

## Original Article

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# Macrobenthic fauna associated with *Diopatra cuprea* (Onuphidae: Polychaeta) tubes on a macrotidal sandy beach of the Brazilian Amazon Coast

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## Abstract

Tube-building polychaetes are an important group of marine bioengineers in soft-bottom habitats, where they provide structures that potentially influence the composition of the benthic community. The present study investigated the effects of *Diopatra cuprea* tubes on the structure of the macrobenthic fauna found on a sandy beach of the Amazon coast. Samples were collected in June (rainy season) and September (dry season) 2012 in two different areas: (1) an area in which *D. cuprea* tubes were present, and (2) a control area, in which worm tubes were absent. A total of 53 taxa were found, of which 30 were associated exclusively with *D. cuprea* tubes. While large aggregations of *D. cuprea* were not found in the study area, the presence of even a single tube may have a significant influence on the environmental conditions available for other organisms, especially those adapted to consolidated or muddy substrates. The two areas presented different seasonal patterns. A significant increase in the abundance and richness of the macrofauna was observed in area 1 in the rainy season, when the density of worm tubes increased and the hydrodynamic conditions were less intense. The results of the study highlight the importance of this organism as an ecosystem engineer on the sandy beaches of the Amazon coast.

## Introduction

Organisms that create, modify or maintain habitats (or microhabitats) are known as ecosystem engineers (Jones *et al.*, 1994, 1997). Many organisms are known to modify the physical structure, complexity and heterogeneity of marine environments, and thus influence the characteristics of the associated communities (Jones *et al.*, 1994, 1997; Crooks, 2002) including mussel beds, reef-building organisms and tube-building worms (Khaitov *et al.*, 1999; Callaway, 2006; Commiato *et al.*, 2008). Tubicolous polychaetes can build their tubes from a number of different materials (e.g. mud, sand, shell, sandstone). These tubes play an especially important ecological role by providing structures that increase the physical complexity and biodiversity of habitats (Dauer *et al.*, 1982; Bailey-Brock, 1984; Dubois *et al.*, 2002; Thomsen *et al.*, 2011).

Polychaete tubes are known to influence near-bed hydrodynamics (Jumars & Nowell, 1984), by either stabilizing (Bolam & Fernandes, 2003) or destabilizing sediments (Eckman *et al.*, 1981; Carey, 1983; Luckenbach, 1986). In general, tube structures have three principal effects, influencing the properties of the sediment, the hydrodynamic regime and the availability of surfaces for attachment. The intensity of the effect on hydrodynamics and sediments depends on the density of the tubes (Eckman, 1983).

The genus *Diopatra* includes ~50 tubicolous species (Budaeva & Fauchald, 2008), which are common in the intertidal and shallow subtidal waters of all the major oceans, but are more diverse in warmer waters. These worms often reinforce the walls of their simple tubes of mucous-bound particles with fragments of shell, algae and other debris (Hartman, 1969). *Diopatra cuprea* (Bosc, 1802) occurs in coastal waters between Cape Cod and Brazil (Mangum *et al.*, 1968). This species builds vertical tubes, which typically penetrate the substratum to a depth of 50–60 cm (Myers, 1972), with a hook-shaped ‘tube cap’ emerging 2–5 cm above the sediment surface. Isolated *D. cuprea* tubes or aggregations of tubes are especially common in intertidal estuarine areas or other sheltered coastal environments.

The construction of *Diopatra* tubes on unconsolidated bottoms may influence the structure of the meiofauna (Bell & Coen, 1982a, 1982b; Bell & Woodin, 1984; Bell, 1985; Guilherme, 2011) and benthic macrofauna (Woodin, 1978; Bell & Devlin, 1983; Thomsen *et al.*, 2009) communities, as well as the bacteria (Phillips and Lovell, 1999; Matsui *et al.*, 2004) and algae (Thomsen, 2004, 2009). In general, there is a positive influence on the species richness and abundance of the fauna associated with these tubes.

While some studies have focused on the fauna associated with worm tubes, there are virtually no data from tropical regions. On the Brazilian Amazon coast, in particular, no



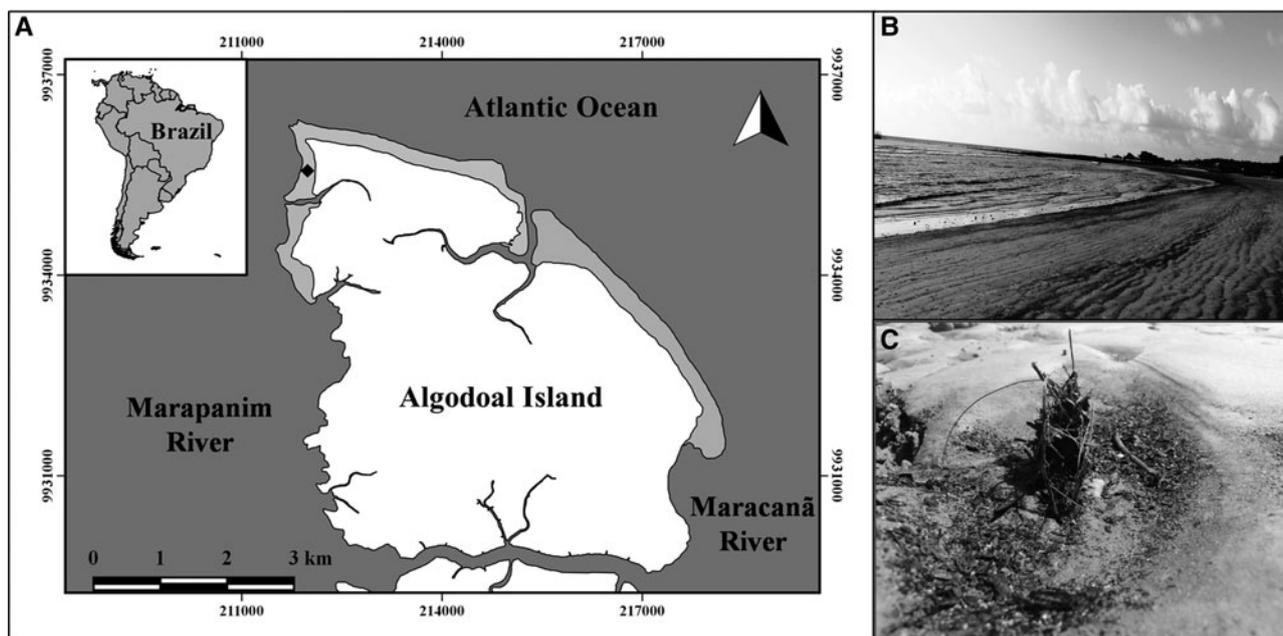


Fig. 1. Map (UTM: 23S zone) of Algodão-Maiandeuá Island (A); Farol Beach (B); the exposed portion of a *Diopatra cuprea* tube (C).

information is available on even the occurrence or ecology of *D. cuprea*, despite the fact that this species is common on mudflats and protected sandy beaches. This coastal region has a number of unique features, including high volumes of river discharge, a macrotidal regime and intense dry and rainy seasons, which contribute to marked fluctuations in the salinity and hydrodynamics of the coastal environments (Dittmar and Lara, 2001; Souza-Filho *et al.*, 2009; Pereira *et al.*, 2012). This provokes extreme temporal variations in the characteristics of Amazonian benthic communities (Rosa Filho *et al.*, 2009, 2011; Silva *et al.*, 2011; Braga *et al.*, 2013).

This study describes the structure of the macrobenthic fauna associated with *D. cuprea* tubes on a sandy beach of the Amazon coast. Two hypotheses were tested: (i) the presence of tubes contributes to the establishment of a macrobenthic assemblage distinct from that found on sediments with no tubes, and (ii) the structure of the benthic macrofauna associated with the tubes varies significantly between climatic seasons.

## Materials and methods

### Study area

The island of Algodão-Maiandeuá is located on the northern coast of Brazil ( $0^{\circ}34'45''$ – $0^{\circ}37'30''$ S  $47^{\circ}32'05''$ – $47^{\circ}34'12''$ W), and is surrounded on three sides by rivers and estuarine channels (Figure 1A). The region is dominated by semidiurnal macrotides, with amplitude of between 4 and 7 m (Silva *et al.*, 2011). The local climate is humid tropical with a mean annual temperature of  $27.7 \pm 1.1^{\circ}\text{C}$  (Martorano *et al.*, 1993) and mean annual precipitation (30-year records) of 2300–2800 mm (Moraes *et al.*, 2005). Precipitation varies considerably over the course of the year, however, with a well-defined rainy season from January to July (total rainfall  $\sim 1657$  mm), and a dry season from August to December, with total rainfall of 490 mm (Moraes *et al.*, 2005).

Algodão-Maiandeuá Island has 35 km of sandy beaches, which vary considerably in their slope, extension and width, and their exposure to wave action, and are covered in substrates ranging from mud to sand (Mendes, 2005). The study beach, Farol, is located on the western margin of the island, which is

bathed by the Marapanim River and is a low-tide terrace beach with a wide intertidal zone (200–400 m) composed mainly of fine sediments (Rosa Filho *et al.*, 2011). *Diopatra cuprea* tubes are common in the intertidal zone of this beach (Figure 1B).

### Sampling and sample processing

Samples were collected in June (rainy season) and September (dry season) 2012 from two different areas of the intertidal zone, each with an area of  $\sim 250$  m<sup>2</sup>, at the same distance from the tideline. One of these areas was populated with *D. cuprea* tubes (area 1), the other had no tube worms (area 2). During each survey, 20 replicate samples were collected haphazardly in each area using cylindrical cores (0.0079 m<sup>2</sup>, 20 cm deep). In area 1, a *D. cuprea* tube (occupied by a single worm) was positioned at the centre of each cylindrical core (Figure 1C). The samples were filtered through a 0.3 mm mesh screen, and all the macrofauna was retrieved and fixed in 4% formalin saline. To estimate the density of the *D. cuprea* within area 1, the number of tubes were counted in eight randomly distributed square subplots (25 m<sup>2</sup>), in both study months.

Simultaneously to the biological sampling, a sediment sample was collected from each area for granulometric analyses using the same core sampler. The temperature of the sediment was determined from three random replicates taken with a soil thermometer in each sampling area. The salinity of the seawater was also determined from a sample of the surface water of the infralittoral, taken with a manual refractometer. Data on air temperatures and precipitation levels were obtained from the meteorological station in Salinópolis ( $\sim 30$  km from the study site), and were provided by the Brazilian National Meteorological Institute (INMET).

In the laboratory, the biological samples were examined under a stereoscopic microscope, and the organisms observed were counted and identified to the lowest possible taxonomic level. The granulometric analysis was conducted by sieving out the coarse sediments and pipetting the fine sediments, as proposed by Suguio (1973). The textural parameters (mean grain size, sorting, sand and percentage gravel) were calculated using the equations of Folk & Ward (1957). Grain sizes were determined by sieving the sediment in an automatic shaker and classifying the grains according to the Wentworth scale (Buchanan, 1984).

**Table 1.** Environmental characteristics of the study area

Climate conditions/water	Rainy (June)		Dry (September)	
Total rainfall (mm)	112.7		2.0	
Air temperature (°C)				
Max	32.2		32.9	
Min	18.9		21.4	
Water salinity	29		35	
Characteristics of sediment	Control	Tubes	Control	Tubes
Temperature (°C)	30.6 ± 0.33	28.33 ± 0.33	31.36 ± 0.63	28.66 ± 0.33
Organic matter (g)	0.13 ± 0.04	2.40 ± 0.15	0.22 ± 0.07	1.96 ± 0.29
Textural classification	FS/MS	VFS	MS	VFS/FS
Mean grain size (Φ)	2.10 ± 0.11	3.92 ± 0.06	1.78 ± 0.07	2.83 ± 0.46
% Clay	0	2.32	0	0
% Silt	1.45	56.43	0	1.73
% Very fine sand	3.42	31.28	1.07	66.67
% Fine sand	58.91	9.25	2.87	28.0
% Median sand	65.82	6.15	53.81	2.51

VFS, very fine sand; FS, fine sand; MS, Medium sand.

### Statistical analysis

We calculated the total taxon richness and density (ind. m<sup>-2</sup>) for each biological sample, and the variation in these parameters was analysed using a two-way (area and season) analysis of variance (ANOVA) after verifying the normality and homogeneity of variances assumptions, using the Kolmogorov–Smirnov and Levene tests, respectively. When necessary, the data were transformed (fourth root or Log(*x* + 1)). When the ANOVA detected a significant difference, Tukey's *a posteriori* test was applied to identify significant pairwise differences. The data on the abundance of *D. cuprea* were analysed separately from those of the associated fauna, and were tested between seasons using a one-way ANOVA.

To assess the effects of the *D. cuprea* tubes on the macrofauna and validate our *a priori* grouping (area 1 and 2; dry and rainy seasons), a Principal Coordinates Analysis (PCO) was run on a Bray–Curtis similarity matrix of the fourth root-transformed species abundance data. To identify the species that characterized each area and season, species that correlated (Spearman's coefficient) more than 60% with one of the first two axes were plotted in each PCO. Simultaneously, the same density matrices used for the PCO were analysed using a two-way permutational ANOVA (PERMANOVA) designed using the same layout as the ANOVA. The contribution of each taxon to the similarity and dissimilarity found among the groups was assessed using the SIMPER (similarity percentage) routine. A 5% significance level was considered in all analyses.

## Results

### Environmental parameters

Precipitation was much higher during the rainy season month (June), whereas the air and sediment temperatures and the salinity were higher during the dry season (Table 1). Overall, temperatures were higher in area 2 (control) in comparison with area 1 (with *D. cuprea* tubes). The sediment in area 1 was classified as fine sand, with some finer sediments (silt and clay) in both months, whereas in area 2, the sediment was classified as fine to medium sand in June (rainy season) and medium sand in the dry season (Table 1).

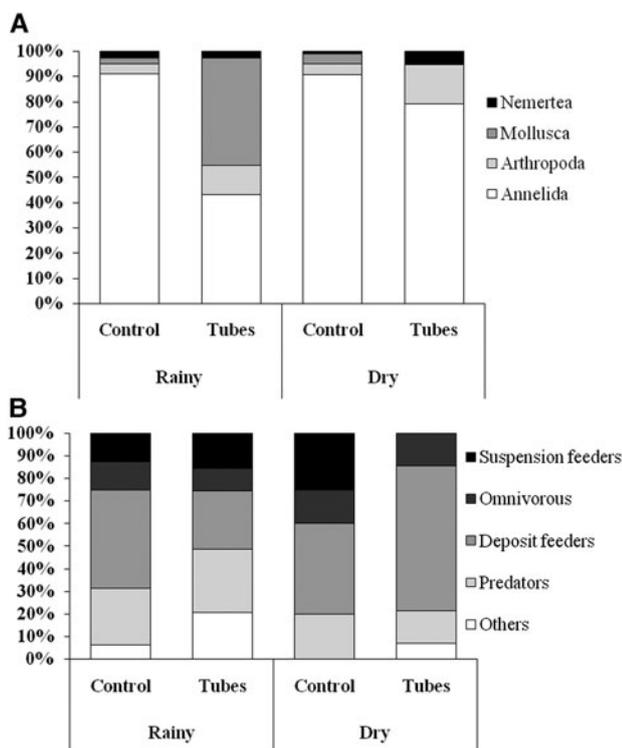
### Macrofauna

The mean density of *D. cuprea* was 69.6 ± 14.4 ind. m<sup>-2</sup> in the rainy season and 38.0 ± 13.3 ind. m<sup>-2</sup> in the dry season, although there was no significant difference between seasons (ANOVA,  $F_{(1,38)} = 2.59$ ,  $P = 0.11$ ). Fifty-three macrobenthic taxa (excluding *D. cuprea*) were recorded during the present study, of which 26 were found exclusively in area 1 (with *D. cuprea* tubes), and 12 exclusively in area 2 (control) (Supplementary Material 1). The Annelida was the phylum represented by the largest number of taxa (23), and was the most abundant group in both areas in both seasons (Figure 2), with *Orbinia* sp. (20% of total abundance) being most abundant.

Molluscs and arthropods were recorded at higher densities in area 1, in particular during the rainy season. In the dry season, molluscs were less abundant in area 1 and more abundant in area 2 (Figure 2A). With regard to the contribution of the feeding guilds to total abundance, deposit-feeders dominated the trophic web in both areas, in particular during the dry season (Figure 2B). A greater diversity of functional groups was recorded in area 1 during the rainy season, in comparison with both the dry season in area 1, and both months in area 2. An increase in deposit-feeders and a marked decrease in suspension feeders were observed in area 1 in the dry season (Figure 2B).

The mean macroinvertebrate densities and total number of taxa varied significantly among areas and seasons. The ANOVA indicated a significant interaction between site and month for both taxon richness ( $F_{(1,76)} = 46.23$ ;  $P = 0.00$ ) and density ( $F_{(1,76)} = 18.72$ ;  $P = 0.00$ ). In the rainy season (Figure 3), the taxon richness and density were higher in area 1 (1525.32 ± 343.29 ind. m<sup>-2</sup>; 38 taxa) than in area 2 (506.33 ± 126.58 ind. m<sup>-2</sup>; 17 taxa). The opposite pattern was observed during the dry season, however, when diversity and density were both higher in area 2 (1436.71 ± 170.88 ind. m<sup>-2</sup>; 22 taxa), in comparison with area 1 (607.59 ± 122.03 ind. m<sup>-2</sup>; 16 taxa). The results of Tukey's test indicated that significant differences between areas in these parameters occurred only during the rainy season, and that significant differences between seasons were recorded in both areas (Figure 3).

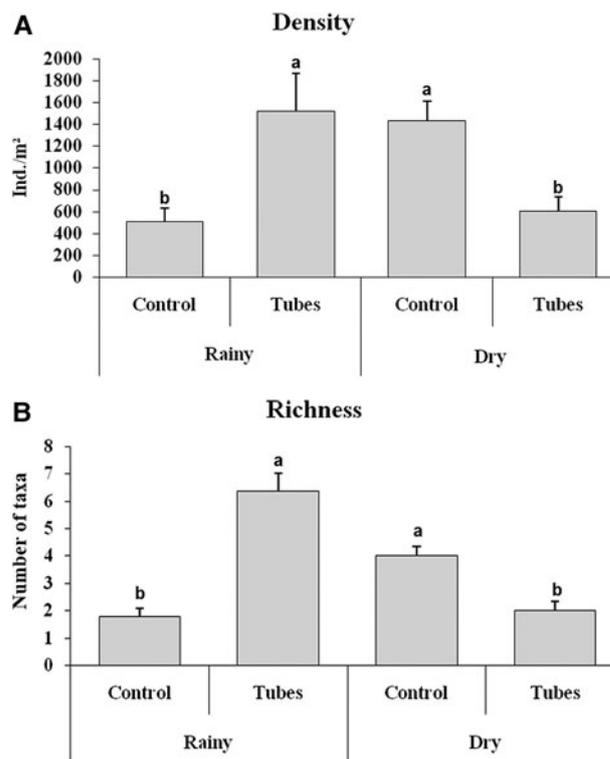
The PCO plots distinguished the macrofauna samples between the two study areas and seasons (Figure 4A). In the rainy season



**Fig. 2.** Relative abundance (%) of taxonomic (A) and feeding groups (B) of the macrobenthic fauna of the two sampling plots in the two study months. (N = 20 samples by area/season).

(Figure 4B), axis 1 explained 24.3% of the variation in the data and was responsible for separating the two areas. The species most correlated with this axis were more abundant in area 1, including the hermit crab, *Clibanarius symmetricus* (Randall, 1840), the molluscs *Leukoma pectorina* (Lamarck, 1818), *Mytella guyanensis* (Lamarck, 1819), *Phrontis vibex* (Say, 1822) and *Littoraria angulifera* (Lamarck, 1822), as well as the polychaetes *Nephtys simoni* (Perkins, 1980) and *Laeonereis culveri* (Webster, 1879). In the dry season (Figure 4C), axes 1 and 2 explained 39.2% and 14.6% of the variation in the data, respectively, with the samples of the two areas grouping in opposite directions along each axis. The species most associated with area 1 were the isopod *Excirrolana armata* (Dana, 1853), the worms *Sigambra* sp. and *Mediomastus* sp. and the Nemertea. By contrast, the polychaetes *Armandia* sp., *Nephtys simoni* and *Orbinia* sp. were most closely associated with area 2. The PERMANOVA confirmed the spatial configuration of the samples, showing significant differences between seasons and areas (Table 2).

The SIMPER analysis indicated a mean dissimilarity of more than 90% between areas in both months. The dissimilarity between seasons was also high (>80%) in both areas (Table 3). Most of the species highlighted by the SIMPER were those most closely correlated with the PCO axes. Comparing sites, most of the species indicated by SIMPER were more abundant in area 1 during the rainy season, in particular polychaetes (*N. simoni* and *Nereis* sp.), molluscs – *Olivella minuta* (Link, 1807), *P. vibex* and *M. guyanensis* – and *C. symmetricus*. In the dry season, polychaetes (*Orbinia* sp., *Armandia* sp. and *N. simoni*) contributed more than 40% of the dissimilarity, and were more abundant in area 2 (Table 3). Most of the predominant species found in area 1 (e.g. *Nereis* sp., *C. symmetricus*, *N. simoni*, *Anachis obesa* (Adams, 1845) and *P. vibex*) were more frequent and abundant in this area during the rainy season. In the control area, by contrast, four species (*Orbinia* sp., *Armandia* sp.,



**Fig. 3.** Mean density (ind. m<sup>-2</sup> ± standard error) and taxon richness (B) of the macrobenthic fauna of the two sampling plots in the two study months. (N = 20 samples by area/season).

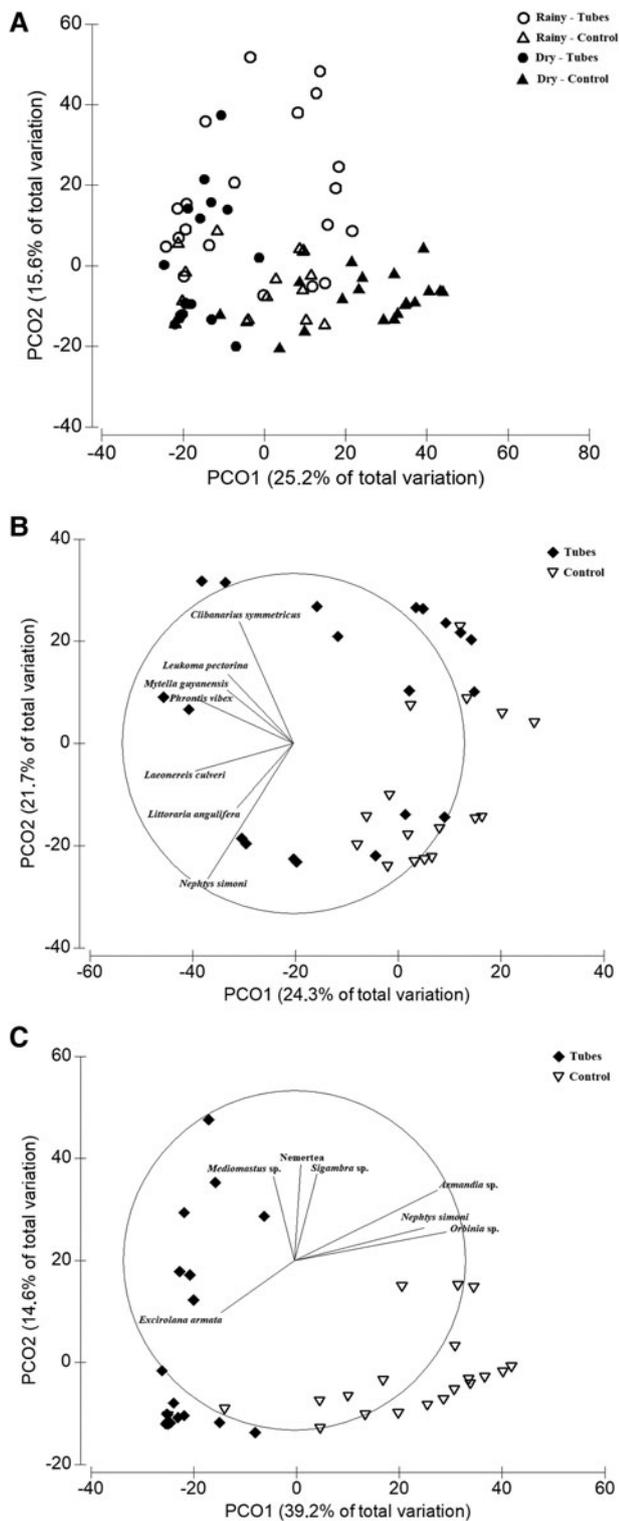
*N. simoni* and *Macoma* sp.) were responsible for more than 55% of the dissimilarity between months, due to their increased frequency and density in the dry season (Table 3).

## Discussion

The dynamics of coastal benthic communities are mediated by a combination of physical, chemical and biological processes. Benthic species are known to be active agents in the interaction between these different components (Berke *et al.*, 2010; Breitburg *et al.*, 2010; Callaway *et al.*, 2010; Woodin *et al.*, 2010). On Algodual-Maiandeuá Island, the presence of *D. cuprea* tubes is associated with fine sediments. The presence of polychaete tubes is known to influence hydrodynamics (Eckman *et al.*, 1981; Callaway, 2006) by reducing the velocity of the near-bottom flow (Friederichs *et al.*, 2000). This may result in an increase in the deposition of fine sediments and the availability of organic matter (Bolan & Fernandes, 2003).

In Amazonian coastal environments, the major seasonal fluctuations in hydrodynamic conditions and fluvial discharge determine shifts in the sediment load and the dispositional patterns of near-shore environments (Jaeger & Nittrouer, 1995; Souza-Filho *et al.*, 2009). While the sampling of sediment in the present study was limited in scope, some variation was observed between months on Farol beach, in particular in area 2, where particles of fine sand were recorded only during the dry season. The granulometry varied much less in area 1, however, which was dominated by fine sediments (silt and clay). Tube-building polychaetes are known to promote greater sediment stability due to near-bed hydrodynamic effects (Luckenbach, 1986; Bolam & Fernandes, 2003).

Dense aggregations of *Diopatra* tubes are commonly found in protected intertidal areas, where organic debris is deposited (Bailey-Brock, 1984; Dagli *et al.*, 2005; Thomsen & McGlathery, 2005). In general, the density of *D. cuprea* recorded in the present



**Fig. 4.** Plots of the Principal Coordinates Analysis (PCO) of the samples of the macrobenthic fauna collected from the two plots in the different study months. The vectors represent species correlating more than 50% (based on Spearman correlation coefficients) with one of the first two PCO axes. (A) All samples (N=80); (B) Dry season samples (N=20 samples per area); (C) Rainy season samples (N=20 samples per area).

study (means of  $69.6 \pm 14.4$  and  $38.0 \pm 13.3$  ind.  $m^{-2}$  in the rainy and dry seasons, respectively) was relatively low in comparison with the values recorded at many other sandy, intertidal flats. In North Carolina, in the USA, for example, Peckol & Baxter (1986) recorded mean densities of *D. cuprea* of between  $76.7 \pm 7.3$  and  $178.3 \pm 6.0$  ind.  $m^{-2}$ , while Mangum *et al.* (1968)

**Table 2.** Results of the PERMANOVA and pairwise tests for the structure of the benthic macrofauna between plots (with and without tubes) and months (dry and rainy season)

Source	df	MS	Pseudo-F	P (perm)
Area (A)	1	15,465	9.76	0.001*
Season (S)	1	12,734	8.03	0.001*
A × S	1	16,789	10.59	0.001*
Res	76	1585		
Total	79			
Groups compared	T	P (perm)		
<i>S × A – Factor ‘Area’</i>				
Rainy: Control vs Tubes	2.52	0.001*		
Dry: Control vs Tubes	3.88	0.001*		
<i>S × A – Factor ‘Season’</i>				
Tubes: Rainy vs Dry	2.76	0.001*		
Control: Rainy vs Dry	3.48	0.001*		

\*Significant differences ( $P < 0.05$ ).  
df, degrees of freedom; MS, mean squares.

recorded a density of  $101.3 \pm 19.1$  ind.  $m^{-2}$ . The density of *D. cuprea* recorded in the present study is also lower than the densities recorded for other species of the genus, such as *Diopatra leuckarti* Kinberg, 1865, which reached  $21,800$  ind.  $m^{-2}$  in a narrow sediment band adjacent to a sandy beach in the Niu Valley in Hawaii (Bailey-Brock, 1984), and *Diopatra marocensis* Paxton, Fadlaoui & Lechapt, 1995, with a density of  $90$  ind.  $m^{-2}$  being recorded by Çinar *et al.* (2014) in Mersin Bay in Turkey, at depths of 4 m (river mouth) and 25 m, in a lagoon. However, Thomsen *et al.* (2011) recorded a density of only  $2.7$  ind.  $m^{-2}$  for *Diopatra* spp. at two sandy beaches in Mozambique.

On Algodoal-Maiandeu Island, the tubes were typically scattered widely in the intertidal zone, which is probably due to the intense hydrodynamics of the local macrotidal beaches, which may prevent the development of denser aggregations. This is supported by the fact that a lower density of *D. cuprea* was recorded during the dry season (September), when hydrodynamics are more intense, due to the stronger easterly trade winds (Pereira *et al.*, 2009) and the strong tidal currents (Pereira *et al.*, 2012) typically found on Amazonian beaches during this season. Mangum *et al.* (1968) found that the population density of *D. cuprea* is related only weakly to the particle size of the substrate, but is correlated strongly with current velocity. While higher current speeds may benefit the feeding mode of *Diopatra* (Mangum *et al.*, 1968), it is possible that very fast currents will have a negative impact on the physical structure of the tubes, as discussed below.

While many studies have compared bare sediments with high-density tube aggregations, the results of the present study indicated that more scattered *Diopatra* tubes may also influence invertebrate communities. In this study on Algodoal-Maiandeu Island, the area with the *D. cuprea* tubes generally had a more diverse and abundant fauna. Similar findings have been obtained for the fauna associated with dense aggregations of *D. cuprea* and *Lanice conchilega* (Pallas, 1766) in the North Atlantic (e.g. Woodin, 1978; Bell & Coen, 1982a, 1982b; Callaway, 2003; Van

**Table 3.** The results of the SIMPER analysis, showing the means abundance (ind. m<sup>-2</sup> ± standard error) and similarity of the species that most contributed the samples from the two plots (in the different study months)

Comparison: Control × Tubes	Average abundance (ind. m <sup>-2</sup> )		Contrib%	Cum.%
	Control	Tubes		
Rainy Average dissimilarity = 91.3%				
<i>Nephtys simoni</i>	2531.6 ± 164.3	2658.2 ± 176.5	14.88	14.88
<i>Nereis</i> sp.	1012.7 ± 176.2	3544.3 ± 257.8	14.08	28.96
<i>Laeonereis cuvieri</i>	3417.7 ± 495.0	2784.8 ± 235.6	7.01	35.96
<i>Clibanarius symmetricus</i>	126.6 ± 28.3	2911.4 ± 193.8	6.72	42.69
<i>Olivella minuta</i>	–	886.1 ± 95.2	4.90	47.59
<i>Nassarius vibex</i>	–	253.2 ± 39.0	4.09	51.67
<i>Mytella guyanensis</i>	253.2 ± 39.0	759.5 ± 92.7	3.85	55.52
Dry				
Average dissimilarity = 94.36				
<i>Orbinia</i> sp.	15443.0 ± 540.0	379.7 ± 61.9	19.53	19.53
<i>Armandia</i> sp.	4303.8 ± 229.0	126.6 ± 28.3	12.78	32.31
<i>Nephtys simoni</i>	3291.1 ± 148.6	–	12.15	44.46
<i>Mediomastus</i> sp.	1265.8 ± 166.8	4557.0 ± 567.0	6.50	50.96
Nemertea sp.	253.2 ± 39.0	632.9 ± 69.6	4.35	55.30
<i>Sigambra</i> sp.	379.7 ± 61.9	1139.2 ± 145.1	3.79	59.10
Comparison: Rainy × Dry				
Control	Rainy	Dry	Contrib%	Cum.%
Average dissimilarity = 84.87				
<i>Orbinia</i> sp.	379.7 ± 61.9	15443.0 ± 540.0	22.82	22.82
<i>Armandia</i> sp.	2531.6 ± 164.3	3291.1 ± 148.6	14.69	37.51
<i>Nephtys simoni</i>	2531.6 ± 164.3	3291.1 ± 148.6	13.56	51.07
<i>Macoma</i> sp.	–	1012.7 ± 103.9	4.36	55.43
<i>Laeonereis cuvieri</i>	3417.7 ± 495.0	126.6 ± 28.3	4.30	59.73
Tubes	Rainy	Dry	Contrib%	Cum.%
Average dissimilarity = 94.95				
<i>Nereis</i> sp.	3544.3 ± 257.8	253.2 ± 39.0	9.78	9.78
<i>Clibanarius symmetricus</i>	2911.4 ± 193.8	1265.8 ± 176.6	8.13	17.91
<i>Nephtys simoni</i>	2658.2 ± 176.5	–	7.08	24.99
<i>Laeonereis cuvieri</i>	2784.8 ± 235.6	–	5.38	30.37
<i>Mediomastus</i> sp.	–	4557.0 ± 567.0	4.53	34.90
Nemertea sp.	759.5 ± 92.7	632.9 ± 69.6	4.49	39.39
<i>Olivella minuta</i>	–	886.1 ± 95.2	4.13	43.52
<i>Leukoma pectorina</i>	3544.3 ± 507.0	–	3.42	46.94
<i>Capitella capitata</i>	126.6 ± 28.3	1012.7 ± 111.7	3.16	50.10

Hoey *et al.*, 2008; Thomsen *et al.*, 2010), as well as for *D. cuprea* in Brazil (Guilherme *et al.*, 2011). Previous studies have shown that even solitary tubes in low-density landscapes may have strong effects on the invertebrate community (Callaway, 2006; Thomsen *et al.*, 2011), although on a much smaller spatial scale. In addition to their influence on hydrodynamics and the texture of the substrate, solitary tubes may increase the complexity and heterogeneity of habitats, facilitating the establishment of a more diverse and abundant macrobenthic community (Rabaut *et al.*, 2007; Toupoint *et al.*, 2008).

While there are obvious limitations to the comparison of regions and/or habitats, the composition of the macrofauna

associated with *D. cuprea* on Algodoal-Maiandeuá Island was similar to that found in association with *D. cuprea* and *L. conchilega* in temperate habitats (e.g. Callaway, 2006; Van Hoey *et al.*, 2008; Callaway *et al.*, 2010; Thomsen *et al.*, 2010). The fauna was composed primarily of estuarine and marine taxa, such as crustaceans, polychaetes and molluscs, in addition to taxa typically found on sandy beaches (Rosa Filho *et al.*, 2009, 2011), in muddy environments (Rosa Filho *et al.*, 2006; Beasley *et al.*, 2010; Braga *et al.*, 2011, 2013), and on consolidated substrate (Morais & Lee, 2013) of the Amazon coast. For example, the molluscs, which were more diverse in the area with *D. cuprea* tubes, were represented primarily by species not normally found on sandy beaches,

but in usually on hard substrates, such as rocks, mangrove roots and other biogenic materials. These taxa include *Mytella* spp., *Littoraria angulifera* (Lamarck, 1822), *Littoraria flava* (King, 1832), *Hiatella* sp., *Sphenia* sp. and *Thaisella coronata* (Lamarck, 1816) (Beasley *et al.*, 2010).

The *Diopatra* tubes provide a wider range of infaunal niches, including mud, detritus, algae, and various types of infaunal prey (Lana *et al.*, 1991; Attolini *et al.*, 1997; Flynn *et al.*, 1998). The aggregation of organisms with different life strategies results in an increase in both the taxonomic and functional richness of the benthic assembly. However, while other studies typically have a broader spatial comparative perspective – i.e. multiple environments with colonies of *Diopatra* vs mud flats with no tubes – the design of the present study, which only compared a single area with and without tubes on the same beach, is limited to a more local scale.

A significant increase in abundance and taxon richness of the samples associated with *D. cuprea* was recorded only in the rainy season, when tube density was higher. The temporal variation of the macrofauna in the two areas also followed a different pattern. Whereas the density and diversity of the macrofauna were higher in the rainy season in the area colonized by *D. cuprea*, the values in the control area were higher in the dry season. As in other Amazonian coastal environments, this may be related to an increase in salinity, since the significant decrease in salinity in the rainy season causes physiological stress to marine organisms (Beasley *et al.*, 2005; Rosa Filho *et al.*, 2011; Silva *et al.*, 2011; Braga *et al.*, 2013). In addition, the more intense hydrodynamic conditions and the resuspension of sediments during the dry season may have a negative effect on the *D. cuprea* population and its associated fauna.

The *D. cuprea* tubes display two types of construction, those constructed only of mucous and sand particles, and those reinforced with debris, primarily in the external section, that rises above the sediment surface (Myers, 1972; Berke & Woodin, 2008). The incorporation of items reflects the diversity of the available substrates and surface debris (Bell & Coen, 1982a), and the tubes of this species may be ornamented with shells, algae or assorted debris (Mangum *et al.*, 1968). On Algodão-Maiandea Island, however, the tubes are relatively simple, being decorated primarily with small fragments of plants. The complexity of the tube is further reduced during the dry season, as a result of the increased physical disruption, and perhaps also the greater difficulty of obtaining and incorporating materials under the stronger hydrodynamic conditions typical of this period. In the dry season, in fact, the tubes may often be buried (personal observation), and the restructuring process may have a negative effect on the presence of other organisms, in particular those that inhabit the reinforced portion of the tube, such as epifaunal molluscs and polychaetes, which are practically absent during this season.

As the samples were taken from different areas of the same beach, certain components of the natural variation in the characteristics of the community may not have been evaluated comprehensively, and this should be taken into account in future studies of the role of *D. cuprea* tubes in the ecology of the region. The exact influence of environmental variables on the populations of this bioconstructor and the characteristics of its tubes, and its effects on the associated fauna, require further investigation. In general, however, the results of the present study are consistent with those of previous research, which found changes in the composition of the benthic macrofauna, that is, higher species richness and densities of fauna in areas inhabited by these tube-building polychaetes in comparison with areas of bare sand, even though *D. cuprea* was sparsely distributed on the study beach.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315418000711>

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