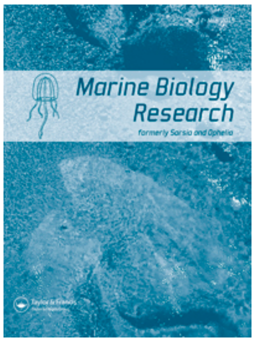

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ORIGINAL ARTICLE

Distribution pattern of zoanthids (Cnidaria: Zoantharia) on a tropical reef

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Abstract
Coastal reef environments support a great diversity of benthic species, which are physically arrayed according to their adaptations to biotic factors such as competition and to abiotic factors such as salinity and desiccation. Few studies have described adaptive strategies on rocky shores in tropical regions. This contribution deals with the spatial distribution of three species of zoanthids (*Palythoa caribaeorum*, *Protopalythoa variabilis* and *Zoanthus sociatus*) on flat sandstone reefs in north-eastern Brazil. Zoanthid distribution and abundances were determined as the percentage of cover along six transects, where 50 × 50 cm quadrats were sampled. Biotic data (influence of macroalgal cover) and abiotic data (relief, substrate type, temperature and salinity) were also taken along the transects to attempt to explain the zoanthid distribution. These species tended to colonize the middle and low intertidal zones, which are least exposed to air. *Zoanthus sociatus* apparently resists desiccation better than *P. caribaeorum. Protopalythoa variabilis* showed the highest abundance and frequency, occurring in the entire middle intertidal zone and colonized areas with high proportions of unconsolidated sediment. Desiccation was the main factor limiting the spatial distributions of the three species, although substrate composition and probably interspecific competition with macroalgae were also important. The results suggest that the zoanthids use a variety of these adaptive strategies, which account for their success on consolidated substrates. Continuous monitoring of changes in distribution patterns can be useful for indicating human impacts on marine biodiversity, providing insights for monitoring and conservation programmes.

Key words: *Adaptation, north-eastern Brazilian coast, sandstone reefs, zonation*

Introduction

Consolidated substrates are usually highly complex environments, which are important for algae and sessile animals (Denovaro & Fraschetti 2002). The distribution of the organisms or zonation is one of the remarkable characteristics of rocky intertidal communities, and each species has a characteristic limited distribution along a vertical or horizontal gradient (Raffaelli & Hawkins 1999; Little et al. 2010). Zonation is limited primarily by physical factors such as desiccation, high temperatures and intense solar radiation, and by biological factors such as competition and predation (Dayton 1971; Connell 1972). On rocky substrates, the structure of the community and the distribution of the organisms are governed by a complex interplay between physical limitations and biological interactions (Little et al. 2010), and predation and competition for space are among several major biological factors that control density and distribution on coastal rocky substrates (Tanner 1997; Suchanek & Green 1981). According to Little et al. (2010), many studies of the causes of zonation have shown that species have different abilities to survive exposure to air during spring low tides. These strategies include specialized morphological, physiological and behavioural adaptations, which allow them to survive for long periods without submersion.

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Among the invertebrates that show a visible distribution pattern are the zoanthids. Zoanthids are common benthic taxa on coral reefs and on intertidal rocky shores and affect the distribution of many other marine invertebrates by competing for space, forming dense colonies on the substrate (Suchanek & Green 1981; Rabelo et al. 2013). Zoanthids are widely distributed along the Brazilian coast, where they form dense aggregations in intertidal environments and shallow waters (Villaça & Pitombo 1997; Oigman-Pszczol et al. 2004; Floeter et al. 2007; Rabelo et al. 2013). Despite the considerable abundance of zoanthids on tropical rocky shores, especially in Brazil, current knowledge of their zonation is based on studies conducted on coral reefs in subtropical climates (Shiroma & Reimer 2010; Irei et al. 2011), with relatively few studies on their spatial distribution and ecology in tropical regions (Sebens 1982; Karlson 1983, 1988a, 1988b; Bastidas & Bone 1996; Belford & Phillip 2012), particularly on rocky shores and sandstone reefs. The present study evaluates the pattern of spatial distribution of *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860), *Protopalythoa variabilis* (Duerden, 1898) and *Zoanthus sociatus* (Ellis, 1768) along a flat sandstone reef in north-eastern Brazil, correlating with different environmental gradients. This study aimed to advance knowledge of the ecology of benthic cnidarians, provide useful insights for future monitoring and conservation projects of marine habitats, and generate data that can be used to predict the effects of climate change on the distribution and consequently the survival of zoanthids.

Materials and methods

Study site

North-eastern Brazil offers diverse coastal habitats including coral reefs, sandstone reefs, sand beaches and dunes. The climate is tropical, with annual sea water temperature ranging from 27 to 29°C, without significant seasonal variations. A rainy period extends from January to June, and a dry period from July to December. Tides are semidiurnal with a maximum tidal amplitude of about 3.5 m and a minimum of −0.1 m; during spring low tides, the intertidal zone is exposed for about 3 h. Common coastal features are the sandstone reefs or beach rocks, with flat surfaces that are tilted slightly seaward. These reefs differ from a typical rocky shore mainly in their gentle slope and sandstone composition.

The fieldwork was conducted at Paracuru Beach, Ceará State in north-eastern Brazil (03°23′53″ S, 39°00′38″ W), 90 km from the city of Fortaleza (Figure 1). The study site was a sandstone reef with large tide pools, which extends for 3 km along the coast and is about 100 m wide. During spring low tides, this reef is fully exposed (Figure 2A).

The study site harbours abundant species of sessile invertebrates, including sea anemones, starfish, molluscs, sponges, ascidians, hydrozoans and crustaceans (Matthews-Cascon & Lotufo 2006). A few scleractinian corals appear in small colonies along the reef. The zoanthids form large colonies on the hard substrate (Figure 2B–E).

Sampling methods

Three subdivisions of the intertidal zone perpendicular to the sandstone reef were defined, according to the length of time that the reef is exposed: (1) Inner Mid-Littoral, a 20-m-wide belt on the outer edge, flooded only during high tide; (2) Middle Mid-Littoral, an intermediate zone 60 m wide, which is submerged for approximately equal periods of time per tidal cycle; and (3) Outer Mid-Littoral, 20 m wide, nearest the sea.

Six horizontal transects were delimited in an area of the reef, perpendicular to the shoreline. Each transect was around 100 m long, depending on the width of the reef, with 300 m between transects. The transects extended from the upper littoral to the sublittoral, in order to sample the entire habitat during spring low tide periods in March and April 2007 (three transects/month). Continuously along each transect, 50 × 50 cm quadrats subdivided into 100 smaller quadrats were positioned on the substrate. In each quadrat we analysed the percentage cover of zoanthids and macroalgae and the type of predominant substrate (rock or sand). Spatial zoanthid distributions were determined as the percentage of zoanthid cover (relative abundance) in each quadrat along the transects.

Abiotic data, including water salinity and temperature, were taken every 10 m on all transects to also relate them to the zoanthid distribution. Temperature and salinity were measured in the water retained in the crevices of rocks and in small pools, with a refractometer, using the Practical Salinity Scale, and a field mercury thermometer, respectively. A horizontal profile of each transect was constructed in order to observe differences in the slope and substrate irregularity, according to the methodology proposed by Emery (1961). The substrate was classified as either consolidated (rock) or unconsolidated (sand).

Statistical analyses

For the analysis of the spatial distribution, asymmetrical graphs were constructed to show the cover and abundance of zoanthids and macroalgae on each

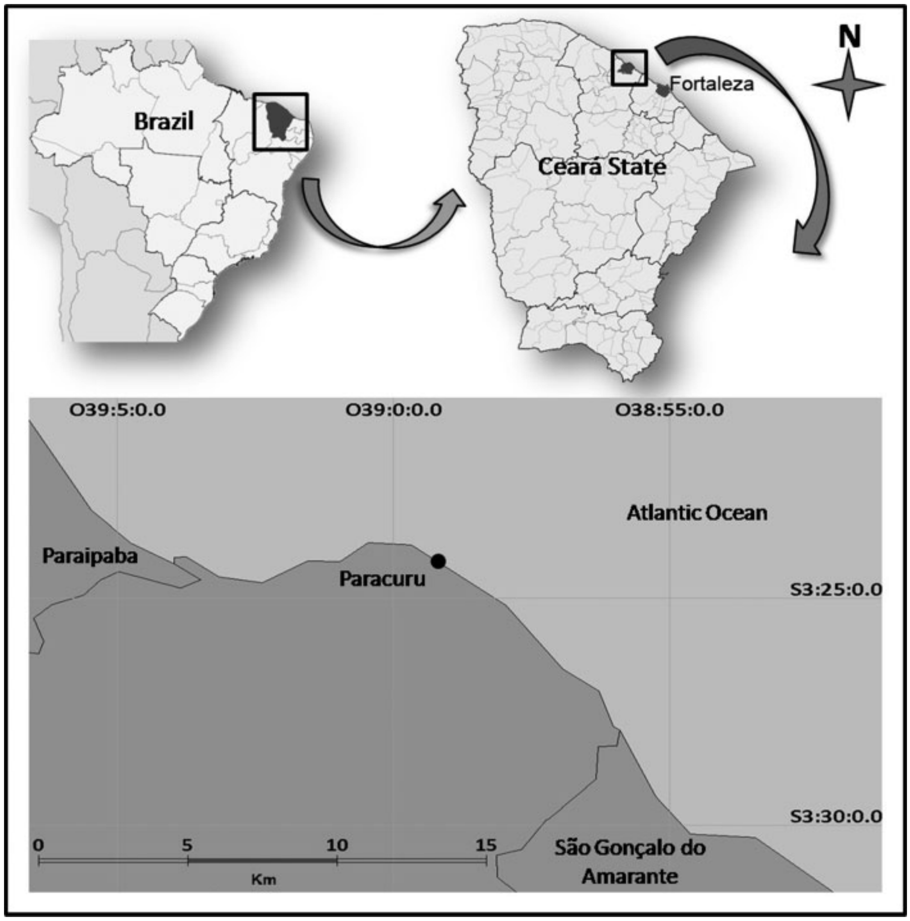

Figure 1. Map of the study area at Paracuru Beach, Ceará State, north-eastern Brazil.

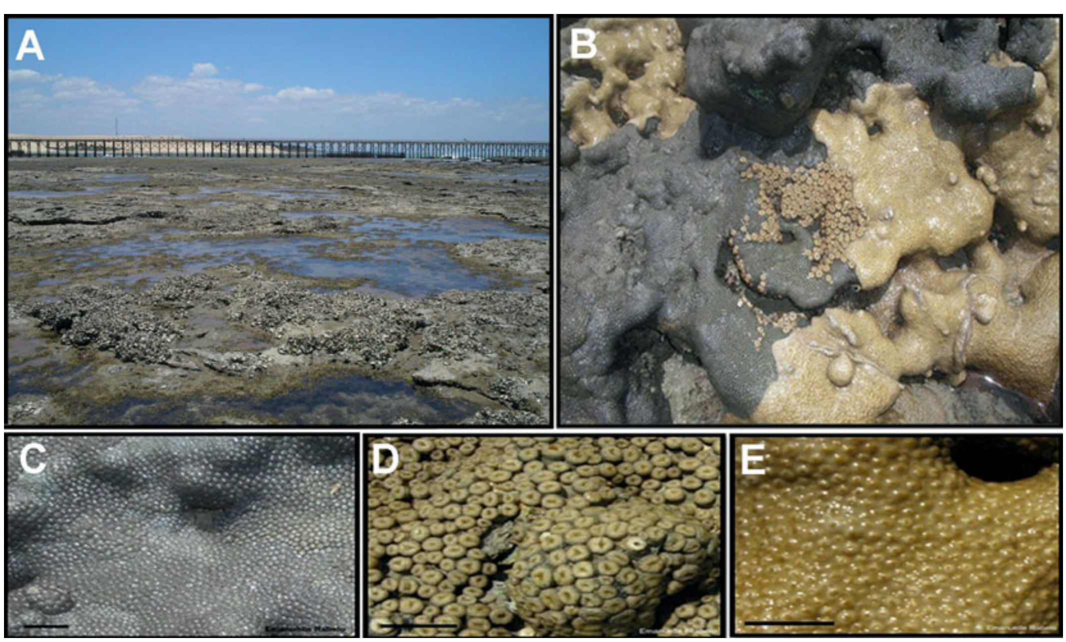

Figure 2. Study site on Paracuru Beach, Ceará State in north-eastern Brazil, showing the sandstone reef (A). Zoanthid colonies in contact with each other (B). Detail of *Zoanthus sociatus* (C); *Protopalythoa variabilis* (D) and *Palythoa caribaeorum* (E). Scale: 2 cm.

transect. The Pearson correlation was used to evaluate the influence of abiotic factors (temperature and salinity) on the distribution of zoanthids and to analyse the effect of macroalgae on zoanthid cover. The significance level (α = 5%) of the correlation coefficient was determined. The Pearson correlation coefficient was calculated using the software Statistica 8.

Results

The zoanthids showed a distinct zonation, mainly in the Middle Mid-Littoral and Outer Mid-Littoral, and covered about 60% and 47% of the total area, respectively. Although both rock and sand substrates were present in the entire Mid-Littoral zone, each species had a particular distribution pattern. The abundance and frequency of the three species differed.

Palythoa caribaeorum was most abundant in the Middle and Outer Mid-Littoral; its dense colonies covered about 5% and 6% of the substrate respectively (Figure 3B). This species was abundant and frequent in shaded and protected areas.

Protopalythoa variabilis was present in almost the entire intertidal zone. It was most abundant in the Middle Mid-Littoral, covering 40% of the substrate, where there were deposits of sand and abundant macroalgae (Figure 3B). *Protopalythoa variabilis* was the only species that colonized substrates with large deposits of unconsolidated sediments, and formed large aggregations on the sand banks where it was found with the column buried, exposing only the oral disc. This zoanthid was the most frequent species at the study site (Figure 3A).

Zoanthus sociatus colonized mainly the Inner and Outer Mid-Littoral zones, covering about 12% and 25% of the substrate, respectively (Figure 3B). In the Outer Mid-Littoral, *Z. sociatus* colonized more exposed areas, such as the top of elevated and exposed rocks, where no other organism occurred. The relief in the Inner Mid-Littoral was irregular,

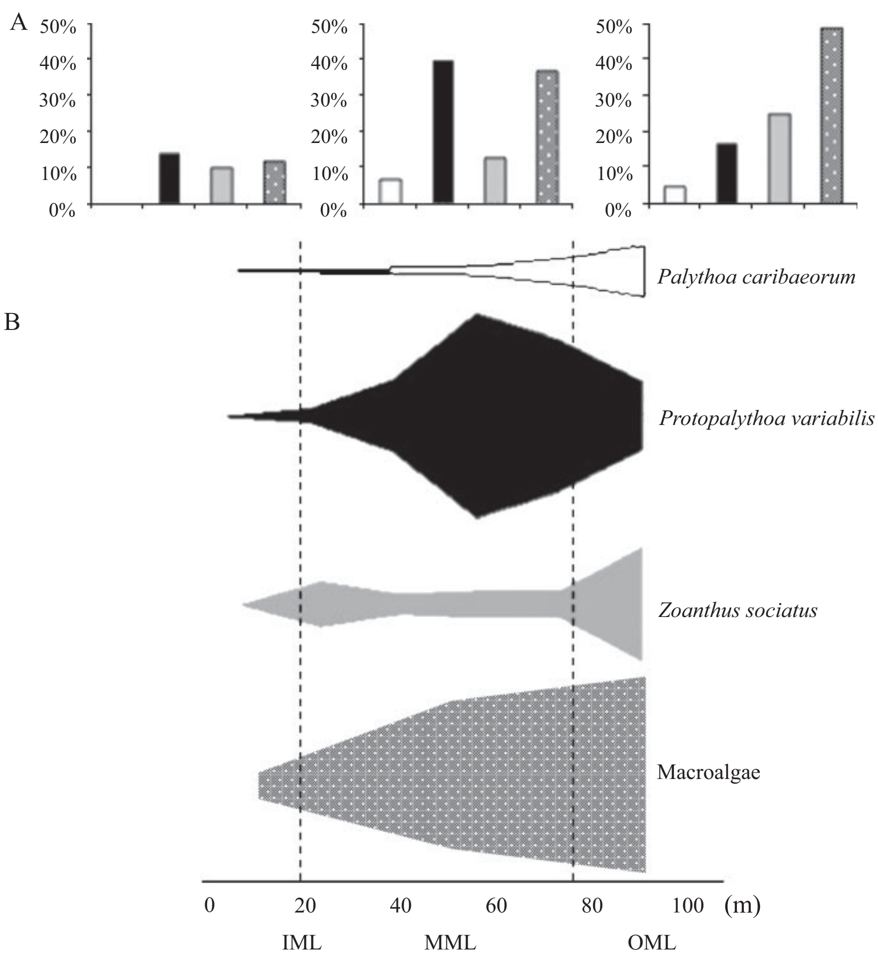

Figure 3. Frequency (A) and percentage cover (B) (relative abundance) of *Palythoa caribaeorum*, *Protopalythoa variabilis*, *Zoanthus sociatus* and macroalgae along the intertidal zone. IML, Inner Mid-Littoral; MML, Middle Mid-Littoral; OML, Outer Mid-Littoral.

and together with some higher rocky areas in the Outer Mid-Littoral remained exposed for long periods during low tide.

The frequency of each species coincided with its abundance in all areas of the littoral zone (Figure 3A,B).

Mean temperature (31.0 °C ± 1.1) and salinity (39.0 psu ± 0.7) showed little variation along the transects. Neither temperature nor salinity showed a correlation with the distribution of zoanthids over the entire study site ($P > 0.05$).

Macroalgae were present in the entire Mid-Littoral, with their highest abundance in the Middle and Outer Mid-Littoral, covering 37% and 49%, respectively. The most abundant macroalgae were *Caulerpa racemosa* (Forsskål) J. Agardh, *Caulerpa sertularioides* (S. G. Gmelin) M. A. Howe, *Ulva lactuca* Linnaeus, *Gracilaria* sp. and *Hypnea* sp. *Protopalythoa variabilis* was most abundant on substrates with large amounts of macroalgae, i.e. in the Middle and Outer Mid-Littoral. In contrast, *P. caribaeorum* and *Z. sociatus* were relatively sparse on substrates where algae were present. Macroalgae and zoanthids were negatively correlated (−0.72, $P < 0.05$) (Figure 4). Rocky substrate was predominant in both the Inner Mid-Littoral and Outer Mid-Littoral, covering about 80% and 90% of these zones, respectively. In the Middle Mid-Littoral sand was predominant, covering about 70% of this zone. Empty spaces and other organisms such as barnacles and limpets occupied 64%, 3% and 4% of the Inner, Middle and Outer Mid-Littoral, respectively.

Zones of zoanthid distribution

According to the sampling results and field observations, four zones of zoanthid distribution could be identified: (1) Inner *Zoanthus* Zone, with dense colonies of *Z. sociatus* in the Inner Mid-Littoral; (2) *Protopalythoa* Zone, composed mainly of *P. variabilis*, with sand substrate and a high density of macroalgae; (3) Interaction Zone, where the three species competed for space, with a high abundance of *P. caribaeorum*; and finally, (4) a second zone of *Zoanthus*, termed the Outer *Zoanthus* Zone, with higher rocks and consequently greater exposure to air. In this zone, very large colonies of *Z. sociatus* formed a bed on high, permanently exposed rocks that receive only splashing water from waves during low tide. Figure 5 shows a schematic representation of the zoanthid zones along the topographic profile of the study area.

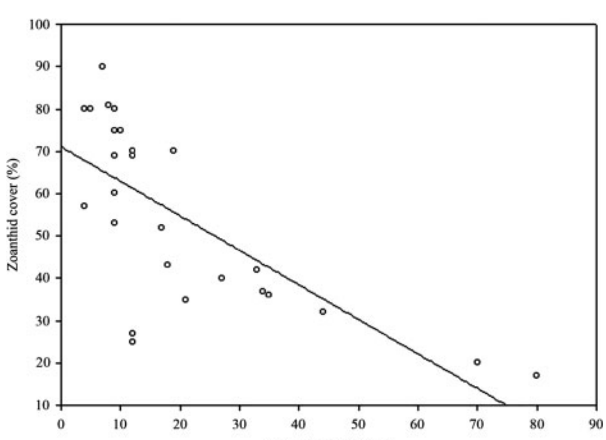

Figure 4. Scatter plot for the relationship between percent cover of zoanthids and seaweed on a rocky reef at Paracuru, northeastern Brazil. The zoanthid cover decreases where there is greater coverage of macroalgae.

Discussion

In this study we evaluated the pattern of distribution of three species of zoanthids, correlating with biotic and abiotic factors.

The results suggest that the zoanthids have morphological, physiological and behavioural adaptations to environmental stress, which account for their success on consolidated substrates, as observed by Karlson (1988a) and Karlson et al. (1996). Zoanthids primarily colonize more stable environments such as the Middle and Outer Mid-Littoral. The spatial distribution of the zoanthids studied here might be affected directly by their different tolerances to desiccation and substrate type.

The topographic profile determined the degree of air and sunlight (UV) exposure, influencing the distribution of the zoanthids. Our observations suggest that *Zoanthus sociatus* is the most resistant species, occurring in the most exposed zones such as high rocks that are more subject to drying. These data agree with those of Sebens (1982), Karlson (1983, 1988b) and Bastidas & Bone (1996), who found that *Z. sociatus* occurs in the most exposed reef areas.

Bastidas & Bone (1996) also showed that *Z. sociatus* is a poor competitor, which would explain the formation of large isolated colonies, favoured by the absence of antagonists. According to Connell (1972), the most likely reason that species of the Mid-Littoral live in physiologically difficult situations, where they are strongly affected by drying, is that they are less competitive than other species that occupy the lowest tidal levels.

The symbiotic zooxanthellae of the genus *Symbiodinium* may influence their host's resistance to adverse environmental factors (Glynn et al. 2001). Rabelo (2012) showed that among the zoanthids found on the coast of Ceará, only *Z. sociatus* hosts *Symbiodinium* clade A. Data from the literature indicate that clade A occurs only in the genus *Zoanthus* among members of the family Zoanthidae

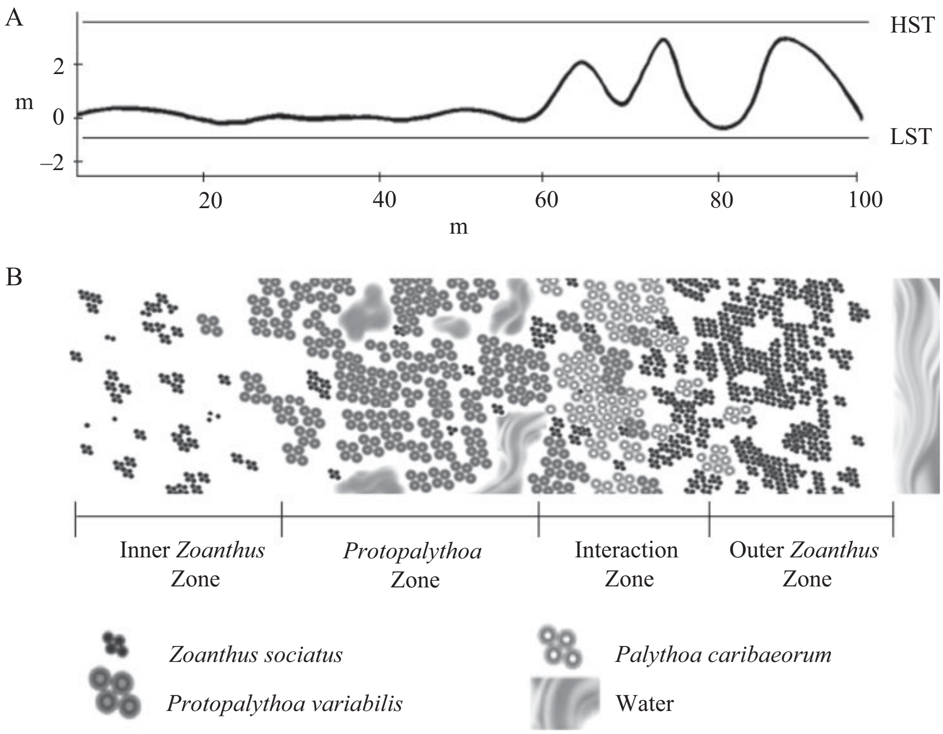

Figure 5. (A) Schematic topographic profile of Paracuru Beach. (B) Schematic representation of the zonation of zoanthids at Paracuru Beach. The Inner *Zoanthus* zone is exposed to intense solar radiation for long periods during low tide; the *Protopalythoa* zone is characterized by large amounts of sand; and the Outer *Zoanthus* zone by higher rock that dries during low tide. HST, High Spring Tide; LST, Low Spring Tide.

(Lajeunesse 2001, 2002; Reimer et al. 2007; Lajeunesse et al. 2008). According to Kinzie et al. (2001) and Magalon et al. (2007), this clade seems to be adapted to environmental stress. The identification of clade A only in *Z. sociatus* supports this hypothesis, suggesting that this species is more resistant to desiccation and sun (UV) exposure, occurring at sites that are well exposed during low tide and where no other cnidarian occurs. Only zooxanthellae clade A are capable of producing considerable amounts of mycosporine-like amino acids (MAAs) (Banaszak et al. 2000), which help to protect the host against damage from UV radiation (Neale et al. 1998) and may confer a competitive advantage on the host, in this case *Z. sociatus* under conditions of high radiation, influencing the host's zonation pattern. We found only 1 °C difference along the transects and, although a small change in temperature can be limiting for the survival of zooxanthellae (Baker 2003), on this reef *Z. sociatus* colonies were healthy. Further studies are needed to evaluate the possibility of any negative consequence of temperature variation on the morphology, types and survival of zooxanthellae of *Z. sociatus* in different areas of the Mid-Littoral.

For many animals of rocky shores, desiccation tolerance involves aspects of cellular biochemistry, such as lowering the water content of the cells and the ability to deal with the rise in osmotic pressure due to water loss (Little et al. 2010). However, the biochemical and physiological mechanisms that account for the resistance of *Z. sociatus* are unknown. Apparently, *Z. sociatus* is able to cope with these problems better than the other zoanthids studied.

Palythoa caribaeorum, on the other hand, occurred in areas that are exposed only occasionally, where it formed dense colonies. On the Brazilian coast, *P. caribaeorum* is found mainly in shallow submerged areas, where it is abundant (Echeverría et al. 1997; Villaça & Pitombo 1997; Oigman-Pszczol et al. 2004; Segal & Castro 2011), or in areas with strong currents (Koehl 1977). Its limited occurrence in the Outer Mid-Littoral suggests that *P. caribaeorum* is less adapted to adverse factors than other species, and although it is a strong competitor (Suchanek & Green 1981; Rabelo et al. 2013), it lacks resistance to drying and long periods of exposure to sunlight. Sebens (1982) observed that *P. caribaeorum* can survive only a few hours of exposure to the sun because of its inability to retain water. According to Herberts (1972), the degree of exposure appears to be the determining factor in the distribution of intertidal zoanthids. Belford & Phillip (2012) found a similar pattern, with *Z. sociatus* colonizing stressed areas and *P. caribaeorum* preferring areas with less-intense stress factors.

Protopalythoa variabilis shows greater resistance to desiccation compared with *P. caribaeorum*, as indicated by its wide distribution along the entire intertidal zone, especially in the Middle Mid-Littoral. At a Caribbean coral reef, Koehl (1977) observed a similar pattern, where *P. caribaeorum* colonized areas near the sublittoral, in areas with high water flow, whereas *P. variabilis* inhabited drier areas.

The distribution of zoanthids also appears to be influenced by the type of substrate, as suggested by Irei et al. (2011). *Palythoa caribaeorum* and *Z. sociatus* were highly abundant on the rock substrate and were not found on the sand substrate. *Protopalythoa variabilis* was more abundant on the rock substrate, and only *P. variabilis* showed a significant presence on unconsolidated substrate. Areas surrounded by sand, therefore, appeared to be a factor of exclusion for *P. caribaeorum* and *Z. sociatus*. The higher frequency of *P. variabilis* could be explained by its ability to colonize unconsolidated substrates where other zoanthids cannot survive. In a similar study, Koehl (1977) showed that 33% of the *P. variabilis* colonies were on cobble surrounded by sand, whereas only 2% of the *P. caribaeorum* colonies were found in these conditions. Polyps of *P. variabilis* colonies tend to be taller than those of *P. caribaeorum* (Koehl 1977), and the oral disc that emerges from the sand can facilitate colonization and feeding, even on sandbars. Few studies have examined the ecological and physiological characteristics of *P. variabilis*, and the unique ability of this zoanthid to colonize sand banks is unreported. However, it is clear from the present observations that the species is able to survive in situations with high sedimentation with the column buried, exposing only the oral disc. Perhaps *P. variabilis* resists desiccation during low tide by using the interstitial water in the sediment.

Because only *P. variabilis* colonizes areas with unconsolidated substrate, human actions such as burying the rocky reefs of Paracuru Beach, as on the nearby Pecém Beach where the reef was buried during the construction of a port terminal, could lead to local extinction of *Z. sociatus* and *P. caribaeorum*.

The morphology of polyps can also influence the distribution of zoanthids in intertidal zones. *Palythoa caribaeorum* and *Z. sociatus* were found in areas subject to strong wave action, whereas *P. variabilis* occurred in more sheltered areas. Colonies of *P. variabilis* have large polyps connected to each other only by basal stolons, whereas *P. caribaeorum* has smaller polyps with shared column walls (Koehl 1977). Koehl suggested that the small, connected polyps of *P. caribaeorum* can minimize the mechanical effect of constant water flow, facilitating their occurrence near the sublittoral, compared with the large, separate polyps of *P. variabilis*. The tight interpolyp attachment of colonies of *P. caribaeorum* may increase the resistance of a polyp colony to waves and constant water flow, generating a distribution pattern based on their adaptive morphological characteristics.

On this reef, *Z. sociatus* and *P. caribaeorum* appeared in large colonies at sites without macroalgae. The relatively high density of macroalgae in the Middle Mid-Littoral might exclude both *P. caribaeorum* and *Z. sociatus*, since only *P. variabilis* can coexist in some abundance with the algae; however, this possibility requires further study. According to Tanner (1995), macroalgae are among the main components of many reef communities and may compete with corals. The negative correlation found here between algal cover and zoanthid cover suggests that the algae compete for space and probably inhibit the growth of these sessile cnidarians. Birrell et al. (2005) showed that coral cover and growth might be retarded by algae in some locations due to reduction or even inhibition of coral settlement; nevertheless, this needs to be better investigated at the study site to confirm this hypothesis.

We believe that interspecific competition among zoanthids also influences their distribution on these reefs. Rabelo et al. (2013) showed that *P. caribaeorum* and *Z. sociatus* grow faster and have better competitive abilities than *P. variabilis*, killing the colonies of *P. variabilis* as they grow. This apparent low competitive ability of *P. variabilis* and its capacity to survive in areas where competitor zoanthids are absent may further explain its distribution. Glynn (1976) noted that competitive processes limit some species by exclusion, or species may be confined to sheltered areas where competition is reduced. The possible effects of competition on zoanthid distribution must be considered together with the indirect effects of other biological factors such as predation.

There were small differences in temperature and salinity along the transects, and we believe that these factors did not influence the zonation of the zoanthids.

In summary, the present study identified some physical and biological factors responsible for the distribution of zoanthids on a sandstone reef in north-eastern Brazil. The distribution in the intertidal zone is apparently influenced by both physical and biological factors. Exposure to desiccation seems to be one of the main reasons for the distribution of zoanthid species at the study site, given that these animals are exposed during spring low tides; therefore, the time of exposure determines the area of occurrence, some species being less resistant than others. The type of substrate and competition with macroalgae also had measurable effects.

Knowledge of the ecology of zoanthids and their spatial distribution is important for understanding the survival capability and dynamics of marine communities developed on hard substrates, and continuous monitoring is necessary to follow the changes in the long term. Changes in the distribution pattern of zoanthids over time can be used as indicators of human impact, encouraging the implementation of reef conservation programmes.

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