Journal of the Marine Biological Association of the United Kingdom, 2017, 97(2), 377–385. © Marine Biological Association of the United Kingdom, 2016
doi:10.1017/S0025315416000485

Distribution of benthic fauna in sediment grains and prop roots of a mangrove channel in south-eastern Brazil

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We examined the benthic fauna in four areas along a mangrove tidal channel in south-eastern Brazil, between October 2008 and August 2009. The tested hypothesis is that the most abundant groups avoid competition as they occupy different types of substrata and that the longitudinal distance from the sea also affects the occurrence of benthic fauna along the channel. We also examined the prop root epibiont fauna to describe this different community. Polychaeta was the dominant group in the sediment whereas Isopoda and Tanaidacea were the dominant groups on the prop roots. We found a tendency for higher infauna species richness and diversity in the innermost channel area during the summer. Higher abundance of epibiont fauna was also found in summer with tidal movements allowing the colonization of the prop roots of the mangrove forest by some taxa. The polychaetes Ceratocephale *sp. and* Laeonereis acuta *had indication of habitat partitioning, with the first occurring mainly in very fine sand sediment whereas the latter preferred medium sand sediment. The microcrustaceans* Chelorchestia darwini *and Tanaidacea sp. 1 occurred in high abundance colonizing the prop roots.* Exosphaeroma *sp. was found in high abundance in infauna and epibiont fauna. The tested hypothesis of spatial partitioning of the mangrove channel by the benthic fauna was confirmed with the most abundant species occupying the substrata with different grain fractions and prop roots in different stations.*

Keywords: Benthic invertebrates, habitat partitioning, zonation, mangrove forest

Submitted 22 June 2015; accepted 9 March 2016; first published online 11 April 2016

INTRODUCTION

Mangroves are a major component of tropical and subtropical semi-closed intertidal regions that support rich fauna and play an important role in estuarine and coastal food webs (Alongi & Christoffersen, 1992; Barbier *et al.*, 2011; Gajdzik *et al.*, 2014). These areas are commonly colonized by associations of benthic invertebrates living in or on the substrate, having a high taxonomic diversity and occupying different microhabitats according to their life habits (Nagelkerken *et al.*, 2008).

Benthic invertebrates play an important role in the mangroves by helping to cycle and conserve nutrients in the system including the consumption of microphytobenthic individuals, plant debris and detritus deposited in the sediment, thus incorporating organic matter in their biomass (Koch & Wolff, 2002). They are also responsible for the transformation of detritus, facilitating mineralization by bacteria, and also promoting oxygenation of the substrate through bioturbation and sediment remobilization (Coull, 1999; Koch & Wolff, 2002).

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Knowing the relationship between benthic fauna and sediment is a prerequisite for understanding the structure and dynamics of benthic associations. Several authors, studying the relationships between organisms and sediments in marine and estuarine environments (Forbes & Lopez, 1990; Snelgrove & Buttman, 1994), found that the benthic invertebrates are closely related to the sediments they inhabit. The highest density of these organisms occurs in unconsolidated substrate, consisting predominantly of quartz sand, reducing dark mud, shell fragments, oyster beds and mangrove remains (Snelgrove & Buttman, 1994; Giere, 2009). Individual occurrences tend to be higher in mud or fine sand, rich in organic matter, and lower in coarse and medium sand (Selleslagh *et al.*, 2011).

Species distribution is controlled by characteristics of the mangrove community, sediment properties and tidal changes (Yijie & Shixiao, 2007; Lee, 2008). The mangrove fauna often show horizontal and vertical zonation (Farrapeira *et al.*, 2009; Santos *et al.*, 2014). Some of them dominate in mud areas whereas others are dominant on the shrubs and leaves and around pneumatophore roots (McLachlan *et al.*, 1977). The pattern of vertical distribution of infauna is an important aspect of the structure, species interactions and organism activity in the soft bottom sediments (Safahieh *et al.*, 2012). Notwithstanding, highest macroinfauna densities were always observed in the surface sediments and both predation and physical disturbance act mainly on the upper layer of sediments, where their effects are more visible than in deeper layers (Alongi & Christoffersen, 1992; Dittmann, 2000; Valença & Santos, 2013).

The mangrove vegetation also plays an essential role related to protection of many species that dwell there. The prop-roots and pneumatophores of mangrove trees form a habitat for a wide variety of species and become home to terrestrial as well as marine plants, algae, invertebrates and vertebrates, some occurring in high densities (Manson *et al.*, 2005). Mangrove roots work as filters to retain sediment, preventing erosion and stabilizing the coast (Barbier *et al.*, 2011). At the same time, the structural complexity of the substrate increases the rate of colonization and the available area for the fauna establishment (Jacobi & Langevin, 1996). In addition, the mangrove vegetation protects organisms which suffer the influence of tides, predation and competition (Corrêa *et al.*, 2008).

Despite their ecological importance, little is known about the relationship between benthic invertebrates distribution and the local habitat characteristics in south-eastern Brazil mangroves. It is very important to provide information on the benthic fauna in mangroves to improve our understanding of the importance of these coastal systems and to help support effective management plans and actions for ensuring their wise use and protection. The aim of this study was to investigate the spatial and temporal distribution of the benthic community in a mangrove channel located in the inner area of the Sepetiba Bay. In addition, we attempted to describe the type of substrate determinant on the distribution of species and the role of the prop roots on the maintenance of local benthic fauna. The tested hypotheses are that the most abundant groups avoid competition as they occupy different types of substrata, and that the longitudinal distance from the sea also affect the occurrence and distribution of the benthic fauna across the channel.

MATERIALS AND METHODS

Study area

The Guaratiba mangrove is located in the inner area of the Sepetiba Bay in a protected area, the Biological and Archaeological Reserve of Guaratiba (RBAG) (Figure 1). This reserve was created by the State Law no. 7.549 of 20 November 1974, which defined the first limits of this area, incorporating in its perimeter the Guaratiba mangrove. Guaratiba coastal plains are located between coordinates 43°35′–44°01′W and 22°53′–23°05′S, in the north-east part of the Sepetiba Bay (Figure 1). The tidal wave is stationary type, modulated by other physical factors such as winds, bottom morphology and channel morphology. Annual average water temperature is 23.5°C and average rainfall is ~1300 mm, with peaks of rainfall in January and March and drought in June and August (Soares & Schaeffer-Novelli, 2005). This study was conducted in the Guaratiba mangrove main channel, which has a length of ~2.2 km and connects the bay to the Atlantic Ocean.

The mangroves have well-preserved forests and hypersaline plains with integrated systems: ocean, estuary, rivers, mangrove forests and channels, forming a complex ecosystem. This region is characterized by a microtidal regime, with a tidal range below 2 m. The mangrove forest is composed of *Avicennia schaueriana, Laguncularia racemosa* and *Rhizophora mangle.* The areas near tidal channels are dominated by *R. mangle* with an

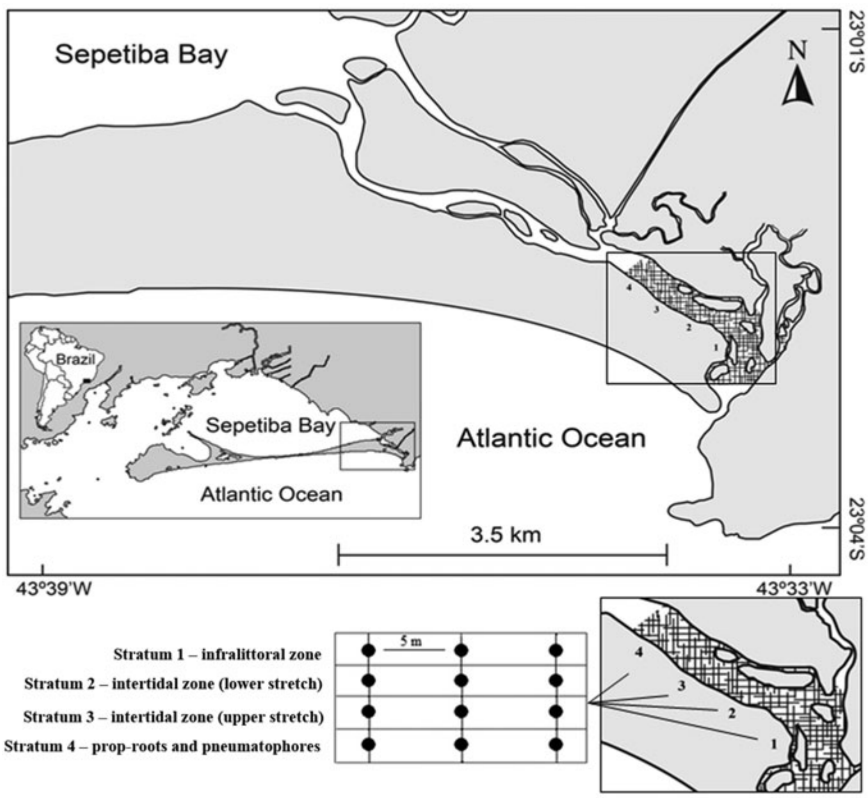

Fig. 1. Study area with indication of the four stations and four strata sampled in the Guaratiba Mangrove main channel.

increase in the contribution of *A. schaueriana* and *L. racemosa* towards the continent (Soares & Schaeffer-Novelli, 2005). This ecosystem is ecologically important for its high productivity, retention of fine sediment, preventing channels silting and trapping of heavy metals.

Field sampling

Data collection was conducted between October 2008 and August 2009, according to a systematic design (Figure 1) in four areas of the main mangrove channel (station 1, the outermost station – near the sea connection; stations 2 and 3, intermediate stations; station 4, the innermost station). Samplings were designed to cover well-characterized conditions of different seasons: spring (October and November), summer (January and February), autumn (April and May) and winter (July and August). In each station, three sampling sites in the sediment were defined (strata 1, 2 and 3), distributed at the infralittoral zone (stratum 1), at the intertidal zone – lower stretch (stratum 2), and at the intertidal zone – upper stretch (stratum 3). In addition, prop roots that could be used as substrate to invertebrate fauna were also collected. Sediment was collected at each site during low tide, with a PVC 'corer' (50 cm long, 10 cm diameter) with a collecting area of 0.00785 m^2 at a depth of 15 cm. Roots were cut at ground level nearly 15 cm and placed in plastic bags. Biological samples were collected at each stratum (in three transects/replicates) and each station, in eight excursions, totalling 384 samples (3 transects × 4 strata × 4 stations × 8 months). Sediment samples for particle-size and organic carbon analyses totalled 96 samples (3 strata × 4 stations × 8 months). At each sampling occasion, we measured the environmental variables of temperature (degree Celsius), salinity (ppt), dissolved oxygen ($mg\,l^{-1}$) pH, turbidity (NTU) and conductivity ($\mu S\,cm^{-1}$). These measurements were performed using a multiprobe YSI 556.

Data processing

A sub-sample of 300 g of sediment was used for the particle-size analyses in sieves of different mesh size over 15 min (Suguio, 1973) gathering the silt and clay fractions. Grain size was classified in accordance to Wentworth (1922) with corresponding values of phi. Per cent of organic carbon was determined through the oxidation of organic matter wet with potassium dichromate in sulphuric acid medium, employing as an energy source the heat given off from the sulphuric acid and/or heating (McLeod, 1975).

Grain size parameters were calculated according to Folk & Ward (1957) and classified according to Shepard (1954). The mean granules size was determined from each granulometric fraction weight retained in each sieve, using the software SysGran 3.0 (Camargo, 2006).

Biological samples were initially screened in plastic trays (80 cm × 40 cm × 7 cm) using tap water for removal of the largest specimens, then sieved through a 0.5 mm mesh and examined under light stereo microscope for identification of the smallest specimens. All identified specimens were preserved in 70% ethanol solution. Voucher specimens were deposited in the macroinfauna collection of the Laboratory of Fish Ecology, Universidade Federal Rural do Rio de Janeiro.

Data analyses

The relative abundance as the number of individuals and percentage (RA) were calculated for the benthic community of the sediment and prop roots. In addition, Shannon diversity indices (H′) and Margalef's richness (D) were performed considering the organisms that were identified to genus and species level or taxa represented by single species.

Environmental variables and biological descriptors (H′, D and number of abundant species) were compared among stations and seasons (fixed factors) by Permutational Analysis of Variance (PERMANOVA) (Anderson, 2001; McArdle & Anderson, 2001). Prior to analyses, biological data and environmental variables of the water were $\log_{10}(x+1)$ transformed whereas % sediment type was arcsin transformed. Euclidean distance matrices were calculated for univariate variables (species abundance, Shannon index, Margalef richness and % sediment type).

Data were converted to triangular similarity matrices using the Bray–Curtis similarity coefficient. One-way analysis of similarity (ANOSIM; Clarke & Warwick, 2001) was used to compare significant differences in community structure among stations, and seasons. Canonical correspondence analysis (CCA) was performed to assess environmental and sediment influences on benthic organisms. The Fine Sand (FS) and Very Fine Sand (VFS) sediment variables were grouped for being collinear. Multivariate analyses were performed with the software PRIMER-E + version 6.02, and CANOCO v.4.5.

RESULTS

A total of 4217 individuals in 35 taxa were observed during the study period. Polychaeta, Isopoda and Tanaidacea were the numerically dominant groups. *Ceratocephale* sp. and *Laeonereis acuta* were the most abundant species in the sediment, whereas *Exosphaeroma* sp. and Tanaidacea sp.1 were the most abundant species on the prop roots (Table 1).

The granolometric fractions did not change among seasons. Therefore, only the comparisons among stations were shown. Most of the samples were classified as fine sand according to Folk & Ward (1957). Sediment was composed of different fractions, as shown by the low value of sorting (poorly sorted), and the curves ranged from approximately symmetric to negative (Table 2). Organic carbon was higher in stations 2, 3 and 4 compared with 1. Granules and very coarse sand were comparatively higher in station 2, whereas coarse sand and medium sand were higher in station 1. Very fine sand was higher in station 3 whereas silt and clay were higher in stations 3 and 4.

No significant differences in physico-chemical variables were found among the stations. However, seasonal differences were found for some of these variables (Table 3). Temperature was significantly higher in summer and lower in winter. Dissolved oxygen was higher in autumn and spring compared with winter, whereas turbidity was higher in summer and spring and lower in autumn.

Longitudinal (or spatial) and temporal changes in infaunal assemblages

Significant differences in species abundance among stations were found for the dominant taxons *Exosphaeroma* sp.,

Table 1. Relative abundance (%RA) of the benthic community of the sediment and prop roots at Guaratiba mangrove channel, south-eastern Brazil. ni., not identified.

Taxa	Code	Sediment	Prop roots
Annelida			
Polychaeta			
Polychaeta ni.	Pn	30.85	0.95
Nereididae			
Ceratocephale sp.	Cs	31.68	0.19
Neanthes sp.	Ns	3.89	1.58
Laeonereis acuta (Treadwell,1923)	La	13.03	0
Perinereis sp.	Ps	0.58	0.95
Spionidae			
Dipolydora sp.	Dp	0.35	0.36
Lysaretidae			
Oenone fulgida (Savigny, 1818)	Of	0.17	0
Pilargidae			
Sigambra grubii (Muller, 1858)	Sg	2.53	0.04
Arthropoda			
Crustacea			
Malacostraca			
Peracarida			
Isopoda			
Exosphaeroma sp.	Es	6.78	43.25
Excirolana armata (Dana, 1852)	Ea	2.71	0.04
Sphaeroma terebrans (Bate, 1866)	St	0	0.11
Tanaidacea			
Tanaidacea sp.1	Ta1	1.35	37.15
Tanaidacea sp.2	Ta2	0.65	0.24
Tanaidacea sp.3	Ta3	0	0.04
Amphipoda			
Caprella equilibra (Say, 1818)	Ce	0	0.55
Chelorchestia darwini (Muller, 1864)	Cd	0.76	6.38
Cymadusa filosa (Savigny, 1816)	Cf	0	0.27
Melita sp.	Mes	0.05	0
Microphotis sp.	Mis	0	0.27
Monocorophium tuberculatum (Shoemaker, 1934)	Mt	0	0.12
Monocorophium acherusicum (Costa, 1857)	Ma	0	0.19
Eucarida			
Decapoda			
Brachyura ni.	Bn	0.23	0.11
Brachyuran larvae	Bl	0.29	0.31
Xanthidae	Xn	0.23	0.04
Grapsidae	Ga	0.05	0.27
Armases benedicti (Rathbun, 1897)	Ab	0	0.04
Portunidae			
Callinectes ornatus (Ordway, 1563)	Co	0.05	0
Ocypodidae			
Uca maracoani (Latreille, 1802–1803)	Um	0.06	0
Uca sp.	Us	1.88	0.03
Hexapoda			
Classe Insecta			
Diptera	Dp	0.71	5.07
Orthoptera	Ot	0.11	0.12
Hymenoptera	Hm	0.12	0.07
Hemiptera	Hm	0.23	0.23
Coleoptera	Cl	0.11	0.31
Lepidoptera	Lp	0.23	0.35

Ceratocephale sp. and *Laeonereis acuta*. The highest abundance of *Exosphaeroma* sp was recorded in station 1, for *Ceratocephale* sp. in sites 2, 3 and 4, and for *Laeonereis acuta* in site 3. Species richness and Shannon diversity were

Table 2. Results for PERMANOVA comparisons, mean and standard deviation of granulometric composition and organic carbon in sediment among stations in Guaratiba mangrove main channel, south-eastern Brazil.

Stations	%OC	%G	%VCS	%CS	%MS	%FS	%VFS	%S + C	GD(φ)	SD	Sorting	Skewness	Terminology
1	0.13 ± 0.01	0.03 ± 0.01	1.56 ± 0.41	12.70 ± 2.26	35.35 ± 2.28	28.11 ± 2.53	16.11 ± 2.58	6.12 ± 1.26	2.40	1.06	PS	−0.07	SYM
2	1.63 ± 0.49	1.16 ± 0.32	3.66 ± 0.54	9.72 ± 0.91	26.78 ± 3.06	24.64 ± 1.77	23.60 ± 2.02	10.44 ± 1.84	2.41	1.29	PS	−0.12	NEG
3	1.90 ± 0.50	0.13 ± 0.07	0.59 ± 0.16	5.04 ± 0.76	22.65 ± 2.82	27.11 ± 2.08	27.51 ± 1.93	16.96 ± 3.46	2.32	1.21	PS	0.05	SYM
4	2.45 ± 0.38	0.17 ± 0.12	2.56 ± 0.45	11.30 ± 2.92	23.07 ± 1.93	25.67 ± 1.89	21.38 ± 2.23	15.82 ± 2.49	2.13	1.29	PS	0.05	SYM
Pairwise comparisons	2, 3, 4 > 1	2 > 1.4	2 > 3	1 > 3	1 > 3.4	NS	3 > 1	3.4 > 1	NS				
Pseudo-f; P(perm)	19.89;0.001	11.7;0.001	9.910.001	3.920.008	5.930.001		5.530.002	8.360.001	19.890.001				

OC, organic carbon; G, granules; VCS, very coarse sand; CS, coarse sand; MS, medium sand; FS, fine sand; VFS, very fine sand; S + C, silt + clay; SD, standard deviation; GD, grain diameter (φ); PS, poorly sorted; SYM, symmetrical; NEG, negative. NS, non-significant difference.

Table 3. Results of PERMANOVA comparisons, mean and standard deviation of environmental variables of the water among seasons at Guaratiba mangrove main channel, south-eastern Brazil. NS, non-significant difference.

Seasons	Temperature (°C)	Salinity (ppt)	pH	Dissolved oxygen (%)	Conductivity (mS cm^{-1})	Turbidity (NTU)
Summer (Su)	26.38 ± 1.93	28.16 ± 3.36	7.93 ± 0.19	3.29 ± 1.56	46.17 ± 4.33	11.83 ± 2.33
Autumn (Au)	23.78 ± 1.39	29.11 ± 2.61	7.88 ± 0.14	3.38 ± 1.38	45.07 ± 2.58	7.93 ± 2.58
Winter (Wi)	21.5 ± 1.32	28.33 ± 0.96	7.91 ± 0.58	4.42 ± 0.70	46.68 ± 2.88	10.03 ± 2.88
Spring (Sp)	23.62 ± 1.49	27.28 ± 3.13	7.76 ± 0.21	4.37 ± 1.38	40.86 ± 5.38	17.72 ± 1.38
Pairwise comparisons	Su > Sp, Au > Wi	NS	NS	Au, Sp > Wi	NS	Sp, Su > A
Pseudo-f; P (perm)	13.56; 0.001			3.72; 0.02		5.81; 0.004

significantly higher in station 4 than in stations 1 and 2 (Table 4). For seasons, *Ceratocephale* sp. was more abundant in summer than in winter, spring and autumn. Species richness and Shannon diversity were also significantly higher in summer. The ANOSIM analysis did not reveal any significant differences in sediment assemblage structure among stations (Global $R = 0.069$, significance level of 0.1%) and seasons (Global $R = 0.036$, significance level of 0.3%) suggesting an overlap in faunal composition at different areas and seasons.

The first two axes of CCA explained 44.9% of the total variance of the species environment correlation. Axis 1 showed positive correlation with coarse sand and medium sand and negative correlation with silt + clay. Medium sand and organic carbon presented positive correlation with axis 2 (Table 5).

Samples from station 1, with medium and coarse sediment, were associated with higher abundance of *Exosphaeroma* sp. and *Chelorchestia darwini* (Muller, 1864). Station 2 and 3 are formed mainly by granules and sandy sediment ranging from fine to very coarse, and were associated with *Melita* sp. Station 4 had samples of sediment with silt + clay and high organic carbon associated with *Oenone fulgida* (Savigny, 1818), Decapoda Xanthidae and *Callinectes ornatus* (Ordway, 1563) (Figure 2).

Spatial and temporal changes in epibiont fauna assemblages

In the prop roots, significant differences in species abundance among stations were found for *Chelorchestia darwini*, *Exosphaeroma* sp. and Tanaidacea sp.1, with the two first being more abundant in station 3, and the latter in stations 1 and 2. Species richness and Shannon diversity did not differ significantly among stations (Table 4). For seasons, *Chelorchestia darwini* was more abundant in autumn than summer and winter. Species richness and Shannon diversity were also significantly higher in autumn. ANOSIM analysis also did not reveal any significant differences in prop roots community structure among stations (Global $R = 0.095$, significance level of 0.2%) and seasons (Global $R = 0.093$, significance level of 0.1%).

The first two axes of CCA explained 56.8% of the total variance of the species-environment correlation. Axis 1 showed positive correlation with salinity and negative correlation with temperature. Dissolved oxygen had negative correlation with axis 2 (Table 6). *Uca maracoani* was associated with higher temperature and turbidity during the summer. *Melita* sp., *Callinectes ornatus* (Ordway, 1563), Decapoda of Xanthidae family were associated with higher dissolved oxygen and pH in spring. Species of the Grapsidae family and *Armases benedicti* (Rathbun, 1897) were associated with conductivity, whereas *Cymadusa filosa* (Savigny, 1816) and *Excirolana armata* (Dana, 1852) with salinity (Figure 3).

DISCUSSION

The benthic community of Guaratiba mangrove main channel was predominantly composed of polychaetes and microcrustaceans, namely of the Isopoda and Tanaidacea orders. Crustaceans and polychaetes worms have also been recorded in other mangrove areas as main organisms of the benthic fauna (Pravinkumar *et al.*, 2013; Musale *et al.*, 2015). The sediment has predominantly sandy fractions, spatially stratified. It was possible to determine a coarser sediment gradient at the station with the closest connection with the ocean compared

Table 4. Results of PERMANOVA for comparisons of numerical abundance of dominant species and descriptors of the benthic community among stations and seasons in Guaratiba mangrove main channel, south-eastern Brazil. NS, non-significant difference.

	Station		Season	
Infauna	Pseudo-F; P (perm)	Pairwise comparisons	Pseudo-F; P (perm)	Pairwise comparisons
Exosphaeroma sp.	12.19; 0.001	1 > 2, 3, 4	NS	
Ceratocephale sp.	4.98; 0.002	2, 3, 4 > 1	4.27; 0.006	Su > Sp, Wi, Au
Laeonereis acuta	6.60; 0.001	3 > 1, 2, 4	NS	
H'	8.86; 0.001	4 > 1, 2	8.65; 0.001	Su > Sp, Wi, Au
D	5.37; 0.002	4 > 1, 2	7.66; 0.001	Su > Sp,Wi, Au
Epibiont fauna				
Chelorchestia darwini	3.44; 0.013	3 > 2	3.41; 0.01	Au < Wi, Su
Exosphaeroma sp.	5.34; 0.006	3 > 1, 2	NS	
Tanaidacea sp.1	2.66; 0.050	1, 2 > 3, 4	NS	
H'	2.45; 0.062	NS	4.07; 0.01	Au < Su, Sp
D	1.78; 0.164	NS	3.80; 0.009	Au < Su, Wi, Sp

Table 5. Results of Canonical Correspondence Analyses of benthic numerical abundance and scores of correlation of sediment variables at Guaratiba mangrove main channel, south-eastern Brazil. Significant correlation between sediment variables and the first two CCA axes in bold.

Axis	1	2	3	4	Total
Eigenvalues	0.140	0.118	0.099	0.077	5.406
Species-environment correlations	0.482	0.545	0.540	0.470	
Cumulative percentage variance					
Species data	2.6	4.8	6.6	8.0	
Species–environment relationship	26.0	47.9	66.2	80.6	
Sum of all Eigenvalues					5.406
Sum of all canonical Eigenvalues					0.538
Variables	1	2			
% Granules	−0.05	−0.17			
% Very coarse sand	0.12	−0.18			
% Coarse sand	**0.39**	−0.07			
% Medium sand	**0.32**	**0.33**			
% Fine sand	−0.20	−0.15			
% Silt + clay	**−0.39**	−0.01			
% Organic Carbon	−0.02	**0.23**			

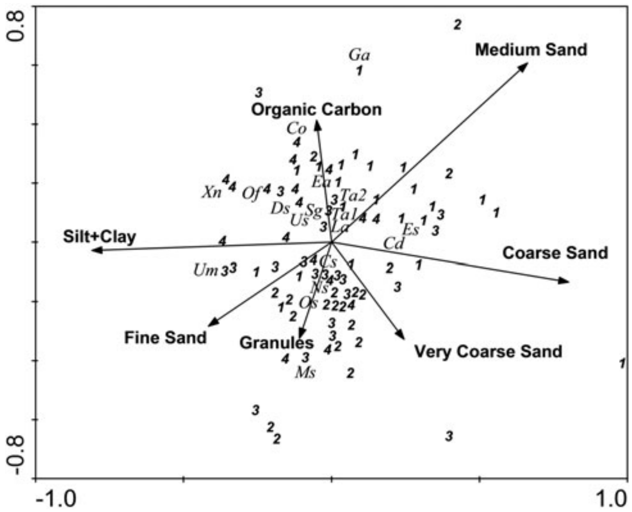

Fig. 2. Ordination plots of the first two axis of Canonical Correspondence Analysis on abundance of benthic community and characteristics of the sediment in the Guaratiba mangrove main channel, south-eastern Brazil. Bi-plot of species, samples coded by stations (1, 2, 3 and 4) and environmental variables. Code of species as in Table 1.

with the inner stations in the mangrove channel. These results are typical of fringe mangroves (Cintrón *et al.*, 1985) whose connection to the sea allows the presence of coarse sediments. Difference in sediment texture is, therefore, an important component of mangrove habitat to define the benthic assemblage.

Infaunal assemblage

Station 4, located in the innermost part of the channel is the farthest area from the connection with the sea, and had the highest richness and diversity of species, showing consistent faunal composition. This pattern shows how the type of sediment influences species distribution, with species selecting substrates with more silt and clay fractions. These fractions have most of the organic carbon content, in non-labile fraction, demonstrating the great ground potential in storing carbon in finer fractions by the formation of an organic-mineral complex (Stevenson, 1994).

Both, the fine grain size of the sediment and the largest organic carbon content seem to exhibit direct influence on the distribution of species of Polychaeta. Indeed, the percentage of silt and clay, as well as the amount of organic matter are main factors structuring the Polychaeta community (Riera *et al.*, 2015). The polychaetes *Laeonereis acuta* and *Ceratocephale* sp. were dominant in the study area with the greatest abundance being recorded in silty-clay substrate. This configuration of the substrate seems to be a preferred habitat for these species, as previously described by Santos & Lana (2001) for estuarine regions of north-eastern Brazil.

Generally, microcrustacean species were associated with coarser fractions of the sediment (Mariano & Barros, 2015). The coarser sand fraction is associated with organic matter free or labile and according to Hook & Burke (2000) is especially important to nitrogen retention, playing an important role in the cycling of soil nutrients. McLachlan *et al.* (1977) and Coull (1988) point out that sediments with coarser fractions have more space between the grains, which promotes a greater variety of niches that can be occupied by other individuals. However, only the isopod *Exosphaeroma* sp. was significantly more abundant in station 1, where the sediment was mainly composed of medium and coarse sand. Since the presence of coarser fractions in the sediment indicates a greater hydrodynamics (Yaacob & Mustapa, 2010), station 1 can be considered a more unstable environment where few species adapt, specializing in occupying these niches with more space between the grains, where other species cannot colonize. Thus, the dynamism and force of currents in the areas near the connection to the sea can be considered as determining factors for the dominance of a few species.

Sediment differences are of crucial importance for most benthic animals, since their feeding strategies tend to be highly adapted to sediment type (McLachlan *et al.*, 1995; Zhuang *et al.*, 2004). Considering the particle size distribution of the Guaratiba mangrove main channel, the pattern of species distribution may be related to structural habitat complexity, since it presents a great mix of grains and allows the

Table 6. Results of Canonical Correspondence Analyses of benthic numerical abundance and scores of correlation of environmental variables at Guaratiba mangrove main channel, south-eastern Brazil.

Axis	1	2	3	4	**Total**
Eigenvalues	0.103	0.062	0.043	0.032	1.699
Species-environment correlations	0.805	0.728	0.603	0.654	
Cumulative percentage variance					
Species data	6.0	9.7	12.2	14.1	
Species–environment relationship	34.9	56.0	70.7	81.6	
Sum of all Eigenvalues					1.699
Sum of all canonical Eigenvalues					0.294
Variables	1	2			
Temperature	**−0.58**	−0.09			
Salinity	**0.42**	0.30			
pH	0.04	−0.16			
Dissolved oxygen	0.16	**−0.43**			
Conductivity	0.22	0.28			
Turbidity	−0.34	0.01			

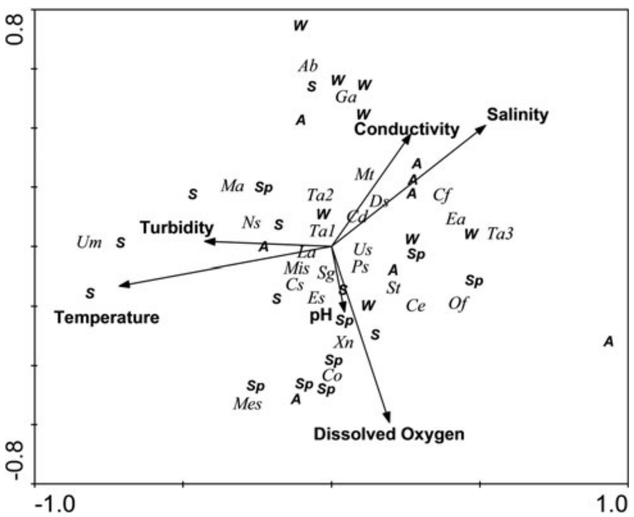

Fig. 3. Ordination plots of the first two axis of Canonical Correspondence Analysis on abundance of benthic community and physic-chemical characteristics of the water in the Guaratiba mangrove main channel, south-eastern Brazil. Bi-plot of species, samples coded by seasons (S, summer; A, autumn; W, winter; Sp, spring) and environmental variables. Code of species as in Table 1.

movement of organisms. According to Centurión & López Gappa (2013), poorly sorted sediments provide many micro-habitats that can support a high biodiversity of benthic organisms, and the presence of a large fraction of sediment generally confers a greater heterogeneity in the microhabitat but are unstable and highly mobile environments.

Epibiont faunal assemblage

In this study, we did not observe significant differences in richness and diversity among stations for the epibiont fauna. These results can be explained by the homogeneous character of the evaluated environmental parameters. On the other hand, the warmer seasons were richer and more diverse than the colder seasons.

The species of microcrustaceans *Exosphaeroma* sp., *Tanaidacea* sp.1 and *Chelorchestia darwini*, and dipteran larvae were significantly more abundant in samples of the prop roots. Recent studies have demonstrated the preference of aquatic invertebrates in colonizing the mangrove vegetation or increase the densities near the prop-roots (Jaxion-Harm *et al.*, 2013), such as Diptera that were found associated with other groups like Isopoda, Amphipoda and Tanaidacea forming a diverse and abundant community (Corrêa *et al.*, 2008). Corroborating the preference of Amphipoda, by this type of habitat, Serejo (2004) reported that *C. darwini* is commonly found in mangrove habitats in both the sediment and the associated vegetation. Likewise, isopods are commonly found inhabiting *Rhizophora mangle* trunks and roots as was also observed by Hendrickx & García-Guerrero (2003). The colonization of marginal vegetation by microcrustaceans contributes to increase habitat complexity by enhancing the number of available niches, and providing shelters (Coull & Wells, 1983; Gillikin & Kamanu, 2005), thus reducing predation effect and increasing the efficiency of the species foraging (Corrêa *et al.*, 2008). Countless studies over the years have demonstrated the importance of plant species in the structuring of different taxa of benthic invertebrates (Heck & Thoman, 1981; Corrêa *et al.*, 2008).

Exosphaeroma sp., although much more abundant in the prop roots, had a significant contribution in the sediment. This suggests that the microtidal regime of the area and the limited channel area favour the marginal vegetation as an attractive habitat for certain species and an efficient mechanism to avoid competition and predation in the sediment. Therefore, the distribution of species is a feature that varies greatly from one habitat to another, and from a set of environmental variables and specific biotic interactions of each region it is difficult to establish a preferred pattern. Moreover, the high hydrodynamic condition of the mangrove channel that connects the bay to the sea contributes to the unstable characteristics of this system. On the other hand, the tidal elevation is an important factor structuring benthic assemblages since the marginal vegetation is exposed to tidal inundation and accessible for colonization.

The tested hypothesis that the benthic fauna uses different mangrove areas to avoid competition seems to be confirmed since the most abundant species coexist occupying the marginal vegetation in different seasons or stations or in different sediment grain fractions. In fact, this is the first time that the benthic invertebrate community of a mangrove area in south-eastern Brazil is described and a spatial partitioning by dominant species was detected. This study is of extreme importance for future comparisons with similar areas of south-eastern Brazil, and to provide subsidies for management measures of this system threatened by anthropic activities.

ACKNOWLEDGEMENTS

The authors thank technicians from Laboratory of Fish Ecology for helping in fieldwork. We also thank Dr Paulo Cesar de Paiva for helping to identify the polychaetes and Dra. Cristiana Serejo and Dr André Senna for helping to identify the isopods and amphipods. Laboratory of Soils of Universidade Federal Rural do Rio de Janeiro helped with the sediment analyses.

FINANCIAL SUPPORT

This work was funded by FAPERJ – Carlos Chagas Foundation for Supporting Research of the Rio de Janeiro State and by CNPq – Brazilian National Council for Research Development. F.G.A. receives funding from FAPERJ and CNPq and D.S.S. received scholarship from CNPq.

REFERENCES

Alongi D.M. and Christoffersen P. (1992) Benthic infauna and organism-sediment relations in a shallow, tropical coastal area: influence of outwelled mangrove detritus and physical disturbance. *Marine Ecology Progress Series* 81, 229–245.

Anderson M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.

Barbier E.B., Hacker S.D., Kennedy C., Koch E.W., Stier A.C. and Silliman B.R. (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81, 169–193.

Camargo M.G. (2006) SYSGRAN: Um sistema de código aberto para análises granulométricas. *Revista Brasileira de Geociências* 36, 371–378.

Centurión R. and López Gappa J. (2013) Benthic biodiversity off the eastern mouth of the Strait of Magellan (Argentina, south-west Atlantic). *Journal of the Marine Biological Association of the United Kingdom* 93, 1–7.

Cintrón G., Lugo A.E. and Martinez R. (1985) Structural and functional properties of mangrove forests. In D'Arcy W.G. and Corrêa M.D.A. (eds) *The botany and natural history of Panama*. Saint Louis, MI: Missouri Botanical Garden, pp. 53–66.

Clarke K.R. and Warwick R.M. (2001) *Changes in marine communities: an approach to statistical analyses and interpretation*. 2nd edition. Plymouth: PRIMER-E.

Corrêa D.A., Oliveira M. and Uieda V.S. (2008) Composition of the aquatic invertebrate fauna associated to the mangrove vegetation of a coastal river, analyzed through a manipulative experiment. *Pan-American Journal of Aquatic Sciences* 3, 23–31.

Coull B.C. (1988) Ecology of the marine meiofauna. In Higgins R.P. and Thiel H. (eds) *Introduction to the study of meiofauna*. Washington, DC: Smithsonian Institution, pp. 18–38.

Coull B.C. (1999) Role of meiofauna in estuarine soft-bottom habitats. *Australian Journal of Ecology* 24, 327–343.

Coull B.C. and Wells J.B.J. (1983) Refuges from fish predation: experiments with phytal meiofauna from the New Zealand Rocky intertidal. *Ecology* 64, 1599–1609.

Dittmann S. (2000) Zonation of benthic communities in a tropical tidal flat of north-east Australia. *Journal of Sea Research* 43, 33–51.

Farrapeira C.M.R., Ramos C.A.C., Barbosa D.F., Melo A.V.O.M., Pinto S.L., Verçosa M.M., Oliveira D.A.S. and Francisco J.A. (2009) Zonación vertical del macrobentos de sustratos sólidos del estuario del río Massangana, Bahía de Suape, Pernambuco, Brasil. *Biota Neotropica* 9, 87–100.

Folk L.R. and Ward W.C. (1957) Brazos river bar: a study in the significance of grain size parameters. *Journal of Sedimentary Petrology* 27, 3–26.

Forbes V.E. and Lopez G.R. (1990) The role of sediment type in growth and fecundity of mud snails (Hydrobiidae). *Oecologia* 83, 53–61.

Gajdzik L., Vanreusel A., Koedam N., Reubens J. and Muthumbi A.W.N. (2014) The mangrove forests as nursery habitats for the ichthyofauna of Mida Creek (Kenya, East Africa). *Journal of the Marine Biological Association of the United Kingdom* 94, 865–877.

Giere O. (2009) *Meiobenthology—the microscopic motile fauna of aquatic sediments*, 2nd edition. Berlin: Springer.

Gillikin D.P. and Kamanu C.P. (2005) Burrowing in the East African mangrove crab, *Chiromantes ortmanni* (Crosnier, 1965) (Decapoda, Brachyura, Sesarmidae). *Crustaceana* 78, 1273–1275.

Heck K.L. Jr and Thoman T.A. (1981) Experiments on predator-prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology* 53, 125–134.

Hendrickx M. and García-Guerrero M. (2003) Distribution of isopods (Peracarida, Isopoda) associated with prop roots of *Rhizophora mangle* in a tropical coastal lagoon, southeastern Gulf of California, Mexico. *Crustaceana* 76, 1153–1169.

Hook P.B. and Burke I.C. (2000) Biogeochemistry in a shortgrass landscape: control by topography, soil texture, and microclimate. *Ecology* 81, 2686–2703.

Jacobi C.M. and Langevin R. (1996) Habitat geometry of benthic substrata: effects on arrival and settlement of mobile epifauna. *Journal of Experimental Marine Biology and Ecology* 206, 39–54.

Jaxion-Harm J., Pien C., Saunders J.E. and Speight M.R. (2013) Distribution of fish, crustacea and zooplankton at different distances from mangrove prop roots within a semi-isolated lagoon. *Journal of the Marine Biological Association of the United Kingdom* 93, 1471–1479.

Koch V. and Wolff M. (2002) Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. *Marine Ecology Progress Series* 228, 119–130.

Lee S.Y. (2008) Mangrove macrobenthos: assemblages, services, and linkages. *Journal of Sea Research* 59, 16–29.

Manson F.J., Loneragan N.R., Skilleter G.A. and Phinn S.R. (2005) An evaluation of the evidence for linkages between mangroves and fisheries: a synthesis of the literature and identification of research directions. *Oceanography and Marine Biology – An Annual Review* 43, 483–513.

Mariano D.L.S. and Barros F. (2015) Intertidal benthic macrofaunal assemblages: changes in structure along entire tropical estuarine salinity gradients. *Journal of the Marine Biological Association of the United Kingdom* 95, 5–15.

McArdle B.H. and Anderson M.J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82, 290–297.

McLachlan A., Jaramillo E., Defeo O., Dugan J., Ruyck A. and Coetzee P. (1995) Adaptation of bivalves to different beach types. *Journal of Experimental Marine. Biology and Ecology* 187, 147–160.

McLachlan A., Winter P.E.D. and Botha A.L. (1977) Vertical and horizontal distribution of sub-littoral meiofauna in Algoa Bay, South Africa. *Marine Biology* 40, 355–364.

McLeod S. (1975) Studies on wet oxidation procedures for the determination of organic carbon in soil. In *Notes on soil techniques*. Adelaide: CSIRO Division of Soils, pp. 73–79.

Musale A.S., Desai D.V., Sawant S.S., Venkat K. and Anil A.C. (2015) Distribution and abundance of benthic macroorganisms in and around Visakhapatnam Harbour on the east coast of India. *Journal of the Marine Biological Association of the United Kingdom* 95, 215–231.

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

Pravinkumar M., Murugesan P., Prakash R.K., Elumalai V., Viswanathan C. and Raffi S.M. (2013) Benthic biodiversity in the Pichavaram mangroves, Southeast Coast of India. *Journal of Oceanography and Marine Science* 4, 1–11.

Riera R., Tuya F., Pérez Ó., Ramos E., Rodríguez M. and Monterroso Ó. (2015) Effects of proximity to offshore fish farms over soft-bottom macrofauna. *Journal of the Marine Biological Association of the United Kingdom* 95, 255–263.

Safahieh A., Nabavi M., Vazirizadeh A., Ronagh M. and Kamalifar R. (2012) Horizontal zonation in macrofauna community of Bardestan mangrove Creek, Persian Gulf. *World Journal of Fish and Marine Sciences* 4, 142–149.

Santos C.S.G. and Lana P.C. (2001) Nereididae (Annelida, Polychaeta) da costa nordeste do Brasil. II. Gêneros Namalycastis, Ceratocephale, Laeonereis e Rullierinereis. *Iheringia – Série Zoologia* 91, 137–149.

Santos J.N.S., Gomes R.S., Vasconcellos R.M., Silva D.S. and Araujo F.G. (2014) Effects of morphodynamics and across-shore physical gradients on benthic macroinfauna on two sandy beaches in south-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom* 94, 671–680.

Selleslagh J., Lesourd S. and Amara R. (2011) Comparison of macrobenthic assemblages of three fish estuarine nurseries and their importance as foraging grounds. *Journal of the Marine Biological Association of the United Kingdom* 92, 85–97.

Serejo C.S. (2004) Talitridae (Amphipoda, Gammaridea) from the Brazilian coastline. *Zootaxa* 29, 1–29.

Shepard F.P. (1954) Nomenclature based on sand–silt–clay ratios. *Journal of Sedimentary Petrology* 24, 151–158.

Snelgrove P.V.R., Buttman C.A. (1994) Animal-sediment relationship revisited: cause versus effect. *Oceanography and Marine Biology – An Annual Review* 32, 111–177.

Soares M.L.G. and Schaeffer-Novelli Y. (2005) Above-ground biomass of mangrove species. I. Analysis of models. *Estuarine, Coastal and Shelf Science* 65, 1–18.

Stevenson F.J. (1994) *Humus Chemistry: genesis, composition, reactions*, 2nd edition. New York: Wiley-Interscience.

Suguio K. (1973) *Introdução a sedimentologia*, 1st edition. São Paulo: Edgard Blücher, Editora da Universidade de São Paulo.

Valença A.P.M.C. and Santos P.J.P. (2013) Macrobenthic community structure in tropical estuaries: the effect of sieve mesh-size and sampling depth on estimated abundance, biomass and composition. *Journal of the Marine Biological Association of the United Kingdom* 93, 1441–1456.

Wentworth C.K. (1922) A scale of grade and class terms for clastic sediments. *Journal of Geology* 30, 377–392.

Yaacob R. and Mustapa M.Z. (2010) Grain-size distribution and subsurface mapping at the Setiu wetlands, Setiu, Terengganu. *Environmental Earth Sciences* 60, 975–984.

Yijie T. and Shixiao T. (2007) Spatial zonation of macrobenthic fauna in Zhanjiang Mangrove Nature Reserve, Guangdong, China. *Acta Ecologica Sinica* 27, 1703–1714.

and

Zhuang S., Zhang M., Zhang X. and Wang Z. (2004) The influence of body size, habitat and diet concentration on feeding of *Laternula marilina* Reeve. *Aquaculture Research* 35, 622–628.

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