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ARTICLE

Macrobenthic community of an estuarine tidal flat on the Amazon coast: spatial variations and presence of polychaetes tubes

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Abstract. The present study characterized the macrobenthic fauna found on a muddy-sandy tidal flat of the Amazon coast in areas with and without the presence of *Diopatra cuprea* (Bosc, 1802) (Onuphidae: Annelida) tubes. In addition, a brief review of records of *D. cuprea* on the Brazilian Amazon coast is presented. Samples were collected in February 2014 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 21 taxa were found, of which 10 were associated exclusively with *D. cuprea* tubes. Although richness did not vary significantly among areas, there were changes in the abundance and composition of species and trophic guilds. In the area with tubes, there was a higher abundance of filter-feeders and the presence of species adapted to consolidated and muddy substrates. Our results and those of other studies indicate that *D. cuprea* commonly presents low density in the Amazon coastal, and its tubes are typically scattered widely in the intertidal zone. The present findings add knowledge about the presence of the bioconstructor in coastal areas and reinforce the role of tube-building polychaetes as ecosystem engineers.

Keywords. *Diopatra cuprea;* Ecosystem engineers; Macrotide; Soft-bottom; Tropical region.

INTRODUCTION

Numerous marine habitat-formers build external physical structures such as shells or tubes that can provide space and shelter from predators (Giangrande *et al.,* 2020). In soft-bottom habitats, tube-building polychaetes represent an important group of marine organisms that build such external structures. The polychaete tubes can be made from several different materials (*e.g.,* mud, sand, shell, sandstone) and are known to influence near-bed hydrodynamics (Jumars & Nowell, 1984), stabilizing the sediments (Bolam & Fernandes, 2003). Moreover, 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). For these reasons, several tube-building polychaetes are designated as ecosystem engineers: organisms capable of modifying the environment by mechanically transforming materials from one state to another, resulting in marked alterations of the distribution of other species (Jones *et al.,* 1994, 2010).

Diopatra cuprea (Bosc, 1802) is a tubicolous species that occurs in coastal waters between Cape Cod and Brazil (Mangum *et al.,* 1968). This species inhabits protected mud and sand flats from the low-tide line to water up to 80 m, building vertical tubes, which typically penetrate the substratum to a depth of 50-60 cm (Myers, 1972). Overall, the construction of these tubes on soft bottoms may influence the structure of the benthic communities, such as the meiofauna (Bell & Coen, 1982a, b; Bell & Woodin, 1984; Bell, 1985; Guilherme *et al.,* 2011) and macrofauna (Woodin, 1978; Thomsen *et al.,* 2011; Santos & Aviz, 2018), as well as the bacteria (Phillips & Lovell, 1999; Matsui *et al.,* 2004) and algae (Thomsen, 2004; Thomsen *et al.,* 2009). In general, there is a positive influence on the species richness and abundance of the fauna associated with these tubes (Santos & Aviz, 2018).

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The literature on the fauna associated with polychaetes tubes is impressive, especially regarding the temperate latitudes where they are widespread (*e.g.,* Woodin, 1978; Bell & Coen, 1982a, b; Callaway, 2003; Dubois *et al.,* 2006; Thomsen *et al.,* 2011; Jones *et al.,* 2018). However, unlike intertidal habitats at temperate latitudes, there are few studies regarding the fauna associated with polychaetes tubes in tropical regions (*e.g.,* Fournier, 2010; Guilherme *et al.,* 2011; Ataide *et al.,* 2014; Aviz *et al.,* 2018, 2021; Lane-Medeiros *et al.,* 2021). In addition, there is virtually no data from tropical regions, especially for the Amazon coast, about studies regarding the fauna associated with *D. cuprea* tubes, even though this species is common in intertidal estuarine areas and protected beaches of the region (Santos & Aviz, 2018), thus providing limited information on community structure in Amazon coastal areas. In this region, studies on benthic communities have been limited to record this species, with only one study on the effect of the bioconstructor on local biodiversity (Santos & Aviz, 2018).

Tidal flats are distributed widely along the world's coastline, typically in association with estuaries or other coastal environments (*e.g.,* lagoons and bays) (Dyer *et al.,* 2000). These environments are formed in areas where there is a sufficient supply of fine-grained sediment and gentle bed slopes (Gao, 2019). In addition, these environments are characterized by relatively strong tidal currents, resulting in high mobility of bed materials (Black *et al.,* 2002; Gao, 2019). The Amazon coastal region is dominated by tidal flat systems that extend for almost 480 km (Kjerfve & Lacerda, 1993), and are influenced by unique conditions, such as macrotidal regime (> 4 m), high river discharge, and rainfall regime, the latter characterized by two contrasting periods, which lead to marked salinity variation (Dittmar & Lara, 2001; Souza-Filho *et al.,* 2009; Pereira *et al.,* 2012). Under such conditions, the intertidal benthic macrofauna of the soft-bottom habitats is known for its remarkable spatial and seasonal variations (Rosa-Filho *et al.,* 2018; Venekey *et al.,* 2019; Danin *et al.,* 2020; Baia *et al.,* 2021).

Therefore, this study aimed to investigate the effects of *D. cuprea* tubes on macrobenthic fauna found on a tidal flat area. The tested hypothesis was that the presence of tubes contributes to the establishment of a macrobenthic assemblage distinct, in terms of composition, abundance and functional structure from that found on sediments with no tubes. In addition, a brief review of records of *D. cuprea* on the Brazilian Amazon coast is presented.

MATERIAL AND METHODS

Study area

This study was conducted on a tidal muddy-sandy flat located in the estuary of the Piriá river (00°59′26.11″S, 46°11′08.73″W) (Fig. 1A) in the city of Vizeu (northeast Pará, Brazil). The Piriá river is part of the Gurupi-Piriá Marine Extractive Reserve and covers an area of 74,081 ha distributed in mangrove ecosystems and marine area (ICMBio, 2010). The Reserve is surrounded by the Araí-

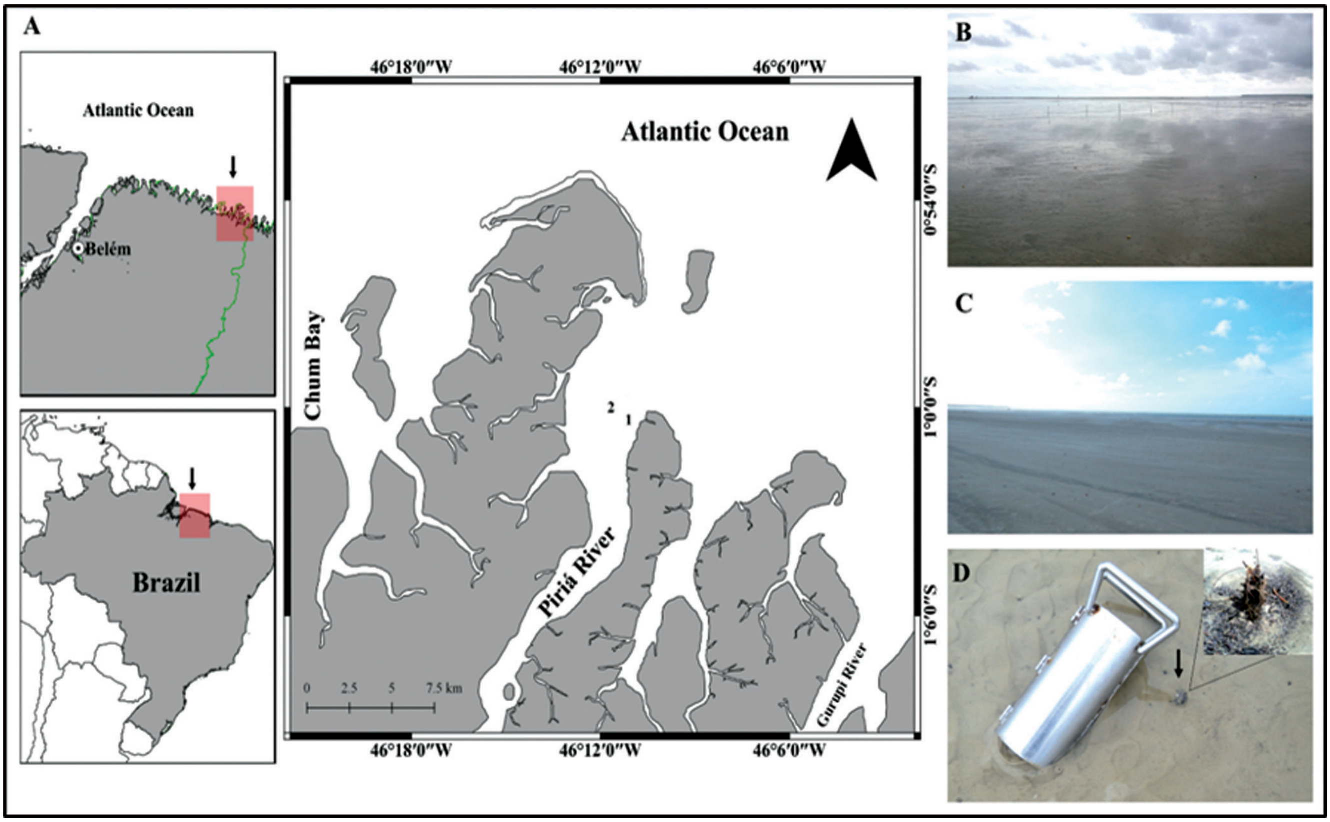

Figure 1. Map of the Piriá river estuary showing the study area (A); Area 1 (B); Area 2 (C); exposed portion of a *Diopatra cuprea* tube found in the study area and metallic sampler (D).

Peroba Marine Extractive Reserve to the west and the Reentrâncias Maranhenses Environmental Protection Area in the state of Maranhão to the east.

The region is dominated by semidiurnal macrotides and the amplitude may reach more than 5 m (Souza-Filho *et al.,* 2009). The climate is humid tropical with a mean annual temperature of 27.7 ± 1.1°C (Martorano *et al.,* 1993) and annual rainfall (30-year series) ranging from 2,200 to 2,800 mm (Moraes *et al.,* 2005). Rainfall rates vary considerably over the year, with a well-marked rainy season from January to July, with total precipitation of ~ 1,657 mm, and a dry season from August to December, with total rainfall of 490 mm (Moraes *et al.,* 2005).

Sampling and laboratory procedures

Samples were collected in February 2014 (rainy season) from two different areas (equidistant ~ 400 m) of the tidal muddy-sandy flat during the low tide, each with an area of ~ 50 m^2, at the same distance from the tideline. One of these areas was populated with *D. cuprea* tubes (area 1) (Fig. 1B), whereas the other had no visible tubes (area 2) (Fig. 1C). Ten replicate samples were collected in each area using cylindrical cores (0.0079 m^2, 20 cm deep) (Fig. 1D). In area 1, the corer was positioned so that a single *D. cuprea* tube (Fig. 1D) stood in its center. The samples were filtered through a 0.3 mm mesh screen, and all the macrofauna was retrieved and fixed in 4% saline formalin. To estimate the density of *D. cuprea* within area 1, the number of tubes were counted in five distributed square subplots (25 m^2).

In the laboratory, the organisms were examined under a stereoscopic microscope, counted, and identified to the lowest possible taxonomic level based on Amaral & Nonato (1996), Melo (1999), Amaral *et al.,* (2006), de León-González *et al.,* (2009) and Rios (2009). Macrofauna was further classified into functional groups, considering feeding habits (predator/carnivore, suspensivores, depositive, detritivore and omnivore), based on the primary literature (*e.g.,* Fauchald & Jumars, 1979; Dauby, *et al.,* 2001; De Broyer *et al.,* 2003; Macdonald *et al.,* 2010). Voucher specimens were deposited in the collections of the Museu Paraense Emílio Goeldi (catalog numbers: MPEG.MOL 003415-003417; MPEG.ANL 002684-002696; MPEG.CRU 003500-003502).

Statistical analysis

We calculated the total taxon richness and abundance for each biological sample, and, to compare variation in these parameters in areas with and without tubes, the generalized linear models (GLM) based on Poisson distributions was used, appropriate to analyze count data. The GLM was implemented with the package of R statistical software (version 3.3.0) (Warton *et al.,* 2012). Principal Coordinates Analysis (PCO) was run on a Bray-Curtis similarity matrix of the fourth root-transformed species and functional groups abundance data, to explore and visualize the similarity between samples across areas. To identify the species/functional groups that characterized each area, those correlated (Spearman's coefficient) more than 50% with one of the first two axes were plotted in each PCO. To test differences in assemblage composition (taxonomic and functional groups) among areas, we applied a permutational multivariate analysis of variance (PERMANOVA), using the same similarity matrix.

RESULTS

The mean density of *D. cuprea* tubes recorded at area 1 was 37.9 ± 12.1 ind./m^2. Twenty-one macrobenthic taxa (excluding *D. cuprea*) were recorded during the present study, of which 10 were found exclusively in area 1 (with *D. cuprea* tubes), and three exclusively in area 2 (without tubes) (Table 1). The Annelida (polychaetes) was represented by the largest number of taxa (13) and the most abundant group in both areas (Fig. 2A). Among these, *Magelona* sp. (13.1% of total abundance) was the most abundant taxa at area 1, and *Nephtys simoni* (Perkins, 1980) (18.6%) and *Thoracophelia papillata* (Santos, Nonato & Petersen, 2004) (15.2%) were the most abundant at area 2. Mollusks (bivalves and gastropods) and arthropods were recorded at higher abundance in area 1. A lower abundance of mollusks was observed in area 2, with an absence of gastropods (Fig. 2A).

Regarding the contribution of the feeding guilds to total abundance, deposit-feeders dominated the trophic web in both areas. However, differences were found in the abundance of the other groups. A higher abundance

Table 1. Mean abundance (ind./0.0079 m^2 ± SE) of the benthic macrofauna found in the study areas (Area 1: With *Diopatra cuprea* tubes; Area 2: Without tube) with their trophic group.

Taxa	Area 1	Area 2	Trophic Guild
Nemertea	0.2 ± 0.1		Predator
Bivalve sp. (B)	0.1 ± 0.1.7		Suspension/filter feeder
Mytella guyanensis (B)	0.3 ± 0.1		Suspension/filter feeder
Donax striatus (B)	0.4 ± 0.1	0.3 ± 0.1	Suspension/filter feeder
Olivela minuta (G)	0.3 ± 0.1		Omnivore
Diopatra cuprea (A)	0.3 ± 0.1		Omnivore
Hemipodia sp. (A)		0.4 ± 0.1	Predator/Carnivores
Glycera sp. (A)		1.6 ± 0.7	Predator/Carnivores
Nephtys simoni (A)	0.4 ± 0.2	1.1 ± 0.3	Predator/Carnivores
Eteone sp. (A)	0.1 ± 0.1	0.5 ± 0.3	Predator/Carnivores
Thoracophelia papillata (A)	0.8 ± 0.4	1.7 ± 0.7	Deposit feeder
Armandia sp. (A)	0.2 ± 0.2	1.1 ± 0.4	Deposit feeder
Sigambra grubii (A)	0.6 ± 0.3		Omnivore
Scolelepis squamata (A)	0.1 ± 0.1	0.8 ± 0.3	Deposit feeder
Capitella spp. (A)	0.7 ± 0.3		Deposit feeder
Mediomastus sp. (A)	0.3 ± 0.2		Deposit feeder
Nereis sp. (A)	0.1 ± 0.1	2.1 ± 1.2	Omnivore
Magelona sp. (A)	0.5 ± 0.2		Deposit feeder
Phoxocephalidae (Cr)	0.6 ± 0.4	1.1 ± 0.5	Detritive scavengers
Cyprideis sp (Cr)	0.3 ± 0.1	0.5 ± 0.2	Suspension/filter feeder
Brachyura (Zoea) (Cr)	0.1 ± 0.1		—
Mysida sp. (Cr)		0.2 ± 0.1	Omnivore

* Taxa: A = Annelida; B = Bivalvia; G = Gastropoda; Cr = Crustacea.

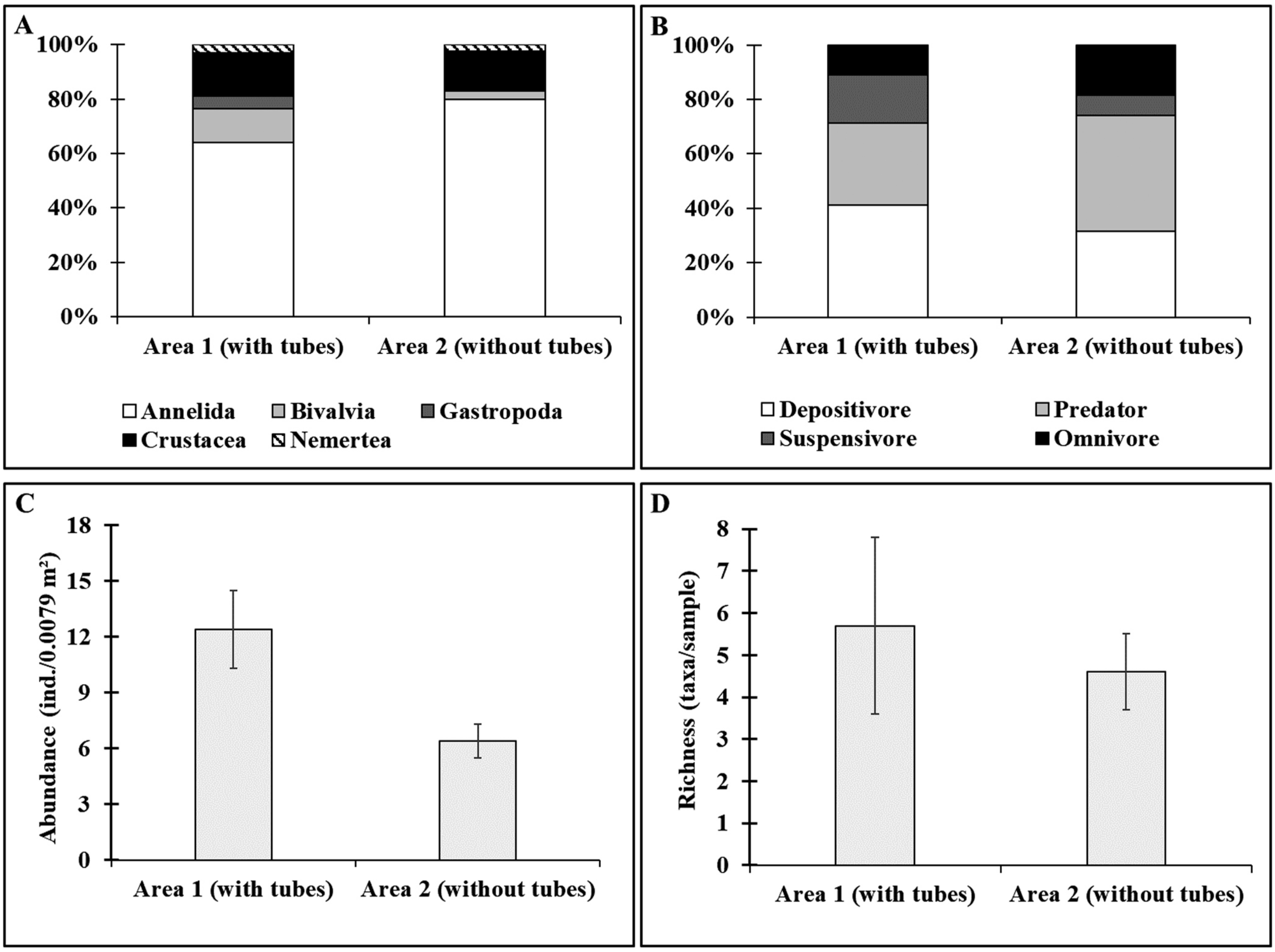

Figure 2. Relative abundance (%) of taxonomic (A) and feeding groups (B); mean abundance (± standard error) (C) and taxon richness (D) of the macrobenthic fauna of the two sampling plots in the study area.

of suspension/filter feeders occurred at area 1. By contrast, omnivores and predators were more abundant in area 2 (Fig. 2B). The mean macroinvertebrate abundance ($F_{1,18}$: 4.35; $p < 0.01$) vary significantly among areas, however, no difference was found to richness ($F_{1,18}$: 2.0; $p = 0.18$). In both cases, the highest values were found in area 1 (Figs. 2C, 2D).

The PCO plots distinguished the macrofauna samples between the two study areas (Fig. 3). Regarding species, axis 1 explained 28.8% of the variation in the data and was responsible for separating the two areas. The species most correlated with area 1 samples were gastropod *Olivela* sp. and the polychaetes *Capitella* spp. and *Magelona* sp. In contrast, the species most associated with area 2 were the amphipod Phoxocephalidae and polychaetes *T. papillata* and *Glycera* sp. Axis 2 also associated samples from area 1 with the bivalve *Mytella guyanensis* (Lamarck, 1819). Using the trophic functional groups, the PCO had greater explanatory capacity, with axis 1 explained 72.3% of the variation in the data. The groups best correlated with this axis were predators (most correlated with area 2) and suspension feeder (most correlated with area 1). The PERMANOVA confirmed the spatial configuration of the samples, showing significant differences for species ($F = 2.4$; $p = 0.021$) and functional ($F = 4.2$; $p = 0.027$) composition between areas.

DISCUSSION

In the study area, the *D. cuprea* tubes were typically scattered widely in the intertidal zone and the extrapolated density recorded (37.9 ind./m^2) was relatively low in comparison with the values at many other intertidal flats (mean densities between 76.7 and 178.3 ind./m^2) (Peckol & Baxter, 1986; Mangum *et al.,* 1968), but close to that found on beaches (mean 42.5 to 53.8 ind./m^2) (Rosa-Filho *et al.,* 2009; Santos & Aviz, 2018) and other Amazon soft-bottom habitats (mean 5.3 to 10.6 ind./m^2) (Table 2). The species prefers sandy and muddy-sandy substrates, with no records in the essentially muddy sediments (Table 2). Dense aggregations of *Diopatra* tubes are commonly found in protected intertidal areas, where organic debris are deposited (Bailey-Brock, 1984; Dagli *et al.,* 2005; Thomsen & McGlathery, 2005). 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), fast currents may harm the physical structure of the tubes, as well as their density. In fact, the low density of *D. cuprea* found on Amazon coastal is probably due to the intense hydrodynamics of the local estuaries (Santos & Aviz, 2018). Overall, the Amazonian

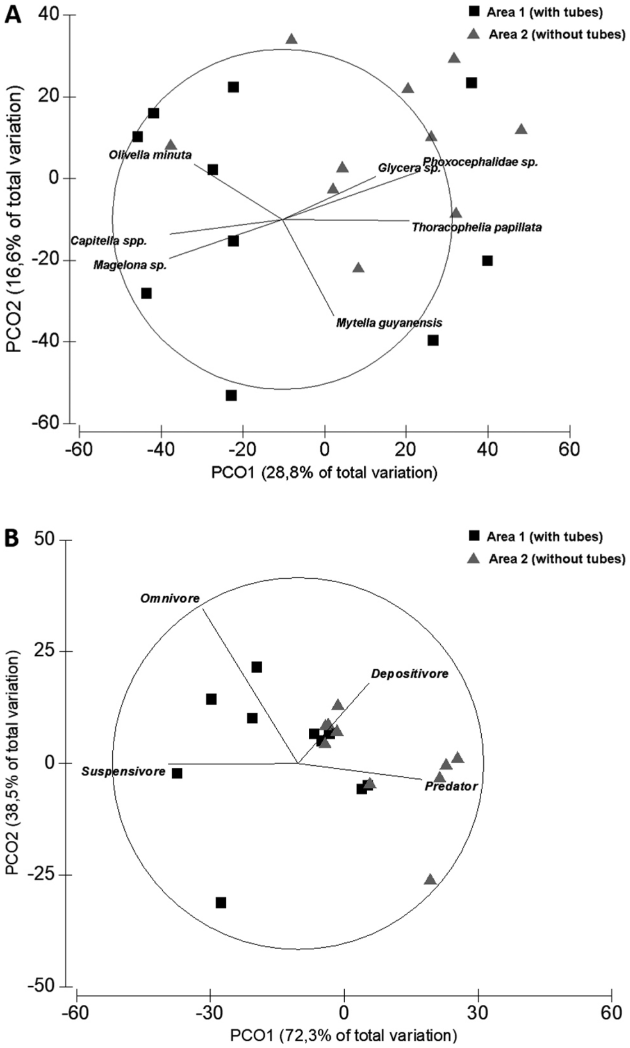

Figure 3. Principal Coordinates Analysis (PCO) of the samples of the macrobenthic fauna considering the (A) taxonomic composition and (B) functional group. The vectors represent species/groups correlating more than 50% (based on Spearman correlation coefficients) with one of the first two PCO axes.

estuaries are dynamic environments formed by the interaction of waters from the Amazon River and its tributaries with waters of the Atlantic Ocean, and these enormous discharges of water dictate unusual and strong hydrodynamic patterns (Nittrouer & Demaster, 1996).

While many studies have compared bare sediments with high-density polychaetes tubes aggregations (*e.g.,* Bell & Coen, 1982a, b; Callaway, 2003; Thomsen *et al.,* 2010), previous studies have shown that even in extremely low density, polychaete tubes can have a strong impact on invertebrate communities in various areas (Callaway, 2006; Thomsen *et al.,* 2011; Santos & Aviz, 2018). In general, although at a much smaller spatial scale, sparsely distributed tubes increase the complexity and heterogeneity of habitats, thus promoting the establishment of more diverse and abundant macrobenthic communities (Rabaut *et al.,* 2007; Toupoint *et al.,* 2008). Biologic structures commonly influence the composition and organization of benthic communities, facilitate the occurrence of organisms by offering new habitats, increasing protection against abiotic and predation pressures, or contributing to the availability of food (Bouma *et al.,* 2009; Jones *et al.,* 2010).

The taxonomic composition of the macrofauna in the studied area is similar to other estuarine tidal flats tropical as well as to that found in association with *D. cuprea* and other polychaetes tubes (*e.g., Lanice conchilega* Pallas, 1976) in temperate regions (*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 and other soft bottoms environments on the Amazon coast, with a dominance of polychaete worms, as well as crustaceans and mollusks as common groups. Also, the composition is similar to the composition found in other soft bottoms environments on the Amazon coast such as sandy beaches (Rosa-Filho *et al.,* 2009, 2011; Santos & Aviz, 2018, 2020), in muddy environments (Rosa-Filho *et al.,* 2006; Beasley *et al.,* 2010; Braga *et al.,* 2011, 2013; Santos *et al.,* 2020), in addition to the presence of typical species of hard substrates (Morais & Lee, 2014).

Annelida was the most dominant phylum in both study areas, with polychaetes being the most abundant group. The dominance of annelids on the study areas is probably due to the elongated shape of their bodies, which facilitates burrowing activities in fine sand bottoms (Giangrande & Gambi, 1998); their high tolerance to environmental stress (Dauvin *et al.,* 2016), which allows them to survive in environments with intense hydrody-

Table 2. Records of *Diopatra cuprea* observed in soft bottom environments in the Brazilian Amazon Coast.

Environment	Locality	Coordinates	*D. cuprea* mean density (ind./m^2)	Reference
Tidal flat (muddy-sand bottom)	Piriá River Estuary (Pará, Brazil)	00°59′26.11″S – 46°11′08.73″W	37.97	This study
Sandy beach (muddy-sand bottom)	Algodoal Island (Pará, Brazil)	00°34′45″S – 47°32′05″W	53.8	Santos & Aviz (2018)
Sandy beach (sandy bottom)	Ajuruteua (Pará, Brazil)	46°35′31.2″W – 00°50′19.5″S	42.5	Rosa-Filho *et al.* (2009)
Sandy beach (sandy bottom)	Algodoal Island (Pará, Brazil)	00°34′45″S – 47°32′05″W	—	Rosa-Filho *et al.* (2011)
Sandy beach (muddy-sand bottom)	Algodoal Island (Pará, Brazil)	00°34′45″S – 47°32′05″W	—	Santos & Aviz, 2020
Saltmarsh (muddy-sand bottom)	Algodoal Island (Pará, Brazil)	00°34′45″S – 47°32′05″W	10.6	Braga *et al.* (2011, 2013)
Saltmarsh (muddy-sand bottom)	Canela Island (Pará, Brazil	00°47′20″S – 46°43′63″W	—	Braga *et al.,* 2009
Mangrove (sandy-mud bottom)	Curuça Estuary (Pará, Brazil)	00°43′48″S – 47°51′06″W	5.3	Vasconcelos (2006)
Mangrove (muddy bottom)	Algodoal Island (Pará, Brazil)	00°34′45″S – 47°32′05″W	—	Monteiro (2009)
Mangrove (muddy bottom)	Caeté Estuary (Pará, Brazil)	00°50′19.5″S – 46°38′14.9″W	—	Rosa-Filho *et al.* (2006)
Mangrove (muddy bottom)	Caeté Estuary (Pará, Brazil)	00°50′19.5″S – 46°38′14.9″W	—	Beasley *et al.* (2010)
Mangrove (muddy bottom)	São Luis Island (Maranhão, Brazil)	02°37′27″S – 44°20′36″W	—	Oliveira & Mochel (1999)
Mangrove (muddy bottom)	Maracá Island (Amapá, Brazil)	01°50′54″N – 50°12′00″W	—	Fernandes (2003)

namics (Omena & Amaral, 2003; Purschke, 1981); and their diversity of feeding habits, which allows them to explore a wide range of food resources (Fauchald & Jumars, 1979; Jumars *et al.,* 2015). Also, this dominance is mainly related to the great abundance of *Magelona* sp. at area 1 and *Nephtys simoni* at area 2. The magelonids are common in the muddy sand substrates of intertidal zones and continental shelves (Hartman, 1971; Fauchald & Jumars, 1979). On the other hand, *N. simoni* is commonly found on sandy areas being present in great abundance in areas with granulometry ranging from medium to fine sand (Lana, *et al.,* 1996; Rosa-Filho *et al.,* 2011).

While there are obvious limitations to the comparison of regions and/or habitats, the total number of taxa (21) recorded in the estuary of the Piriá river was lower than that recorded in most studies on the Amazon coast (Table 2). In the present study, this lower richness probably results from two factors: (1) the low spatial and temporal effort of sampling; and (2) the greater instability of the tidal flat, when compared to more protected and/or vegetated environments, such as mangroves and saltmarsh. Tidal flats are highly dynamic environments, with sediments in constant motion through several processes (*e.g.,* transportation, deposition, and erosion), depending on the hydrodynamic characteristics (*e.g.,* tide, waves, and wind) of the local area (Black *et al.,* 2002).

In the present study, although there was no significant increase in richness in the area with tubes, changes in abundance and composition and trophic groups were observed. Although the sedimentary composition of the sediment could not be evaluated in this study, the presence of *D. cuprea* tubes has been associated with an increase in fine sediment, due to reducing the velocity of the near-bottom flow and increase in the deposition (Eckman *et al.,* 1981; Friederichs *et al.,* 2000; Bolam & Fernandes, 2003; Callaway, 2006). Fine, organically rich muds tend to contain more burrowing deposit feeders, whereas coarser sandy sediments typically harbor more mobile animals and predators (Pearson & Rosenberg, 1978). Although, in general, the assemblages of the study area were dominated by deposit feeders, the deposit feeders and filter-feeders were more representatives in area 1 (with tubes), while predators and omnivores in area 2 (without tubes).

The higher abundance of deposit feeders in area 1 was related principally to polychaetes *Magelona* sp., *Capitella* spp. and *Mediomastus* sp. Both magelonids and capitellids are deposit feeders, of surface and sub-surface, respectively, which are common in the muddy sand substrates of intertidal zones and continental shelves (Hartman, 1971; Fauchald & Jumars, 1979). On the other hand, mollusk bivalves were the main responsible for the greater abundance of filter-feeders in area 1. These organisms were represented primarily by species (*e.g., Sphenia* sp. and *Mytella guyanensis*) not normally found on soft bottoms, but on hard substrates, such as rocks, mangrove roots, and other biogenic materials, and in the present study, they were found attached to the *D. cuprea* tubes. Additionally, the gastropod *Olivella minuta* (Link, 1807) occurred exclusively in the area with tubes and was the main responsible for the abundance of omnivores in this area. This gastropod is commonly found in protected environments with finer sediments (Viana *et al.,* 2005) and, although in small scale, in the present study these characteristics would probably be found near the *D. cuprea*. In area 2, higher predator abundance was related principally to *Nephtys simoni,* which prefers fine to medium sand (Lana, 1986; Rosa-Filho *et al.,* 2011).

CONCLUSION

Although the present study presents a small spatial scale and we did not test for temporal effects, its results are consistent with those of previous research, which found changes in the composition of the benthic macrofauna in areas with and without polychaete tubes, even though *D. cuprea* was sparsely distributed on the study area. This conclusion would be reinforced by a broader sampling, which would include a larger number of tubes and areas, larger-scale effects, as well the sedimentary and hydrodynamic parameters. The present findings add knowledge about the presence of the bioconstructor in other types of habitats in the Amazon.

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AUTHORS' CONTRIBUTIONS

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