Marine Environmental Research 81 (2012) 43–52

Contents lists available at SciVerse ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Subtidal benthic macroinfaunal assemblages in tropical estuaries: Generality amongst highly variable gradients

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ARTICLE INFO

Article history:
Received 29 May 2012
Received in revised form
14 August 2012
Accepted 18 August 2012

Keywords:
Benthic assemblages
Estuarine gradients
General patterns
Empirical model
Baía de Todos os Santos

ABSTRACT

South American estuaries are frequently not included in the search for general ecological models and studies dealing with biological assemblages in estuaries frequently do not sample the entire salinity gradient. We sampled three tropical estuaries, two times each, on ten stations distributed along each system. Six replicates were collected in each station for the benthic macroinfauna and sediment samples for grain size and inorganic contaminant analyses. There were finer sediments at the lower than at the upper estuarine portions. There was a decrease in the diversity, at family level, from marine to freshwater and the differences on the structure of the benthic assemblages were mostly spatial. In spite of the many different characteristics of the three estuaries (e.g. catchment size, pollution levels, proximity with the inner continental shelf) several consistent patterns of benthic macrofauna distribution along these systems were still observed. It suggested a general empirical model regarding the distribution of different benthic invertebrates along tropical salinity gradients which can be tested in different estuaries around the world.

1. Introduction

Estuaries provide a wider variety of ecosystem functions and societal benefits (Elliott and Whitfield, 2011). They are widely recognized as one of the most important transition systems on earth, highly productive and can be feeding areas and nursery grounds for many commercial species. The great majority of the world's estuaries are influenced by human activities, mostly as consequences of the rapid human growth and poor management (Edgar et al., 2000; Kennish, 2002). As a result they have been pushed far from their historical baseline of rich, diverse, and productive ecosystems (Lotze et al., 2006; Merrifield et al., 2011). Very few tropical estuaries are, nowadays, near pristine conditions and estuaries in South America are frequently unnoticed by studies dealing with general patterns in large scales (e.g. Borja et al., 2008; Elliott and Whitfield, 2011; Klemas, 2012). Although estuaries across the globe share similar driving forces (e.g. salinity gradient), there are substantial differences among different geographic regions (e.g. tidal range, seasonality) (Perillo et al., 2009). There is still an urgent need to identify consistent spatial and temporal patterns of estuarine benthic assemblages, specially in tropical systems, to allow further investigations about ecological processes (Underwood et al., 2000). The identification of the patterns caused by deterministic processes evolving populations, and its interactions, is a major challenge in ecology (Maurer, 1999). Most ecologists work at scales where complexity tends to be greatest (i.e. local) and is likely to be explained by special and unique events (Fowler-Walker et al., 2005). Furthermore, the search for general rules governing environmental systems is extremely difficult due to the lack of predictability and due to the fact that long-term data is generally needed (Boero, 2009; Dolbeth et al., 2011).

Benthic assemblages are frequently mentioned as good indicators of environmental quality and are included in impact assessment studies of marine and coastal areas. However, the establishment of causal relationships between anthropogenic stressors and its effects on the structure of benthic assemblages is difficult (Elliott and Quintino, 2007). This is essentially due to the chemical, physical and biological complexity of these systems with interacting anthropogenic stresses (e.g. Adams, 2005). Transitional systems present high complexity with strong natural gradients that may confound the evaluation of anthropogenic stressors (de Paz et al., 2008). It have been suggested that the management of estuaries has to not only accommodate the causes and consequences of pressures within the estuarine system but also need to

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http://dx.doi.org/10.1016/j.marenvres.2012.08.006

respond to the consequences of external natural and anthropogenic influences (Elliott and Whitfield, 2011). Nevertheless, some studies have been showing predictive responses of the benthic assemblages (e.g. Gogina et al., 2010).

Salinity is the environmental factor of utmost importance in estuarine systems (e.g. Cognetti and Maltagliati, 2000; Telesh and Khlebovich, 2010; Telesh et al., 2011), actually it defines the system, and alterations in the salinity regime might cause changes in the distribution of estuarine invertebrates (Gillanders and Kingsford, 2002; Mcleod and Wing, 2008).

Many studies described the variation on the structure of several biological assemblages along salinity gradients, these included saltmarshes (e.g. Khedr, 1998; Netto and Lana, 1999), benthic invertebrates (e.g. Bulger et al., 1993; Rossi et al., 2006), benthic diatom (e.g. Sgro et al., 2006), bacteria (e.g. Cottrell and Kirchman, 2004; Freitag et al., 2006), phytoplankton (e.g. Gobler et al., 2006) and fish (e.g. Hampel et al., 2004; Marancik and Hare, 2007; Simier et al., 2006). Nevertheless, studies dealing with biological assemblages in estuarine gradients frequently sample a few portions (e.g. upper, middle and lower estuary) from the entire salinity gradient (e.g. Dye and Barros, 2005a, 2005b; Gobler et al., 2006; de Paz et al., 2008; Lu et al., 2008; Carvalho et al., 2010) potentially obscuring broad general patterns (Lawton, 1999). Nevertheless, knowing the patterns of distribution of benthic assemblages along different estuarine gradients is essential in order to understand of the general functioning of these systems.

The present work had the objective of identifying the main spatial patterns of the structure of the benthic macrofaunal assemblages along three different tropical estuarine systems, to test its relationships with environmental variables and propose a general empirical model of broad application.

2. Methods

2.1. Sampling

The Baía de Todos os Santos (BTS) is the second largest bay in Brazil and has several large rivers flow into it. The bay's tides are characteristically semi-diurnal and the currents inside the bay are tide driven (Cirano and Lessa, 2007). The estuarine portion of the main tributaries of BTS was sampled in this study. The Paraguaçu River has the larger drainage basin, with 56,300 km^2 followed by Jaguaripe River (2200 km^2) and Subaé River (600 km^2) (Cirano and Lessa, 2007).

Macrozoobenthic assemblages from 10 subtidal stations in each main of the tributaries of BTS were sampled along the entire salinity gradient (Fig. 1) on two different occasions. The Subaé estuary was sampled on June (rainy season) of 2004 and March of 2006 (dry season), Paraguaçu on May 2005 (rainy) and December 2005 (dry) and Jaguaripe on May 2006 (rainy) and August 2007 (dry). Six replicates were collected in each sampling station yielding 360 samples (2 times or sampling occasions × 3 estuaries × 10 sampling station × 6 replicates). The stations were numbered 1 to 10, stations numbered 1 were most seaward and deepest and stations 10 were furthest inland and shallowest. The salinity of the superficial water was measured at spring low ebb tides and recorded using a Hydrolab DataSonde.

In Paraguaçu estuary six replicate samples were collected at each station using a 0.05 m^2 van Veen grab (see details in Barros et al., 2008). In Jaguaripe and Subaé estuaries six replicate samples were manually collected at each station using a 0.008 m^2 corer by divers. Core sampling was not suitable to Paraguaçu River due to large depth in some stations and also due to very strong

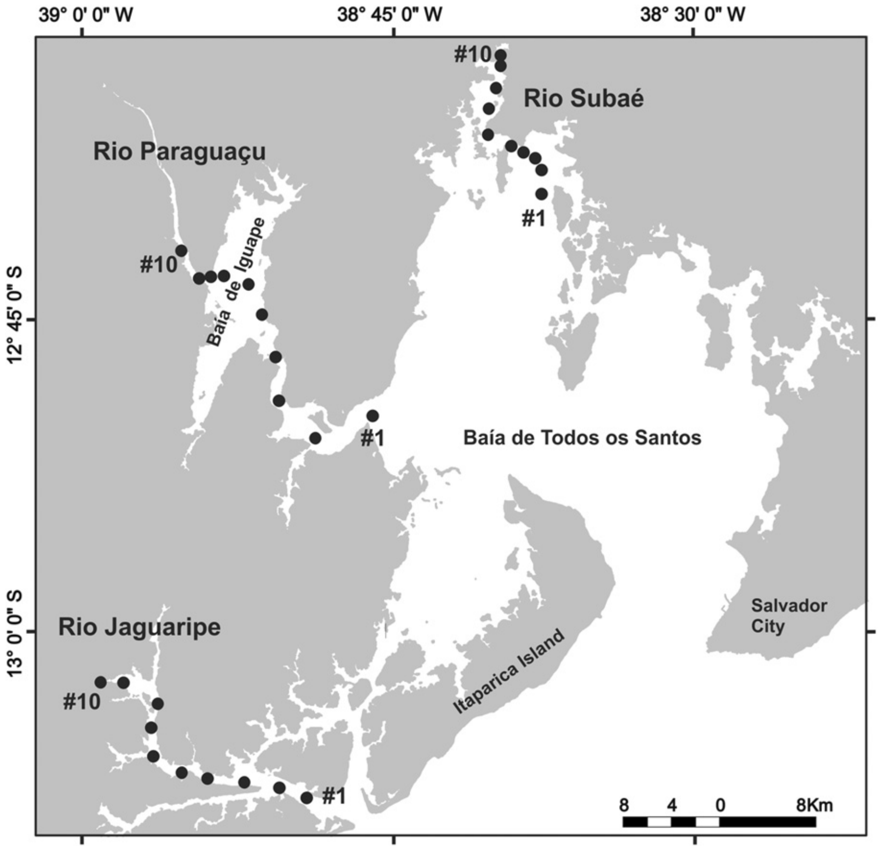

Fig. 1. Map of the studies area showing the sampled stations (black dots) of each estuary (Subaé, Paraguaçu and Jaguaripe) at Baía de Todos os Santos, Brazil.

currents and zero visibility. All macrofaunal samples were sieved through a 0.5 mm mesh in the field and preserved in 70% alcohol until sorting in the laboratory. Invertebrates were identified mostly to family considering that family level is enough to show the estuarine macrofaunal changes (De Biasi et al., 2003) and due to (i) the scarcity of taxonomical studies of the local benthic invertebrates (with numerous or substantial numbers of undescribed species) and (ii) to investigate a general model of taxa distribution which might be tested in other regions.

One sediment sample was collected at each stations at each sampling occasion (dry and wet seasons) for grain size analysis, using a 0.05 m^2 van Veen grab for Paraguaçu River and a 0.008 m^2 corer for Jaguaripe and Subaé River. Mean particle diameter, Sorting, Skewness, and Kurtosis were calculated using the software SysGran 3.0 (Camargo, 2006) and following (Folk and Ward, 1957) methods.

Trace metals (Ba, Cd, Cr, Co, Cu, Mn, Ni, Pb and Zn) were extracted with 1.0 mol L^1 HCl and determined by ICP OES (VARIAN Vista-Pro). Blanks were included in each batch of analysis. The precision and accuracy of the analytical technique were assessed by the analysis of a Certified Reference Material, MESS-2 (National Research Council of Canada) with each batch of samples (see details in Hatje et al., 2006).

2.2. Data analysis

Benthic taxa used in the statistical analysis were those which contributed to more than 90% of the total abundance and that were sampled in at least two sampling. Taxa that were colonial (i.e. cnidarians, bryozoans, sponges) attached, for instance, to shells or pebbles within the samples, were excluded as they were not properly quantified. A dummy variable was introduced to include stations with no invertebrates in the analyses (Clarke et al., 2006).

For the analyses, abundances were expressed as densities due to the different size of the sampling devices. In order to understand the sources of variation in the estuarine benthic assemblages we performed a hierarchical component of variation with the biological data. A sequence of partial hierarchical multivariate analysis was then performed following Leps and Smilauer (2003). For this analysis, all replicates in each sampling station were summed and the hierarchical structure was based on all of the spatial and temporal data. The balanced design of three estuaries (Es) sampled on ten stations (St) in the two seasons (Se) the variation to be partitioned and assessed across the three sources of variation. To assess the effects of the temporal (season) and spatial scales (estuaries and stations) upon the benthic community, the individual samples were not permuted at random. The groups representing each individual cases of the different levels (season, estuary or station) immediately below the tested level was held together (this was achieved using the split-plot design permutation option in Canoco; Leps and Smilauer, 2003).

To visualize patterns in benthic assemblages and environmental data, two partial principal component analysis (pPCA) were conducted using seasons as co-variables (Ter Braak and Prentice, 1988; Leps and Smilauer, 2003). Partial analyses were used because season was not significant (see the results section, Table 1). In all multivariate analyses, the biological data was hellinger transformed to make the biological data amenable to linear ordination method (Legendre and Gallagher, 2001). Before performing the direct gradient analysis, aiming to explain the detected pattern in the benthic assemblage, a search for multicollinearity in the set of explanatory environmental data was made. First, a pair plot with all environmental variables (% of gravel, % of sand, % of silt, distance Cd, As, Co, Cr, Cu, Mn, Ni, Pb, Zn and salinity) showing the Pearson's correlation coefficients was carried out. Second, we conduct a variance inflation factor analysis (VIF) based in a partial redundancy analysis (pRDA) with season as co-variables and all environmental variables as explanatory variables. We used a >10 VIF criteria as an exclusion rule (Zuur et al., 2009, 2007). A direct gradient analysis was performed using variables that passed by the VIF and correlation criteria as explanatory variables. A partial redundancy analysis (pRDA) was used to construct a model relating environmental data to biological data. A dummy variable was used to represent season and was used to partition out the effect of this design variables from the adjusted model. A Monte Carlo's permutation procedure was performed with all variables in the analysis to test axis significance considering the trace test rather than individual axis test. The forward selection procedure was used to construct final model only with significant variables.

Table 1
(a) Sources of variation used to partition the total variance in the benthic assemblages of the main estuarine systems of Baía de Todos os Santos (n.a. = not applicable). (b) Results of variance decomposition (significant results in bold).

(a) Sources of variation

Variance component	Environmental variables	Co-variables	Permuting blocks	Whole plot represent
Season (Se)	Se	None	No	Es
Estuaries (Es)	Es	Se	Se	St
Sampling Stations (St)	St	Es	Es	None
Residual	None (PCA)	St	n.a.	n.a.
Total	None (PCA)	None	n.a.	n.a.

(b) Variance decomposition

Component	DF	Explained variability (%)	R^2 adj.	*F*	Test significance
Se	1	0.9	0.9	3.318	0.796
Es	**4**	**8.8**	**2.2**	**8.616**	**0.001**
St	**54**	**46.5**	**0.861**	**5.886**	**0.001**
Residual	300	43.8	0.146	n.a.	n.a.
Total	359	100	0.276	n.a.	n.a.

A pRDA model was constructed partialling out season and estuary effect, this model was an attempt to create a more general model. A LOESS function was adjusted to the most important variable to explain benthic assemblage structure and was superimposed in ordination diagram of the general pRDA model. Two pPCAs were performed with the same co-variables used in this two pRDAs aiming to extract the largest explained variance at the same model complexity. Those calculated thresholds, rather than 100%, were used to evaluate the achieved total variance explained by the two proposed pRDAs models (Leps and Smilauer, 2003).

3. Results

All the estuarine samples collected around 3100 invertebrates belonging to 87 different taxa (Table 2, Supplementary material). Several taxa were abundant in the three estuaries. The polychaetes from the family Nereididae represented 10% of the total number of individuals collected at Subaé, 10.7% at Jaguaripe and 3.9% in Paraguaçu, manly in the oligohaline zones (Fig. 2). Bivalves from the family Tellinidae represented 11% of the total number of individuals in Subaé 7.5% at Jaguaripe and was the most abundant taxa at Paraguaçu with 18% with greater abundances in mesohaline and oligohaline zones (Fig. 2). Cirratulids were 2.8%, 13.6% and 9% of the total number of invertebrates collected at Subaé, Jaguaripe and Paraguaçu, respectively, more abundant in the mixohaline zones (Fig. 2). At Subaé and Jaguaripe, orbiniids were within the most abundant taxa with 9.6% and 18.5% of the total number of individuals, respectively (Fig. 2). Glycerids contributed to 1.5% and 4.6% of the total number of invertebrates collected at Jaguaripe and

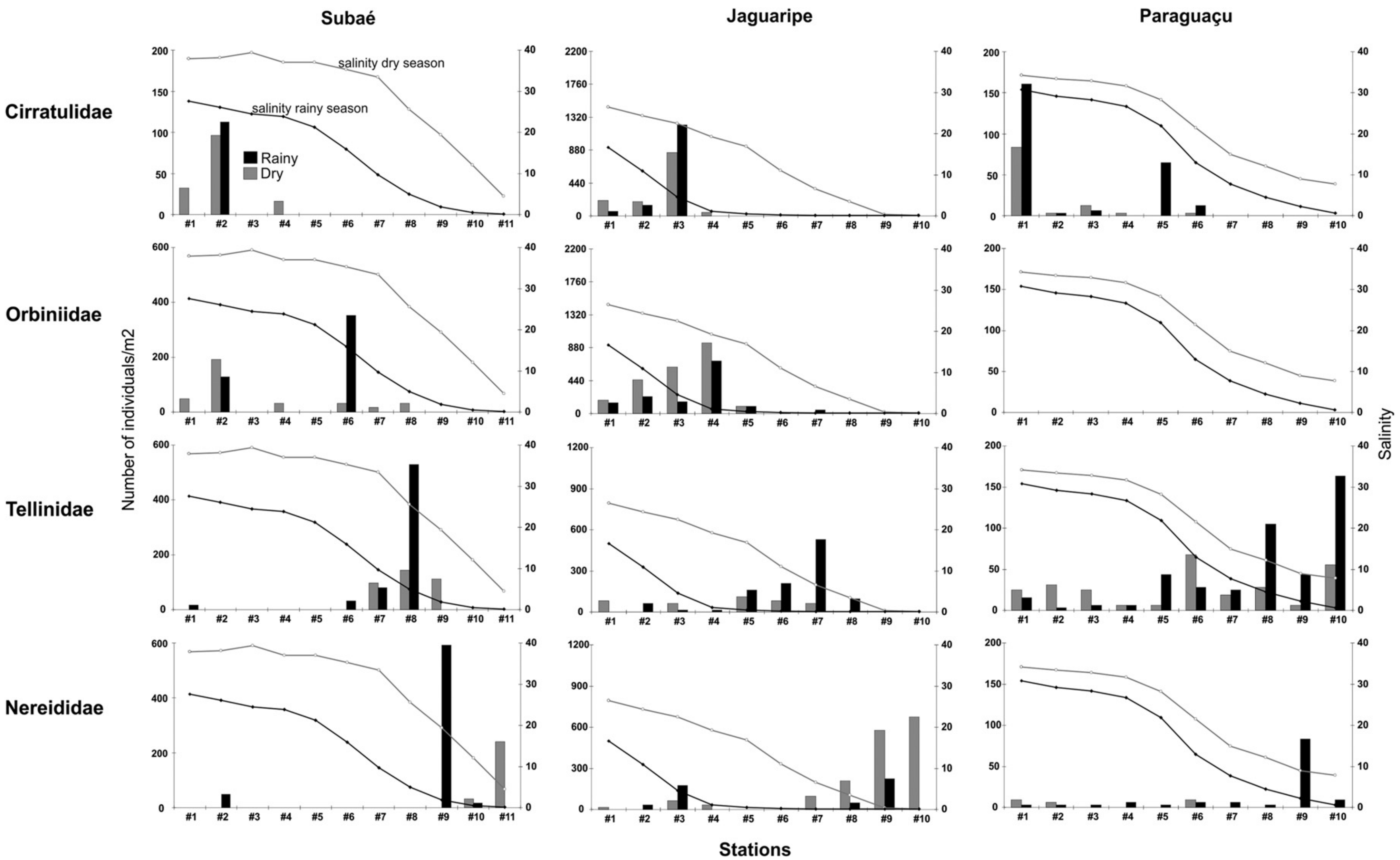

Fig. 2. Abundance (number of individuals/m^2, left vertical axis) of some very frequent taxa in the two sampling occasions (dry season: grey bars, rainy season: black bars) along the three estuarine systems. The continuous lines are showing the surface water salinity (scale on the right vertical axis) on each occasion (dry season: grey line, rainy season: black line).

Paraguaçu, respectively. Magelonids were the most abundant taxa at Jaguaripe (35%) and represented only 1.4% of the total number of individuals at Subaé. Sternaspids polychaetes were the most abundant taxa at Subaé (12.5% of the total number of individuals), but were rare at Jaguaripe (less than 1%) and did not occur at Paraguaçu. The total number of taxa (at family level) generally decreased in the inner portion (i.e. towards the oligohaline zone; sensu Venice System, 1959) of all estuarine systems (Fig. 3), but in the middle estuary of Paraguaçu (Baía de Iguape), there was an increased in the number of taxa.

Variation in the structure of the benthic assemblages at the estuaries level was relatively high compared with other spatial (station) or temporal (season) scales. Variation in estuaries ($p = 0.001$) and stations ($p = 0.001$) was significant (Table 1). While the variation at the temporal scale (i.e. season) was not significant ($p = 0.796$), indicating that there was no need of partialling out season effect in all subsequent analysis. Nevertheless, season was sustained as a co-variable to account for sampling design when performing a complete comparison using inter-season samples as replicates (Table 1a).

In the partial principal components analysis (pPCA), performed to characterize the environment of the three estuaries (Fig. 4), the first two axes explained 54.4% of total variation. The estuarine systems were also separated, but in this ordination, Subaé estuary did not overlap the other two systems. The first axis explained 34.5% of total variation and was related with increased metal contamination of Cu, Zn, Ni, Pb and Cd, especially in Subaé River (Fig. 4). Magnesium, in the left side of the ordination, was associated with the Jaguaripe stations and Paraguaçu stations were distributed in the middle of the ordination (Fig. 4). The second axis explained 19.9% of total variation and was related with the increase of silt and salinity, plotted in the upper part of the ordination, which varied from 34 to freshwater. An increase in sand, with distance from the mouth, was also observed in the three systems, plotted in the lower part of the ordination.

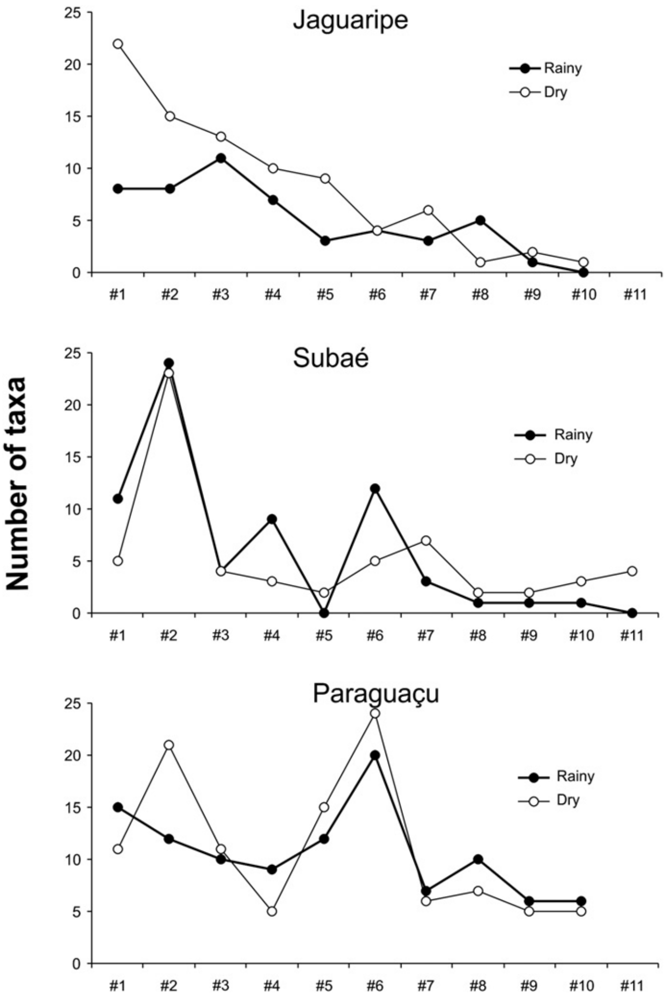

Fig. 3. Number of taxa along the three estuaries (Jaguaripe, Subaé and Paraguaçu) at two occasions (dry season: grey line, rainy season: black line).

In the partial principal components analysis (pPCA) using the benthic assemblage data (Fig. 5) the first two axes explained 23.4% of the total variation. The main pattern was the partial separation of the estuarine systems, mainly Paraguaçu from Jaguaripe, while Subaé stations were plotted in the centre of the ordination. The first axis explained 12.5% of total variation and was related with increase densities of Penaeoidae, Grapsidae, Lucinidae, Nuculidae, Amphiuridae and Corbulidae, in the right side of the ordination, mostly associated with the low estuary of Paraguaçu River. Sampling stations from each estuary were observed, with some variation, from inner to outer estuary (i.e. 1–10) on the second axis. This axis explained 10.9% of total variation and was related with the increase in the densities of Anthuridae, Branchiostomidae, Amphipoda, Orbiniidae and Magelonidae, more abundant in the outer estuary of Jaguaripe than in other estuaries. The bottom part of diagram was associated with increase densities of Donacidae and, to a lesser extent, Tellinidae. Both were abundant in the three estuarine systems (Fig. 5).

Zinc, sand and distance were multicollinear, based in both procedures used to identify multicollinear variables, thus, they were excluded from the partial redundancy analysis (pRDA). This analysis was performed with the inclusion of gravel, silt, Cd, As, Co, Cr, Cu, Mn, Ni, Pb and salinity. The general pRDA model was significant according to Monte Carlo permutation procedure ($p = 0.002$). Forward selection results indicated that variables gravel, As, Cr, Cu and salinity were significant and improved the variance explained by the model ($p < 0.05$) thus, only those variables were maintained in the final model. In this pRDA model (Fig. 6) the first two axes explained 13.6% of total variance. This model has a relatively low explained variance, indicating that there is noise, but an interpretable ecologically pattern can be observed. The first 5 axis of a pPCA with the same partialling out variable, explained 44% of total variance in data. This result weakens the importance of small variability explained by the pRDA. The first axis explained 8.0% of total variation and was related with increase in As and Cr concentration plotted in the right/upper portion of ordination diagram. This pattern was associated manly with an increase in the densities of Cirratulidae, Anthuridae, Brachiostomidae, Amphipoda, Orbiniidae, Onuphidae and Maldanidae. The upper right quadrant of the ordination diagram was related with outer stations of Jaguaripe. The lower right quadrant was related with increase of salinity, mainly in Subaé and Paraguaçu and associated with different taxa (e.g. Nuculidae, Amphiuridae, Paguridae). The left side of ordination diagram was related with increase of Cu concentration, manly in inner stations of Subaé River. The second axis explained 5.6% of total variation and was related with low salinity plotted in upper/left portion of diagram, it is noteworthy that the Jaguaripe River has lower mean salinity when compared with other two estuaries.

When a pRDA model was constructed, partialling out the season and estuary, a general model was constructed (Fig. 7). In this model, a gradient of increased salinity and Cr concentration provided the strongest correlation with the benthic assemblages. This analysis showed (see also Fig. 3) an increase in macrofaunal diversity, at family level, with an increase in salinity. Some taxa like Cirratulidae

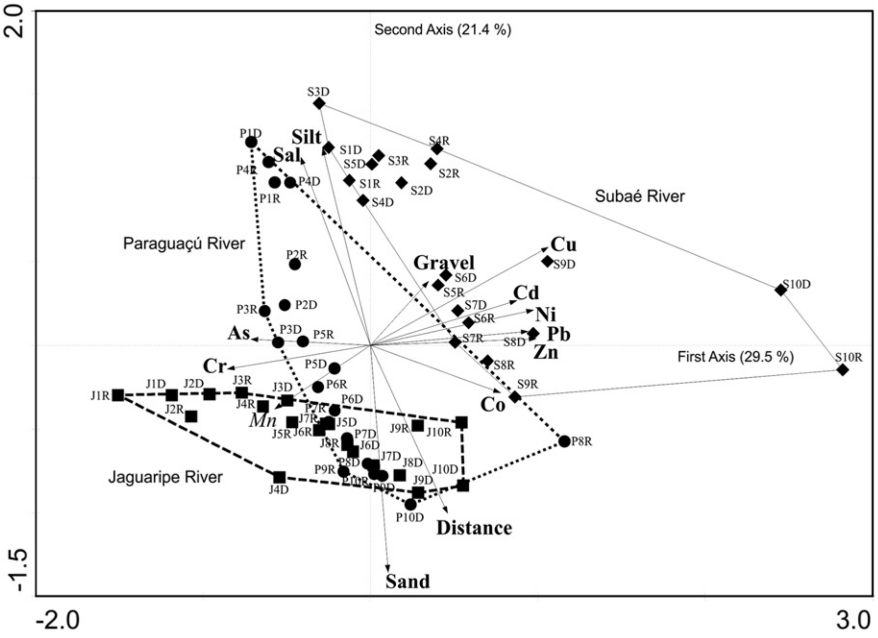

Fig. 4. Partial principal components analysis (pPCA) using the environmental data from the three estuaries (S: Subaé, P: Paraguaçu, J: Jaguaripe; Numbers 1–10: stations, D = dry season, R = rainy season). The sampling stations of each estuary are contained in an envelop (Subaé: continuous line, Paraguaçu: short intermittent line, Jaguaripe: long intermittent line).

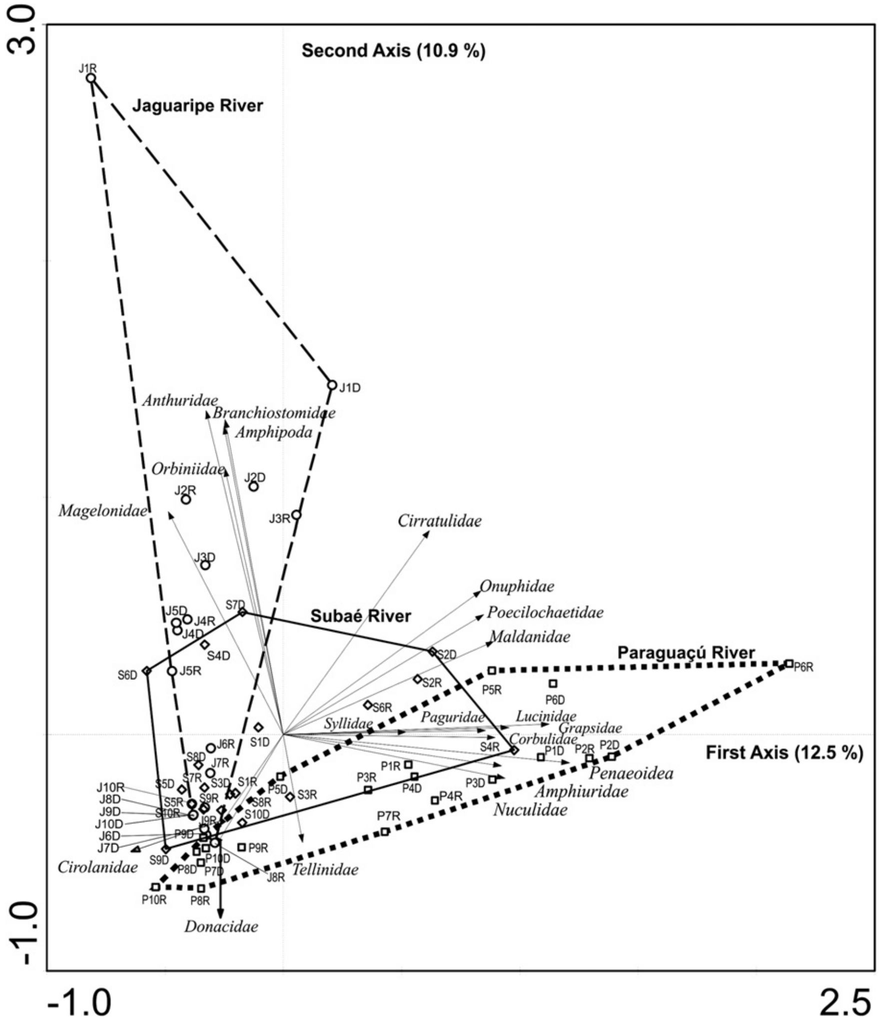

Fig. 5. Partial principal components analysis (pPCA) using the benthic assemblage data sampled at the three estuaries (legends same as in Fig. 4).

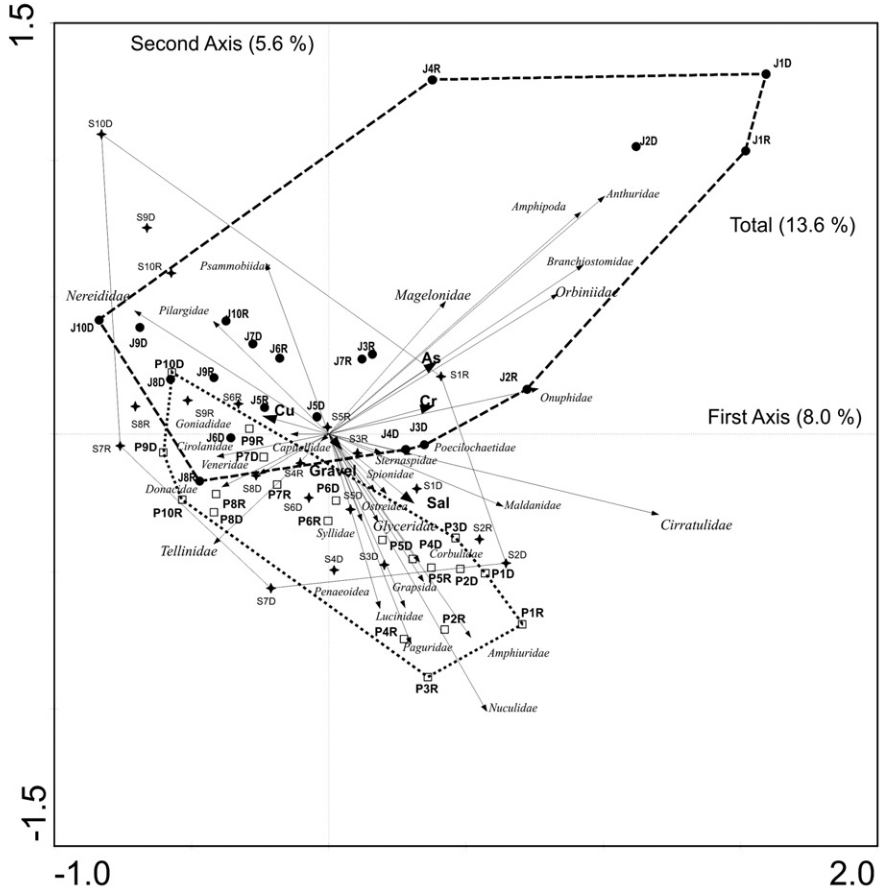

Fig. 6. Partial redundancy analysis (pRDA) using benthic and environmental data (legends same as in Fig. 4).

and Orbiniidae were associated to higher salinities, in the outer part of estuaries. A less diverse assemblage was observed in inner estuary regions and few taxa (e.g. Tellinidae, Nereididae) were more abundant in this lower salinity estuarine environment. Most of the families were represented by one or few species or morphotypes as previously observed for polychaetes in these estuaries (Magalhães and Barros, 2011).

This final general pRDA model (Fig. 7) explained 13% of the total variance, great part of the total variance explained by pRDA model with only season as co-variable, showing that this amount of variation can be attributed to an overall gradient independent of seasons and variation among estuaries. This model also achieved relatively low explained variance too, but an interpretable ecologically pattern can be observed. In the same way, the first 5 axis of a pPCA with the same partialling out of variables (i.e. seasons and estuaries) explained 39% of total variance in data. This result weakens the importance of small variability explained by the general pRDA model.

Distance showed high correlation with Salinity ($r = -0.66$) and As ($r = -0.55$), sand showed high correlation with silt ($r = -0.88$) and Salinity ($r = -0.66$) and Zn showed high correlation with Pb ($r = 0.99$). Once Salinity, As and Silt showed to be significant by the forward selection, the interpretation of those variables must be done with careful (i.e. the effects may be in reality the effects of the multicollinear variables deleted from the analysis).

4. Discussion

High salinity values were generally associated with fine sediments and with an increase in the abundance of several taxa, especially with Cirratulidae, in the outer part of the three estuaries. A less diverse assemblage was observed in inner estuary regions and few taxa, especially Tellinidae, Nereididae and Cirolanidae, were more abundant in this lower salinity estuarine environment. In general, there was a decrease in the diversity, at family level, of macrofaunal assemblages from marine to freshwater. This contradicts one of the oldest paradigms in estuarine ecology, the Artenminimum zone (Remane, 1934), where between salinities of 5–8 the relative number of “true brackish water species” reach a maximum while species richness of organisms of freshwater or marine origin decreases to minimum and then increase again towards marine waters. This zone is considered as a physiological and evolutionary barrier (Telesh and Khlebovich, 2010). However, recently studies, had challenged this pattern regarding its application for all taxa, not only benthic assemblages (Elliott and Whitfield, 2011), and suggested a new conceptual model (Whitfield et al., 2012) where estuaries with marked salinity fluctuations (i.e. not static as in Baltic Sea for instance) might not present the Remane’s pattern. However, only a well design and comprehensive meta-analysis can test, in the future, if a general model regarding diversity of benthic assemblages can be in fact generally observed and how these patterns will vary with different taxonomic levels. Certainly, to avoid the inclusion of freshwater and marine habitats, the starting point is the definition of the estuarine environment itself. The present study, which worked with the upper limit of tidal influence (above 0 of salinity) till oceanic salinities (i.e. 34–35), observed an increase in families with increasing salinities.

The results showed that the differences on the structure of the benthic assemblages were mostly spatial. Season was not of major

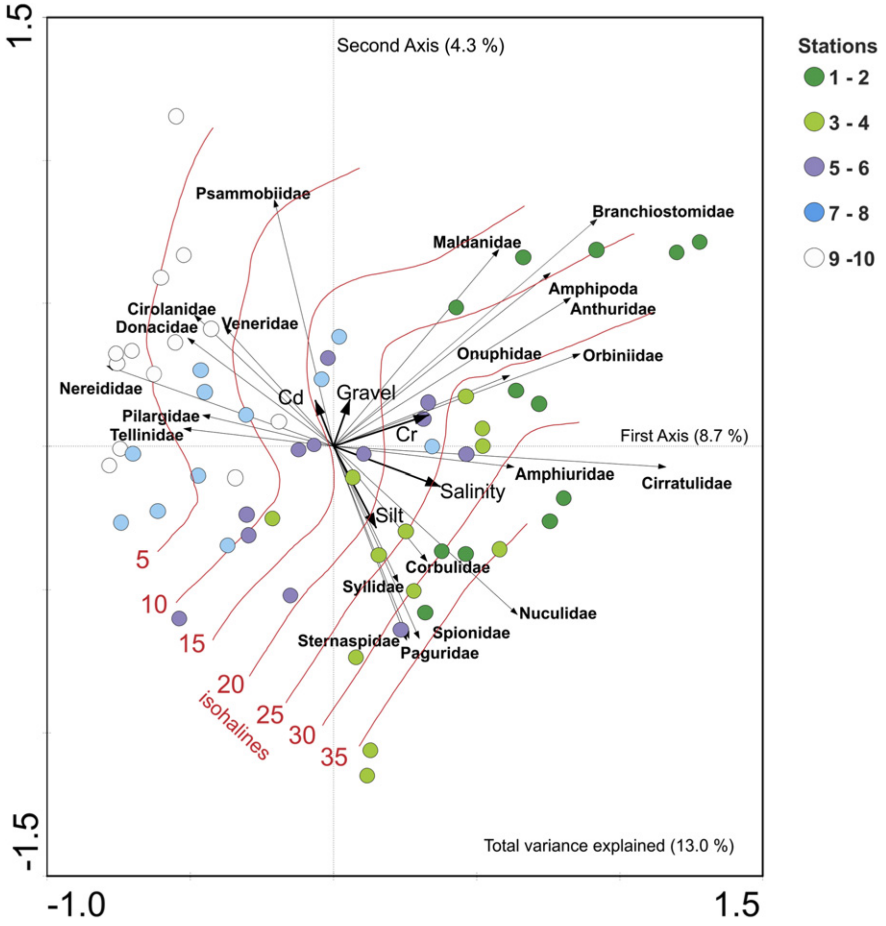

Fig. 7. Final partial redundancy analysis (pRDA) based on three tropical estuarine systems at Baía de Todos os Santos (groups of two stations were coloured to facilitate visualization). The empirical model is showing that different taxa are associated with different salinities (isohaline in red) along tropical estuaries. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

importance and significant differences were found between and within the estuarine gradients (i.e. estuaries and stations, respectively). The benthic assemblages in Paraguaçu were mostly different from Jaguaripe, but Subaé assemblages had some similarities with both estuaries. This indicates two important points. First that, in spite of the fact that each system have some particularities and preserves some degree of differentiation, some taxa can be found at the three systems. Secondly, and more important, that future benthic studies in these region, and likely in other tropical regions, should be very aware of spatial variability among and within estuaries. Nevertheless, well structured long-term monitoring (e.g. Ferreira et al., 2007) in tropical estuarine systems are scarce and must be one of the major objective of estuarine research around the globe as well as the development of data repository (Reichman et al., 2011) for these systems.

Regarding the environmental variables, a general trend was that there were more fine sediments at the lower estuary than at the upper estuary, where the sediments were composed by greater proportions of sand. Another important result was that Subaé estuary was quite dissimilar form the other two systems due to high levels of inorganic contaminants specially at the upper estuary, as reported elsewhere (Hatje et al., 2006; Hatje and Barros, 2012). Some trace metals were important in the structure of the benthic assemblages, especially in the upper Subaé estuary. Nevertheless, it seems that all the three systems are still developing important ecological and, certainly, economical functions with several human populations depending on them as their major income.

It have been suggested that 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 and Maltagliati, 2000). However, the same authors also suggested that in estuarine systems found in the same biogeographical region, it is expected that the same species would occupy similar estuarine regions. In the present study, in spite of the many different characteristics of the three estuaries (e.g. catchment size, pollution levels, proximity with the inner continental shelf) several consistent patterns of benthic macrofaunal distribution along these systems were still observed. For instance, the upper regions of the three systems showed peaks of abundance of nereidids and this was also observed in estuaries in other regions of the world (e.g. Deaton and Greenberg, 1986; Pook et al., 2009). In a similar way (i.e. consistent peaks of abundance at certain regions) there were tellinids, also more abundant in the upper regions, cirratulids more abundant at lower estuarine regions. Further studies must to address if there are differences in these taxa that can be found in different estuaries. For instance, how the populations of nereidids (*Laonereis culveri*, Magalhães and Barros, 2011) can cope with sediments with different levels of contamination must be investigated.

These results suggest a general empirical model regarding the distribution of different benthic invertebrates along tropical salinity gradients. In interpreting this model it must be kept in mind that the goal was not explaining 100%, because part of the total variance is due to noise in the data. Moreover, the percentage of the explained variance is dependent on the number of variables in the analysis (e.g. with only two environmental variables in the analysis, the two canonical axes would explain 100%) regardless of whether the result is ecologically meaningful (Teer Braak and Smilauer, 1998). Several other studies achieved low explained total variance and found meaningfully interpretable results (e.g. Booth, 2001; Quinlan et al., 2003; Dantas and Batalha, 2011). Therefore, it must be kept in mind that the empirical model presented here is not a definitive and universal one, but it is ecologically meaningful and can be properly tested and further developed by future studies. These should look at broad general patterns and general rules governing estuarine tropical systems to propose robust and general models of wide application.

Acknowledgements

We thank several colleagues who helped with the fieldwork and gave laboratory assistance. We also thank Dr. N. Knott and two anonymous referees for the corrections and valuable comments on the manuscript. This research was funded by CNPq (No. 478265/2008-5). F Barros was supported by a CNPq fellowship (No. 302642/2008-0).

Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.marenvres.2012.08.006.

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