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Moon and tide effects on fish capture in a tropical tidal flat

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The influence of the lunar phases and tidal range on the fish capture was analysed in a tidal flat in Barra do Paraguaçu (Baía de Todos os Santos). The sampling was realized in the flood tide and ebb tide of the spring (full moon) and neap (waning moon) tides, between June 2007 and May 2008. At all sampling occasions, two parallel drags were accomplished to the tidal flat, in the same direction of the current, in a 100 m long area marked on the beach beforehand, using a seine net of 15 m × 2.0 m with a mesh of 12 mm between adjacent knots. A total of 2312 fish specimens were captured (26.5 kg), belonging to 75 species from 45 families. The mean number of captured fish was significantly larger in full moon at ebb tides, while the mean weight in the captures was larger in ebb tides. There was significant difference in number of species, number of fish, richness and diversity between full and waning moons. The number of fish and biomass were significantly different between tides. Significant differences were found in community structure regarding trophic groups in relation to tide and moon, although the classic diversity indices did not capture this effect between tides. Furthermore, it was possible to identify preferences of occurrence related to the change of tide in dominant species.

Keywords: ichthyofauna, lunar phase, tidal effect, Baía de Todos os Santos, Brazil

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INTRODUCTION

In estuarine systems, environmental variations of short and long periods can limit the diversity of species (Nagelkerken *et al*., 2008). However, the maintenance of great numbers of individuals in these ecosystems is assured by the large amount of food sources and by the great structural complexity which promotes the occurrence of several ecological niches (Odum & Herald, 1972). Among the different estuarine habitats, tidal flats are areas that are exposed and submerged regularly by tides and that can be distributed from estuarine to marine areas. These flats are transitional systems between the terrestrial and the aquatic environments and, generally, they limit the narrow strips between salt marshes and/or mangroves and brackish waters (Reise, 1985).

Tidal flats are important for the growth of several fish species (Manderson *et al*., 2004) and characterized by large variations in environmental conditions and in the structure of fish assemblages (Godefroid *et al*., 2003). The species of fish that inhabit these places are generally small and most of them do not present migratory behaviour (Weinstein & Heck, 1979). In tropical tidal flats tides are usually important to distribute nutritious and minerals resources especially where primary productivity is reduced (Carter, 1988). The intertidal zone provides an important, but temporary, accessible foraging ground for coastal fish and other nektonic species (e.g. shrimps and gastropods) (e.g. Wolff *et al*., 2005). Thus, it is expected that spatial and temporal patterns of fish abundance in tidal flats are related to patterns of feeding, although avoidance of predation, reproduction, and appropriate environmental conditions may also explain changes in abundance (Gibson, 1992, 1996; Rountree & Able, 1993; Gibson *et al*., 1998).

The Paraguaçu River, the main tributary of the Baía de Todos os Santos (BTS) is one of the most important aquatic systems of the Bahia State. This system is of high value for wildlife conservation and provides the main source of protein and income (i.e. consumption and commercialization of fish and shellfish) for the local communities (Barros *et al*., 2008). In spite of the ecological and economic importance of the Paraguaçu River estuary, there is no published work addressing communities of fish, only work addressing expansion of geographical distribution (Santos *et al*., 2008).

In Brazil, a few studies considered the influence of the moon and tide for estuarine fish, most for sub-tropical areas (Corrêa *et al*., 1988; Godefroid *et al*., 1998, 2003; 2004). The variation of the level of water with the tide and the lunar phase, in tidal flats, are ecologically relevant, for instance air exposure can affect the maturation time and patterns of feeding (Nybakken & Bertness, 2004). These changes can modify the distribution and the density of fish species (Rozas & Minello, 1998). A review of the literature shows that, despite studies on seasonal variations of the ichthyofauna

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in estuaries (Rozas & Minello, 1998; Lin & Shao, 1999; Giarrizzo & Krumme, 2009), few studies evaluated the influence of time (Santos & Nash, 1995; Gray *et al.*, 1998), tide (Rozas, 1995; Catellanos & Rozas, 2001) and phase of the moon (Quinn & Kojis, 1981) on the structure of the ichthyofauna assemblages. Furthermore, information about temporal variations of intertidal fish from estuarine environments (Brenner & Krumme, 2007) are scarce, thus making predictions of general patterns of intertidal fish is difficult. This way, the present study evaluates the following null hypothesis that the structure and composition the ichthyofauna are the same in different lunar phases (waning and full) and tidal stages (ebb and flood).

MATERIALS AND METHODS

Study area

The studied tidal flat is located at Barra do Paraguaçu (12°50′S 38°47′W), in the western section of the Baía de Todos os Santos (BTS), in the estuarine portion of the Paraguaçu River (Figure 1). This river is the main contributor of freshwater for BTS. The sediments are a mixture of terrigenous material with biogenic material produced in or near the tidal flat. In this area, the bottom is predominantly sandy with deposition of coarse fractions, mainly biogenic gravel (shell and coral fragments) and plant debris. The deposition of fine sediment or organic matter is generally restricted to nearby areas of low energy. The tides are semi-diurnal with currents in the bay mainly bi-directional and stronger during the ebb tide in most of the bay (Lessa *et al.*, 2001). The circulation inside the BTS is mostly tidally driven and does not vary significantly throughout the year (Cirano & Lessa, 2007).

Sampling design

Fish assemblages of the tidal flat were sampled monthly at flood and ebb tide of the spring (full moon) and neap (waning moon) tides, between June 2007 and May 2008. At each sampling occasion two parallel drags were accomplished to the coast, in the same direction as the current, in 100 m long areas marked on the beach beforehand, using a seine net (15 m × 2 m, 12 mm between knots). After capture, all individuals were identified and the length (mm) and the biomass (weight of individual fish; g) were recorded.

Trophic categories

The feeding habits of each species were described using a trophic classification adapted from Bouchon-Navarro *et al.* (1992): herbivores, fish that consume algae and seagrass beds; planktivores, fish that consume plankton; omnivores, which eat invertebrates and algae; first-order carnivores (CI) that preferentially consume small benthic invertebrates; second-order carnivores (CII) that mostly eat invertebrates and fish; and third-order carnivores (CIII), whose diet consists of more than 80% of fish. One category, illiophagy-scavenger, was added to this classification (Zavala-Camin, 1996). The

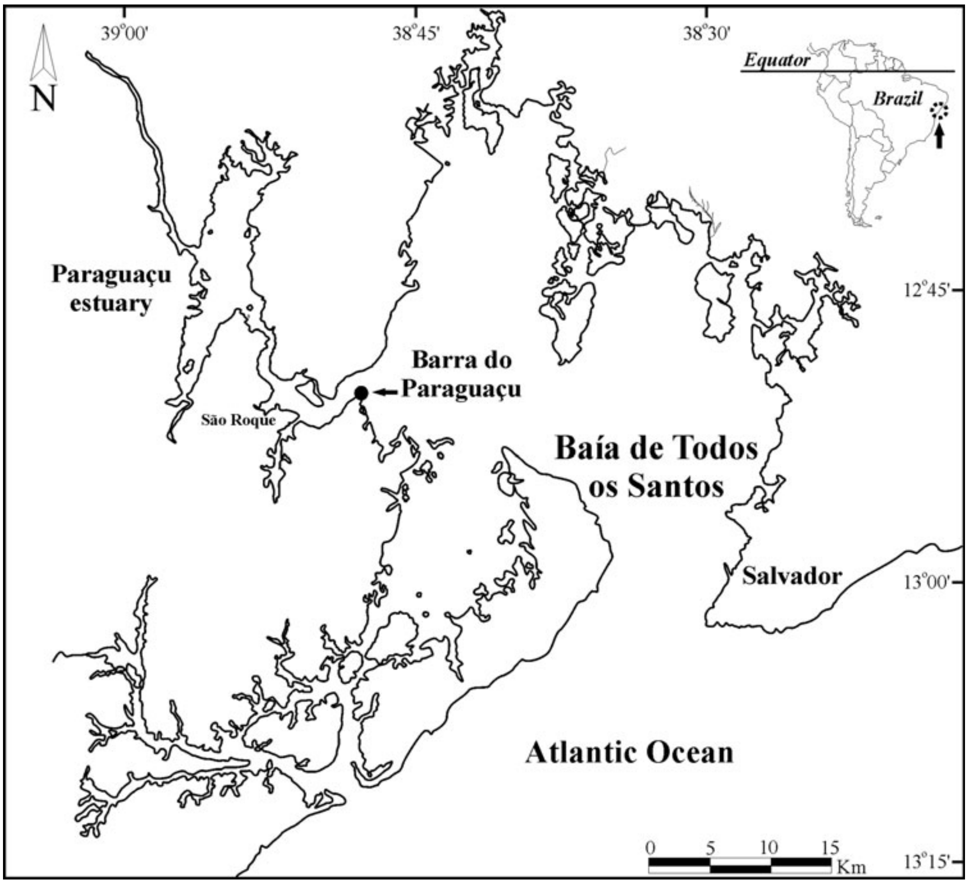

Fig. 1. Map of the channel of outlet of Paraguaçu River locating the sampling point in the tidal flat.

scientific nomenclature followed Nelson (1994), Eschmeyer (2006) and Froese & Pauly (2006).

Statistical analysis

Differences in fish assemblage composition and in abundance were tested by analysis of variance (ANOVA) using STATISTICA 8.0 software (Statsoft, Inc.) where tide and moon were fixed factors both with two levels. The monthly averages of the numbers of fish, number of species, weight of the capture and the indices of richness (Margalef), diversity (Shannon–Wiener) and evenness (Pielou) were also tested. The alpha value was corrected by the Bonferroni method (0.008) to avoid the Type I error. Before the ANOVA, data were fourth-root transformed to down-weight the influence of dominant species and reduce the significant correlation between the variance and mean (Chang & Winnell, 1981). The independence of the means were evaluated by the correlation among the mean and the standard deviation, and the homogeneity of the variances and data normality were tested by the Bartlett and Shapiro–Wilk tests, respectively (Sokal & Rohlf, 1995).

A Bray–Curtis distance was computed where the most abundant species were considered attributes (Clarke & Warwick, 2001). These data were log $(x + 1)$ transformed, to avoid the high value units, and used to compare samples and identify groupings graphically using cluster analysis. A similarity matrix using the Bray–Curtis index was computed using PRIMER 5 following Clarke & Warwick (2001).

In the tidal flat, the associations of fish were identified through the ordering technique non-metric multidimensional scaling (nMDS). As abundances between the species differed by two orders of magnitude, so data were log $(x + 1)$ transformed. To evaluate the similarity between groups of samples corresponding tide and moon analysis of similarity (ANOSIM) were performed.

RESULTS

There were 2312 fish captured, weighing 26.53 kg, belonging to 75 species of 45 families (Table 1). The captures of the ebb tide of full moon (EF) were 948 individuals, weighing 8.30 kg, belonging to 49 species and 35 families, while in the flood tide of the full moon (FF) 551 individuals were collected, weighing 6.84 kg, belonging to 46 species of 30 families. In periods of the ebb tide of the waning moon (EW) 442 fish were captured, with weight of 5.88 kg corresponding to 44 species of 29 families, and, in the flood tide of the waning moon (FW), 375 fish, weighing 5.69 kg, belonging to 44 species of 27 families (Table 1).

The dominant species and their biomass in the EF were *Haemulon steindachneri* (Jordan & Gilbert, 1882), *Sphoeroides greeleyi* Gilbert, 1900, *Lutjanus synagris* Linnaeus, 1758 and *Eucinostomus argenteus* (Baird & Girard, 1855), corresponding to 52.6% of the total number of individuals and 67.8% of the total biomass in these conditions. In FF the species *Lile piquitinga* (Schneider & Miranda Ribeiro, 1903), *Sphoeroides greeleyi*, *Hemiramphus brasiliensis* Linnaeus, 1758 and *Sphoeroides testudineus* Linnaeus, 1758 prevailed, representing 47.1% of the total of fish captured (Figure 2). At EW, the dominant species and biomass were *Sphoeroides greeleyi*, *Sphoeroides testudineus*, *Eucinostomus argenteus* and *Atherinella brasiliensis* (Quoy & Gaimard, 1824), representing 45.1% of the total captured and 59.8% of the total biomass. In the FW, the dominant species were *Hemiramphus brasiliensis*, *Atherinella brasiliensis*, *Albula vulpes* Linnaeus, 1758 and *Lile piquitinga* accounting for 42.6% of the total captured (Figure 2).

In the present work several species (i.e. *L. synagris*, *H. steindachneri*, *E. argenteus*, *S. testudineus*, *S. spengleri* (Bloch, 1785), *S. greeleyi*, *Pellona harroweri* (Fowler, 1917), *L. piquitinga*, *A. vulpes*, *Caranx latus* (Agassiz, 1831) and *Etropus crossotus* Jordan & Gilbert, 1882) occurred frequently during the full moon, and some species were specifically captured in singular situations (e.g. 80% of *S. spengleri* in the full moon of April). *Narcine brasiliensis* (Olfers, 1831), *Anchoa januaria* (Steindachner, 1879), *Anchoa tricolor* (Agassiz, 1829), *C. bartholomaei* (Cuvier, 1833), *Chloroscombrus crhysurus* (Linnaeus, 1766), *Sparisoma radians* (Valenciennes, 1840), *Paraclinus arcanus* (Guimarães & Bacelar, 2002) and *Gobionellus oceanicus* (Pallas, 1770) were captured only at waning moons.

There was significant difference in number of species ($P = 0.001$), number of fish ($P = 0.001$), richness ($P = 0.004$) and diversity ($P = 0.001$) between full and waning moons. At each tide, the number of fish ($P = 0.007$) and biomass ($P = 0.006$) were also significantly different. The number of species, individuals, richness and diversity were significantly higher in the full than in the waning moon. The number of fish and biomass were significantly higher at ebb than at flood tide (Table 2). The trophic groups of the full moon were dominated by the carnivores. In the ebb tide, the first order carnivores, followed by omnivores, were more abundant. At flood tide, planktivores followed by omnivores were more abundant. In the waning moon, omnivores dominated overall. At ebb tide, omnivores followed by first order carnivores were the most abundant, and in the flood tide, planktivores followed by omnivores reached the higher values of capture (Figure 3). The ANOSIM test revealed significant differences on fish assemblages during the flood and ebb tides (R global = 0.58; $P = 0.002$) and the full and waning moon (R global = 0.55; $P = 0.006$), which can be observed in the nMDS plots (Figure 4A and Figure 4B, respectively).

The cluster analysis distinguished three main groups among the 10 most frequent species (Figure 5A). Group I was formed by the species *Sphoeroides greeleyi*, *S. testudineus* and *Eucinostomus argenteus* grouped in a level above 90% similarity. These species were the most abundant of the assemblage and occurred in all months of the year, occurring more frequently in the full moon, with *Sphoeroides greeleyi* and *E. argenteus* more often captured in ebb tides with full moon. Group II was formed by the species *Atherinella brasiliensis* and *Lile piquitinga*, with similarity of 77%, in the area throughout the sampling period. But, *L. piquitinga* used primarily the flood tide with emphasis on full moon, while *Atherinella brasiliensis* was numerically similar between the tides and moons. Group III consisted of *Albula vulpes*, *Hemiramphus brasiliensis* and *Rypticus randalli* Courtenay, 1967, with the first two together at a level of 100% similarity. These two species followed a similar variation in their abundances, with larger values in August, September, October, December and January with decline from February until May. However, *Hemiramphus brasiliensis* was numerically dominant in the flood tide. The species *Lutjanus synagris* and *Haemulon stendachneri* became isolated probably due to the high number of captures in the dry period (January to March) and had preferential dominance in the EF. The

Table 1. Species collected, trophic categories, number of individuals and biomass (weight of individual fish) (maximum, minimum and standard deviation) of the different moons and tides sampled in the tidal flat of Barra do Paraguaçu, during the period June 2007–May 2008.

Species	Trophic categories	EF	FF	EW	FW
Acanthostraciun quadricornis	Omnivore	5 (5–17 g ± 4.5)			4 (6–10 g ± 2.3)
Achirus lineatus	Carnivore I	2 (15–23 g)	2 (8–12 g)	1 (13 g)	2 (12–14 g)
Achirus sp.	Carnivore I			1 (19.5 g)	
Albula vulpes	Carnivore I	39 (3–57 g ± 8.7)	24 (4.5–59 g ± 7.7)	18 (3.5–25 g ± 7.2)	38 (4–60.5 ± 6.5)
Aluterus heudeloti	Omnivore		1 (23 g)		
Amphychthys criptocentrus	Carnivore II	1 (87 g)		1 (76 g)	
Anchovia clupeoides	Planktivore	1 (65 g)	3 (60–61–60 g)		7 (55–67 g ± 3.2)
Anchoa januaria	Planktivore			1 (39 g)	
Anchoa tricolor	Planktivore				9 (35–67 ± 4.2)
Archosargus romboidalis	Carnivore I	13 (25–78 g ± 5.6)	6 (17–34 g ± 2.9)		3 (12–16–56 g)
Atherinella brasilensis	Omnivore	36 (5–25 g ± 4.6)	27 (4–20 g ± 6.2)	36 (5–17 ± 5.9)	42 (4–16 ± 3.5)
Bathygobius soporator	Omnivore	3 (7–8–13 g)	3 (6–6.6–13 g)	2 (4–5.6 g)	9 (5–18 g ± 5.6)
Bothus ocelatus	Carnivore II		1 (43 g)		
Calamus calamus	Carnivore I	1 (19 g)			
Caranx latus	Carnivore II	9 (34–78 g ± 5.7)	2 (60–76 g)	3 (55–67–89 g)	
Carangoides bartholomaei	Carnivore III			1 (15 g)	1 (30 g)
Chloroscombrus crhysurus	Omnivore			1 (5 g)	1 (8.5 g)
Centropomus undecimalis	Carnivore II			3 (40–67–68 g)	
Centropomus parallelus	Carnivore II		2 (44–56 g)	1 (78 g)	
Centegraulis edentulus	Planktivore		1 (77g)		
Citharichthys spilopterus	Carnivore II	10 (4–20 g ± 3.9)	5 (10–24 g ± 4.5)	8 (12–23 g ± 3.4)	1 (13 g)
Chaetodipterus faber	Omnivore	3 (12–13.4–17 g)	7 (5–18.4 g ± 2.4)	3 (6–8.8–23 g)	3 (7.6–8–10.7 g)
Chilomycterus spinosus	Omnivore	22 (17–239 g ± 8.9)	26 (19–189 g ± 8.1)	16 (23–154 g ± 7.6)	12 (12–89 g ± 4.7)
Ctenogobius boleassoma	Omnivore	1 (2.3 g)	1 (2g)		2 (2–2.7 g)
Dactylopterus volitans	Carnivore I	30 (7–67 g ± 9.8)	23 (6–66 g ± 6.7)	11 (5–55 g ± 5.9)	10 (34–56 ± 4.9)
Diapterus auratus	Omnivore	2 (12–21 g)		1 (16 g)	1 (11.4 g)
Diapterus rhombeus	Omnivore	4 (30–67 g ± 5.4)		4 (18–23 g ± 3.6)	2 (17–20 g ± 2.9)
Diplectrum radiale	Carnivore II	9 (20–32 g ± 3.4)	5 (15–50 g ± 8.3)	14 (20–40 g ± 5.9)	4 (21–27g ± 1.3)
Eucinostomus gula	Carnivore I	32 (4–19 g ± 4.1)	20 (3–18 g ± 3.8)	15 (5–29 g ± 6.6)	14 (5–17 g ± 7.8)
Eucinostomus argenteus	Carnivore I	99 (15–40 ± 5.5)	36 (20–40 ± 2.3)	40 (5–39 ± 7.5)	30 (30–41 ± 2.3)
E. melanopterus	Omnivore	2 (15–17 g)	6 (6–18 g ± 2.7)	2 (10–14 g)	2 (3–8 g)
E. havana	Carnivore I		2 (12–17 g)		
Etropus crossotus	Carnivore I	24 (8–24 g ± 5.6)	9 (7.3–22 g ± 4.2)	13 (6.5–18 g ± 3.1)	4 (7.8–17 g ± 4.1)
Fistularia tabacaria	Carnivore III	2 (67–89 g)	7 (55–88 g ± 7.8)	12 (44–76 g ± 3.4)	5 (60–70 g ± 2.9)
Gerres cinereus	Carnivore I	1 (13 g)	2 (17–27 g)	1 (18 g)	1 (10 g)
Gobionellus oceanicus	Illiophagy-scavenger			3 (10–12–15 g)	
Haemulon steindachneri	Carnivore I	166 (32–62 g ± 4.5)	6 (35–65 g ± 4.6)	28 (45–55 g ± 2.5)	1 (43–60 g ± 3.9)
Hemiramphus brasiliensis	Carnivore II	7 (20–24 g ± 1.8)	52 (25–30 g ± 3.3)	1 (34 g)	45 (28–40 g ± 3.1)
Lile piquitinga	Planktivore	9 (30–35 g ± 2.1)	97 (30–40 g ± 2.8)	9 (32–41 g ± 2.7)	35 (30–36 g ± 2.2)
Lobotes surinamensis	Carnivore II		1 (8.9 g)		1 (10.9 g)
Lutjanus synagris	Carnivore II	116 (7–45 ± 9.8)	16 (10–39 ±3.4)	14 (10–40 ± 4.5)	12 (8–40 ± 3.9)
Mugil curema	Illiophagy-scavenger	4 (60–70 g ± 3.8)	2 (69–75 g)		6 (67–90 g ± 4.5)
Narcine brasiliensis	Carnivore II			2 (156–189 g)	
Ocyurus chrysurus	Carnivore II	2 (2.3–3.4 g)		1 (3.6 g)	
Ogcocephalus vespertilio	CarnivoresII	1 (124 g)			
Oligoplites saurus	Carnivore II		1 (69.6 g)		1 (78.1 g)
Opistognathus cuvieri	Planktivore	2 (39–44 g)		1 (50 g)	
Paraclinus arcanus	Carnivore I				1 (2.6 g)
Pellona harroweri	Planktivore	4 (66–76 g ± 4.3)	10 (65–78 g ± 4.8)		
Pomadasis corvaeniformes	Omnivore				1 (34 g)
Prionotus punctatus	Carnivore II	22 (6–55 g ± 6.9)	7 (67–69 ± 0.2)	15 (10–80 ± 8.7)	5 (12–59 ± 6.6)
Pseudopenaeus maculatus	Carnivore I		1 (14 g)		
Rhinobatos percellens	Carnivore II	1 (201 g)			
Rypticus randalli	Carnivore II	45 (8–45 g ± 10.9)	13 (12–39 g ± 4.3)	27 (12–40 g ± 7.6)	4 (10–20 g ± 4.3)
Scorpaena plumieri	Carnivore II	1 (44 g)		1 (50 g)	
Selene setapinnis	Carnivore II		2 (70–100.4g)		1 (89.7 g)
Selene vomer	Carnivore II		1 (56 g)		
Serranus flaviventris	Carnivore II	3 (10–12–15 g)		2 (5–8 g)	7 (34 g ± 2.3)
Sparisoma axillare	Herbivore	5 (18–23 g ± 2.4)			
Sparisoma radians	Herbivore				1 (5.6 g)
Sphoeroides testudineus	Omnivore	45 (10–40 ± 7.6)	46 (15–39 ± 3.4)	68 (15–35 ± 3.4)	13 (20–39 ± 4.1)
Sphoeroides greeleyi	Omnivore	119 (12–45 ± 6.7)	65 (10–55 g ± 8.3)	55 (12–44 ± 4.5)	29 (15–50 ± 6.5)
Sphoeroides spengleri	Omnivore	24 (8–67 g ± 6.5)	3 (12–15–16 g)		2 (13–20 g)

Continued

Table 1. Continued

Species	Trophic categories	EF	FF	EW	FW
Sphyraena barracuda	Carnivore III		2 (56–79 g)	1 (77.4 g)	
Stephanolepis setifer	Omnivore	2 (5–7 g)	1 (6.5 g)		
Strongylura marina	Carnivore III	1 (101 g)	6 (98–109 g ± 4.3)		1 (109 g)
Strongylura timuco	Carnivore III	1 (78 g)		2 (109–111 g)	1 (89 g)
Syacium micrurum	Carnivore II	1 (79 g)			
Syngnathus sp.	Planktivore	2 (5–7 g)			
Synodus foetens	Carnivore II	1 (98 g)	2 (70–78 g)		
Symphurus diomedianus	Carnivore I			1 (15.5 g)	
Symphurus plagusia	Carnivore I			1 (18 g)	
Thalassophryne punctata	Carnivore II	2 (60–98 g)	1 (64 g)	1 (68 g)	1 (50 g)
Trachinotus falcatus	Carnivore II		1 (45.9 g)		
Trinectes microphthalmus	Carnivore I	1 (5 g)			

EF, ebb tide full moon; FF, flood tide full moon; EW, ebb tide waning moon; FW, flood tide waning moon. Carnivores I, first order; II, second order; III, third order.

obvious groups over 65% of the cluster are also visible in the nMDS, indicating that the proximity between the species is almost equivalent to the original similarities (Figure 5B).

DISCUSSION

Moon and tide effects

In the studied tidal flat, there was a clear separation of fish assemblages in relation to the tide, as shown by Bonecker *et al.* (2009) in another tropical estuary in Brazil. The significant differences observed in abundance and composition between assemblages sampled in the different tide stages emphasizes the importance of the tidal cycles in the structure of the ichthyofauna. Tidal variation can change behaviour in fish, making them more active in slow currents and less active when current increases (Kleypas & Dean, 1983).

In the present study, the diversity showed no significant differences between tides, only a small increase in ebb tide. However, the abundance and biomass were greater on ebb than on flood, contrasting with the results of Godefroid

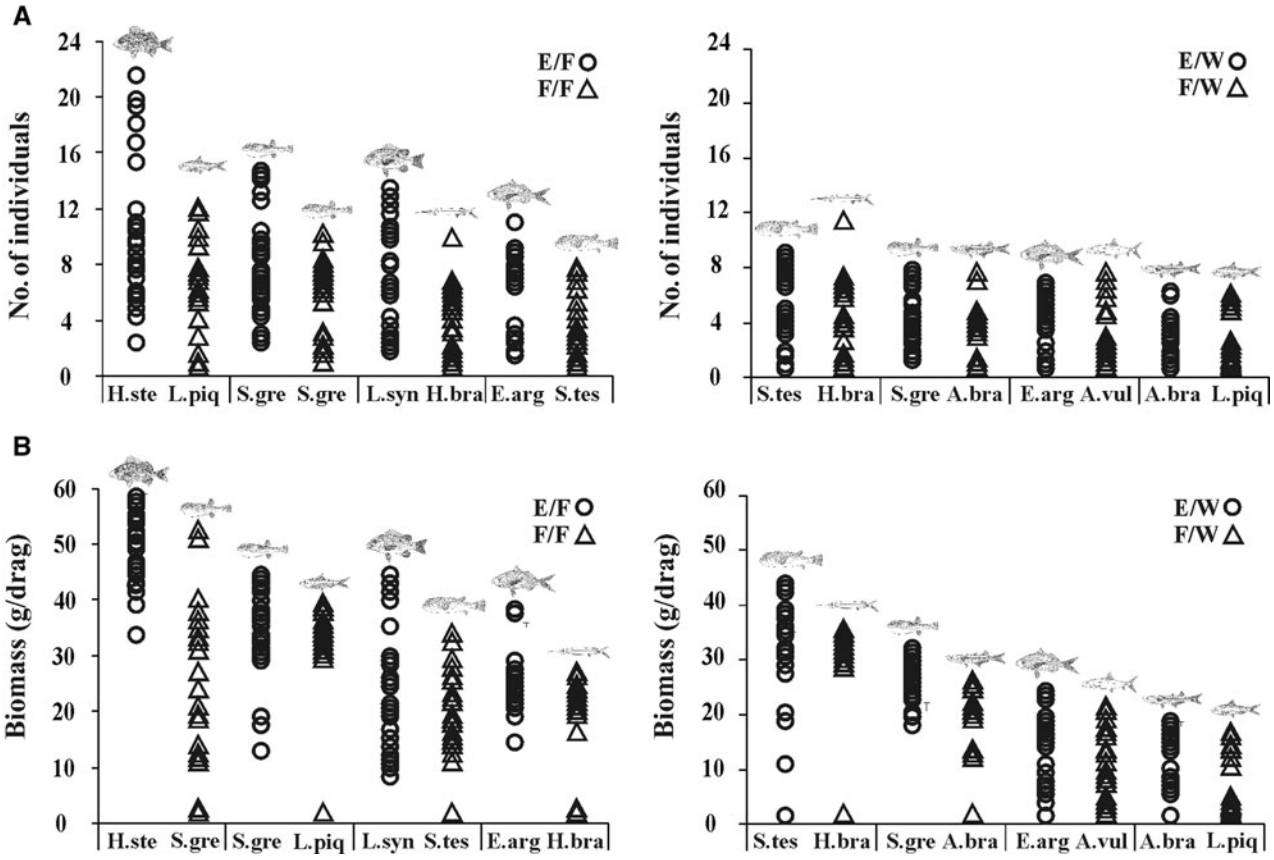

Fig. 2. Dominant species, number of individuals (A) and biomass (B) in the flood and ebb tide of the full moon and waning moon. E/F, ebb tide/full moon; F/F, flood tide/full moon; E/W, ebb tide/waning moon; F/W, flood tide/waning moon; H.ste, *Haemulon stendachneri*; L.piq, *Lile piquitinga*; S.gre, *Sphoeroides greeleyi*; L.syn, *Lutjanus synagris*; H.bra, *Hemiramphus brasiliensis*; E.arg, *Eucinostomus argenteus*; A.bra, *Atherinella brasiliensis*; A.vul, *Albula vulpes*.

Table 2. Result of two-way analysis of variance, analysing the effect of the moon and of the tide on the number of species, number of individuals, biomass, richness of Margalef, diversity of Shannon–Wiener, and evenness of Pielou, of the fish assemblages in the tidal flat of Barra do Paraguaçu, during the period June 2007–May 2008.

	Moon		Tide		Moon × tide	
	F	*P* value	F	*P* value	F	*P* value
No. of species	15.55	0.001 FM > WM	1.36	0.24 NS	0.01	0.89 NS
No. of fish	14.34	0.001 FM > WM	9.18	0.007 ET > FT	0.89	0.64 NS
Biomass	2.34	0.11 NS	10.77	0.006 ET > FT	3.45	0.09 NS
Richness	9.1	0.004 FM > WM	2.39	0.12 NS	1.91	0.28 NS
Diversity	13.65	0.001 FM > WM	1.55	0.21 NS	2.34	0.12 NS
Evenness	0.09	0.75 NS	0.15	0.69 NS	2.17	0.14 NS

FM, full moon; WM, waning moon; FT, flood tide; ET, ebb tide; NS, not significant.

et al. (2003), where diversity was greater in flood tide and abundance and weight did not show any significant differences. The species *Lile piquitinga*, *Hemiramphus brasiliensis, S. greeleyi, A. brasiliensis* and *A. vulpes* were more abundant in flood tides. These results suggest that these species follow the movements of the tides for food or protection. Godefroid *et al.* (2003) also observed this pattern in *Albula vulpes* in the south of Brazil.

The lunar phases may influence the specific composition of the ichthyofauna, either by its action on the tidal level (Quinn & Kojis, 1981), and/or caused by variation in light (Rooker & Dennis, 1991). Moreover, it was suggested that reproductive aggregations associated with lunar cycles can have significant implications in the abundance of fish (Johannes, 1978). Krumme *et al.* (2004) observed for mangrove creeks that the structure of fish assemblages was more homogeneous in the full moon of spring tide than at other situations corroborating Reis-Filho *et al.* (2010) in a semi-urban estuary on the northern coast of Bahia, Brazil. Differently, we found a more heterogeneous structure associated with the full moon. Perhaps this difference can be attributed to the distinction of topographical and hydrological features peculiar to these estuarine environments (mangrove creeks versus tidal flats). Furthermore, functional characteristics of the use of this estuarine habitat by fish species may explain this difference. According to Elliot *et al.* (2007), fish that occur in the river mouths (salinities below 35) are marine stragglers that spawn at sea and typically enter estuaries only in low numbers, most frequently in the lower reaches. On the other hand, mangrove creeks species may be estuarine residents capable of completing their entire life cycle within the estuary environment. Although the effect of the moon on the structure of fish communities is still little studied, works conducted in Baía de Paranaguá, south-east Brazil (Godefroid *et al.*, 1998, 2003) and Joanes River estuary, north-east Brazil (Reis-Filho *et al.*, 2010) found that the moon influenced the occurrence of species.

Rooker & Dennis (1991) and Krumme *et al.* (2004) found no significant difference between the average number of individuals collected during the full and waning moons and Reis-Filho *et al.* (2010) found no significant difference between number of individuals and species. Contrasting with the data found in the present study, where the number of fish captured were greater in the full than at the waning moon. However, Godefroid *et al.* (2003) showed significant differences between the number of species during the two moon stages, with more species in the full moon. This corresponds to what was observed in the present study where significant differences were found in the number of species captured in full and waning moons. Although Krumme *et al.* (2008) have suggested that the factor moon phase can only be sampled once every month, efficient temporal sampling is difficult within a short period (i.e. to avoid

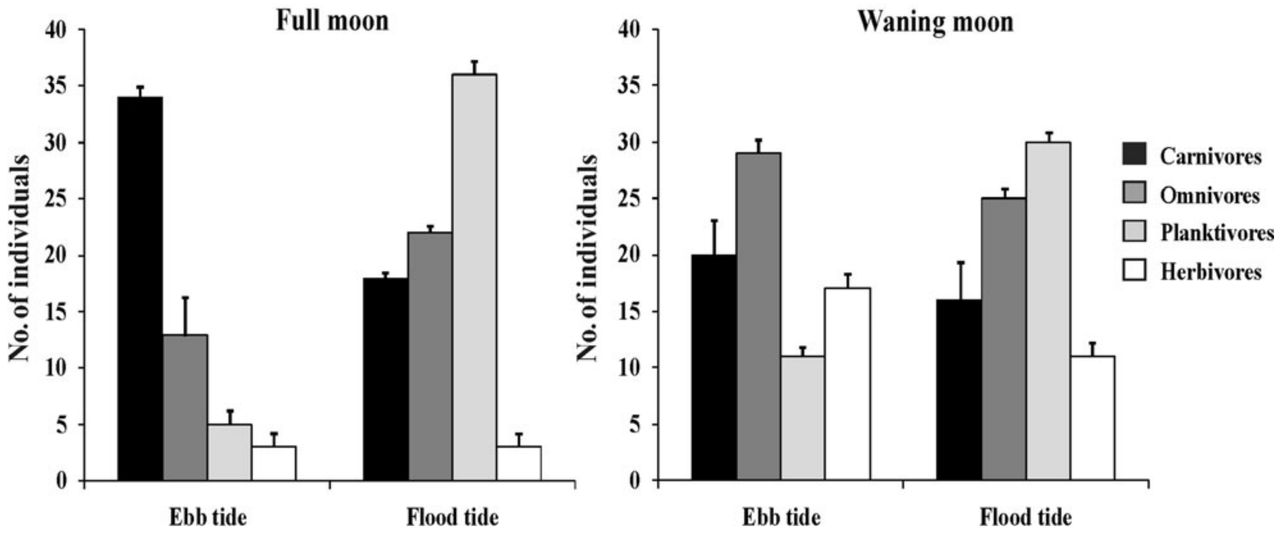

Fig. 3. Number of individuals (mean and standard deviation) for trophic groups in the ebb and flood tide of full and waning moon.

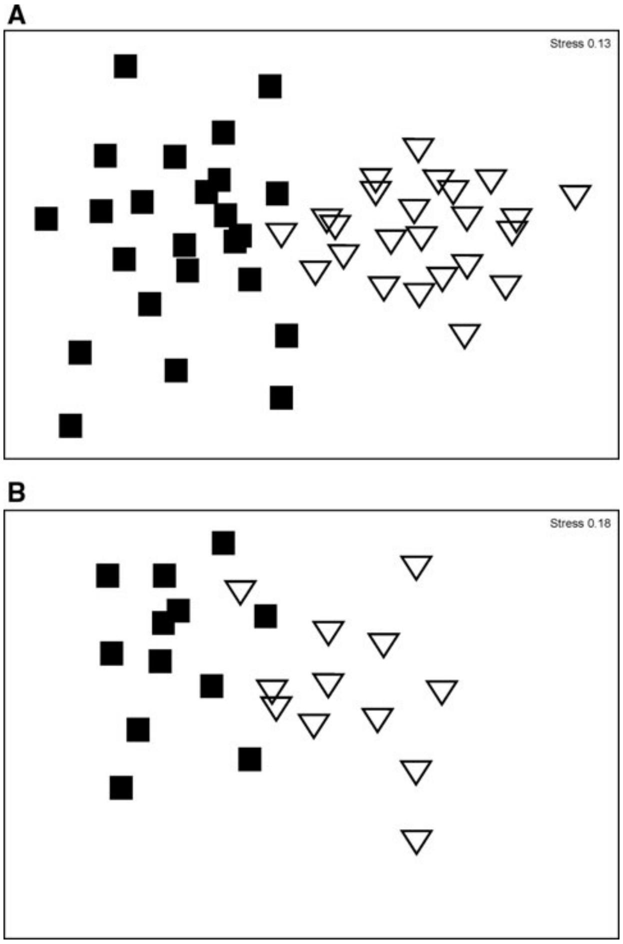

Fig. 4. Non-metric multidimensional scaling ordination showing differences between ebb and flood assemblages (A) and between full and waning assemblages (B). Each individual point represents a sample. Squares, flood tide and waning moon; triangles, ebb tide and full moon.

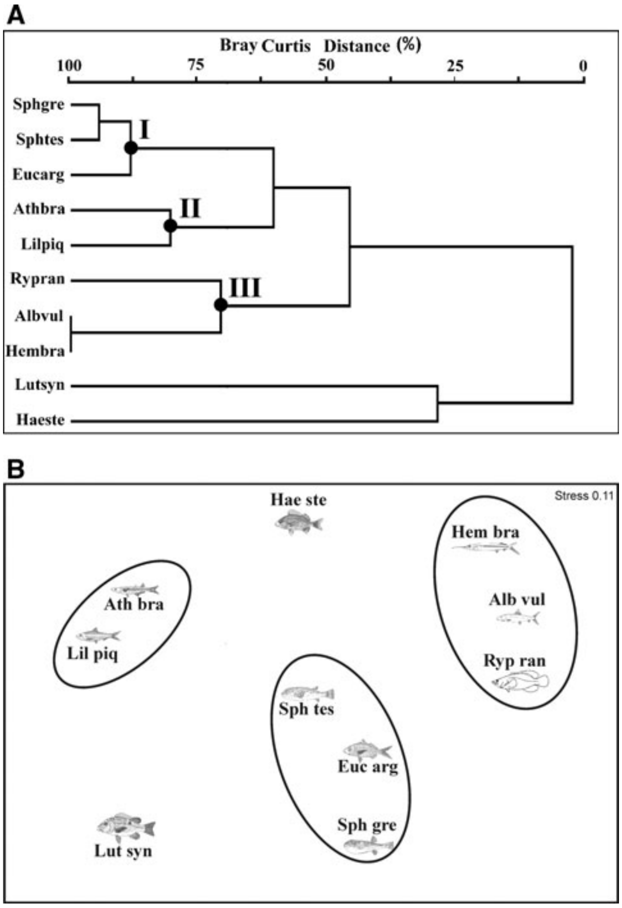

Fig. 5. Cluster (A) and non-metric multidimensional scaling (B), based on the abundance of the dominant species data, sampled in the tidal flat of Barra do Paraguaçu. The groups of the species delineated in the similarity level above 65% are surrounded in the ordering graph. Sph gre, *Sphoeroides greeleyi*; Sph tes, *Sphoeroides testudineus*; Euc arg, *Eucinostomus argenteus*; Hem bra, *Hemiramphus brasiliensis*; Hae ste, *Haemulon stendachneri*; Ryp ran, *Rypticus randalli*; Lut syn, *Lutjanus synagris*; Ath bra, *Atherinella brasiliensis*; Lil piq, *Lile piquitinga*; Alb vul, *Albula vulpes*.

confusion between month and moon phase). Thus, we advocate the need to evaluate the lunar cycle effect on the variation of water level and the consequent availability of habitat for fish.

The ichthyofauna of the tidal flat studied was characterized by dominance of juvenile of marine migrant forms with small size that use it as areas of growth and feeding, a fact confirmed in the same region by Oliveira-Silva *et al.* (2008) and in an estuary of southern Brazil by Barletta *et al.* (2008). An important characteristic of fish assemblages in intertidal mangrove zones is that there are several residents (Barletta *et al.* 2000) that do not move over large distances during their tidal migration (Horn *et al.* 1999). However, we observed a small number of resident species that regularly frequent the tidal flat, which does not mean that the same group of individuals is constantly present in the area throughout the period. Although there are differences between the tidal flats in relation to the pattern of species dominance, the dominant fish are a few taxonomic groups (Day *et al.*, 1989) as shown in the present study.

Functional aspects

In the present study more than 60% of species were carnivores. The dominance of species with generalized diet with a strong tendency to carnivory (especially invertebrates) was also documented in other tropical estuaries (Blaber, 2000; Paiva *et al.*, 2008). The carnivores and omnivores dominance found in the present study indicates that tide changes modified trophic categories, just altering the dominant species. Another observation associated with change of tide is the preference of planktivore species for the flood tide. During high tide, the physical and chemical conditions of the water in the tidal flat almost mirror those of the adjacent marine area, tending to be uniform during flood tide (Barletta *et al.*, 2003). Thus, this condition is favourable to these species (generally nektonic) for entering the tidal flat. Krumme *et al.* (2004), studying mangrove creeks, explained that many species emigrate with filled stomachs, feeding being considered the most important factor for fish immigration into the tidal flat. Thus, the territorial occupation may be linked to behavioural characteristics and availability of food (Koch, 1999) due to the implications of the lunar cycle and flood–ebb tide cycle on the movement of water (Krumme *et al.*, 2008).

Another aspect that the results of this study show is about traditional measures of species diversity, which few estimates are predictive of the structure and functioning of the community (Webb, 2000; Díaz & Cabido, 2001; Petchey, 2004; Ricotta *et al.*, 2005). Cianciaruso *et al.* (2009) provides an example where, due to the environmental change, the community that had species in the different genus was replaced by another with most species belonging to the same genus. Keeping the same number of species and the same abundance distribution, traditional analysis of diversity will not reveal any effect. In the present study, we faced the problem that the species composition and the trophic guild showed differences in the community structure, but there were no observed differences in the diversity indices. Therefore, we suggest that diversity measures that incorporate information about the functional characteristics (Diaz & Cabido, 2001; Petchey & Gaston, 2006) and even phylogeny (Webb, 2000; Ricotta *et al.*, 2005) should be better than traditional measures.

The strategy of different fish species to use the tidal flats, conditioned by the tolerance of some species to certain environmental conditions, follows short term variations. The interplay of the ebb–flood tide pulse together with the lunar phase affects the fish assemblage composition. Additionally, the trophic category in the tidal flat studied also changed. Thus, despite the different forces that imply movement of immigration and emigration of species in the tidal flat, the functional structure responds to environmental variation. Therefore, we argue that the functional diversity has been more sensitive to detect community responses to environmental changes compared to species diversity.

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REFERENCES

Barletta M., Saint-Paul U., Barletta-Bergan A., Ekau W. and Schories D. (2000) Spatial and temporal distribution of *Myrophis punctatus* (Ophichthidae) and associated fish fauna in a northern Brazilian intertidal mangrove forest. *Hydrobiologia* 426, 65–74.

Barletta M., Barletta-Bergan A., Saint-Paul U. and Hubold G. (2003) Seasonal changes in density, biomass, and diversity of estuarine fishes in tidal mangrove creeks of the lower Caeté Estuary (northern Brazilian coast, east Amazon). *Marine Ecology Progress Series* 256, 217–228.

Barletta M., Amaral C.S., Corrêa M.F.M., Guelbert F., Dantas D.V., Lorenzi L. and Saint-Paul U. (2008) Factors affecting seasonal variations in demersal fish assemblages at an ecoline in a tropical–subtropical estuary. *Journal of Fish Biology* 73, 1314–1336.

Barros F., Hatje V., Figueiredo M.B., Magalhães W.F., Dórea H.S. and Emídio E.S. (2008) The structure of the benthic macrofaunal assemblages and sediments characteristics of the Paraguaçu estuarine system, NE, Brazil. *Estuarine, Coastal and Shelf Science* 78, 758–762.

Blaber S.J.M. (2000) *Tropical estuarine fishes: ecology, exploitation and conservation.* Oxford: Blackwell Science, 372 pp.

Bonecker F.T., Castro M.S. and Bonecker A.C.T. (2009) Larval fish assemblage in a tropical estuary in relation to tidal cycles, day/night and seasonal variations. *Pan-American Journal of Aquatic Sciences* 4, 230–246.

Bouchon-Navaro Y., Bouchon C. and Louis M. (1992) L'ichtyofaune des herbiers de phanérogames marines de la baie de Frot-de-France (Martinique, Antiles Françaises). *Cybium* 16, 307–330.

Brenner M. and Krumme U. (2007) Tidal migration and patterns in feeding of the four-eyed fish *Anableps anableps* L. in a north Brazilian mangrove. *Journal of Fish Biology* 70, 406–427.

Carter R.W.G. (1988) *Coastal environments. An introduction to the physical, ecological and cultural systems of coastlines.* London: Academic Press, 617 pp.

Castellanos D.P. and Rozas L.P. (2001) Nekton use of submerged aquatic vegetation, marsh, and shallow unvegetated bottom in the Atchafayc River Delta, a Lousiana tidal freshwater ecosystem. *Estuaries* 24, 184–197.

Chang W.Y.B. and Winnell M.H. (1981) Comment on the fourth-root transformation. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 126–129.

Cianciaruso M.V., Silva I.A. and Batalha M.A. (2009) Diversidade filogenética e funcional: novas abordagens para Ecologia de Comunidades. *Biota Neotropica* 9, 93–103.

Cirano M. and Lessa G.C. (2007) Oceanographic characteristics of Baía de Todos os Santos, Brazil. *Revista Brasileira de Geofísica* 25, 363–387.

Clarke K.R. and Warwick R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation.* 2nd edition. Plymouth: Plymouth Marine Laboratory, PRIMER-E.

Corrêa M.F.M., Cerdeiras P.C.R. and Peckzarka J.C. (1988) Levantamento ictiológico do Guanandi, subbacia do rio Nhundiaquara (Morretes, PR, Brasil). *Nerítica* 3, 37–60.

Day J.W., Hall C.A.S., Kemp W.M. and Yanez-Arancibia A. (1989) *Estuarine ecology.* 1st edition. New York: John Wiley & Sons, 558 pp.

Diaz S. and Cabido M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16, 646–655.

Elliot M., Whittfield A.K., Potter I.C., Blaber S.J.M., Cyrus D.P., Nordlie F.G. and Harrison T.D. (2007) The guild approach to categorizing estuarine fish assemblages: a global review. *Fish and Fisheries* 8, 241–268.

Eschmeyer W.N. (2006) *Catalog of fishes.* 1st edition. San Francisco, CA: California Academy of Sciences.

Froese R. and Pauly D. (2006) *FishBase.* Available from www.fishbase.org (accessed 18 November 2009).

Giarrizzo T. and Krumme U. (2009) Temporal patterns in the occurrence of selected tropical fish to mangrove creeks: implication for the fisheries management in north Brazil. *Brazilian Archives of Biology and Technology* 52, 679–688.

Gibson R.N. (1992) Tidally-synchronised behaviour in marine fishes. In Ali M.A. (ed.) *Rhythms in fishes.* New York: Plenum Press, pp. 63–81. [NATO ASI Series Life Sciences, No. 236.]

Gibson R.N. (1996) Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. *Marine Ecology Progress Series* 130, 1–17.

Gibson R.N., Pihl L., Burrows M.T., Modin J., Wennhage H. and Nickell L.A. (1998) Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Marine Ecology Progress Series* 165, 145–159.

Godefroid R.S., Hofstaetter M. and Spach H.L. (1998) Moon, tidal and diel influences on catch composition of fishes in the surf zone of Pontal do Sul beach, Paraná. *Revista Brasileira de Zoologia* 15, 647–701.

Godefroid R.S., Spach H.L., Schwarz Jr R., Queiroz G.M.N. and Oliveira-Neto J.F. (2003) Efeito da Lua e da Maré na Captura de Peixes em uma Planície de Maré da Baía de Paranaguá, Paraná, Brasil. *Boletim do Instituto de Pesca* 29, 47–55.

Godefroid R.S., Spach H.L., Santos C., McLaren G. and Schwarz Jr R. (2004) Mudanças temporais na abundância e diversidade da fauna de peixes do infralitoral raso de uma praia do sul do Brasil. *Iheringia, Série Zoologia* 94, 95–104

Gray C.A., Check R.C. and Mcellegot D.J. (1998) Diel changes in assemblages of fishes associated with shallow seagrass and bare sand. *Estuarine, Coastal and Shelf Science* 46, 849–859.

Horn M.H., Martin K.L.M. and Chotkowski M.A. (1999) *Intertidal fishes. Life in two worlds.* 1st edition. San Diego, CA: Academic Press, 399 pp.

Johannes R.E. (1978) Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes* 3, 65–84.

Kleypas J. and Dean J.M. (1983) Migration and feeding of the predatory fish, *Bairdiella chrysoura* Lacépède, in an intertidal creek. *Journal of Experimental Marine Biology and Ecology* 72, 199–209.

Koch V. (1999) *Epibenthic production and energy flow in the Caeté mangrove estuary, North Brazil.* PhD thesis. Center for Tropical Marine Ecology (ZMT), Bremen, GE.

Krumme U., Saint-Paul U. and Rosenthal H. (2004) Tidal and diurnal changes in the structure of a nekton assemblage in small intertidal mangrove creeks in northern Brazil. *Aquatic Living Resources* 17, 215–229.

Krumme U., Brenner M. and Saint-Paul U. (2008) Spring–neap cycle as a major driver of temporal variations in feeding of intertidal fishes: evidence from the sea catfish *Sciades herzbergii* (Ariidae) of equatorial West Atlantic mangrove creeks. *Journal of Experimental Marine Biology and Ecology* 367, 91–99.

Lessa G.G., Dominguez J.M.L., Bittencourt A.C.S.P. and Brichta A. (2001) The tides and tidal circulation of Todos os Santos Bay, Northeast Brazil: a general characterization. *Anais da Academia Brasileira de Ciências* 73, 245–261

Lin H.J. and Shao K.T. (1999) Seasonal and diel changes in a subtropical mangrove fish assemblage. *Bulletin of Marine Science* 65, 775–794.

Manderson J.P., Pessuti J., Hilbert J.G. and Juanes F. (2004) Shallow water predation risk for a juvenile flatfish (winter flounder; *Pseudopleuronectes americanus*, Walbaum) in a northwest Atlantic estuary. *Journal of Experimental Marine Biology and Ecology* 304, 137–157.

Nagelkerken I., Blaber S.J.M., Bouillon S., Green P., Haywood M., Kirton L.G., Meynecke J.O., Pawlik J., Penrose H.M., Sasekumar A. and Somerfield P.J. (2008) The habitat function of mangroves for terrestrial and marine fauna. *Aquatic Botany* 89, 155–185.

Nelson J.S. (1994) *Fish of the world.* 3rd edition. New York: John Wiley & Sons.

Nybakken J.W. and Bertness M.D. (2004) *Marine biology: an ecological approach.* 6th edition. San Francisco, CA: Pearson.

Odum W.E. and Herald E.J. (1972) Trophic analyses of an estuarine mangrove community. *Bulletin of Marine Science* 22, 671–738.

Oliveira-Silva J.T., Peso-Aguiar M.C. and Lopes P.R. (2008) Ictiofauna das praias de Cabuçu e Berlinque: uma contribuição ao conhecimento das comunidades de peixes na Baía de Todos os Santos—Bahia—Brasil. *Biotemas* 21, 105–115.

Paiva A.C.G., Chaves P.T.C. and Araújo M.E. (2008) Estrutura e organiação tróficada ictiofauna de ágas rasas em um estuário tropical. *Revista Brasileira de Zoologia* 25, 647–661.

Petchey O.L. (2004) On the statistical significance of functional diversity. *Functional Ecology* 18, 297–303.

Petchey O.L. and Gaston K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters* 9, 741–758.

Quinn N.J. and Kojis B.L. (1981) The lack of changes in nocturnal estuarine fish assemblages between new and full moon phases in Serpentine Creek Queensland. *Environmental Biology of Fishes* 6, 213–218.

Reise K. (1985) *Tidal flat ecology*. 1st edition. Berlin: Springer-Verlag, 191 pp.

Reis-Filho J.A., Nunes L.D.C., Menezes B.L. and Souza G.B.G. (2010) Variação espaço-temporal e efeito do ciclo lunar na ictiofauna estuarina: evidências para o estuário do Rio Joanes—Bahia. *Biotemas* 23, 111–122

Ricotta C., Avena G. and Chiarucci A. (2005) Quantifying the effects of nutrient addition on the taxonomic distinctness of serpentine vegetation. *Plant Ecology* 179, 21–29.

Rooker J.R. and Dennis G.D. (1991) Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bulletin of Marine Science* 49, 684–698.

Routree R.A. and Able K.W. (1993) Diel variation in decapod and fish assemblages in New Jersey polyhaline marsh creeks. *Estuarine, Coastal and Shelf Science* 37, 181–201.

Rozas L.P. (1995) Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries* 18, 579–590.

Rozas L.P. and Minello T.J. (1998) Nekton use of salt marsh, seagrass, and nonvegetated habitats in a south Texas (USA) estuary. *Bulletin of Marine Science* 63, 481–501.

Santos R.S. and Nash R.D.M. (1995) Seasonal changes in sandy beach fish assemblage at Porto Pim, Faial, Azores. *Estuarine, Coastal and Shelf Science* 41, 579–591.

Santos A.C.A., Oliveira-Silva J.T., Moura P.E.S. and Sena M.P. (2008) Ampliação do limite norte de distribuição geográfica de *Catathyridium garmani* (Jordan & Goss 1889) (Actinopterygii: Achiridae). *Biota Neotropica* 9, 275–277.

Sokal R.R. and Rohlf F.J. (1995) *Biometry.* 1st ed. New York: W.H. Freeman and Company, 859 pp.

Webb C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist* 156, 145–155.

Weinstein M.P. and Heck K. (1979) Ichthyofauna of seagrass meadows along the Caribbean coast of Panama and in the Gulf of Mexico: composition, structure and community ecology. *Marine Biology* 50, 97–108.

Wolff W.J., Vand Etten J.P.C., Hiddink J.G., Montserrat F., Schaffmeister B.E., Vonk J.A. and De Vries A.B. (2005) Predation on the benthic fauna of the tidal flats of the Banc d'Arguin (Mauritanie). In Symoens J.J. (ed.) *Coastal ecosystems of West-Africa biological diversity resources conservation.* Brussels: Foundation for the Promotion of Scientific Research in Africa, pp. 43–59.

and

Zavala-Camin L.A. (1996) *Introdução aos estudos sobre alimentação natural em peixes.* Maringá: Nupélia, 127 pp.

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