximity of the sampling sites and the fact the individuals were preserved on ice immediately after capture, associated with quick digestion of the food items, probably contributed to the great similarity among the diets of the studied species. Moreover, the identification of items in broad food categories probably contributed to the high level of similarity observed in the cluster dendrogram.

A generalist feeding strategy was observed in some of the studied fish in the present work. For instance, the sea catfish (*S. herzbergii*) showed the tendency to have a generalist trophic strategy, with a wide range of prey occurring in its diet. Similar results were reported to *S. herzbergii* in the Curuçá estuary, Pará (Giarrizzo and Saint-Paul 2008). This feeding strategy was also observed in other Ariidae species, which fed on a great variety of items, including small fishes, crabs, amphipods, isopods, copepods, and polychaeta e.g. *Cathorops spixii* (Le Bail et al. 2000), *Aspistor luniscutis* and *Genidens genidens*. In this study, diets of both catfishes (*S. herzbergii* and *S. parkeri*) were dominated by Polychaeta and Brachyura crabs. Studies elsewhere on Ariidae species with a similar size range also found a pattern of dominance of the diet by two benthonic preys (Mendoza-Carranza and Vieira 2008), which suggest that the two catfish species forage on or just above the substratum (Krumme et al. 2008). This conclusion is consistent with observations

that catfishes frequently swim close to the substratum surface browsing for benthonic preys. Moreover, anatomical features of catfishes, such as a large mouth gape, allow them to capture entire preys, including those associated with the substrate. Similarly with *Sciades herzbergii* and *S. parkeri*, the diets of *E. argenteus* and *D. rhombeus* were also comprised of infauna species, such as Polychaeta and Nematoda, thereby implying these two species also feed on or just above the substratum.

The Gerreidae are mainly benthic feeders with highly protrusible mouths, which limit the extent of substratum penetration, and have been observed foraging for epifaunal invertebrates (Cyrus and Blaber 1983). The Polychaeta fragments found in the stomach content of the specimens probably originated from prey captured in the water column or larval stages on the substratum surface (Kerschner et al. 1985), since the Gerreidae protrudes its feeding apparatus directly above the prey (Cyrus and Blaber 1982). These items were also reported as important in diet of Gerreidae species in other ecosystems, such a bays (Denadai et al. 2012), beaches (Teixeira and Helmer 1997) and coastal waters (Cyrus and Blaber 1984).

Although shallow waters have been not considered a habitat for large piscivorous fish in estuaries (Paterson and Whitfield 2000), we found two piscivorous species (*C. parallelus* and *C. undecimalis*) in our studied system. Acurate vision and prey attacking techniques are two factors considered important when capturing very active swimming organisms such as fishes and shrimps (Hajisamae 2009), which were items with higher frequency of occurrence in the diet of the studied species. The presence of piscivorous along the estuaries, especially in the mangroves, may be related to the fact that the spatial heterogeneity created by the mangrove roots provides a suitable place to stay in ambush (McDonald et al. 2009).

CONCLUSION

Our findings revealed that the nine studied carnivorous fishes feed on similar food items (mainly crustaceans, fish and polychaets), but in different amounts and proportions. The niche overlap among them was relatively low for most of the species, although there were several cases of highly overlapped food niches (e.g., 0.97 between *E. argenteus* and *D. rhombeus*; 0.94 between *L. alexandrei* and *L. jocu*, *B. saporator* and *L. jocu*; 0.92 between *C. parallelus* and *C. undecimalis*). These findings contribute to an understanding of how resource partitioning could determine species coexistence in estuarine tropical environments and highlights the need for further studies to evaluate the effect of partitioning on space and time in this ecosystem. Future investigations are needed to evaluate if competitive exclusion principle does occur or how much it influences on fish estuarine assemblages.

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