PANAMJAS
Pan-American Journal of Aquatic Sciences

Spatio-temporal changes in macroinfaunal assemblages of tropical saltmarshes, northern Brazil

CESAR F. BRAGA[1*], ROSEANNE F. DA SILVA[1], JOSÉ S. R. FILHO[1] & COLIN R. BEASLEY[2]

[1]*Universidade Federal do Pará (UFPA), Instituto de Geociências, Laboratório de Bentos, Avenida Perimetral s/n, CEP 66075-100, Belém, PA, Brazil.* [*]*Corresponding author: c_fbraga@yahoo.com.br*
[2]*Universidade Federal do Pará (UFPA), Campus de Bragança, Laboratório de Moluscos, Alameda Leandro Ribeiro s/n, Bragança, CEP 68600-000, Bragança, PA, Brazil.*

Abstract. Spatio and temporal variation in benthic macroinfaunal structure in saltmarshes from the Pará coast was described at four sites, sampled in April and November of 2008, representing peak conditions in the wet and dry periods, respectively. Differences in abundance and taxa were found among sites and between dates. High macroinfaunal abundance and number of taxa were associated with tall, dense vegetation and sand, and with high salinity, higher temperatures and low sediment organic matter content in November. Typically marine organisms, such as *Halmyrapseudes spaansi*, *Capitella* cf. *capitata* and ostracods of the Family Cypridae were identified as dominant taxa at this time and associated with relatively lower organic matter content in the sediment.

Key words: benthos, invertebrates, variation in structure, *Spartina* habitat, Amazon coast

Resumo. Mudanças espaço-temporais nas assembléias macroinfaunais de marismas tropicais, norte do Brasil. Variações espaciais e temporais na estrutura da macroinfauna bentônica em marismas da costa do Pará foram descritas para quatro locais amostrados em Abril e Novembro de 2008, representando condições extremas dos períodos chuvosos e secos, respectivamente. Diferenças na abundância e número de espécies foram encontradas entre sites e datas. Elevados valores de abundância e número de táxons foram associados com vegetação alta e densa e sedimento arenoso com alta salinidade e temperatura e baixo conteúdo de matéria orgânica em Novembro. Organismos tipicamente marinhos, como *Halmyrapseudes spaansi*, *Capitella* cf. *capitata* e ostrácodes da Família Cypridae foram identificados como táxons dominantes no período seco e foram associados com relativa baixa quantidade de matéria orgânica no sedimento.

Palavras chave: bentos, invertebrados, variabilidade em estrutura, habitat de *Spartina*, costa amazônica

Introduction

Coastal benthic macroinfaunal assemblages have both ecological and economic importance (Snelgrove & Butman 1994, Dittmann 2002) and are characterized by high spatial and temporal variability in abundance and species richness (Morrisey *et al.* 1992 a,b) Such variation may be caused by changes in sediment characteristics (Snelgrove & Butman 1994), salinity (Montagna & Kalke 1992, Ritter *et al.* 2005), temperature (Dippner & Ikauniece 2001) and hydrodynamics (Snelgrove & Butman 1994).

Salinity and temperature in intertidal porewater sediments are positively correlated (Kinne 1970, 1971, Elliott & McLusky 2002) and may be major factors affecting macroinfaunal density (Montagna & Kalke 1992, Palmer *et al.* 2011), diversity (Manino & Montagna 1997, Kim & Montagna 2009) and biomass (Kalke & Montagna 1991). Increases in abundance and biomass of the benthic infauna are also associated with riverine organic matter inputs that favor both deposit and suspension feeders (Montagna & Kalke 1992, Snelgrove & Butman 1994).

In the tropics, rainfall patterns and associated runoff may differ greatly throughout the year and commonly influence the biota of coastal habitats such as mangroves and saltmarshes (Alongi

1989, Dittmann 1995, 2002). Tropical saltmarshes are pioneer intertidal coastal plant systems associated with the seaward fringes of mangrove forest (Pennings & Bertness 2001). Saltmarshes along the Amazon coast, northern Brazil, are composed of *Spartina alterniflora* Loiseleur 1807 (Panitz 1992).

To date, only a few studies have focused on the temporal variation of the benthic fauna associated with saltmarshes, such as those in Galveston Bay, Texas, USA (Vaughn & Fisher 1992, Minello 2000). In Brazil, the saltmarsh macrofauna has been studied in the subtropical Paranaguá Bay in the south (Lana & Guiss 1991, Netto & Lana 1997, Pagliosa & Lana 2000) where high abundance and number of species were associated with colder months. Along the Pará coast, in the tropical northern coast, the saltmarsh macroinfauna in the Taperaçú estuary is most abundant and diverse in the drier period (Braga *et al.* 2009). Spatial differences in the saltmarsh macroinfauna were found among eight other locations in the same region, albeit during the dry season (Braga *et al.* 2011).

Based on these observations, we hypothesize that the macroinfaunal structure associated with saltmarshes should differ among sampling sites and dates at the peak of the wet and dry seasons along the Pará coast, northern Brazil. Thus, we intend to provide more comprehensive data on temporal variation in saltmarsh macroinfaunal composition and abundance in relation to associated changes in vegetation and sediment characteristics.

Materials and Methods

Study area

The eastern Amazon coast including Pará and Maranhão states (Dominguez 2009), also known as the Brazilian macrotidal mangrove coast (Silva *et al.* 2009) is 480 km long with a 7600 km^2 dense strip of mangroves and saltmarshes (Souza-Filho *et al.* 2009). The climate is equatorial and humid with a mean air temperature of 27.7°C (Martorano *et al.* 1993). The annual mean precipitation (thirty year record) ranges from 2300 to 2800 mm (Moraes *et al.* 2005). A dry season occurs from September to November when mean precipitation is near-to-zero, and a wet season from January to April, when 73% of the annual precipitation occurs (Martorano *et al.* 1993).

Sampling was carried out at the end of the wet (April) and dry (November) periods of 2008. On each sampling date, four sites at three estuaries were selected to represent two distinct environments: island (Algodoal: S 0° 36’ 0.9”, W 47° 35’ 11.4”; Canela: S 0° 47’ 21.6”, W 46° 43’ 25.2”) and continent (Marudá: S 0° 37’ 13.6”, W 47° 37’ 59.2”; Ajuruteua Beach at Bragança: S 0° 50’ 17.3”, W 46° 36’ 13.3”). All sites possess several coastal ecosystems including extensive well-developed mangrove forests (Menezes *et al.* 2008) and saltmarshes (Braga *et al.* 2011).

There is a geographical pattern in climate along the Pará coast, with mean annual rainfall increasing westward (Souza-Filho *et al.* 2009). Moreover, the sites are also geographically distinct, with Algodoal and Marudá from the Marapanim estuary in the west, where the wet season begins earlier and lasts longer (Moraes *et al.* 2005) and Bragança, from the Caeté estuary, and Canela, from the Taperaçú estuary, both in the east.

Few hydrogeological data are available for the sites sampled in the present study. The Pará coast is dominated by semidiurnal macrotides ranging from 3.5 m during neap tide to over 6 m during spring tides (Dominguez 2009). Differences in salinity among sites may be associated with river discharges that vary according to catchment size, which range from 508 km^2 to 35200 km^2 (Souza-Filho *et al.* 2009). The Marapanim catchment area is 2500 km^2 (Silva *et al.* 2009), 1546 km^2 for the Caeté and 40 km^2 for the Taperaçu (Araújo Jr & Asp 2013), which lacks a significant freshwater input (Asp *et al.* 2012). Surface water salinity varies from 1 to 35 at Marapanim (Berredo *et al.* 2009), 5 to 38 in the Caeté (Schories *et al.* 2003) and 6 to 35 at the Taperaçu estuary (Dittmar & Lara 2001a).

Sampling and study design

At each site, three saltmarshes (M1, M2, M3) were randomly selected and their areas (m^2) were individually measured and divided into 1 m^2 plots for sampling of four random replicate cores of sediment for benthic macroinfauna with a tube (10 cm diameter, 20 cm height, approximate volume 0.0016 m^3). In order to avoid border effects, sampling was carried out at least 1 meter from the edge of the saltmarsh. For macroinfaunal samples, cores were sieved through a 0.3 mm mesh and all organisms were fixed in 5% buffered formalin and identified to the lowest taxonomic level possible.

A single additional random core was obtained for sediment analyzes, which consisted of granulometry (mean grain size (Φ), sorting, % sand, % silt, % clay) by sieving and pipette analyzes (Suguio 1973), water (mg, 60 °C/4 h) and organic matter (g, 550 °C/4h) (Dean 1974) contents of the sediment. Pore water salinity and temperature (°C) were recorded in the field using a temperature-compensating refractometer and a digital thermometer probe.

Three 0.25 m^2 quadrats were randomly selected for sampling the saltmarsh vegetation. The area of each plot was dug to a depth of 20 cm and all plant material was removed and separated into above (stems and leaves) and below-ground (roots) components. The average height (cm) of the vegetation in the plot was obtained by measuring all the stems. The vegetation density (stems/0.25m^2) was obtained by counting the number of saltmarsh stems inside each plot. Estimates of vegetation above and below-ground water (mg) and organic matter contents (g) were obtained from a random subsample, 25% by volume, dried at 60°C/4h and incinerated in an oven at 500°C/4h, respectively, methodology adapted from Netto & Lana (1997).

Statistical analysis

The total number of individuals (N), number of taxa (S), Pielou´s evenness (J') and Shannon diversity (log10, H') were calculated for each sampling unit. The data were analyzed for differences in N, S, J' and H' among sites and between dates using two-way crossed analysis of variance (ANOVA) (Underwood 1997, Zar 1998). Tukey's multiple comparison tests were used when significant differences ($p<0.05$) were detected (Sokal & Rohlf 1997).

Due to low abundance or the absence of macroinfauna from some cores (23.44%), data from the four replicate cores in each of the three saltmarshes (n=12) were pooled (n=3) for subsequent analysis. Macroinfaunal data were analyzed using multivariate methods in the PRIMER 5.1 statistical package (Clarke & Warwick 1994, Clarke & Gorley 2001). Bray-Curtis similarity (fourth root transformed macroinfaunal abundance) was calculated for each pair of sampling units. Ordination by non-metric multidimensional scaling (MDS) was followed by a formal significance test for differences among sites and between dates using two-way crossed permutational multivariate analysis of variance (PERMANOVA). As there were marked differences in macroinfaunal structure between dates, differences among sites may not have been obvious. Thus, a one-way PERMANOVA was performed among sites within each date. The contributions of each taxon to similarity and dissimilarity among sites and between seasons were assessed using the similarity percentage (SIMPER) routine. Taxa with a contribution of less than 10% to total abundance were excluded to minimize the influence of rare taxa. The Draftsman Plot procedure was used to check for collinearity among vegetation and sediment data. These variables were log (x+1) transformed, except for variables expressed in percentages (sand, silt and clay), which were arcsine transformed. Data were then normalized, and analyzed using Principal Components Analysis (PCA, Euclidian distance). Two-way crossed ANOVAs were used to test for potential significant differences among sites and dates in sediment and vegetation data. The relationship between multivariate patterns in sediment and vegetation variables and the macroinfaunal assemblage structure was explored using the biota-environment matching (BIOENV) procedure between and within sites and sampling dates.

Results

Environmental variables

There was no significant interaction between site and date for most of the sediment variables indicating that variation in mean values among sites was similar on each sampling date. There was no significant difference among sites or dates in relation to sediment water and organic matter contents (Table I). Mean grain size differed significantly among sites and dates. In both April and November, silty sediments predominated at Bragança and Marudá whereas silty and sandy sediments predominated at Algodoal and Canela (Table II). Sediment sorting also differed significantly among sites (Table I). The sediments at Algodoal and Canela tended to be poorly selected whereas those at Bragança and Marudá were moderately to well selected (Table II). Proportions of sand and silt differed significantly among sites and dates and there was significant interaction between these factors (Table I). In April, there is relatively low variation in proportions of sand and silt among sites. However, in November, proportions of sand increased and those of silt decreased to a greater extent in Algodoal and Canela in comparison to those at Bragança and Marudá (Table II). No differences in proportions of clay were found among sites or between dates (Table I). Pore water salinity varied significantly among sites and dates (Table I) and was higher in November at all sites. Values were highest at Canela on both sampling dates, especially in November (Table I). Sediment temperature was significantly higher in November at all sites, especially at Canela and Marudá (Table II).

No significant interaction between sites and dates was detected for vegetation characteristics (Table III). Mean height was significantly different between sites and dates (Table III), with highest values at Bragança and Canela in November (Table IV). Mean density was significantly higher in November at all sites, especially at Canela (Table III) with the greatest temporal difference at Bragança (Table IV). Vegetation area was significantly different among sites (Table III) with highest values at Canela (Table IV). There were no significant differences in above-ground vegetation water or organic matter contents among sites or dates (Table III). Below-ground vegetation water content was significantly higher in November (Table III) with the greatest temporal difference at Canela (Table IV).

Table I. Results of 2 way ANOVA and interaction between factors (F values) evaluating effects of Site and Date on sediment variables in saltmarshes at four sites along the Pará coast in April (Apr) and November (Nov) of 2008 (NS = not significant; * p<0.05, ** p<0.01 and *** p<0.001) and Tukey´s *post hoc* test. Br= Bragança, Ma= Marudá, Al= Algodoal island, Ca= Canela island. Residual degrees of freedom (df) = 16. ≈ approximately equal to.

Variable	Factors		Interaction
	Site (S), df=3	Date (D), df=1	SxD, df=3
Water Content (mg)	0.60 NS	0.00 NS	0.46 NS
Organic Matter (g)	0.55 NS	0.32 NS	0.74 NS
Mean Grain Size (Φ)	3.53 * Br≈Ma>Al≈Ca	9.85 ** Apr>Nov	0.17 NS
Sorting	3.28 * Al≈Ca>Br≈Ma	2.36 NS	2.32 NS
% Sand	6.85 ** Al>Ma>Br≈Ca	13.92 ** Nov>Apr	3.77 *
% Silt	5.31 ** Br≈Ma>Ca>Al	10.74 ** Apr>Nov	4.28 ***
% Clay	0.64 NS	1.29 NS	0.59 NS
Salinity	3.77 * Ca>Al≈Ma≈Br	954.24 *** Nov>Apr	0.51 NS
Temperature (°C)	7.76 ** Ca>Ma≈Br>Al	307.55 *** Nov>Apr	12.30 ***

Table II. Mean values (± SD) of sediment variables in saltmarshes at four sites along the Pará coast in April (Apr) and November (Nov) of 2008 (n=3).

Variable	Date	Sites			
		Algodoal	Bragança	Canela	Marudá
Water Content (mg)	**Apr**	4.40±1.21	3.91±1.06	3.49±0.52	4.01±0.38
	Nov	4.16±1.03	4.18±0.99	3.98±0.34	3.49±0.61
Organic Matter (g)	**Apr**	0.30±0.11	0.20±1.12	0.25±0.16	0.35±0.02
	Nov	0.22±0.07	0.22±1.13	0.24±0.10	0.25±0.04
Mean Grain Size (Φ)	**Apr**	4.13±0.49	5.35±1.62	4.71±0.63	5.09±1.01
	Nov	2.85±1.00	4.28±0.00	3.54±0.06	4.44±0.15
Sorting	**Apr**	0.80±0.93	0.60±0.36	0.68±0.58	0.68±0.65
	Nov	1.49±0.33	0.21±0.01	1.69±0.29	0.65±0.40
% Sand	**Apr**	14.16±22.56	5.30±6.01	3.70±3.16	1.13±1.96
	Nov	61.76±33.86	0.61±1.06	39.91±4.80	12.77±6.78
% Silt	**Apr**	85.84±22.56	88.37±7.48	94.80±4.51	95.96±7.00
	Nov	38.24±33.86	99.39±1.06	60.09±4.80	84.98±9.22
% Clay	**Apr**	0	6.34±10.98	1.50±2.60	2.91±5.05
	Nov	0	0	0	2.25±3.89
Salinity	**Apr**	18.33±1.15	16.33±0.58	19.00±1.73	17.33±0.58
	Nov	36.33±1.53	36.00±0.00	38.67±2.08	35.67±2.52
Temperature (°C)	**Apr**	24.13±1.29	25.73±0.29	24.63±0.55	23.7±0.36
	Nov	28.50±0.98	29.50±0.60	32.67±1.12	32.30±1.11

Three variables were correlated: vegetation mean density with salinity (r_s=0.782), vegetation mean density with temperature (r_s=0.803) and salinity with temperature (r_s=0.896). On the basis of sediment and vegetation variables, the first two principal components (PC) explained 48.1% of the variance in saltmarshes among sites and dates. Along PC1, there is a clear separation of saltmarshes according to date (Fig. 1). On the left-hand side of the ordination, saltmarshes in November, especially those at Algodoal and Canela, were characterized by sediments with high salinity and temperatures, greater percent sand and denser vegetation. On the right-hand side, saltmarshes were associated with silty sediments with high organic matter content in April. Along PC2, saltmarshes tend to separate among sites (Fig. 1). Those on the upper half (especially at Algodoal) were characterized by an increase in percent sand, sorting and vegetation below-ground water content. On the lower half, saltmarshes, especially those from Bragança and Canela, are associated with greater vegetation density, area, above-ground water content and percent silt. Island sites (Algodoal, Canela) differ (higher salinity, sandier and heterogeneous sediments) with respect to continental sites (Bragança, Marudá), especially in November.

Table III. Results of 2 way ANOVA and interaction between factors (F values) evaluating effects of Site and Date on vegetation variables in saltmarshes at four sites along the Pará coast in April (Apr) and November (Nov) of 2008 (NS= not significant; * $p<0.05$, ** $p<0.01$ and *** $p<0.001$) and Tukey´s *post hoc* test. Br= Bragança, Ma= Marudá, Al= Algodoal island, Ca= Canela island. A-G = Above Ground, B-G = Below Ground. Residual degrees of freedom (df) = 16. ≈ approximately equal to.

Variable	Factors		Interaction
	Site (S), df=3	Date (D), df=1	SxD, df=3
Mean Height (cm)	19.83*** Br≈Ca>Al≈Ma	10.64 ** Nov>Apr	1.89 NS
Mean Density (stems/0.25 m^2)	13.18 *** Ca>Al≈Br≈Ma	76.83 *** Nov>Apr	0.51 NS
Area (m^2)	4.77 * Ca>Al≈Br≈Ma	0.71 NS	0.44 NS
A-G Water Content (mg)	1.04 NS	1.41 NS	0.42 NS
A-G Organic Matter (g)	1.06 NS	1.62 NS	0.19 NS
B-G Water Content (mg)	2.63 NS	4.51 * Nov>Apr	0.61 NS
B-G Organic Matter (g)	0.24 NS	2.14 NS	0.01 NS

Table IV. Mean values (± SD) of vegetation variables in saltmarshes at four sites along the Pará coast in April (Apr) and November (Nov) of 2008 (n=3). A-G = Above Ground, B-G = Below Ground.

Variable	Date	Sites			
		Algodoal	Bragança	Canela	Marudá
Mean Height (cm)	**Apr**	35.05±5.84	53.20±9.35	56.04±2.80	37.99±2.21
	Nov	39.47±2.60	70.86±9.29	78.87±17.71	35.56±9.56
Mean Density	**Apr**	46.67±5.03	102.67±9.02	160.00±26.46	67.33±6.11
(stems/0.25 m^2)	**Nov**	159.33±89.11	265.33±11.02	289.33±21.94	190.67±38.70
Area (m^2)	**Apr**	272.58±288.80	796.40±389.05	4071.33±416.61	445.10±450.62
	Nov	435.95±367.46	1129.73±839.22	7404.67±703.31	601.02±573.32
A-G Water Content (mg)	**Apr**	0.50±0.21	0.59±0.21	0.70±0.12	0.63±0.30
	Nov	0.60±0.17	0.72±0.08	1.30±1.24	0.72±0.14
A-G Organic Matter (g)	**Apr**	2.91±1.00	4.02±0.60	3.15±0.79	2.58±0.76
	Nov	3.01±1.17	4.67±0.23	4.72±0.80	3.70±1.79
B-G Water Content (mg)	**Apr**	0.17±0.06	0.20±0.06	0.23±0.03	0.21±0.08
	Nov	0.20±0.04	0.24±0.02	0.32±0.21	0.23±0.04
B-G Organic Matter (g)	**Apr**	0.39±0.24	0.51±0.19	0.52±0.19	0.46±0.19
	Nov	0.56±0.20	0.63±0.10	0.64±0.42	0.61±0.21

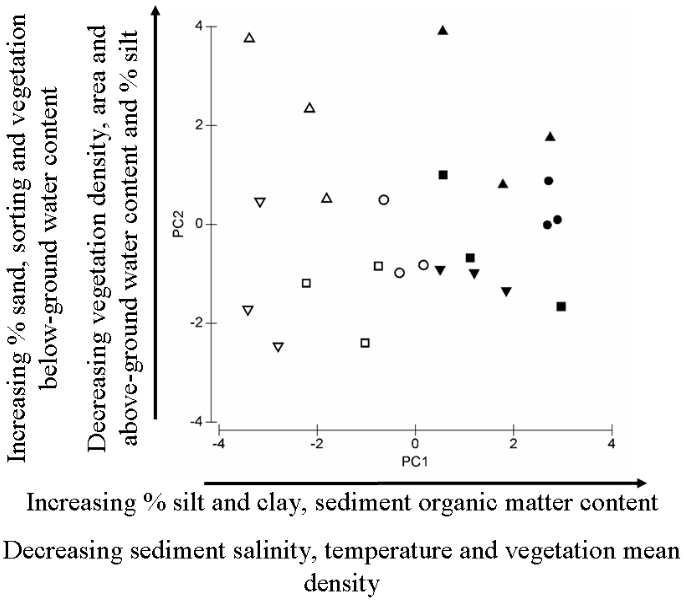

Figure 1. PCA ordination of saltmarshes (n=3) sampled at four sites along the Pará coast in April (closed symbols) and November (open symbols) of 2008. Algodoal (▲, △), Bragança (■, □), Canela (▼, ▽) and Marudá (●, ○). PC1 and PC2 explain 29.7% and 18.4% of the variation, respectively.

Macroinfaunal variables

Differences in assemblage structure were found among sites (PERMANOVA, *pseudo-F*=3.8475, p<0.001) and between dates (PERMANOVA, *pseudo-F*=11.011, p<0.001). Saltmarshes sampled in April were placed on the right-hand side of the MDS ordination (Fig. 2a) and were clearly separated from those sampled in November, on the left-hand side, indicating a well defined temporal difference in macroinfaunal structure. Saltmarshes were distributed along a gradient, from right to left on the ordination, of both increasing numbers of individuals (N) and number of taxa (S), and decreasing values of Pielou’s evenness (J') and Shannon diversity (H') (Fig. 2b-2e). The macroinfaunal structure of island sites (Algodoal, Canela) is distinct from that of continental sites (Bragança, Marudá), especially in November.

In April, numbers of individuals and taxa are lower (Fig. 2b and 2c) and macroinfaunal structure is more variable, particularly at Bragança and Marudá (Fig. 2a). In contrast, in November, numbers of individuals and taxa are higher and there is greater similarity in macroinfaunal composition among sites. Temporal differences in macroinfaunal structure were particularly pronounced for Bragança and Marudá (Fig. 2a). Differences in assemblage structure among sites were found to be significant in April (PERMANOVA, *pseudo-F*=2.3829, p<0.001) and highly significant in November (PERMANOVA, *pseudo-F*=4.7033, p<0.001).

A total of 10043 individuals among 62 taxa were found associated with saltmarshes from the four sites sampled in April and November of 2008 (Table V). Total macroinfaunal abundance (sum of 4 cores) among sites ranged from 1137 at Bragança to 4060 at Algodoal and from 971 to 9072 in April and November, respectively. The number of taxa ranged from 33 at Bragança to 43 at Canela and from 41 to 54 in April and November, respectively. Malacostraca was the dominant group with 51.34% of the total abundance, mostly represented by 5018 individuals of *Halmyrapseudes spaansi* in November at Algodoal and Canela. The Maxillipoda was the least abundant group with a single individual occurring in November at Canela. The Polychaeta was the second most abundant group with 2581 individuals and contained the greatest number of taxa (23) of which the Capitellidae was the most abundant family with 1613 individuals.

Mean number of individuals (N) was relatively similar among sites in April and increased in November, especially at Algodoal and Canela, although interaction was not significant (Tables VI and VII). Mean number of taxa (S) varied significantly among sites and between dates and there was significant interaction between both factors (Table VI). Values increased from April to November, but this increase was much greater at Marudá and Canela (Tables VI and VII). Pielou´s evenness (J') and Shannon diversity (H') were higher in April at Algodoal, Bragança and Canela whereas at Marudá, J' and H' were similar and lower in April, respectively (Tables VI and VII).

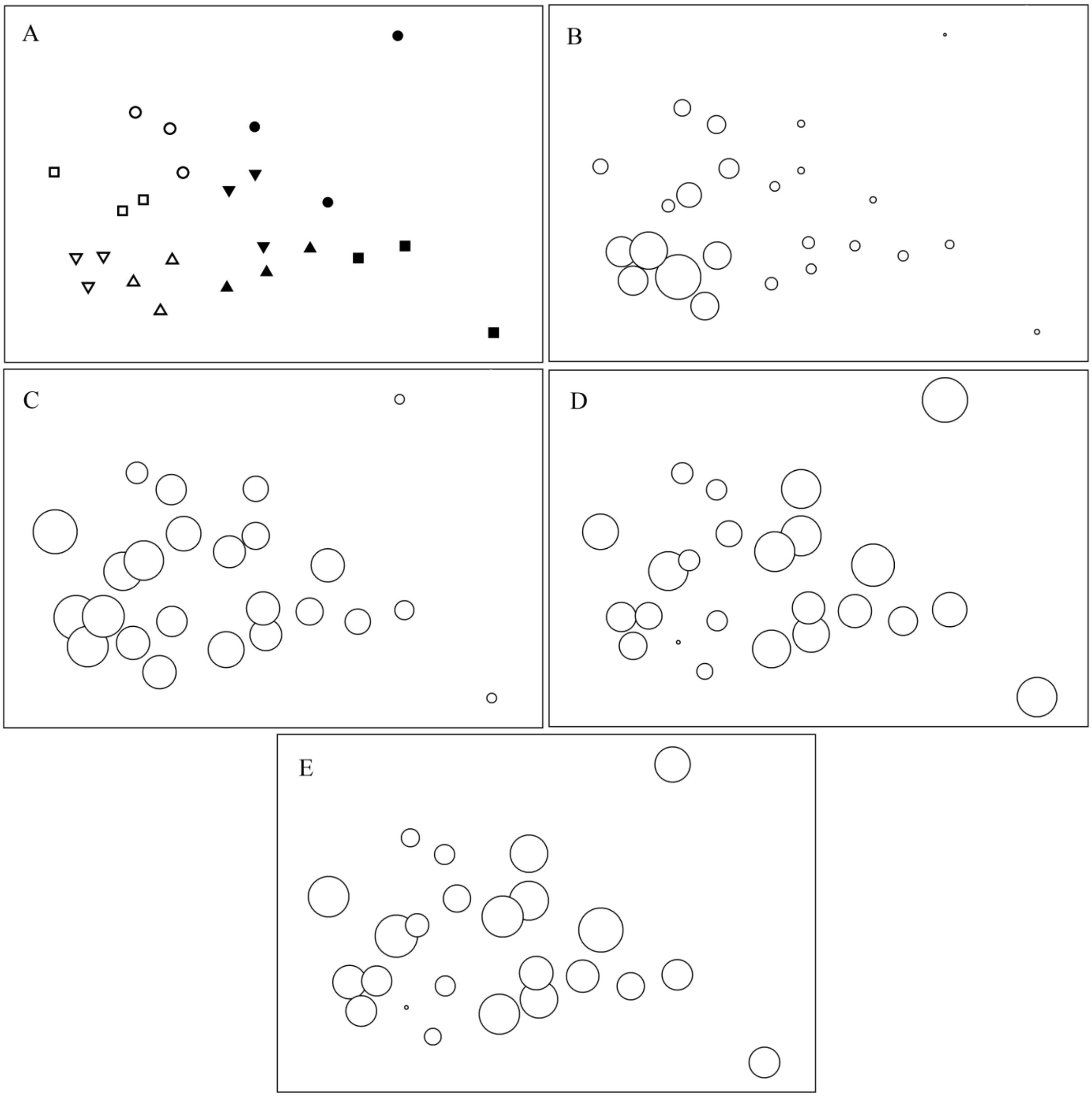

Figure 2. A. Ordination of saltmarshes (n=3) sampled at four sites along the Pará coast in April (closed symbols) and November (open symbols) of 2008 by MDS using a distance matrix (Bray Curtis dissimilarity) based on macroinfaunal abundance and composition with fourth root transformation. 2D stress=0.16. Algodoal (▲, △), Bragança (■, □), Canela (▼, ▽) and Marudá (●, ○). Superimposed values of B. Number of individuals (N); C. Number of taxa (S); D. Pielou's Evenness (J') and E. Shannon diversity (H'). Diameter of circle is proportional to the value of each variable.

Table V. Abundance (total number of individuals summed over 12 sediment cores (4 cores, 3 saltmarshes) of macroinfaunal taxa sampled from saltmarshes at four sites along the Pará coast in April (Apr) and November (Nov) of 2008.

Class	Taxa	Algodoal		Bragança		Canela		Marudá	
		Apr	Nov	Apr	Nov	Apr	Nov	Apr	Nov
Aracnida									
	Acarina sp.	0	0	0	4	0	5	0	0
Bivalvia									
	Anadara sp.	0	0	0	0	0	0	0	1
	Anomalocardia flexuosa	0	0	0	7	0	5	0	13
	Bivalve (juvenile)	6	4	4	12	33	84	0	44

	Codakia costata	0	1	0	0	0	2	0	2
	Eurytellina lineata	0	2	1	0	0	0	1	0
	Iphigenia brasiliensis	0	1	0	0	3	1	0	1
	Lucinidae	0	0	0	0	1	0	0	0
	Macoma constricta	0	0	1	0	0	0	0	0
	Macoma tageliformis	0	0	2	0	0	0	0	0
	Mytella guyanensis	0	0	0	0	0	2	0	1
	Odostomia laevigata	0	0	0	0	1	0	0	0
	Phacoides pectinata	6	5	0	1	0	0	0	2
	Protothaca pectorina	0	0	0	0	1	3	0	2
	Semele sp.	4	0	0	3	3	4	0	0
	Sphenia antillensis	0	0	0	0	0	0	0	12
	Tagelus plebeius	0	0	0	0	1	6	0	7
	Veneridae	4	4	0	3	8	43	0	0
Clitellata									
	Tubificidae	123	20	5	1	2	879	1	3
Gastropoda									
	Gastropoda (juvenile)	0	6	0	4	1	16	0	48
	Hydrobiidae	0	0	1	3	31	0	0	0
	Nerita ascensionis	0	0	0	0	0	0	0	8
Insecta									
	Ceratopogonidae (larvae)	5	2	0	0	0	0	0	0
	Ceratopogonidae (pupae)	1	0	1	0	0	0	0	1
	Chironomidae (larvae)	0	0	0	0	2	0	0	0
	Coleoptera	0	0	0	0	0	4	0	0
	Dolichopodidae (larvae)	11	3	0	2	2	5	0	0
Malacostraca									
	Alpheus sp.	0	1	0	0	0	0	0	0
	Cassidinidea fluminensis	6	1	0	0	6	5	4	20
	Dogielinotidae	1	1	0	1	1	2	16	4
	Eurytium limosum	0	0	0	0	1	1	0	3
	Halmyrapseudes spaansi	1	3220	5	3	1	1765	0	23
	Spelaeomysis siriboia	1	0	2	0	2	0	10	0
	Ocypode quadrata	0	2	1	3	1	3	0	2
	Pseudosphaeroma jakobii	4	2	3	5	2	7	5	7
	Uca cumulanta	1	0	0	0	1	0	0	0
Maxillopoda									
	Cyclopidae	0	0	0	0	0	1	0	0
Nemertea									
	Nemertea	6	4	4	7	7	5	6	8
Ostracoda									
	Cyprinidae	1	1	0	36	3	32	3	624
Polychaeta									
	Alitta succinea	24	20	1	0	6	14	3	22
	Boccardiella sp.	0	0	0	0	0	9	0	1
	Capitella cf. *capitata*	23	309	24	818	73	152	0	102
	Diopatra sp.	0	1	0	0	0	0	0	0
	Eteone sp.	0	0	0	1	0	0	0	0
	Hemipodia sp.	0	0	0	0	0	2	0	0
	Hermundura sp.	0	0	0	0	0	1	0	1
	Hesionidae sp.	0	1	0	0	0	0	0	1
	Heteromastus sp.	3	0	0	1	1	53	0	0
	Isolda pulchella	0	9	0	0	0	132	0	21
	Laeonereis culveri	114	32	13	40	21	23	29	5

Lumbrineridae	0	0	0	0	0	0	0	3
Magelona sp.	0	0	0	0	0	1	0	1
Mediomastus sp.	1	0	3	0	0	0	0	2
Namalycastis abiuma	2	3	0	0	1	0	0	0
Nephtys fluviatilis	0	0	1	0	0	0	0	1
Nephtys simoni	4	0	1	0	1	0	8	0
Notomastus lobatus	0	2	0	31	1	11	0	3
Onuphidae	0	0	0	0	0	0	0	1
Sigambra grubii	16	30	15	49	69	35	10	26
Streblospio sp.	0	2	5	0	0	0	0	0
Terebellidae	0	0	0	0	0	8	0	0
Thoracophelia sp.	3	0	8	1	0	0	116	0

Table VI. Results of 2 way ANOVA and interaction between factors (F values) evaluating effects of Site and Date on macroinfaunal variables associated with saltmarshes at four sites along the Pará coast in April (Apr) and November (Nov) of 2008 (NS= not significant; * p<0.05, ** p<0.01 and *** p<0.001) and Tukey´s *post hoc* test. Br= Bragança, Ma= Marudá, Al= Algodoal island, Ca= Canela island. Residual degrees of freedom (df) = 16. ≈ approximately equal to.

Variable	**Factors**		**Interaction**
	Site (S), df=3	**Date (D), df=1**	**SxD, df=3**
Number of Individuals (N)	4.29 ** Ca≈Al>Ma≈Br	29.72 *** Nov>Apr	3.23 NS
Number of Taxa (S)	4.71 * Ca>Al≈Ma>Br	25.46 *** Nov>Apr	5.79 **
Pielou's Evenness (J')	2.30 NS	39.91 *** Apr>Nov	4.38 *
Shannon Diversity (H')	1.74 NS	16.02 *** Apr>Nov	7.22 **

Table VII. Mean values (± SD) of macroinfaunal variables associated with saltmarshes at four sites along the Pará coast in April (Apr) and November (Nov) of 2008 (n=3).

Variable		**Sites**			
	Date	**Algodoal**	**Bragança**	**Canela**	**Marudá**
Number of Individuals (N)	**Apr**	123.67±32.38	33.67±23.63	95.67±51.05	70.67±41.26
	Nov	1229.67±752.89	345.33±61.61	1107.00±308.49	342.00±253.44
Number of Taxa (S)	**Apr**	16.00±3.00	11.67±5.51	15.33±2.08	9.00±3.00
	Nov	16.33±1.15	14.33±4.04	24.33±1.53	23.00±2.65
Pielou's Evenness (J')	**Apr**	0.67±0.07	0.88±0.10	0.73±0.13	0.63±0.16
	Nov	0.23±0.08	0.34±0.06	0.46±0.03	0.58±0.24
Shannon Diversity (H')	**Apr**	1.87±0.32	2.06±0.32	1.97±0.32	1.33±0.12
	Nov	0.63±0.22	0.91±0.24	1.46±0.13	1.83±0.75

Some taxa such as *Laeonereis culveri*, *Sigambra grubii*, Nemertea, *Pseudospheroma jakobii* and *Alitta succinea* were common to both sites through subject to large temporal variation in abundance. Other taxa, such as the bivalves *Anadara* sp. and Lucinidae, the gastropod *Nerita ascensionis*, Coleoptera, the crustacean *Alpheus* sp. and the polychaetes *Diopatra* sp., *Eteone* sp., *Hemipodia* sp. Lumbrineridae, *Magelona* sp. and Terebellidae were present at only one site and in low abundance. The difference in macroinfaunal structure between saltmarshes in April and November is mainly due to the consistently greater abundance of *Halmyrapseudes spaansi*, *Capitella* cf. *capitata* and cyprid ostracods in November.

Other taxa were more abundant in April and include the polychaetes *Nephtys simoni*, *Thoracophelia* sp., *Namalycastis abiuma* and

Mediomastus, the crustacean *Spelaeomysis siriboia*, the gastropod family Hydrobiidae, the bivalve *Eurytellina lineata* and juvenile ceratopogonid dipterans. In April, differences among sites were due to the greater abundance of Tubificidae, *L. culveri* and *A. succinea* at Algodoal; Hyalellidae and *Thoracophelia* at Marudá; and *S. grubii* at Canela. *Capitella* cf. *capitata* occurred at all sites, except for Marudá.

In November, *H. spaansi*, Tubificidae, Veneridae, *Heteromastus*, *Isolda pulchella*, Terebellidae and juvenile gastropods were very abundant at Canela. At Marudá, abundance of cassidinid isopods was relatively high, whereas those of cyprid ostracods and juvenile gastropods were much greater than at other sites. Juvenile bivalves, Cyprididae and *H. spaansi* were least abundant at Algodoal. Abundance of *Capitella* cf. *capitata* was greater at Bragança in relation to other sites, whereas *A. succinea* was absent from Bragança and abundant at the other sites.

Relationship between environmental variables and macroinfaunal structure

Considering both sampling dates, there was a significant correlation between environmental and macroinfaunal distance matrices. Only a single variable, sediment pore water salinity, best explained the pattern of differences in macroinfaunal structure (BIOENV, r_s=0.518, p<0.05). The second best set of environmental variables (BIOENV, r_s=0.483, p<0.05) related to the macroinfaunal assemblage was composed of sediment organic matter content and temperature. These variables are correlated with the arrangement of saltmarshes based on macroinfaunal structure, with an increase in both salinity and temperature from the right-hand side (saltmarshes in April with low abundance and number of taxa) to the left-hand side (saltmarshes in November with high abundance and number of taxa) (Fig 3a-c). Sediment organic matter content (g) was greater in saltmarshes in November (right-hand side) (Fig 3d). Considering only data from April, salinity, organic matter content and vegetation height (Fig 3e) were positively correlated with macroinfaunal structure (BIOENV, r_s=0.362, p<0.05), whereas with data only from November, % sand (Fig 3f) was the most important variable directly associated with the fauna (BIOENV, r_s=0.550, p<0.05).

Discussion

Macroinfaunal densities (1-3220) and number of taxa (62) in the present study were higher than those found by Braga *et al*. (2009) at a single site in the wet and dry periods, (1-74, 46) and Braga *et al*. (2011) (1-2605, 51) at eight sites in the dry period in the same region, perhaps as a result of sampling greater spatio-temporal heterogeneity. The total number of macroinfaunal species from saltmarsh assemblages along the Pará coast may, in fact, be greater since taxonomic difficulties precluded the identification of all individuals to species level in both the above studies.

The macroinfauna was composed of typically estuarine and marine taxa such as crustaceans, polychaetes and mollusks, as well as those, such as oligochaetes and insect larvae, associated with freshwater. Such a diverse faunal composition is the result of the influence of freshwater as well as associated temporal changes in saltmarsh sediment and vegetation characteristics. Similar wide-ranging diversity has been observed in macroinfaunal assemblages from non-vegetated estuarine habitats (Currier & Small 2005). Crustacea was the faunal group with highest abundance (51.2%), mostly due to that of the tanaid *H. spaansi* at Algodoal and Canela, particularly in November, at the end of the dry period.

Polychaeta was the second most abundant faunal group (25.7%) and was the most diverse macroinfaunal group with 23 taxa. Such polychaete diversity may be related to a wider range of infaunal niches among saltmarsh roots and rhizomes that provide refuges, detritus and various types of infaunal prey (Lana *et al.* 1991, Attolini *et al.* 1997, Flynn *et al.* 1998). The high diversity of polychaetes in the present study suggests a similarly high trophic diversity (Fauchald & Jumars 1979) and thus a well-established assemblage (Froján *et al.* 2006). The infaunal *I. pulchella, L. culveri, S. grubii* and non-selective deposit feeding capitellids, such as *N. lobatus* and *Capitella* cf. *capitata*, are common polychaete taxa found in saltmarsh assemblages in southern (Lana *et al.* 1991, Lana & Guiss 1992), southeastern (Flynn *et al.* 1996, Netto & Lana 1997, Flynn *et al.* 1998), and northern Brazil (Braga *et al.* 2009, 2011). Similarity in the polychaete macroinfauna among saltmarshes along the Brazilian coast may be due to high below-ground structural similarity.

Despite the high abundance of crustacean and polychaete groups, the composition of species may be similar among locations at different latitudes due to ecological equivalence (Nybakken & Bertness 2005). For example, high densities of *H. spaansi* in saltmarshes in northern Brazil (Braga *et al.* 2011) and in the present study, appear not to occur in Paranaguá Bay, subtropical Brazil, where another tanaid crustacean (*Kalliapseudes schubarti*) occurs in very high densities in July but is absent during the rest of the year (Lana & Guiss 1991, Wakabara *et al.* 1996). Similarly, the infaunal polychaete *I. pulchella* is a dominant deposit feeder in subtropical saltmarshes in the south (Lana & Guiss 1992) and southeast of Brazil (Netto & Lana 1997) whereas it is scarce in saltmarshes along the Pará coast, which were dominated by other deposit feeders such as the Tubificidae and the capitelid *Capitella* cf. *capitata*.

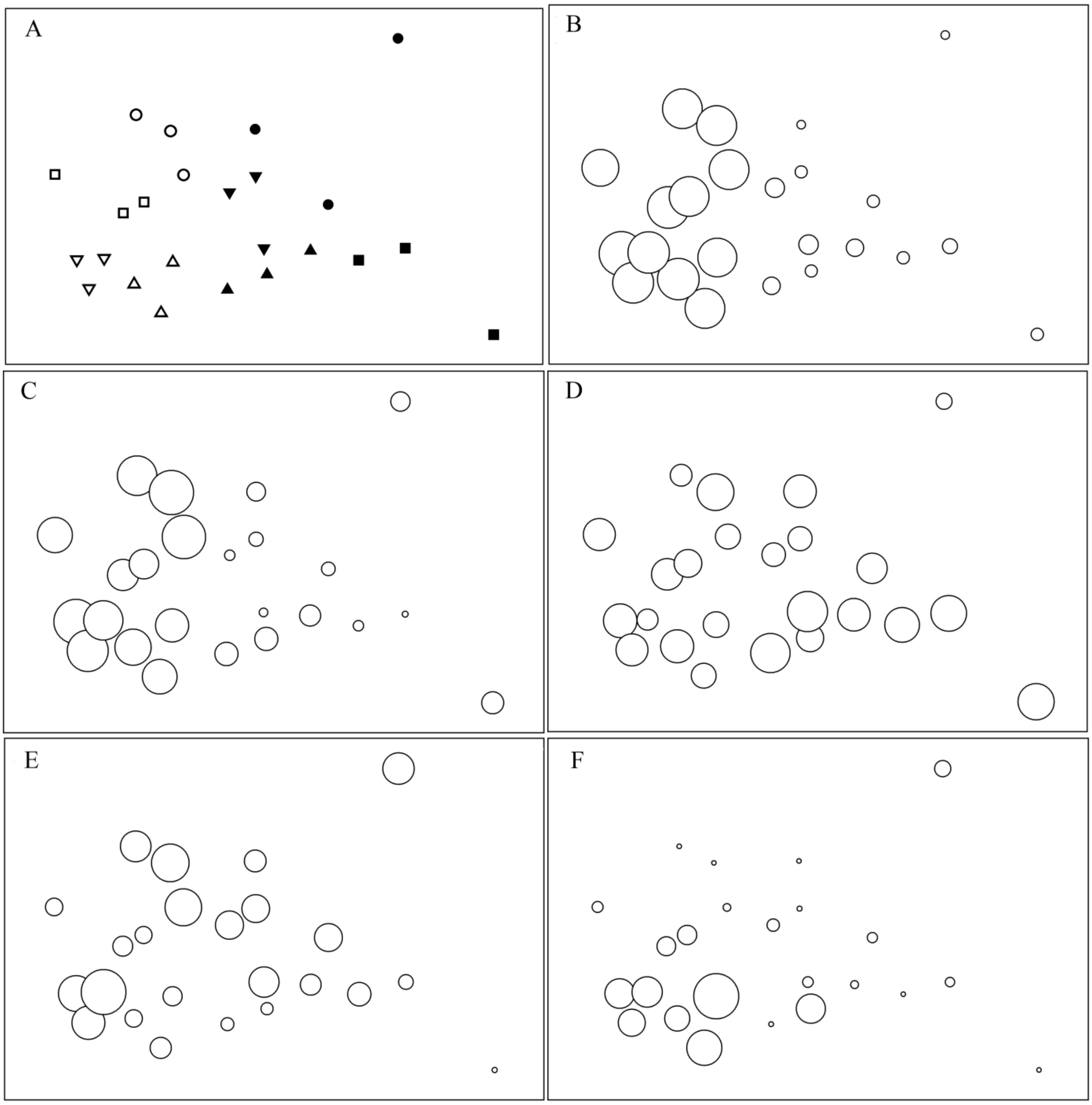

Figure 3. A. Ordination of saltmarshes (n=3) sampled at four sites along the Pará coast in April (closed symbols) and November (open symbols) of 2008 by MDS using a distance matrix (Bray Curtis dissimilarity) based on macroinfaunal abundance and composition with fourth root transformation. 2D stress=0.16. Algodoal (▲, △), Bragança (■, □), Canela (▼, ▽) and Marudá (●, ○). Superimposed values of B. Sediment salinity; C. Sediment temperature (°C); D. Sediment organic matter content (g); E. Vegetation height (cm) and F. % sand. Diameter of circle is proportional to the value of each variable.

Saline, sandier and heterogeneous sediments are associated with greater macroinfaunal abundance at island sites, especially in November, at the end of the dry period, and may be due to a greater marine influence whereas continental sites are subject to a relatively stronger year-round riverine influence resulting in lower abundance. Similar patterns of decreasing macroinfaunal abundance due to increasing freshwater inflow have been described for other intertidal estuarine habitats (Dittmar & Lara 2001b, Nybakken & Bertness 2005, Whitcraft & Levin 2007).

In the present study, greater dominance was recorded in November, at the end of the dry period, due to the very high abundance of marine taxa such as *H. spaansi*, *Capitella* cf. *capitata* and cyprid ostracods in some sampling units. Evidence for small-scale aggregation of infaunal organisms has been demonstrated in saltmarshes (Rader 1984). Braga *et al*. (2011) suggested that the aggregation of these same species in saltmarshes along the Pará coast may be a opportunistic response to an increase in salinity. For example, the population size of *Capitella* cf. *capitata* in estuaries subject to abrupt temporal changes in salinity, may fluctuate due to its short life cycle and rapid reproduction (Hutchings 2000).

At both island and continental sites, strong temporal variation in sediment and saltmarsh vegetation characteristics occurred during the present study resulting in changes in macroinfaunal structure. High macroinfaunal abundance and number of taxa were associated with tall and dense vegetation, sand, high salinity, higher temperatures and low sediment organic matter content in November, at the end of the dry period. Increases in sediment organic matter content and salinity in this period appear to lead to high abundance and diversity of the benthic macrofauna in a range of habitats (Montagna & Kalke 1992, Manino & Montagna 1997, Ysebaert & Herman 2002).

Saltmarshes are halophytes that tolerate fluctuations in salinity and greater height, density and area have been associated with higher salinity (Pennings & Bertness 2001) and saltmarshes along the Pará coast appear to be no exception to this rule (Braga *et al.* 2009). In turn, taller and denser saltmarsh vegetation has been related to a more abundant and diverse macroinfaunal assemblage (Adam 1990, Boorman 1999, Bortolus *et al.* 2002)

Variation in precipitation between April and November of 2008 affecting the influx of freshwater could lead to changes in inputs of organic matter, salinity and temperature (Longley 1994, Russell *et al.* 2006, Xu & Wu 2006) and may be a major factor driving estuarine ecology and function (Elliott & McLusky 2002, Palmer *et al.* 2011). Along the Pará coast, seasonally high precipitation between January and May increases freshwater inflow to coastal areas (Dittmar & Lara 2001b, Schwendenmann *et al.* 2006), increasing rates of fine sediment deposition and decreasing salinity (Alongi 1989, Aller & Stupakoff 1996, Geyer *et al.* 1996). The benthic fauna of non-vegetated tropical tidal flats appears to be generally characterized by high numbers of taxa and low abundances as a result of wide temporal variation in the above factors (Alongi 1989, Dittmann 2002, Guzmán-Alvis *et al.* 2006).

High organic matter contents in the sediment were related to lower abundance and number of taxa in the present study. Organic matter quantity and quality may be key factors structuring marine benthic communities (Rossi *et al.* 2001, Heip *et al.* 2005, Wieking & Kroncke 2005). The Pará and Maranhão coasts in northern Brazil appear to be subject to a high supply of organic matter due to mangrove productivity and riverine input (Dittmar *et al.* 2001) enriching coastal habitats. Very high organic matter contents lead to high rates of decomposition and deoxygenation of the sediment with a reduction in macroinfaunal diversity as a result (Snelgrove & Butman 1994) through the dominance of a limited number of opportunistic species, such as capitellid and nephytid polychaetes (Manino & Montagna 1997, Harmelin-Vivien *et al.* 2009).

In the present study, enrichment with organic matter in April may initially promote macroinfaunal abundance and diversity, but continued enrichment may lead to dominance of opportunistic taxa. For example, highest abundance and diversity of saltmarsh macroinfauna along the Pará coast was associated with intermediate values of organic matter content at Salinas (Braga *et al.* 2011). Positive correlations between organic matter inputs and macroinfaunal structure have been described in saltmarshes from northern (Braga *et al.* 2011), southeastern (Netto & Lana 1997, Flynn *et al.* 1998, Pagliosa & Lana 2000) and southern (Lana *et al.* 1991) Brazil. As long as such inputs of organic matter are not excessive, benthic production may be enhanced (Manino & Montagna 1997).

Salinity and temperature have been positively correlated with greater abundance and number of taxa of macrobenthos along the Amazon coast (Beasley *et al.* 2005, Rosa Filho *et al.* 2005, Aviz *et al.* 2009, Rosa Filho *et al.* 2009). For example, wide variation in nematode abundance and distribution appears related to changes in temperature and salinity associated with seasonal rainfall in the region (Alongi 1987). Strong temporal patterns in settlement of barnacles and oysters were clearly associated with low and high salinities, respectively, in mangrove creeks in northern Brazil (Marques-Silva *et al.* 2006).

Wide variation in salinity has been observed among saltmarshes along the Pará coast where mean pore water salinity varies between 17 and 45 in the dry season (Braga *et al.* 2011). This variation may regulate benthic structure by increasing macrobenthic abundance, productivity and diversity in estuaries (Dexter 1992, Montagna & Kalke 1992, Nielsen *et al.* 2003). In the present study, although mean pore water salinity was much greater in November at the end of the dry season, variation on each sampling date was relatively low (April: 16.5-19; November: 36-39). In contrast, mean values of surface water salinity in estuaries along the Pará coast vary widely, from near zero to over 40 (Santos Filho *et al.* 2008, Berredo *et al.* 2009, Magalhães *et al.* 2009, Sousa *et al.* 2009). Saltmarsh vegetation may buffer strong variation in pore water salinity, through retention of denser saline water among roots in the surrounding sediment whereas taller and denser vegetation slows wind speed and provides shading, thereby reducing evaporation rates (Adam 1990, Whitcraft & Levin 2007). In *Spartina* marshes along the Pacific coast of North America, average sediment salinity varied only 7‰ across 5 embayments (Levin *et al.* 1998). Such a buffering effect of saltmarsh vegetation may also be observed in southern Brazil, where despite inter-seasonal differences, intra-seasonal variation in salinity (23.5-31), temperature (19-34°C) and organic matter content (0.9-3.3 g) was low (Lana & Guiss 1991, Netto & Lana 1997).

In tropical and subtropical estuaries, increases in salinity appear to be directly correlated with sediment temperature as a result of high rates of insolation and evaporation (Dittmar & Lara 2001b, Nybakken & Bertness 2005, Whitcraft & Levin 2007). For example, warm saline waters during summer and spring may have favored greater recruitment of benthic estuarine species in Patos lagoon, southern Brazil (Colling *et al.* 2007, Pinotti *et al.* 2011). The high salinity and temperature observed at Canela, in the present study, where greatest abundance and number of taxa were observed, may be due to its location in an open estuary (Magalhães *et al.* 2009) with greater marine influence and low riverine inflow as well as high rates of evaporation in the sediment, especially during the dry period. At this time, the predominantly easterly trade winds are stronger, increasing evaporation rates along the Pará coast (Souza-Filho *et al.* 2009).

In conclusion, macroinfaunal assemblages associated with saltmarshes along the Pará coast appear to be strongly influenced by increases in salinity and temperature and a decrease in sediment organic matter content in November at the end of the dry period. Greater abundance and number of taxa of macroinfauna at this time appear to be due to a greater contribution of marine taxa, associated with relatively lower organic matter content in the sediment.

Acknowledgments

This study was financed by the Brazilian National Research Council (CNPq) (Edital Universal Process No. 472234/2007-2) and the Instituto de Educação do Brasil (Bolsas de Estudos para o Desenvolvimento da Amazônia). A scholarship to first author/CFB was financed by the CNPq. Special thanks go to V. Ferreira Monteiro, F. Noel dos Santos, M. Vinícius Barros da Silva and D. Mary Lima Rabelo for their help in both the field and in the laboratory.

References

Adam, P. 1990. **Saltmarsh ecology**. Cambridge University Press, Cambridge, 461 p.

Aller, J. Y. & Stupakoff, I. 1996. The distribution and seasonal characteristics of benthic communities on the Amazon shelf as indicators of physical processes. **Continental Shelf Research**, 16(5/6): 717-751.

Alongi, D. M. 1987. Inter-estuary variation and intertidal zonation of free-living nematode communities in tropical mangrove systems. **Marine Ecology Progress Series**, 40: 103-114.

Alongi, D. M. 1989. Ecology of tropical soft-bottom benthos: a review with emphasis on emerging concepts. **Revista de Biologia Tropical**, 31(1): 85-100.

Araújo Jr, W. P. & Asp, N. E. 2013. Hydrodynamic connectivity between two macrotidal Amazonian estuaries. **Journal of Coastal Research**, SI65: 1086-1091.

Asp, N. E., Schettini, C. A. F., Siegle, E., Silva, M. S. & Brito, R. N. R. 2012. The dynamics of a frictionally-dominated Amazonian estuary. **Brazilian Journal of Oceanography**, 60(3): 391-403.

Attolini, F. S., Flynn, M. N. & Tararam, A. S. 1997. Influence of *Spartina alterniflora* and tide level on the structure of polychaete associations in an euryhaline salt marsh in Cananéia lagoon estuarine region (SE Brazil). **Revista Brasileira de Oceanografia**, 45(1/2): 25-34.

Aviz, D., Melo, C. F. & Silva, P. F. 2009. Macrofauna associada às galerias de *Neoteredo reynei* (Bartsch, 1920) (Mollusca: Bivalvia) em troncos de *Rhizophora mangle* Linnaeus durante o período menos chuvoso, em manguezal de São Caetano de Odivelas, Pará (costa norte do Brasil). **Boletim do Museu Paraense Emilio Goeldi, Série Ciências Naturais**, 4(1): 47-55.

Beasley, C. R., Fernandes, C. M., Gomes, C. P., Brito, B. A., Santos, S. M. L. & Tagliaro, C. H. 2005. Molluscan diversity and abundance among coastal habitats of northern Brazil. **Ecotropica**, 11: 9-20.

Berredo, J. F., Costa, M. L. & Progene, M. P. S. 2009. Efeitos das variações sazonais do clima tropical úmido sobre as águas e sedimentos de manguezais do estuário do rio Marapanim, costa nordeste do Estado do Pará. **Acta Amazonica**, 38(3): 473-482.

Boorman, L. A. 1999. Salt marshes - present functioning and future change. **Mangroves and Salt Marshes**, 3: 227-241.

Bortolus, A., Schwindt, E. & Iribarne, O. 2002. Positive plant-animal interactions in the high marsh of an Argentinean coastal lagoon. **Ecology**, 83: 733-742.

Braga, C. F., Beasley, C. R. & Isaac, V. J. 2009. Effects of plant cover on the macrofauna of *Spartina* marshes in northern Brazil. **Brazilian Archives of Biology and Technology**, 52(6): 1409-1420.

Braga, C. F., Monteiro, V. F., Rosa-Filho, J. S. & Beasley, C. R. 2011. Benthic macroinfaunal assemblages associated with Amazonian saltmarshes. **Wetlands Ecology and Management**, 19: 257-272.

Clarke, K. R. & Gorley, R. N. 2001. **PRIMER v5: user manual/tutorial**. Plymouth Marine Laboratory, Primer-E-Ltd, Prospect Place, West Hoe, Plymouth PL1 3DH. U.K., 91 p.

Clarke, K. R. & Warwick, R. M. 1994. **Change in marine communities: an approach to statistical analysis and interpretation**. Natural Environment Research Council, U.K., 144 p.

Colling, L. A., Benvenuti, C. E. & Gandra, M. S. 2007. Seasonal variability on the structure of sublittoral macrozoobenthic association in the Patos Lagoon estuary, southern Brazil. **Iheringia, Série Zoologia**, 93(3): 257-262.

Currier, D. R. & Small, K. J. 2005. Macrobenthic community responses to long-term environmental change in an east Australian sub-tropical estuary. **Estuarine, Coastal and Shelf Science**, 63: 315-331.

Dean, W. E. J. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. **Journal of Sedimentary Petrology,** 44: 242-248.

Dexter, D. M. 1992. Sandy beach community structure: the role of exposure and latitude. **Journal of Biogeography**, 19: 59-66.

Dippner, J. W. & Ikauniece, A. 2001. Long-term zoobenthos variability in the Gulf of Riga in relation to climate variability. **Journal of Marine Systems**, 30: 155-164.

Dittmann, S. 1995. Benthic structure on tropical tidal flats of Australia. **Helgoland Marine Research,** 49: 539-551.

Dittmann, S. 2002. Benthic fauna in tropical tidal flats – a comparative perspective. **Wetlands Ecology and Management**, 10: 189-195.

Dittmar, T. & Lara, R. J. 2001a. Do mangroves rather than rivers provide nutrients to coastal environments south of the Amazon river? Evidence from long-term flux measurements. **Marine Ecology Progress Series**, 213: 67-77.

Dittmar, T. & Lara, R. J. 2001b. Driving forces behind nutrient and organic matter dynamics in a mangrove tidal creek in North Brazil. **Estuarine, Coastal and Shelf Science**, 52: 249-259.

Dittmar, T., Lara, R. J. & Kattner, G. 2001. River or mangrove? Tracing major organic matter sources in tropical Brazilian coastal waters. **Marine Chemistry**, 73: 253–271.

Dominguez, J. M. L. 2009. The coastal zone of Brazil. Pp. 17-51. *In*: Dillenburg, S. & Hesp, P. (Eds.). **Geology and geomorphology of Holocene coastal barriers of Brazil**. Springer-Verlag, Berlin, 380 p.

Elliott, M. & McLusky, D. S. 2002. The need for definitions in understanding estuaries. **Estuarine, Coastal and Shelf Science**, 55: 815-827.

Fauchald, K. & Jumars, P. A. 1979. The diet of worms: a study of polychaete feeding guilds. **Oceanography and Marine Biology**, 17: 193-284.

Flynn, M. N., Tararam, A. S. & Wakabara, Y. 1996. Effects of habitat complexity on the structure of macrobenthic associations in a *Spartina alterniflora* marsh. **Revista Brasileira de Oceanografia**, 44: 9-21.

Flynn, M. N., Wakabara, Y. & Tararam, A. S. 1998. Macrobenthic associations of the lower and upper marshes of a tidal flat colonized by *Spartina alterniflora* in Cananéia lagoon estuarine region (southeastern Brazil). **Bulletin of Marine Science**, 63: 427-442.

Froján, C. R. S. B., Kendall, M. A., Paterson, G. L. J., Hawkins, L. E., Nimsantijaroen, S. & Aryuthaka, C. 2006. Patterns of polychaete diversity in selected tropical intertidal habitats. **Scientia Marina**, 70(3): 239-248.

Geyer, W. R., Beardsley, R. C., Lentz, S. J., Candela, J., Limeburner, R., Johns, W. E., Castro, B. M. & Soares, I. D. 1996. Physical oceanography of the Amazon shelf. **Continental Shelf Research**, 16(5/6): 575-616.

Guzmán-Alvis, A., Lattig, P. & Ruiz, J. A. 2006. Spatial and temporal characterization of soft bottom polychaetes in a shallow tropical bay (Colombian Caribbean). **Boletín de Investigaciones Marinas y Costeras**, 35: 19-36.

Harmelin-Vivien, M. L., Bănaru, D., Dierking, J., Hermand, R., Letourneur, Y. & Salen–Picard, C. 2009. Linking benthic biodiversity to the functioning of coastal ecosystems subjected to river runoff (NW Mediterranean). **Animal Biodiversity and Conservation**, 32(2): 135-145.

Heip, C. H. R., Herman, P. M. J., Middelburg, J. J., Moodley, L., Soetaert, H. & Ysebaert, T. 2005. The ecology of estuarine intertidal flats – the example of the Westerschelde. Pp. 179–195. *In*: Wilson, J. G. (Ed.). **The Intertidal Ecosystem: The Value of Ireland's Shores**. Royal Irish Academy, Dublin, 206 p.

Hutchings, P. A. 2000. Family Capitellidae. Pp. 67-72. *In*: Beesley, P. L., Ross, G. J. B. & Glasby, C. J. (Eds.). **Polychaetes & Allies: The Southern Synthesis.** CSIRO Publishing, Melbourne, 465 p.

Kalke, R. D. & Montagna, P. A. 1991. The effect of freshwater inflow on macrobenthos in the Lavaca River Delta and Upper Lavaca Bay, Texas. **Contributions in Marine Science**, 32: 49-71.

Kim, H. C. & Montagna, P. A. 2009. Implications of Colorado river (Texas, USA) freshwater inflow to benthic ecosystem dynamics: A modeling study. **Estuarine, Coastal and Shelf Science** 83, 491–504.

Kinne, O. 1970. Temperature: invertebrates. Pp. 407-514. *In*: Kinne, O. (Ed.). **Marine Ecology**. Wiley-Interscience, New York, 681 p.

Kinne, O. 1971. Salinity: invertebrates. Pp. 821-995. *In*: Kinne, O. (Ed.). **Marine Ecology**. Willey–Interscience, New York, 681 p.

Lana, P. C. & Guiss, C. 1991. Influence of *Spartina alterniflora* on structure and temporal variability of macrobenthic associations in a tidal flat of Paranaguá bay (southeastern Brazil). **Marine Ecology Progress Series**, 73(2/3): 231-244.

Lana, P. C. & Guiss, C. 1992. Macrofauna - plant-biomass interactions in a euhaline salt-marsh in Paranaguá Bay (SE Brazil). **Marine Ecology Progress Series**, 80(1): 57-64.

Lana, P. C., Guiss, C. & Disaró, S. T. 1991. Seasonal variation of biomass and production dynamics for above and below-ground components of a *Spartina alterniflora* marsh in the euhaline sector of Paranaguá Bay (SE Brazil). **Estuarine, Coastal and Shelf Science**, 32: 231-241.

Levin, L. A., Talley, T. S. & Hewitt, J. 1998. Macrobenthos of *Spartina fofiosa* (Pacific cordgrass) salt marshes in southern California: community structure and comparison to a Pacific mudflat and a *Spartina alterniflora* (Atlantic smooth cordgrass) marsh. **Estuaries and Coasts**, 21(1): 129-144.

Longley, W. L. 1994. **Freshwater inflows to Texas bays and estuaries: ecological relationships and methods for determination of needs**. Texas Water Development Board and Texas Parks and Wildlife Department, Austin, Texas, 386 p.

Magalhães, A., Bessa, R. S. C., Pereira, L. C. & Costa, R. M. 2009. Variação temporal da composição, ocorrência e distribuição dos Copepoda (Crustacea) do estuário do Taperaçu, Pará, Brasil. **Boletim do Museu Paraense Emilio Goeldi, Série Ciências Naturais**, 4(2): 133-148.

Manino, A. & Montagna, P. A. 1997. Small-scale spatial variation of macrobenthic community structure. **Estuaries**, 20(1): 159-173.

Marques-Silva, N. S., Beasley, C. R., Gomes, C. P., Gardunho, D. C. L., Tagliaro, C. H., Schories, D. & Mehlig, U. 2006. Settlement dynamics of the encrusting epibenthic macrofauna in two creeks of the Caeté mangrove estuary (north Brazil). **Wetlands Ecology and Management**, 14: 67-78.

Martorano, L. G., Pereira, L. C., Cezar, E. G. M. & Pereira, I. C. B. 1993. **Estudos climatológicos do Estado do Pará, classificação climática (Köppen) e deficiência hídrica (Thorntwaite, Mather).** SUDAM/EMBRAPA, Belém, Pará, Brazil, 53 p.

Menezes, M. P. M., Berger, U. & Mehlig, U. 2008. Mangrove vegetation in Amazonia: a review of studies from the coast of Pará and Maranhão States, north Brazil. **Acta Amazonica**, 38(3): 403-420.

Minello, T. J. 2000. Temporal development of salt marsh value for nekton and epifauna: utilization of dredged material marshes in Galveston Bay, Texas, USA. **Wetlands Ecology and Management**, 8: 327-341.

Montagna, P. A. & Kalke, R. D. 1992. The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces estuaries, Texas. **Estuaries**, 15(3): 307-326.

Moraes, B. C., Costa, J. M. N., Costa, A. C. L. & Costa, M. H. 2005. Variação espacial e temporal da precipitação no Estado do Pará. **Acta Amazonica**, 35: 207-214.

Morrisey, D. J., Howitt, L., Underwood, A. J. & Stark, J. S. 1992a. Spatial variation in soft-sediment benthos. **Marine Ecology Progress Series**, 81(2): 197-204.

Morrisey, D. J., Underwood, A. J., Howitt, L. & Stark, J. S. 1992b. Temporal variation in soft-sediment benthos. **Journal of Experimental Marine Biology and Ecology**, 164(2): 233-245.

Netto, S. A. & Lana, P. C. 1997. Intertidal zonation of benthic macrofauna in a subtropical salt marsh and nearby unvegetated flat (SE, Brazil). **Hydrobiologia**, 353: 171-180.

Nielsen, D. L., Brock, M. A., Rees, G. N. & Baldwin, D. S. 2003. Effects of increasing salinity on freshwater ecosystems in Australia. **Australian Journal of Botany**, 51: 655-665.

Nybakken, J. W. & Bertness, M. D. 2005. **Marine biology: an ecological approach**. Pearson/Benjamin Cummings, San Francisco, 592 p.

Pagliosa, P. R. & Lana, P. C. 2000. Population dynamics and secondary production of *Nereis oligohalina* (Nereididae, Polychaeta) from a subtropical marsh in southeast Brazil. **Bulletin of Marine Science**, 67(1): 259-268.

Palmer, T. A., Montagna, P. A., Pollack, J. B., Kalke, R. D. & DeYoe, H. R. 2011. The role of freshwater inflow in lagoons, rivers, and bays. **Hydrobiologia**, 667: 49-67.

Panitz, C. M. N. 1992. Ecological aspects of salt marsh ecosystems in Santa Catarina Island, Brazil. Pp. 213-230 *In*: Seeliger, U. (Ed.). **Coastal plant communities of Latin America**. Academic Press, New York, 392 p.

Pennings, S. C. & Bertness, M. D. 2001. Salt marsh communities. Pp. 313-351.. *In*: Bertness, M. D., Gaines, S. D. & Hay, M. E. (Eds.). **Marine Community Ecology**. Sinauer Associates, Sunderland, USA, 550 p.

Pinotti, R. M., Colling, L. A. & Benvenuti, C. E. 2011. Temporal dynamics of deep infralittoral macrobenthic fauna inside a subtropical estuarine environment. **Brazilian Journal of Aquatic Science and Technology**, 15(1): 26-41.

Rader, D. N. 1984. Salt-marsh benthic invertebrates: small-scale patterns of distribution and abundance. **Estuaries**, 7: 413-420.

Ritter, C., Montagna, P. A. & Applebaum, S. 2005. Short-term succession dynamics of macrobenthos in a salinity-stressed estuary. **Journal of Experimental Marine Biology and Ecology**, 323(1): 57-69.

Rosa Filho, J. S., Almeida, M. F. & Silva, D. E. A. 2009. Spatial and temporal changes in the benthic fauna of a macrotidal Amazon sandy beach, Ajuruteua, Brazil. **Journal of Coastal Research**, SI56: 1823-1827.

Rosa Filho, J. S., Busman, D. V., Viana, A. P., Gregório, A. M. & Oliveira, D. M. 2005. Macrobenthos bentônica de zonas entre-marés não vegetadas do estuário do rio Caeté (Bragança-PA). **Boletim do Museu Paraense Emilio Goeldi, Série Zoologia**, 2: 109-121.

Rossi, F., Como, S., Corti, S. & Lardicci, C. 2001. Seasonal variation of a deposit-feeder assemblage and sedimentary organic matter in a brackish basin mudflat (Western Mediterranean, Italy). **Estuarine, Coastal and Shelf Science**, 53: 181-191.

Russell, M. J., Montagna, P. A. & Kalke, R. D. 2006. The effect of freshwater inflow on net ecosystem metabolism in Lavaca Bay, Texas. **Estuarine, Coastal and Shelf Science**, 68: 231-244.

Santos Filho, C., Tagliaro, C. H. & Beasley, C. R. 2008. Seasonal abundance of the shipworm *Neoteredo reynei* (Bivalvia, Teredinidae) in mangrove driftwood from a northern Brazilian beach. **Iheringia**, **Série Zoologia**, 98(1): 17-23.

Schories, D., Barletta-Bergan, A., Barletta, M., Krumme, U., Mehlig, U. & Verena, R. 2003. The keystone role of leaf-removing crabs in mangrove forests of north Brazil. **Wetlands Ecology and Management**, 11: 243-255.

Schwendenmann, L., Riecke, R. & Lara, R. J. 2006. Solute dynamics in a North Brazilian mangrove: the influence of sediment permeability and freshwater input. **Wetlands Ecology and Management**, 14: 463–475.

Silva, C. A., Souza-Filho, P. W. M. & Rodrigues, S. W. P. 2009. Morphology and modern sedimentary deposits of the macrotidal Marapanim Estuary (Amazon, Brazil). **Continental Shelf Research**, 29: 619–631.

Snelgrove, P. V. R. & Butman, C. A. 1994. Animal sediment relationships revisited: cause versus effect. **Oceanography and Marine Biology**, 32: 111-117.

Sokal, R. R. & Rohlf, J. F. 1997. **Biometry: the principles and practice of statistics in biological research**, 3rd Edition. W. H. Freeman and Company, New York, 850 p.

Sousa, E. B., Costa, V. B., Pereira, L. C. & Costa, R. M. 2009. Variação temporal do fitoplâncton e dos parâmetros hidrológicos da zona de arrebentação da Ilha Canela (Bragança, Pará, Brasil). **Acta Botanica Brasilica**, 23(4): 1084-1095.

Souza-Filho, P. W. M., Lessa, G. C., Cohen, M. C. L., Costa, F. R. & Lara, R. J. 2009. The subsiding macrotidal barrier estuarine system of the eastern Amazon coast, northern Brazil. Pp. 347-375. *In*: Dillenburg, S. & Hesp, P. (Eds.). **Geology and geomorphology of Holocene coastal barriers of Brazil**. Springer-Verlag, Berlin, 380 p.

Suguio, K. 1973. **Introdução à sedimentologia**. Edgard Blucher, São Paulo, 317 p.

Underwood, A. J. 1997. **Experiments in ecology. Their logical design and interpretation using analysis of variance**. Cambridge University Press, Cambridge University, 522 p.

Vaughn, C. C. & Fisher, F. M. 1992. Dispersion of the salt-marsh periwinkle *Littoraria irrorata* - effects of water level, size and season. **Estuaries**, 15(2): 246-250.

Wakabara, Y., Nicoletti, A. & Tararam, A. S. 1996. Ingestion and selection of suprabenthic crustaceans by small-sized fishes in a lower saltmarsh system. **Revista Brasileira de Oceanografia**, 44(2): 89-103.

Whitcraft, C. R. & Levin, L. A. 2007. Regulation of benthic algal and animal communities by salt marsh plants: impact of shading. **Ecology**, 88(4): 904-917.

Wieking, G. & Kroncke, I. 2005. Is benthic trophic structure affected by food quality? The Dogger Bank example. **Marine Biology**, 146: 387-400.

Xu, Y. J. & Wu, K. 2006. Seasonality and interannual variability of freshwater inflow to a large oligohaline estuary in the Northern Gulf of Mexico. **Estuarine, Coastal and Shelf Science**, 68: 619-626.

Ysebaert, T. & Herman, P. M. J. 2002. Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. **Marine Ecology Progress Series**, 244: 103-124.

Zar, J. H. 1998. **Biostatistical analysis**, 4th Edition. Prentice Hall, New Jersey, 929 p.

Received December 2012
Accepted August 2013
Published online December 2013