

Spatial and temporal variation in the abundance and taxonomic composition of estuarine and terrestrial macrofauna associated with mangrove logs

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Brazilian mangroves have ecological and economic importance, with molluscs, crustaceans and polychaetes being diverse and common faunal groups. The present study characterizes the macrofauna associated with logs from two mangrove forests in Pará State, northern Brazil, sampled in September, January and April, between 2008 and 2010, at three different distances from a tidal channel (2, 10, 20 m). In each forest, five logs (diameter/length: 10/40 cm) were randomly selected at each distance, totalling 15 logs per sampling date. The macrofauna was removed, counted and identified. Three-way analysis of variance was used to compare mean numbers of individuals, numbers of taxa and Berger–Parker dominance per log, between forests and among sampling dates and distances from the tidal channel. Non-metric multidimensional scaling and permutational multivariate analyses of variance were used to investigate macrofaunal structure in relation to the three factors. A total of 5437 individuals from both estuarine and terrestrial faunas was found in both forests, with 85 taxa distributed among Mollusca, Annelida, Arthropoda and Nemertea. Abundance increased from September through January to April in both mangrove forests. The most dominant species was Neoterredo reynei, representing 48% of total abundance. No significant difference in any variable was found among the two forests and between the three distances. Logs may represent a stable microhabitat for the macrofauna, with little variation in humidity, salinity or temperature, despite different distances from the tidal channel. However, macrofaunal structure varied significantly between forests and among sampling dates, probably due to seasonal differences in precipitation and salinity between both locations.

Keywords: infauna, benthos, invertebrates, wood, shipworm, tropical estuary

Submitted 19 February 2013; accepted 10 August 2013; first published online 10 September 2013

INTRODUCTION

Brazilian mangroves are among the largest in the world (Lara, 2003), extending from the States of Amapá to Santa Catarina (Schaeffer-Novelli *et al.*, 1990). The Amazon macrotidal mangrove coast has an estimated area of 7591 km², representing a little over half (56.6%) the total mangrove area in Brazil (Souza-Filho *et al.*, 2009). The mangrove is a coastal ecosystem representing the transition between terrestrial and marine environments, providing food, protection and nursery areas for many animal species (Schaeffer-Novelli, 1995).

The benthic fauna is composed of animals that are associated with mangrove substrates, at least during part of their life cycle, where individuals usually either attach to, move about or burrow into the substrate (Levinton *et al.*, 2001). The epifauna is found on the mangrove sediment surface and logs, as well as on roots, trunks and branches of mangrove trees

(Alongi & Sasekumar, 1992; Nagelkerken *et al.*, 2008). The mangrove infauna spends part or all of their life cycle within the substrate (Nagelkerken *et al.*, 2008), either boring or burrowing into hard or soft substrates, respectively (Oliveira & Mochel, 1999; Thurman & Trujillo, 2004).

The burrows created by shipworms inside logs and fallen trunks are ideal habitats for many animal groups, especially for small benthic invertebrates (Turner & Johnson, 1971). Aviz *et al.* (2009) is the only study of the Amazon macrotidal mangrove coast log fauna, which is dominated by the phyla Annelida, Arthropoda and Mollusca, notably class Polychaeta, sub-phylum Crustacea (Decapoda and Isopoda) and class Bivalvia, respectively. This fauna is important for the decomposition of mangrove wood (Santos Filho *et al.*, 2008), promoting mineralization, nutrient recycling and mangrove primary productivity (Koch & Wolff, 2002).

The richness, abundance and composition of estuarine benthic assemblages may vary on a spatial scale (Morrisey *et al.*, 1992a), for example, among different tidal levels in the mangrove forest (Frith *et al.*, 1976). The level of flooding in mangroves may cause changes in salinity, nutrient availability and structure of mangrove forests (Lara *et al.*, 2010),

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and in the distribution of macrofaunal assemblages on different substrates (Cantera *et al.*, 1999), which may be composed of members of both the terrestrial and estuarine faunas (Nagelkerken *et al.*, 2008). In order to survive and reproduce in the mangrove habitat, the fauna exhibits certain behaviours, for example, climbing up tree trunks at high tide (Nilsen, 1997) and adaptations, such as physiological mechanisms that allow individuals to remain in the substrate during high tide (Nilsen, 2006).

Seasonal variation in the abundance and composition of the macrofauna (Morrisey *et al.*, 1992b; Ysebaert & Herman, 2002) is influenced by factors such as precipitation (Dippner & Ikauniece, 2001), salinity (da Silva *et al.*, 2011), temperature (Nagelkerken *et al.*, 2008) and relative humidity (Omena *et al.*, 1990). Variation in these factors may cause a temporal shift in species composition (Kathiresan & Bingham, 2001). This paper investigates the effects of distance from tidal channel and sampling date on the abundance and taxonomic composition of the macrofauna associated with logs in two mangrove forests from northern Brazil.

MATERIALS AND METHODS

Study area

Sampling was carried out in two mangrove forests: Ilha da Fortaleza (00°46'47.27"S47°10'51.88"W) near São João de Pirabas in September 2008, January 2009 and April 2009, and Furo do Meio (00°52'26.00"S46°38'59.00"W) near Bragança in September 2009, January 2010 and April 2010. *Rhizophora mangle* L. is the predominant mangrove species in both study areas (Menezes *et al.*, 2008).

Both mangrove forests are located on the macrotidal mangrove coast of Pará State, northern Brazil (Saint-Paul & Schneider, 2010; see map in Supplementary Materials). The tidal regime is semi-diurnal, varying from 4 to 6 m (Moraes & Lopes, 2003). The climate is hot and humid, with well-defined seasonality (Martorano *et al.*, 1993) with over 75% of the annual precipitation falling between January and June. From September to November, rainfall is usually less than 30 mm (INMET, 2013). Annual rainfall in the region (Tracuateua weather station) was 2897 mm in 2008, 3284 mm in 2009 and 1987 mm in 2010 with 16.6 and 1 mm in September 2008 and 2009, 173 and 118.2 mm in January 2009 and 2010, and 507.8 and 379.5 mm in April 2009 and 2010, respectively (INMET, 2013).

Sampling

A 20 × 250 m area was delimited parallel to the main tidal channel in each mangrove forest. Within each area, a search was carried out for *Rhizophora mangle* logs with a diameter of approximately 10 cm every 10 m to ensure independence of observations. Searching took place at each of the distances 2, 10 and 20 m from the tidal channel. When logs were abundant, these were labelled and a random sample of five logs was selected at each distance. When logs were scarce searching continued until at least five logs were found at each distance. On each sampling date, a total of 15 logs were obtained at each forest, giving a grand total of 90 logs.

The selected logs were cut to a standard length of 40 cm from either one of the free ends, or from the free end if

attached to a larger trunk (Santos Filho *et al.*, 2008). Logs were cut and excavated over a plastic sheet to prevent loss of animals. Logs were opened initially using a small hatchet and afterwards excavated using forceps to carefully remove macrofauna and wood fragments. The logs were occasionally washed with water during excavation in order to remove animals and fine detritus. All washes took place over a 0.3 mm sieve, which was also used to rinse away mud and fine detritus from the animals and debris removed from the log. Animals were anaesthetized in magnesium chloride (10%) and kept in labelled plastic bags in the field until arrival in the laboratory. Individuals were then fixed in neutral formalin (5%) for approximately 24 h and then stored in ethyl alcohol (70%) for subsequent counting and identification. Individuals that could not be identified but were morphologically distinct were numbered to distinguish them from others of the same taxon.

Statistical analysis

Two logs from Ilha da Fortaleza sampled in September at distances 10 and 20 m, did not contain any macrofauna and were not included in the data analysis. The density (number of individuals), number of taxa and the reciprocal Berger–Parker dominance index were calculated for each log. A three-factor analysis of variance (ANOVA) was used to compare mean values of density, number of taxa and Berger–Parker dominance between mangrove forests (Ilha da Fortaleza, Furo do Meio), and among sampling dates (September, January and April) and distances from the tidal channel (2, 10, 20 m). Diagnostic graphs were used to verify ANOVA assumptions of normality and homogeneity of variances, residual distribution and outliers. A Box–Cox transformation was used if variances were heterogeneous. Tukey's multiple comparison tests were used when significant ($P < 0.05$) differences were detected by ANOVA.

Abundance data from the individual logs at each combination of forest, sampling date and distance were aggregated to create a reduced dataset of (2 mangrove forests × 3 sampling dates × 3 distances) 18 replicates. A distance matrix using the Czekanowski dissimilarity index was calculated from non-standardized fourth root transformed (to increase the contribution of rarer species to dissimilarity) macrofaunal abundance. Patterns in macrofaunal structure (abundance and composition) in relation to mangrove forests, sampling dates and distances from tidal channel were investigated using ordination by non-metric multidimensional scaling (nMDS) (Clarke & Ainsworth, 1993). Permutational multivariate analysis of variance (perMANOVA), using function *adonis* in the GNU-R vegan package (Oksanen *et al.*, 2012) was used to formally test for differences in macrofaunal structure among mangrove forests, sampling dates and distances from tidal channel. All data were analysed using the software GNU-R (R-Project, 2012).

RESULTS

The total number of individuals found in both mangrove forests was 5437, with an overall average (\pm SD) of 61.8 ± 60.4 individuals per log (see complete data set in Supplementary Materials). Numbers of individuals increased from September through January to April with 1397, 1459

Table 1. Summaries of analyses of variance of numbers of individuals, numbers of taxa and Berger–Parker dominance of macrofauna in mangrove logs sampled at distances of 2, 10 and 20 m from the tidal channel in September 2008, and January and April 2009 at Ilha da Fortaleza, and in September 2009, and January and April 2010 at Furo do Meio, Pará, Brazil.

Source of variation	Number of individuals				Number of taxa			Berger–Parker dominance		
	df	MS	F	P	MS	F	P	MS	F	P
Mangrove forest (M)	1	7881	2.534	0.116	1.51	0.104	0.748	0.281	0.424	0.517
Date (Dt)	2	13176	4.237	0.018*	224.65	15.524	<0.001***	6.756	10.205	<0.001***
Distance (Ds)	2	2836	0.912	0.406	0.31	0.022	0.979	0.511	0.771	0.466
M×Dt	2	19456	6.256	0.003**	65.63	4.535	0.014*	3.089	4.665	0.013*
M×Ds	2	3754	1.207	0.305	13.70	0.947	0.393	2.078	3.140	0.049*
Dt×Ds	4	2351	0.756	0.557	50.27	3.474	0.012*	1.538	2.323	0.065
M×Dt×Ds	4	1007	0.324	0.861	8.21	0.567	0.677	0.293	0.443	0.777
Error	70	3110			14.47			0.662		

df, degrees of freedom; MS, Mean Square; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

and 2581 individuals with average values (\pm SD) of 49.9 ± 59.6 , 48.6 ± 57.2 and 86.0 ± 58.6 individuals per log, respectively. A total of 85 taxa were distributed among four phyla: Mollusca (14 taxa), Annelida (17 taxa), Arthropoda (53 taxa) and Nemertea (one taxon). The most abundant species with 2609 individuals was *Neoterredo reynei* (Bartsch, 1920), representing 48% of total abundance. Other abundant ($\geq 2\%$ total abundance) taxa represented 30.5% of total abundance: Isopoda 2 (6.5%), the ant *Pheidole* sp. (4.4%), Capitellidae (4%), Tubificidae (3.8%), *Littoridina* sp. 1 (3.7%), *Littoridina*

sp. 2 (3.5%), *Melampus monilis* (Bruguiere, 1789) (2.6%) and Nereididae (2%).

A total of 3073 and 2364 individuals were found at Ilha da Fortaleza and Furo do Meio, with an average (\pm SD) of 71.5 ± 70.3 and 52.5 ± 48.1 individuals per log, respectively. At Ilha da Fortaleza, the macrofauna was represented by 61 taxa, 19 of which were unique, whereas at Furo do Meio, 66 taxa were found, 22 of which were unique. In both mangrove forests, the most abundant taxon was *Neoterredo reynei*, with 45% and 52% of total abundance at Ilha da Fortaleza and Furo do Meio, respectively. At Ilha da Fortaleza, other abundant taxa represented 40.8% of the total abundance: Isopoda 2 (7.3%), Capitellidae (7%), Tubificidae (5.6%), *Littoridina* sp. 1 (5%), *Littoridina* sp. 2 (4.8%), *Sphaeroma annandalei* Stebbing, 1911 (3.4%), Nereididae (2.9%), *Blauneria heteroclita* (Montagu, 1808) (2.5%) and *Littoridina* sp. 3 (2.3%). At Furo do Meio, other abundant taxa represented 25.7% of the total abundance: *Pheidole* sp. (10%), Isopoda 2 (5.5%), *Melampus monilis* (4.7%), *Solenopsis* sp. (2.9%) and *Namalycastis* sp. 2 (2.6%).

Numbers of individuals, numbers of taxa and Berger–Parker dominance differed significantly among sampling dates but not between forests nor among distances (Table 1). Interaction between forest and sampling date was significant for all three variables. At Ilha da Fortaleza,

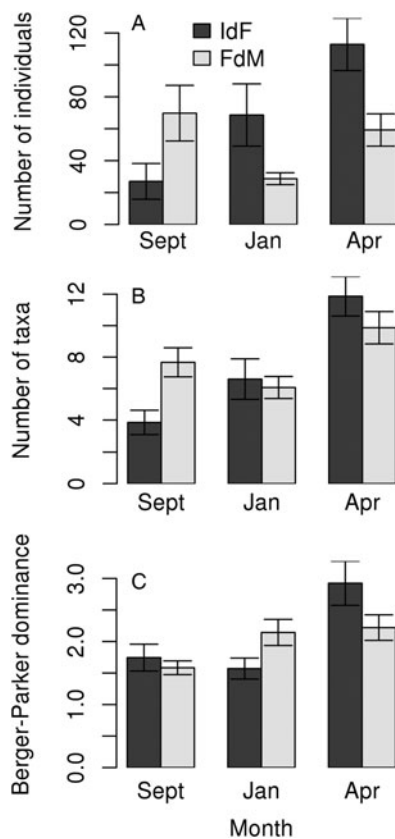


Fig. 1. Mean number (\pm SD) of individuals (A), taxa (B) and Berger–Parker dominance per log (C) from mangrove forests sampled in September 2008, and January and April 2009 at Ilha da Fortaleza (IdF), and in September 2009, and January and April 2010 at Furo do Meio (FdM), Pará, Brazil. Data were aggregated for distances of 2, 10 and 20 m from the tidal channel at each forest.

Table 2. Summary of permutational multivariate analysis of variance of macrofaunal abundance and composition in mangrove logs sampled at distances of 2, 10 and 20 m from the tidal channel in September 2008, and January and April 2009 at Ilha da Fortaleza, and in September 2009, and January and April 2010 at Furo do Meio, Pará, Brazil.

Source of variation	df	Sum of squares	Mean square	F	R	P
Mangrove forest (M)	1	1.298	1.288	4.926	0.049	0.001***
Date (Dt)	2	1.511	0.755	2.889	0.058	0.002**
Distance (Ds)	2	0.616	0.308	1.178	0.024	0.216
M×Dt	2	1.447	0.724	2.768	0.056	0.002**
M×Ds	2	0.464	0.232	0.887	0.179	0.601
Dt×Ds	4	1.208	0.302	1.155	0.047	0.214
M×Dt×Ds	4	1.054	0.263	1.007	0.041	0.449
Error	70	18.301	0.261		0.707	
Total	87	25.888			1	

df, degrees of freedom; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

numbers of individuals and numbers of taxa increased during the study (Figure 1A, B), whereas dominance was similar in September and January, but increased in April (Figure 1C). At Furo do Meio, the number of individuals (around half of which were *Neoterredo reynei*) was initially high in September, decreasing in January and increasing again in April (Figure 1A). The number of taxa at Furo do Meio was similar in September and January (Figure 1B) and increased in April, whereas dominance was low in September, increasing in January and April (Figure 1C).

There were significant differences in macrofaunal structure (see aggregated data set in Supplementary Materials) between mangrove forests and among sampling dates with significant interaction between these factors (Table 2). Two groups of macrofauna associated with logs from each mangrove forest

(Ilha da Fortaleza and Furo do Meio) are clearly distinct in the ordination (Figure 2A), which had a final stress value of 15%. The groups differed in terms of the taxa unique to each forest (Table 3) where more insect taxa were unique to Furo do Meio and more polychaete taxa unique to Ilha da Fortaleza. There were also differences in the abundance of taxa common to both mangrove forests (Table 4). *Blauneria heteroclita*, *Littoridina* sp. 1 and sp. 2, Tubificidae, Nereididae and Isopoda 2 were more abundant at Ilha da Fortaleza whereas *Melampus monilis* and *Namalycastis* sp. 2 were more abundant at Furo do Meio (Table 4).

Differences in macrofaunal structure between sampling dates were more obvious at Ilha da Fortaleza than at Furo do Meio (Figure 2B). At Ilha da Fortaleza, abundance of *Neoterredo reynei*, *Blauneria heteroclita*, *Littoridina* sp. 1 and sp. 2,

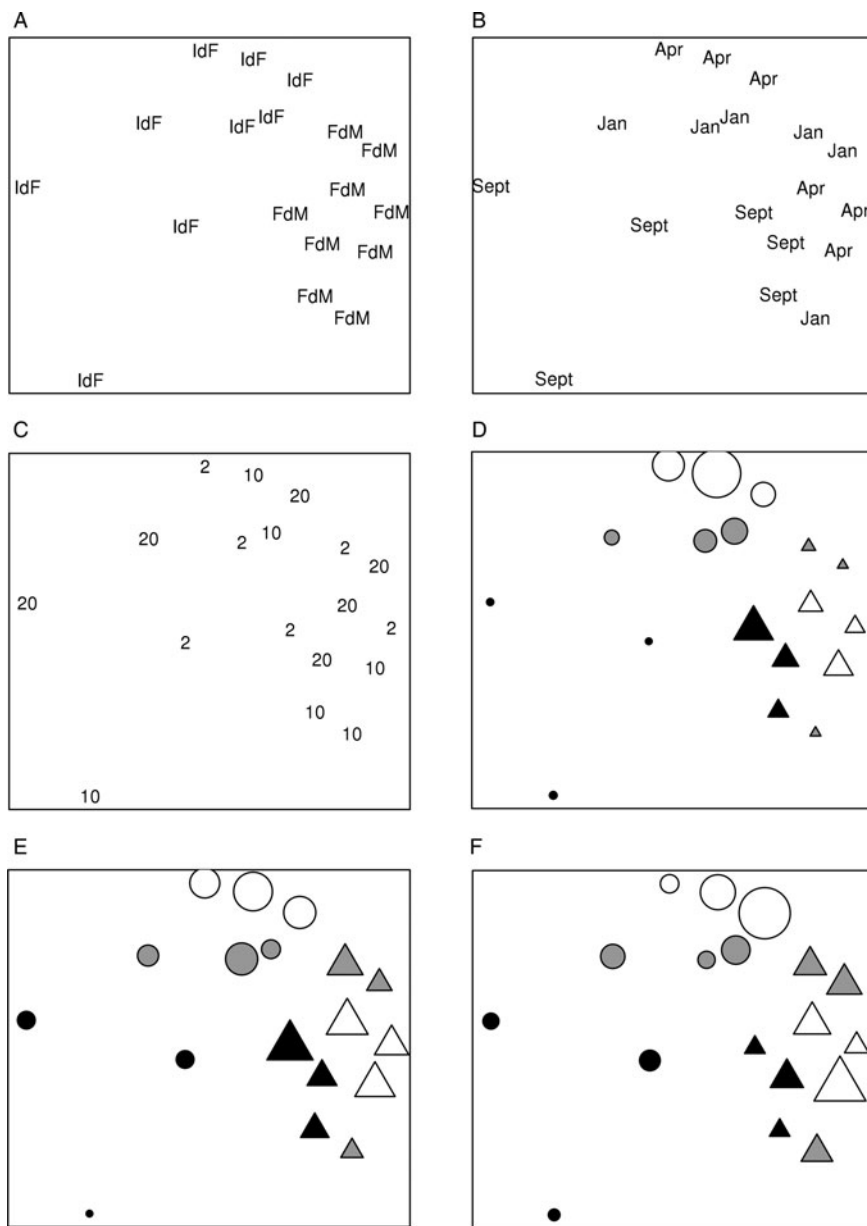


Fig. 2. Ordination by non-metric multidimensional scaling of mangrove logs sampled in September 2008, and January and April 2009 at Ilha da Fortaleza (IdF), and in September 2009, and January and April 2010 at Furo do Meio (FdM), Pará, Brazil, based on a Czekanowski distance matrix using fourth root transformed macrofaunal abundance data. Mangrove forests (A), sampling date (B) and distance from tidal channel (C). Overlays of numbers of individuals (D), numbers of taxa (E) and Berger-Parker dominance (F), where symbols represent the mangrove forests: circles (IdF) and triangles (FdM), and colours represent the sampling dates: black (September), grey (January) and white (April). Final stress value 15%.

Table 3. List of mangrove log macrofaunal taxa occurring uniquely at either Ilha da Fortaleza or Furo do Meio, Pará, Brazil. Numbered taxa are morphologically distinct from others of the same taxon.

Phylum or class	Taxon	Ilha da Fortaleza	Furo do Meio	
Gastropoda	<i>Littoridina</i> sp. 3	+		
Malacostraca	<i>Petrolisthes</i> sp.	+		
	<i>Corallana</i> sp. 2	+		
	Isopoda 5	+		
	<i>Ucides cordatus</i>		+	
	<i>Sphaeroma</i> sp.		+	
Arachnida	Isopoda 4		+	
	Amphipoda 2		+	
	Araneae 2	+		
	Araneae 1		+	
Nemertea	Acari 4		+	
	Unidentified species	+		
Insecta	Poduridae	+		
	Diptera 12	+		
	<i>Paratrechina</i> sp.		+	
	<i>Pheidole</i> sp.		+	
	<i>Solenopsis</i> sp.		+	
	Coleoptera		+	
	Hemiptera		+	
	Ephemeroptera		+	
	Philodaetidae		+	
	Diptera 1–3		+	
	Diptera 5–10		+	
	Polychaeta	Capitellidae	+	
		<i>Capitella</i> sp.	+	
		<i>Heteromastus</i> sp.	+	
		<i>Laeonereis</i> sp.	+	
<i>Mediomastus</i> sp.		+		
<i>Namalycastis abiuma</i>		+		
<i>Neanthes</i> sp.		+		
<i>Neanthes succinea</i>		+		
<i>Nereis oligoalina</i>		+		
<i>Phyllodoce</i> sp.		+		
<i>Perinereis vancaurica</i>		+		

Tubificidae, Capitellidae, Nereididae, *Desoria trispinata* (Mac Gillivray, 1896) and Poduridae increased from September to April. Certain taxa were present only in April (Nemertea, Amphipoda 3, Orthoptera, Dolichopodidae and Xylophagidae). At Furo do Meio, patterns in macrofaunal abundance were less clear where some taxa, such as *Littoridina* sp. 1 and sp. 2 and *Namalycastis* sp. 2, remained at similar abundances over the study period and others either increased (Tubificidae, Nereididae, Isopoda 2 and *Solenopsis* sp.) or decreased (*Desoria trispinata* and Acari 2) from September to April. Other taxa were more (*Blauneria heteroclita*) or less (*Melampus monilis* and *Pheidole* sp.) abundant in January. Certain taxa were only present (Diptera 8, 9, 10, 11, Dolichopodidae, Chilopoda and Acari 4) in April at Furo do Meio (see examples in Table 4). There were no clear patterns in macrofaunal structure among distances from the tidal channel at either Ilha da Fortaleza or at Furo do Meio (Figure 2C).

At Ilha da Fortaleza, an increase from September to April in the number of individuals, taxa and Berger–Parker dominance (Figure 2D–F) is clear, whereas for Furo do Meio, this pattern is not so clear, where there is a reduction in the number of individuals and taxa in January (Figure 2D, E). However, Berger–Parker dominance did appear to increase from September to April at Furo do Meio (Figure 2F).

Table 4. Total number of individuals of the most common taxa of macrofauna associated with mangrove logs ($N = 15$) sampled in September 2008, and January and April 2009 at Ilha da Fortaleza, and in September 2009, and January and April 2010 at Furo do Meio, Pará, Brazil. Numbered taxa are morphologically distinct from others of the same taxon.

	Ilha da Fortaleza			Furo do Meio		
	Sept	Jan	Apr	Sept	Jan	Apr
<i>Neoteredo reynei</i>	259	474	644	671	194	367
<i>Blauneria heteroclita</i>	0	6	72	1	20	2
<i>Littoridina</i> sp. 1	13	81	64	16	18	10
<i>Littoridina</i> sp. 2	9	58	81	18	10	12
<i>Littoridina</i> sp. 3	0	2	68	0	0	0
<i>Melampus monilis</i>	13	2	13	34	5	73
Tubificidae	14	49	110	4	6	24
Capitellidae	1	45	170	0	0	0
<i>Namalycastis</i> sp. 2	0	2	0	23	23	16
Nereididae	0	14	74	6	4	12
Isopoda 2	0	170	54	23	42	66
<i>Desoria trispinata</i>	0	2	38	32	2	6
Poduridae	0	8	95	0	0	0
<i>Pheidole</i> sp.	0	0	0	132	22	84
<i>Solenopsis</i> sp.	0	0	0	5	18	45
Acari 3	1	0	7	0	3	38
Dolichopodidae	0	0	3	0	0	10
Diptera 7	0	0	0	0	2	13
Diptera 8	0	0	0	0	0	20

DISCUSSION

The number of macrofaunal taxa associated with mangrove logs in the present study was 85, which is higher than the 31 taxa recorded by Aviz *et al.* (2009) in mangrove logs from São Caetano de Odivelas, Pará. The values are reasonably comparable since the total volume of logs sampled by Aviz *et al.* (2009), 0.38 m³, was similar to the 0.28 m³ sampled in the present study. The number of taxa in mangrove logs appears to be much higher than that found in surveys by Fernandes (2003) in mangrove sediment at Ilha de Maracá, Amapá (15) and in muddy sediment along the Caeté estuary, Pará (17) (Rosa-Filho *et al.*, 2006). However, the total volume sampled in both studies (0.071 m³ and 0.025 m³, respectively) was much lower than that of the present study, and so further sampling effort could potentially reveal more taxa associated with mangrove sediments.

The macrofauna surveyed in mangrove forests from São João de Pirabas and Bragança was composed of both estuarine and terrestrial taxa. Aviz *et al.* (2009) found a similar estuarine–terrestrial division in the macrofauna associated with logs from a mangrove forest in São Caetano de Odivelas, Pará, which is in the same region as the present study. Such a diverse composition of benthic macrofauna indicates the influence of terrestrial environments adjacent to the mangroves (Kathiresan & Bingham, 2001). Terrestrial environments contribute to increased macrofaunal diversity in mangroves, insects being a good example, which may be either permanent or temporary residents in mangroves (Kathiresan & Bingham, 2001). In the present study, insects made a significant contribution to macrofaunal diversity in mangrove logs. The diversity of insects in mangroves may be high, and they may belong to different trophic levels, such as herbivores, saprophages, parasites or predators

(Nagelkerken *et al.*, 2008). Insect survival may be enhanced by the availability of microhabitats in which to live or shelter, such as trunks, roots and decaying wood (Kathiresan & Bingham, 2001; Nagelkerken *et al.*, 2008).

Annelida, Crustacea and Mollusca are the predominant groups in the macrofauna of mangrove sediments (Oliveira & Mochel, 1999; Aviz *et al.*, 2009) and logs (Aviz *et al.*, 2009; present study) in northern Brazil. The relative abundances of Mollusca (61.7%), Annelida (12.7%), Crustacea (11.1%) and non-crustacean Arthropoda (14.1%) in the present study were greater, similar, lower and higher, respectively, than those recorded in a mangrove forest in the same region as the present study by Aviz *et al.* (2009): Mollusca (27.5%), Annelida (10.8%), Crustacea (53.4%) and non-crustacean Arthropoda (6.3%).

The macrofauna of sediments is usually dominated by polychaetes, which generally have the highest relative abundance (da Silva *et al.*, 2011), whereas in mangrove logs the most abundant taxon is Bivalvia (present study) or Crustacea (Aviz *et al.*, 2009). In the sediment infauna of mangroves at Ilha de Maracá, Amapá State, Brazil, marine taxa, such as Mollusca, Annelida and Crustacea, were relatively more abundant (0.18, 0.41 and 96.3%) than terrestrial ones, such as Collembola, Coleoptera and Chilopoda, (0.04, 0.09 and 0.22%) (Fernandes, 2003). In sediments from the Furo do Meio mangrove forest, Bragança, Pará, the most abundant faunal group was Polychaeta (Beasley *et al.*, 2010). The relatively lower proportion of terrestrial fauna in mangrove sediment may be due to very low concentrations of oxygen and high concentrations of sulphides and other toxic substances. The mangrove log may provide the macrofauna, especially those of terrestrial origin, an island of microhabitat with more favourable conditions than that of the sediment.

In the present study, Mollusca (class Bivalvia) was the most abundant faunal group, dominated by *Neoteredo reynei*. The teredinids (shipworms) are capable of entering and excavating mangrove logs (Moraes & Lopes, 2003), thereby facilitating the entry of other macrofauna and providing refuge and a food supply for other benthic organisms (Dame, 1996). The larger surface area of the exposed log (Reis, 1995) enables an increasing number of bacteria (Alongi & Sasekumar, 1992) and fungi (Sotão *et al.*, 2003) to colonize the log, thus increasing the rate of their decomposition (Kohlmeyer *et al.*, 1995). *Neoteredo reynei* tolerates wide fluctuation in salinity (Reis, 1995), has adaptations for gas exchange and desiccation (Turner, 1966) and are not dependent on suspension-feeding (Moraes & Lopes, 2003). Such characteristics contribute to their survival in mangrove areas that are not frequently flooded by tides (Lopes *et al.*, 2000) allowing these shipworms to resist changes in air humidity and tidal inundation all year round.

Isopoda was the second most abundant taxon in the present study. A total of 3154 species of marine isopods have been described from different habitats, with 40% of these species from tropical regions (Poore & Bruce, 2012). Isopoda are often associated with mangrove roots and logs, aiding in their decomposition (Svavarsson *et al.*, 2002). Mangrove logs provide refuge from predators for isopods (Ellison & Farnsworth, 1992) and food in the form of woody detritus (Poore & Bruce, 2012), although some are filter feeders (Si *et al.*, 2002). The logs serve as habitat for reproduction as some females give parental care, sheltering the offspring in logs (Thiel, 1999). Poore & Bruce (2012)

found that the number of isopods varied from 1 to 48 individuals per log, whereas in the present study, the numbers varied from 1 to 162 per log, distributed in two genera (*Corallana* and *Sphaeroma*), the species *Sphaeroma annandalei* and four unknown morphospecies.

The ant genus *Pheidole* sp., which despite being a member of a typically terrestrial faunal group (family Formicidae), is adapted to survive in the microhabitat found in mangrove logs (Nagelkerken *et al.*, 2008). To prevent drowning, some species find refuge on trunks or branches above the high tide mark as their galleries may become partially or totally submerged during high tide (Cannicci *et al.*, 2008). Other species of ant are able to survive submerged during high tide by means of physiological adaptations that allow partial anaerobic respiration, and thus no longer need to seek a place of refuge (Nilsen, 2006).

The family Nereididae was relatively abundant in both mangrove forests. Varying in size from a few millimetres to a metre, they are considered sedentary, with detritivorous or herbivorous feeding habits (Santos & Lana, 2001). The genus *Namalycastis*, the most abundant member of this family in the present study, is commonly associated with fallen logs in mangroves (Glasby, 1999) and in roots of *Rhizophora mangle* (Santos & Lana, 2001)

Zonation and the distribution of mangrove species are related to tidal amplitude. In the high intertidal zone, decapod crustaceans dominate, whereas in the low intertidal zone, the fauna consists of filter-feeders, such as oysters and barnacles (Koch & Wolff, 2002). Zonation of species also depends on the coastal topography (Alongi & Sasekumar, 1992), variation in temperature (Koch & Wolff, 2002) and the distribution of organic matter, which is an important food source (Wolff *et al.*, 2000). In the present study, no significant difference in macrofaunal structure occurred among distances up to 20 m from the tidal channel in either of the mangrove forests. The relative homogeneity of the macrofauna at this spatial scale may indicate relatively similar conditions in mangrove logs despite different distances from the tidal channel. Although the study area is situated in a high intertidal zone and is subject to infrequent tidal flooding, mangrove logs may represent a stable island microhabitat for the macrofauna, retaining humidity, maintaining a stable temperature and protecting against desiccation.

Macrofaunal structure also depends on seasonal variation (Ysebaert & Herman, 2002). In the present study, macrofaunal structure associated with mangrove logs varied greatly among sampling dates with higher abundance and numbers of taxa in the wetter season. Similarly, marked temporal differences were found in the composition and abundance of the macrofauna associated with aggregates of the polychaete *Phyllochaetopterus socialis* Claparède, 1870 (Albano & Obenat, 2009). In general, such variation in macrofaunal structure may be caused by seasonal changes in precipitation (Dippner & Ikauniece, 2001), salinity (da Silva *et al.*, 2011), temperature (Nagelkerken *et al.*, 2008), tidal level (Dittmann, 2000), and air humidity (Omena *et al.*, 1990).

Seasonal variation in macrofaunal structure differed in each mangrove forest. At Ilha da Fortaleza, seasonal variability was high, where the abundance and number of taxa increased threefold during the study. This may occur due to the fact that Ilha da Fortaleza is less influenced by river discharge and is thus a more marine environment. However, seasonal rainfall may cause wide variation in salinity along the Amazon

mangrove macrotidal coast (Souza-Filho *et al.*, 2009). In the Furo do Meio mangrove forest, seasonal variation in macrofaunal structure was much lower. Although the same seasonal pattern occurred in Furo do Meio, there was greater similarity among sampling dates. This may be due to the greater influence of river discharge at this mangrove forest (Souza-Filho & El-Robrini, 1997), which tends to reduce seasonal variation in salinity and thus reduce variation in the macrofauna. In conclusion, the mangrove log macrofauna appears to be relatively diverse at both forests in this study. However, macrofaunal structure was dominated by estuarine taxa at Ilha da Fortaleza and by terrestrial taxa at Furo do Meio. Such differences between sites are greater at certain times of the year when rainfall and salinity change.

ACKNOWLEDGEMENTS

J. Andrade and N. Palhano are grateful to the Programa Institucional de Bolsas de Iniciação Científica/Conselho Nacional de Desenvolvimento Científico e Tecnológico at the Universidade Federal do Pará (UFPA) for undergraduate scholarships. J. Andrade also thanks the Fundação de Amparo à Pesquisa do Estado do Pará for a postgraduate scholarship. We thank L.R.L. Simone (Museu de Zoologia da Universidade de São Paulo) for identifying gastropods, T.M.C. Ferreira (UFPA) for identifying ants and A.S. Souza (UFPA) for identifying decapods. We are also grateful to T.C. Sousa for help in the field and to two anonymous referees for greatly improving the manuscript.

FINANCIAL SUPPORT

This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

REFERENCES

- Albano M.J. and Obenat S.M.** (2009) Assemblage of benthic macrofauna in the aggregates of the tubicolous worm *Phyllochaetopterus socialis* in the Mar del Plata harbour, Argentina. *Journal of the Marine Biological Association of the United Kingdom* 89, 1099–1108.
- Alongi D.M. and Sasekumar A.** (1992) Benthic communities. In Robertson A.I. and Alongi D.M. (eds) *Tropical mangrove ecosystems*. Washington, DC: American Geophysical Union, pp. 137–171.
- Aviz D., Mello C.F. and 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 Emílio Goeldi, Série Ciências Naturais* 4, 47–55.
- Beasley C.R., Fernandes M.E.B., Figueira E.A.G., Sampaio D.S., Melo K.R. and Barros R.S.** (2010) Mangrove infauna and sessile epifauna. In Saint-Paul U. and Schneider H. (eds) *Mangrove dynamics and management in north Brazil*. Berlin & Heidelberg: Springer, pp. 109–123.
- Cannici S., Burrows D., Fratini S., Smith III T.J., Offenberg J. and Dahdouh-Guebas F.** (2008) Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. *Aquatic Botany* 89, 186–200.
- Cantera J.R., Thomassin B.A. and Arnaud P.M.** (1999) Faunal zonation and assemblages in the Pacific Colombian mangroves. *Hydrobiologia* 413, 17–33.
- Clarke K.R. and Ainsworth M.** (1993) A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* 92, 205–219.
- Dame R.F.** (1996) *Ecology of marine bivalves: an ecosystem approach*. 1st edition. Boca Raton; FL: CRC Press.
- Dippner J.W. and Ikaunieca 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.** (2000) Zonation of benthic communities in a tropical tidal flat of north-east Australia. *Journal of Sea Research* 44, 33–51.
- Ellison A.M. and Farnsworth E.J.** (1992) The ecology of Belizean mangrove-root fouling communities: patterns of epibiont distribution and abundance, and effects on root growth. *Hydrobiologia* 247, 87–98.
- Fernandes M.E.B.** (2003) Macroendofauna bêmica de substrato móvel. In Fernandes M.E.B. (ed.) *Os manguezais da costa norte brasileira*. São Luís, MA: Fundação Rio Bacanga, pp. 87–104.
- Frith D.W., Tantanasiwong R. and Bathia O.** (1976) Zonation and abundance of macrofauna on a mangrove shore, Phuket island. *Phuket Marine Biological Center* 10, 1–38.
- Glasby C.J.** (1999) The Namanereidinae (Polychaeta: Nereididae). Part 1. Taxonomy and Phylogeny. *Records of the Australian Museum* 25, 1–129.
- INMET** (2013) *Banco de Dados Meteorológicos para Ensino e Pesquisa (BDMEP)*. Instituto Nacional de Meteorologia. Dados da Rede INMET. Available at: <http://www.inmet.gov.br/projetos/rede/pesquisa> (accessed 16 August 2013).
- Kathiresan K. and Bingham B.L.** (2001) Biology of mangroves and mangrove ecosystems. *Advances in Marine Biology* 40, 81–251.
- Koch V. and Wolff M.** (2002) Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. *Marine Ecology Progress Series* 228, 119–130.
- Kohlmeyer J., Bebout B. and Volkmann-Kohlmeyer B.** (1995) Decomposition of mangrove wood by marine fungi and teredinids in Belize. *Publicazioni della Stazioni Zoologica di Napoli* 16, 27–39.
- Lara R., Cohen M. and Szlafsztajn C.** (2010) Drivers of temporal changes in mangrove vegetation boundaries and consequences for land use. In Saint-Paul U. and Schneider H. (eds) *Mangrove dynamics and management in north Brazil*. Berlin & Heidelberg: Springer, pp. 127–141.
- Lara R.J.** (2003) Amazonian mangroves—a multidisciplinary case study in Pará State, North Brazil: Introduction. *Wetlands Ecology and Management* 11, 217–221.
- Levinton J.S.** (2001) *Marine biology: function biodiversity, ecology*. 2nd edition. New York: Oxford University Press.
- Lopes S.G.B.C., Domaneschi O., Moraes D.T., Morita M. and Meserani G.L.C.** (2000) Functional anatomy of the digestive system of *Neoteredo reynei* (Bartsch, 1920) and *Psiloteredo healdi* (Bartsch, 1931) (Bivalvia: Teredinidae). In Harper E.M., Taylor J.D. and Crane J.A. (eds) *The evolutionary biology of Bivalvia*. London: Geological Society of London, pp. 257–271.
- Martorano L.G., Pereira L.C., César E.G.M. and Pereira I.C.B.** (1993) *Estudos climáticos do Estado do Pará: classificação climática (Köppen) e deficiência hídrica (Thorntwhite, Mather)*. 1st edition. Belém: SUDAM/EMBRAPA, SNLCS.
- Menezes M.P.M., Berger U. and Mehlig U.** (2008) Mangrove vegetation in Amazonia: a review of studies from the coast of Pará and Maranhão States, north Brazil. *Acta Amazonica* 38, 403–420.

- Moraes D.T. and Lopes S.G.B.C.** (2003) The functional morphology of *Neoteredo reyni* (Bartsch, 1920) (Bivalvia, Teredinidae). *Journal of Molluscan Studies* 69, 311–318.
- Morrisey D.J., Howitt L., Underwood A.J. and Stark J.S.** (1992a) Spatial variation in soft-sediment benthos. *Marine Ecology Progress Series* 81, 197–204.
- Morrisey D.J., Underwood A.J., Howitt L. and Stark J.S.** (1992b) Temporal variation in soft-sediment benthos. *Journal of Experimental Marine Biology and Ecology* 146, 233–245.
- Nagelkerken I., Blaber S.J.M., Bouillon S., Green P., Haywood M., Kirton L., Meynecke J.O., Pawlik J., Penrose H.M., Sasekumar A. and Somerfield P.J.** (2008) The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquatic Botany* 89, 155–185.
- Nilsen M.G.** (1997) Nesting biology of the mangrove mud-nesting ant *Polyrhachis sokolova* Forel (Hymenoptera, Formicidae) in Northern Australia. *Insectes Sociaux* 44, 15–21.
- Nilsen M.G.** (2006) Respiration by mangrove ants *Camponotus anderseni* during nest submersion associated with tidal inundation in Northern Australia. *Physiological Entomology* 31, 120–126.
- Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H. and Wagner H.** (2012) *Vegan: community ecology package*. Available at: <http://CRAN.R-project.org/package=vegan> (accessed 16 August 2013).
- Oliveira M. and Mochel F.** (1999) Macrofauna bêntica de substratos móveis de um manguezal sob impacto das atividades humanas no Sudoeste da Ilha de São Luis, Maranhão, Brasil. *Boletim do Laboratório de Hidrobiologia* 12, 75–93.
- Omena E.P., Junqueira A.O.R. and Silva S.H.G.** (1990) Resistência de Teredinidae Rafinesque, 1815 (Mollusca: Bivalvia) a diferentes períodos de exposição ao ar. *Revista Brasileira de Biologia* 50, 701–707.
- Poore G.C.B. and Bruce N.L.** (2012) Global diversity of marine isopods (except *Asellota* and crustacean symbionts). *PLoS ONE* 7, e43529. doi:10.1371/journal.pone.0043529.
- Reis R.E.M.L.** (1995) Moluscos bivalves perfuradores de madeira do Estado do Pará, Brasil: caracterização taxonômica, distribuição e resistência de madeiras. *Boletim do Museu Paraense Emílio Goeldi, Série Zoologia* 11, 125–203.
- Rosa-Filho J.S., Busman D., Viana A.P., Gregório A.M. and Oliveira D.M.** (2006) Macrofauna bentônica de zonas entre-marés não vegetadas do estuário do rio Caeté, Bragança, Pará. *Boletim do Museu Paraense Emílio Goeldi, Série Ciências Naturais* 1, 85–96.
- R-Project** (2012) *The R project for statistical computing*. Available at: <http://www.r-project.org/> (accessed 16 August 2013).
- Saint-Paul U. and Schneider H.** (2010) *Mangrove dynamics and management in North Brazil*. 1st edition. Berlin & Heidelberg: Springer.
- Santos C.S.G. and Lana P.C.** (2001) Nereididae (Annelida, Polychaeta) da costa nordeste do Brasil. II. Gêneros *Namalycastis*, *Ceratocephale*, *Laonereis* e *Rullierinereis*. *Iheringia, Série Zoologia* 91, 137–149.
- Santos Filho C., Tagliaro C.H. and Beasley C.R.** (2008) Seasonal abundance of the shipworm *Neoteredo reyni* (Bivalvia, Teredinidae) in mangrove driftwood from a northern Brazilian beach. *Iheringia, Série Zoologia* 98, 17–23.
- Schaeffer-Novelli Y.** (1995) *Manguezal: ecossistema entre a terra e o mar*. 1st edition. São Paulo: Caribbean Ecological Research.
- Schaeffer-Novelli Y., Cintrón M.G., Rothleder A. Daime R. and Camargo T.M.D.** (1990) Variability of mangrove ecosystems along the Brazilian coast. *Estuaries* 13, 204–218.
- Si A., Bellwood O. and Alexander C.G.** (2002) Evidence for filter-feeding by the wood-boring isopod, *Sphaeroma terebrans* (Crustacea: Peracarida). *Journal of Zoology* 256, 463–471.
- Silva R.F. da, de Souza S.R., Souza-Filho P.W.M. and Rosa-Filho J.S.** (2011) Spatial and temporal changes in the structure of soft-bottom benthic communities in an Amazon estuary, Caeté estuary, Pará, Brazil. *Journal of Coastal Research* 64, 440–444.
- Sotão H.M.P., Campos E.L., Gugliotta A.M. and Costa S.P.S.E.** (2003) Fungos macroscópicos Basidiomycetes. In Fernandes M.E.B. (ed.) *Os manguezais da costa norte brasileira*. São Luís, MA: Fundação Rio Bacanga, pp. 45–59.
- Souza-Filho P.W.M. and El-RObrini M.** (1997) Morfologia, processos de sedimentação e litofácies dos ambientes morfo-sedimentares da Planície Costeira Bragantina, nordeste do Pará, Brasil. *Geonomos* 4, 1–16.
- Souza-Filho P.W.M., Lessa G.C., Cohen M.C.L., Costa F.R. and Lara R.J.** (2009) The subsiding macrotidal barrier estuarine system of the eastern Amazon coast, northern Brazil. In Dillenburg S.F. and Hesp P.A. (eds) *Geology and geomorphology of Holocene coastal barriers of Brazil*. Berlin & Heidelberg: Springer, pp. 347–375.
- Svavarsson J., Osore M.K.W. and Ólafsson E.** (2002) Does the wood-borer *Sphaeroma terebrans* (Crustacea) shape the distribution of the mangrove *Rhizophora mucronata*? *Ambio* 31, 574–579.
- Thiel M.** (1999) Reproductive biology of a wood-boring isopod, *Sphaeroma terebrans*, with extended parental care. *Marine Biology* 135, 321–333.
- Thurman H.V. and Trujillo A.P.** (2004) *Introductory oceanography*. 10th edition. Upper Saddle River, NJ: Pearson Prentice Hall.
- Turner R.D.** (1966) *A survey and illustrated catalogue of Teredinidae (Mollusca, Bivalvia)*. 1st edition. Cambridge, MA: Museum of Comparative Zoology, Harvard University.
- Turner R.D. and Johnson A.C.** (1971) Biology of marine wood-boring molluscs. In Jones E.B.G. and Eltringham S.K. (eds) *Marine borers, fungi and fouling organisms of wood*. Paris: Organisation for Economic Co-operation and Development (OECD), pp. 259–301.
- Wolff M., Koch V. and Isaac V.** (2000) A trophic flow model of the Caeté mangrove estuary (North Brazil) with considerations for the sustainable use of its resources. *Estuarine, Coastal and Shelf Science* 50, 789–803.
- and
- Ysebaert T. and 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, 105–124.

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