

Relationships between copepod community structure, rainfall regimes, and hydrological variables in a tropical mangrove estuary (Amazon coast, Brazil)

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Abstract The influence of rainfall and hydrological variables on the abundance and diversity of the copepod community was investigated on a monthly basis over an annual cycle in the Taperaçu mangrove estuary. In general, the results show that there were no clear spatial or tidal patterns in any biological variables during the study period, which was related to the reduced horizontal gradient in abiotic parameters, determined mainly by the morphological and morphodynamic features of the estuary. Nevertheless, seasonal and monthly trends were recorded in both the hydrological data and the abundance of the dominant copepod species. In particular, *Pseudodiaptomus marshi* ($6,004.6 \pm 22,231.6 \text{ ind m}^{-3}$; $F = 5.0$, $p < 0.05$) and *Acartia tonsa* ($905.6 \pm 2,400.9 \text{ ind m}^{-3}$; $F = 14.6$, $p < 0.001$) predominated during the rainy season, whereas *Acartia lilljeborgii* ($750.8 \pm 808.3 \text{ ind m}^{-3}$; $U = 413.0$, $p < 0.01$) was the most abundant species in the dry season. A distinct process of succession was observed in the relative abundance of these species, driven by the shift in the rainfall regime, which affected hydrological, in particular salinity, and consequently the abundance of copepod species. We suggest that this may be a general pattern governing the dynamics of copepod populations in the estuaries of the Brazilian Amazonian region.

Keywords Copepod temporal variation · Rainfall levels · Ecological succession · Salinity · Amazonian estuary

Introduction

Brazil has the second largest area of mangrove forest on Earth, distributed along a coast of approximately 6,800 km (Kjerfve et al. 1997). The country's northernmost coastline is extremely irregular, with innumerable bays, muddy, and sand beaches, salt and freshwater swamps, islands, and estuaries, among other ecosystems (Souza-Filho et al. 2005) that shelter highly complex and productive ecosystems, in which the biological dynamics are influenced by combined effects of the local climate and the physical–chemical characteristics of the water (Giarrizzo and Saint-Paul 2008; Costa et al. 2011). The hydrological and hydrodynamic conditions of these environments are favorable for the development of the planktonic larvae of a wide range of marine fish and shellfish species, which use these habitats as nurseries by providing a rich food source (e.g., phytoplankton and detritus) and protection from predation, as reported to other coastal ecosystems worldwide (Dauvin and Desroy 2005; Nagelkerken et al. 2008).

The estuaries of the Amazonian coast are characterized by a relatively hot and humid equatorial climate which, combined with a semidiurnal macrotidal regime and vast areas of mangrove forest, creates a unique aquatic ecosystem, in terms of its physical–chemical and biological characteristics, especially in comparison with other tropical coastal environments in India (Dalal and Goswami 2001; Madhu et al. 2007), Africa (Champalbert et al. 2007), Australia (Duggan et al. 2008), Costa Rica (Brugnoli-Oliviera and Morales-Ramírez 2008), and other regions of Brazil (Sankaranakutty et al. 1995; Marcolin et al. 2010). In recent years, research into the region's zooplankton (Krumme and Liang 2004; Costa et al. 2008) and especially its copepods Magalhães et al. (2006, 2009a, b, 2011; Leite et al. 2010) has increased considerably.

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In temperate waters, the seasonal relationship of phyto- and mesozooplankton populations often shows what resembles coupled oscillations which might suggest a classical Lotka–Volterra predator–prey relationship (Kjørboe 1997), i.e., the phytoplankton populations are limited by predation, while the zooplankton (predator) populations are limited by the availability of feeding resources. This top-down versus bottom-up control has been observed in several tropical and subtropical estuaries around the world (Rios-Jara 1998; Ara 2002; Marques et al. 2007). However, ecological studies in the mangroves estuaries of the Amazonian coast (Atique 2009; Magalhães et al. 2011) suggest that the high productivity of these systems can be related to its detritus-based food web, in which the forest represents one of the main sources of carbon for aquatic consumers (Dobson and Frid 2009). Giarrizzo et al. (2011) confirmed the importance of the mangroves in this region as a source of carbon using stable isotopes, showing that this compound enters the food web indirectly as particulate organic matter (POM), which is assimilated by Calanoida copepods and transferred to higher trophic levels through the ingestion of these invertebrates by chaetognaths and small zooplanktivores pelagic fishes. Clearly, the role of the copepods as a direct and efficient path for the transfer of energy to higher level consumers is pivotal to the functioning of this system. Given this, understanding the biological attributes of copepod populations is essential for the reliable assessment of their contribution to the processes that structure the aquatic systems they inhabit, as well as the evaluation of the effects of anthropogenic impacts on these systems, to which these organisms are particularly sensitive (Park and Marshall 2000).

Despite the importance of copepods at the secondary trophic level, the scale and pattern of temporal variations in abundance and biodiversity are still poorly known in the specific context of tropical estuaries. Estimates of copepods abundance are fundamental to the determination of biomass and productivity, which are crucial for the understanding of energy flow and the trophodynamics of estuarine systems. In addition to all these considerations, the assessment of biodiversity on both a regional and global scale is an increasingly important issue in ecology, given the growing evidence of profound anthropogenic modifications to the biosphere (Palumbi 2001).

Given these considerations, the present study focused on a continuous 12-month analysis of the abundance and ecological indices (species diversity, evenness, and richness) of copepods in a tropical, tide-dominated estuary, the Taperaçu, in northern Brazil. These biological parameters provide an annual profile of the zooplankton community structure in an estuary with unique characteristics, such as the absence of fluvial discharge, a small catchment area, shallow waters, and strong tidal currents, which may be

especially useful for comparative studies with similar systems in Brazil and in other parts of the world. A primary aim of this survey was to contribute to the understanding of the effects of regional coastal conditions (e.g., climatological and hydrological) on the temporal variation of copepod populations in tropical estuarine ecosystems.

Materials and methods

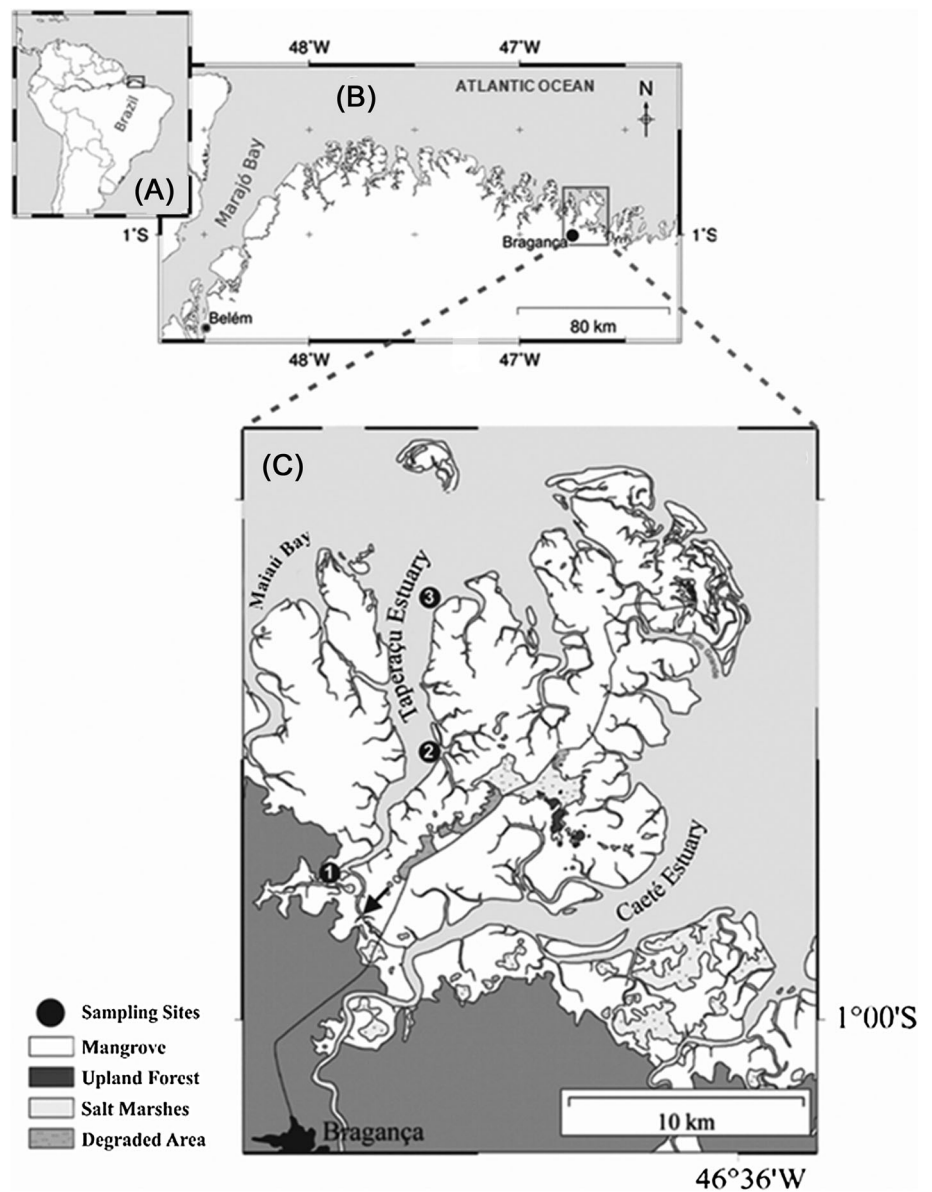
This study was carried out in the Taperaçu estuary (46°42′–46°45′W and 00°50′–00°57′S), located about 200 km southeast of the mouth of the Amazon River, in the municipality of Bragança, northern Brazil. It is classified as a shallow (mean depth = 4.2 m), permanently open estuary, with many sandbanks running down the middle, high turbidity (mean 378.1), and strong tidal currents of up to 2.04 m s^{-1} (Asp et al. 2012). Delimited by the Atlantic Ocean and the Maiaú Bay and Caeté estuary (Fig. 1), the Taperaçu has 21 km² of surface water and a catchment area of approximately 40 km², but no effective source of freshwater. A recent study conducted in this estuary indicates that the system is characterized by discreet vertical gradients in hydrological parameters (Asp et al. 2012). The main hydrodynamic feature is a semidiurnal tidal range of about 5 m, which may reach 6 m during the equinoctial spring tides (DHN 2008).

The local climate is humid equatorial, with a rainy season normally between January and July, and a dry (or less rainy) season between August and December (Moraes et al. 2005), although considerable variation may be observed in some years. This seasonal pattern is controlled primarily by shifts in the intertropical convergence zone (ITCZ), which provokes intense convective activity during the first half of the year. Mean annual rainfall is 2,401 mm (INMET 2012), with 75 % of the precipitation falling during the rainy season. Average monthly air temperatures are between 25.2 and 26.7 °C, with maximum daily amplitude between 20.4 and 32.8 °C (Schories and Mehlig 2000).

The Taperaçu estuary is surrounded by wetlands and extensive mangrove forests, with trees reaching up to 20 m in height, and a complex network of tidal creeks, which link the Taperaçu with the neighboring Maiaú Bay and Caeté estuary. Due to its biogeochemical, ecological, and socioeconomic importance, this ecosystem has been designated a conservation unit (RESEX Caeté-Taperaçu) by the Brazilian government.

Zooplankton samples were collected at monthly intervals in the Taperaçu estuary from January to December 2006 during spring tides at three stations located in the upper (1), middle (2), and lower (3) sectors of the estuary (Fig. 1). Each sample consisted of a 3-min subsurface

Fig. 1 Study area: **a** South America; **b** Location of the Taperaçu estuary on the Amazonian coast of northern Brazil; **c** Positions of the sampling stations in the upper (1), middle (2), and lower (3) sectors of the Taperaçu estuary, with the *black arrow* indicating the position of Taici creek, which connects the Taperaçu and Caeté estuaries (modified from Mehlig 2001)



horizontal tow of a conical plankton net (300 μ m mesh) fitted with a mechanical flowmeter to estimate the volume of water filtered through the net. Two tows per station were conducted each month—one on the ebb tide and the other on the flood tide—resulting in a total of 72 samples. The tows were performed during the diurnal period, using a small powerboat running at an average speed of 1.5 knot. As soon as they were collected, the samples were preserved in a 4 % buffered formaldehyde seawater solution. Physical and chemical parameters of the water (salinity, temperature, pH, and dissolved oxygen (DO) concentrations) were measured in situ using a multiparameter analyzer. The salinity was measured using the Practical Salinity Scale. The transparency of the water was determined using a Secchi disk. Rainfall data for the sampling periods were

obtained from the Tracuateua station of the National Meteorological Institute, which is located at 01°05'S, 47°10'W, about 20 km from the study area.

In the laboratory, the preserved zooplankton samples were rinsed to remove the formalin buffer and divided into aliquots between one and nine times in a Folsom splitter to provide standardized subsamples containing ~500 copepods, which were then identified (Björnberg 1981; Bradford-Grieve et al. 1999), classified taxonomically (WoRMS 2012), and counted in a gridded Petri dish under a stereomicroscope. The counts for each species were multiplied by the subsampling factor (1–9) to obtain the estimate of the total number of individuals in the full sample. The adult copepods were identified to species or the lowest possible taxonomic level. Copepodites were identified to the genus

level. Adults and juveniles that could not be identified to the genus or species level were classified as unidentified copepod, together with copepod nauplii.

To analyze the monthly and seasonal patterns of variation in the biological attributes of the local copepod populations, the quantitative data obtained for each sample were used to calculate abundance and ecological indices (diversity, evenness, and species richness). Abundance was expressed as the number of individuals per m^3 (ind m^{-3}). Copepod diversity (H') and evenness (J') were calculated, respectively according to:

$$\text{Shannon–Wiener index } (H') = - \sum_{i=1}^s (pi \log_2 pi), \text{ Shannon}$$

(1948);

$$\text{Pielou index } (J') = H' / \log_2 S, \text{ Pielou (1977);}$$

where $pi = ni/N$ (proportion of the sample belonging to the i th species). S = the total number of species recorded in the sample (species richness) and N = the total number of individuals of all the species in a sample. The relative frequency of occurrence (FO) of a given species was determined by the proportion of samples in which the species was recorded.

The one-way analysis of variance (ANOVA) and the nonparametric Mann–Whitney U test were applied to compare variation in abiotic parameters, the abundance of the two principal groups of copepod taxa (total copepod fauna and the dominant species), and their ecological indices between sampling stations (S1, S2, and S3), tides (flood/ebb), months (January–December), and seasons (rainy/dry). When significant F values were recorded in the ANOVA, Tukey's multiple comparisons test was used to discern significant differences between treatments (Zar 2010). All analyses were conducted in STATISTICA 5, with $\alpha = 0.05$. In the present study, species contributing more than 10 % of the total number of copepods in a given month were classified as dominant.

A multivariate redundancy analysis (RDA) was carried out to determine the relationships between environmental variables and the abundance of copepod taxa, using the CANOCO 4.5 software package (ter Braak and Smilauer 1998). The results are presented as a biplot, in which species and environmental variables are plotted together. To assess the similarity among months, a hierarchical agglomerative cluster analysis and non-metric multidimensional scaling (NMDS) ordination were computed using the Bray–Curtis similarity index for log-transformed ($x + 1$) abundance data. A one-way analysis of similarity (ANOSIM) was subsequently used to test whether copepod community varied significantly between seasons. In addition, a similarity percentage (SIMPER) analysis was used to identify the species that contributed most to the similarities within and dissimilarities between the groups

formed by the cluster and NMDS analyses. These analyses were run in the PRIMER 6 software package, following Clarke and Warwick (1994).

Results

Mean monthly rainfall in the dry season (42.7 ± 33.9 mm) was considerably lower than that recorded in the rainy season (313.9 ± 151.6 mm), with 88 % of the year's total precipitation (1,883.3 mm) falling between February and July, which was thus defined as the rainy season (Fig. 2). During the rainy season months, significant reductions were recorded in salinity ($U = 1.0$, $p < 0.01$), pH ($F = 30.6$, $p < 0.01$), and water temperature ($U = 232.5$, $p < 0.01$), which appeared to be linked to the massive inflow of freshwater from rainfall runoff occurring during this period (Fig. 2). Mesohaline–marine regimes were

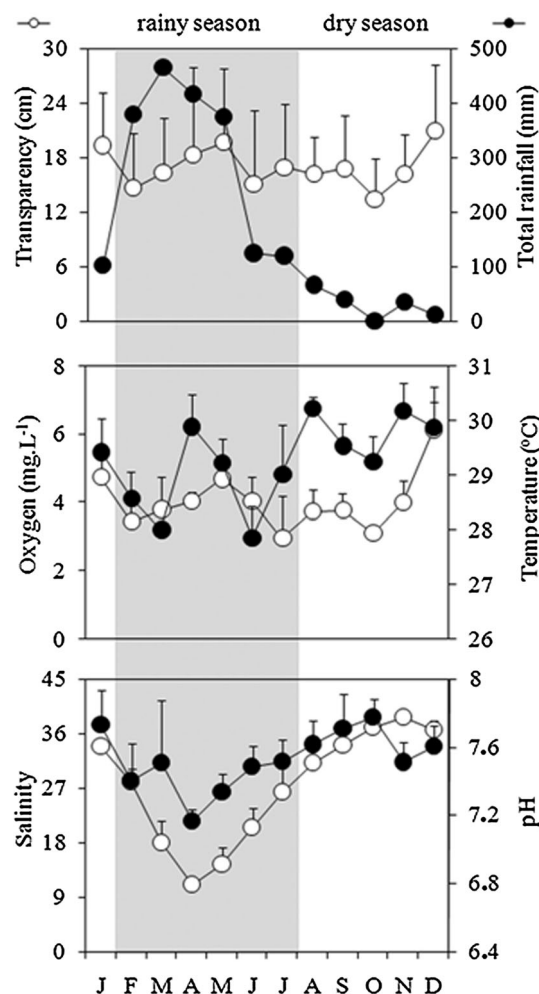


Fig. 2 Total monthly rainfall and Mean ($\pm$ SD) variation in hydrological variables in the Taperaqu estuary, northern Brazil. The shaded portion of the graph indicates the rainy season (February–July)

predominant throughout the study period, with mean salinity ranging from 11.0 ± 0.6 in April to 38.7 ± 0.8 in November. The pH values were generally alkaline, ranging from 7.2 ± 0.1 in April to 7.8 ± 0.1 in October. While seasonal differences in mean water temperatures were highly significant ($p < 0.01$), temperatures were relatively constant throughout the year—which is typical of tropical environments—with an amplitude of only 2.3°C .

Dissolved oxygen (DO) concentrations also varied little between seasons ($p > 0.05$), with water being slightly less oxygenated during the rainy season. The mean DO ranged from $3.0 \pm 1.2 \text{ mg L}^{-1}$ in July to $6.1 \pm 1.3 \text{ mg L}^{-1}$ in December. A similar trend was observed in the transparency of the water, with mean values varying from $13.5 \pm 4.5 \text{ cm}$ in October to $21.0 \pm 7.3 \text{ cm}$ in December. The reduced transparency recorded throughout the year was due to the high concentrations of suspended particulate material and nebulosity typical of this type of environment (Fig. 2).

Overall, no significant spatial patterns were identified in the biological data collected in the Taperacu estuary, which allowed for the pooling of the data from the three sectors (mean $\pm$ standard deviation) for the analysis of monthly and seasonal patterns. In general, short-term variation, related to tidal cycles, was negligible.

The seasonal variation in the copepod populations tended to reflect that of the total abundance of zooplankton during the study period. The Copepoda was the dominant taxon, accounting for up to 57.9 % of total zooplankton abundance in the dry season and 90.6 % in the rainy season. The lowest copepod abundance was recorded in June (4.3 %) and January (28.1 %), when the abundance of brachyuran crab larvae increased considerably. A total of 22 copepods species, belonging to four orders (Calanoida, Cyclopoida, Harpacticoida, and Poecilostomatoida), were identified (Table 1). The Calanoida was the most abundant order and the richest in taxa, with seven families, nine genera, and 15 species, of which *Pseudodiaptomus marshi* Wright, 1936, *Acartia tonsa* Dana, 1849, *Acartia lilljeborgii* Giesbrecht, 1889, and *Subeucalanus pileatus* (Giesbrecht, 1888) were numerically dominant, contributing up to 99.6 % of total copepod abundance (in February).

While no clear seasonal pattern of abundance ($p > 0.05$) was recorded for the copepod community as a whole, marked seasonal variation was observed in some individual species (Fig. 3; Table 1). In particular, *P. marshi* presented marked seasonal fluctuations in abundance ($F = 5.0$, $p < 0.05$), increasing significantly from a mean of $1,418.7 \pm 5,621.9 \text{ ind m}^{-3}$ in the dry season to $6,004.6 \pm 22,231.6 \text{ ind m}^{-3}$ in the rainy season. This species accounted for 90.5 % of the total copepod abundance in February ($20,909.69 \pm 50,527.07 \text{ ind m}^{-3}$)

(Fig. 3). Spikes in the abundance of this species were also recorded in April, when it accounted for 63.8 % of total copepod abundance ($9,260.0 \pm 21,482.7 \text{ ind m}^{-3}$) and August, when it contributed 75.9 % ($7,644.6 \pm 12,769.4 \text{ ind m}^{-3}$). A similar seasonal trend was recorded in *A. tonsa*, with a mean abundance of $119.3 \pm 246.9 \text{ ind m}^{-3}$ in the dry season and $905.6 \pm 2,400.9 \text{ ind m}^{-3}$ in the rainy season ($F = 14.6$, $p < 0.001$). In this case, there was only a single peak in abundance, in April ($4,604.182 \pm 4,521.736 \text{ ind m}^{-3}$; $F = 5.9$, $p < 0.001$), representing 31.7 % of total copepod abundance (Fig. 3).

By contrast, the abundance of *A. lilljeborgii* was significantly higher ($U = 413.0$, $p < 0.01$) in the dry season ($750.8 \pm 808.3 \text{ ind m}^{-3}$) in comparison with the rainy season ($709.5 \pm 1,286.3 \text{ ind m}^{-3}$), although a significant peak was observed in the late rainy season month of July ($2,227.9 \pm 2,082.0 \text{ ind m}^{-3}$; $F = 4.5$, $p < 0.05$), when it contributed 62.2 % of total copepod abundance (Fig. 3). Peaks in the abundance of this species were also recorded in February ($1,646.4 \pm 1,237.3 \text{ ind m}^{-3}$; 7.1 %), August ($1,445.5 \pm 1,222.7 \text{ ind m}^{-3}$; 14.4 %), September ($1,208.6 \pm 1,117.4 \text{ ind m}^{-3}$; 62.8 %), and January ($961.4 \pm 307.8 \text{ ind m}^{-3}$; 69.6 %). Of the four predominant species, *S. pileatus* was the least representative and was absent from the samples collected between May and July, when mesohaline–polyhaline conditions prevailed. While the mean abundance of *S. pileatus* was also higher in the dry season ($24.3 \pm 31.0 \text{ ind m}^{-3}$), there was no significant seasonal variation in its abundance. Classified as a non-dominant species (<10 % of the total copepod abundance in a given month), *Paracalanus quasimodo* Bowman, 1971, had a high relative frequency of occurrence (61.1 %), with mean abundance varying significantly from $17.5 \pm 64.1 \text{ ind m}^{-3}$ in the dry season to $86.8 \pm 219.5 \text{ ind m}^{-3}$ in the rainy season ($U = 434.0$, $p < 0.05$; Table 1).

No evidence was found of any significant variation in the abundance of *A. tonsa* and *A. lilljeborgii* related to the tidal cycle or estuarine sector. This lack of any tidal or spatial pattern was also observed in *S. pileatus*, although the abundance of this species increased slightly toward the lower estuary during the ebb and flood tides of the rainy season (Fig. 4). However, significant spatial and tidal differences were recorded in *P. marshi*, which was most abundant at stations 1 ($34,322.3 \pm 47,972.6 \text{ ind m}^{-3}$) and 2 ($1,595.8 \pm 1,114.9 \text{ ind m}^{-3}$) during the flood tide in the rainy season, decreasing considerably toward the mouth of the estuary ($31.2 \pm 46.1 \text{ ind m}^{-3}$), and during the ebb tide (Fig. 4; Table 2). A similar pattern was observed in this species during the dry season, although the difference was not statistically significant.

Copepod diversity (0.5 ± 0.2 to $1.2 \pm 0.3 \text{ bits ind}^{-1}$), evenness (0.2 ± 0.0 to 0.5 ± 0.3), and richness (4.2 ± 2.3 to 7.8 ± 2.3) were all relatively low overall (Fig. 5) and

Table 1 List of the copepod taxa collected in the Taperaçú estuary, Brazil, and their mean ($\pm$ SD) and relative abundance, and frequency of occurrence during the rainy and dry seasons, and over the study period as a whole

Taxa/periods	Rainy season		Dry season		Annual		FO
	Ind m ³ $\pm$ SD	%	Ind m ³ $\pm$ SD	%	Ind m ³ $\pm$ SD	%	
Unidentified copepods*	28.9 $\pm$ 87.8	0.4	16.5 $\pm$ 66.0	0.7	22.7 $\pm$ 77.4	0.4	58.3
<i>Acartia</i> (copepodite)	146.4 $\pm$ 537.7	1.8	0.3 $\pm$ 0.9	<0.1	73.3 $\pm$ 384.7	1.4	18.1
<i>A. lilljeborgii</i> Giesbrecht, 1889 ^{N, E}	709.5 $\pm$ 1,286.3	8.7	750.8 $\pm$ 808.3	30.8	730.1 $\pm$ 1,066.9	13.8	87.5
<i>A. tonsa</i> Dana, 1849 ^{E,C,O}	905.6 $\pm$ 2,400.9	11.1	119.3 $\pm$ 246.9	4.9	512.4 $\pm$ 1,740.2	9.7	94.4
<i>Centropages velificatus</i> (Oliveira, 1947) ^{N,C}	0.0 $\pm$ 0.0	0.0	1.1 $\pm$ 2.4	<0.1	0.5 $\pm$ 1.8	<0.1	15.3
<i>Paracalanus</i> (copepodite)	<0.1 $\pm$ 0.2	<0.1	0.1 $\pm$ 0.8	<0.1	0.1 $\pm$ 0.6	<0.1	2.8
<i>P. quasimodo</i> Bowman, 1971 ^C	86.8 $\pm$ 219.5	1.1	17.5 $\pm$ 64.1	0.7	52.2 $\pm$ 164.3	1.0	61.1
<i>Parvocalanus crassirostris</i> (Dahl F., 1894) ^E	2.8 $\pm$ 11.8	<0.1	0.1 $\pm$ 0.4	<0.1	1.4 $\pm$ 8.4	<0.1	8.3
<i>Calanopia</i> (copepodite)	0.0 $\pm$ 0.0	0.0	1.2 $\pm$ 7.4	0.1	0.6 $\pm$ 5.2	<0.1	1.4
<i>C. americana</i> Dahl F., 1894 ^{N,C}	<0.1 $\pm$ 0.1	<0.1	0.1 $\pm$ 0.4	<0.1	<0.1 $\pm$ 0.3	<0.1	4.2
<i>Labidocera</i> (copepodite)	1.1 $\pm$ 3.6	<0.1	0.0 $\pm$ 0.0	0.0	0.5 $\pm$ 2.6	<0.1	5.6
<i>L. fluviatilis</i> Dahl F., 1894 ^N	6.9 $\pm$ 15.5	0.1	1.5 $\pm$ 4.3	0.1	4.2 $\pm$ 11.6	0.1	20.8
<i>Pseudodiaptomus</i> (copepodite)	195.8 $\pm$ 746.9	2.4	2.5 $\pm$ 14.7	0.1	99.1 $\pm$ 533.5	1.9	12.5
<i>P. acutus</i> (Dahl F., 1894) ^E	4.8 $\pm$ 13.5	0.1	6.9 $\pm$ 17.0	0.3	5.8 $\pm$ 15.3	0.1	23.6
<i>P. marshi</i> Wright S., 1936 ^E	6,004.6 $\pm$ 22,231.6	73.8	1,418.7 $\pm$ 5,621.9	58.1	3,711.7 $\pm$ 16,265.1	70.2	84.7
<i>P. richardi</i> (Dahl F., 1894) ^E	5.9 $\pm$ 28.1	<0.1	0.8 $\pm$ 4.6	<0.1	3.3 $\pm$ 20.2	0.1	12.5
<i>Pseudodiaptomus</i> sp.	<0.1 $\pm$ 0.1	<0.1	25.1 $\pm$ 90.6	0.9	10.7 $\pm$ 64.5	0.2	5.6
<i>Subeucalanus</i> (copepodite)	2.9 $\pm$ 8.2	<0.1	6.4 $\pm$ 11.2	0.3	4.6 $\pm$ 9.9	0.1	34.7
<i>S. crassus</i> (Giesbrecht, 1888) ^O	0.1 $\pm$ 0.8	<0.1	0.3 $\pm$ 0.9	<0.1	0.2 $\pm$ 0.8	<0.1	6.9
<i>S. pileatus</i> (Giesbrecht, 1888) ^O	11.7 $\pm$ 39.8	0.1	24.3 $\pm$ 31.0	1.0	18.0 $\pm$ 36.0	0.3	51.4
<i>Subeucalanus</i> sp.	<0.1 $\pm$ 0.1	<0.1	0.0 $\pm$ 0.0	0.0	<0.1 $\pm$ 0.1	<0.1	1.4
<i>Temora stylifera</i> (Dana, 1849) ^{C, O}	0.0 $\pm$ 0.0	0.0	<0.1 $\pm$ 0.3	<0.1	<0.1 $\pm$ 0.2	<0.1	1.4
<i>Oithona</i> (copepodite)	0.0 $\pm$ 0.0	0.0	<0.1 $\pm$ 0.1	<0.1	<0.1 $\pm$ 0.1	<0.1	1.4
<i>O. hebes</i> Giesbrecht, 1891 ^{C,E}	7.1 $\pm$ 22.9	0.1	12.6 $\pm$ 38.3	0.5	9.9 $\pm$ 31.5	0.2	38.9
<i>O. oswaldocruzi</i> Oliveira, 1945 ^{C,E}	7.7 $\pm$ 23.9	0.1	20.8 $\pm$ 64.5	0.9	14.2 $\pm$ 48.7	0.3	45.8
<i>Oithona</i> sp.	0.1 $\pm$ 0.4	<0.1	0.1 $\pm$ 0.8	<0.1	0.1 $\pm$ 0.6	<0.1	2.8
<i>Microsetella</i> (copepodite)	0.0 $\pm$ 0.0	0.0	<0.1 $\pm$ 0.1	<0.1	<0.1 $\pm$ 0.1	<0.1	1.4
<i>M. rosea</i> (Dana, 1848) ^O	3.0 $\pm$ 17.7	<0.1	3.8 $\pm$ 16.3	0.2	3.4 $\pm$ 16.9	0.1	9.7
<i>Euterpina</i> (copepodite)	0.0 $\pm$ 0.0	0.0	<0.1 $\pm$ 0.2	<0.1	<0.1 $\pm$ 0.1	<0.1	1.4
<i>E. acutifrons</i> (Dana, 1847) ^C	0.5 $\pm$ 1.8	<0.1	7.5 $\pm$ 17.7	0.3	4.1 $\pm$ 13.1	0.1	25.0
<i>Tisbe</i> sp.	1.2 $\pm$ 5.9	<0.1	5.0 $\pm$ 16.4	0.2	3.1 $\pm$ 12.4	0.1	26.4
Harpacticoida	1.1 $\pm$ 3.7	<0.1	0.3 $\pm$ 1.5	<0.1	0.7 $\pm$ 2.8	<0.1	8.3
<i>Oncaea</i> sp.	0.5 $\pm$ 2.9	<0.1	0.2 $\pm$ 1.1	<0.1	0.4 $\pm$ 2.2	<0.1	5.6
Total	8,874.4 $\pm$ 37,886.7	100	2,661.9 $\pm$ 9,884.9	100	11,536.4 $\pm$ 47,186.5	100	

* Adults, copepodites and nauplii of unidentified copepods, C coastal, E estuarine, N neritic, O oceanic (according to Björnberg 1981; Bradford-Grieve et al. 1999). FO relative frequency of occurrence in the 72 samples analyzed

varied little ($p > 0.05$) between stations, tide cycles, months, or between seasons, indicating relative spatial and temporal homogeneity in comparison with other tropical and temperate estuaries worldwide (e.g., Islam et al. 2006; Rakhesh et al. 2013). The low species diversity recorded in the Taperaçú estuary was partly related to the large mesh size of the plankton net (300 μ m) used for the collection of samples, which almost certainly underestimated species richness. This was also reflected in the overwhelming abundance of large species (e.g., *P. marshi* and *A.*

lilljeborgii) in comparison with the smaller ones, such as *Oithona oswaldocruzi* Oliveira, 1945, and *Euterpina acutifrons* Dana, 1847 (Table 1).

The relationship between copepod abundance and environmental parameters is shown in the RDA ordination diagram (Fig. 6). Of the four predominant species, *A. lilljeborgii* and *S. pileatus* were positively correlated with salinity, which accounts for the higher values recorded in the dry season, when salinity was significantly higher. The opposite pattern was observed in *P. marshi*, *A. tonsa*, and

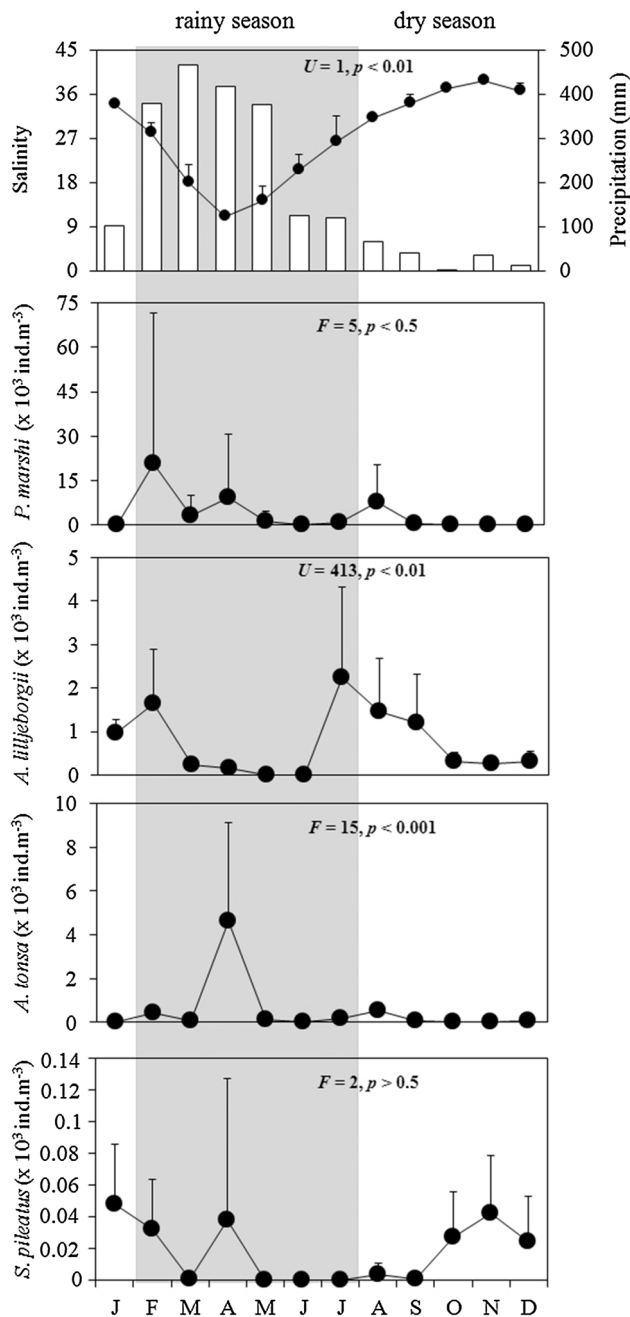


Fig. 3 Total monthly rainfall (histogram) and Mean ($\pm$ SD) variation in the salinity and abundance (filled circle) of the principal copepod species in the Taperaçu estuary, northern Brazil. The results of the statistical tests refer to the differences between seasons

P. quasimodo, which were influenced negatively by this parameter.

The hierarchical cluster analysis illustrated clear temporal changes in the copepod community of the Taperaçu estuary (Fig. 7a). In particular, two distinct groups of months were delineated with 60 % similarity. Group I was characterized by the predominance of *P. marshi* and *A. tonsa* and included primarily rainy season months. In group

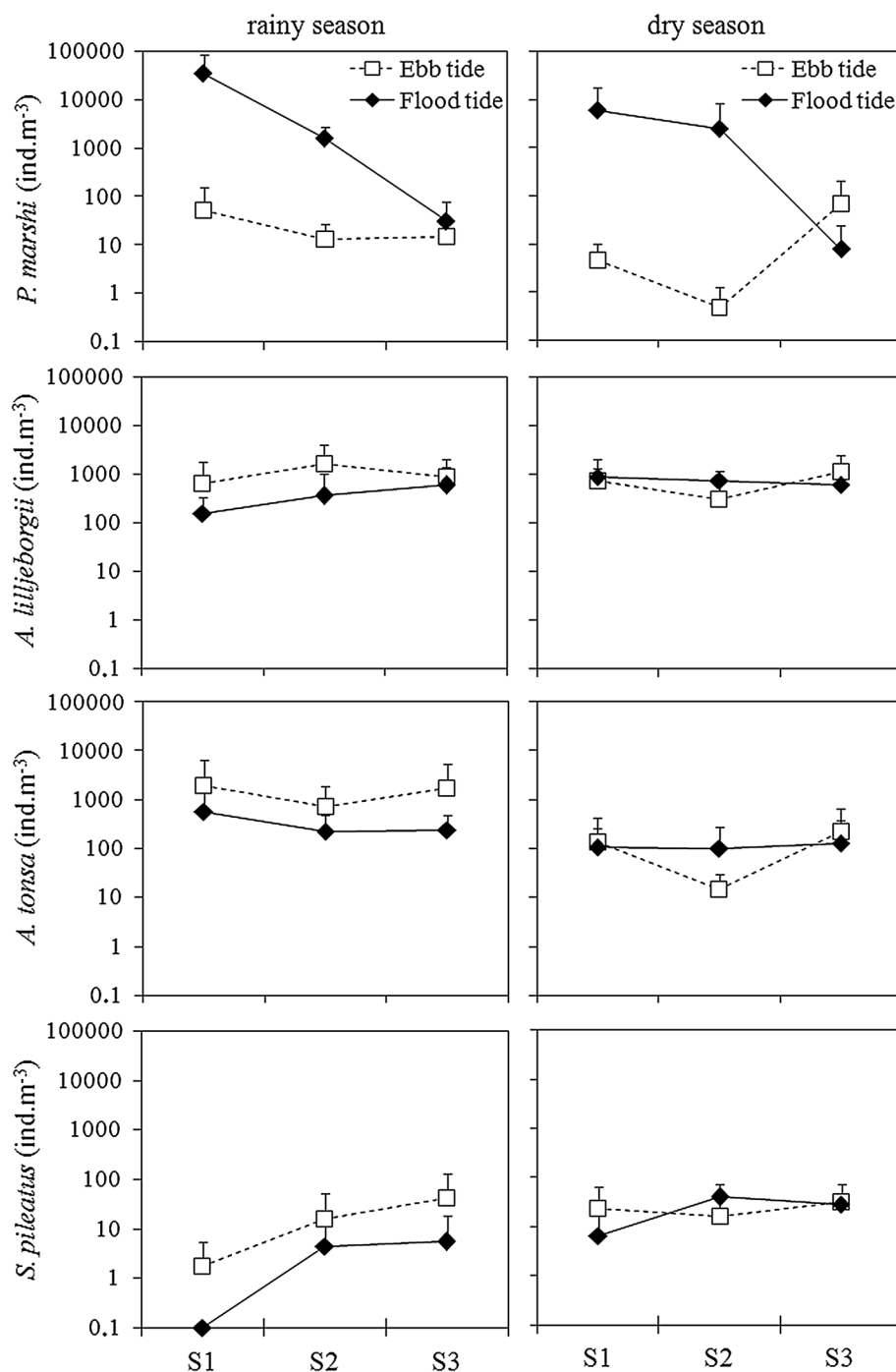
II, by contrast, which contained mainly dry season months, there was a decline in the contribution of *P. marshi* and *A. tonsa* to total copepod abundance, and an increase in that of *A. lilljeborgii* (Fig. 7c). The clustering pattern was further confirmed by a NMDS two-dimensional plot (stress: 0.03) with no overlap between groups (Fig. 7b). There was 70.8 % similarity within the rainy season group (group I) and 73.2 % in the dry season group (group II). The results of the NMDS ordination analysis were supported by the ANOSIM (global $R = 0.9$, $p < 0.01$). Overall, *P. marshi*, *A. lilljeborgii*, *A. tonsa*, and *S. pileatus* accounted for over 85 % of the similarity within these groups and for 74 % of the dissimilarity between them. The SIMPER also indicated that *P. marshi* (62.1 %) and *A. lilljeborgii* (57.8 %) were the species that most contributed to the similarity within groups I and II, respectively, highlighting the importance of these species in the structural dynamics of the copepod community.

Discussion

The horizontal gradients in hydrological parameters such as salinity, temperature, and turbidity constitute a crucial determinant of the distribution of copepods within estuarine environments (Lawrence et al. 2004; Chew and Chong 2011). The virtual absence of such gradients in the Taperaçu estuary is probably related to a number of morphological and morphodynamic factors, including the effective absence of fluvial discharge, the small catchment area (minimal, sporadic freshwater inflow), shallow depths, and strong tidal currents, which facilitate both horizontal and vertical mixing of the water column. Overall, the lack of any significant spatial variation in biological parameters presumably reflects the absence of any horizontal gradient in hydrological variables, especially salinity.

The Amazonian coast is characterized by pronounced annual fluctuations in rainfall, which, together with the associated variation in fluvial discharge, cause drastic seasonal changes in hydrological parameters. These fluctuations are related with the displacement of the ITCZ, which shifts to the southern hemisphere during the first half of the year, provoking an increase in precipitation levels, whereas in the second half of the year, it shifts back to the northern hemisphere, creating drier conditions (Marengo 1995). In the rainy season, the significant reduction in salinity, pH, and temperature were closely related to the increased in precipitation levels, which leads to a major increment in the discharge of local rivers (e.g., Caeté, Quatipuru), with a knock-on effect in the hydrological parameters, and consequently in the abundance of copepods. During the course of the dry season (<13 % of total annual precipitation), these abiotic variables increased

Fig. 4 Variation in the Mean ($\pm$ SD) abundance of the four dominant copepod species in the Taperaçu estuary, northern Brazil, by season (rainy/dry), station (S1, S2, and S3), and tide (ebb/flood)



progressively. By contrast, water transparency was relatively low overall due to the large amount of particulate material suspended in the water column, a typical characteristic of shallow Amazonian estuaries. In addition, the Taperaçu was different from other estuarine systems in northern (Guimarães et al. 2009) and northeastern Brazil (Cavalcanti et al. 2008), in the lack of any clear seasonal variation in dissolved oxygen concentrations.

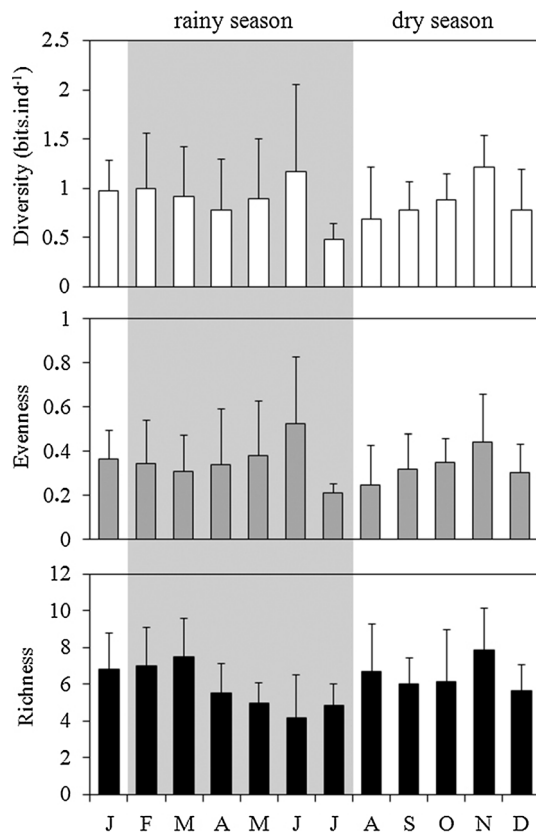
Copepods were by far the most prominent zooplankton group, as found in other mangrove systems in different

parts of the world, where they typically account for more than 80 % of total abundance (Rios-Jara 1998; Dias and Bonecker 2008). The copepod community in the Taperaçu estuary was characterized by the predominance of *Pseudodiaptomus marshi*, *Acartia tonsa*, *Acartia lilljeborgii*, and *Subeucalanus pileatus*. A similar composition has been recorded at the same site in previous studies (Costa et al. 2008; Magalhães et al. 2009a) and in other mangrove estuaries on the Brazilian coast (Almeida Prado-Por and Lansac-Tôha 1984; Sterza and Fernandes 2006). The

Table 2 Results of the Tukey (HSD) test for pair-wise multiple comparisons of the abundance of *Pseudodiaptomus marshi* between stations (S1, S2, and S3) and tides (flood and ebb) during the rainy season in the Taperaçu estuary, Brazil

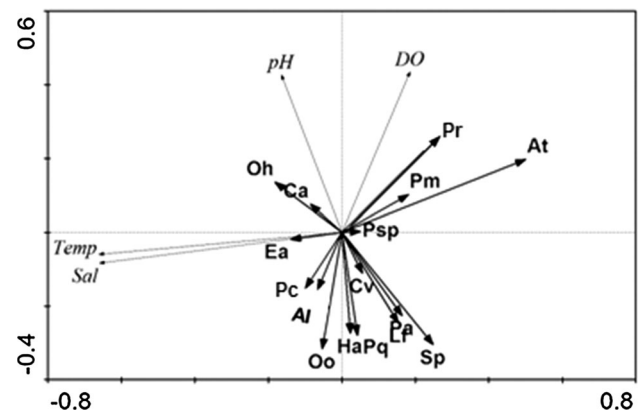
Station–tide	(1)	(2)	(3)	(4)	(5)	(6)
S1–flood (1)		0.000182	0.409853	0.000141	0.000146	0.000140
S1–ebb (2)	0.000182		0.009795	0.990692	0.998510	0.988097
S2–flood (3)	0.409853	0.009795		0.002126	0.003469	0.001955
S2–ebb (4)	0.000141	0.990692	0.002126		0.999965	1.000000
S3–flood (5)	0.000146	0.998510	0.003469	0.999965		0.999922
S3–ebb (6)	0.000140	0.988097	0.001955	1.000000	0.999922	

p values in bold are <0.05


Fig. 5 Mean ($\pm$ SD) ecological indices recorded over an annual cycle in the Taperaçu estuary, northern Brazil

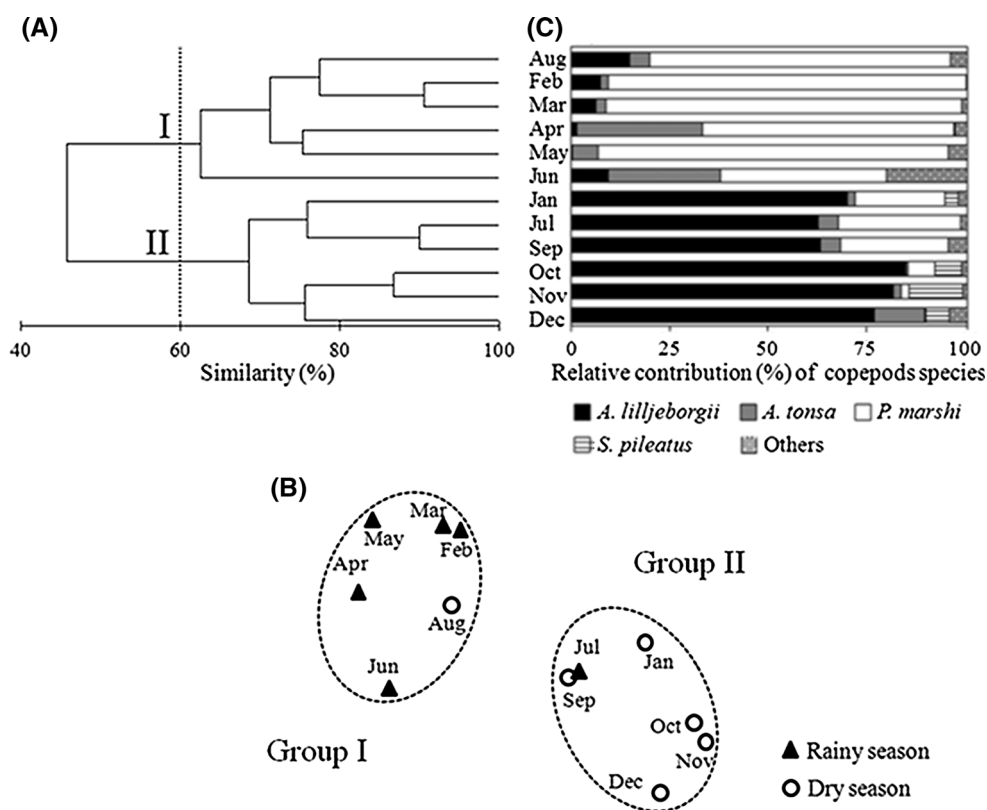
contribution of other zooplankton groups, e.g., foraminifers, cnidarians, mollusks, amphipods, chaetognaths, brachyurans, appendicularians, and chordates, was highly variable, but together accounted for an average of 38.5 % of total zooplankton abundance. The contribution of the non-copepod zooplankton was greatest in January and June, due to the abundance of the larvae of the brachyuran crabs, which spawns during these months in this region (Diele 2000; Koch et al. 2005).

The variability in the abundance, biomass, and productivity of copepods in shallow tidal estuaries has been associated with the combined effects of regional climate


Fig. 6 RDA analysis showing biplot of copepod taxa (large arrows heads) and environmental variables (small arrow heads). Environmental variables are as follows: *Sal* salinity, *pH* pH, *DO* dissolved oxygen, and *Temp* temperature. Copepods taxa are as follows: *Al* = *Acartia lilljeborgii*, *At* = *Acartia tonsa*, *Pm* = *Pseudodiaptomus marshi*, *Pr* = *Pseudodiaptomus richardi*, *Sp* = *Subeucalanus pileatus*, *Pa* = *Pseudodiaptomus acutus*, *Psp* = *Pseudodiaptomus* sp., *Ca* = copepodite of *Acartia*, *Ea* = *Euterpina acutifrons*, *Ha* = *Harpacticoida*, *Pq* = *Paracalanus quasimodo*, *Oh* = *Oithona hebes*, *Oo* = *Oithona oswaldocruzi*, *Lf* = *Labidocera fluviatilis*, *Cv* = *Centropages velificatus*, *Pc* = *Parvocalanus crassirostris*

patterns and local hydrological factors (Leandro et al. 2007; Muxagata et al. 2012), in addition to other multifactorial processes involving both biotic and abiotic parameters (Dalal and Goswami 2001; Azeiteiro et al. 2005). In the present study, the seasonal variation in the abundance of copepods appeared to be influenced primarily by the interaction of precipitation levels and salinity. In Taperaçu estuary, this seasonality was defined mainly by shifts in the relative contribution of the four predominant species (*P. marshi*, *A. tonsa*, *A. lilljeborgii*, and *S. pileatus*). Overall, *P. marshi* was the dominant taxon, especially in the rainy season months, when salinity decreased. During the dry season, by contrast, *P. marshi* declined sharply in abundance and was replaced by *A. lilljeborgii*. While *P. marshi* may be able to survive and even reproduce in hypersaline water (Medeiros et al. 2006), the results of redundancy analysis suggest a preference for the low to

Fig. 7 **a** Cluster and **b** NMDS analyses of the abundance of copepod species recorded during the study period in the Taperaçu estuary, northern Brazil. **c** Relative contributions of the dominant species to total copepod abundance. Dominance of oligomesohaline species (*group I*); dominance of marine species (*group II*). The main groups shown in the Cluster and NMDS (stress: 0.03) are separated by *dashed lines* at a similarity level of 60 %



intermediate saline conditions of estuarine environments. *P. marshi* was more abundant in the Taperaçu estuary than in the neighboring Caeté estuary (Magalhães et al. 2010). These two estuaries are connected by the Taici creek (Fig. 1), through which water flows from the Caeté to the upper Taperaçu during the flood tide (Araújo and Asp 2013). This may have contributed to the recruitment of copepods, such as *P. marshi* and *Pseudodiaptomus richardi* (Dahl F., 1894), from the oligomesohaline Caeté estuary (Magalhães unpub. data). Considering the morphological, morphodynamic, and hydrological characteristics of the Taperaçu estuary, this process would account for the variation in the abundance of *P. marshi* during the rainy season (Fig. 4, Table 2), as well as the presence of organisms more typical of the inner Caeté estuary when marine conditions—as defined by the Venice classification system (Anonymous 1959)—prevailed (i.e., during the dry season months). These results suggest that *P. marshi*, together with other oligohaline copepods, does not establish resident populations throughout the year, or at least during the dry season. The presence of this species during the dry season months, when the system is clearly more marine in nature, was probably the result of immigration through the Taici creek. This would explain the peak in abundance of *P. marshi* recorded in August, which contradicts the decrease in precipitation and the increase in salinity recorded during this month.

In estuarine environments, two or more species of *Acartia* may coexist, with seasonal alternations in dominance (Lee and McAlice 1979; Sullivan and McManus 1986). In the case of the Taperaçu estuary, the increasing freshwater runoff in April, May, and June resulted in a sharp decline in salinity and consequently the progressive substitution of *A. lilljeborgii* by *A. tonsa*, due presumably to the relative tolerance of *A. tonsa* to lower salinity levels.

The planktonic copepod *A. tonsa* is a cosmopolitan species which occurs in the Atlantic, Indian, and Pacific oceans, and the Azov, Baltic, Black, and Mediterranean Seas, as well as the Caspian Sea, where it is a recent invader. The species is nevertheless distributed preferentially in estuarine and coastal areas (Paffenhöfer and Stearns 1988; Tester and Turner 1991) and is one of the most prominent in the estuaries of the Atlantic coast of South America, being present year-round, but exhibiting major seasonal fluctuations in population density (Gómez-Erache et al. 2000; Costa et al. 2009). Despite being considered a euryhaline and eurythermal species, capable of tolerating salinity levels ranging from 0 to 31.5 (Montú and Gloeden 1986), optimal salinity for *A. tonsa* is considered to be between 15 and 22 (Cervetto et al. 1999); although in the present study, the greatest abundance was recorded at a salinity of 11.

A number of field and laboratory studies have reported enhanced growth rates in *A. tonsa* at lower salinity levels

(Peck and Holste 2006; Putland and Iverson 2007). The significant negative effects of salinity on the population dynamics of *A. tonsa* underpin its temporal distribution in the Taperaçu estuary, because the organism's ability to osmoregulate affects its ecological tolerance. In the present study, the species presented a single annual peak of abundance in the rainy season month of April. This pattern differed from that observed in other Amazonian coastal systems (Leite et al. 2009; Magalhães et al. 2009b), where the species was abundant and predominant throughout much of the rainy season, when salinity was between seven and 19. The reduction in the abundance of *A. tonsa* during the dry season was determined by its ecological affinity with environments characterized by moderate salinity levels and suggests resting (diapause) eggs production, which is used as a survival strategy in response to seasonal and longitudinal fluctuations in conditions, as observed previously in temperate coastal and marine habitats (Castro-Longoria 2001; Katajisto 2006), where the eggs were maintaining in a resting state by environmental cues such as temperature and salinity. The benthic diapause phase could be one of the bases of the seasonal replacement of *Acartia* species at the present study site, in addition to the resumption of growth in the remaining adult population under favorable conditions.

Copepods of the genus *Acartia* inhabit many coastal and offshore environments, where they are usually among the most abundant zooplankton taxa (Greenwood 1981; Hubareva et al. 2008). This was also confirmed in the present study, given the predominance of *A. lilljeborgii* during most of the second half of the year. This marine–estuarine species is an indicator of coastal waters (Björnberg 1981) and is dominant in many Brazilian estuaries (Schwamborn et al. 2004; Dias et al. 2009). In the Taperaçu, the temporal fluctuations in the abundance of *A. lilljeborgii* can be explained by its preference for a given range of salinity. In the present study, values peaked at between 25 and 35, which may be the optimal range for egg production in this species. Ara (2001) recorded an increase in the production of eggs in *A. lilljeborgii* with increasing salinity and found that during periods of reduced abundance related to low salinity (<17), populations of this species were unable to recover rapidly through egg production. Temporal fluctuations in the abundance of this species are thus derived not only from its reproductive output, but also from the modification of this process by extrinsic biological factors and physical conditions, such as salinity. The affinity of this species for highly saline environments has been reported from a number of other tropical estuaries (Brugnoli-Olivera et al. 2004; Dias and Bonecker 2008), as a result of its greater tolerance to high salinities.

As mentioned above, the peak in the abundance of *S. pileatus*, a species typical of the warm coastal waters of the

tropical and subtropical regions of the southwest Atlantic (Björnberg 1981), occurred primarily during the dry season, when marine conditions predominated, suggesting that the presence of this species in the studied area depends on recruitment from the adjacent coastal zone. This could account for the slight increase in its abundance toward the mouth of the estuary during the ebb and flood periods in the rainy season (Fig. 4). Dominant in most Brazilian coastal areas (Magalhães et al. 2009b; Eskinazi-Sant'Anna and Björnberg 2006), *P. quasimodo* is a marine–euryhaline species, occurring preferentially in waters of high salinity in tide-dominated areas (Lopes et al. 1998; Araújo et al. 2008). However, the opposite tendency was observed in the Taperaçu estuary, where the highest density of this species was recorded during the period of lowest salinity. The euryhaline character of *P. quasimodo* associated with the strong tidal currents may account for this pattern, as well as the high frequency of occurrence of the species (61.1 %) during the study period.

The lack of any significant variation in ecological indices in relation to estuary sector, tide cycle or climatic variables may be related to the unique configuration of the Taperaçu estuary, and the absence of any major and continuous inflow of freshwater, thus minimizing the horizontal gradients in these indices. Magalhães et al. (2011) also recorded a lack of circadian and tidal level variations in copepod diversity within the Taperaçu estuary, which was attributed to the shallow depths of the estuary combined with its strong tidal currents, which make the water column relatively homogeneous, and eliminate the effects of the vertical migration of the zooplankton on diversity patterns. This process may impede the mechanisms that retain resident copepods in the estuary (e.g., DVM and TVM—diel- and tide-induced vertical migrations), which would account for the reduced spatial–temporal variation recorded in the ecological indices during the course of the study period. The ecological indices recorded in the present study reflect the relatively low diversity typical of estuarine environments (Hopcroft et al. 1998). In tropical areas, however, this may be at least partly due to the presence of small-bodied species, which may be under sampled in nets with mesh sizes over 64 µm (Chisholm and Roff 1990). In this case, it would be necessary to collect further samples using nets of finer mesh in order to evaluate the full diversity of copepods in the study area. A negative effect of mesh size on zooplankton diversity has been recorded in other aquatic ecosystems (Favareto et al. 2009; Riccardi 2010).

Monthly and seasonal changes in the relative contributions of the four principal copepod species, in particular *P. marshi* and *A. lilljeborgii*, did not have a direct affect on the ecological indices, which were spatially and temporally homogeneous. However, the present study found a clear

seasonal pattern of abundance in the copepod community, characterized by the ecological succession of the main species. The multivariate analyses confirmed the dominance of oligomesohaline species during the rainy season, in contrast with the predominance of estuarine–marine species during the dry season. These fluctuations may play a fundamental role in community structure, especially where salinity exceeds the levels tolerated by the different species and interferes with their osmoregulatory processes, leading to alterations in their reproductive potential and ultimately a decrease in the size of the population. In the present study, the absence of freshwater organisms was related to the lack of an effective river discharge.

The temporal variability of copepods in coastal waters is controlled mainly by salinity and temperature (Rodríguez et al. 1995; Mouny and Dauvin 2002), although bottom-up as well as top-down controls (i.e., food availability and predation pressure) also play an important role in this process (Hoffmeyer and Torres 2001; Islam et al. 2006). In the Taperaçu estuary, some of the dominant copepod species, such as *A. lilljeborgii* and *A. tonsa*, are classified as omnivores (Uye et al. 1987; Paffenhöfer 1991; Ara 2001) and present an ample range of feeding behavior, which likely reduces interspecific competition for resources, and may represent a secondary factor in the ecological succession of the different species. This is further supported by the relative abundance and diversity of autotrophic food sources (e.g., benthic and planktonic microalgae, mangrove macroalgae, and detritus) available in the local aquatic food web (Koch and Wolff 2002; Brenner and Krumme 2007; Matos et al. 2011), which may also contribute to a reduction in interspecific competition among the copepods. While predation may also have been an important mechanism of population control, data are only available for *P. marshi* and *A. lilljeborgii* in the neighboring Caeté estuary (Camargo and Isaac 2004). In this estuary, these two copepods were the main food items ingested by juvenile fishes of three species, *Macrodon ancylodon* (Bloch and Schneider, 1801), *Stellifer rastrifer* (Jordan, 1889), and *Stellifer naso* (Jordan, 1889). This scarcity of data on the role of predation as a control mechanism for copepod populations in Amazonian estuaries impedes the conclusive evaluation of the contribution of this factor to the structure of the zooplankton community of the Taperaçu estuary as a whole.

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