The distribution of macrofauna on the inner continental shelf of southeastern Brazil: The major influence of an estuarine system

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ARTICLE INFO

ABSTRACT

The environmental heterogeneity of the Campos Basin on the northern coast of Rio de Janeiro State was assessed by the benthic macrofauna on the platform adjacent to the Paraíba do Sul River (PSR) on the dry and rainy seasons. The samples were collected in triplicate from 33 sites using a van Veen grab during March 2009 − a period of higher precipitation and flow rate − and July 2009 − a period of lower precipitation and flow rate. The grab depths ranged from 12 to 97 m and were grouped into three strata: 1: <25 m, 2: 25−50 m and 3: >50 m. The particle size, total carbonate and total organic carbon in each sample were analyzed. Subsamples for the macrofauna analysis were washed, sieved with a 500 μm mesh and identified. The sediment was predominantly composed of sand, with mud pockets near the mouth of the river. The macrofauna included annelids, crustaceans, mollusks, echinoderms, cnidarians, nemerteans, cephalochordates, sipunculids and bryozoans. The density and richness were directly related to the depth, with both descriptors being higher during the rainy season and at depths greater than 50 m. This result is probably due to the higher availability of food in the river during this period and is corroborated by the predominance of deposit feeders in the deepest stratum. The number of individuals of each species was higher in the shallowest stratum, probably due to the higher productivity of this stratum. The rate of organic particulate matter flow from the coastal regions to the deeper regions can also be influenced by the material export dynamics of the river, which are more intense during the rainy season. These dynamics explain why a significantly higher number of individuals were observed in the rainy period in comparison to the dry one. Multivariate analyses identified differences between the sampling sites in the deepest stratum during both periods and revealed a stronger similarity between the shallow and intermediate strata, especially during the rainy season, which has a higher flow rate. These findings reinforce the influence of the Paraíba do Sul River on the structural pattern and composition of the benthic macrofauna of the internal platform (<50 m) on the northern coast of Rio de Janeiro.

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1. Introduction

Benthic macrofauna play an important role in the physical structure of their habitats (Thrush and Dayton, 2002). By excavating the substrate and building tubes, they change the circulation of the water, participate in sediment aeration, modify the pattern of sedimentation and create microhabitats (Gray, 1981; Pereira and Soares-Gomes, 2009). By feeding, macrofauna convert particulate organic matter into animal biomass and reprocess deposited particles (Amaral and Migotto, 1980; McCall and Tevesz, 1982; Kawakami and Amaral, 1983; Gray and Elliot, 2009).

The occurrence and distribution of macrofaunal organisms are often correlated with the predominant environmental characteristics of the ecosystem (Zajac and Whitlatch, 1982). Hydrodynamics and sediment characteristics like grain size, organic matter and carbonate content, have repeatedly been referred to as factors that contribute to the variability of soft-bottom communities (Snelgrove and Butman, 1994), which are influenced by the ability of the bottom currents to favor sedimentation and/or resuspension and sediment transport, particularly in shallow waters (Sternberg, 1984). In addition to sedimentation features, the availability of food and the physicochemical characteristics of the water such as

salinity, oxygen content and temperature directly influence the richness and abundance of the macrofauna (Gray, 1974, 1981; Leninhan and Micheli, 2001).

Tropical continental margins are of particular relevance, because they receive the majority of global riverine water and sediment inputs (in Jennerjahn et al., 2010) The Paraíba do Sul River (PSR) plays an important role in the ecosystem of the north continental shelf of Rio de Janeiro State, with the export dynamics of dissolved and particulate materials correlated to the rainfall and flow rate (Souza and Knoppers, 2003; Figueiredo, 2011). This river is a multiple source system derived from its land use (urban, industrialization and agriculture) and over the last five decades the continuous sewage outflow in all basis (180 municipalities have ∼50% of sewage treatment), industrial spills (Hoag, 2003) and agriculture (Dittmar et al., 2012) have promoted several disruptions in the structure and functioning into the aquatic ecosystem. All these transformations together will certainly compromise the coastal region considering that the latter authors have identified an outwelling at least of 20 km and a mixture rate of 1.6–2.6 km d^{-1} (Souza et al., 2010). The Paraíba do Sul River seasonal discharge

exhibits a dry period between the months of May and September and a rainy one from October to April (Carvalho et al., 2002). The temporal variations in the flow rate induce variations on the coastal water's salinity and temperature (Rudorff et al., 2011), in the concentrations of nutrients (Gatts et al., 2005) and pollutants and on the export (Lacerda et al., 1993) and sediment dynamics (Ribeiro et al., 2004).

The present study aimed to evaluate the effect of the flow rate of the Paraíba do Sul River on the benthic macrofauna of the inner platform (<50 m), where different discharge periods of the river and rainfall are well defined. We tested the hypotheses that spatial variations on the structure and composition of the macrofauna respond to the sedimentary variations that result from hydrodynamic processes on the inner platform adjacent to the Paraíba do Sul River.

2. Study site

The study area is located at 21°36′S, 41°00′W, on the continental shelf north of the Rio de Janeiro State, and it is adjacent to the
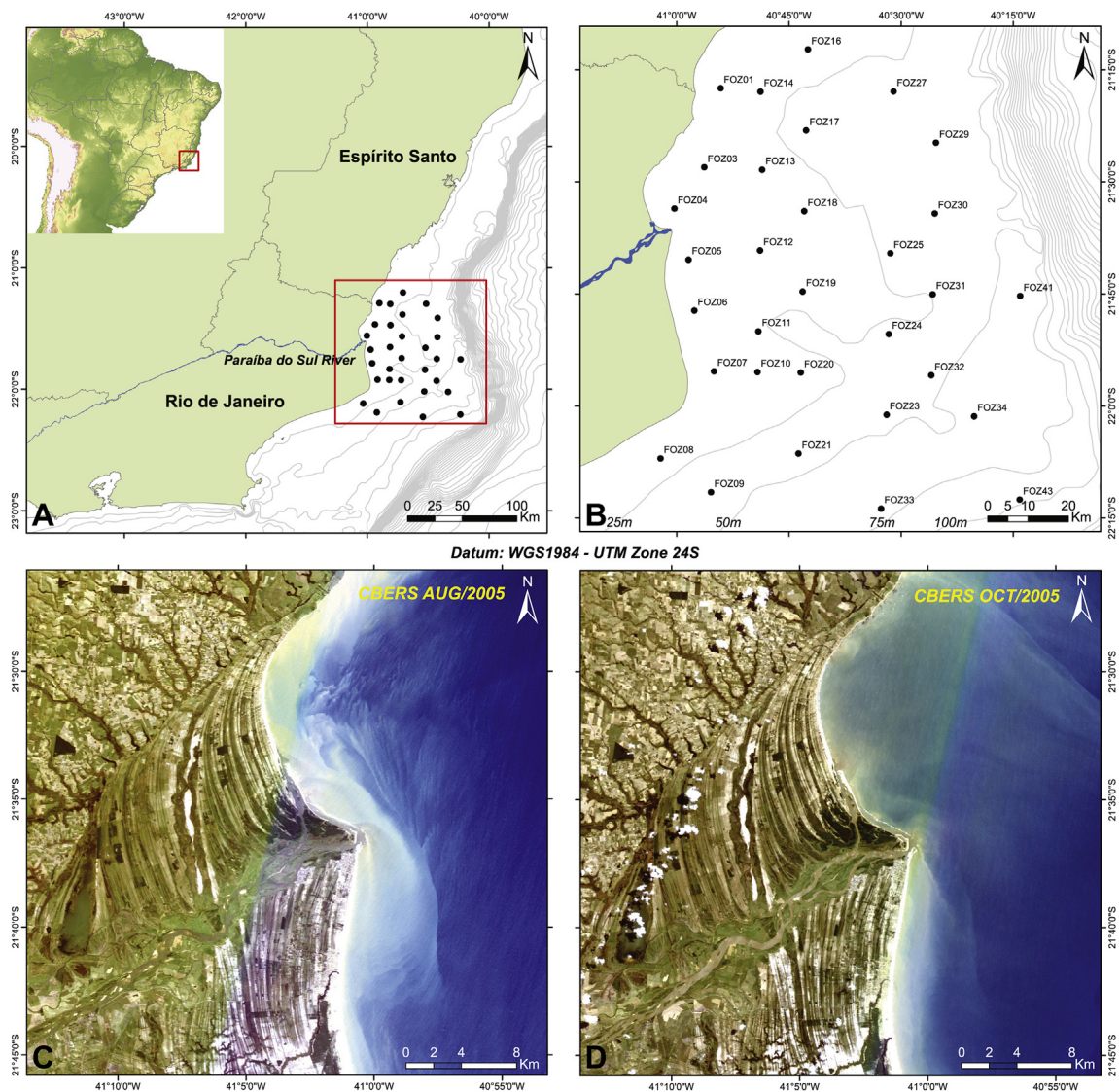

Fig. 1. A) The study area on the northern coast of the State of Rio de Janeiro. B) A map showing the locations and depths of the sampling sites at the mouth of the Paraíba do Sul river. C) The plume of the Paraíba do Sul river (PSR) identified using satellite images during the period with the lowest flow rate and (D) during the period of greatest flow rate.

mouth of the Paraíba do Sul River (Fig. 1A). The Tropical Water, Coastal Water and South Atlantic Central Water masses all influence the study area. The latter penetrates the continental shelf during the spring and summer, bringing nutrient-rich waters (Silveira et al., 2000; Soares-Gomes et al., 2000). The climate of the drainage basin of this river is characterized as warm subtropical, with average annual temperatures ranging from 18 to 24 °C (Marengo and Alves, 2005).

3. Methods

3.1. Field sampling

Two oceanographic sampling campaigns were completed: one in March 2009 (rainy season: RS) and another in July 2009 (dry season: DS). As there is no valid temporal comparison possible (because of lack of replicated wet/dry season sampling), both surveys were considered as spatial replicates to reinforce riverine influence, which have to be discerned using spatial difference alone. The samples were collected in triplicate using a 231-L van Veen grab at 33 sampling sites and represented a range of potential penetration depths in the sediment plume on the platform (Fig. 1B–D). Four steel templates measuring $10 \times 10 \times 10$ cm were collected from the inside of the sampler from a total volume of 0.004 m^3 of the superficial sediment. Two sampling sites (02 and 15) could not be sampled during the rainy season for logistical reasons. The samples were taken from 12 to 97 m deep and were analyzed in three predetermined bathymetric strata: Stratum 1 was designated as depths <25 m, Stratum 2 ranged from 26 to 50 m, and Stratum 3 included depths >50 m (Table 1).

3.2. Laboratory analysis

Subsamples were obtained from each sample for macrofauna, grain size distribution, total carbonate and total organic carbon analyses. The subsamples with the macrofauna were fixed in 10% formaldehyde, sieved through a 500-μm mesh, sorted and identified at the lowest taxonomic level. The depth, temperature and salinity were measured *in situ* using a CTD multiparameter profiler. Total carbonate was determined by acid treatment using 1 g of dry sediment with 20 mL of HCl 1.0M overnight; grain size distribution was determined by the particle analyzer by laser diffraction (Shimadzu Model SALD-3101) in several fractions as Wentworth scale (Suguio, 1973); and total organic carbon were determined by CHN analyzer after removing carbonate with HCl vapor (Hedges and Stern, 1984).

3.3. Data analysis

To test for differences on water temperature and salinity, we compare these values using two-sample *t*-tests of surveys-specific estimates ($n = 93$ for March 2009, $n = 99$ for July 2009). The biotic data obtained from the taxonomic identification processes included the taxonomic composition, frequency of occurrence, density, richness, and Simpson's dominance (λ), Shannon's diversity and Pielou evenness (log$_2$) in relation to the spatial distribution of the main taxa in the two sampling campaigns. The statistical significance of the spatial differences in the community structure descriptors among the depth strata in each sampling campaign was evaluated using an analysis of variance (ANOVA), using log$_{10}$ (X + 1) transformations when necessary to reduce variance heterogeneity.

The comparative analysis of the macrofauna at the sampling sites and depths in both sampling campaigns included an analysis of similarity (ANOSIM) to test for significant differences in the three

strata. The species' contributions to the similarity were calculated using the identification of faunal associations (Clarke and Warwick, 2001). Diversity indices and multivariate analysis were performed using PRIMER V 6.

A canonical correspondence analysis (CCA) was used to correlate the macrofauna (species with a relative abundance >0.5%) in each campaign with the depth strata and the environmental variables mentioned above. The significances of the canonical axes and variables were determined with Monte Carlo tests and permutation (Ter Braak, 1986) using CANOCO and MVSP 3.13 software, respectively.

4. Results

4.1. Abiotic data

The bottom water mass samples exhibited salinity values between 34.3 and 36.9 during the rainy season and 35.2 and 36.4 during the dry one ($t_{est.} = 5.33$, *D.F.* $= 160.3$, $p < 0.0001$), and temperatures ranging from 14.5 °C to 26.1 °C and 14.0 °C to 23.1 °C, respectively ($t_{est.} = 2.03$, *D.F.* $= 133.5$, $p = 0.04$). The sediment samples were predominantly composed of sand (Table 1), with the exception of sampling sites 04 and 08 during the rainy period and 04 during the dry one, which exhibited a predominance of silt-clay. The mean particle size ranged from very coarse sand to medium silt in the rainy period and from coarse sand to fine silt in the dry period. The samples were classified using the degree of sorting from very poorly to moderately selected, with the latter being predominant within the study area (Table 1).

4.2. Taxonomic composition

The benthic macrofauna included annelids, crustaceans, mollusks, echinoderms, cnidarians, nemerteans, cephalochordates, sipunculids and bryozoans. A total of 37,213 individuals belonging to 1112 species were collected during the two sampling campaigns, of which 24,165 individuals and 855 species were sampled during the rainy period and 13,048 individuals and 659 species during the dry period. Twenty-four taxa with frequencies of occurrence above 60% were recorded in the rainy period, whereas 13 taxa were obtained during the dry one. The relative densities of the main taxonomic groups of both campaigns were Polychaeta (64%) and Crustacea (∼28%), followed by Nemertinea, Sipuncula, Mollusca and Echinodermata, each with values below 6% (Fig. 2A, B).

4.3. Community structure descriptors

Higher taxa richness and density values were registered at depths >50 m in both campaigns (Figs. 3 and 4), and the average values were 2–3 times higher during the rainy season than on the dry one. In both campaigns, the richness and density differed significantly among the three depth strata (Table 2).

The mean species diversity values were higher in the intermediate depth stratum (Fig. 5) and significantly lower in the shallowest one during the dry period (Table 2), reflecting reduced richness and density. The significantly higher dominance in Stratum 3 indicates that the smallest mean diversities were observed in the deeper waters, especially during the rainy period (Fig. 5, Table 2).

4.4. Species association – spatial comparative analysis

The analysis of similarity (ANOSIM) in the rainy season revealed significant differences ($P = 0.1\%$, $R = 0.271$) between the depth strata, reflecting the greater contributions (41%) of the polychaetes

Table 1
Abiotic data (temperature (°C), salinity, granulometric composition: sand (%), silt-clay (%), mean particle size and degree of sorting) for the sampling sites under the influence of the mouth of the PSR during the dry and rainy seasons of 2009 (RS: rainy season, DS: dry season). Strata 1: <25 m, strata 2: 26–50 m, strata 3: >50 m.

| Station	Strata	Depth	Temperature		Salinity		Coarse (%)		Silte-clay (%)		Mean grain size		Sort-selected	
			RS	DS	RS	DS	RS	DS	RS	DS	RS	DS	RS	DS
1	1	15	24.6	22.4	36.4	35.5	89 ± 12	98 ± 3	0	0	Coarse sand	Coarse sand	Poorly selected	Moderately selected
2	1	20		22.3		35.8		90 ± 2		3 ± 3		Medium sand		Poorly selected
3	1	16	23.9	22.4	36.6	35.3	100 ± 0.1	81 ± 7	0	1 ± 1	Very coarse sand	Coarse sand	Moderately selected	Poorly selected
4	1	12	25.4	22.4	35.5	35.4	28 ± 22	3 ± 0.4	57 ± 31	97 ± 0.4	Very fine sand	Fine silt	Very poorly selected	Poorly selected
5	1	17	26.1	22.4	34.3	35.3	43 ± 9	41 ± 12	25 ± 9	32 ± 29	Medium sand	Fine sand	Very poorly selected	Very poorly selected
6	1	17	24.6	22.3	36.2	35.2	100 ± 0.5	94 ± 9	0.4 ± 1	5 ± 7	Medium sand	Medium sand	Moderately selected	Poorly selected
7	1	16	24.8	21.2	36.3	35.8	81 ± 6	99 ± 1	19 ± 6	0.3 ± 0.5	Fine sand	Medium sand	Poorly selected	Moderately selected
8	1	16	16.7	21.7	35.7	35.9	24 ± 3	64 ± 49	76 ± 4	36 ± 49	Medium silt	Fine sand	Very poorly selected	Poorly selected
9	2	44	16.8	20.8	35.8	36.0	99 ± 1	100 ± 0.3	1 ± 1	0.2 ± 0.3	Coarse sand	Coarse sand	Moderately selected	Moderately selected
10	1	21	25.0	21.3	36.6	36.8	100 ± 0	100 ± 0.1	0	0	Coarse sand	Medium sand	Moderately selected	Moderately selected
11	1	22	24.5	22.3	36.6	36.0	100 ± 0	100 ± 0.4	0	0.01 ± 0	Medium sand	Medium sand	Moderately selected	Moderately selected
12	1	22	24.4	22.6	36.5	36.3	89 ± 10	94 ± 6	0.1 ± 0.2	0.02 ± 0	Medium sand	Medium sand	Poorly selected	Poorly selected
13	1	21	23.7	22.4	36.6	36.9	100 ± 0.1	98 ± 2	0	2 ± 2	Medium sand	Medium sand	Moderately selected	Moderately selected
14	1	24	23.7	22.4	36.5	35.7	53 ± 7	99 ± 1	14 ± 4	1 ± 1	Medium sand	Medium sand	Very poorly selected	Moderately selected
15	1	21		22.4		35.6		85 ± 7		2 ± 2		Medium sand		Poorly selected
16	1	15	23.5	22.4	36.5	35.7	70 ± 16	71 ± 14	1 ± 1	0.3 ± 0.5	Coarse sand	Coarse sand	Poorly selected	Poorly selected
17	2	28	23.3	22.3	36.7	36.1	99 ± 2	99 ± 1	1 ± 2	0	Medium sand	Medium sand	Moderately selected	Moderately selected
18	1	22	24.4	22.1	36.6	35.8	100 ± 0.1	99 ± 1	0	1 ± 1	Coarse sand	Medium sand	Moderately selected	Moderately selected
19	1	21	24.4	22.6	36.6	36.4	99 ± 2	100 ± 0.1	1 ± 2	0	Coarse sand	Coarse sand	Moderately selected	Moderately selected
20	1	20	24.8	21.3	36.6	35.8	100 ± 0	100 ± 0	0	0	Fine sand	Fine sand	Moderately selected	Moderately selected
21	2	47	16.7	20.2	35.8	35.9	92 ± 0.2	98 ± 1	0	0	Coarse sand	Coarse sand	Moderately selected	Moderately selected
23	2	49	19.0	21.1	36.2	35.9	62 ± 19	73 ± 3	9 ± 1	9 ± 7	Coarse sand	Medium sand	Very poorly selected	Very poorly selected
24	2	27	23.7	22.0	36.7	36.1	99 ± 1	100 ± 0	1 ± 1	0	Coarse sand	Medium sand	Moderately selected	Moderately selected
25	2	28	23.1	22.1	36.7	36.4	100 ± 0	96 ± 2	0	0	Coarse sand	Coarse sand	Moderately selected	Moderately selected
27	2	29	22.2	22.0	36.6	36.3	100 ± 0	97 ± 2	0	0	Coarse sand	Coarse sand	Moderately selected	Moderately selected
29	2	33	21.2	22.2	36.5	36.4	91 ± 4	93 ± 6	0	0.2 ± 0.2	Coarse sand	Coarse sand	Moderately selected	Moderately selected
30	2	29	24.2	21.9	36.7	36.4	99 ± 1	100 ± 0.1	1 ± 1	0	Coarse sand	Coarse sand	Moderately selected	Moderately selected
31	2	26	23.3	23.1	36.7	36.6	99 ± 2	99 ± 1	1 ± 2	1 ± 1	Medium sand	Medium sand	Moderately selected	Moderately selected
32	2	48	19.8	21.7	36.3	36.1	88 ± 3	98 ± 1	12 ± 4	1 ± 1	Very fine sand	Medium sand	Poorly selected	Very poorly selected
33	3	68	14.9	14.0	35.5	35.3	99 ± 1	72 ± 9	1 ± 1	9 ± 3	Medium sand	Medium sand	Moderately selected	Moderately selected
34	3	59	22.2	20.0	36.7	36.2	96 ± 2	98 ± 3	5 ± 2	2 ± 3	Fine sand	Medium sand	Poorly selected	Poorly selected
41	3	67	23.1	21.1	36.9	36.5	64 ± 2	97 ± 1	13 ± 4	3 ± 1	Medium sand	Coarse sand	Very poorly selected	Moderately selected
43	3	97	14.5	18.6	35.4	36.1	87 ± 2	91 ± 1	13 ± 2	9 ± 1	Fine sand	Fine sand	Poorly selected	Poorly selected
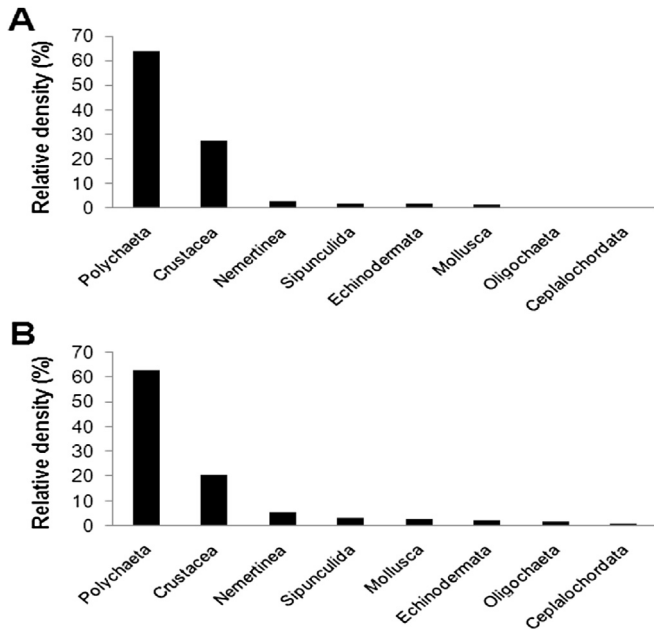
Fig. 2. The relative densities (%) of the taxonomic groups recorded during the rainy (A) and dry (B) seasons of 2009.

Goniadides carolinae and *Chone americana* (15%) in the shallow and intermediate strata and the crustacean *Phtisica marina* (42%) and the polychaete *Spiophanes* sp. (26%), both deposit feeders, in the deeper stratum. During the dry period the ANOSIM showed significant differences between Strata 1 and 3 ($P = 0.1\%, R = 0.358$) and Strata 2 and 3 ($P = 0.1\%. R = 0.672$). *G. carolinae* and the polychaete *Protodorvillea kefersteini* contributed the most to Strata 1 and 2 (>15%), while *Spiophanes* sp. on Stratum 3 (31%) during the dry period.

The canonical correspondence analysis confirmed the close association between Strata 1 (<25 m) and 2 (25–50 m) during the rainy period (Fig. 6A), when the flow rate is highest (Fig. 6B). The two principal axes indicated by the CCA explained ~72% of the total variance in the rainy season and ~66% in the dry one (Table 3). Canonical Axis 1 was significant in both campaigns, with the

parameters depth and temperature as the most explanatory variables, and Stratum 3 (>50 m) positively associated with the first one (Fig. 6A, B). The degree of sorting and mean particle size were identified as secondary variables and were negatively correlated with Strata 1 and 2. *Spiophanes* sp., *Phtisica marina*, Kamakidae, *Exogone* (*Exogone*) sp., *Chevalia* sp., *Parexogone* sp., *Laonice weddellia* and *Microphoxus uroserratus* were highlighted as associated taxa exclusively in Stratum 3 in both campaigns. Strata 1 and 2 featured a group of 18 related taxa during the rainy period, but different groups of taxa were associated to these two strata during the dry period, when a greater separation of the shallow and intermediate sampling sites was noted.

5. Discussion

The structure of the macrobenthic community, which is influenced by species richness, abundance, diversity and dominance, revealed that the spatial variability throughout the study area is influenced by the PSR discharge in both surveys. The highest relative abundance and frequency of occurrence were found in the group of polychaetes, followed by the crustaceans, which were preferentially found in the deeper sampling sites. This pattern of dominance in the benthic macrofauna, of which the polychaetes are the most representative, is often observed in studies addressing these communities in coastal regions worldwide (Diener et al., 1995; Tselepides et al., 2000; Probert et al., 2001; Ellingsen, 2002). The large number of feeding strategies the polychaetes exhibit confers upon them a key role in marine food webs, improving nutritional value (Bessa et al., 2007). The crustaceans' preference for deeper regions has also been reported in several studies (Martinez and Adarraga, 2001; Occhipinti-Ambrogi et al., 2002; Jayaraj et al., 2007) and is positively associated with the sand fraction of the sediment and negatively associated with temperature.

The high densities and richness found in the deepest stratum, especially during the rainy period, might be related to the deeper penetration of the South Atlantic Central Water (SACW) in the region of Cabo de São Tomé during the upwelling phenomenon in the spring and summer, a process that brings nutrient-rich waters to the study area (Silveira et al., 2000, 2004). Depth and latitude have been reported as the primary factors responsible for the higher gradients of species richness in soft substrate fauna (Gray, 2002).
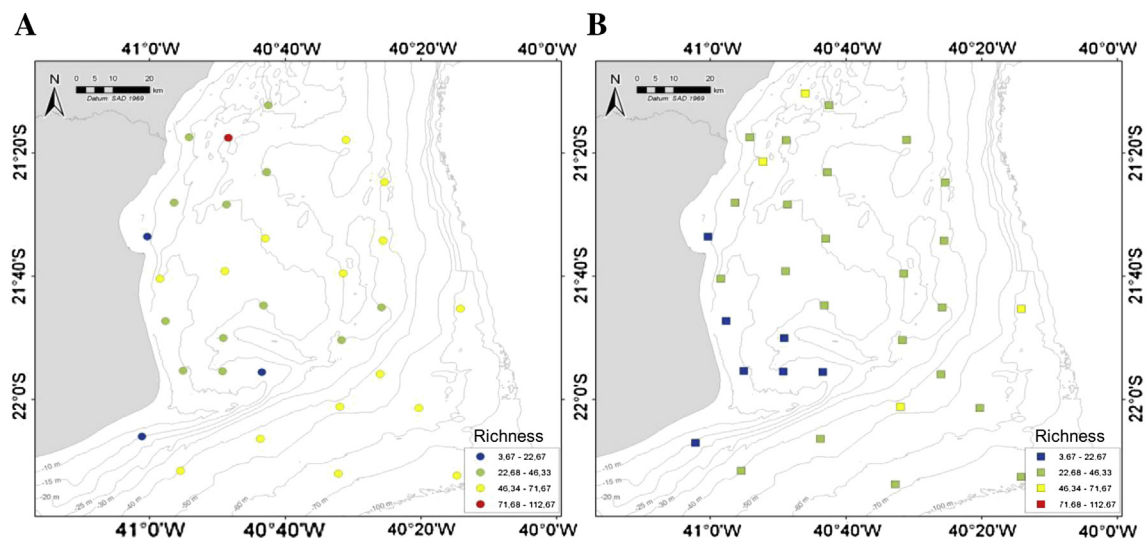

Fig. 3. The mean taxa richness values at the 33 sampling sites located in the area influenced by the mouth of the Paraíba do Sul river (A: rainy period, B: dry period).
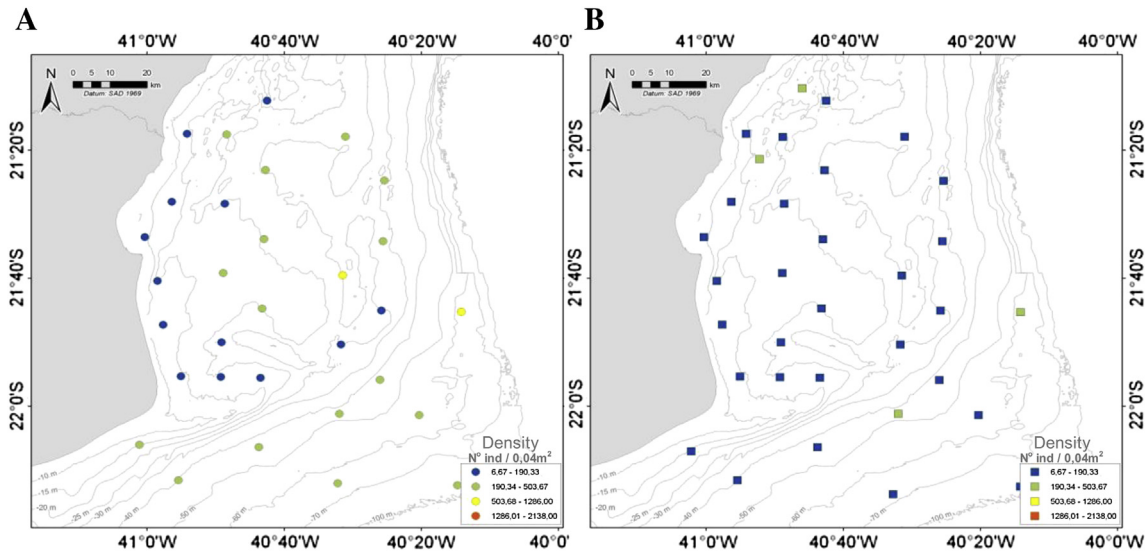
Fig. 4. The mean density (no. of individuals/0.04 m^2) at the 33 sampling sites located in the area influenced by the mouth of the Paraíba do Sul river (A: rainy period, B: dry period).

The depth of the water column can influence the pattern of sedimentation and the hydrodynamic conditions. The mouth region of the Paraíba do Sul River (PSR) is shallow and is strongly influenced by northeastern winds that connect the pelagic and benthic processes. In addition to these natural processes, the intense fishing activity of the region is concentrated in the isobaths below 25 m and certainly influences the dynamics of the benthic communities. It should be noted that bottom trawl fishery, a very common source of income for the local population on the north coast of Rio de Janeiro (Costa and Di Beneditto, 2009), could also reduce diversity. Among the main effects caused by fishing are the resuspension of sediments, changes in the conformity of the physical environment, changes in biogeochemistry and in the structure and composition of the macrofauna (Kenchington et al., 2001; Thrush and Dayton, 2002). It is suggested that a weakened 'top down' control is resulting from intense fishing pressure at below 25 m, with a decreasing effect on the macrofauna abundance. Dredging and other types of bottom fishing reduces habitat complexity by impacting sessile species, and by extension their associated organisms (Jennings and Kaiser, 1998; Kaiser et al., 2002). The implications of this disturbance on the shallower stratum could be a decrease of biodiversity and/or species abundance by removing the macrofauna.

The environmental instability that arises from the fluctuating flow rates in the Paraíba do Sul River can severely disturb the shallowest stratum, thus explaining its lower diversity. Similar studies performed on the southern (Capitoli and Bemvenuti, 2004) and southeastern (Paiva, 1993) continental shelves showed that the reduced diversity in the shallower areas was a result of physical changes. Paiva (op. cit.) argues that the sand beds in shallow regions are more unstable than those in deeper regions because of the stronger hydrodynamics induced by the waves that occur almost all year round, which, when combined with the river's flow rate, could explain the lower diversity in this stratum.

Higher diversity values were observed in the intermediate stratum in both periods, forming a unimodal distribution characteristic of the Intermediate Disturbance Hypothesis (IDH), in which the diversity of species increases in the presence of moderate environmental disturbances due to reduced competitive exclusion (Connell, 1978). This hypothesis is corroborated by the greater dominance of taxa observed in the deeper stratum, where the disturbances caused by fluctuations in flow rate, waves and even bottom trawl fishery are minimized.

Higher diversity was also found in the locations where the mean particle size was smaller and the sediment was less sorted (more heterogeneous). Gray (1981), Levinton (1995) and Capitoli and Bemvenuti (2004) observed that sediments with greater heterogeneity in their granulometric composition support more abundant, rich and diverse communities, as noted in the area influenced by the PSR mouth. This observation probably results from the

Table 2
ANOVA results for the diversity indices among the three depth strata (1: <25 m, 2: 25–50 m, 3: >50 m) in March 2009 (rainy period) and July 2009 (dry period).

| Descriptors	Rainy period					Dry period				
Richness	SS	LD	MS	F	p	SS	LD	MS	F	p
Depth strata	5810.9	2	2905.5	8.55	0.0004	2682.11	2	1341.06	5.79	0.0042
St. error	30588.9	90	339.9		**	22238.21	96	231.65		**
Density										
Depth strata	862568	2	431284	5.84	0.0041	80931	2	40466	3.17	0.0463
St. error	6645328	90	73837		**	1224267	96	12753		*
Diversity (H')										
Depth strata	2.296	2	1.148	1.1	0.3347	9.01	2	4.51	6.71	0.0019
St. error	93.247	90	1.036		NS	64.39	96	0.67		**
Dominance (S)										
Depth strata	0.18804	2	0.094	3.63	0.0305	0.1	2	0.048	3.56	0.0324
St. Error	2.33246	90	0.026		*	1.3	96	0.014		*

*p < 0.05; **p < 0.01; NS: not significative.
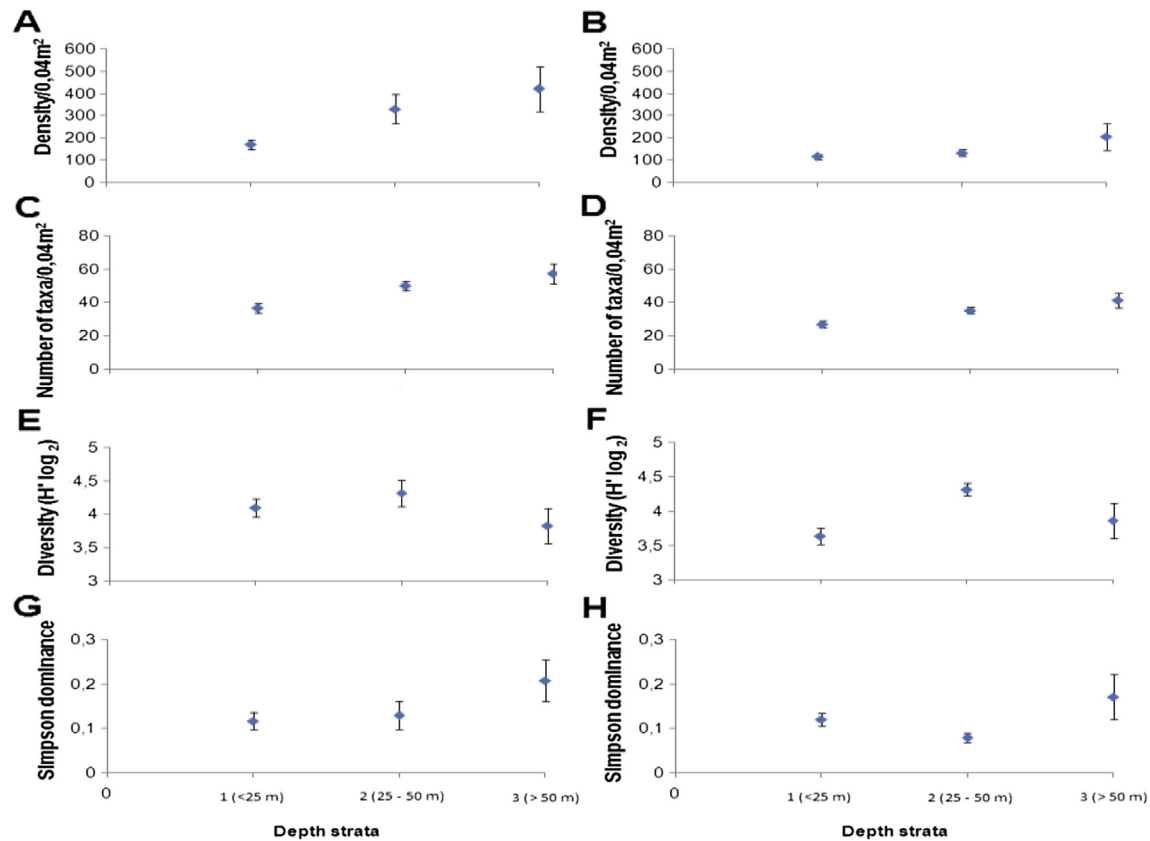
Fig. 5. The mean values and SE of the number of taxa, density of individuals, diversity and dominance of benthic macrofauna species in the three depth strata (1: <25 m, 2: 25–50 m, 3: >50 m) for the campaigns undertaken during the rainy (left column) and dry (right column) periods of 2009. SE = standard error.

increased availability of niches, which can result from interactions between physical and biological factors. These interactions may allow for an increase (not necessarily prominent) in hydrodynamics to increase diversity, especially in regions that are already subject to wide variations over time such as those areas influenced by the increased flow rate of the PSR during the rainy season, when the hydrodynamic influence can reach the 25 to 50-m range in the intermediate stratum (Souza et al., 2010). Also, the relationship between diversity and granulometry could actually be explained in the opposite direction – a more diverse benthos would likely result in more heterogeneous sediment because bioturbation would effectively increase sediment heterogeneity through for example, vertical sediment transportation.

The significant differences in the diversities of the depth strata during the dry period suggest the influence of the PSR on the benthic macrofauna. During this period, the flow rate of the river ranges from 300 to 600 m^3 s^{-1}. In contrast, in the rainy period ranges from 1200 to 2400 m^3 s^{-1} and may reach even more extreme values. This fluctuation in river flow may cause large differences in the dissolved and particulate matter input and affects the coverage area of the flow's influence on the adjacent coastal region. Another point worth noting is that the mixing ratio of the contribution varies from 14 to 60 km^2 d^{-1} in the dry and rainy periods, respectively, and can reach approximately 40 km off the coast (Souza et al., 2010). A corroborating analysis of the quality of organic matter in the sediments revealed a significant difference in the organic material input during both seasons, with the highest lipid values found during the rainy period. This result demonstrates the interdependence of the coastal processes and the continental input, in addition to the connection between the pelagic and benthic compartments.

The larger number of individuals per species observed in the shallower stratum is probably related to this stratum's higher productivity. A decrease in the flow of particulate organic matter from coastal to deeper regions influences the material export dynamics of rivers. In the PSR, this process is more intense during the rainy period, which may explain the significantly larger number of individuals present in the rainy period. Another contributing factor is the dynamics of the bottom nepheloid layer of sediments, which has a low density and is often rich in organic matter. In the case of the region adjacent to the PSR, it can be assumed that there is an intense movement directly associated with the exchange of tides, winds and continental contributions.

The species associations in the three ranges were related primarily to depth and secondarily to the mean particle size and degree of sorting, which reflect the type of sediment present. Both factors are often identified as determinants of the distribution of benthic species and the formation of species associations (Gray, 1974; Levinton, 1995). In general, the groups of species present on both surveys distinguished the three depth ranges and are characteristic of sandy sediments. The shallower stratum is represented by the polychaete *Goniadides carolinae*, a small predator of the meiofauna (Fauchald and Jumars, 1979). The polychaete *Chone americanos* contributed the most to the intermediate stratum, and it is a filter feeder *par excellence*, indicating the availability of food in the water column (Pagliosa, 2005). The prevalence of potentially deposit-feeding species such as *Spiophanes* sp. A and *Phtisica marina* in Stratum 3 reflects the decreased hydrodynamics that results from the increased depth, distance from the coast and, primarily, the reduced sediment sorting in both surveys. This pattern shows a bathymetric stratification of feeding habits of the dominant species in the three ranges.
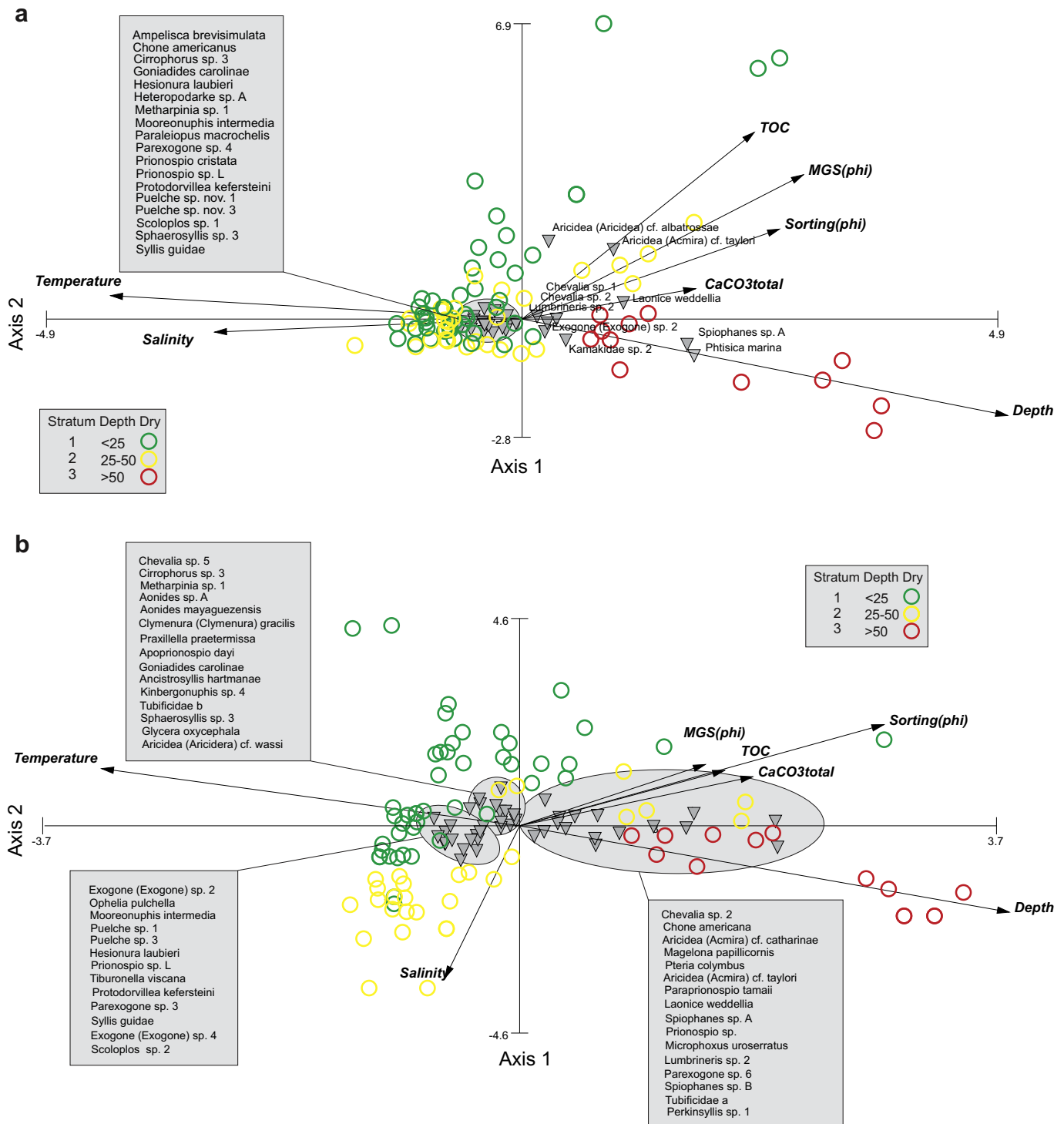
Fig. 6. The canonical correspondence analysis (CCA) for the three depth strata (1: <25 m, 2: 25–50 m, 3: >50 m) at the 31 sampling sites on March 2009 – rainy period (A) and July 2009 – dry period (B). The CCA considered macrobenthic species with an abundance greater than 0.5%; the environmental parameters depth, temperature and salinity; and the sediment parameters mean particle size (MPS), sorting, total organic carbon (TOC) and total carbonate ($CaCO_3$).

In summary, the results of the analyses indicate that, when species assemblages and environmental variations are considered, more than 60% of the variation in the system was related to factors associated with changes in the discharge of the Paraíba do Sul River, which in turn seems to influence the patterns of abundance, richness, diversity and dominance. The pattern of species association in the study area was characterized by a distinction between the deepest stratum (>50 m) and the other strata in both surveys. The

changes in the shallow and intermediate strata reflected the influence of the mouth of the Paraíba do Sul River and were more pronounced during the rainy period, when two significantly different associations were identified. In the dry period, however, the reduced penetration of the plume of the Paraíba do Sul River caused the association of stratum 1 (below 25 m) to be similar to the association of stratum 2 (between 25 and 50 m), probably reflecting greater environmental stability during this period.

Table 3
CCA analysis: eigenvalues and variable loadings on axis 1 and 2.

	Axis 1	Axis 2
Rainy season		
Eigenvalues	0.358	0.263
Percentage	12.912	9.475
Cum. percentage	12.912	22.387
Cum. constr. percentage	41.546	72.032
Spec.-env. correlations	0.914	0.872
Dry season		
Eigenvalues	0.378	0.119
Percentage	12.034	3.778
Cum. percentage	12.034	15.812
Cum. constr. percentage	50.330	66.130
Spec.-env. correlations	0.939	0.709

Therefore, we conclude that the Paraíba do Sul River influences the structural pattern and composition of the benthic macrofauna of the inner shelf (<50 m) of the northern coast of Rio de Janeiro.

Acknowledgments

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