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Structural and functional approaches to describe polychaete assemblages: ecological implications for estuarine ecosystems

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Abstract. Polychaete assemblages are of special interest when studying dynamic environments such as estuaries because of their high plasticity in life strategies to cope with environmental variability. We tested the hypothesis that polychaete feeding guilds would be more related to environmental characteristics than to taxonomic composition. Polychaetes were sampled on two different occasions along three tropical estuarine systems in north-eastern Brazil. Different polychaete taxa replaced one another along the entire salinity gradient and the overall pattern from high- to low-salinity regions was from high species and feeding-guild diversities to dominance by a single species or a feeding group. We suggest that the relationships between structure and function of polychaete assemblages might provide a measure of the resilience of estuarine conditions; estuaries with a high redundancy in the trophic role of polychaetes might recover faster from disturbance and retain more natural ecological functions than those estuaries with low or no redundancy, because more species would have the capacity to expand their niches to compensate for the loss of neighbouring species. Integrative approaches allying species composition to their trophic role need to be thoroughly investigated to help understand such complex temporal and spatial organisation of benthic assemblages in estuaries.

Additional keywords: ecosystem resilience, feeding guilds, polychaeta, tropics, zoobenthos.

Introduction

Polychaete assemblages typically contribute to a high percentage of total macrofaunal diversity and abundance (Hutchings 1998) and frequently represent more than half of the number of organisms in soft-bottom habitats (Olsgard *et al*. 2003). In general, they are the group that most contributes to the diversity and abundance patterns of the benthic communities (Olsgard and Somerfield 2000).

Biological traits of marine invertebrates, including polychaetes, provide a great deal of information on their roles in ecosystem function (Bremner *et al*. 2006), and feeding characteristics are commonly used to address the functional role of the fauna in benthic environments. The use of morphological characteristics to categorise feeding mode adds information to survey data, beyond species names and abundances (Woodin 1987). The feeding-guild approach delineated by Fauchald and Jumars (1979) appears to be more relevant than is the use of other functional groups in polychaetes (e.g. reproductive functional groups; see Wilson 1991), because morphology and feeding behaviour of polychaetes largely determine most ecological patterns. The conceptual framework of feeding guilds by Fauchald and Jumars (1979) has been widely used to investigate polychaete assemblages (e.g. Pagliosa 2005; Antoniadou and Chintiroglou 2006; Cheung *et al*. 2008), even though some studies focussed only on the feeding modes (e.g. Barroso *et al*. 2002; Dolbeth *et al*. 2009; Box *et al*. 2010).

Ecological studies of polychaete assemblages often use taxonomic criteria to describe assemblage structure; fewer studies have incorporated functional approaches. The relationship between both approaches has never been investigated in depth, although it might be relevant for understanding how benthic ecosystems behave after perturbations. Walker (1995) suggested that the level of functional redundancy may be a useful measure of ecological resilience. Thus, if there is only a single taxon for each role, there will be low functional redundancy. After disturbance, an estuarine ecosystem in this 'one taxon per role' situation will have greater risk of losing one function (low resilience) by losing one taxon, than estuarine systems with multiple taxa performing each ecological role (high resilience). In the latter, different taxa can expand their niches to compensate for taxa that disappeared, and the function would still remain after disturbances (Johnson *et al*. 1996).

The feeding-guild approach seems to be an effective method for understanding the environmental constraints on the trophic structure, mobility and morphological mode of food acquisition of polychaetes and it is also helpful for reducing large taxonomic

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lists to biological datasets. Thus, it is relevant to ask whether this new variable is related to an environmental gradient (Dauer 1984) and, if so, this approach has potential value in posing and testing explicit hypotheses.

The aim of the present study was to evaluate whether the feeding guilds of polychaetes could provide a strong link between benthic communities and ecosystem function. We tested the hypothesis that polychaete data expressed as feeding guilds would be more significantly correlated with estuarine environmental variables than with data expressed as taxonomic groupings. The use of an integrated analysis (functional and structural) to describe estuarine macrobenthic assemblages was also assessed.

Materials and methods

Study area

The study area was in the main estuarine regions of the Baía de Todos os Santos, north-eastern Brazil (Fig. 1), a bay with a total area of 1223 km^2 and an average depth of 9.8 m (Cirano and Lessa 2007). The semi-diurnal tides drive the currents inside the bay (Cirano and Lessa 2007). The climate at the entrance of the bay is tropical with high humidity, whereas the inner part of the bay is semiarid throughout the year.

The macrobenthic assemblages of the Baía de Todos os Santos have been poorly studied and the most comprehensive study is that by Alves *et al*. (2006). The northern part of this bay has been severely affected by the petroleum industry and Peso-Aguiar *et al*. (2000), Venturini and Tommasi (2004) and Venturini *et al*. (2008) showed severe impacts, with reduced diversity and abundance, and altered trophic function of macrobenthic organisms. The main sources of freshwater and suspended material to the Baía de Todos os Santos are the Paraguaçu River (drainage area of 56 300 km^2), Jaguaripe River (2200 km^2) and the Subaé River (600 km^2) (Cirano and Lessa 2007). The upper part of the Subaé estuary is potentially unfavourable for the macrobenthic assemblages because of high concentrations of several heavy metals (Hatje *et al*. 2006). In contrast, the macrobenthic assemblages of the largest estuarine system (Paraguaçu estuary) have been shown not to be severely affected by anthropogenic activities (Barros *et al*. 2008).

Data collection

Macrobenthic polychaetes from 31 subtidal stations in the main tributary estuaries of Baía de Todos os Santos were sampled along the entire salinity gradient (Fig. 1) on two different occasions (i.e. dry and wet seasons), yielding 456 samples. The stations were numbered 1–10 for the Jaguaripe and Paraguaçu estuaries and 1–11 for the Subaé estuary. Station 1 was the most seaward and the deepest, Stations 10 and 11 were the furthest inland and the shallowest; the salinity gradient was from 34 at Station 1 to near freshwater at Stations 10 and 11. The salinity of the superficial water was measured at spring low-ebb tides and recorded with a Hydrolab Data Sonde (Loveland, CO, USA).

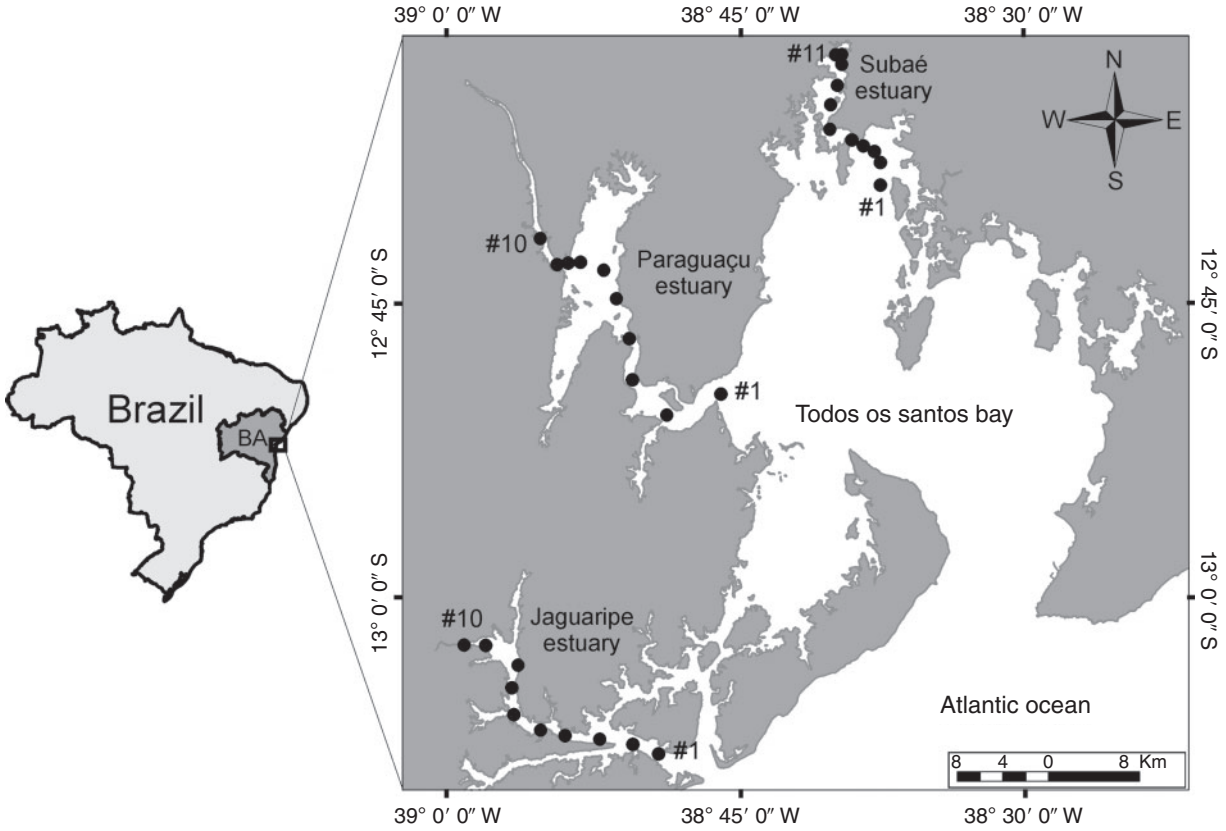

Fig. 1. Study area with sampling stations in Jaguaripe (10 stations), Paraguaçu (10 stations) and Subaé (11 stations) estuaries in Baía de Todos os Santos, north-east of Brazil.

In Paraguaçu estuary, six replicate samples were collected at each station with a 0.05-m^2 van Veen grab (see details in Barros *et al*. 2008). In Jaguaripe and Subaé estuaries, eight replicate samples were collected at each station with a 0.008-m^2 corer (for Subaé estuary, see details in Hatje *et al*. 2006). The different choice of sample size (i.e. 6 replicates collected with a van Veen grab for Paraguaçu estuary and 8 replicates collected with corers for Jaguaripe and Subaé estuaries) was because some of the stations at Paraguaçu River were substantially deeper and subjected to stronger currents than were those of the other two estuaries, preventing safe sampling by SCUBA divers. Because of the different sampling designs, the data from each estuary were analysed independently as replicates to test the same hypothesis. Sediment samples were collected at all stations during the dry and wet seasons for sediment analysis. Mean particle diameter, sorting, skewness and kurtosis were calculated using the software SysGran 3.0 (Camargo 2006) and following Folk and Ward (1957). Sediment diversity (or sediment complexity) was calculated by the Shannon–Wiener diversity index, using the suite of particle sizes as proposed by Whitlatch (1981).

All macrofaunal samples were sieved through a 0.5-mm mesh and stored in 70% alcohol. Polychaetes were sorted and identified to the lowest possible taxonomic level, most to species. There have been few taxonomic studies of the local estuarine polychaete fauna and several unidentified species may be undescribed. The guts were classified as complete (non-empty or empty) or incomplete (i.e. fragmented) and contents were extracted and ingested material was described. Afterwards, all polychaete species were placed in feeding guilds according to Fauchald and Jumars (1979), with modifications exclusively for Spionidae (Dauer *et al*. 1981). This classification, explained in detail by several authors (Jumars and Fauchald 1977; Fauchald and Jumars 1979; Pagliosa 2005; Cheung *et al*. 2008), classifies polychaetes on the basis of the feeding mode (defined on particle size and composition; i.e. macrophagous and microphagous) and submode (based on the trophic origin of their food or to the stratum from which their food is derived; e.g. surface deposit-feeder and carnivore), motility (based on locomotion used for feeding; e.g. motile and sessile) and feeding apparatus (based on functional morphology used for feeding; e.g. tentaculate or jawed). Environmental variables analysed were related to sediment characteristics (i.e. mean particle diameter, sorting, skewness, kurtosis, sediment diversity and sediment grain size) and salinity, because in estuaries these variables are intimately associated with general distribution patterns of polychaetes (e.g. Wolff 1983; Pagliosa 2005).

Data analysis

The software package PRIMER V.6 was used for all analyses (Clarke and Warwick 2001). The DIVERSE routine was used to calculate Shannon–Wiener diversity of species (H') and the feeding-guild abundance (H'–FG). To assess the potential differences between functional and structural approaches, the RELATE procedure (the equivalent of a non-parametric Mantel test using the Spearman rank correlations), and non-metric multidimensional scaling (nMDS) ordinations were performed to investigate (1) the relationship between structural and functional approaches, (2) the relationship between environmental variables and polychaete species matrices, and (3) the relationship between environmental variables and feeding-guild matrices. The BIO-ENV procedure was carried out to verify which groups of environmental variables were more related to polychaete species than to polychaete feeding guilds.

For all analyses with biological data, replicates of each sample station were pooled, densities of organisms (individuals per m^2) were calculated, and untransformed data were used. All environmental variables were transformed to $\log(x+1)$ and auto-collinearity was verified before the procedure BIO-ENV (Clarke and Warwick 2001). The sequential Bonferroni correction was applied to adjust significance levels for multiple comparisons among species abundance, feeding guilds and environmental variables.

Results

Structural analysis

The samples contained 1551 polychaete specimens distributed among 26 families and 58 species (see Table A1, available as an Accessory Publication to this paper). The magelonid *Magelona papillicornis*, orbiniid *Scoloplos* (*Leodamas*) *ohlini* and nereid *Laeonereis culveri* were the dominant species, constituting 55% of the total polychaete abundance.

In all three estuaries, we found a different set of polychaete species being replaced according to the salinity gradient, during the rainy and dry seasons (Fig. 2). The cirratulids *Aphelochaeta* sp. C and *Timarete* sp. and the sternaspid *Sternaspis capillata* were the most abundant at the mouth region of the rivers Jaguaripe, Paraguaçu and Subaé, respectively (Fig. 2). These species were then replaced in dominance in the lower estuarine region by the magelonid *M. papillicornis* at Jaguaripe estuary, the poecilochaetid *Poecilochaetus johnsoni* at Paraguaçu estuary and the orbiniid *Scoloplos* (*L.*) *ohlini* at Subaé estuary (Fig. 2). Within the upper region of the three estuaries, with salinity ranging from 0 to 10, the nereid *Laeonereis culveri* was the dominant and sometimes the only polychaete found (Fig. 2).

The Shannon–Wiener diversity index showed higher values at the outer estuarine stations (Stations 1–3) than in the other stations in Jaguaripe estuary (Fig. 3). In Paraguaçu estuary, the most diverse stations were Stations 2 and 6, whereas the least diverse was Station 9. In Subaé estuary, Station 2 had the highest Shannon–Wiener diversity value, whereas lower values were found at Stations 5, 8 and 9.

Functional analysis

Stomach-content analysis of 625 polychaetes belonging to 21 species revealed that microphages represented by the submode deposit-feeder were dominant in several species and individuals (Table 1). Some selectivity in relation to composition and size of sediment particles ingested by some species of polychaetes was found. The polychaete species *M. papillicornis*, *Poecilochaetous johnsoni* and *Spiophanes bombyx* appear to be capable of selecting and ingesting superficial detritus with palps or feeding tentacles. Cirratulids, *Laeonereis culveri* and *Scoloplos ohlini* do not select only detritus but also ingest sediment grains. All deposit-feeder specimens analysed were found with full gut contents, whereas typically, carnivorous species had empty guts.

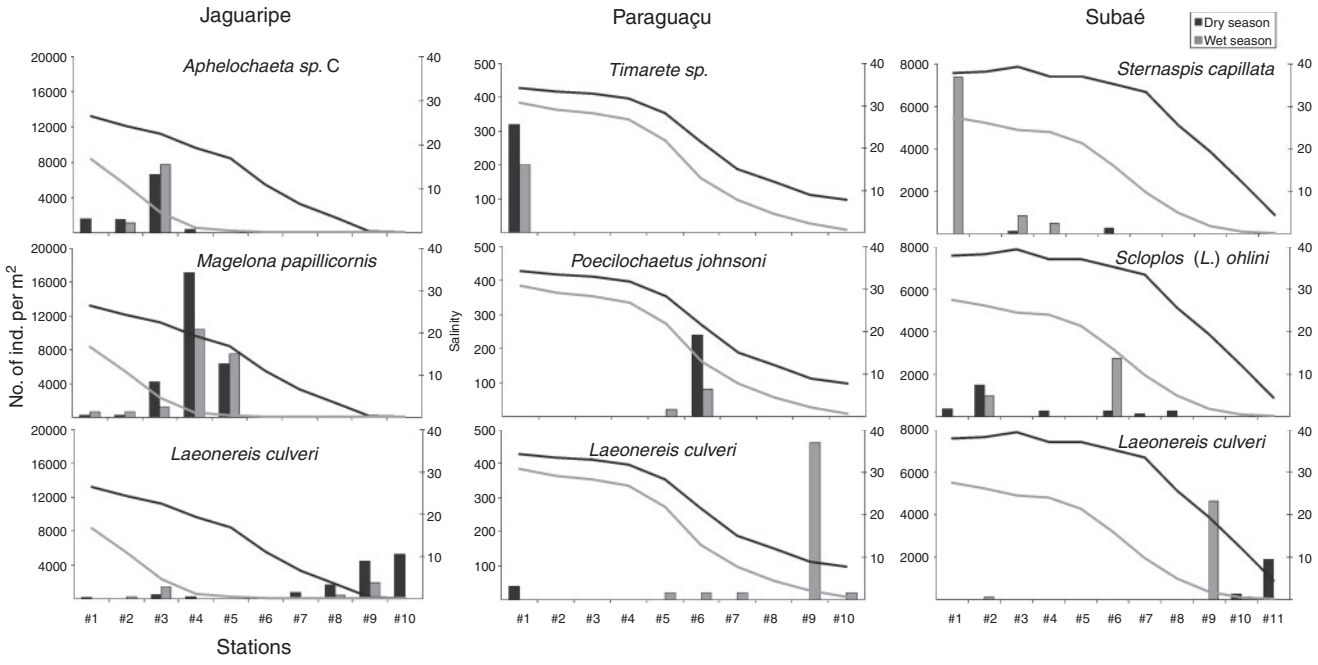

Fig. 2. Replacement of the three most abundant polychaete species along the entire salinity gradient at Jaguaripe, Paraguaçu and Subaé estuaries in dry and wet seasons (salinity range was roughly 34 (Station 1) to 0 (Station 10/11) on low spring tide).

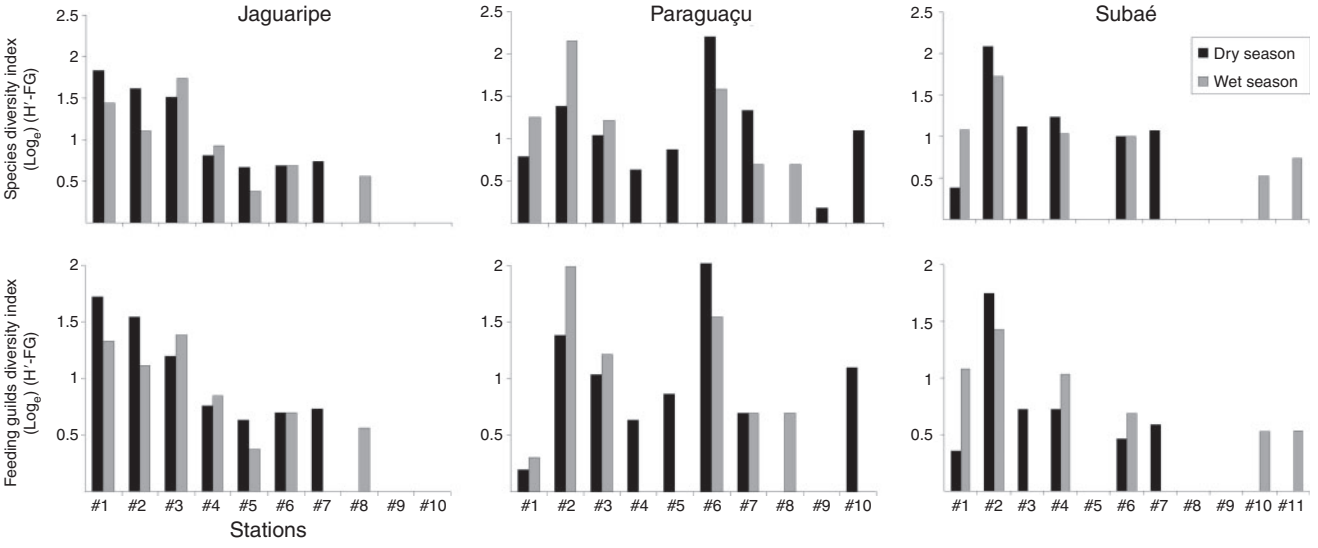

Fig. 3. Shannon–Wiener diversity index for polychaetes species (H') and feeding guilds (H'–FG) in dry and wet seasons at Jaguaripe, Paraguaçu and Subaé estuaries.

All species collected were classified to 14 feeding guilds (see Table 1 for the feeding-guild codes) and the dominant ones were SDT (30.4%), BMX (22.4%), SMT (19.1%) and BMJ (14.8%). The distribution of the most abundant feeding guilds along the estuarine gradient is shown in Fig. A1, available as an Accessory Publication to this paper. The feeding guilds BMX, SMT and BMX were the most abundant at the mouth region of the rivers Jaguaripe, Paraguaçu and Subaé, respectively (Fig. A1). In the lower estuarine region, these feeding guilds were replaced by SDT, ODJ and SMT, respectively, whereas the feeding guild BMJ, composed only by the species *Laeonereis culveri*, was dominant in the upper region of the three estuaries.

The sessile polychaetes were relatively scarce, whereas the motile and discretely motile species showed broad distributions along the salinity gradients of the three estuaries. Tentaculate polychaetes were the most abundant at high-salinity stations (frequently Stations 1–5) where the substrate was composed of fine grain particles (see Fig. A2, available as an Accessory

Table 1. Gut-content analyses and feeding classifications of the 21 polychaete species in the study

The classification of the polychaetes in feeding guilds is a three-letter code, where the first letter indicates the major feeding mode, the second indicates the motility and the third indicates the morphological structure used in feeding. S, surface deposit-feeder; B, subsurface deposit-feeder; C, carnivore; O, omnivore; I, interface-feeder; M, motile; D, discretely motile; S, sessile; T, tentaculate; X, unarmed proboscides; J, jawed

Species	Gut contents			Ingested material	Present classification
	Complete		Incomplete		
	Non-empty	Empty			
Ampharetidae					
Unidentified Ampharetidae	1	–	–	Detritus + medium sand	SST
Arenicolidae					
Arenicola sp.	2	–	–	Detritus	SDX
Capitellidae					
Capitella sp.	1	–	5	Detritus	BMX
Cirratulidae					
Protocirrineris sp.	18	–	6	Detritus + fine sand + very fine sand	SMT
Timarete sp.	5	–	2	Detritus + very fine sand	SMT
Aphelochaeta sp. A	6	–	–	Detritus + very fine sand	SMT
Aphelochaeta sp. B	30	–	18	Detritus + very fine sand	SMT
Glyceridae					
Glycera dibranchiata	–	8	–	–	CDJ
Glycera lapidum	–	5	–	–	CDJ
Hemipodia californiensis	1	5	1	Polychaete chaetae	CDJ
Goniadidae					
Glycinde picta	–	5	1	Unidentified material	CDJ
Magelonidae					
Magelona papillicornis	110	–	50	Detritus	SDT
Magelona variomellata	4	–	11	Detritus + fine sand	SDT
Maldanidae					
Petaloproctus sp.	5	–	–	Detritus + very fine sand	BSX
Nereididae					
Laeonereis culveri	91	–	37	Detritus + fine sand	BMJ
Onuphidae					
Mooreonuphis lineata	–	19	3	Polychaete chaetae + medium sand + unidentified material	ODJ
Orbiniidae					
Scoloplos (*L.*) *ohlini*	54	–	24	Detritus + very fine sand	BMX
Pilargidae					
Sigambra grubei	1	6	3	Unidentified material	CMJ
Poecilochaetidae					
Poecilochaetus johnsoni	–	–	16	Detritus	SDT
Spionidae					
Spiophanes bombyx	1	–	8	Detritus	IDT
Sternaspidae					
Sternaspis capillata	62	–	–	Detritus	BMX

Publication to this paper). Jawed polychaetes were mainly found at low-salinity stations (Stations 7–10/11) where the substrate is composed of coarse grain sediments (Fig. A2).

In Jaguaripe and Subaé estuaries, the number and diversity of polychaete feeding guilds varied, being highest at high-salinity stations and lowest at low-salinity regions, which were dominated by a single feeding group (Fig. 3). However, in Paraguaçu estuary, this pattern was not observed.

Structural versus *functional analysis*

Non-metric multidimensional scaling (nMDS) of species and feeding-guild matrices of the Jaguaripe and Paraguaçu estuaries (Fig. 4) showed resembling patterns, with greater similarities within high-salinity stations (Stations 1–5) and within the low-salinity (Stations 6–10) stations than between them, whereas no resembling pattern was seen for the Subaé nMDS ordinations.

In general, there were few differences between the species and feeding-guild nMDS ordinations. In the Jaguaripe's nMDS ordinations, for example, the same group of stations is seen either for the species or feeding-guild ordinations (Stations 1–5 and Stations 6–10) (Fig. 4). In addition, there were always smaller similarities among samples from Stations 1–5 and 6–10 (or 11) with the species data than with feeding-guild data (see Table A2, available as an Accessory Publication to this paper). The correlations between the similarity matrices of polychaete species found

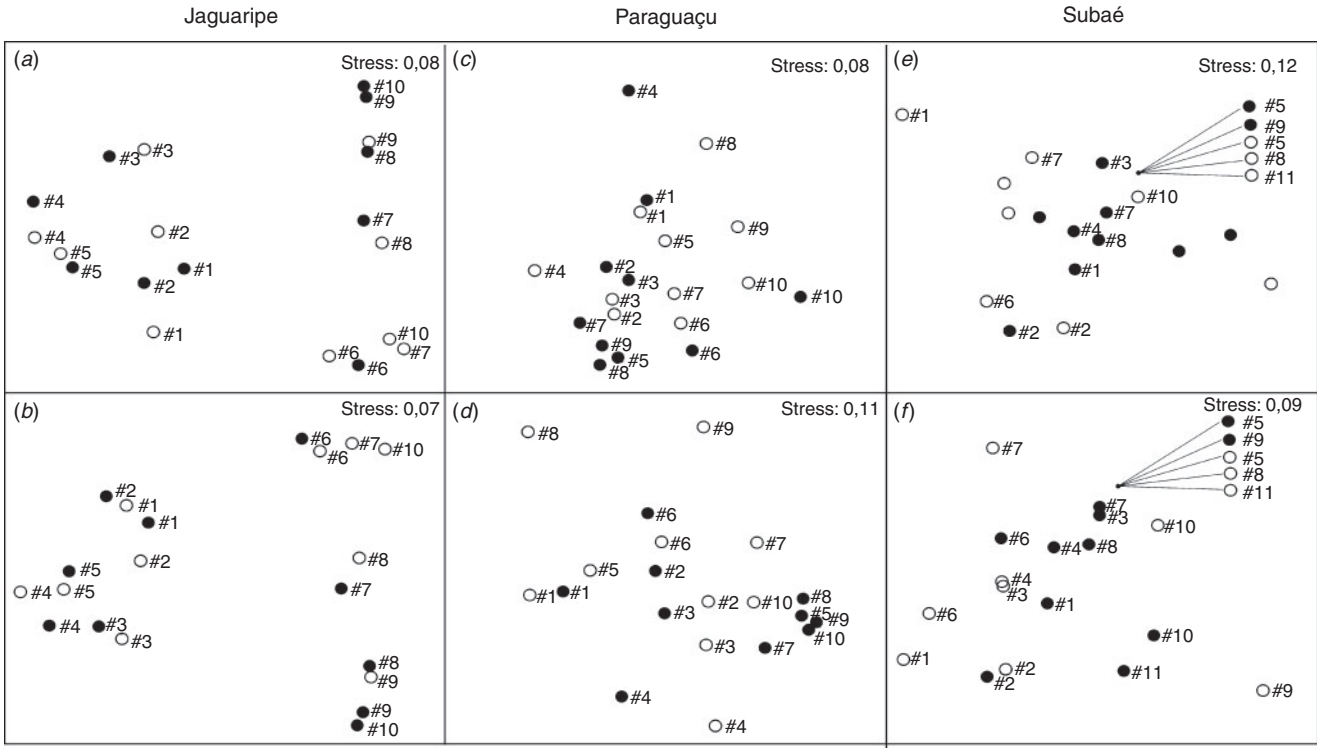

Fig. 4. Two-dimensional non-metric multidimensional scaling (2D nMDS) ordinations plots of polychaetes species and feeding guilds from Jaguaripe, Paraguaçu and Subaé estuaries in dry (open circles) and wet seasons (solid circles). (*A*, *C*, *E*) Species. (*B*, *D*, *F*) Feeding guilds.

Table 2. Results of RELATE procedure between polychaete species and feeding guilds in Jaguaripe, Subaé and Paraguaçu estuaries in wet and dry seasons, showing Spearman rank correlations (r_s)

Estuary	r_s	*P*
Jaguaripe	0.970	0.001
Paraguaçu	0.666	0.001
Subaé	0.858	0.001

Table 3. Results of RELATE procedure where both polychaete-species (sp) and feeding-guild (fg) matrices were correlated with environmental variables (env) at Jaguaripe, Paraguaçu and Subaé estuary in wet and dry seasons, showing Spearman rank correlations (r_s)

Estuary	r_s (sp × env)	*P*	r_s (fg × env)	*P*
Jaguaripe	0.022	0.377	0.002	0.235
Paraguaçu	0.384	0.001	0.319	0.022
Subaé	−0.142	0.806	−0.150	0.671

and their feeding guilds at Jaguaripe and Subaé were greater than was the correlation at the Paraguaçu estuary (Table 2).

In Jaguaripe and Subaé estuaries, most polychaete feeding guilds were composed of one or few species, whereas at Paraguaçu estuary, polychaete feeding guilds usually contained five or six species.

Relationships with environmental variables

The RELATE procedure showed that only in Paraguaçu estuary were polychaete species and feeding guilds significantly correlated with the environmental variables (Table 3). The environmental variables that showed the best correlations with polychaete-species or feeding-guild datasets varied among estuaries (Table 4). In Jaguaripe estuary, sediment sorting and salinity were strongly associated with polychaete feeding guilds. In Paraguaçu estuary, different combinations of variables were significantly correlated with feeding guilds and in Subaé estuary the sediment diversity and salinity appeared to be correlated, although not significantly, to polychaete species and their trophic roles in the estuarine gradient.

Table 4. BIOENV results showing Spearman rank correlations (r_s) and the level of significance

CS, coarse Sand; MS, medium sand; VFS, very fine sand; VCS, very coarse sand; FS, fine sand

Data type	Best variable(s) matched	r_s	*P*
Jaguaripe species	Sorting and salinity	0.533	0.017
Jaguaripe guilds	Sorting and salinity	0.582	0.016
Paraguaçu species	Gravel, pebble, CS, MS, silt + clay	0.384	0.203
Paraguaçu guilds	Pebble, VCS, CS, silt + clay, salinity	0.347	0.031
Subaé species	Silt + clay, sediment diversity and salinity	0.332	0.329
Subaé guilds	Sediment diversity and salinity	0.265	0.644

Discussion

Ecological implications in estuarine ecosystems

The correlation between the similarity matrices of polychaete species and feeding guilds indicates the potential to assess estuarine resilience. In Jaguaripe and Subaé estuaries, these correlations were high, once the feeding guilds were represented by one or a few species. This indicates high numbers of taxa with specific roles in these estuarine systems and low functional redundancy. These species have a specific role in the estuarine ecosystem that could be lost after some sort of disturbance (e.g. changes in the percentage of fine grains caused by flooding might reduce the number of detritus-feeding polychaetes morphologically specialised to capture finer sediment grains). The correlations were lower in the Paraguaçu estuary, and a large number of species were classified and placed in the same feeding guild. Therefore, the Paraguaçu estuary is likely to have a greater possibility of recovering from disturbance and less risk of losing ecological functions than do Jaguaripe and Subaé estuaries, because the species in the Paraguaçu estuary might have a greater capacity to expand their niches to compensate for the neighbouring species that could decrease or even disappear (Johnson *et al*. 1996).

The results for the Paraguaçu estuary agree with those of Gray *et al*. (1988) and Clarke and Warwick (1998), and show a considerable redundancy in the number of species that describe the macrobenthic assemblages. The redundancy hypothesis presented by Walker (1992) proposes that some species may be expendable in terms of ecosystem maintenance if any extant species can take the functional place of the extinct species in the community (see also Johnson *et al*. 1996). From this perspective, in assemblages that have species functionally equivalent in their ecological role, the level of redundancy may be a useful measure of assemblage resilience (Holling 1973; Walker 1995). Thus, polychaete species and their respective feeding guilds could provide a useful way to measure the level of environmental resilience of estuarine systems.

Although it is only by conducting experimental studies such as removing species of a specific functional type from a particular community, that it would be possible to understand the functional redundancy (Clarke and Warwick 1998), the temporal and spatial role observed for the species and reposition of polychaetes in feeding guilds might provide a framework to understand the behaviour of the ecosystem after disturbance (e.g. Fig. A3, available as an Accessory Publication to this paper). Therefore, ecological functions represented by feeding guilds are more likely to persist after disturbances in environments with higher trophic redundancy. These ecosystems with several species overlapping in ecological functions would be more resilient than those with ecological functions carried out by a single or few species.

Structural and functional analysis of polychaetes in estuarine environments and its relation with environmental variables

Most of the diversity patterns of benthic communities in estuaries and others coastal habitats are based on information from temperate regions (e.g. Gray 1997; Attrill 2002; Puente *et al*. 2008; Wildsmith *et al*. 2011), whereas the distributional pattern of polychaetes and others marine invertebrates in tropical estuaries is still poorly known. The estuarine polychaetes from the Brazilian coast have been studied by few authors, mostly from the southern regions (e.g. Lana *et al*. 1997; Santos and Pires-Vanin 2004; Rosa and Bemvenuti 2006).

As expected from such a broad region of estuaries, the polychaete species and their trophic composition from the Baía de Todos os Santos estuaries varied widely. Polychaete species replace one another along the entire salinity gradient (as do all macrobenthic taxa in Paraguaçu estuary; Barros *et al*. 2008). However, the feeding-guild distributions are probably a result of a complex of physical (e.g. sediment characteristics), physicochemical (e.g. salinity) and biotic factors (e.g. food availability from detritus, microbial and macrofauna).

In general, from high- to low-salinity regions, species and feeding-guild diversities varied from high values to dominance by a single species or a feeding group tolerant of these low-salinity conditions. This is particularly true for Jaguaripe and Subaé estuaries where the species and feeding-guild diversities were higher in high-salinity regions and lower in low-salinity regions. However, in the Paraguaçu estuary, the distribution of polychaete species and feeding guilds seems to be influenced by distinct hydrodynamic conditions owing to an embayment (Baía de Iguape) containing Stations 5–7. This embayment reduces the high hydrodynamic energy from the discharge of Paraguaçu River and forms low-energy habitats where the tube-builder *Mooreonuphis lineata* is particularly abundant.

The increase in species richness and feeding-guild diversity with salinity seems to be a common trend in estuaries (e.g. Brown *et al*. 2000; Rakocinski *et al*. 2000). This variety of species and the feeding-guild diversity across the estuarine gradients could provide a useful background for analyses of macrobenthic functional responses to natural and polluted conditions, as has been used for levels of sediment contamination (Rakocinski *et al*. 1997; Gaston *et al*. 1998; Cheung *et al*. 2008). Subaé estuary is contaminated by trace metals (Hatje *et al.* 2006); however, the highest concentrations of metals are found in the upper estuarine region, which is more likely to have low species and feeding-guild diversities.

The estuarine polychaete assemblages of the main estuaries from Baía de Todos os Santos are composed mainly of deposit-feeders and comprise species with different feeding-apparatus and mobility types, especially those adapted to exploit detritus as a food source. This trophic category is expected to show considerable morphological variation (i.e. protrusible oral apparatus, thoracic feeding and anterior sensory structures), which may allow them to capture detritus efficiently (Woodin 1987). In addition, they were always found with full guts, indicative of opportunistic behaviour, probably to compensate for the low nutrient content of the detritus (Jumars 1993). In high-salinity estuarine regions (generally deeper and finer grained), tentaculate polychaetes (e.g. magelonids and cirratulids) were more abundant, whereas in low-salinity regions (generally shallower depths, more dynamic, and coarser grained) the non-tentaculate polychaetes (e.g. nereids) were more abundant. Tentaculate deposit-feeders are expected to be absent or rare in freshwater environments (Lopez 1988), because they need a continuous sediment supply provided by tidal motion in marine environments (Newell *et al*. 1984).

The overall pattern of the relationship among polychaete species, feeding guilds and environmental variables is not clear because the results varied among estuaries. Additionally, a large number of correlations were not significant. Thus, the hypothesis that the polychaete feeding guilds would be more closely related to environmental variables than to the composition of polychaete species was not supported. Further tests should include other variables such as natural organic content and inorganic and organic contaminants, which are likely to have some influence on these benthic assemblages (Hatje *et al*. 2006).

Despite the fact that the initial hypothesis was not supported, an integrated analysis of the structural and functional aspects of polychaetes is recommended to help understand the complex organisation across space and time of the benthic communities. In addition, different recovery levels of degraded estuarine ecosystems could be assessed by an integrative approach. As a result, the understanding of the estuaries as an ecosystem could be enhanced, the priority species for conservation could be established, and management-risk plans could be developed and put into practice.

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