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Intertidal benthic macrofaunal assemblages: changes in structure along entire tropical estuarine salinity gradients

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Spatial variation in the structure of macrobenthic assemblages on intertidal flats is known to be related to different environmental variables. Most of the studies have observed that along the estuarine gradient, salinity is the most important variable driving the patterns of the macrobenthic assemblages. However, the great majority of studies have been done on single estuarine systems in temperate regions. We investigated the relationship between the macrobenthic assemblages in intertidal habitats and the environmental variables along three tropical estuaries. From lower to upper estuarine regions we sampled benthic macrofauna, salinity and sediments. The structure of the benthic assemblages was primarily related to salinity. There was a decrease in the number of taxa from the upper to the lower estuarine regions, indicating important deviation from Remane's model of estuarine diversity. There were important similarities of taxa abundance along different estuarine salinity gradients which can be properly tested in other tropical and temperate regions. We advocate that in order to adopt general and robust management practices it is essential to identify broad patterns and general rules governing estuarine systems.

Keywords: intertidal environment, salinity gradients, sediments, zoobenthos

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INTRODUCTION

The intertidal estuarine environment is recognized for its great ecological and economic value (Dittmann, 2000; Fujii, 2007). Many human communities use natural resources (e.g. shellfish and fish) from intertidal flats as their main source of food and/or income (e.g. Rondinelli & Barros, 2010). This habitat retains a large amount of nutrients, allowing macrobenthic assemblages to exhibit high values of abundance and biomass, which is used as a resource by higher trophic levels (e.g. Lunardi *et al.*, 2012).

The structure of estuarine intertidal macrobenthic assemblages often has high spatial and temporal variability due to the variation of physical and chemical factors. Among the most studied variables are particle size, organic content (e.g. Dittmann, 2002; Rodrigues *et al.*, 2006), tidal height (e.g. Sasekumar, 1974), salinity (e.g. Attrill, 2002; Ysebaert & Herman, 2002) and also biological variables (e.g. Peterson, 1991; Netto & Lana, 1994; Beauchard *et al.*, 2012). Additionally, the structure of macrobenthic assemblages can also be affected by human impacts, often leading to a decrease in diversity, biomass and abundance of certain groups or to an increase of opportunistic species (e.g. Hatje *et al.*, 2006).

In estuarine intertidal habitats, studies of spatial patterns of macrobenthic assemblages have been undertaken at different scales and have frequently described zonation patterns (i.e. intertidal gradients; Dittmann, 2002). These studies are especially abundant in temperate regions (e.g. Rodrigues & Manning, 1992; Mannino & Montagna, 1997; Rodrigues *et al.*, 2006; Fujii, 2007), and less common in tropical environments (e.g. Dittmann, 2000). These studies have generally aimed to associate zonation patterns with sediment type, organic matter content and tidal height.

A scale relatively less studied is the longitudinal gradient (i.e. along the entire salinity gradient). Some studies have been made in temperate zones (e.g. Ysebaert *et al.*, 2002; Gimenez *et al.*, 2005) and have suggested that the macrobenthic assemblages are primarily influenced by changes in salinity and, secondarily, by sediment characteristics (e.g. particle size, organic matter content and concentration of contaminants). Temperate studies were frequently made at a single estuary making them of great local interest (e.g. Chainho *et al.*, 2006; Conde *et al.*, 2013), but their conclusions are of limited application. Some of these temperate studies also suggested a zonation pattern in the structure of the assemblages throughout the estuary, where different assemblages inhabit different portions of the estuarine gradient (i.e. upper, middle and lower estuary; Ysebaert *et al.*, 1998; Lu *et al.*, 2008), and similar studies in tropical regions are scarce (e.g. Barros *et al.*, 2008, 2012).

Distinct biogeographical regions may show different patterns of variation in several estuarine characteristics (e.g. tidal range, temperature and rainfall regimes), that may affect the structure of macrobenthic assemblages (e.g. Whitfield *et al.*, 2012). There is a clear lack of knowledge

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about the relationship between tropical intertidal benthic assemblages and environmental variables throughout entire estuarine gradients (i.e. from freshwater to marine waters) which, coupled with the scarcity of tropical studies, may obscure the description of general patterns.

To better understand general estuarine ecosystem services (e.g. decomposition, nutrient cycling and nutrient production; Levin *et al.*, 2001) and also to allow the development of general predictive models, tropical systems must be studied. Attempts to provide a unitary and synthetic picture of the biological features of estuaries, considered extremely heterogeneous environments, can lead to general conclusions that may be true for one situation, but untrue for another (Cognetti & Maltagliati, 2000). However, in spite of the many peculiarities of each estuary (e.g. catchment size, fishing pressure and pollution level) it seems that consistent patterns of subtidal benthic macrofaunal distribution along different systems can be observed (e.g. Barros *et al.*, 2012). Therefore, the present study evaluates if there are similarities in the structure of intertidal macrofaunal assemblages between tropical estuarine systems and the relationship between these assemblages and environmental variables, and discusses potential similarities with other estuarine systems and habitats.

MATERIALS AND METHODS

Study area

Baía de Todos os Santos (BTS) is the second largest bay in Brazil with an area of 1223 km^2 (Figure 1). It is essentially marine, with an average depth of 9.8 m, semidiurnal tides, with a range of 0.9–3.1 m in amplitude of neap and spring tides, respectively (Cirano & Lessa, 2007). The intertidal area in BTS is 327 km^2, where 152 km^2 is occupied by mangroves, 160 km^2 by non-vegetated flats and 15 km^2 by non-vegetated supratidal flats (Cirano & Lessa, 2007). BTS is recognized for its great economic and ecological relevance (e.g. Hatje & Barros, 2012) and the truly estuarine regions are associated with the major tributaries, Rivers Paraguaçu, Jaguaripe and Subaé, with drainage basins of 56,300, 2200 and 600 km^2, respectively. These systems have other different characteristics such as contamination level (Hatje & Barros, 2012), toxicity (Krull *et al.*, 2014) and proximity with the inner continental shelf (Figure 1).

Sample collection and processing

Samples were collected during 2011 in the Jaguaripe (March), Paraguaçu (June) and Subaé (October) estuaries. Ten sampling

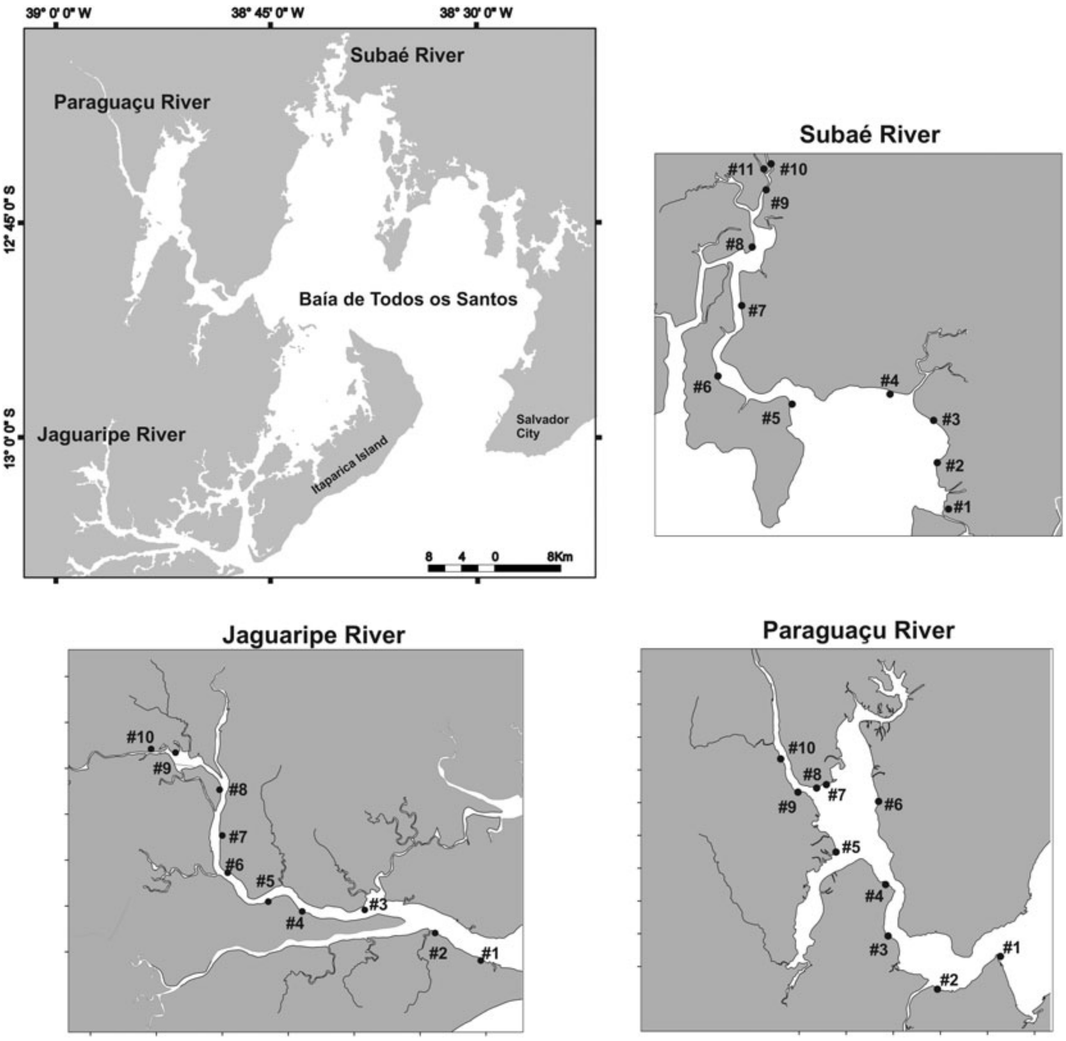

Fig. 1. Location map of the studied area and sampling stations along the estuaries of Jaguaripe (1–10), Paraguaçu (1–10) and Subaé (1–11).

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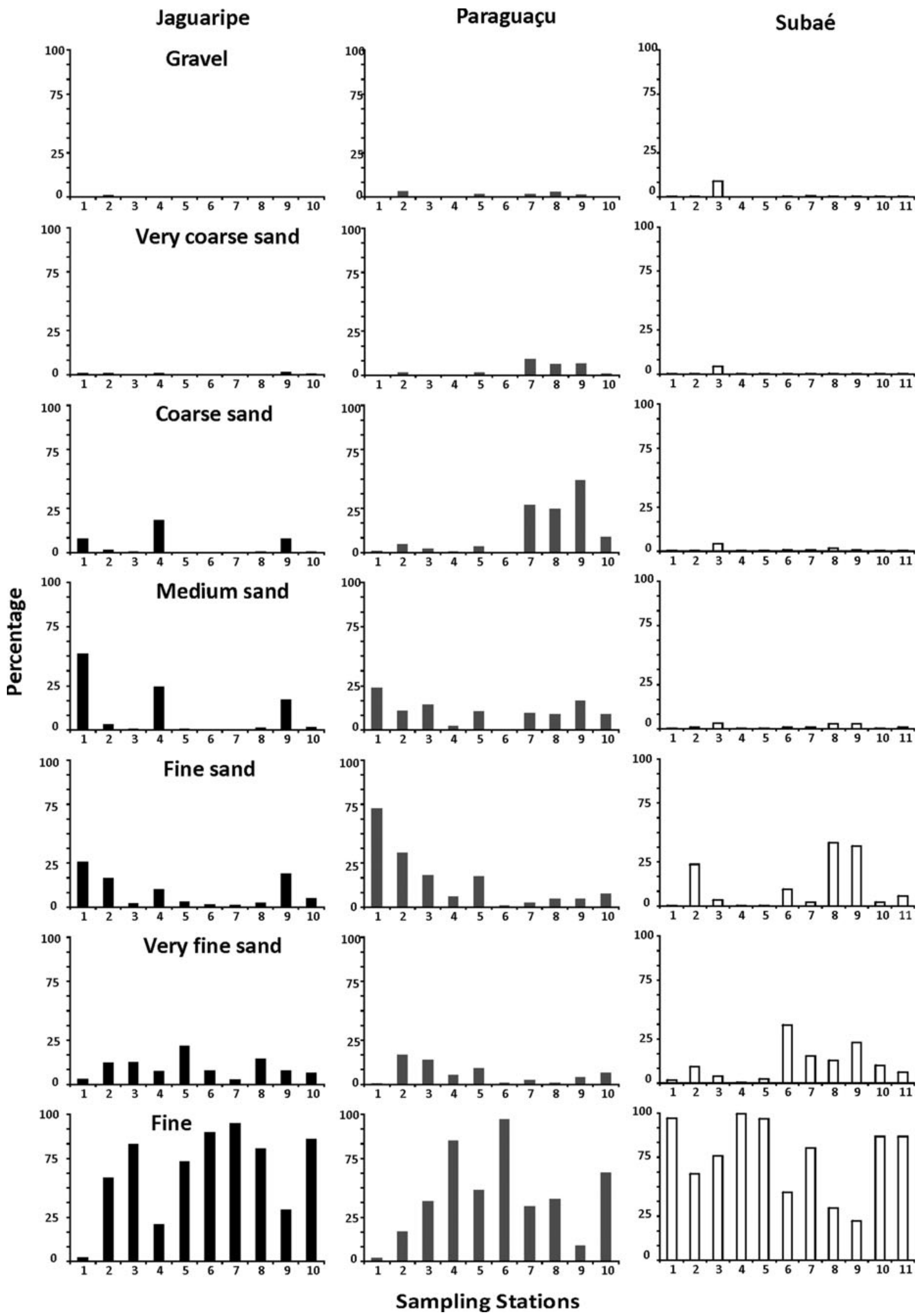

Fig. 2. Percentage of sediment grain sizes in stations along Jaguaripe, Paraguaçu and Subaé estuaries.

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stations were positioned in Jaguaripe and Paraguaçu estuaries and 11 stations were positioned in the Subaé estuary, along the entire salinity gradient (Figure 1). At each station, macrozoobenthic assemblages were sampled in eight random replicates (total = 248 samples), using a corer of 15 cm diameter (≈177 cm^2 surface area) pushed 15 cm into the sediment. Samples were collected during low tide standardized at about two metres below the boundary between the tidal flat and the mangrove forest to minimize variability due to vertical differences along the estuarine gradient. The samples were washed through a 0.5 mm sieve in the field and preserved in 70% alcohol. In the laboratory, the organisms were sorted, counted and identified to the lowest possible taxonomic level, usually family. Invertebrates were identified mostly to family considering that family level is enough to show the estuarine macrofaunal changes (e.g. De Biasi *et al.*, 2003; Chainho *et al.*, 2007) and due to the scarcity of taxonomic studies of the local benthic invertebrates (with numerous or substantial numbers of undescribed species) and to investigate a general model of taxa distribution which might be tested in other tropical regions.

Superficial and interstitial salinity were collected in rainy and dry periods (July 2011 and March 2012). In each of the estuaries, in both periods, the stations were sampled on the same day during the period of low tide, thus minimizing the effect of temporal variation in salinity between stations. One sediment sample was collected at each sampling station for grain size analysis using a corer of 177 cm^2 surface area. Sediment particle size was determined by standard procedures. The fractions of gravel (>4 mm) were pooled. Fractions of silt and clay (<0.062 mm), also pooled, are referred to in this work as 'fine sediments'.

Approximately 10 g, was subsampled from each sediment sample to estimate the percentage of organic matter (OM) and calcium carbonate ($CaCO_3$). First, the samples were dried in an oven at 60°C. Organic matter and calcium carbonate were then obtained by combustion in a muffle furnace at 550°C and 1000°C, respectively, for a period of 1 h (Dean, 1974).

Data analyses

Station replicates (N = 8) were summed and the similarity among the macrobenthic assemblages were calculated using Bray–Curtis. Data were fourth root transformed to down-weight the influence of dominant taxa. Non-metric multidimensional scaling (nMDS) ordination was used to investigate patterns in the structure of the macrofaunal assemblages in each estuarine system (Clarke & Warwick, 2001).

To test if the benthic invertebrates would show replacement along each estuary, seriation tests were performed, with 999 permutations, using Spearman correlation (Relate routine, Primer 6). Principal components analysis (PCA) was used to assess differences in the environmental variables (salinity, OM, $CaCO_3$ and particle sizes) from each station in each estuary. For the PCAs, abiotic data were transformed to log $(x + 1)$ and normalized (Clarke & Gorley, 2006).

The spatial patterns of the macrobenthic assemblages were correlated with environmental variables using the routine BIOENV (Primer 6). These analyses were performed for each estuary based on the correlation of Bray–Curtis dissimilarity matrices, of the fourth root transformed biological data, with Euclidean distance matrices, of the log $(x + 1)$ transformed environmental data. Due to the high correlation among salinity data (superficial and interstitial at both sample period, $r > 0.95$), only the salinity of surface water during the rainy season was included in the analysis. *Uca* spp. crabs were excluded from multivariate analysis because the sampling method used in the present study was not suitable to catch this highly mobile organism. The Monte Carlo permutation test (999 permutations) was used to test the effects of each environmental variable in explaining the total variance of macrofauna, assuming $\alpha = 0.05$.

RESULTS

Environmental variables

In the Jaguaripe estuary, the composition of the sediment was dominated by fine sediments, except at Stations 1, 4 and 9, which had a higher percentage of sand (Figure 2). In Paraguaçu, the sediments were composed of relatively larger percentages of sand, but Stations 4, 6 and 10 were mostly composed of fine sediments (Figure 2). The Subaé estuary was

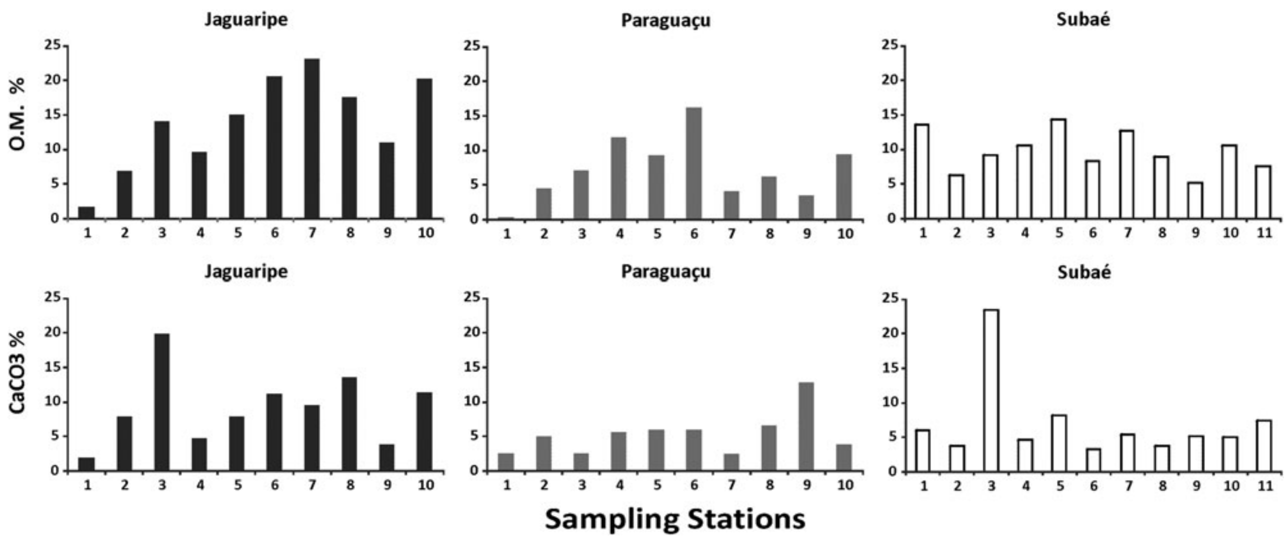

Fig. 3. Percentage of organic matter and $CaCO_3$ in sampling stations along Jaguaripe, Paraguaçu and Subaé estuaries.

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dominated by fine sediments. There were very small amounts of gravel in the three estuaries (Figure 2).

In the dry season, superficial water salinity ranged from 4 (at Station 10) to 39 (at Station 1), in Jaguaripe, 6 to 36 in Paraguaçu, and 0 to 38 in Subaé. In the rainy season, the variation was between 0 and 34, 4 and 34 and 0 and 33 in Jaguaripe, Paraguaçu and Subaé estuaries, respectively. There was a relatively smaller variation in the interstitial water of all estuaries in the dry period, ranging from 2 to 34 in Jaguaripe, 19 to 39 in Paraguaçu and 20 to 40 in Subaé. In the rainy season, interstitial salinity varied from 10 to 38, 7 to 35 and 11 to 35, in Jaguaripe, Paraguaçu and Subaé, respectively.

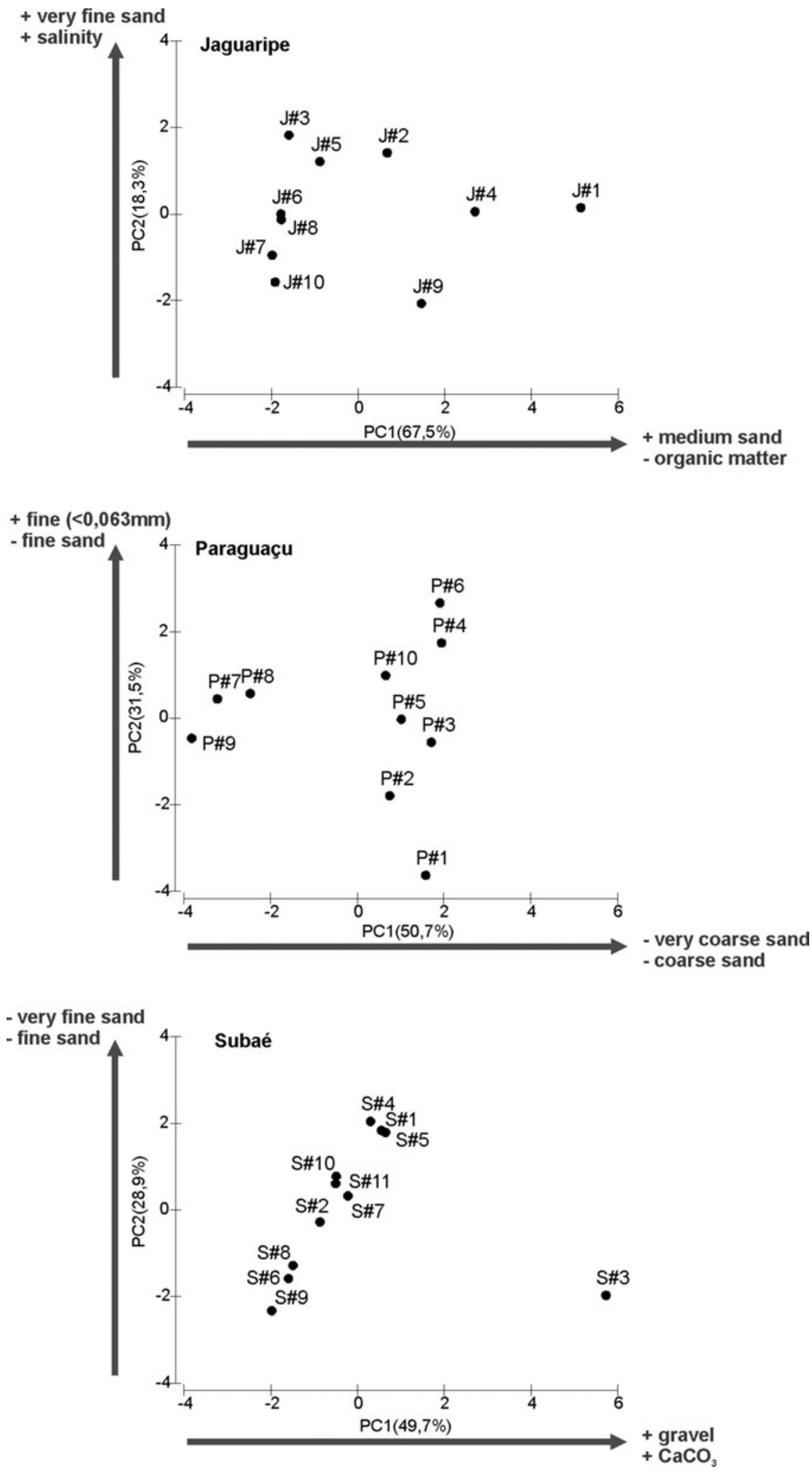

Fig. 4. Principal components analysis for abiotic data in sampling stations along Jaguaripe, Paraguaçu and Subaé estuaries.

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The content of OM and $CaCO_3$ was always smaller than 25% in all systems (Figure 3). There was higher OM at Jaguaripe (between 1.7 and 23.1%) than in the other systems. In the Paraguaçu estuary, the organic matter content ranged from 0.3 to 16.2%, with higher OM at Stations 4 and 6. In Subaé Stations 1, 5 and 7 had the highest percentage of OM, respectively 13.6, 14.3 and 12.8%. The percentages of $CaCO_3$ ranged between 2 and 19.8% in the Jaguaripe estuary, and 2.4 and 12.7%, in Paraguaçu. The Subaé estuary showed a range of 3.7 to 23.4%, with Station 3 having a value far greater than the others (Figure 3).

The PCA performed with abiotic data in the Jaguaripe estuarine system showed 85.8% of the total variability explained by the first two axes (Figure 4). The first principal component (PC) was mainly correlated with medium sand ($r = 0.57$) and negatively correlated with organic matter ($r = -0.45$), while the second PC correlated with surface salinity of the rainy season ($r = 0.81$) and very fine sand ($r = 0.35$). In the Paraguaçu estuary, the first two PCs explained 82.2% of the total variability, and the first PC was correlated negatively with very coarse sand ($r = -0.64$) and coarse sand ($r = -0.63$), and the second PC with fine sand ($r = -0.61$) and positively with fine sediments (i.e. silt + clay; $r = 0.53$). For the Subaé estuary, the first two PCs explained 78.6% (Figure 4) of the total variance. The first PC was mostly positively correlated with gravel and $CaCO_3$ ($r = 0.66$, $r = 0.51$, respectively), whereas the second was negatively correlated with very fine sand ($r = -0.56$) and fine sand ($r = -0.45$).

Benthic macrofauna

Jaguaripe estuary had a total of 1435 individuals distributed in 26 taxa, of which 57% were molluscs, 39% were polychaetes and 2% were crustaceans. There were 753 individuals in Paraguaçu distributed among 28 taxa, of which 76% were polychaetes, 14% were crustaceans and 7% were molluscs. In the Subaé estuarine system 1758 individuals were collected, represented by 28 taxa (92% polychaetes, 4% molluscs and 3% crustaceans). In general, the highest abundances were found in the regions of lower salinity (Figure 5A, B), except for Station 10 of the Paraguaçu estuary (low abundance) and Station 1 of the Jaguaripe (high abundance). In this latter station, there was high abundance of the gastropod *Neritina virginea* (Figure 6). Highest richness values were generally observed on tidal flats in the lower estuary zones (Figure 5A, B). Figure 6 shows the distribution of the most abundant groups (those that, combined, contributed to 80% of total abundance in each estuary) and Nereididae, Spionidae and Capitellidae were found especially at the upper estuarine regions.

The nMDS ordination for Jaguaripe showed greater dissimilarity of Station 1 and, to a lesser extent, Stations 9 and 10, from the other stations (Figure 7). The upper estuary, characterized by low salinity, was dominated by polychaete families Spionidae, Nereididae and Capitellidae (Figure 6). Station 1 (region with high salinity) was dominated by the gastropod *Neritina virginea*. The polychaete family Pilargidae was abundant in the intermediate regions of the Jaguaripe estuary. In the Paraguaçu estuary the nMDS ordination showed a higher dissimilarity between Stations 1, 4 and the others (Figure 7). Station 4 was differentiated by the extremely low abundance of organisms and it was also the least rich station within this estuary, with only 2 taxa (Pilargidae, Goniadidae) and Station 1 was dominated by the isopods of the genus *Excirolana*. In the Subaé estuarine system, Stations 8, 9, 10 and 11 (Figure 7) were dissimilar

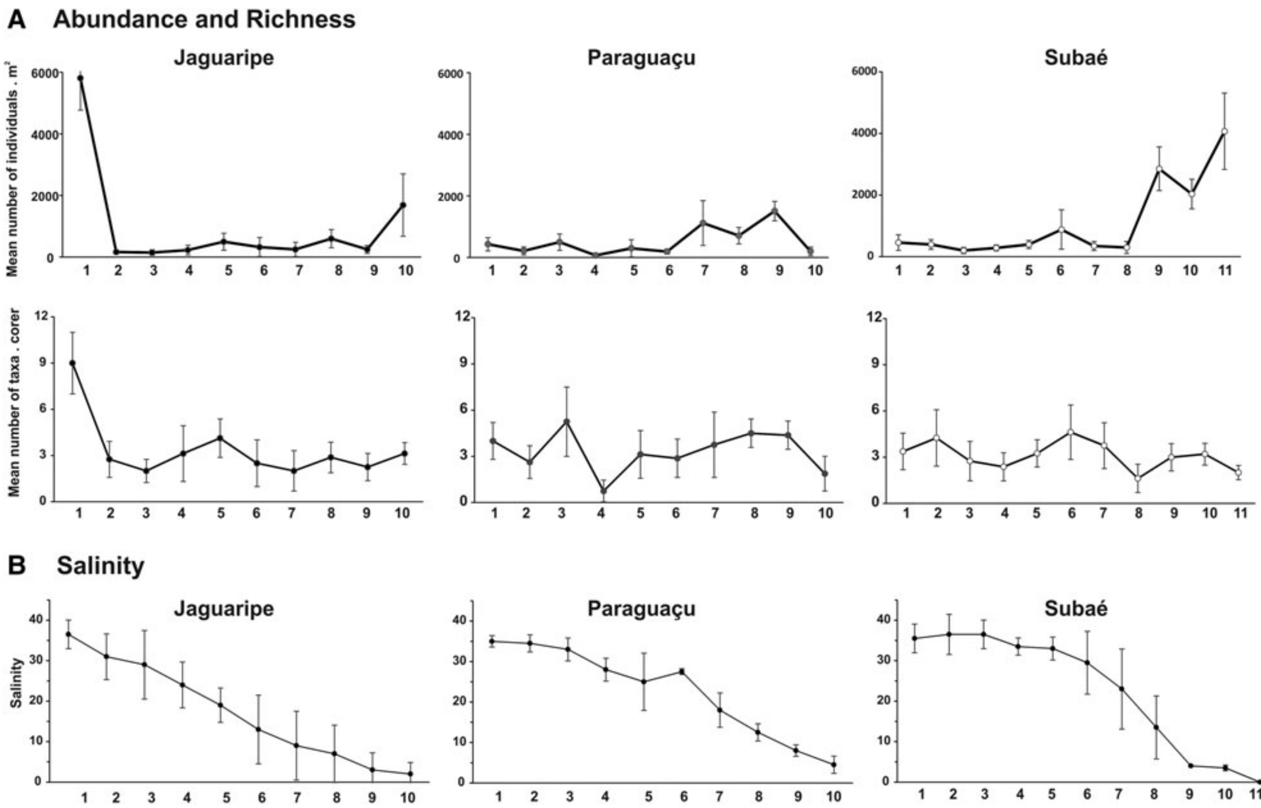

Fig. 5. (A) Distribution of mean (±standard deviation (SD)) total abundance and richness at each sampling station along the estuaries of Jaguaripe, Paraguaçu and Subaé (N=8); (B) mean (±SD) salinity (N = 2).

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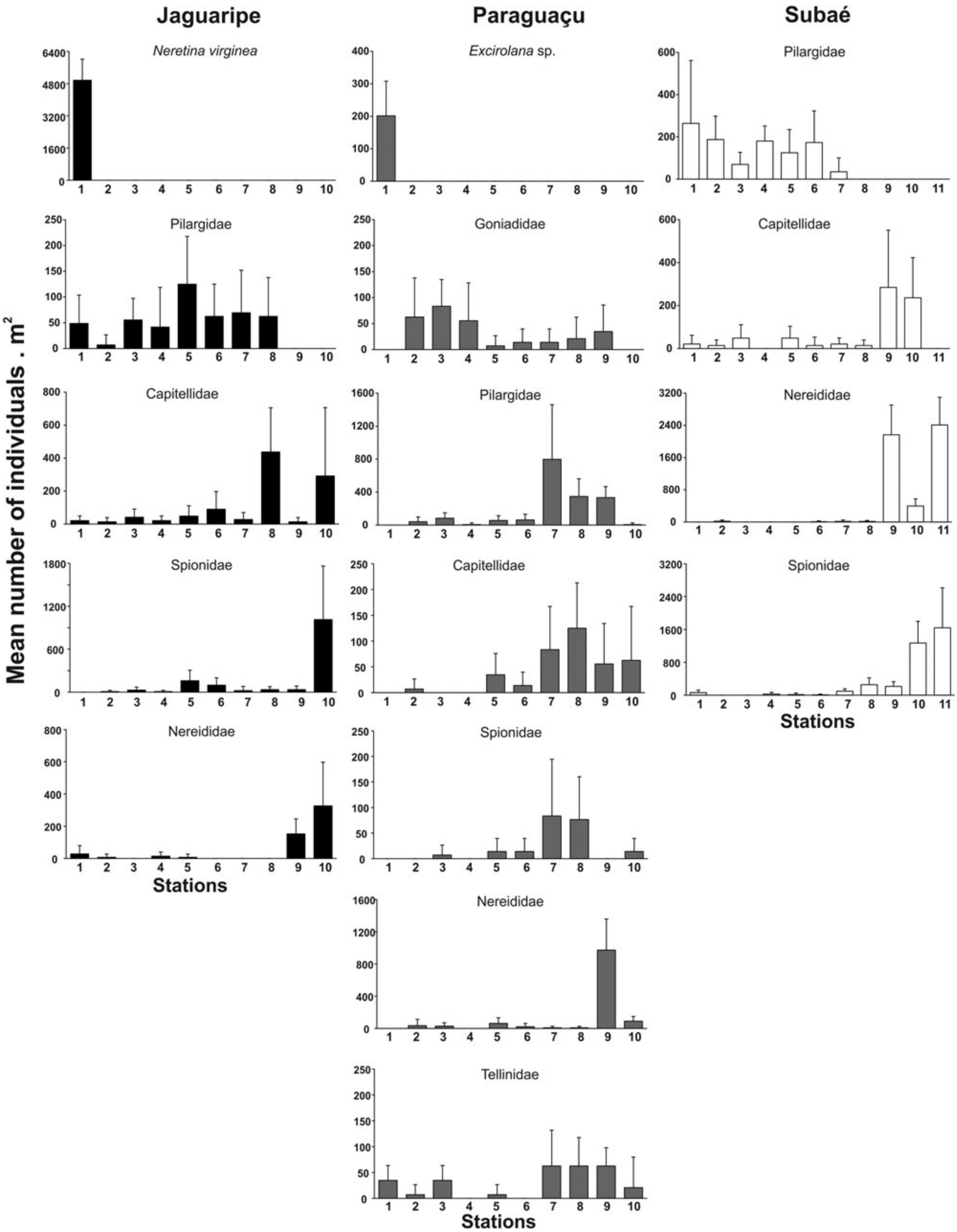

Fig. 6. Mean (±standard deviation) abundance of the most abundant taxa (i.e. those that contributed 80% of the total number of individuals of each estuary) at each sampling stations in the estuaries of Jaguaripe, Paraguaçu and Subaé.

from Stations 1–7. In these latter stations, Pilargidae was dominant, while Spionidae, Capitellidae and Nereididae prevailed in the former (Figure 6).

The three estuarine systems showed significant patterns of seriation. The Jaguaripe estuarine system had a significance level of 0.001 and a rho value of 0.59, and none of the

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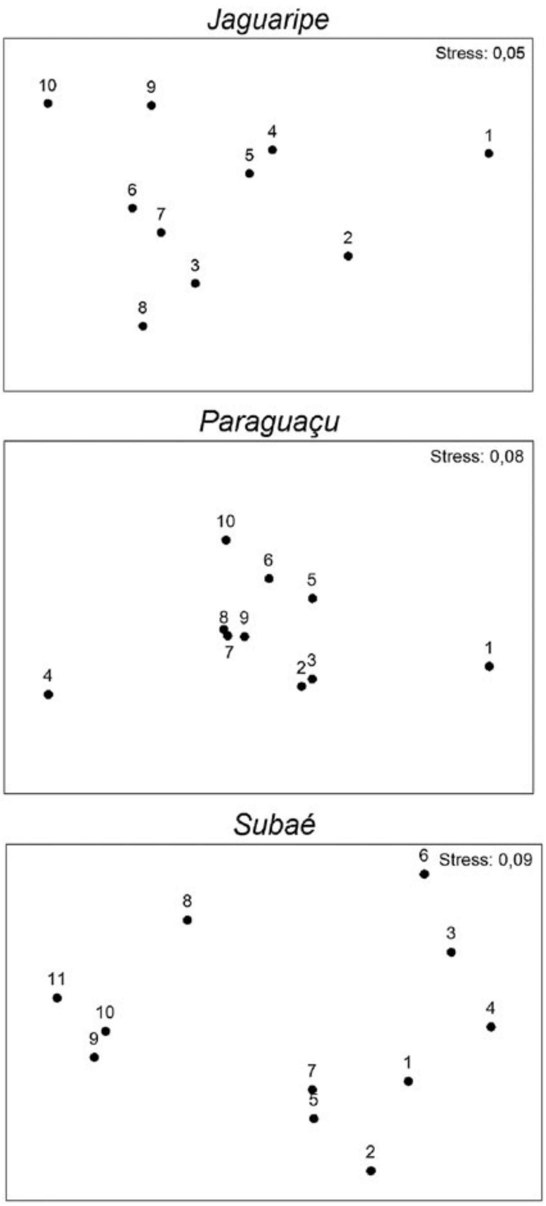

Fig. 7. Non-metric multidimensional scaling with the macrofauna of all sampling stations along the Jaguaripe, Paraguaçu and Subaé estuaries.

permutations showed similar or higher values than the observed rho. For the Paraguaçu estuary the seriation was also significant ($P = 0.001$ and rho $= 0.41$) and only nine values of the permutations were greater than or equal to the rho observed. The Subaé system showed a rho value of 0.61, with a significance level of 0.003, and only two values of the permutations were equal to or greater than the observed Rho.

In the Jaguaripe estuarine system, BIOENV analysis (Table 1) showed that the best correlation with the benthic macrofauna was with salinity, organic matter and fine sand. In the Paraguaçu estuary, four environmental variables were best correlated with macrofauna (salinity, organic matter, medium sand and fine sand) and in the Subaé, salinity alone showed the best correlation with the macrofauna (Table 1).

DISCUSSION

The ordinations of the stations based on environmental variables (PCAs) indicated differences between sampling stations due to salinity, organic matter content and $CaCO_3$ and also due to differences in sediment grain size. However, there were no consistent differences in sediment size at distinct estuarine regions, as observed in subtidal habitats of the same estuaries (Barros *et al.*, 2012) or in other regions (Ysebaert *et al.*, 2003; Gimenez *et al.*, 2005). Several studies, mostly in temperate regions, suggested strong relationships between the structure of the intertidal benthic assemblages and grain size. For instance, Lu *et al.* (2008) observed a positive correlation between the fine fractions (silt and clay) and richness and diversity. Thrush *et al.* (2003) used mud to predict macrofaunal species occurrence along an estuarine gradient. However, the sediments of the intertidal habitats in the present study did not show a clear gradient in grain size. The intertidal habitats were predominantly composed of fine fractions (silt and clay) but medium and fine sands were more correlated with the structure of macrobenthic assemblages. In the tropical systems studied, salinity seems to exert a stronger influence on the structure of benthic assemblages than sediment size. Additionally, there are other variables, not measured in this study, which

Table 1. Summary of the results of the BIOENV analysis for each estuarine system (Sal, salinity; OM, organic matter; G, gravel; VCS, very coarse sand; CS, coarse sand; MS, medium sand; FS, fine sand; VFS, very fine sand; F, fine; $^*P < 0.05$; ns, not significant).

	Jaguaripe		**Paraguaçu**		**Subaé**	
No. of variables	**Variable**	***P***	**Variable**	***P***	**Variable**	***P***
1	FS	0.54 (ns)	MS	0.59*	Sal	0.74*
	Sal	0.53*	FS	0.47 (ns)	VFS	0.13 (ns)
2	Sal, FS	0.70*	MS, FS	0.60 (ns)	Sal, CS	0.73*
	OM, VCS	0.48 (ns)			VCS, VFS	0.15 (ns)
3	Sal, OM, FS	0.74*	OM, MS, FS	0.63 (ns)	Sal, CS, MS	0.73*
	G, VCS, MS	0.46 (ns)			G, $CaCO_3$, VFS	0.11 (ns)
4	Sal, OM, FS, G	0.73*	Sal, OM, MS, FS	0.64*	Sal, OM, CS, MS	0.71*
	$CaCO_3$, CS, MS, F	0.35 (ns)	VCS, CS, VFS, F	0.15 (ns)	VCS, $CaCO_3$, VFS, F	0.09 (ns)
5	Sal, G, VCS, FS, F	0.73*	Sal, OM, MS, FS, F	0.61 (ns)	Sal, OM, MS FS, F	0.51*
	MO, $CaCO_3$ CS, MS, VFS	0.35 (ns)			$CaCO_3$, G, VCS, CS, VFS	0.10 (ns)

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may also be important (e.g. nutrients, chlorophyll and oxygen content).

The results indicated that there were similarities in the structure of intertidal macrofaunal assemblages; several abundant taxa showed distinct preferences for different salinity ranges along the salinity gradient. The polychaete families Spionidae, Nereididae and Capitellidae occurred mainly in low salinity areas. Individuals of the Pilargidae family showed a greater range of distribution, tolerating a variety of salinities. Our results showed that there was an important relationship between the structure (i.e. composition and abundance) of the intertidal benthic assemblages and salinity. The replacement of species within an estuarine gradient was observed in several studies where salinity was also an important explanatory variable (e.g. Ysebaert *et al.*, 2003; Gimenez *et al.*, 2005), while other factors (e.g. fractions of sediment and depth) had secondary influence on the structure of the assemblages. In the present study, peaks of abundance of different taxa were reported at different estuarine regions (e.g. upper, middle and lower estuary), some of these taxa showed similar patterns in subtidal regions (Barros *et al.*, 2012). We believe that this replacement might be observed in intertidal and subtidal fauna in other tropical estuaries around the world; however, this needs further test.

Samples from the three estuaries presented high macrofaunal abundance at the upper estuarine region, contrary to studies where an inverse pattern was reported (Ysebaert *et al.*, 2003; Hatje *et al.*, 2006; Fujii, 2007; Barros *et al.*, 2008). The high number of individuals in lower salinity areas was mainly due to capitellid and spionid polychaetes. Dominance of these organisms may indicate organically enriched areas (Yokoyama, 1995; Mendez *et al.*, 2001; Venturini *et al.*, 2008). In fact, the upstream sampling stations are close to urbanized areas with untreated effluents, especially in the Subaé (Hatje & Barros, 2012). The high abundance of the gastropod *Neritina virginea* observed in the lower Jaguaripe estuarine system probably occurred due to the relatively higher percentage of medium sand combined with high salinity values, conditions ideal for this euryhaline species (Ortiz & Blanco, 2012). Furthermore, *Neritina virginea* uses seagrasses for feeding (Lana & Guiss, 1992) and a seagrass bed was observed near this station.

It has been suggested that marine and/or freshwater organisms occupy intermediate regions of the estuaries up to the limit of their physiological tolerance to salinity changes (Attrill & Rundle, 2002). Thus, the fauna would occupy two overlapping gradients or stressors (i.e. two ecoclines), one from the river to the intermediate region and another from intermediate region to the sea. In the present study, the most abundant invertebrates showed peaks of abundance in specific regions of the estuaries, suggesting that there is a continuum of intertidal estuarine benthic assemblages. However, there were very few individuals of typical freshwater species (chironomids), indicating that these taxa might be further upstream, above the tidal influence (i.e. above the estuary), but this requires future studies.

We observed that most of the stations located downstream showed a greater number of taxa than those upstream (under the influence of freshwater) which exhibited relatively smaller values. These results do not fit into the well-known Remane model of estuarine diversity (see also Whitfield *et al.*, 2012). This model predicts a minimum point of richness in places with salinities between 5 and 8, but this was not observed in the Jaguaripe, Paraguaçu and Subaé estuaries. Instead, the pattern observed resembles those found in the subtidal portion of these tropical estuaries (Barros *et al.*, 2012) and on other estuaries in temperate regions (e.g. Ysebaert *et al.*, 1998; Gimenez *et al.*, 2005; Fujii, 2007) where there are greater numbers of species at lower than at upper estuarine zones. These results reinforce the need to develop new models to understand and to predict the diversity of benthic invertebrates along estuarine gradients.

The present work shows important similarities in taxa replacement along different tropical systems; these patterns are ecologically meaningful and can be properly tested in future studies over different tropical and subtropical estuarine systems. It is clear that the structure (i.e. composition and abundance) of the benthic assemblages is primarily related to salinity. Future studies should consider not only the entire salinity gradient but different spatial scales (e.g. longitudinal and intertidal) to reach a complete understanding of estuarine intertidal flats. We advocate that it is still necessary to investigate broad general patterns and general rules governing estuarine tropical and temperate systems in order to propose robust and general management models of wide application.

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