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).
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 Piria river is part of the Gurupi-Piria 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 Arai.

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 m², at the same distance from the tide line. 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 m², 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 m²).

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./m². 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

| Taxa                | Area 1          | Area 2          | Trophic Group        |
|--------------------|-----------------|-----------------|----------------------|
| Nemertea           | 0.2 ± 0.1       | Predator        |
| Bivalve sp. (B)    | 0.1 ± 0.17      | Suspension/filter feeder |
| Mytilopsis gynanensis (B) | 0.3 ± 0.1 | Suspension/filter feeder |
| Donax striatus (B) | 0.4 ± 0.1       | Suspension/filter feeder |
| Olivella minuta (G) | 0.3 ± 0.1       | Omnivore        |
| Diopatra cuprea (A) | 0.3 ± 0.1      | Omnivore        |
| Hemipoda sp. (A)   | 0.4 ± 0.1       | Predator/Carnivores |
| Glycera sp. (A)    | 1.6 ± 0.7       | Predator/Carnivores |
| Nephtys simoni (A) | 0.4 ± 0.2       | Predator/Carnivores |
| Etoxone sp. (A)    | 0.1 ± 0.1       | Predator/Carnivores |
| Thoracophelia papillata (A) | 0.8 ± 0.4 | Deposit feeder |
| Armadus sp. (A)    | 0.2 ± 0.2       | Deposit feeder |
| Sigambra grubhi (A) | 0.6 ± 0.3     | Omnivore        |
| Scalepsis squamata (A) | 0.1 ± 0.1 | Deposit feeder |
| Capitella sp. (A)  | 0.7 ± 0.3       | Deposit feeder |
| Mediomastus sp. (A) | 0.3 ± 0.2       | Deposit feeder |
| Nepes sp. (A)      | 0.1 ± 0.1       | 2.1 ± 1.2       |
| Magelona sp. (A)   | 0.5 ± 0.2       | Deposit feeder |
| Phoacophila (Cr)   | 0.6 ± 0.4       | Detritive scavengers |
| Gymnodiis sp (Cr)  | 0.3 ± 0.1       | 0.5 ± 0.2       |
| Brachyura (Zoea) (Cr) | 0.1 ± 0.1 | Suspension/filter feeder |
| Mysida sp. (Cr)    | 0.2 ± 0.1       | Omnivore        |

* Taxa: A = Annelida; B = Bivalvia; G = Gastropoda; Cr = Crustacea.
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./m²) was relatively low in comparison with the values at many other intertidal flats (mean densities between 76.7 and 178.3 ind./m²) (Peckol & Baxter, 1986; Mangum et al., 1968), but close to that found on beaches (mean 42.5 to 53.8 ind./m²) (Rosa-Filho et al., 2009; Santos & Aviz, 2018) and other Amazon soft-bottom habitats (mean 5.3 to 10.6 ind./m²) (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
Table 2. Records of Diopatra cuprea observed in soft bottom environments in the Brazilian Amazon Coast.

| Environment                        | Locality                               | Coordinates                  | D. cuprea mean density (ind./m²) | Reference                  |
|------------------------------------|----------------------------------------|------------------------------|--------------------------------|---------------------------|
| Tidal flat (muddy-sand bottom)     | Pará River Estuary (Pará, Brazil)      | 00°59'26.11"S – 46°11'08.73"W | 17.97                          | This study                |
| Sandy beach (muddy-sand bottom)    | Algodoal Island (Pará, Brazil)         | 00°34'45.5"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°34'45.5"S – 47°32'05"W    | —                              | Rosa-Filho et al. (2011)  |
| Sandy beach (muddy-sand bottom)    | Algodoal Island (Pará, Brazil)         | 00°34'45.5"S – 47°32'05"W    | —                              | Santos & Aviz, 2020       |
| Saltmarsh (muddy-sand bottom)      | Algodoal Island (Pará, Brazil)         | 00°34'45.5"S – 47°32'05"W    | 10.6                           | Braga et al. (2011, 2013) |
| Saltmarsh (sandy-bottom)           | Canela Island (Pará, Brazil)           | 00°47'20.5"S – 46°43'63"W    | —                              | Braga et al. (2009)       |
| Mangrove (sandy-mud bottom)        | Curuça Estuary (Pará, Brazil)          | 00°43'48.5"S – 47°51'06"W    | 5.3                            | Vasconcelos (2006)        |
| Mangrove (muddy bottom)            | Algodoal Island (Pará, Brazil)         | 00°34'45.5"S – 47°32'05"W    | —                              | Monteiro (2009)           |
| Mangrove (muddy bottom)            | Caeté Estuary (Pará, Brazil)           | 00°30'19.5"S – 46°38'14.9"W  | —                              | Rosa-Filho et al. (2006)  |
| Mangrove (muddy bottom)            | Caeté Estuary (Pará, Brazil)           | 00°30'19.5"S – 46°38'14.9"W  | —                              | Beasley et al. (2010)     |
| Mangrove (muddy bottom)            | São Luís Island (Maranhão, Brazil)     | 02°37'27.5"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)          |

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., Lance 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., 2006; Beasley et al., 2010). The occurrence of organisms by offering new habitats, in increasing protection against abiotic and predation pressures, or contributing to the availability of food (Bouma et al., 2009; Jones et al., 2010).

Table 2. Records of Diopatra cuprea observed in soft bottom environments in the Brazilian Amazon Coast.
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 representative in area 1 (with tubes), while predators and omnvores 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 omnvores 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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