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Fish assemblages along a morphodynamic continuum on three tropical beaches

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A comparative study involving three mesotidal beaches from reflective to estuarine states was conducted between October 2010 and September 2011 in the estuary of Mamanguape River, northeastern Brazil. The aim was to test for differences in fish assemblages along a morphodynamic *continuum*, particularly the effects of wave action. In total, 3,732 fish from 71 species were examined; *Rhinosardinia bahiensis* and *Atherinella brasiliensis* dominated the estuarine beach, whereas *Trachinotus carolinus* dominated the reflective beach. Fish assemblages were structured by spatial differences among the sites, and overall abundance, richness and biomass demonstrated a clear increasing trend from the reflective to the estuarine beaches, indicating a primary influence of wave exposure in the measured parameters. The Mamanguape River estuary plays a crucial ecological role as a nursery for several species that depend on its resources and have adapted to the high variability of its physical and chemical factors and the diversity of its habitats.

Um estudo comparativo envolvendo três praias mesotidais do estado refletivo para o estuarino foi realizado entre outubro de 2010 e setembro de 2011 no estuário do rio Mamanguape, Nordeste do Brasil. O objetivo foi testar as diferenças nas assembleias de peixes ao longo de um *continuum* morfodinâmico, particularmente os efeitos da ação das ondas. No total, 3.732 peixes de 71 espécies foram examinados; *Rhinosardinia bahiensis* e *Atherinella brasiliensis* dominaram a praia estuarina, enquanto *Trachinotus carolinus* dominou a praia refletiva. As assembleias de peixes foram estruturadas por diferenças espaciais entre locais de amostragem, e a abundância total, riqueza e biomassa demonstraram uma clara tendência crescente da praia refletiva à praia estuarina, indicando uma influência primária de exposição às ondas nos parâmetros medidos. O estuário do rio Mamanguape desempenha um papel ecológico importante como um berçário para várias espécies que dependem de seus recursos e se adaptaram à alta variabilidade de seus fatores físico-químicos e da diversidade de seus habitats.

Key words: Community descriptors, Juveniles, Nursery, Spatial patterns, Wave action.

Introduction

The importance of shallow coastal biotopes in the maintenance of fish assemblages has been clearly demonstrated by studies conducted worldwide (Layman, 2000; Ramos *et al*., 2006; Kruger & Strydom, 2010; Woodland *et al*., 2012). These biotopes are often described as nursery habitats or recruitment areas for fish because they provide a great abundance of food resources and protection from predation. They may also act as a temporary habitat during a particular life cycle phase and/or as a permanent habitat for young-of-the-year, thereby ensuring the renewal of fish stock (McLachlan, 1983; Pessanha *et al*., 2000; Beck *et al*., 2001; Able, 2005).

Beaches are defined by McLachlan (1983) as a range of environments on a gradient from open sea to protected sands or mudflats in estuaries. The classification of beaches is performed using several models, including those that consider the beach morphodynamics (Wright & Short, 1984) and the influence of tides (Short, 1982; Masselink, 1993). In the case of reflective beaches, wave action generates physical stress at these sites that affects sedimentary structure and makes food resources available for fish that can adapt to these conditions (Calliari *et al*., 2003; Vasconcellos *et al*., 2007; Niang *et al*., 2010). Moreover, fish in such environments, with physical conditions created by tides and waves, possess adaptations that may be morphological (Palmeira & Monteiro-Neto,

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2010), or even behavioural adaptations, such as migration to the intertidal zones or other habitats (Harvey, 1998).

In contrast, estuarine beaches are characterized as calmer environments that result from a reduced influence of wave energy (Bernabeu *et al*., 2012). Several fish species utilize these environments at some stage of their life cycle because of factors such as availability of food from high primary production; availability of refuge provided by structural complexity, especially for juveniles; high water turbidity; and a lower number of large carnivorous fish (Potter *et al*., 1986; Whitfield, 1999; Beck *et al*., 2001; Spach *et al*., 2003; Hajisamae *et al*., 2006; Paiva *et al*., 2008).

One of the primary bases for understanding fish assemblages is the knowledge of their distribution and abundance and their relationship with abiotic factors (Inoue *et al*., 2008), as well as factors that will limit or affect a change in population (Levin *et al*., 1997). Several studies from different regions have emphasized abiotic factors, such as temperature and salinity (Harrison & Whitfield, 2006), salinity and turbidity (Cyrus & Blaber, 1992; Barletta *et al*., 2005), turbidity (Cyrus & Blaber, 1987; Abou-Seedo *et al*., 1990), morphodynamic models (Inui *et al*., 2010), and input of freshwater and river flow (Barletta *et al*., 2005; Vinagre *et al*., 2009; Baptista *et al*., 2010; Castillo-Rivera, 2013) as factors that influence the abundance of young fish in these shallow water habitats. Additionally, factors such as recruitment, competition, predation, and structural complexity are listed as ecological processes that determine the structure of these communities, so that the fish assemblages are the result of the complex interaction of abiotic and biotic factors (Mariani, 2001; Laegdsgaard & Johnson, 2001).

In tropical northeastern Brazilian estuaries, information regarding juvenile fish composition, seasonal variations in abundance, and biomass in shallow water is still largely unavailable. This study aimed to describe the structure and dynamics of fish assemblages on three beaches in the Mamanguape River estuary, and to test the hypothesis that distinct fish assemblages occur along a morphodynamic continuum as the result of changes in environmental variables, particularly the effects of wave action.

Material and Methods

Study site

The study was conducted in the Mamanguape River estuary (6º43'02"S 35º67'46"W), which is the second largest estuary in the state of Paraíba (northeastern Brazil). The estuary is located in an environmental protection area ("EPA") (CERHPB, 2004), whose goal is to protect coastal ecosystems as well as the marine manatee *Trichechus manatus* Linnaeus, 1758 (Mourão & Nordi, 2003). The climate is tropical and humid, as its annual total rainfall varies from 2000 mm to less than 30 mm. Temperatures are high, as the annual average temperature is between 24ºC and 26ºC (Macedo *et al*., 2010). The beaches display a mesotidal, semi-diurnal tidal regime. The mouth of the river forms a 6-km-wide bay that is nearly closed off by a coastal reef line, which results in calm and quiet waters (Paludo & Klonowski, 1999). In this area, well-preserved mangroves are present that are principally represented by *Rhizophora mangle*, *Avicennia schaueriana*, *Avicennia germinans*, *Laguncularia racemosa*, and *Conocarpus erectus*, which grow around the main channel and its intertidal creeks to encompass approximately 6,000 hectares, in addition to the remnants of the Atlantic rainforest (Rocha *et al*., 2008).

Sampling

Samples were collected between October 2010 and September 2011, on monthly daytime excursions during spring tides. Sampling was performed at three sites defined according to their locations relative to the mouth of the river (Fig. 1): Curva do Pontal Beach (CPO) (6º46'27"S 34º55'20"W), which is situated in a protected estuarine region, and presents predominantly muddy sediment, calm waters and seagrass meadows; Pontal Beach (PON) (6º46'22"S 34º55'07"W), situated beyond the mouth of Mamanguape River, with sandy sediment and a barrier reef parallel to the shoreline which absorbs most of the wave energy; and Campina Beach (CAM) (6º48'43"S 34º54'49"W), which presents sandy sediment, gravels and high wave energy.

The fish were sampled using a beach seine net (10 m x 1.5 m, with an 8-mm mesh). The seine hauls were 30 m long, parallel to and close to the shore, and were taken out to a depth of approximately 1.5 m. This procedure was replicated five times at each site, separated 5 m apart to minimize the influence on the following haul. The fish collected were fixed in 10% formalin and later identified (Figueiredo & Menezes, 1978, 1980, 2000; Menezes & Figueiredo, 1980, 1985; Araujo *et al*., 2004), counted, measured (total length in mm), and weighed (g).

For each sample, environmental factors such as water temperature, salinity and transparency were also measured five times at each site, using a mercury thermometer, an optical refractometer and a Secchi disc, respectively. Samples from the sediment were collected in at each beach in five replicates. Granulometric analysis was performed according to Embrapa (1997), with the method using a combination of sieving and sedimentation steps and is designed to be used in conjunction with analysis of particulate organic matter (POM). Wave height and wave period were measured by visually estimating the height of the breaker waves during one minute for three times and the time interval between five successive breaker waves was recorded.

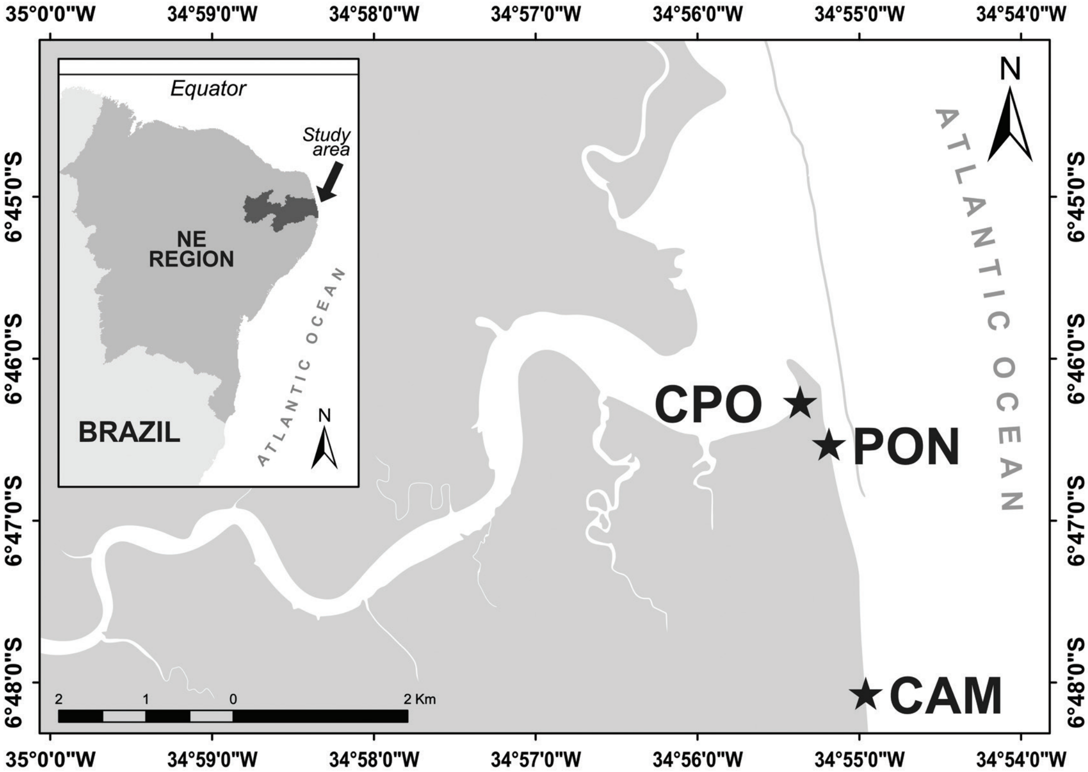

Fig. 1. Map of Mamanguape River estuary with locations of the sampling sites: CPO, Curva do Pontal Beach; PON, Pontal Beach; and CAM, Campina Beach.

Data analysis

The morphological classification of beaches was performed according to the RTR (Relative Tide Range), which takes into account the average variation of tides and the wave height, whose reference values are: $3<RTR<7$: group III (reflective state); $7<RTR<15$: group II (intermediate state); $RTR>15$ (dissipative state) (Masselink 1993; Calliari *et al.*, 2003).

The environmental variables and the fish abundance (weight and number) were transformed ($\log_{10}x+1$) to meet the assumptions of normality and homoscedasticity prior to comparison using one-way analysis of variance (ANOVA). Analyses were used for spatial comparison between abundance and environmental variables. A *post hoc* comparison of means was performed using the Tukey HSD test (Zar, 1982).

The data matrix to be analysed via multivariate techniques was created from the numerical abundance data for the species, using the Bray-Curtis similarity coefficient as a measure. An ANOSIM was used to test for differences in fish assemblage structure between beaches. When the ANOSIM test comparisons detected a significant difference, SIMPER was used to identify the species that were related to each beach type. These analyses were undertaken using PRIMER 6.0® statistical software.

Influences of environmental variables on fish assemblages were analysed using Canonical Correspondence Analysis (CCA), and the results were tested with the Monte Carlo test with 499 permutations. Direct analysis of the gradients through CCA clarified the role that environmental factors play in the structuring of fish assemblage by comparing species composition between sampling sites. A forward selection procedure was performed to identify variables that accounted for the greatest variation. The significance of these variables, defined as $p < 0.05$, was tested in Monte Carlo simulations. The Monte Carlo permutation test, at $\alpha = 0.05$, was also used to test the statistical significance of the relationship between species and environmental variables. The software used to perform the analyses was CANOCO ® for Windows.

Results

Environmental factors

The RTR varied between 4.40 and 21.11, and according to the morphodynamic classification, where Pontal Beach (PON) fell within the Intermediate beach (RTR = 8.73), while Campina Beach (CAM) was characterized within the Reflective beach (RTR = 4.40). Although being classified as a Dissipative beach (RTR > 15), Curva do Pontal Beach (CPO) was dominated by the tide that transition to a tidal flat, and was thus classified as estuarine.

Table 1. Results from ANOVA for comparisons of abiotic (temperature, salinity and transparency) and biotic (CPUE, Species number and Biomass) factors between beaches and hydrological regime in the Mamanguape River estuary, Brazil. **, $p < 0.01$; ns, not significant.

	F	Tukey
Temperature	ns	-
Salinity	6.88**	Reflective > Dissipative
Transparency	14.27**	Dissipative > Reflective
Abundance (CPUE)	43.745**	Dissipative > Intermediate, Reflective
Species number	39.705**	Dissipative > Intermediate, Reflective
Biomass	36.801**	Dissipative > Intermediate, Reflective

Spatially, no significant differences were found for temperature among the beaches. Highest salinity levels were recorded at Reflective Beach (41.3±0.3) and lowest at Dissipative Beach (11.3±0.9), the highest transparency values were found at Dissipative Beach (99.0±10.6) and lowest at Reflective Beach (10.0±0.6).The results were significantly different (Table 1).

Structure and composition

In total, 3,732 individuals belonging to 71 species (27 families) were collected during 174 beach seine hauls at beaches in the Mamanguape River estuary during the study period (Table 2). The family Carangidae had the largest number of species (7), followed by Sciaenidae (6) and Engraulidae, Gerreidae, Gobiidae, and Tetraodontidae (each with 5). The families with the highest number of individuals were Clupeidae, Atherinopsidae, Engraulidae, and Mugilidae, which collectively represented 79% of the total number of fish. The families Tetraodontidae, Clupeidae, Atherinopsidae, and Engraulidae, in decreasing order, contributed the most to the weight frequency and accounted for 73% of the total weight of the fish. Bahia sprat herring *Rhinosardinia bahiensis* (Steindachner, 1879) contributed the most to numerical abundance, as it accounted for 32% of the total, followed by the Brazilian silverside, *Atherinella brasiliensis* (Quoy & Gaimard, 1825), which represented 16% of the total abundance. The highest biomass contribution was from the puffer fish *Sphoeroides testudineus* (Linnaeus, 1758) which contributed 29% of the total biomass. Among the species, 18 occurred only once in the samples and 7 accounted for less than 0.01% of the biomass.

The families with the highest number of individuals in the dissipative beach were Clupeidae, Atherinopsidae, Engraulidae, and Mugilidae (81% of total number of individuals). In the intermediary beach, Engraulidae, Clupeidae, Haemulidae, Carangidae, and Sciaenidae were the abundant families (75%), whereas in the reflective beach, Engraulidae, Clupeidae, Haemulidae, Carangidae, and Sciaenidae were the most abundant families (96%).

The species that accounted for the majority of the total number of individuals in each beach were: *R. bahiensis*, *A. brasiliensis*, *Lycengraulis grossidens* (Agassiz, 1829) and *Mugil liza* Valenciennes, 1836 in dissipative beach, comprising 74% of the total number of individuals; *L. grossidens*, *Lile piquitinga* (Schreiner & Miranda Ribeiro, 1903), *Anchoa januaria* (Steindachner, 1879), *Polydactilus virginicus* (Linnaeus, 1758) and *Anchoviella lepidentostole* (Fowler, 1911) in the intermediate beach (51%); and *M. liza*, *L. grossidens*, *Mugil gaimardianus* Desmarest, 1831 and *Trachinotus carolinus* (Linnaeus, 1766) in the reflective beach (80%).

The analysis of the fish assemblages at the three beaches showed that there was a higher abundance, biomass and richness in the dissipative beach than at reflective and intermediary beaches, which demonstrates a significant increase at the site with the lowest exposure to wave activity (Fig. 3). This spatial difference was significant as determined by ANOSIM (Global R = 0.431; P> 0.1), with the dissipative beach being different from intermediary (Global R = 0.495;

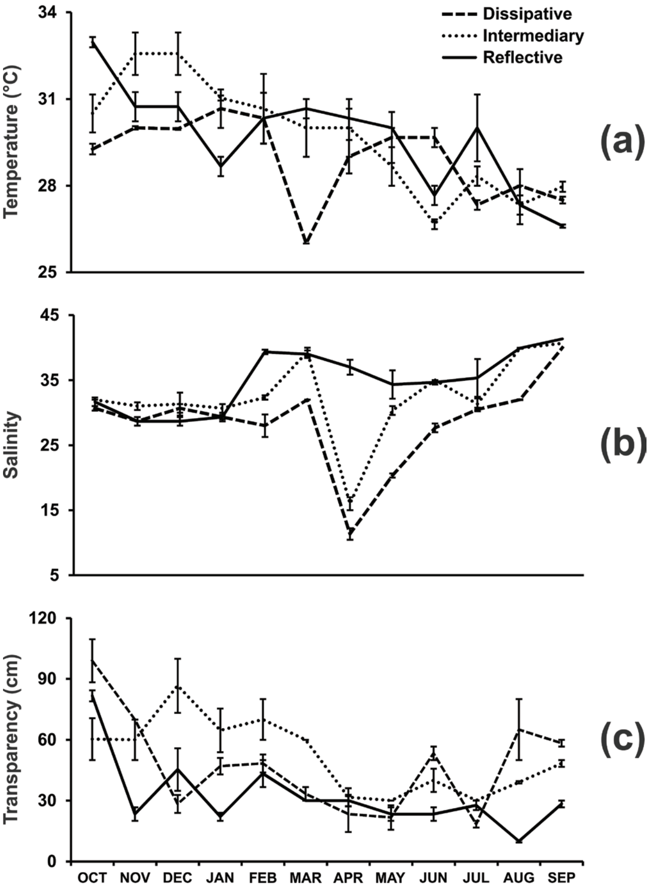

Fig. 2. Mean monthly variations of the environmental variables (±SE) for the study period.

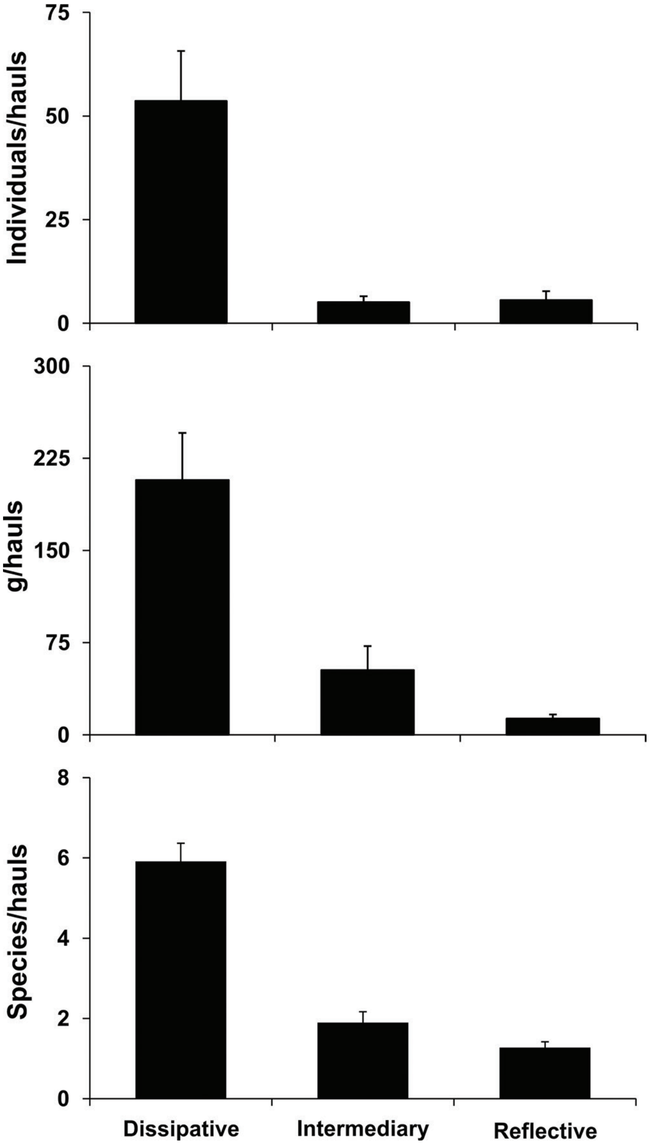

Fig. 3. Variation in the mean number of individuals (CPUE average ±SE), biomass (±SE) and number of species (±SE) at Mamanguape River estuary in Brazil.

P > 0.1) and reflective (Global R = 0.747; P > 0.1) beaches. SIMPER showed higher contributions from *L. grossidens*, *R. bahiensis*, *A. brasiliensis*, *S. testudineus*, and *Hyporhamphus unifasciatus* (Ranzani, 1841) for dissipative beach, whereas *T. carolinus*, *Trachinotus goodei* Jordan and Evermann, 1896, *M. liza* and *P. virginicus* showed higher contributions for intermediary and reflective beaches.

Influence of environmental factors

The first two axes from canonical correspondence analysis accounted for 63.1% of the cumulative percentage of variance for the environmental-species relationship (Fig. 4), with the Monte Carlo analysis revealing that RTR and characteristics of sediment (percentage of sand, silt, and clay) contributed most to species distribution. Samples representing the beaches were separated along the first axis. Axis 1 was positively correlated with RTR and silt clay, and negatively correlated with sand. Axis 2 was negatively correlated with salinity (Table 3).

The species *Atherinella blackburni* (Schultz, 1949), *T. carolinus*, *Mugil hospes* Jordan & Culver, 1895, *M. liza*, *T. goodei*, *Menticirrhus littoralis* (Holbrook, 1847), and *L. grossidens* were associated with sandy bottoms and higher salinity, conditions of the reflective beaches. A considerable amount of species (such as *Achirus lineatus*, *Citharichthys spilopterus*, *Citharichthys macrops* Dresel, 1885, *Gobionellus stomatus* Starks, 1913, *R. bahiensis* and others) was influenced by high values of RTR, silt and clay, suggesting a preference for dissipative beaches (Figure 4).

Discussion

Spatial differences in the structure for fish assemblages was demonstrated among the three tropical beaches that are strongly influenced by wave action, which is thought by many authors to be synonymous with exposure. This heterogeneous spatial distribution pattern of fish species showed a higher abundance, biomass and richness for the estuarine beach compared with the reflective beach with different species being characteristics of each beaches. These observations corroborate the hypothesis that the degree of exposure is a primary factor shaping local assemblages of fishes. This pattern has been demonstrated in other studies in tropical and subtropical regions (Romer, 1990; Clark, 1997; Jovanovic *et al*., 2007, Vasconcellos *et al*., 2007).

Estuarine beaches, which are also called “low energy” beaches, differ from the most exposed beaches in having additional features such as a narrow and abrupt sandy upper beach portion, a marked break in profile and a broad coastal plain with a smooth gradient (Rosa & Borzone, 2008). In estuarine beaches, the high fish abundance observed results from the aggregation of Clupeiforms species (such as *R. bahiensis*, *A. clupeioides* (Swainson, 1839), and *L. grossidens* in this study). Therefore, these beaches have been considered to be recruitment areas during the life cycles of these species (Oliveira-Silva *et al*., 2008; Hackradt *et al*., 2009). Moreover, the aggregation serves as a temporary refuge in calmer habitats close to the coast because high-energy sites do not permit such behaviour, mainly because of the high dynamic of the water column, which potentially results in high energy consumption (Felix *et al*., 2007). The use of calmer sites, such as those inside of bays and estuaries (Blaber & Blaber, 1980; Pessanha & Araújo, 2003) and even sheltered sandy beaches (Barreiros *et al*., 2004), plays an important recruitment role for pelagic species.

Table 2. Numerical abundance, biomass, frequency of occurrence, spatial distribution and maximum and minimum length of fish species captured on three beaches in the Mamanguape River estuary of Brazil. The species are ordered in accordance with Nelson (2006).

			Total abundance		Total biomass			Spatial distribution			Length (mm)	
Family	Species	Code	N	%	W(g)	%	%OF	CPO	PON	CAM	L_{min}	L_{max}
Engraulidae	*Anchoa januaria* (Steindachner, 1879)	ANJA	30	0.8	24.47	0.15	4.02	X	X		48	62
	Anchovia clupeoides (Swainson, 1839)	ANCL	69	1.85	405.77	2.56	5.17	X	X		50	134
	Anchoviella lepidentostole (Fowler, 1911)	ANLE	58	1.55	105.59	0.67	4.02	X	X		38	122
	Cetengraulis edentulus (Cuvier, 1829)	CEED	2	0.05	17.55	0.11	1.15	X	X		63	120
	Lycengraulis grossidens (Agassiz, 1829)	LYGR	428	11.47	624.43	3.95	22.99	X	X	X	31	110
Clupeidae	*Harengula clupeola* (Cuvier, 1829)	HACL	17	0.46	56.28	0.36	2.3	X			60	96
	Lile piquitinga (Schreiner & Miranda Ribeiro, 1903)	LIPI	33	0.88	224.76	1.42	3.45	X	X		74	114
	Opisthonema oglinum (Lesueur, 1818)	OPOG	14	0.38	301.88	1.91	0.57		X		99	154
	Rhinosardinia bahiensis (Steindachner, 1879)	RHBA	1204	32.26	2781.05	17.57	9.77	X	X		24	106
Ariidae	*Sciades herzbergii* (Bloch, 1794)	SCHE	2	0.05	7.43	0.05	0.57		X		65	73
Batrachoididae	*Thalassophryne nattereri* Steindachner, 1876	THNA	1	0.03	7.59	0.05	0.57	X			79	-
Mugilidae	*Mugil curema* Valenciennes, 1836	MUCU	17	0.46	93.8	0.59	2.87	X	X		46	110
	Mugil hospes Jordan & Culver, 1895	MUHO	101	2.71	146.96	0.93	5.75	X	X	X	27	95
	Mugil incilis Hancock, 1830	MUIN	1	0.03	4.53	0.03	0.57	X			82	-
	Mugil liza Valenciennes, 1836	MULI	371	9.94	108.55	0.69	15.52	X	X	X	17	39
Atherinopsidae	*Atherinella blackburni* (Schultz, 1949)	ATBL	7	0.19	38.14	0.24	3.45			X	90	104
	Atherinella brasiliensis (Quoy & Gaimard, 1825)	ATBR	601	16.1	1764.6	11.15	22.99	X	X		17	127
Hemiramphidae	*Hyporhamphus unifasciatus* (Ranzani, 1841)	HYUN	83	2.22	631.61	3.99	9.77	X	X		81	202
Belonidae	*Strongylura timucu* (Walbaum, 1792)	STTI	1	0.03	0.06	<0.01	0.57	X			43	-
Syngnathidae	*Syngnathus folletti* Herald, 1942	SYFO	1	0.03	0.11	<0.01	0.57		X		110	-
Dactylopteridae	*Dactylopterus volitans* (Linnaeus, 1758)	DAVO	2	0.05	8.38	0.05	1.15	X			60	-
Centropomidae	*Centropomus parallelus* Poey, 1860	CEPA	1	0.03	20.76	0.13	0.57	X			52	-
	Centropomus undecimalis (Bloch, 1792)	CEUN	1	0.03	83.64	0.53	0.57			X	220	-
Serranidae	*Diplectrum radiale* (Quoy & Gaimard, 1824)	DIRA	1	0.03	1.03	0.01	0.57		X		46	-
Carangidae	*Caranx latus* Agassiz, 1831	CALA	46	1.23	186.86	1.18	9.2	X	X	X	26	95
	Chloroscombrus chrysurus (Linnaeus, 1766)	CLCH	1	0.03	0.23	<0.01	0.57		X		28	-
	Oligoplites saurus (Bloch & Schneider, 1801)	OLSA	15	0.4	30.96	0.2	6.32	X	X		31	102
	Selene setapinnis (Mitchill, 1815)	SESE	1	0.03	0.29	<0.01	0.57		X		25	-
	Trachinotus carolinus (Linnaeus, 1766)	TRCA	35	0.94	87.52	0.55	9.2		X	X	15	87
	Trachinotus falcatus (Linnaeus, 1758)	TRFA	6	0.16	17.76	0.11	2.3	X	X	X	42	86
	Trachinotus goodei Jordan & Evermann, 1896	TRGO	31	0.83	265.56	1.68	9.77		X	X	18	153
Lutjanidae	*Lutjanus synagris* (Linnaeus, 1758)	LUSY	17	0.46	241.32	1.52	4.6	X			27	157
Gerreidae	*Diapterus rhombeus* (Cuvier, 1829)	DIRH	4	0.11	35.71	0.23	1.72	X			43	115
	Eucinostomus argenteus Girard & Baird, 1855	EUAR	62	1.66	137.4	0.87	6.9	X			10	105
	Eucinostomus gula (Quoy & Gaimard, 1824)	EUGU	3	0.08	26.85	0.17	1.72	X			65	112

Table 2. Cont. Numerical abundance, biomass, frequency of occurrence, spatial distribution and maximum and minimum length of fish species captured on three beaches in the Mamanguape River estuary of Brazil. The species are ordered in accordance with Nelson (2006).

	Eucinostomus melanopterus (Bleeker, 1863)	EUME	35	0.94	13.75	0.09	5.17	X			15	68
	Eugerres brasilianus (Cuvier, 1830)	EUBR	13	0.35	43.18	0.27	5.17	X			26	99
Haemulidae	*Conodon nobilis* (Linnaeus, 1758)	CONO	20	0.54	123.43	0.78	1.15		X	X	25	100
	Pomadasys corvinaeformis (Steindachner, 1868)	POCO	12	0.32	365.03	2.31	2.3	X	X		59	165
	Pomadasys crocro (Cuvier, 1830)	POCR	5	0.13	3.23	0.02	0.57		X		30	46
	Pomadasys ramosus (Poey, 1860)	PORA	4	0.11	67.67	0.43	1.15	X	X		72	77
Polynemidae	*Polydactylus virginicus* (Linnaeus, 1758)	POVI	28	0.75	122.63	0.77	9.77		X	X		
Sciaenidae	*Bairdiella ronchus* (Cuvier, 1830)	BARO	1	0.03	15.38	0.1	0.57		X		110	-
	Menticirrhus americanus (Linnaeus, 1758)	MEAM	2	0.05	85.59	0.54	1.15		X	X	126	193
	Menticirrhus littoralis (Holbrook, 1847)	MELI	24	0.64	352.47	2.23	10.92	X	X	X	34	236
	Pogonias cromis (Linnaeus, 1766)	POCM	1	0.03	0.64	<0.01	0.57		X		36	-
	Stellifer brasiliensis (Schultz, 1945)	STBR	4	0.11	17.73	0.11	1.15		X		33	104
	Stellifer naso (Jordan, 1889)	STNA	1	0.03	5.14	0.03	0.57		X		75	-
Eleotridae	*Erotelis smaragdus* (Valenciennes, 1837)	ERSM	9	0.24	14.06	0.09	4.02	X	X		14	85
Gobiidae	*Bathygobius soporator* (Valenciennes, 1837)	BASO	22	0.59	192.5	1.22	9.2	X			88	124
	Ctenogobius boleosoma (Jordan & Gilbert, 1882)	CTBO	22	0.59	6.13	0.04	4.6	X			26	52
	Ctenogobius smaragdus (Valenciennes, 1837)	CTSM	11	0.29	17.27	0.11	4.6	X			24	92
	Ctenogobius stigmaticus (Poey, 1860)	CTST	7	0.19	0.69	<0.01	2.3	X			22	33
	Gobionellus stomatus Starks, 1913	GOST	12	0.32	8.73	0.06	4.6	X			30	93
Acanthuridae	*Acanthurus bahianus* Castelnau, 1855	ACBA	1	0.03	1	0.01	0.57	X			38	-
Scombridae	*Scomberomorus brasiliensis* Collette, Russo & Zavala-Camin, 1978	SCBR	1	0.03	2.96	0.02	0.57	X			83	-
Paralichthyidae	*Citharichthys arenaceus* Evermann & Marsh, 1900	CIAR	6	0.16	57.08	0.36	2.87	X	X		76	94
	Citharichthys macrops Dresel, 1885	CIMA	42	1.13	81.04	0.51	7.47	X			18	140
	Citharichthys spilopterus Günther, 1862	CISP	23	0.62	124.8	0.79	5.75	X			52	121
	Etropus crossotus Jordan & Gilbert, 1882	ETCR	1	0.03	0.1	<0.01	0.57		X		25	-
Achiridae	*Achirus lineatus* (Linnaeus, 1758)	ACLI	24	0.64	69.81	0.44	4.6	X			15	114
	Trinectes paulistanus (MirandaRibeiro, 1915)	TRPA	1	0.03	1.15	0.01	0.57	X			45	-
Cynoglossidae	*Symphurus plagusia* (Bloch & Schneider, 1801)	SYPL	7	0.19	126.89	0.8	2.87	X			113	171
	Symphurus tessellatus (Quoy & Gaimard, 1824)	SYTE	19	0.51	159.54	1.01	4.6	X			39	153
Tetraodontidae	*Lagocephalus laevigatus* (Linnaeus, 1766)	LALA	1	0.03	402.32	2.54	0.57		X		283	-
	Sphoeroides greeleyi Gilbert, 1900	SPGR	11	0.29	142.84	0.9	4.02	X			39	105
	Sphoeroides spengleri (Bloch, 1785)	SPSP	8	0.21	46.37	0.29	3.45	X			23	74
	Sphoeroides testudineus (Linnaeus, 1758)	SPTE	81	2.17	4658.1	29.43	18.97	X	X		12	236
	Sphoeroides tyleri Shipp, 1972	SPTY	1	0.03	1.24	0.01	0.57	X			38	-
Diodontidae	*Chilomycterus antillarum* Jordan & Rutter, 1897	CHAN	2	0.05	2.81	0.02	1.15	X	X		33	-

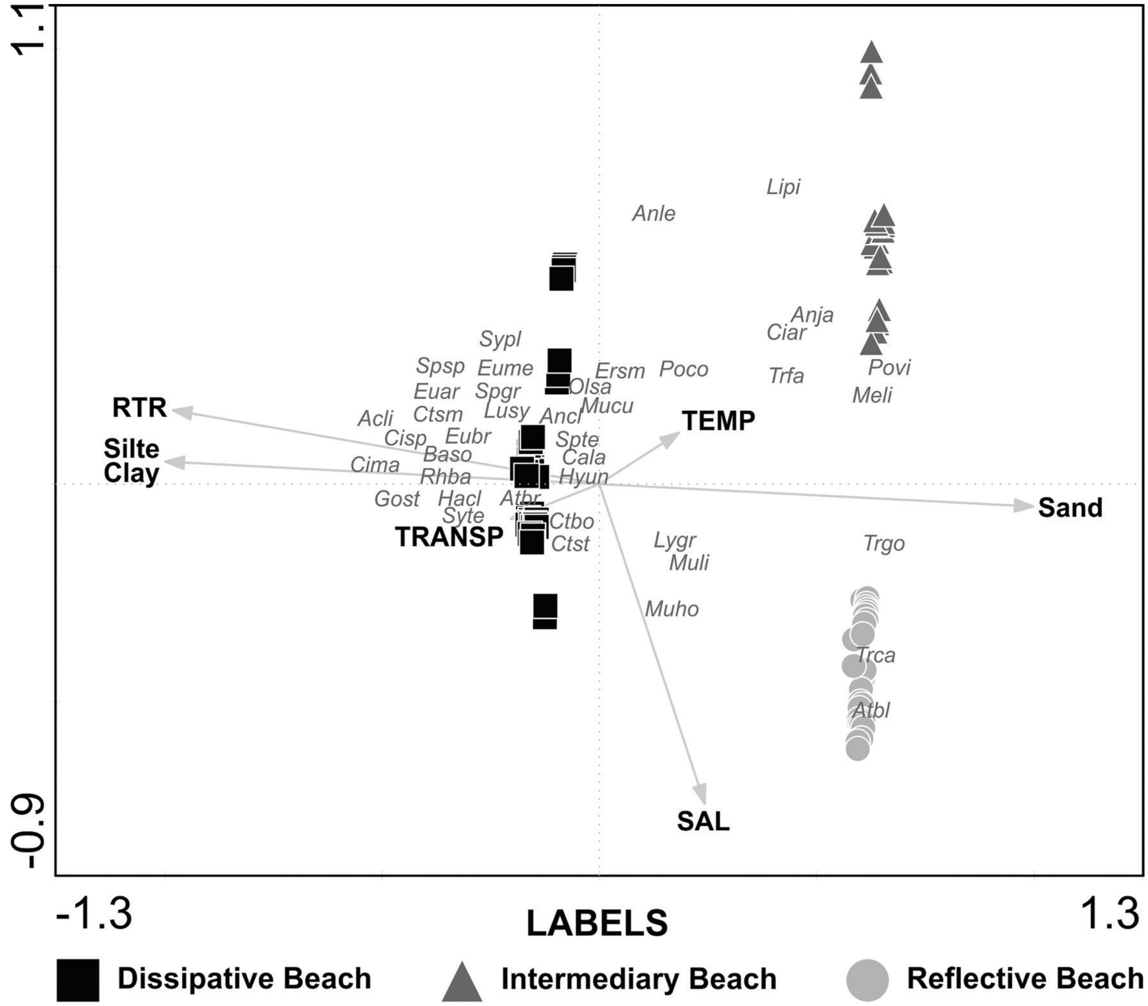

Fig. 4. Ordination diagram (tripolot) from Canonical Correspondence Analysis for the numerical abundance of fish species and environmental variables. (TEMP= Temperature; SAL= Salinity; TRANSP= Transparency and RTR= Relative Tide Range). (Acli = *Achirus lineatus*; Ancl = *Anchovia clupeoides*; Anja = *Anchoa januaria*; Anle = *Anchoviella lepidentostole*; Atbl = *Atherinella blackburni*; Atbr = *Atherinella brasiliensis*; Baso = *Bathygobius soporator*; Cala = *Caranx latus*; Ciar = *Citharichthys arenaceus*; Cima = *Citharichthys macrops*; Cisp = *Citharichthys spilopterus*; Ctbo = *Ctenogobius boleosoma*; Ctsm = *Ctenogobius smaragdus*; Ctst = *Ctenogobius stigmaticus*; Ersm = *Erotelis smaragdus*; Euar = *Eucinostomus argentus*; Eubr = *Eugerres brasilianus*; Eume = *Eucinostomus melanopterus*; Gost = *Gobionellus stomatus*; Hacl = *Harengula clupeola*; Hyun = *Hyporhamphus unifasciatus*; Lipi = *Lile piquitinga*; Lusy = *Lutjanus synagris*; Lygr = *Lycengraulis grossidens*; Meli = *Menticirrhus littoralis*; Mucu = *Mugil curema*; Muho = *Mugil hospes*; Muli = *Mugil liza*; Olsa = *Oligoplites saurus*; Poco = *Pomadasys corvinaeformis*; Povi = *Polydactylus virginicus*; Rhba = *Rhinosardinia bahiensis*; Spgr = *Sphoeroides greeleyi*; Spsp = *Sphoeroides spengleri*; Spte = *Sphoeroides testudineus*; Sypl = *Symphurus plagusia*; Syte = *Symphurus tesselatus*; Trca = *Trachinotus carolinus*; Trfa = *Trachinotus falcatus*; Trgo = *Trachinotus goodei*).

For juvenile and young-of-the-year fishes, beaches located within estuaries provide an ideal site for growth and protection. At these beaches, a constant supply of food has been observed because of the primary production and the absence of large predators (Inui *et al*., 2010). As species indicative of sheltered environments, *S. testudineus* (Felix *et al*., 2007), *M. liza* (Pessanha & Araújo, 2003; Vasconcellos *et al*., 2007) and *Bathygobius soporator* (Valenciennes, 1837) (Oliveira-Silva *et al*., 2008) are prominent. Furthermore, the small size of the individuals increases their agility in shallow coastal water and thus increases their success rate when catching suspended prey, as most of the juveniles are zooplanktivorous (Lasiak, 1986; Inoue *et al*., 2008). These characteristics indicate that estuarine beaches function more effectively than reflective beaches as nursery areas for a larger number of species.

Reflective beach has the lowest abundance and richness among the three studied beaches because of limiting factors such as increased wave energy and the high variability of abiotic factors. The degree of wave exposure is one of the characteristics that contributes most to determine fish assemblage structure, with typical of surf zones supporting high numbers of fish species, such as *Trachinotus* (*T. carolinus* and *T. goodei*) (Gomes *et al*., 2003; McLachlan & Brown, 2006), *Menticirrhus* [*M. americanus* (Linnaeus, 1758) and *M. littoralis*) (Layman, 2000; McLachlan & Brown, 2006) and *Polydactylus* (*P. virginicus*) (Gianinni & Paiva-Filho, 1995; McLachlan & Brown, 2006; Oliveira-Silva *et al*., 2008)]. These species can be considered to be residents of the surf zones of reflective beaches, as indicated by McLachlan & Brown (2006). Few species can adapt and colonize highly dynamic environments such as the surf zones of reflective beaches (Vasconcellos *et al*., 2007), although these beaches provide protection from predation and a wide availability of zooplankton for feeding juvenile and larval fish (Lasiak, 1986). Wootton (1992) explains that fish from high-energy zones developed during their evolutionary history appropriate body shapes for minimizing energy costs by effectively counteracting the effects of waves, *i.e.*, a more hydrodynamic form that minimizes the effects of wave energy.

The low number of individuals captured at the intermediate and reflective beaches indicates that these beaches act as nursery areas for a limited number of species. According to Beck *et al*. (2001), a characteristic that is considered primary for defining nursery areas is their great contribution to the production of individuals that recruit for adult populations. Nonetheless, some studies suggest that selective capture by the net, as well as the difficulty of seine hauling on high-exposure beaches, could influence the low abundance at reflective and intermediate beaches (Romer, 1990; Vasconcelos *et al*., 2007).

The beaches have functional ecological connections with adjacent ecosystems, such as estuaries and coastal lagoons, and may serve as passage routes and/or habitats, especially for juvenile individuals (Inui *et al*., 2010). On beaches adjacent to estuaries, the surf zone could provide water masses with low salinity that have been shown to be important in attracting juvenile fish, which are usually recruited within protected environments (Fisher & Pearcy, 1995). Therefore, the distribution of such species is determined according to a *continuum* or environmental gradient (herein represented by the gradual change in the degree of wave exposure along the estuary) where species turnover occurs along gradients of physical conditions, and where there are no well-defined barriers that isolate different communities (Ricklefs, 2003). The occurrence of certain species, such as *M. littoralis*, *P. virginicus*, and *T. goodei* in reflective and intermediate beaches, and *A. brasiliensis* and *L. grossidens* through all three beaches, demonstrates that there is connectivity between the beaches and the estuary, which may represent an open community pattern. Among other species that had a significant representation at the reflective beach in this study, *M. liza* and *M. hospes* are noteworthy because they had a high abundance of juveniles recruited at the estuarine beach, which suggests connectivity between the fish assemblage. This connectivity between beaches and estuarine environments has been described for subtropical environments (Monteiro-Neto *et al*., 2008) for species of Clupeiformes, and also in a study by Xavier *et al*. (2012) that observed connectivity between reef systems and mangroves within the same study area.

Results of this study indicate that two factors, namely the RTR and characteristics of sediment, play a major role determining spatial variations in fish abundance and community structure. Some other variables, *e.g.*, salinity and transparency, also play an important role, but are probably of secondary importance. Species-specific preferences for varying combinations of these variables result in variations in the structure and overall abundance of fish assemblages in different areas. Overall, the following trends were observed: the dissipative beaches were found to harbor the most diverse assemblage of fishes, while the reflective beach harbored the lowest densities of fishes.

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