

## Fish assemblage of the Mamanguape Environmental Protection Area, NE Brazil: abundance, composition and microhabitat availability along the mangrove-reef gradient

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Reefs, mangroves and seagrass biotopes often occur in close association, forming a complex and highly productive ecosystem that provide significant ecologic and economic goods and services. Different anthropogenic disturbances are increasingly affecting these tropical coastal habitats leading to growing conservation concern. In this field-based study, we used a visual census technique (belt transects 50 m x 2 m) to investigate the interactions between fishes and microhabitats at the Mamanguape Mangrove-Reef system, NE Brazil. Overall, 144 belt transects were performed from October 2007 to September 2008 to assess the structure of the fish assemblage. Fish trophic groups and life stage (juveniles and adults) were recorded according to literature, the percent cover of the substrate was estimated using the point contact method. Our results revealed that fish composition gradually changed from the Estuarine to the Reef zone, and that fish assemblage was strongly related to the microhabitat availability, as suggested by the predominance of carnivores at the Estuarine zone and presence of herbivores at the Reef zone. Fish abundance and diversity were higher in the Reef zone and estuary margins, highlighting the importance of structural complexity. A pattern of nursery area utilization, with larger specimens at the Transition and Reef Zone and smaller individuals at the Estuarine zone, was recorded for *Abudefduf saxatilis*, *Anisotremus surinamensis*, *Lutjanus alexandrei*, and *Lutjanus jocu*. Our findings clearly suggests ecosystem connectivity between mangrove, seagrass and reef biotopes, and highlighted the importance of Mamanguape Mangrove-Reef System as a priority area for conservation and research, whose habitat mosaics should be further studied and protected.

Recifes, manguezais e bancos de fanerógamas marinhas são biótopos frequentemente associados, formando um ecossistema complexo e altamente produtivo que proporciona significativos bens e serviços ecológicos e econômicos. Diferentes impactos antrópicos estão crescentemente afetando esses habitats costeiros tropicais, trazendo preocupações acerca de sua conservação. Neste estudo de campo, utilizamos uma técnica de censo visual subaquático (transecções de 50 x 2 m) para investigar as interações entre os peixes e microhabitats no complexo estuarino-recifal de Mamanguape, no Nordeste do Brasil. Entre outubro de 2007 e setembro de 2008 foram realizadas 144 transecções para avaliar a estrutura da assembleia de peixes. Grupos tróficos e estágios de vida dos peixes (jovens e adultos) foram registrados segundo a literatura, enquanto a porcentagem de cobertura do substrato foi estimada através do método de pontos de contato. Nossos resultados mostraram que a composição da ictiofauna mudou gradualmente da Zona Estuarina para a Zona Recifal, e que a assembleia de peixes esteve fortemente relacionada com a disponibilidade de microhabitats – como sugerido pela predominância de carnívoros na zona estuarina e presença de herbívoros na zona recifal. A abundância e diversidade de peixes foram maiores na zona recifal e nas margens do estuário, destacando a importância da complexidade estrutural. O padrão de uso da área como berçário, com indivíduos maiores nas zonas de transição e recifal, e os menores na zona estuarina, foi registrado para *Abudefduf saxatilis*, *Anisotremus surinamensis*, *Hippocampus reidi*, *Lutjanus alexandrei* e *Lutjanus jocu*. Nossos resultados sugerem que há conectividade entre os biótopos de manguezal, bancos de fanerógamas e recifes, e destacam a importância do Sistema Manguezal-Recife de Mamanguape como uma área prioritária para conservação e pesquisa, cujos mosaicos de habitats devem ser ainda estudados e protegidos.

**Key words:** Conservation, Conservation unit, Ichthyofauna, Nursery habitats.

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## Introduction

Reefs, mangroves and seagrass beds are the major coastal habitats in tropical areas (Nagelkerken *et al.*, 2000; Ikejima *et al.*, 2003; Mumby *et al.*, 2004; Mumby *et al.*, 2008; Nagelkerken & Faunce, 2008; Nagelkerken *et al.*, 2008). They often occur in close association, forming a complex and highly productive ecosystem that provide significant economic goods and services and contribute to the livelihoods, food security and safety of millions of people around the world (Moberg & Folke, 1999; Nagelkerken *et al.*, 2008; Unsworth *et al.*, 2009). Several anthropogenic disturbances are increasingly affecting those coastal habitats (see Rönnbäch, 1999), leading to growing conservation concern.

Reefs are known for the diversity and abundance of their fish and invertebrate faunas, while seagrass beds and mangrove areas are recognized as important nursery areas for many commercially important and forage organisms (Nagelkerken *et al.*, 2008), as well as to some of the reef species (Ogden & Gladfelter, 1983). Mangroves are also characterized by a high abundance of fish, crustaceans and mollusks (Nagelkerken *et al.*, 2008).

Many studies have long discussed the nursery role of mangroves and estuaries (Ogden & Gladfelter, 1983; Arrivillaga & Baltz, 1999; Nagelkerken *et al.*, 2000; Ikejima *et al.*, 2003; Mumby *et al.*, 2004; Nagelkerken & Faunce, 2008), and how juvenile fish use habitats like seagrass beds and small, protected patch reefs before venturing out to large reefs. In that line, some studies have suggested that current rates of mangrove deforestation are likely to have severe deleterious consequences for the ecosystem function, fisheries productivity and resilience of adjacent reefs (Mumby *et al.*, 2004; Mumby & Hastings, 2008).

Knowledge on the nursery function and connectivity of mangroves to other habitats, however, is limited, particularly in areas outside of the Caribbean (Nagelkerken *et al.*, 2000), therefore, studies focusing on the functional roles played by species in those habitats, are relevant to increase our knowledge about on how habitat mosaics must be protected if a complete protection of biodiversity is to be achieved (see Gray, 1997).

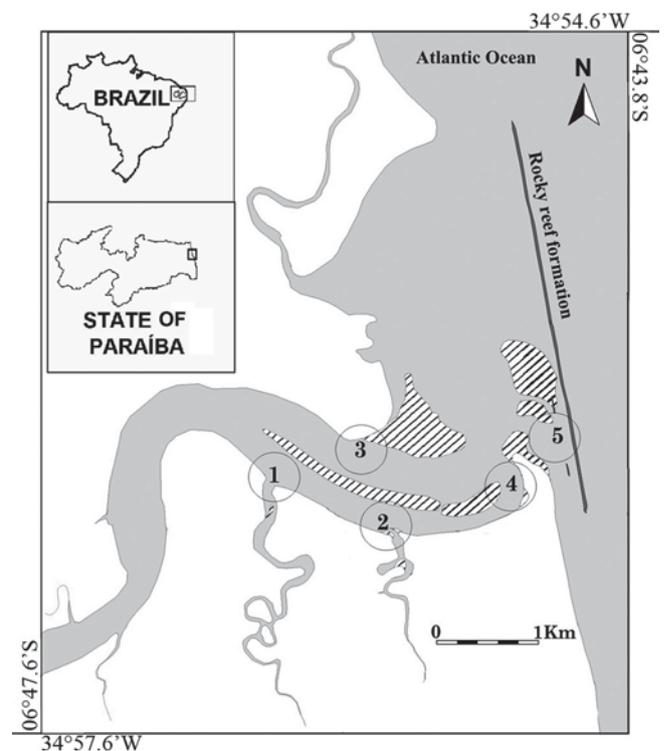
In this field-based study, we used visual census methods to investigate the interactions between fishes and microhabitats at the Mamanguape Mangrove-Reef system (NE Brazil). Published information on the fish fauna of this area is limited to the report of species collected by the Branner-Agassiz Expedition (Gilbert, 1900) and the papers based on an ethnoecological perspective (Mourão & Nordi, 2003; Rocha *et al.*, 2008). Other recent reports on the estuarine and reef fishes remained unpublished (Rosa & Sassi, 2002; Silva, 2002).

Considering the Mamanguape Mangrove-Reef system, with the presence of estuary and reefs as adjacent ecosystems and exposed to similar environmental conditions, this study addressed the following questions: (1) are there differences (*e.g.*, composition, trophic levels, abundance) in the fish assemblages distributed along the estuarine-reef

gradient? (2) how does microhabitat availability influence the spatial distribution of fishes? (3) does structural complexity, herein inferred by rugosity, also influence fish assemblage composition? (4) based on the ontogenetic distribution of fishes, is there indication of connectivity between the Mamanguape mangrove estuary and the adjacent rocky reef ecosystem?

## Material and Methods

**Study area.** The Mamanguape Mangrove-Reef system (NE Brazil) is located at the north coast of Paraíba State, within the boundaries of an Environmental Protection Area considered as a high priority site for biodiversity conservation in Brazil (Ministry of the Environment, 2002). The Mamanguape estuary (06°46'20"S 34°56'00"W) is bordered by a dense mangrove forest, its mouth being partially dammed by a fringe reef, visible at low tide, which extends north up to 8.5 Km (Silva, 2002). Data were collected in five sub-areas (Fig. 1), categorized according to their habitat features, including margin characteristics, bottom type and human use, as summarized in Table 1. Sampling stations referred to as Tanques, Peixe-Boi and Caçõ sub-areas collectively represent mangrove habitats, and were categorized as the Estuarine zone. The Transition sub-area, herein called Transition zone, was delimited as a sandy beach area, adjacent to the Reef sub-area, herein called Reef zone, formed by a fringe



**Fig. 1.** Mamanguape estuary, State of Paraíba, NE Brazil, showing surveyed sub-areas: 1) Tanques; 2) Peixe-Boi; 3) Caçõ; 4) Transition; and 5) Reefs. Dashed areas represent sandbanks.

**Table 1.** Habitat features of studied sub-areas in the Mamanguape Mangrove-Reef system, State of Paraíba, NE Brazil, according to margin and bottom types, depth, currents, sedimentation, and human use. Sub-areas: 1. Ta - Tanques; 2. Pe - Peixe-Boi; 3. Ca -Caçõ; 4. Tr -Transition; 5. Re -Reefs.

Sub-area	Margin	Bottom	Exposure	Maximum depth	Human use/ boats
1 Ta	Well preserved mangrove vegetation	Sand and mud	Calm and sheltered	6 m	Artisanal fisheries: cast-net and gill-net; Shellfish harvesting; transportation of tourists by local sail boats
2 Pe	Well preserved mangrove vegetation	Sand and mud	Calm and sheltered	4 m	Artisanal fisheries: cast-net and gill-net; transportation of tourists by local sail boats
3 Ca	Sparse and lower mangrove vegetation	Sand and mud	Unsheltered; exposed to currents	4 m	Artisanal fisheries: cast-net; Shellfish harvesting; Transportation of tourists by local sail boats
4 Tr	Beach area	Sand	Unsheltered; exposed to currents	4 m	Artisanal fisheries: cast-net and gill-net; larger-scale tourism, including the presence of motorized boats. Fishing boats stored in huts built along the margins.
5 Re	Rocky reef area, 200 m far from the beach.	Sand and rocks	Unsheltered; exposed to currents, except inside tide pools	6 m	Recreational fishing (fish rods); presence of sail and motorized boats.

rocky reef. Sampling points and margin limits, including sandbanks, when appropriate, were recorded using GPS and plotted on a georeferenced map using the software AutoCAD® 2005.

**Fish assemblage composition and spatial distribution.** Data on fish assemblage composition and abundance were recorded from October 2007 to September 2008, during low tide, on neap tides. Throughout the study 144 belt transects (50 x 2 m) were performed, covering non-overlapping areas through SCUBA diving, totaling an area of 14,400 m<sup>2</sup>. All transects were conducted during daylight between 07:00 am h and 05:00 pm h. Due to the shade and decreased visibility at the mangroves, which ranged from zero to 2 m in the study area, fish were counted within 1 m either side of the transect.

Transects were distributed across sampling sub-areas as follows: 1) Tanques, n=40 transects; 2) Peixe-Boi, n=28; 3) Caçõ, n=30; 4) Transition, n=29, and 5) Reefs, n=17. Transects were separated from one another by approximately 50 m, and encompassed both margin and channel portions of the estuary. Surveys were undertaken in both dry (September to February) and rainy seasons (March to August). Tanques, Peixe-Boi and Transition sub-areas were sampled from October 2007 to April 2008, while Caçõ and Reefs sub-areas were sampled from April to September 2008. Each sub-area was sampled in both seasons.

Fishes sighted on transects were quantified, categorized by size classes and then classified as juveniles or adults, according to information on their size at first maturity (Thomsom *et al.*, 2000; Dias *et al.*, 2005; Rosa *et al.*, 2007; Souza *et al.*, 2007; Souza & Chaves, 2007; Afonso *et al.*, 2008; Poot-Salazar *et al.*, 2009; Froese & Pauly, 2010). When size at first maturity was not available for a species, we used data from another species of the same genus as a reference point. Reported fish sizes are total length (TL) in cm. Since our size data did not fit to normal distribution, they were compared between sub-areas by using Mann-Whitney Test (non-parametric analysis). Statistical analyses were performed using Statistica® Software, version 6.0 (Statsoft, 2004). Confidence level was defined as 95%.

Species were also checked on their trophic group and categorized as omnivores, carnivores, invertivores of mobile prey, invertivores of sessile prey, roving herbivores, and territorial herbivores, based on the literature (Randall, 1967; Ferreira *et al.*, 2001, 2004; Guedes *et al.*, 2004; Froese & Pauly, 2010). Individuals of *Stegastes variabilis* were categorized as invertivores of mobile prey when juveniles and as territorial herbivores when adults (Froese & Pauly, 2010). Taxa that could not be visually identified with confidence to species level are cited by genus only, which was the case of *Antennarius* sp., *Centropomus* sp., *Mugil* sp., *Scarus* sp., *Sparisoma* sp., and *Strongylura* sp.

Percentage cover of benthic organisms and of other items found on the substrate was estimated using the point contact method (Ferreira & Maida, 2006), in which 100 points were distributed at 0.50 m intervals, along the same transect used to assess fish abundance. Substrate characteristics found at the pre-defined points were recorded and classified into categories: sand/ muddy, mangrove, seagrass, bivalves, sessile invertebrates, macroalgal beds and other algae.

Topographic complexity of the bottom (rugosity) was estimated using the 'chain link method' (adapted from Luckhurst & Luckhurst, 1978), as follows: a chain of 5 m was draped over the substrate, to conform as close as possible to all contours and crevices, and a measure of the actual surface distance relative to the linear distance was thus obtained. This measure is termed the rugosity index. Salinity was also measured for each transect with a portable refractometer.

Canonical Correspondence Analyses (CCA) were performed to describe the relationship between microhabitats categories and individual fish species, where fishes are presented as symbols and microhabitats as environmental vectors. For environmental data, we used the following categories, based on our substrate data: MUDDYSAND - sandy or muddy bottom, without visually detectable organisms; MANGROVE - roots, leaves and fallen branches of mangrove trees, mainly *Rhizophora mangle*; SEAGRASS - *Halophila* sp. and *Halodule wrightii*; BIVALVES - bivalve shells, mainly *Crassostrea rhizophorae*, *Anomalocardia*

*brasiliensis*, and *Lucina pectinata*; SESSILE INV - sponges, including *Haliclona* sp., *Cinachyrella alloclada*, and cnidarians, including *Carijoa* sp.; ALGAE - included macroalgal beds, mainly composed by *Hypnea musciformis*, *Hypnea spinella*, *Cryptonemia* sp., and *Acanthophora* sp., and other drift or attached algae but not forming beds, which included *Gracilaria* sp., *Gelidiella acerosa*, *Pterocladia* sp., *Gelidium* sp., *Corynomorpha* sp., and *Acetabularia* sp. The proximity of symbols to the vectors indicates the relationship between fishes and environmental variables. Abundance data were log transformed to improve fit to Normality, and rare species (only sighted once in transects) were excluded from the analysis. A Monte-Carlo randomization test (999 permutations) was used to assess the probability of the observed pattern being due to chance (see Ter Braak, 1986).

## Results

**Fish abundance and composition.** The fish assemblage recorded during the underwater surveys in the study area was represented by 37 species distributed in 23 families, as shown on Table 2. In addition to the fish species found within the area covered by transects, we recorded the presence of four other species along the margins of the Estuarine zone: *Antennarius* sp., *Gymnothorax funebris*, *Sphoeroides greeleyi*, and *Strongylura* sp. These, however, did not enter the analyses.

Overall, *Abudefduf saxatilis*, *Anisotremus surinamensis*, *Eucinostomus melanopterus*, and *Lutjanus alexandrei* were the most abundant species; their abundance, however, was unequally distributed according to sub-area and to microhabitat features. The Reef zone exhibited the highest fish abundance, mainly represented by *Abudefduf saxatilis* and *Anisotremus surinamensis*. Also, the abundance and diversity of fishes were higher during the rainy season (from March to August 2008). Fish abundance and population densities (number of individuals per transect), as well as size parameters (mean  $\pm$  standard deviation), are given for each sub-area during dry (Table 3) and rainy season (Table 4).

The majority of individuals (77.1%) recorded at the study site were considered juveniles, and were sighted throughout the year, including *Eucinostomus melanopterus* and *Lutjanus* spp., which are important species for the local artisanal fisheries. Eleven species were exclusively represented by juveniles (*Acanthurus chirurgus*, *Centropomus* sp., *Chaetodon striatus*, *Haemulon parra*, *Lutjanus alexandrei*, *L. analis*, *Ocyurus chrysurus*, *Rypticus randalli*, *Scarus* sp., *Sparisoma* sp., and *Trachinotus falcatus*), while six (*Achirus lineatus*, *Chaetodipterus faber*, *Dactylopterus volitans*, *Dasyatis guttata*, *Mugil* sp., and *Ophichthus ophis*) were represented exclusively by adults. Life stage of species *Thalassophryne nattereri*, *Pareques acuminatus*, *Myrichthys ocellatus*, and *Echeneis naucrates* could not be assessed.

**Percentage cover of the substrate.** Benthic organisms and other items found on the substrate were grouped into categories, as summarized in Table 5. Substrate in Estuarine

and Transition zones was formed by sand and mud, and covered by leaves of *Rhizophorae mangle*, fallen branches of mangrove vegetation and bivalve shells, mainly *Anomalocardia brasiliensis*. Structural complexity at these sub-areas was enhanced by mangrove vegetation (margins), or by fallen logs, branches or rocks (channel). Seagrass beds were commonly found in the Tanques and Peixe-Boi sub-areas, while the Cação sub-area was dominated by bivalve shells and lacked seagrass beds. Unlike the Estuarine zone, transition zone lacked mangrove-related components along the margin, being characterized by strong tidal currents and sandy areas. Fallen logs and branches with attached sessile invertebrates (cnidarians, sponges, polychaetes, and barnacles) were also found there.

The Reef zone was covered by a more diverse group of items, including several species of macroalgae, mostly *Hypnea musciformis* and *Cryptonemia* sp., sessile invertebrates and rocks. Structural complexity in this sub-area was increased by the presence of large rocks found on the sandy bottom.

Salinity ranged from 20 to 43 at the Estuarine zone, while at the Transition and Reef zones it ranged from 31 to 41, a narrower range (Table 5). On the other hand, the structural complexity (rugosity) of Estuarine and Transition zones was similarly low (0.11 to 0.12), while Reef zone presented much higher values (1.13).

**Spatial distribution of the fish assemblage.** Along the Estuarine zone, we recorded 21 fish species, from which six were exclusively sighted there: *Acanthurus bahianus*, *Centropomus* sp., *Chaetodipterus faber*, *Dactylopterus volitans*, *Dasyatis guttata*, and *Ophichthus ophis*.

Juveniles of *Centropomus* sp. were sighted at the Estuarine zone from October to November 2007 (dry season). Fish abundance and diversity were higher along the margin, in mangrove-rich portions of the estuary used as microhabitats, mostly by *Hippocampus reidi*, *Lutjanus alexandrei*, *L. analis*, *L. joco*, and *Bathygobius soporator*. *Bathygobius soporator* and the seahorse *Hippocampus reidi* were frequently found in association with mangrove roots, oysters, sessile invertebrates and seagrass beds. Juveniles of *Lutjanus* were frequently sighted in proximity to mangrove roots. *Rypticus randalli* (sighted at all surveyed zones, generally associated to muddy or sandy bottom) and *Echeneis naucrates* (sighted at the Estuarine and Transition zones) occurred in the estuary channel. The adult life stage of *Eucinostomus melanopterus* was also exclusively found in the Estuarine zone.

The species *Achirus lineatus*, *Bathygobius soporator* (from these two only adults recorded), and *Citharichthys spilopterus* (only juveniles), although mostly found at the Estuarine zone, also occurred in the transition zone. The Transition zone received influence from both estuarine and reef systems, and the 18 species found there also occurred in the Estuarine zone, Reef zone or on both. The highest abundances were obtained for *Eucinostomus melanopterus*, commonly found in the Estuarine zone, *Abudefduf saxatilis* and *Anisotremus surinamensis*, the most abundant species

**Table 2.** Information on family and species, total abundance, trophic group, and maturity size of fishes sighted in the Mamanguape estuary, State of Paraíba, NE Brazil, from October 2007 to September 2008. \* Trophic group (TG): CA - carnivore; IM - invertivore of mobile prey; IS - invertivore of sessile prey; RH - roving herbivore; TH - territorial herbivore; OM - omnivore. \*\* When size at first maturity was not available for the sighted species, it was inferred from other species from the same genus, which were *Abudefduf vaigiensis*, *Anisotremus davidsonii*, *Centropomus undecimalis*, *Eucinostomus gula*, *Haemulon plumierii*, *Mugil curema*, *Ophichthus gomesii*, *Scarus coeruleus*, and *Stegastes variabilis*. Size at maturity not available for *Thalassophryne nattereri*, *Pareques acuminatus*, *Myrichthys ocellatus*, and *Echeneis naucrates*. Maturity information sources: <sup>a</sup>. Afonso *et al.*, 2008; <sup>b</sup>. Dias *et al.*, 2005; <sup>c</sup>. Froese & Pauly, 2010; <sup>d</sup>. Personal observation; <sup>e</sup>. Poot-Salazar *et al.*, 2009; <sup>f</sup>. Rosa *et al.*, 2007; <sup>g</sup>. Souza *et al.*, 2007; <sup>h</sup>. Souza & Chaves, 2007; <sup>i</sup>. Thomsom *et al.*, 2000.

Family	Species	Total abundance	TG*	Maturity (cm)**
Pomacentridae	<i>Abudefduf saxatilis</i>	250	OM	12.0 <sup>c</sup>
Haemulidae	<i>Anisotremus surinamensis</i>	186	IM	5.0 <sup>i</sup>
Gerreidae	<i>Eucinostomus melanopterus</i>	66	IM	11.0 <sup>c</sup>
Lutjanidae	<i>Lutjanus alexandrei</i>	34	CA	30.0 <sup>c</sup>
Scaridae	<i>Sparisoma</i> sp.	32	RH	21.9 <sup>a</sup>
Lutjanidae	<i>Lutjanus jocu</i>	26	CA	30.0 <sup>c</sup>
Serranidae	<i>Rypticus randalli</i>	15	CA	10.9 <sup>b</sup>
Pomacentridae	<i>Stegastes variabilis</i>	15	IM/TH	6.2 <sup>g</sup>
Gobiidae	<i>Bathygobius soporator</i>	15	IM	7.0 <sup>d</sup>
Syngnathidae	<i>Hippocampus reidi</i>	14	IM	10.0 <sup>f</sup>
Pomacentridae	<i>Stegastes fuscus</i>	13	TH	6.2 <sup>g</sup>
Acanthuridae	<i>Acanthurus coeruleus</i>	13	RH	11.0 <sup>c</sup>
Centropomidae	<i>Centropomus</i> sp.	12	CA	30.0 <sup>c</sup>
Lutjanidae	<i>Lutjanus analis</i>	9	CA	38.0 <sup>c</sup>
Gobiidae	<i>Coryphopterus glaucofraenum</i>	8	OM	2.0 <sup>c</sup>
Tetraodontidae	<i>Sphoeroides testudineus</i>	8	IM	13.0 <sup>c</sup>
Haemulidae	<i>Anisotremus virginicus</i>	7	IM	5.0 <sup>i</sup>
Serranidae	<i>Epinephelus adscensionis</i>	6	CA	25.0 <sup>c</sup>
Haemulidae	<i>Haemulon parra</i>	6	IM	16.0 <sup>c</sup>
Scaridae	<i>Scarus</i> sp.	6	RH	30.5 <sup>c</sup>
Achiridae	<i>Achirus lineatus</i>	6	IM	3.1 <sup>e</sup>
Dactylopteridae	<i>Dactylopterus volitans</i>	4	IM	8.9 <sup>b</sup>
Echeneidae	<i>Echeneis naucrates</i>	4	CA	-
Syngnathidae	<i>Microphis brachyurus</i>	3	IM	12.0 <sup>c</sup>
Ophichthidae	<i>Myrichthys ocellatus</i>	2	IM	-
Carangidae	<i>Trachinotus falcatus</i>	2	IM	44.9 <sup>c</sup>
Acanthuridae	<i>Acanthurus bahianus</i>	2	RH	9.0 <sup>c</sup>
Paralichthyidae	<i>Citharichthys spilopterus</i>	2	IM	11.7 <sup>b</sup>
Dasyatidae	<i>Dasyatis guttata</i>	1	CA	66.0 <sup>c</sup>
Ophichthidae	<i>Ophichthus ophis</i>	1	CA	4.7 <sup>h</sup>
Batrachoididae	<i>Thalassophryne nattereri</i>	1	IM	-
Mugilidae	<i>Mugil</i> sp.	1	RH	12.0 <sup>c</sup>
Lutjanidae	<i>Ocyurus chrysurus</i>	1	CA	13.0 <sup>c</sup>
Sciaenidae	<i>Pareques acuminatus</i>	1	CA	-
Chaetodontidae	<i>Chaetodon striatus</i>	1	IS	12.4 <sup>c</sup>
Ephippidae	<i>Chaetodipterus faber</i>	1	IM	9.4 <sup>c</sup>
Acanthuridae	<i>Acanthurus chirurgus</i>	1	RH	14.0 <sup>c</sup>

in the Reef zone. Adults of *Lutjanus jocu* only occurred at the Transition zone. The only species found exclusively at the transition zone, *Thalassophryne nattereri*, is in fact a typically estuarine species and was also sighted at Tanques sub-area, off the area covered by transects.

The Reef zone exhibited the most abundant and diverse fish assemblage, including 25 species, 12 of which exclusively found there: *Acanthurus chirurgus*, *A. coeruleus*, *Anisotremus virginicus*, *Chaetodon striatus*, *Coryphopterus glaucofraenum*, *Haemulon parra*, *Ocyurus chrysurus*, *Pareques acuminatus*, *Scarus* sp., *Sparisoma* sp., *Stegastes fuscus*, and *Trachinotus falcatus*. The most abundant species in the reefs were *Abudefduf saxatilis*, *Anisotremus surinamensis*, and *Sparisoma* sp., represented by juveniles and adult specimens. The two latter species were also

recorded at the Estuarine and Transition zones, throughout the year, but with higher abundances recorded from March to August (rainy season) at the study site. *Stegastes* spp. (adults and juveniles) and *Coryphopterus glaucofraenum* (adults) were typically Reef zone species, with *Stegastes variabilis* also occurring at the Transition zone.

Our data revealed two interconnected fish assemblages, composed of estuarine and reef fishes. Along the mangrove-reef gradient, several estuarine species appear to be gradually replaced by reef species. Additionally, size distribution of several species tend to differ between the estuarine zone and the transition and/or reef zone, with smaller individuals concentrating at the former and larger individuals at the latter zones. This type of distribution is exemplified by *Abudefduf saxatilis*, *Anisotremus surinamensis*, *Lutjanus alexandrei*, and *L. jocu* (Fig. 2).

**Table 3.** Species abundance (N), population density (Dens.) as individuals per 100 m<sup>2</sup> and size (mean ± standard deviation) of fishes sighted at the Mamanguape Mangrove-Reef system, State of Paraíba, NE Brazil, according to each sub-area during the dry season (October 2007 to February 2008, and September 2008). ? = undetermined values.

Species	Tanques			Peixe-Boi			Cação			Transition			Reefs		
	N	Dens.	Size (cm)	N	Dens.	Size (cm)	N	Dens.	Size (cm)	N	Dens.	Size (cm)	N	Dens.	Size (cm)
<i>Abudefduf saxatilis</i>	1	0.034	3.0 ± 0	-	-	-	-	-	-	-	-	-	8	0.888	3.8 ± 2.47
<i>Acanthurus bahianus</i>	2	0.069	6.5 ± 4.95	-	-	-	-	-	-	-	-	-	-	-	-
<i>Acanthurus chirurgus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Acanthurus coeruleus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Achirus lineatus</i>	4	0.138	16.2 ± 4.79	-	-	-	-	-	-	1	0.066	10.0 ± 0	-	-	-
<i>Anisotremus surinamensis</i>	-	-	-	-	-	-	-	-	-	2	0.133	2.0 ± 0	8	0.888	9.1 ± 2.47
<i>Anisotremus virginicus</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	0.111	7.0 ± 0
<i>Bathygobius soporator</i>	4	0.138	5.5 ± 1.00	7	0.269	6.3 ± 2.56	-	-	-	1	0.066	10.0 ± 0	1	0.111	3.0 ± 0
<i>Centropomus sp.</i>	4	0.276	8.3 ± 2.32	4	0.154	10.0 ± 0	-	-	-	-	-	-	-	-	-
<i>Chaetodipterus faber</i>	1	0.034	10.0 ± 0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chaetodon striatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	0.111	5.0 ± 0
<i>Citharichthys spilopterus</i>	-	-	-	-	-	-	-	-	-	1	0.066	5.0 ± 0	-	-	-
<i>Coryphopterus glaucofraenum</i>	-	-	-	-	-	-	-	-	-	-	-	-	3	0.333	4.3 ± 1.15
<i>Dactylopterus volitans</i>	2	0.069	12.5 ± 3.53	2	0.076	22.5 ± 10.6	-	-	-	-	-	-	-	-	-
<i>Dasyatis guttata</i>	1	0.034	?	-	-	-	-	-	-	-	-	-	-	-	-
<i>Echeneis naucrates</i>	1	0.034	6.0 ± 0	-	-	-	-	-	-	1	0.066	20.0 ± 0	-	-	-
<i>Epinephelus adscensionis</i>	-	-	-	1	0.038	30.0 ± 0	-	-	-	2	0.133	10.0 ± 0	-	-	-
<i>Eucinostomus melanopterus</i>	3	0.103	5.0 ± 0	11	0.423	5.9 ± 5.16	1	0.143	10.0	-	-	-	-	-	-
<i>Haemulon parra</i>	-	-	-	-	-	-	-	-	-	5	0.333	4.0 ± 0.7	1	0.111	10.0 ± 0
<i>Hippocampus reidi</i>	4	0.138	7.2 ± 3.86	3	0.115	13.6 ± 0.58	-	-	-	1	0.066	9.0 ± 0	-	-	-
<i>Lutjanus alexandrei</i>	8	0.276	8.7 ± 2.31	20	0.769	10.0 ± 3.62	-	-	-	-	-	-	-	-	-
<i>Lutjanus analis</i>	2	0.069	5 ± 0	4	0.154	8.7 ± 2.50	-	-	-	1	0.067	3.0 ± 0	8	0.889	3.8 ± 2.47
<i>Lutjanus jocu</i>	-	-	-	8	0.308	7.75 ± 3.01	-	-	-	15	1.000	22.0 ± 8.41	-	-	-
<i>Microphis brachyurus</i>	1	0.034	10.0 ± 0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mugil sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Myrichthys ocellatus</i>	1	0.034	?	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ocyurus chrysurus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ophichthus ophis</i>	1	0.034	?	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pareques acuminatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rypticus randalli</i>	6	0.207	10.0 ± 0	2	0.077	10.0 ± 0	-	-	-	5	0.333	10.0 ± 0	-	-	-
<i>Scarus sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sparisoma sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sphoeroides testudineus</i>	3	0.103	8.3 ± 5.77	-	-	-	-	-	-	1	0.067	5.0 ± 0	-	-	-
<i>Stegastes fuscus</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	0.111	5.0 ± 0
<i>Stegastes variabilis</i>	-	-	-	-	-	-	-	-	-	2	0.133	10.0 ± 0	1	0.111	5.0 ± 0
<i>Thalassophryne nattereri</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trachinotus falcatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

**Trophic groups.** Overall, the predominant trophic categories were mobile invertivores, represented by 15 species and carnivores, by 11 species (see Table 2). Considering the Estuarine zone, the most abundant groups were carnivores (55.5% of total abundance), mainly represented by the genus *Lutjanus*, and invertivores of mobile prey (42.1%), mostly represented by *Bathygobius soporator* and *Eucinostomus melanopterus*. Transition zone exhibited a higher abundance of invertivores of mobile prey (69.7%), largely represented by *Anisotremus surinamensis* and *Eucinostomus melanopterus*. Omnivores were the second most abundant group at the Transition zone (11.8%), and were solely represented by juveniles of *Abudefduf saxatilis*. The Reef zone showed the highest abundance of omnivores (50.1%), mainly *Abudefduf saxatilis*, followed by invertivores of mobile prey (31%), mostly represented by *Anisotremus surinamensis*.

The Reef zone exhibited a low abundance of carnivores (2.3%). Instead, it was characterized by a high abundance of herbivores (16.3%), a trophic group either poorly or not represented in the remaining sub-areas (Tanques: 3.4%;

Transition: 2.2%; Peixe-Boi and Cação lacking herbivores). Herbivore species included roving herbivores such as *Acanthurus sp.* and *Sparisoma sp.*, and territorial herbivores, represented by *Stegastes fuscus* and *S. variabilis*.

Canonical Correspondence Analysis (CCA), as performed in the first plot (Fig. 3a), identified mangroves, rocky structures, sessile invertebrates and bivalve shells, as important environmental variables structuring the fish assemblages. The following species were associated to the mangrove structures and hence to the Estuarine zone: *A. bahianus*, *B. soporator*, *Centropomus sp.*, *D. volitans*, *Lutjanus spp.*, *H. reidi*, *R. randalli*, and *S. testudineus*; associated to bivalves, rocky structures and sessile invertebrates, predominant on the Reef zone: *A. saxatilis*, *A. coeruleus*, *A. bahianus*, *A. surinamensis*, *A. virginicus*, *C. glaucofraenum*, *E. adscensionis*, *S. fuscus*, *S. variabilis*, *Scarus sp.*, and *Sparisoma sp.*; and associated to seagrass and algae vectors, encompassing species that predominated on the Transition zone: *A. lineatus*, *C. spilopterus*, *E. naucrates*, and *E. melanopterus*. A second CCA was

**Table 4.** Species abundance (N), population density (Dens.) as individuals per 100 m<sup>2</sup> and size (mean ± standard deviation) of fishes sighted at the Mamanguape Mangrove-Reef System, State of Paraíba, NE Brazil, according to each sub-area during the rainy season (March to August 2008).

Species	Tanques			Peixe-Boi			Cação			Transition			Reefs		
	N	Dens.	Size (cm)	N	Dens.	Size (cm)	N	Dens.	Size (cm)	N	Dens.	Size (cm)	N	Dens.	Size (cm)
<i>Abudefduf saxatilis</i>	-	-	-	-	-	-	-	-	-	21	1.500	3.3 ± 1.53	220	27.500	6.5 ± 2.48
<i>Acanthurus bahianus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Acanthurus chirurgus</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	0.125	10.0 ± 0
<i>Acanthurus coeruleus</i>	-	-	-	-	-	-	-	-	-	-	-	-	13	1.625	10.8 ± 1.87
<i>Achirus lineatus</i>	1	0.091	9.0 ± 0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Anisotremus surinamensis</i>	-	-	-	-	-	-	-	-	-	54	3.857	3.5 ± 1.85	122	15.250	4.8 ± 1.93
<i>Anisotremus virginicus</i>	-	-	-	-	-	-	-	-	-	-	-	-	6	0.750	8.5 ± 4.68
<i>Bathygobius soporator</i>	-	-	-	-	-	-	2	0.087	7.0 ± 0	-	-	-	-	-	-
<i>Centropomus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chaetodipterus faber</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chaetodon striatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Citharichthys spilopterus</i>	1	0.091	10.0 ± 0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Coryphopterus glaucofraenum</i>	-	-	-	-	-	-	-	-	-	-	-	-	5	0.625	4.8 ± 1.09
<i>Dactylopterus volitans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dasyatis guttata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Echeneis naucrates</i>	2	0.182	28.5 ± 4.95	-	-	-	-	-	-	-	-	-	-	-	-
<i>Epinephelus adscensionis</i>	-	-	-	-	-	-	-	-	-	-	-	-	3	0.375	10.0 ± 0
<i>Eucinostomus melanopterus</i>	-	-	-	-	-	-	-	-	-	50	3.571	3.0 ± 0	1	0.125	5.0 ± 0
<i>Haemulon parra</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hippocampus reidi</i>	-	-	-	-	-	-	-	-	-	4	0.286	15.3 ± 1.50	2	0.250	15.0 ± 2.83
<i>Lutjanus alexandrei</i>	-	-	-	-	-	-	1	0.043	10.0 ± 0	5	0.357	25.0 ± 0	-	-	-
<i>Lutjanus analis</i>	-	-	-	-	-	-	-	-	-	-	-	-	2	0.250	7.0 ± 4.24
<i>Lutjanus jocu</i>	-	-	-	-	-	-	-	-	-	-	-	-	3	0.375	15.0 ± 0
<i>Microphis brachyurus</i>	-	-	-	-	-	-	-	-	-	2	0.143	7.0 ± 1.41	-	-	-
<i>Mugil</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	0.125	30.0 ± 0
<i>Myrichthys ocellatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	0.125	60.0 ± 0
<i>Ocyurus chrysurus</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	0.125	7.0 ± 0
<i>Ophichthus ophis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pareques acuminatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	0.125	10.0 ± 0
<i>Rypticus randalli</i>	-	-	-	-	-	-	1	0.043	10.0 ± 0	-	-	-	1	0.125	10.0 ± 0
<i>Scarus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	6	0.750	7.7 ± 2.25
<i>Sparisoma</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	32	4.000	4.7 ± 1.67
<i>Sphoeroides testudineus</i>	1	0.091	20.0	-	-	-	1	0.043	2.0 ± 0	1	0.071	10.0	-	-	-
<i>Stegastes fuscus</i>	-	-	-	-	-	-	-	-	-	-	-	-	12	1.500	8.2 ± 2.75
<i>Stegastes variabilis</i>	-	-	-	-	-	-	-	-	-	2	0.143	3.0	11	1.375	4.2 ± 2.13
<i>Thalassophryne nattereri</i>	-	-	-	-	-	-	-	-	-	1	0.071	10.0	-	-	-
<i>Trachinotus falcatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	2	0.250	15.0 ± 0

performed with mangroves, rocky structures and salinity as the most important environmental variables (vectors), while trophic groups and sub-areas were represented by symbols distributed across environmental ranges. As shown in Fig. 3b, roving and territorial herbivores, as well as omnivores, are clearly associated to the rocky structures, while carnivores remained associated to mangroves. Invertebrates of mobile prey were unrelated to any specific variable.

## Discussion

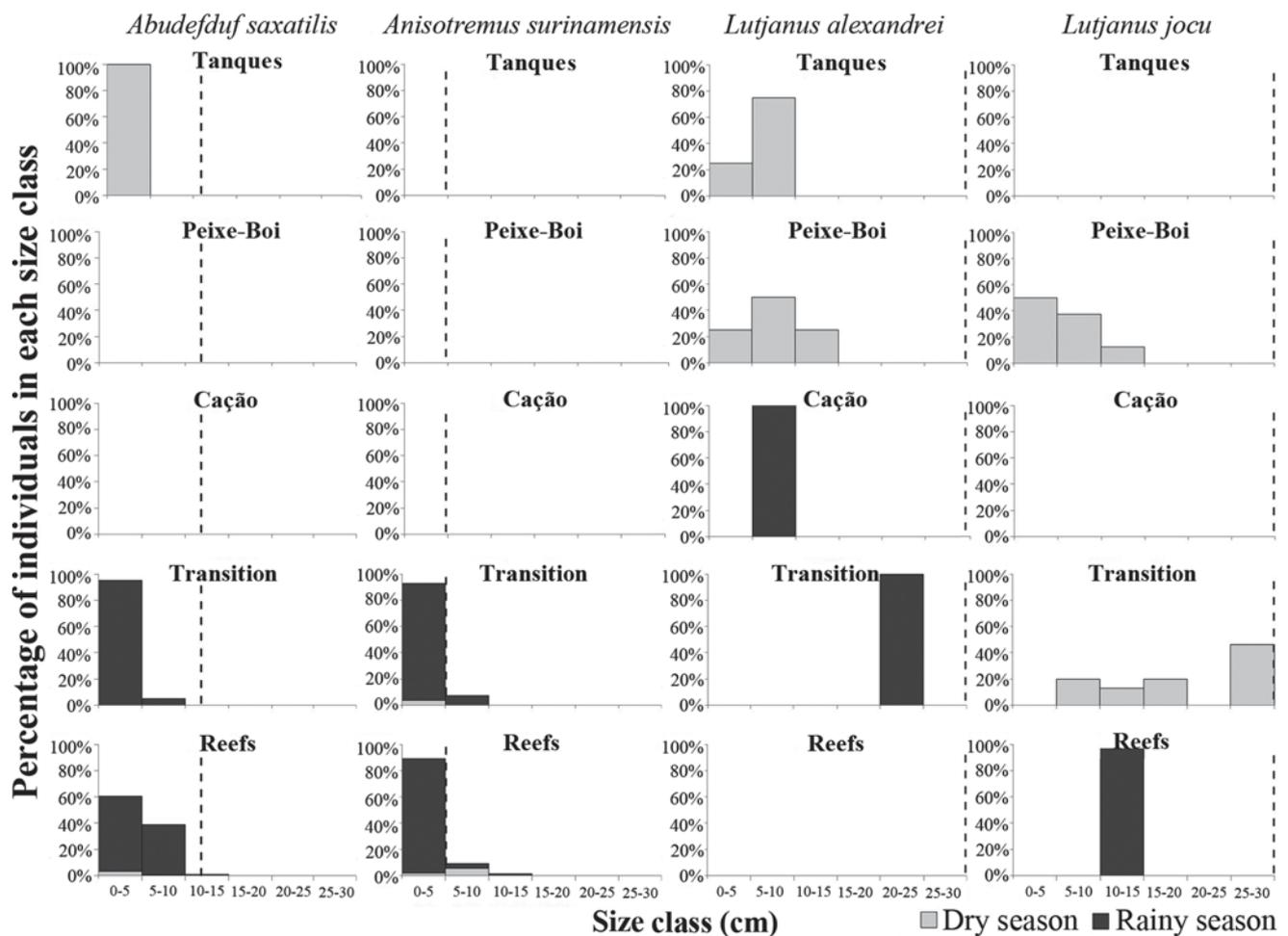
**Fish composition and spatial distribution.** The spatial distribution of fishes may be related to several factors, including the distribution of prey, habitat availability or the physiological capabilities of individual species relative to environmental conditions (Williams, 1991). In Northeast Brazil, Andrade-Tubino *et al.* (2008) estimated that about 51% of estuarine species (mainly represented by families Haemulidae and Lutjanidae) are opportunists, while Osório *et al.* (2011) considered all sighted fish species at the Pacoti estuary (NE

Brazil) as originally marine, which might enter the estuary for feeding, shelter and nursery. The following species, considered as opportunists (Andrade-Tubino *et al.*, 2008), were sighted in our study: *Anisotremus surinamensis*, *Citharichthys spilopterus*, *Datylopterus volitans*, *Gymnothorax funebris*, *Haemulon parra*, *Hippocampus reidi*, *Lutjanus* sp., *Ocyurus chrysurus*, *Rypticus randalli*, *Sparisoma* sp., *Sphoeroides testudineus*, and *Strongylura* sp., comprising 34.1% of all sighted fish species at the Mamanguape estuary.

Fish assemblage along the Mamanguape Mangrove-Reef system was strongly related to the microhabitat availability, as revealed by the representative numbers of carnivores at the Estuarine zone and herbivores at the Reef zone. This result agrees with those obtained in the Indo-Pacific by Unsworth *et al.* (2009), who found that carnivorous fishes were the predominant feeding group in the mangroves, while omnivores dominated on the mangrove edge and seagrass beds, and a representative number of herbivores were present on adjacent coral reefs.

**Table 5.** Percentage of substrate cover (main items), rugosity index and salinity (mean  $\pm$  standard deviation and variation) along the Mamanguape Mangrove-Reef system, Paraíba, NE Brazil, according to the sampling sub-areas from October 2007 to September 2008. \*. Cover categories: S/M - sandy or muddy bottom, without visually detectable organisms; Ma - Mangrove roots, leaves and fallen branches of mangrove trees, mainly *Rhizophora mangle*; Sg - Seagrass beds, *Halophila* sp. and *Halodule wrightii*; Bv - bivalve shells, mainly *Crassostrea rhizophorae*, *Anomalocardia brasiliana*, and *Lucina pectinata*; Si - Sessile invertebrates, sponges, including *Haliclona* sp., *Cinachyrella alloclada*, and cnidarians, including *Carijoia* sp.; Mb - Macroalgae beds, red algal beds, mainly composed by *Hypnea musciformis*, *Hypnea spinella*, *Cryptonemia* sp., and *Acanthophora* sp.; Oa - Other algae, drifting or attached algae (not forming beds), which included *Gracilaria* sp., *Gelidiella acerosa*, *Pterocladia* sp., *Gelidium* sp., *Corynomorpha* sp., and *Acetabularia* sp.

Sub-area	Percentage of substrate cover categories*							Rugosity	Mean salinity
	S/M	Ma	Sg	Bv	Si	Mb	Oa		
1 Tanques	71.5	9.2	8.3	7.1	0.1	1.4	2.4	0.11	31.3 $\pm$ 4.9 (20 – 43)
2 Peixe-Boi	83.1	10.3	2.9	2.2	0.1	0.2	1.2	0.11	34.0 $\pm$ 5.0 (20 – 43)
3 Cação	84.7	3.1	0.0	10.9	0.2	0.0	1.1	0.11	31.3 $\pm$ 4.5 (24 – 39)
4 Transition	85.4	3.3	2.6	1.9	3.0	2.2	1.6	0.12	36.6 $\pm$ 1.8 (35 – 40)
5 Reefs	56.6	0.5	0.9	0.4	2.9	31.9	6.8	1.13	36.9 $\pm$ 3.1 (31 – 41)



**Fig. 2.** Ontogenetic patterns of habitat use in *Abudefduf saxatilis*, *Anisotremus surinamensis*, *Lutjanus alexandrei*, and *L. jocu* along the sub-areas of Mamanguape Mangrove-Reef system, NE Brazil, showing an increase in individual size classes from the Estuarine to the Reef zone. Mann Whitney U Test showed significant size differences between all sub-areas (for *A. saxatilis*, Transition vs. Reefs:  $U = 491$ ,  $Z = -6.02$ ,  $p = 0.00$ ; for *A. surinamensis*, Transition vs. Reefs:  $U = 1338$ ,  $Z = -6.83$ ,  $p = 0.00$ ; for *L. alexandrei*, Peixe-Boi vs. Transition:  $U = 0.00$ ,  $Z = -3.39$ ,  $p = 0.00$ ; and Tanques vs. Transition:  $U = 0.00$ ,  $Z = -2.92$ ,  $p = 0.00$ ; for *L. jocu*, Peixe-Boi vs. Transition:  $U = 7.5$ ,  $Z = -3.38$ ,  $p = 0.00$ ), except between Tanques and Peixe-Boi for *L. alexandrei* ( $U = 65$ ,  $Z = 0.76$ ,  $p = 0.46$ ).

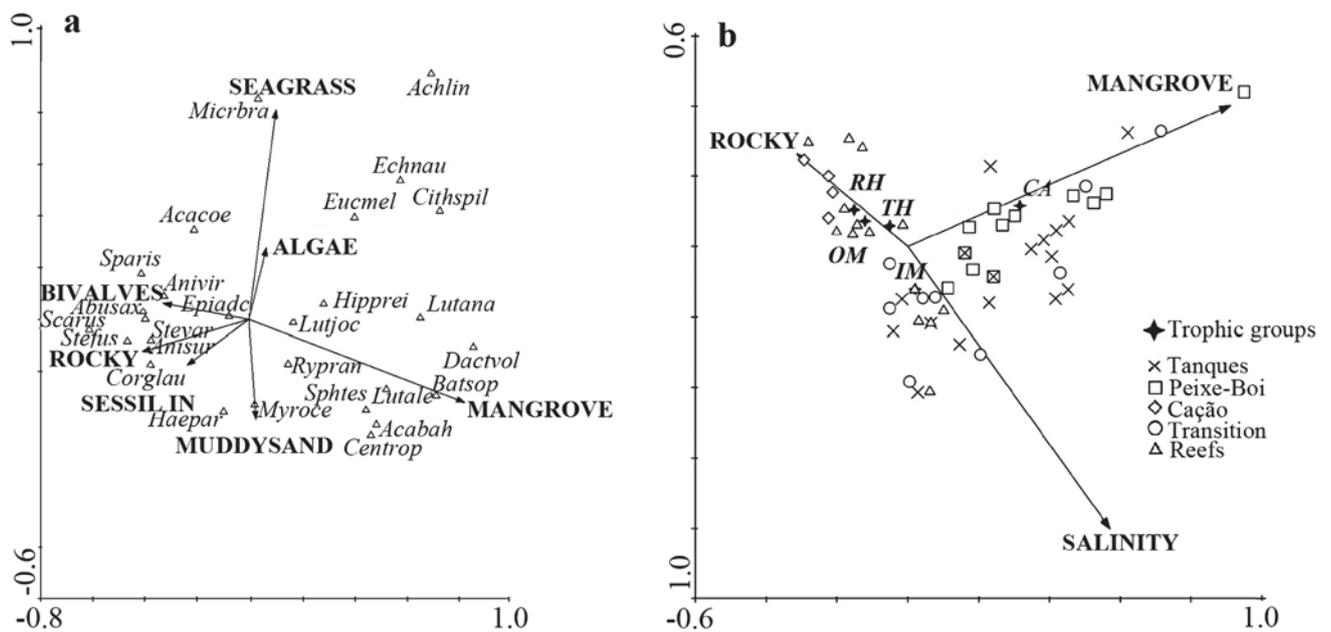
The abundance of Carnivores at the Estuarine zone was probably related to the high abundance of young from a variety of taxa in that area, a result in line with Ogden & Gladfelder (1983), who remarked that those organisms and their relative vulnerability during migrations attract carnivorous fish to mangroves from surrounding systems, such as coral reefs.

The species *Lutjanus alexandrei*, *L. jocu*, and *Bathygobius soporator* were the most representative, in terms of abundance and frequency of occurrence, along the estuarine margins, inhabiting mangrove roots and other complex structures at the Estuarine zone. Osório *et al.* (2011) also considered these species as representative of the mangrove ecosystem, and their presence appear to be a typical feature of mangrove areas in NE Brazil.

Herbivore fishes are known to compose the bulk of fish biomass on coral reefs, where they play a vital role transferring energy from the base to the top of the food web (Horn, 1989; Choat, 1991). Although less diverse than other trophic groups, their huge biomass exerts a strong influence

on the abundance of the epilithic algae community and on sediment transport (Bruggemann, 1994; Bellwood, 1995). Considering the high abundance of macroalgal beds and herbivore fishes in the Reef zone, we can assume that they play an important role on the trophic balance in the area, based on the availability of space, nutrients, and luminosity (see Francini-Filho *et al.*, 2010).

Herbivore species recorded in this study (*Acanthurus* sp., *Stegastes* sp., *Sparisoma* sp., *Scarus* sp.) are conspicuous along the Brazilian coast (Ferreira *et al.*, 2004; Floeter *et al.*, 2005) and abundant in northeastern Brazilian reefs (Rocha *et al.*, 1998; Medeiros *et al.*, 2007; Ilarri *et al.*, 2008; Francini-Filho *et al.*, 2010). Scarids, represented in our study by *Scarus* sp. and *Sparisoma* sp., are known for their feeding plasticity (Bonaldo *et al.*, 2006) which makes them very adaptable to feeding on different sources. Acanthurids are known to tolerate low salinity (Rocha *et al.*, 2002) and thus to explore estuarine habitats, as occurred with *Acanthurus bahianus* in our study. The other species of surgeonfishes (*A. chirurgus* and *A. coeruleus*) were only sighted at the Reef zone.



**Fig. 3.** Canonical Correspondence Analysis of fishes and environmental parameters from Mamanguape Mangrove-Reef system, NE Brazil: (a) fish species (symbols) in relation to microhabitat categories (vectors) - Eigenvalues: axis 1, 0.56; axis 2, 0.20; r species-environment: axis 1, 0.87; axis 2, 0.56; First two axes accounted for 64.9 % of the variance; (b) fish trophic groups and sub-areas (symbols) in relation to environmental categories (vectors) - Eigenvalues: axis 1, 0.49; axis 2, 0.39; r species-environment: axis 1, 0.79; axis 2, 0.76; First two axes accounted for 51.6 % of the variance. Monte-Carlo test of all canonical axes were significant ( $p < 0.01$ ), 999 permutations. Abbreviations as follows - fish species: *Abusax*: *Abudefduf saxatilis*; *Acabah*: *Acanthurus bahianus*; *Acacoe*: *A. coeruleus*; *Achlin*: *Achirus lineatus*; *Anivir*: *A. virginicus*; *Batsop*: *Bathygobius soporator*; *Centrop*: *Centropomus* sp.; *Cithspil* - *Citharichthys spilopterus*; *Corglau* - *Coryphopterus glaucofraenum*; *Dactvol* - *Dactylopterus volitans*; *Echnau*: *Echeneis naucrates*; *Epiadc*: *Epinephelus adscensionis*; *Eucmel*: *Eucinostomus melanopterus*; *Haepar*: *Haemulon parra*; *Hipprei*: *Hippocampus reidi*; *Lutana*: *Lutjanus analis*; *Lutale*: *L. alexandrei*; *Lutjoc*: *L. jocu*; *Micbra*: *Micropphis brachyurus*; *Myroce*: *Myrichthys ocellatus*; *Rypran*: *Rypticus randalli*; *Scarus*: *Scarus* sp.; *Sparis*: *Sparisoma* sp.; *Sphites*: *Sphoeroides testudineus*; *Stefus*: *Stegastes fuscus*; *Stegar*: *S. variabilis*; trophic groups: RH - Roving herbivore; TH - Territorial herbivore; OM - Omnivore; CA - Carnivore; IM - Invertivore of mobile prey.

Finally, the genus *Stegastes*, represented here by *S. fuscus* and *S. variabilis*, seem to be very dependent on the reef matrix and site-attached due to their farming habits (Ferreira *et al.*, 1998; Barneche *et al.*, 2009); nevertheless, representatives of that genus can inhabit brackish waters, as exemplified by *S. otophorus* (Froese & Pauly, 2010) and by *Stegastes variabilis* in this study.

Among the fishes found on our surveys, *Mugil* sp., *C. spilopterus*, *L. jocu*, and *E. melanopterus* are typically found in estuaries at Northeastern Brazil (Andrade-Tubino *et al.*, 2008). On the Reef zone, *Stegastes fuscus*, *S. variabilis*, *Acanthurus* sp., *Chaetodon striatus*, *Pareques acuminatus*, scarids and haemulids, encompass a vast assemblage of fishes found on Brazilian reefs, being generally associated to habitat complexity, reef topography and cover of benthic organisms (Rosa *et al.*, 1997; Ferreira *et al.*, 2001; Ferreira *et al.*, 2004; Floeter *et al.*, 2007).

The abundance and diversity of fishes in the Reef zone, as well as the concentration of fishes along the margins of the estuary, highlighted the importance of structural complexity (in our study, rugosity), which was higher in those habitats. A higher abundance of fishes, and also the higher population densities of the seahorse *Hippocampus reidi*, possibly are related (among other aspects) to this greater habitat complexity. The role played by high structural complexity in providing food, shelter, refuge from predators and settlement places for pelagic fish larvae has been highlighted in various studies (*e.g.*, Ferreira *et al.*, 2001; Gratwicke & Speight, 2005), while the structural complexity resulting from mangrove roots, debris, and other vegetation structures of the intertidal habitat has been shown to enhance the refuge aspect of habitats (Rönnbäck, 1999; Weis & Weis, 2005; Osório *et al.*, 2011).

**Ecosystem connectivity: species along the mangrove-reef gradient.** Connectivity studies between mangrove and reef ecosystems are often complicated by differences in geomorphology and tidal range of estuaries (Barletta *et al.*, 2003) and by local variations of environmental factors such as hydrodynamics, depth, shading and prop-root densities (Nagelkerken & Faunce, 2007). These local variations may determine the mangrove's fish composition and strongly influence the fish community structure on neighboring reefs (Mumby *et al.*, 2004; Nagelkerken & Faunce, 2007). Therefore, connectivity studies of these ecosystems should not be limited to the comparison of shared species, but instead should look at physical processes of connectivity along the ecotones and to assess information on functional groups of fishes (Nagelkerken & Faunce, 2007).

In spite of the limited number of physical factors investigated, our results on fish assemblage composition, microhabitat use and functional groups suggest connectivity among mangrove, seagrass, and reef biotopes in the study area. Results also revealed that the fish composition along the study area gradually changed from the Estuarine to the Reef zone, despite the fact that these

biotopes were distant only a few kilometers from each other. Such change is possibly related to complex interactions of multiple factors, including some that were not assessed in this study. Differences in salinity, turbidity, organic matter, and bottom structure, for example, are variables known to play a role in the structure of fish assemblages in the estuarine environments (see Barletta *et al.*, 2005).

In our study, we highlight the high abundance of mangrove-associated structures, oysters, and seagrass which predominated on the muddy and sandy bottom of the Estuarine zone, and were gradually replaced by the beds of macroalgae and sessile invertebrates (sponges and cnidarians) found on the sandy and rocky substrate of the Reef zone, possibly exerting a significant effect on the structure of the fish assemblage. Additionally, this gradual change in bottom structure may play a role in ontogenetic habitats shifts at the study site. As discussed by Gratwicke *et al.* (2006), the fact that some species appear to have incremental ontogenetic transitions from habitat type to habitat type means that sh assemblage composition may depend not only on the type of habitat available, but on the contiguity and dispersion of adjacent habitat types.

#### **Nursery role of the Mamanguape Mangrove-Reef System.**

Various authors have discussed the nursery potential of certain habitats, such as mangroves, seagrass beds and shallow coral reefs (Nagelkerken *et al.*, 2000; Dorenbosch *et al.*, 2004; Gratwicke *et al.*, 2006; Mumby *et al.*, 2008; Nagelkerken & Faunce, 2008; Nagelkerken *et al.*, 2008; Unsworth *et al.*, 2009), an aspect highlighted in our study by the predominance of juveniles. Fishes at that life stage may benefit from the shelter provided by environmental characteristics observed in this study, such as shallow habitats, high turbidity, and soft mud suitable for burrowing, all as a result of the sediment-trapping capacity of mangroves (see Rönnbäck, 1999).

Nevertheless, even though connectivity between coral reefs and mangroves or seagrass beds can benefit the reef fish fauna (*i.e.* food and shelter for juveniles, additional space and feeding resources for adults), generalizations about the nursery role of these habitats should be avoided. Not all mangrove or seagrass beds appear to offer nursery function, not all fish species use these services as well (Chittaro *et al.*, 2005). As pointed out by Nagelkerken & Faunce (2008), there is a need for a species-based approach towards assessing the benefits provided by nursery habitats for fishes.

Our results revealed the presence of smaller individuals at the Estuarine zone and larger individuals at the Transition and/or Reef zone for *Abudefduf saxatilis*, *Anisotremus surinamensis*, *Lutjanus alexandrei*, and *L. jocu*, a typical pattern for species that use shift between contiguous habitats during ontogeny. Additionally, the Reef zone exhibited an abundant macroalgal cover, where juveniles of many herbivore species were found, suggesting that the reef may provide shelter (high turbidity) and food (algae beds) to juveniles.

It is possible that several other species may present this ontogenetic patterns of distribution along the study area -

**Table 6.** Fishes recorded along the Mamanguape Mangrove-Reef system, State of Paraíba, NE Brazil, according to the zone where they occurred. Species that occurred in our study are marked with an asterisk.

Estuarine species - those exclusively found on the Estuarine zone (sources: Rosa & Sassi, 2002; this study)		
<i>Achirus declivis</i> Chabanaud, 1940	<i>Cynoscion leiarchus</i> (Cuvier, 1830)	<i>Nebris microps</i> Cuvier, 1830
<i>Achirus lineatus</i> (Linnaeus, 1758)*	<i>Cynoscion microlepidotus</i> (Cuvier, 1830)	<i>Odontognathus mucronatus</i> Lacepède, 1800
<i>Albula vulpes</i> (Linnaeus, 1758)	<i>Dactylopterus volitans</i> (Linnaeus, 1758)*	<i>Oligoplites palometa</i> (Cuvier, 1832)
<i>Anchoa januaria</i> (Steindachner, 1879)	<i>Dasyatis guttata</i> (Bloch & Schneider, 1801)*	<i>Ophichthus cylindroideus</i> (Ranzani, 1839)
<i>Anchoa tricolor</i> (Spix & Agassiz, 1829)	<i>Diapterus auratus</i> Ranzani, 1842	<i>Ophichthus ophis</i> (Linnaeus, 1758)*
<i>Anchovia clupeioides</i> (Swainson, 1839)	<i>Diapterus rhombeus</i> (Valenciennes, 1830)	<i>Ophioscion punctatissimus</i> Meek & Hildebrand, 1925
<i>Antennarius</i> sp.*	<i>Echeneis naucrates</i> Linnaeus, 1758*	<i>Opisthonema oglinum</i> (Lesueur, 1818)
<i>Archosargus rhomboidalis</i> (Linnaeus, 1758)	<i>Eleotris pisonis</i> (Gmelin, 1789)	<i>Paralonchurus brasiliensis</i> (Steindachner, 1875)
<i>Arius herzbergii</i> (Bloch, 1794)	<i>Elops saurus</i> Linnaeus, 1766	<i>Pellona harroweri</i> (Fowler, 1919)
<i>Arius proops</i> (Valenciennes, 1840)	<i>Eucinostomus argenteus</i> Baird & Girard, 1855	<i>Peprilus paru</i> (Linnaeus, 1758)
<i>Arius quadriscutis</i> (Valenciennes, 1840)	<i>Eugerres brasiliensis</i> (Valenciennes, 1830)	<i>Polydactylus virginicus</i> (Linnaeus, 1758)
<i>Atherinella brasiliensis</i> (Quoy & Gaimard, 1824)	<i>Gobionellus boleosoma</i> (Jordan & Gilbert, 1882)	<i>Pomadasys corvinaeformis</i> (Steindachner, 1868)
<i>Bagre marinus</i> (Mitchill, 1815)	<i>Gobionellus oceanicus</i> (Pallas, 1770)	<i>Prionotus punctatus</i> (Bloch, 1789)
<i>Bairdiella ronchus</i> (Cuvier, 1830)	<i>Gobionellus smaragdus</i> (Valenciennes, 1837)	<i>Rachycentron canadus</i> (Linnaeus, 1766)
<i>Bothus ocellatus</i> (Agassiz, 1831)	<i>Gymnothorax ocellatus</i> Agassiz, 1831	<i>Rhinocardinia amazonica</i> (Steindachner, 1879)
<i>Caranx latus</i> Agassiz, 1831	<i>Gymnura micrura</i> (Bloch & Schneider, 1801)	<i>Sardinella brasiliensis</i> (Steindachner, 1879)
<i>Cathorops spixii</i> (Agassiz, 1829)	<i>Haemulon steindachneri</i> (Jordan & Gilbert, 1882)	<i>Scorpaena plumieri</i> (Bloch, 1789)
<i>Centropomus ensiferus</i> Poey, 1860	<i>Harengula clupeiola</i> (Cuvier, 1829)	<i>Selene vomer</i> (Linnaeus, 1758)
<i>Centropomus mexicanus</i> Bocourt, 1868	<i>Hemiramphus brasiliensis</i> (Linnaeus, 1758)	<i>Serranus flaviventris</i> (Cuvier, 1829)
<i>Centropomus pectinatus</i> Poey 1860	<i>Hyporhamphus unifasciatus</i> (Ranzani, 1842)	<i>Sphoeroides greeleyi</i> Gilbert, 1900*
<i>Centropomus undecimalis</i> (Bloch, 1796)*	<i>Lagocephalus laevigatus</i> Linnaeus, 1766	<i>Stellifer brasiliensis</i> (Schultz, 1945)
<i>Cetengraulis edentulus</i> (Cuvier, 1829)	<i>Larimus breviceps</i> Cuvier, 1830	<i>Stellifer rastrifer</i> (Jordan, 1889)
<i>Chaetodipterus faber</i> (Broussonet, 1782)*	<i>Lutjanus cyanopterus</i> (Cuvier, 1828)	<i>Strongylura timucu</i> (Walbaum, 1792)*
<i>Chilomycterus antillarum</i> Jordan & Rutter, 1897	<i>Lycengraulis grossidens</i> (Agassiz, 1829)	<i>Symphurus tessellatus</i> (Quoy & Gaimard, 1824)
<i>Chloroscombrus chrysurus</i> (Linnaeus, 1766)	<i>Menticirrhus oceanicus</i> (Linnaeus, 1758)	<i>Thalassophryne punctata</i> Steindachner, 1876
<i>Citharichthys arenaceus</i> Evermann & Marsh, 1900	<i>Menticirrhus littoralis</i> (Holbrook, 1847)	<i>Trachinotus carolinus</i> (Linnaeus, 1766)
<i>Citharichthys spilopterus</i> Günther, 1862*	<i>Micropogonias brachyurus</i> (Bleeker, 1853)*	<i>Trachinotus goodei</i> Jordan & Evermann, 1896
<i>Colomesus psittacus</i> (Bloch & Schneider, 1801)	<i>Micropogonias furnieri</i> (Desmarest, 1823)	<i>Trinectes microphthalmus</i> (Chabanaud, 1928)
<i>Conodon nobilis</i> (Linnaeus, 1758)	<i>Mugil curvidens</i> Valenciennes, 1836	<i>Trinectes paulistanus</i> (Miranda Ribeiro, 1915)
<i>Cynoscion acoupa</i> (Lacepède, 1801)	<i>Mugil gaimardianus</i> Desmarest, 1831	
Transient species - those found in both Estuarine and Reef portions (sources: Rosa & Sassi, 2002; Silva, 2002; this study)		
<i>Abudefduf saxatilis</i> (Linnaeus, 1758)*	<i>Gymnothorax vicinus</i> (Castelnau, 1855)	<i>Megalops atlanticus</i> Valenciennes, 1847
<i>Acanthurus bahianus</i> Castelnau, 1855*	<i>Haemulon parra</i> (Desmarest, 1823)*	<i>Mugil curema</i> Valenciennes, 1836*
<i>Anisotremus surinamensis</i> (Bloch, 1791)*	<i>Haemulon plumieri</i> (Lacepède, 1802)*	<i>Myrichthys ocellatus</i> (Lesueur, 1825)*
<i>Bathygobius soporator</i> (Valenciennes, 1837)*	<i>Hippocampus reidi</i> (Ginsburg, 1933)*	<i>Rypticus randalli</i> Courtenay, 1967*
<i>Epinephelus adscensionis</i> (Osbeck, 1765)*	<i>Lutjanus jocu</i> (Bloch & Schneider, 1801)*	<i>Sphoeroides testudineus</i> (Linnaeus, 1758)
<i>Eucinostomus melanopterus</i> (Bleeker, 1863)*	<i>Lutjanus alexandrei</i> Moura & Lindeman, 2007*	<i>Trachinotus falcatus</i> (Linnaeus, 1758)*
<i>Gymnothorax funebris</i> (Ranzani, 1840)	<i>Lutjanus analis</i> (Cuvier, 1828)*	
Reef species - those exclusively found on the Reef zone (sources: Silva, 2002; this study)		
<i>Acanthurus chirurgus</i> (Bloch, 1787)*	<i>Gobionellus shufeldti</i> (Jordan & Eigenmann, 1887)	<i>Pareques acuminatus</i> (Bloch & Schneider, 1801)*
<i>Acanthurus coeruleus</i> Bloch & Schneider, 1801*	<i>Gymnothorax moringa</i> (Cuvier, 1829)	<i>Pomacanthus paru</i> (Bloch, 1787)
<i>Ahlia egmontis</i> (Jordan, 1884)	<i>Hypleurochilus pseudoaequipinnis</i> Bath, 1994	<i>Scartella</i> aff. <i>crystata</i> (Linnaeus, 1758)
<i>Anisotremus virginicus</i> (Linnaeus, 1758)*	<i>Labrisomus nuchipinnis</i> (Quoy & Gaimard, 1824)	<i>Scarus</i> sp.*
<i>Cephalopholis fulva</i> (Linnaeus, 1758)	<i>Malacoctenus delalandii</i> (Valenciennes, 1836)	<i>Sparisoma</i> sp.*
<i>Chaetodon striatus</i> Linnaeus, 1758*	<i>Nicholsina usta</i> (Valenciennes, 1840)	<i>Stegastes fuscus</i> (Cuvier, 1830)*
<i>Coryphopterus glaucofraenum</i> Gill, 1863*	<i>Ocyurus chrysurus</i> (Bloch, 1971)*	<i>Stegastes variabilis</i> (Castelnau, 1855)*
<i>Entomacrodus vomerinus</i> (Valenciennes, 1836)	<i>Parablennius</i> aff. <i>pilicornis</i> (Cuvier, 1829)	

previous studies have recorded this pattern for *Acanthurus chirurgus* (Nagelkerken *et al.*, 2000; Nagelkerken & Faunce, 2008), *Lutjanus alexandrei* (Nagelkerken *et al.*, 2000; Chittaro *et al.*, 2005; Unsworth *et al.*, 2009), *Sparisoma viride* (Nagelkerken *et al.*, 2000) and *S. chrysopterum* (Nagelkerken & Faunce, 2008), which used mangroves or seagrass beds as nursery biotopes; and also *Abudefduf saxatilis* and *Acanthurus bahianus*, which used shallow reef habitats as nurseries (Nagelkerken *et al.*, 2000).

**Estuarine vs. Reef fish communities.** When combining our data from Estuarine and Reef zones with those sampling data obtained by Silva (2002) and Rosa & Sassi (2002), it was possible to categorize the fish assemblage of the Mamanguape Mangrove-Reef System into three groups, as shown on Table

6: (1) Estuarine species, the group of species that emerged as typically estuarine; (2) Transient species, those found in both estuarine, transition and reef portions of the study area; and (3) Reef species, those exclusively found on the Reef zone.

It should be noted that the spatial distribution of the many fish species recorded in this study was well-known by local artisanal fishers, who applied several criteria for classifying fish, mostly based on behavior and habitat use (Mourão & Nordi, 2003, 2006). For instance, they associated *Thalassophryne nattereri* and the flatfish *Citharichthys spilopterus* to the estuarine bottom (muddy substrate) and *Bathygobius soporator* to the mangrove roots and muddy habitats near that vegetation, in accordance to our study. In addition, fishermen referred to the Reef zone as the area with highest diversity of fishes (Mourão & Nordi, 2006).

**Final remarks.** The number of fish species recorded in our study clearly represents an underestimation of the total number of 103 species, previously reported for the area, based on a study using destructive sampling (Rosa & Sassi, 2002), which surveyed additional habitats when compared to our study, including the upper sections of the estuary, deeper portions of the main channel and tide pools. Visual census techniques tend to underestimate cryptobenthic and highly mobile species (Ferreira *et al.*, 2004). Nevertheless, underwater visual fish census can be a rapid and effective technique for gathering data and making quantitative comparisons of fish distribution, abundance, and size-structure within and among habitat types (Faunce & Serafy, 2006).

The visual censuses performed in our study generated novel data relevant for management of the protected area located at the study site, such as fish associations with habitat features. Additionally, the taxa *Antennarius* sp., *Sphoeroides greeleyi*, *Microphis brachyurus*, *Anisotremus virginicus*, *Chaetodon striatus*, *Ocyurus chrysurus*, *Pareques acuminatus*, and *Scarus* sp. were recorded for the first time at the study site.

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