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Influence of depth on bryozoan richness and distribution from the continental shelf of the northern coast of Bahia State, north-eastern Brazil

ANA C.S. ALMEIDA, FACELUCIA B.C. SOUZA, LEANDRO M. VIEIRA & MARCOS M. NOGUEIRA

Abstract: Biological and abiotic processes influence ecosystem structure and species distribution. For bryozoan assemblages, depth, substratum and habitat structure are among the main factors influencing their distribution. Ecological studies on bryozoan fauna from Brazil are scarce and factors affecting the distribution and/or diversity of this common group are obscure. Here we attempted to verify the influence of bathymetry on bryozoan richness on the north shore of Bahia State, north-eastern Brazil. We identified 57 bryozoan taxa, comprising 35 families and 50 genera, all belonging to the Cheilostomata. *Retevirgula multipunctata* Winston, Vieira & Woollacott, 2014 and *Tetraplaria dichotoma* (Osburn, 1914) and the genus *Aimulosia* Jullien, 1888 were recorded for the first time from Bahia State. Species growing as encrusting sheets were dominant at all depths. There was a significant difference in richness among samples at different depths, with highest values of richness at 40 meters (Kruskal-Wallis Test). Analysis of similarities revealed a significant difference among the bryozoan assemblages, mainly when comparing assemblages from 10 and 20 meters with deeper ones. Also, shallower assemblages composition varied much than assemblages from 30 and 40 meters. Since depth is a proxy for several environmental parameters, further studies are needed to identify other factors influencing bryozoan distribution.

Key words: Atlantic Ocean, bryozoan assemblages, Cheilostomata, colonial growth form.

INTRODUCTION

Understanding how biological and abiotic processes influence ecosystem structure and species distribution is a main goal in ecology (Clark et al. 2017a). Such comprehension may be essential to evaluate factors affecting the distribution of organisms in different marine environments (Kuklinski & Bader 2007, Balazy & Kuklinski 2017, Clark et al. 2017a, Peterson & Herkul 2019). Among the benthic fauna bryozoans are considered a good model for investigations of environmental influences on the community structure: they are not only speciose and abundant but also present in virtually all marine habitats, with many species showing broad bathymetric ranges (McKinney & Jackson 1989, Lidgard 1990, Clarke & Lidgard 2000, Kuklinski et al. 2006, Ben Ismail et al. 2012, Figuerola et al. 2014, Souto & Albuquerque 2019). In this context, many taxa could be model organisms for exploring depth-related changes (e.g. Hageman et al. 1995, Kuklinski et al. 2005, Liuzzi et al. 2018).

Bryozoans comprise colonial invertebrates whose assemblages are mainly influenced by depth, substratum, and habitat structure (e.g. rugosity) (Amini et al. 2004, Kuklinski et al. 2006, Ben Ismail et al. 2012). Some of these key factors may be further affected by other environmental parameters, such as current strength, wave action and topography (e.g. profile) (Kuklinski 2002, Barnes & Kuklinski 2003, Amini et al. 2004). Generally, depth is directly related to changes in bryozoan assemblages due to the influence of driving factors, such as light and temperature, over characteristics of the substratum (Kuklinski et al. 2006, Balazy & Kuklinski 2017). Amini et al. (2004) emphasizes that no bryozoan colonial growth form is exclusive to a single habitat, although specific growth forms may dominate different depths under the influence of a particular set of ecological and environmental conditions. For instance, encrusting bryozoans (i.e. colonies that are fully attached to the substratum, being essentially two-dimensional) can live in high-energy environments (often associated with shallow habitats) and on several types of substrata (McKinney & Jackson 1989, Bone & Wass 1990, Amini et al. 2004, Taylor & James 2013). In contrast, erect rigid delicate and branching bryozoans (i.e. colonies that have only a basal portion attached to the substrata, growing as three-dimensional structures), are more common than encrusting ones at greater depths and in environments lacking hard substrata (e.g., Hayward 1981, Nelson et al. 1988, Amini et al. 2004, Vieira et al. 2010, Almeida et al. 2017). Thus, it is widely known that encrusting species are common in shallow waters and the occurrence of erect species in deeper environments is strongly related to the local hydrodynamics. Once shallower habitats undergo stronger water movements, including tidal fluctuations, erect colony forms that are susceptible to mechanical damage are at a greater disadvantage than encrusting ones that suffer no breakage (e.g. McKinney & Jackson 1989, Amini et al. 2004, Taylor & James 2013, Liuzzi et al. 2018).

Several studies have been carried out to understand those environmental factors that influence the dynamics and composition of marine bryozoan assemblages (e.g. Lagaaij & Gautier 1965, Eggleston 1972, López Gappa & Lichtschein 1988, Hageman et al. 1995, Harmelin 1997, Clarke & Lidgard 2000, López Gappa 2000, Novosel et al. 2004, Kuklinski et al. 2005, 2006, Kuklinski & Bader 2007, Ben Ismail et al. 2012, Denisenko & Grebmeier 2015, Clark et al. 2017b, Souto & Albuquerque 2019). Most of these studies found that depth, substratum availability, and thermal regime are key factors to the occurrence of bryozoan species. Also, bryozoan colonial growth forms are considered as good indicators of environmental conditions mainly because assemblages of different growth forms are influenced by parameters such as temperature, salinity, nutrients, depth, hydrodynamics, and sedimentation (Stach 1936, Smith 1995, Nelson et al. 1988, Hageman et al. 1998, Amini et al. 2004, Taylor & James 2013). The majority of these ecological studies, however, were carried out based on Arctic and Mediterranean fauna, with few studies of the Atlantic Ocean available (Eggleston 1972, López Gappa & Lichtschein 1988, Clarke & Lidgard 2000, López Gappa 2000, Denisenko et al. 2016, Souto & Albuquerque 2019).

Traditionally, most of the research on marine bryozoans from the South-western Atlantic, particularly Brazil, is focused on taxonomy and fauna surveys (e.g. Marcus 1955, Winston et al. 2014, Almeida et al. 2015a, 2017, 2018, Vieira et al. 2016, Ramalho et al. 2018). Bryozoan faunas of Brazil show high taxonomic diversity and variability of growth forms on different types of substrata (Vieira et al. 2012), but they also contain some specific substratum-bryozoan associations, including species growing on sand

(Winston & Vieira 2013), sponges (Almeida et al. 2017), molluscs (Marcus 1938, Almeida et al. 2018), and cnidarians (Vieira & Stampar 2014, Ramalho et al. 2018). The only comparison between bryozoan fauna at different depths along the Brazilian coast was provided in a systematic paper, with no data on richness or distribution related to the environmental factors (Vieira et al. 2010). Since ecological studies are scarce and factors that affect the distribution and diversity of the bryozoans from Brazil are poorly understood, here we present the first study focused on the bathymetric distribution of bryozoan assemblages from a stretch of the coast of Bahia State, north-east Brazil.

MATERIALS AND METHODS

Study area and sampling

Samples were collected in October 1997 with a Van Veen Grab between the localities of Itacimirim and Guarajuba (12° 47’ 45” S; 37° 57’ 09” W and 12° 36’ 55” S; 38° 05’ 49” W), northern coast of Bahia State, north-east Brazil (Figure 1). The continental shelf of the area is narrow (mean of 15 km in width and the shelf edge occurs at a depth of 50 m), with a strong bathymetric gradient and isobaths almost parallel to each other (Bittencourt et al. 2000, Dominguez et al. 2011). The bottom is composed mainly of two types of sediment, siliciclastic and carbonate sands, the former found predominantly closer to the coast (Dominguez et al. 2011).

Five samples were taken from five different depth zones (10, 20, 30, 40, and 50 m) and each sample was separated by 2 km (total of 25 samples). The material was fixed in 4% buffered formaldehyde and transported to the laboratory.

Sample treatment and bryozoan identification

In the laboratory, samples were washed in a 0.25 mm mesh sieve with distilled water and then kept in an oven (60 °C) until totally dry. After drying, the samples were analysed under a stereomicroscope and all bryozoan fragments were separated. Due to this colonial

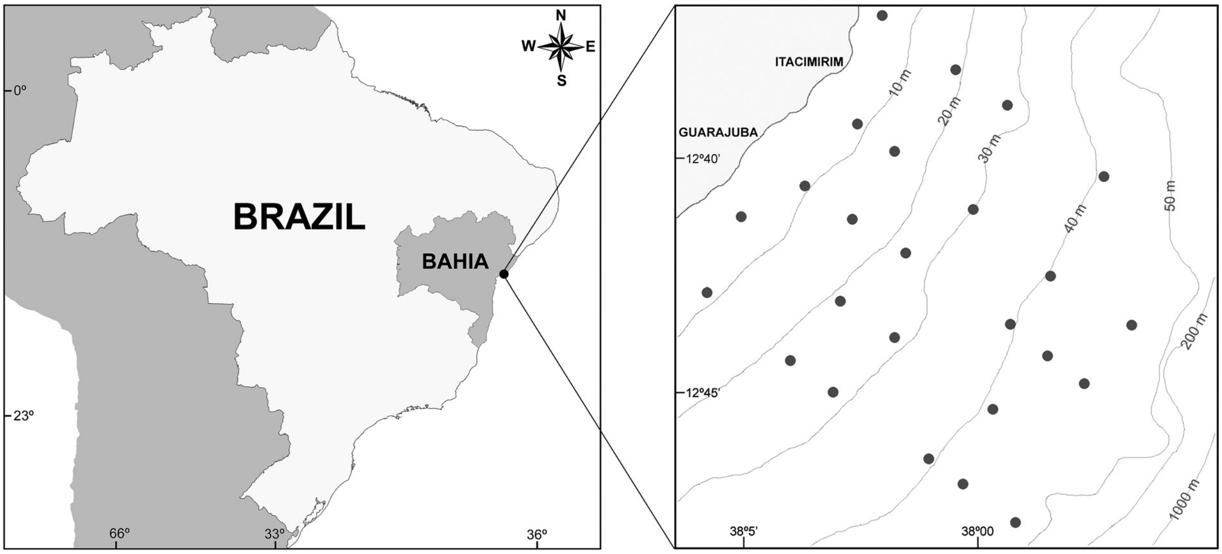

Figure 1. Studied area and sampling sites (indicated as grey circles) at Littoral North of Bahia State, northeast Brazil.

fragmentation, the bryozoan species were counted as present or absent and the data is presented as frequency of occurrence.

For taxonomic identification, bryozoans were first washed in sodium hypochlorite and then immersed in water to remove the external tissues. The bryozoans were then dried naturally before being examined under a stereo microscope. When necessary, selected fragments were mounted on stubs and coated with gold for examination using scanning electron microscopy. Bryozoans were identified at the lower taxonomic level possible, based mainly on external morphology (i.e. characteristics of autozooids, heterozooids, and reproductive structures) and following recent and specific literature (e.g. Vieira et al. 2008, 2010, 2016, Winston & Vieira 2013, Winston et al. 2014, Almeida et al. 2015a, b, 2017, 2018). Voucher specimens were deposited at the Bryozoa collection of the Setor da Zoologia, Museu de História Natural at Universidade Federal da Bahia (UFBA).

The bryozoan colony growth forms (Figure 2; Table I) were classified following Bishop (1989), Taylor & James (2013), and Almeida et al. (2017).

Statistical analysis

Since data did not conform to the assumptions that allow parametric analysis, a non-parametric Kruskal-Wallis one-way analysis of variance was used, using the open-source software R, to verify the differences in richness patterns among depths. The post hoc Dunn's Multiple Comparison Test was performed to identify significant differences among the depth means. In order to illustrate the spatial patterns in samples and to summarize patterns in bryozoan distribution according to depth, the Nonmetric Multidimensional Scaling (NMDS) method was applied using PC-ORD version 5. The NMDS was performed using Bray-Curtis dissimilarity for binary (presence/absence) data.

Analysis of similarities (ANOSIM-test) was performed to compare similarities between the combinations of groups and indicate which habitats have significantly different species communities. Also, to investigate the relationship between the bryozoan assemblages and the different depths, we used similarity percentage analysis (SIMPER) in the PAST program, which indicates the dissimilarities and the most distinctive species at the different depths.

RESULTS

A total of 57 bryozoan taxa were identified, comprising 35 families and 50 genera, belonging to a single order, the Cheilostomata (Table II). Most of the families (29 of 35) were represented by one or two taxa. The Phidoloporidae was the most diverse family, represented by five taxa, followed by the Candidae and Lepraliellidae (four taxa each) and the Calloporidae, Metrarabdotosidae, and Smittinidae (three taxa each).

The Kruskal-Wallis Test indicated that there was significant difference in richness among samples at different depths ($p = 0.0154$). Dunn's Multiple Comparisons test results found differences between 10 – 40 m ($p = 0.012$), 20 – 40 m ($p = 0.040$), and 40 – 50 m ($p = 0.010$) (Figure 3). The results from the NMDS plot showed that the species composition of samples collected at 10 and 20 m were more variable when compared with samples from 30, 40, and 50 m. Samples from depths of 30, 40, and 50 m formed well-defined groups (Figure 4).

The ANOSIM-test showed a significant difference among bryozoan assemblages from different depths ($R = 0.1382$; $p = 0.0092$). The highest dissimilarities were verified by SIMPER when comparing assemblages from depths of 10 and 20 m, with *Licornia* aff. *diadema* (Busk, 1852)

Table I. **Classification of the bryozoan colony growth forms based on criteria from Bishop (1989), Taylor & James (2013) and Almeida et al. (2017). Substratum attachment: abfrontal (colony attached to the substratum by the zooidal basal wall, abfrontal in relation to the zooidal frontal surface); unattached (colony growing free of substratum); proximal (only a proximal ancestrular portion of the colony is attached to the substratum). Zooidal orientation (related to the substratum): horizontal (zooids forming laminar sheets adjacent to the substratum); vertical (zooids forming free erect branches). Zooidal layers: single (colony with a single layer of autozooids); multiple (colony with two or more layers of autozooids on only one side of the colony); cylindrical (colony with zooids growing along an axis). Branching: articulated (branches comprising by zooids forming internodes separated by chitinous articulation); bifurcating (branches comprising by zooids without articulations).**

Growth form	Figure	Substratum attachment	Zooidal orientation	Zooidal layers and branching
Encrusting (EN)				
Creeping	1A	abfrontal	horizontal	single zooids with basal and erect portions
Uniserial	1B	abfrontal	horizontal	single zooid in series
Sheet	1C	abfrontal	horizontal	single or multiple sheets
Spot	1D	abfrontal	horizontal	multiple, zooids mounted
Domal	1E	abfrontal	horizontal	multiple, zooids with vertical relief
Free-living (FL)				
Free-living	1F	unattached	horizontal	single with low conical or disk-like profile
Erect (ER)				
Rigid branching	1G	proximal	vertical	single, multiple or cylindrical, rigid articulated branches with or without elastic joints
Delicate branching	1H	proximal	vertical	single or cylindrical, delicate articulated branches without elastic joints
Palmate	1I	proximal	vertical	flattened strap-like bifurcating at intervals

recognized as the species that most contributed to these dissimilarities. High dissimilarities were also recorded when comparing bryozoan assemblages from depths of 10 and 20 m with deeper sites. However, lower dissimilarities were verified among assemblages from the deeper sites. *Parasmittina loxoides* Winston, Vieira & Woollacott, 2014, *Nellia tenella* (Lamarck, 1816), and *Margaretta buski* Harmer, 1957 represented those species that most contributed to the dissimilarities between assemblages from depths of 30 – 40 m, 30 – 50 m, and 40 – 50 m, respectively (Table III).

The majority of the species found in the area (42 of 57) have encrusting colonies (38 were encrusting sheets; encrusting creeping, uniserial, spot, and domal forms were represented by one species each), followed by erect rigid branching (five species), erect delicate branching and erect palmate (four species each) colonies, and

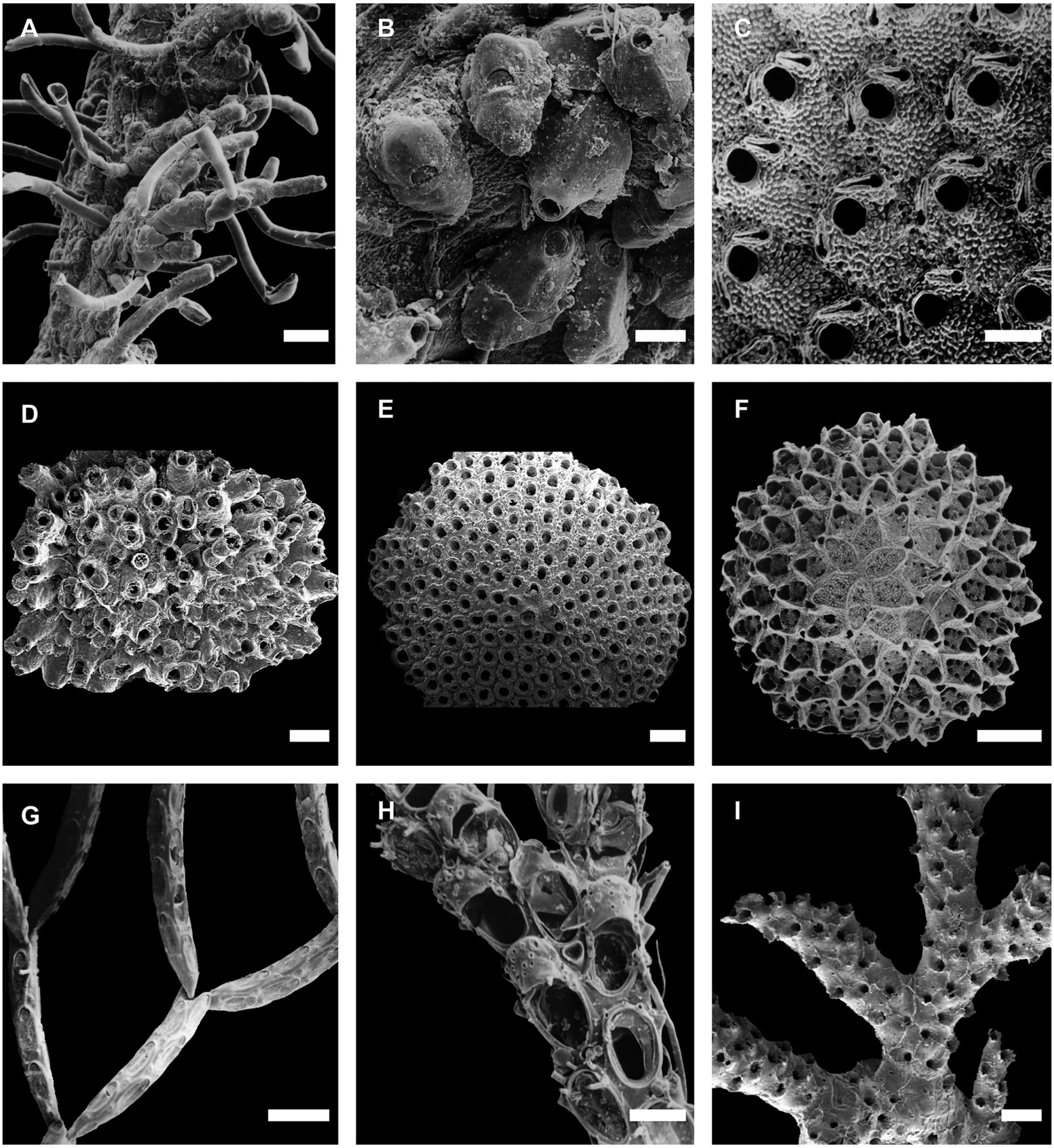

Figure 2. Bryozoan colony growth forms from the North shore of Bahia State, northeast Brazil. **a**, encrusting creeping; b, encrusting uniserial; c, encrusting sheet; d, encrusting spot; e, encrusting domal; f, free-living; g, erect rigid branching; h, erect delicate branching; i, erect palmate. Scale bars: A, C, D, F, H, I = 400 µm; B = 200 µm; E, G = 1 mm.

free-living (two species) (Table II). Encrusting was the most common colony form at all depths, with the highest number of species at a depth of 40 m (Figure 5). Fourteen species (nine encrusting sheets, two erect rigid branching, two erect delicate branching, and one free-living form) were reported at all depths (Table II). Another 10 species were considered stenobathic since they were found at a single depth only (Table II).

Thirty-three species were recorded at a depth of 10 m, most of those forming encrusting colonies (21 encrusting sheets) and erect (four rigid branching and four delicate branching) colonies (Table II; Figure 5). No exclusive species was found at this depth and no species showed higher frequency of occurrence than at other depths. *Nellia tenella* and *Licornia* aff. *diadema* were considered very common among these samples.

Thirty-seven species were collected at a depth of 20 m, 25 species with encrusting colonies and 10 species with erect colonies. *Aimulosia* sp. (encrusting sheet) and *Aetea cultrata* Vieira, Almeida & Winston, 2016 (encrusting creeping) were only collected at this depth (Table II).

The encrusting sheet bryozoans *Ammatophora arenacea* Winston & Vieira, 2013, *Smittipora tuberculata* (Canu & Bassler, 1928), *Puellina* sp., *Reptadeonella leilae* Almeida, Souza, Sanner & Vieira, 2015b, and the free-living *Discoporella salvadorensis* Winston, Vieira & Woollacott, 2014 were the most common taxa at a depth of 30 m. A total of 27 encrusting sheet species were found, with four species (*Hemismittoidea* sp., *Hippopodina pulcherrima* (Canu & Bassler, 1928), *Utinga castanea* (Busk, 1884) and *Fodinella atlantica* Winston, Vieira & Woollacott, 2014) found exclusively at this depth. *Ammatophora arenacea* and *Smittipora tuberculata* recorded their highest frequencies of occurrence when compared with the other depths (Table II).

Fauna from a depth of 40 m was mainly represented by encrusting sheet colonies (31 species), followed by erect species (five rigid branching and three erect palmate) (Table II; Figure 5). The encrusting sheets species *Retevirgula multipunctata* Winston, Vieira & Woollacott, 2014 and *Drepanophora tuberculata* (Osburn, 1914) and the erect palmate *Trematooecia arborescens* were only recorded at a depth of 40 m. *Puellina* sp., *Parasmittina loxoides*, *Hippoporina* sp., *Margaretta buski*, *Bryopesanser pesanseris* (Smitt, 1873) and *Reteporellina evelinae* Marcus, 1955 occurred more frequently than at other depths, being considered very common at 40 m (Tables II and III).

Puellina sp. and *Reptadeonella leilae*, species with encrusting colonies that frequently form small unilaminar sheets, were the most frequent at depths of 30 and 40 m. Also, the encrusting *Plesiocleidochasma* sp. and *Hippoporina* sp. were the most common at depths of 40 and 50 m, respectively. *Steginoporella magnilabris* (Busk, 1854) was the commonest bryozoan from a depth of 30 to 50 m (Table II). At a depth of 50 m, the number of encrusting species (24) decreased when compared to depths of 30 and 40 m (27 and 31 species, respectively). The only exclusive species at this depth was *Calyptotheca* sp. (Table II). We also found five erect rigid branching, three erect palmate, one erect delicate branching and only one free-living bryozoans at 50 m (Table II).

Table II. Bryozoan taxa with respective colony-form from the northern coast of Bahia State, north-eastern Brazil. New records are marked with an asterisk. Colony growth form: EN, encrusting colony (c, creeping; d, domal; sh, sheet; sp, spot; u, uniserial); FL, free-living; ER, erect colony (d, delicate branching; r, rigid branching; p, palmate).

Bryozoan taxa	Colony growth	Frequency of occurrence (%)				
		10 m	20 m	30 m	40 m	50 m
Family Aeteidae Smitt, 1868						
Aetea cultrata Vieira, Almeida & Winston, 2016	ENc	0	20	0	0	0
Family Calloporidae Norman, 1903						
Ammatophora arenacea Winston & Vieira, 2013	ENsh	40	40	100	40	40
Copidozoum tenuirostre (Hincks, 1880)	ENsh	20	40	20	40	40
**Retevirgula multipunctata* Winston, Vieira & Woollacott, 2014	ENsh	0	0	0	20	0
Family Antroporidae Vigneaux, 1949						
Antropora typica (Canu & Bassler, 1928)	ENsh	20	0	20	20	20
Family Quadricellaridae Gordon, 1984						
Nellia tenella (Lamarck, 1816)	ERr	80	80	100	80	20
Family Cupuladriidae Lagaaij, 1952						
Cupuladria monotrema Busk, 1884	FL	20	20	20	40	0
Discoporella salvadorensis Winston, Vieira & Woollacott, 2014	FL	20	60	100	100	80
Family Candidae d'Orbigny, 1851						
Canda alsia Winston, Vieira & Woollacott, 2014	ERd	40	20	40	40	80
Cradoscrupocellaria calypso Vieira, Spencer Jones & Winston, 2013	ERd	40	40	0	0	20
Licornia aff. *diadema* (Busk, 1852)	ERd	80	40	40	60	80
Licornia sp.	ERd	20	40	0	40	60
Family Microporidae Gray, 1848						
Micropora angustiscapulis Winston, Vieira & Woollacott, 2014	ENsh	20	20	40	60	20
Mollia elongata Canu & Bassler, 1928	ENsh	0	20	40	40	0
Family Onychocellidae Jullien, 1882						
Smittipora tuberculata (Canu & Bassler, 1928)	ENsh	40	20	80	40	60

Table II. Continuation

Bryozoan taxa	Colony growth	Frequency of occurrence (%)				
		10 m	20 m	30 m	40 m	50 m
Family Steginoporellidae Hincks, 1884						
Labioporella tuberculata Winston, Vieira & Woollacott, 2014	ENsh	0	20	0	20	0
Steginoporella magnilabris (Busk, 1854)	ENsh	20	0	60	100	100
Family Cellariidae Fleming, 1828						
Cellaria oraneae Almeida, Souza & Vieira, 2017	ERr	20	20	20	0	0
Family Cribilinidae Hincks, 1879						
Puellina sp.	ENsh	20	40	80	100	20
Family Hippothoidae Busk, 1859						
Hippothoa flagellum Manzoni, 1870	ENu	20	20	0	20	0
Family Trypostegidae Gordon, Tilbrook & Winston, 2005						
Trypostega tropicalis Winston, Vieira & Woollacott, 2014	ENsh	20	40	60	40	20
Family Vitrimurellidae Winston, Vieira & Woollacott, 2014						
Vitrimurella fulgens (Marcus, 1955)	ENsh	0	20	0	20	0
Family Arachnopusiidae Jullien, 1888						
Poricella frigorosa Winston, Vieira & Woollacott, 2014	ENsh	40	0	0	40	40
Family Exechonellidae Harmer, 1957						
Exechonella vieirai Cáceres-Chamizo, Sanner, Tilbrook & Ostrovsky, 2017	ENsh	0	0	40	20	20
Family Adeonidae Busk, 1884						
Reptadeonella leilae Almeida, Souza, Sanner & Vieira, 2015b	ENsh	0	40	80	80	20
Reptadeonella brasiliensis Almeida, Souza, Sanner & Vieira, 2015b	ENsh	40	20	40	60	40
Family Lepraliellidae Vigneaux, 1949						
Celleporaria carvalhoi Marcus, 1939	ENsh	20	0	40	60	0
Celleporaria schubarti Marcus, 1939	ENsh	40	0	60	60	20
Celleporaria mordax (Marcus, 1937)	ENsh	20	0	20	60	20

Table II. Continuation

Bryozoan taxa	Colony growth	Frequency of occurrence (%)				
		10 m	20 m	30 m	40 m	50 m
Drepanophora tuberculata (Osburn, 1914)	ENsh	0	0	0	20	0
Family Metrarabdotosidae Vigneaux, 1949						
Metrarabdotos jani Winston, Vieira & Woollacott, 2014	ENsh	20	20	20	0	40
Metrarabdotos tuberosum Canu & Bassler, 1928	ERp	0	20	0	0	20
Metrarabdotos auriculatum Canu & Bassler, 1923	ERp	20	0	0	40	20
Family Smittinidae Levinsen, 1909						
Parasmittina loxoides Winston, Vieira & Woollacott, 2014	ENsh	20	20	0	80	20
Pleurocodonellina marcusi Almeida, Souza, Farias, Alves & Vieira, 2018	ENsh	20	20	0	20	0
Hemismittoidea sp.	ENsh	0	0	20	0	0
Family Bitectiporidae MacGillivray, 1895						
Hippoporina sp.	ENsh	40	0	40	80	0
Family Lanceoporidae Harmer, 1957						
Calyptotheca sp.	ENsh	0	0	0	0	40
Family Schizoporellidae Jullien, 1883						
Schizoporella sp.	ENsh	40	40	40	60	20
Stylopoma aurantiacum (Canu & Bassler, 1928)	ENsh	20	20	0	60	60
Family Tetraplariidae Harmer, 1957						
Tetraplaria dichotoma (Osburn, 1914)	ERr	0	20	20	0	0
Family Margarettidae Harmer, 1957						
Margaretta buski Harmer, 1957	ERr	40	40	60	100	0
Family Buffonellodidae Gordon & d'Hondt, 1997						
Aimulosia sp.	ENsh	0	20	0	0	0
Family Hipoppodinidae Levinsen, 1909						
Hipoppodina pulcherrima (Canu & Bassler, 1928)	ENsh	0	0	20	0	0

Table II. Continuation

Bryozoan taxa	Colony growth	Frequency of occurrence (%)				
		10 m	20 m	30 m	40 m	50 m
Family Escharinidae Tilbrook, 2006						
Bryopesanser pesanseris (Smitt, 1873)	ENsh	0	20	20	80	40
Family Hippaliosinidae Winston, 2005						
Hippaliosina imperfecta (Canu & Bassler, 1928)	ENsh	0	20	20	20	40
Family Petraliellidae Harmer, 1957						
Utinga castanea (Busk, 1884)	ENsh	0	0	20	0	0
Family Mamilloporidae Canu & Bassler, 1927						
Mamillopora cupula Smitt, 1873	ENd	0	20	20	0	0
Family Cleidochasmatidae Cheetham & Sandberg, 1964						
Calyptooecia conuma Almeida & Souza, 2014	ENsp	0	20	0	20	0
Gemelliporina glabra (Smitt, 1873)	ERr	40	40	40	80	80
Family Colatooeciidae Winston, 2005						
Trematooecia arborescens (Canu & Bassler, 1928)	ERp	0	0	0	40	0
Family Hippoporidridae Vigneaux, 1949						
Hippotrema fissurata Almeida & Souza, 2014	ENsh	20	0	20	20	20
Family Phidoloporidae Gabb & Horn, 1862						
Fodinella atlantica Winston, Vieira & Woollacott, 2014	ENsh	0	0	20	0	0
Plesiocleidochasma sp.	ENsh	0	0	0	20	20
Rhynchozoon brasiliensis Almeida, Souza, Menegola & Vieira, 2017	ENsh	20	20	20	60	40
Rhynchozoon sp.	ENsh	0	20	20	40	0
Reteporellina evelinae Marcus, 1955	ERp	0	0	40	80	40

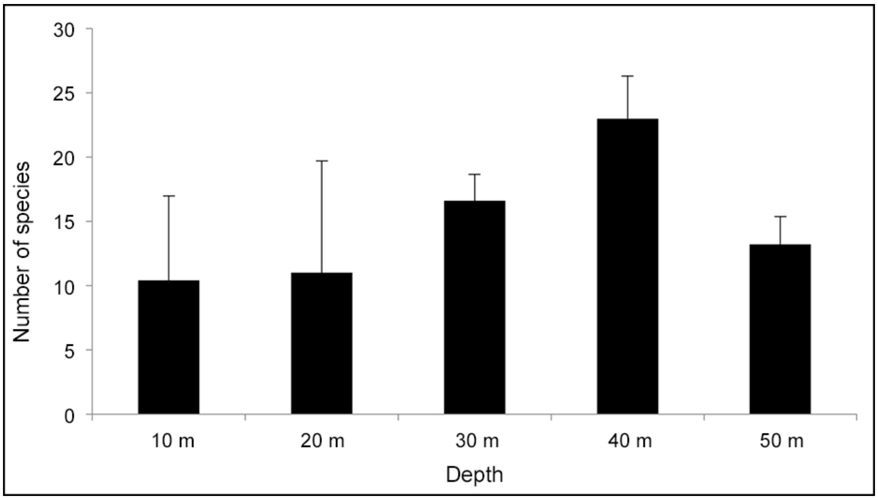

Figure 3. Mean number and standard deviation of bryozoan species per depth on the North shore of Bahia State.

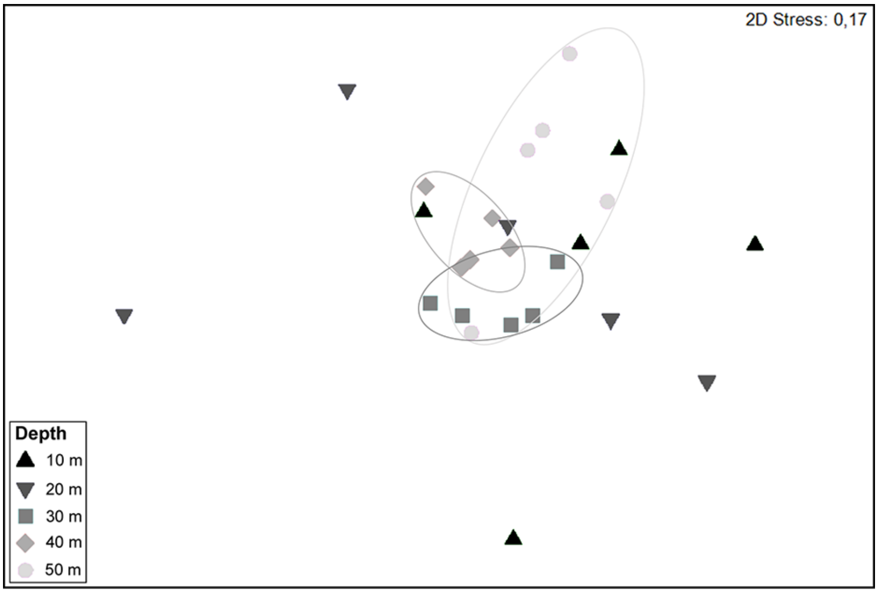

Figure 4. NMDS plot of bryozoan bathymetric distribution on the North shore of Bahia State.

DISCUSSION

Bryozoans belonging to the Order Cheilostomata are recognized as a dominant group in marine environments of the Present (Ryland 1970, Kuklinski et al. 2005). In general terms the composition of the bryozoan assemblages studied here agree with the bryozoan richness already described for the area (Almeida et al. 2015b, 2017, 2018). Almeida et al. (2015b) recognized the families Smittinidae, Phidoloporidae, Candidae, and Schizoporellidae as the most diverse in Bahia State. In this study, three of these (Smittinidae, Phidoloporidae, and Candidae) are considered to be the most diverse families. Representatives of these families are commonly reported from the shallow waters of the Brazilian coast and frequently show high species diversity (e.g. Vieira et al. 2008, Almeida et al. 2015b, 2018). Also, the Smittinidae, Phidoloporidae, and Candidae are among the most diverse cheilostome families in warm tropical and subtropical waters, comprising more than 200 living species each

Table III. Average dissimilarities between bryozoan assemblages from different depths and correlations of the most important species contributing to the dissimilarities. All values in percentage (%).

Average dissimilarity	**10 x 20 m**	**76.71**	**10 x 30 m**	**69.19**	**10 x 40 m**	**67.88**	**10 x 50 m**	**72.24**	**20 x 30 m**	**69.97**
Species contribution	*Licornia* aff. *diadema*	3.86	*Reptadeonella leilae*	3.24	*Steginoporella magnilabris*	2.62	*Steginoporella magnilabris*	3.89	*Smittipora tuberculata*	2.87
	Discoporella salvadorensis	3.44	*Discoporella salvadorensis*	2.94	*Puellina* sp.	2.62	*Nellia tenella*	2.96	*Ammatophora arenacea*	2.71
	Smittipora tuberculata	3.18	*Puellina* sp.	2.84	*Reteporellina evelinae*	2.56	*Discoporella salvadorensis*	2.92	*Reptadeonella leilae*	2.56
	Puellina sp.	2.98	*Ammatophora arenacea*	2.71	*Reptadeonella leilae*	2.54	*Canda alsia*	2.81	*Celleporaria schubarti*	2.42
Average dissimilarity	**20 x 40 m**	**70.83**	**20 x 50 m**	**77.34**	**30 x 40 m**	**52.05**	**30 x 50 m**	**66.38**	**40 x 50 m**	**59.68**
Species contribution	*Steginoporella magnilabris*	3.15	*Steginoporella magnilabris*	4.66	*Parasmittina* sp.	1.99	*Nellia tenella*	2.73	*Margaretta buski*	2.8
	Reteporellina evelinae	2.57	*Canda alsia*	2.99	*Bryopesanser pesanseris*	1.74	*Reptadeonella leilae*	2.36	*Hippoporina* sp.	2.28
	Hippoporina sp.	2.57	*Nellia tenella*	2.93	*Ammatophora arenacea*	1.54	*Puellina* sp.	2.36	*Puellina* sp	2.26
	Bryopesanser pesanseris	2.28	*Licornia* aff. *diadema*	2.91	*Stylopoma* sp.	1.52	*Stylopoma* sp.	2.11	*Nellia tenella*	1.94

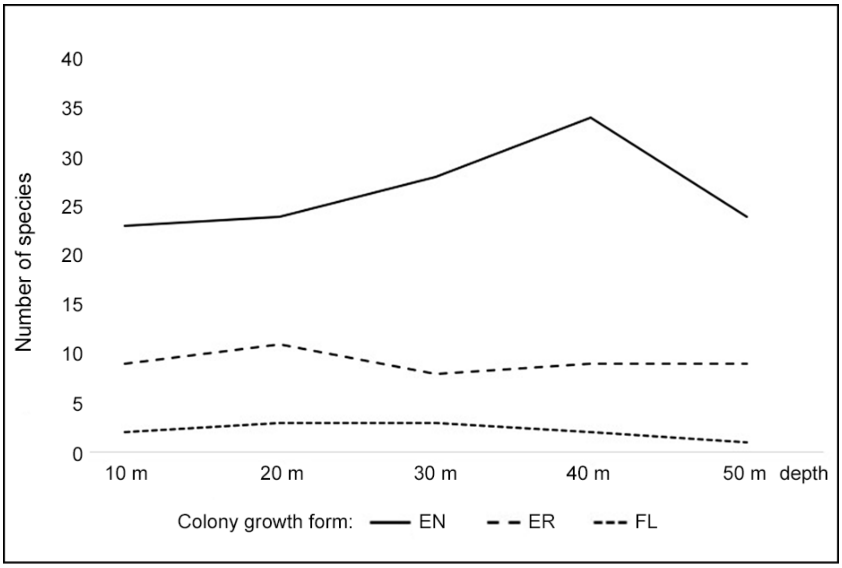

Figure 5. Total number of bryozoan species per growth form in different depth (10 to 50 meters). Colony growth form: EN, encrusting colony; ER, erect colony; FL, free-living.

(Bock & Gordon 2019). Smittinidae species are commonly reported from shallow waters on hard substrata (such as coral reefs), mainly in the Caribbean, Hawaiian, and Australian regions (e.g. Soule & Soule 1973, Winston 1986, Ryland & Hayward 1992). Phidoloporidae are frequently found on bottoms mainly composed of biogenic substrata (e.g. corals, shells, rhodoliths) (e.g. Hayward 2004, Vieira et al. 2010, Almeida et al. 2017, 2018), comprising the most speciose family in Australia, with more than 70 species already recorded from that area (Cook et al. 2018, Bock & Gordon 2019). The family Candidae is generally well-distributed worldwide (Cook et al. 2018, Bock & Gordon 2019) and known to occur on a wide range of natural and artificial substrata (e.g. Vieira et al. 2013, Almeida et al. 2017, 2018).

The species *Retevirgula multipunctata* and *Tetraplaria dichotoma* and the genus *Aimulosia* Jullien, 1888 are recorded for the first time from Bahia State (Figure 6). *Retevirgula multipunctata* was recently described, based on specimens collected at depths of 64 – 82 m from Rio de Janeiro State, south-eastern Brazil. Here we report the second locality known for this species so far, with specimens from Bahia found at a depth of 40 m. *Tetraplaria dichotoma* is distributed through the Western Atlantic, being found in the Gulf of Mexico and the Caribbean, at depths ranging from 18 to 270 m (Montoya-Cavidad et al. 2007, Winston & Maturo 2009). The genus *Aimulosia* is reported here for the first time in Brazilian waters; because specimens of this genus studied here consisted of only small fragments with broken ooecia, it was not possible to confidently assign a specific identification. Species of *Aimulosia* are common in the Caribbean region, frequently found in shallow waters (20 m deep, or less) (Winston 1986), and also known from Patagonia and Antarctica (Figuerola et al. 2014). The occurrence of these taxa in the assemblages studied here is unsurprising and these new records can be attributed to the historical underestimation of bryozoan fauna from Brazil, as highlighted by Almeida et al. (2015b, 2017, 2018).

The majority of bryozoan species from the northern coast region of Bahia State (67%) have colonies that grow as encrusting sheets largely attached to the substratum. Since it allows these species to live on virtually any type of substratum and in high-energy environments,

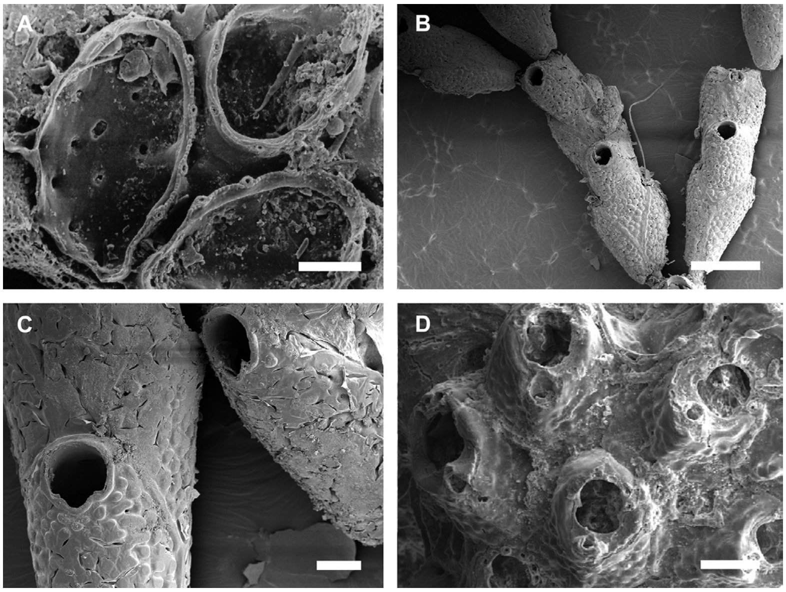

Figure 6. New records of bryozoans from Bahia State. a, *Retevirgula multipunctata*; b, c, *Tetraplaria dichotoma*; d, *Aimulosia* sp. Scale bars: a, d = 100 µm; b = 500 µm; c = 150 µm.

this colony growth form is considered to be the most opportunistic (McKinney & Jackson 1989, Amini et al. 2004). Most of the encrusting species in the assemblages studied here form unilaminar colonies that are common in shallow shelf environments, up to 200 m deep (Nelson et al. 1988, Stach 1936, Smith 1995, Amini et al. 2004) as in the studied area.

Erect colonies (rigid branching, delicate branching, and palmate) were also represented in the studied area. Erect rigid and delicate branching bryozoans are common in environments with moderate to high energy (Stach 1936, Amini et al. 2004). The high frequency of two erect branching species (*Licornia* aff. *diadema* and *Nellia tenella*) at a depth of 10 m found here seem to be in accordance with this trend. Also, erect palmate colonies are commonly related to low energy waters as depth increases (Cheetham & Thomsen 1981, Amini et al. 2004). Here we found that an erect palmate species, *Trematooecia arborescens*, was among the commonest taxa at a depth of 40 m, unlike in the assemblages at shallower depths.

Much more variation was seen in the composition of bryozoan assemblages among the samples collected at depths of 10 and 20 m, with the species composition becoming very similar with increasing depth, especially in the assemblages from 30 and 40 m (see Figure 4). Depth is considered to be among the key factors determining the composition of bryozoan assemblages (e.g. Kuklinski 2002, Barnes & Kuklinski 2003, Ben Ismail et al. 2012, Denisenko & Grebmeier 2015, Denisenko et al. 2016). As highlighted by Hageman et al. (1995), depth is a proxy for several parameters, including nutrient supply, temperature, and bottom-current energy. In this context our results can be related theoretically to a gradient of increasing stability (i.e. less wave action and stable water temperatures) with an increase in depth. In general terms, it is assumed that assemblages are less diverse intertidally than in subtidal to shallow shelf environments (e.g. Lidgard 1990, Kuklinski et al. 2005). Higher diversity of encrusting cheilostome bryozoans, for example, is found between 10 and 50 m deep (Lidgard 1990) and greatest abundance usually terminates at the break of the continental shelf, at depths of around 200 m (Ryland 1970). We found a similar trend here since the highest richness of bryozoans was found at a depth of 40 m with a decrease in richness at 50 m and, also, samples from depths of 30 and 40 m were more similar in composition. Vieira et al. (2010) studied the bryozoan fauna from the southern and south-eastern Brazilian continental shelf and slope (99 to 517 m deep), also collected by benthic samplers (van Veen, Box-corer, and rectangular dredge), and provided a compilation of species reported from deep waters from Brazil; their results are somewhat in accordance with this pattern (see also Ryland 1970, Lidgard 1990, Kuklinski et al. 2005). From the 105 species listed by Vieira et al. (2010), only 60 occurred deeper than 200 m. The composition of the assemblages described by Vieira et al. (2010) is quite distinct from the fauna presented here. Twenty-two species from 16 families were reported from deep waters of southern and south-eastern Brazil and, from those, only seven families (Candidae, Cellariidae, Cribrilinidae, Escharinidae, Smittinidae, Colatooeciidae, Phidoloporidae) and two species (*Smittipora acutirostris* and *Trematooecia arborescens*) were also reported here. These seven families, however, are mainly represented by different genera in the Brazilian coast and only the genera *Cellaria* and *Rhynchozoon* were recorded in both areas. Studies on bryozoan fauna from deep-waters are less common and usually reveal a great number of new taxa, including new genera, indicating a different composition and greater endemism than found in shallower regions (e.g. Vieira et al. 2010, Berning et al. 2017, Figuerola et al. 2018, Souto & Albuquerque 2019).

The continental shelf of Brazil is generally narrow, reaching maximum widths off the mouth of the Amazon River (north; 350 km), Abrolhos Bank (east; 245 km), and Santos (southeast; 200 km) (Berlinck et al. 2004). The shelf break is from 40 to 160 m, being wider in the south-east and south (100 – 160 m) and narrower in the north-east and east (40 – 80 m) (Berlinck et al. 2004), where the studied area is located. In the bryozoan community of the northern coast of Bahia State, the highest values of richness were recorded at 40 m deep, decreasing at 50 m, where is the break of the continental shelf (Bittencourt et al. 2000, Dominguez et al. 2011). However, since ecological studies are scarce in Brazil, other aspects must be evaluated to identify factors influencing the structure of the bryozoan fauna of this region. As noted by López Gappa (2000) there is a trend in species richness, with either increases or decreases associated with increasing depth. It is likely that the depth-diversity relation varies locally (McKinney & Jackson 1989) as it is strongly related to the availability of hard substrata suitable for larval settlement (Lidgard 1990, Kuklinski 2002), which is perhaps the major factor affecting the occurrence and distribution of these animals (López Gappa 2000, Kuklinski et al. 2005, Ben Ismail et al. 2012).

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ANA C.S. ALMEIDA[1,2]
https://orcid.org/0000-0003-4899-1483

FACELUCIA B.C. SOUZA[2]
https://orcid.org/0000-0001-8499-1400

LEANDRO M. VIEIRA[1]
https://orcid.org/0000-0001-8661-8861

MARCOS M. NOGUEIRA[2]
https://orcid.org/0000-0002-9486-5149

[1]Universidade Federal de Pernambuco, Laboratório de
Estudos de Bryozoa (LAEBry), Centro de Biociências,
Avenida da Engenharia, s/n, Departamento de Zoologia,
Cidade Universitária, 50670-810 Recife, PE, Brazil

[2]Universidade Federal da Bahia, Grupo de Estudos Sistemática,
Ecologia e Biologia de Bryozoa, Museu de História Natural,
Rua Barão de Jeremoabo, S/N, Universidade Federal da Bahia,
Instituto de Biologia, Ondina, 40170-290 Salvador, BA, Brazil

Correspondence to: **Ana Carolina Sousa de Almeida**
E-mail: carol.salmeida@gmail.com

Author contributions

ACSA, FBCS and MMN designed the research. ACSA, LMV and MMN analysed data and wrote the manuscript. All authors read and approved the manuscript.

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