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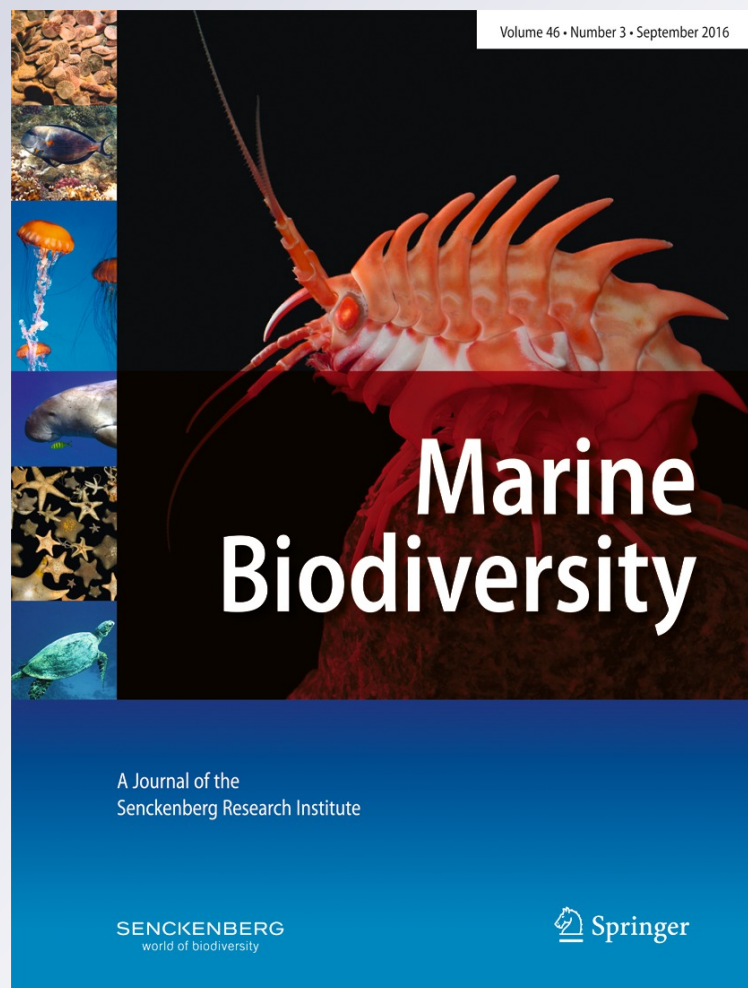
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Overview of the order Zoantharia (Cnidaria: Anthozoa) in Brazil

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Abstract Zoantharia (Hexacorallia) is an order of benthic cnidarians, which are known to play an important ecological role in many marine ecosystems. Although the order has a cosmopolitan distribution, including the tropical southwestern Atlantic, research on Brazilian zoantharian species diversity and distribution patterns is lacking. In order to start addressing this gap, we conducted shallow-water coastal and oceanic island sampling in parallel with an extensive literature review to summarize the knowledge of the order Zoantharia from Brazil. Additionally, mitochondrial 16S ribosomal DNA and cytochrome oxidase subunit I (COI) sequences from

specimens were determined to confirm their identity and phylogenetic position within the order. Our results show the presence of at least 13 zoantharian species in Brazilian waters, including first records of *Palythoa* aff. *clavata* and *Zoanthus* aff. *pulchellus*. Moreover, range extensions were confirmed for *Palythoa caribaeorum*, *P. grandiflora*, *P. variabilis*, *Zoanthus pulchellus*, and *Parazoanthus swiftii*. We also present the first report on the distribution patterns for all studied species in Brazil. The current study is expected to provide a baseline for further surveys in the tropical southwestern Atlantic, where Zoantharia species richness is still understudied and therefore very likely underestimated.

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Introduction

Reported from all oceans, zoantharians (Cnidaria: Anthozoa: Hexacorallia: Zoantharia) occur from the intertidal zone to depths greater than 5,000 m (Ryland et al. 2000; Reimer and Sinniger 2010). Most zoantharians do not produce a hard skeleton and are able to form extensive colonies, covering up to 50% of the substrate at some localities (Karlson 1983; Oigman-Pszczol et al. 2004). These colonies are commonly used for protection or as shelter by various invertebrates (Den Hartog and Holthuis 1984; Den Hartog and Türkay 1991; Messing et al. 1990; Pérez et al. 2005), and also as a food source for other marine animals, such as fishes, sea turtles, and sea stars (Gleibs and Mebs 1999; Stampar et al. 2007; Obuchi and Reimer 2011). Although zoantharians play a considerable ecological role in benthic ecosystems, species identification remains challenging due to their relatively simple body plan and high intraspecific plasticity (Burnett et al.

1997; Ryland and Lancaster 2003; Ong et al. 2013). As a result, they are usually neglected in marine surveys. However, studies combining morphological, ecological, and molecular data have proven to be an excellent way to identify these cnidarians (Reimer et al. 2004; Sinniger et al. 2008; Koupaei et al. 2014) and are also shedding light on their evolutionary relationships (Sinniger et al. 2005, 2010). The knowledge on the systematics of the order has increased with the description of new families, genera, and species, primarily in the Pacific and Indian Oceans (Sinniger et al. 2010; Fujii and Reimer 2011, 2013; Sinniger et al. 2013; Irei et al. 2015). Surveys undertaken at sites in the Atlantic Ocean, such as in the Caribbean (Swain and Wulff 2007; Reimer et al. 2012), Cape Verde islands (Reimer et al. 2010a), and Ascension Island (Reimer et al. 2014b) have reported potential new species and extended the distribution ranges for many others.

In Brazil, taxonomic and biogeographic research on the order Zoantharia is still in its infancy. The Brazilian coast from the mouth of the Amazon River, in the north, to the state of Santa Catarina, in the south, along with the oceanic islands (Rocas Atoll and Archipelagoes of Trindade and Martin Vaz, Fernando de Noronha and Saint Peter and Saint Paul), is recognized as an important biogeographic region, known as the Brazilian Province (Floeter et al. 2008; Briggs and Bowen 2012). Within this province that extends for more than 6,000 km in the tropical southwestern Atlantic, the diversity of other common reef organisms has been relatively well studied (e.g., phylogenetic and distribution patterns of scleractinian corals, sea anemones and reef fishes [Laborel 1970; Russo et al. 1994; Zamponi et al. 1998; Castro and Pires 2001; Floeter et al. 2001, 2008; Nunes et al. 2008, 2011; Bender et al. 2013]). Although zoantharians are broadly distributed in Brazilian waters, data such as species lists and phylogenetic analyses are still lacking. Due to their important ecological role in Brazilian marine ecosystems (Mendonça-Neto et al. 2008; Cruz et al. 2015a), improvement on the knowledge of zoantharian species diversity is needed to provide a foundation for further studies. In addition, a better understanding of zoantharian species' distributions would help in the monitor biotic and abiotic events that affect marine community structures, such as pathogen outbreaks (Acosta 2001), introduction of invasive species (Mantelatto et al. 2011), climate change (Shinzato et al. 2011), and the potential for phase shifts (Cruz et al. 2015a, b). Therefore, the present study aimed to: (1) provide a list of Zoantharia species reported from Brazil along with the placement of species in the phylogeny of the group, and (2) draw the first picture of species distribution patterns in the tropical southwestern Atlantic. This study provides a baseline for future research on Brazilian zoantharians and contributes to the ongoing discussion of the species diversity and evolutionary patterns of the order Zoantharia.

Materials and methods

Bibliographic review

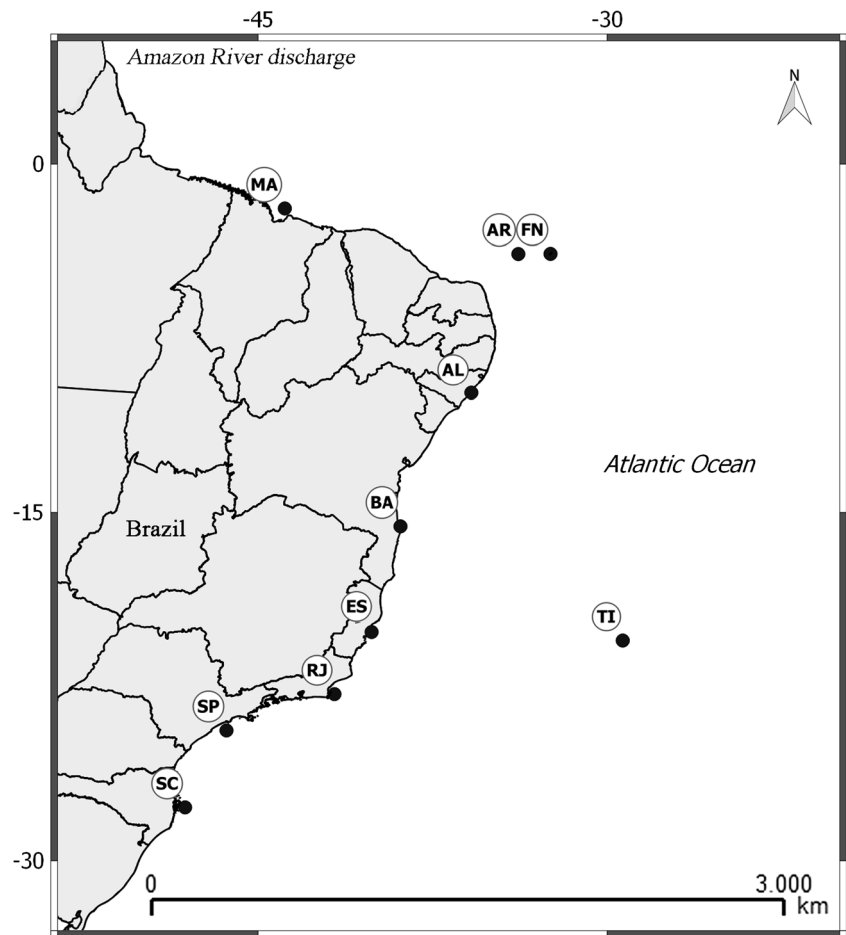
An extensive literature review was undertaken to summarize a list of Zoantharia species recorded from Brazilian waters. We included records from peer-reviewed papers and proceedings from the International Coral Reef Symposiums. In total, data from 69 scientific publications reporting zoantharians on the Brazilian coast and on oceanic islands were compiled. We followed recent revisions of the taxonomic nomenclature used in past literature in making our list of zoantharians from Brazil.

The genus *Protopalythoa*, previously thought to be separate from *Palythoa* (see, for example, Burnett et al. 1997, and Ryland and Lancaster 2003), has been considered as congeneric to *Palythoa* (Reimer et al. 2007b) and we therefore only use *Palythoa* in this study. Considering the anteriority rule, we have used *Savalia* Nardo, 1844 instead of its junior synonym *Gerardia* Lacazr-Duthiers, 1864 (Sinniger et al. 2005, 2007; Altuna et al. 2010). For the same reason, in this work we use *Zoanthus pulchellus* (Duchassaing and Michelotti, 1860) instead of *Z. nymphaeus* (Lesuer, 1817) following Duerden (1902) and Walsh (1967). *Palythoa brasiliensis* Heider, 1895, described from the Brazilian coast, has an incomplete original description (Kelecom and Solé-Cava 1982). In addition, it is most likely a synonym of *P. caribaeorum*, as junior synonyms of this latter species have also been reported from other locations in the Atlantic, such as *P. senegalensis* and *P. vicentina* in Reimer (2010). Furthermore, the holotype of *P. brasiliensis* is lost (Pax and Müller 1957). For these reasons, we have chosen not to include this species in the current study.

Specimen collection

Between 2010 and 2013, expeditions to collect zoantharians were carried out at ten sites along the Brazilian coast and on oceanic islands using SCUBA and snorkeling in depths ranging from 0 to 20 m (Fig. 1). Whenever possible, in situ images were taken prior to specimen sampling. In total, 31 specimens of zoantharians were collected, preserved in 95–100% ethanol and deposited in the Museum of Zoology, São Paulo University (MZUSP; collection numbers MZUSP 002655–002685). Two specimens previously deposited at the National Museum, Federal University of Rio de Janeiro (MNRJ), were also analyzed in the present study (MNRJ 1590 *Epizoanthus* sp. and MNRJ 1995 *Savalia* sp.) as they have been cited in previous literature (Migotto et al. 1999). Specimens were identified to the lowest taxonomic level possible and at least one sample from each morphotype was analyzed molecularly. Therefore, each species analyzed was identified based on the combination of morphological and molecular data, except *Epizoanthus*

Fig. 1 Sampling sites along the Brazilian coast (*AL* Alagoas, *BA* Bahia, *ES* Espírito Santo, *MA* Maranhão, *RJ* Rio de Janeiro, *SC* Santa Catarina and *SP* São Paulo) and at oceanic islands (*AR* Rocas Atol, *FN* Fernando de Noronha Archipelago and *TI* Trindade and Martins Vaz Archipelago)



sp. and *Savalia* sp., as these samples were initially preserved in formalin and it was not possible to extract DNA. In addition, probably due to high sediment content in the tissue from sample BR1 (identified herein as Parazoanthidae), attempts to extract genomic DNA from this specimen were unsuccessful.

Morphological analyses

Species identification and external morphological examination followed Pax (1910), West (1979), Burnett et al. (1997), Reimer (2010), and Reimer et al. (2013a). For each specimen, the following characters were analyzed: polyp and oral disk color(s), polyp form, numbers of tentacles, and presence/absence of sand encrustation.

DNA extraction, polymerase chain reaction (PCR) and sequencing

DNA was extracted from approximately 25 mg of tissue from each specimen using a DNeasy Blood and Tissue kit (Qiagen, Seoul, Korea), following the manufacturer's animal tissue protocol. PCR amplification was performed using HotStarTaq DNA polymerase (Qiagen, Seoul, Korea) according to the

manufacturer's instructions. Partial fragments of the mitochondrial markers 16S ribosomal DNA (mt 16S rDNA) and cytochrome oxidase subunit I (COI) were amplified using primers and procedures outlined in Sinniger et al. (2005) and Reimer et al. (2007a), respectively. Amplified products were visualized by 1% agarose gel electrophoresis and submitted to direct sequencing by Macrogen (Korea).

Phylogenetic analyses

Nucleotide sequences of COI and mt 16S rDNA were aligned and concatenated using Clustal Omega (Sievers et al. 2011). We amplified sequences of both COI and mt 16S rDNA markers for 19 specimens. These sequences were aligned with previously published sequences deposited in GenBank of Parazoanthidae, Sphenopidae, and Zoanthidae species from the Atlantic Ocean, using sequences from Epizoanthidae as an outgroup (Sinniger et al. 2005, 2008; Reimer et al. 2010a, b, 2012, 2013b), once the monophyly of this family and the sister-group relationship with other Zoantharia families was demonstrated (Sinniger et al. 2005). The concatenated (mt 16S rDNA+COI) alignment of Brazilian specimens and respective closely-related species' sequences from GenBank

contained 36 sequences with 1,223 sites, of which 497 sites were from COI and 726 sites were from mt 16S rDNA.

The alignment was inspected by eye and ambiguous positions were manually edited using MEGA6 (Tamura et al. 2013). Phylogenetic analyses were performed using PhyML (Guindon and Gascuel 2003) for Maximum-Likelihood (ML) with a Hasegawa-Kishino-Yano model (Hasegawa et al. 1985) of nucleotide distribution and estimated parameters. Robustness of the ML reconstruction was tested with 1,000 bootstrap replicates. Bayesian inference was performed with MrBayes 3.0 (Ronquist and Huelsenbeck 2003) under the general time-reversible model (Rodriguez et al. 1990) of nucleotide substitution matrix with eight categories. Markov chains Monte Carlo simulations were run for 1,000,000 generations, with log-likelihoods and topologies saved at 100-generations intervals. The first 1,000 topologies were discarded as burn-in, and trees generated from the remaining 9,000 trees. In addition, sequences obtained from specimens BR10 and BR18 were shorter than other sequences analyzed in this study and therefore were only compared for similarity following Bo et al. (2012), with no additional phylogenetic analyses. These sequences were compared with previously reported Zoantharia sequences using the National Center for Biotechnology Information's Basic Local Alignment Search Tool (NCBI-BLAST) search. New sequences determined in the present study were deposited in GenBank (accession numbers KT454341–KT454380).

Results

A total of 11 Zoantharia species has been recorded from Brazil in previous literature (Table 1). Sequences obtained from specimens BR10 and BR18 (COI from BR10, mt 16S rDNA from BR18) were only compared for similarity using BLAST. The COI sequence from BR10 had a length of 722 bp and BLAST comparison indicated it was identical (identity=100%, query coverage=91%) to previously reported sequences of *Palythoa tuberculosa* (KF840072). *P. tuberculosa* is from the Indian/Pacific Oceans and sibling to Atlantic *P. caribaeorum* (Reimer et al. 2012). The mt 16S rDNA sequence from BR18 had a length of 906 bp and BLAST search indicated it was identical (identity=100%, query coverage=83%) to previously reported sequences of *Palythoa* sp. *sakurajimensis* from the Pacific Ocean (DQ997842). Sister zoantharian species from the Atlantic and Indian/Pacific Oceans have high similarity or identical mtDNA sequences (Reimer et al. 2010a, 2012).

Four large clades corresponding to the families Epizoanthidae, Parazoanthidae, Sphenopidae, and Zoanthidae were retrieved in the resulting mt 16S rDNA + COI phylogenetic tree (Fig. 2). Family-level clades of Parazoanthidae, Sphenopidae, and Zoanthidae were generally well supported

in phylogenetic analyses (ML/Bayesian=55/1.0, 89/0.99, 94/1.0, respectively). Sequences from Brazilian specimens BR09 and BR12 grouped within the Sphenopidae and corresponded to the genus *Palythoa*. Sequences from specimen BR09 were identical to previously reported sequences of *P. grandiflora* from the Caribbean (ML/Bayesian=72/0.97), while sequences from BR12 were identical to *P. aff. variabilis* from Caribbean (ML/Bayesian=96/1.0).

Sequences from 13 specimens (BR03, BR05, BR11, BR13–17, BR19–20, BR27–29) grouped within the Zoanthidae clade, and corresponded to species from the genus *Zoanthus*. Specimens BR14, BR16–17, BR19–20 and BR28 had identical sequences and formed a clade with previously reported *Z. sociatus* sequences from the Caribbean (ML/Bayesian=96/0.98). Sequences from BR29 were identical to previously reported *Z. pulchellus* from the Caribbean (ML/Bayesian = 61/59). Sequences from BR03, BR05, BR11, BR13, BR15 and BR27 were identical and formed a clade with previously reported sequences of *Z. aff. pulchellus* from Cape Verde (64/100). Within the Parazoanthidae clade, sequences BR02, BR06, BR07 and BR23 were identical to each other and to previously reported sequences from *Parazoanthus swiftii* from the Caribbean.

A list of 31 specimens identified from Brazil on the basis of molecular data and general external morphological characters is provided (ESM1). Results of these analyses and the literature review confirmed the presence of at least 13 Zoantharia species in Brazil (*Palythoa caribaeorum*, *P. variabilis*, *P. grandiflora*, *P. aff. clavata*, *Zoanthus sociatus*, *Z. solanderi*, *Z. pulchellus*, *Z. aff. pulchellus*, *Isaurus tuberculatus*, *Parazoanthus swiftii*, *P. catenularis*, *Savalia* sp. and *Epizoanthus* sp.; Figs. 3 and 4).

In Brazil, the suborder Brachycnemina is represented by families Sphenopidae and Zoanthidae, whereas the suborder Macrocnemina is represented by the families Parazoanthidae and Epizoanthidae. Reports of *Isaurus tuberculatus* was shown to be limited to the northeastern of Brazil, while *Zoanthus* and *Epizoanthus* have São Paulo State as the southernmost distribution limit (Fig. 3). The genus *Palythoa* and the family Parazoanthidae are reported all the way to Santa Catarina State in Brazil (Fig. 3).

Within *Palythoa*, *P. caribaeorum*, *P. grandiflora* and *P. variabilis* are widespread species, occurring from Santa Catarina State to the northeastern region (Fig. 3). However, their congener *P. aff. clavata* is reported herein only from Trindade Island and represents the first record in Brazil for this species. Within the genus *Zoanthus*, *Z. sociatus*, *Z. solanderi*, and *Z. pulchellus* were reported from several sites along the coast as well as from the oceanic islands. Finally, reports of the potentially undescribed species *Z. aff. pulchellus*, from São Paulo and Rio de Janeiro states as well as from Trindade and Martins Vaz Archipelago are new records for the southwestern Atlantic.

Table 1 Literature review of zoantharian species records from Brazil. Symbols indicate range extensions resulting from this study

Species name	Previous sites recorded ^a	References ^b	Site records from this study
<i>Epizoanthus</i> sp.	BA, ES, RJ, SP	1-2	
<i>Isaurus tuberculatus</i>	BA, CE, FN, RN	1, 3-7	
Parazoanthidae			SC+
<i>Parazoanthus</i> sp.	AS, BA, ES, MA, RJ, SC	1, 8-11	
<i>Parazoanthus swiftii</i>	RJ	12	RJ, SC+, SP+
<i>Parazoanthus catenularis</i>	MA	12	
<i>Palythoa</i> aff. <i>clavata</i>			TI+
<i>Palythoa caribaeorum</i>	AL, AR, AS, BA, CE, FN, PE, RJ, RN, SC, SP	1-2, 7-9, 11, 13-47	AR, BA, ES, FN, RJ, SC, SP, TI+
<i>Palythoa grandiflora</i>	RJ	21	AL+, RJ, SC+, SP+
<i>Palythoa variabilis</i>	BA ^c , CE-SP, FN, SC	1-2, 7, 11, 13-14, 18, 23, 33-34, 38, 42, 46, 48, 50-54, 55c, 56c, 57	TI+
<i>Palythoa</i> sp.	AR, BA, ES, FN, RJ, RN, SP, TI	1, 8, 14-15	
<i>Palythoa</i> spp.	BA, RJ	17, 59	
<i>Savalia</i> sp.	SP	1-2	
<i>Zoanthus pulchellus</i>	AS, BA, ES, RJ	1, 9, 60	SP+
<i>Zoanthus</i> aff. <i>pulchellus</i>			ES+, RJ+, SP+, TI+
<i>Zoanthus sociatus</i>	AL, AS, AR, BA, CE, ES, FN, RJ, RN, PB, PE, SC ^d , SP	1-4, 7-9, 13, 15-16, 18, 21, 29, 33, 36, 45, 61-62, 63 ^d , 64	AR, SP
<i>Zoanthus solanderi</i>	AL, BA, ES, FN, PE, RJ, RN, SP	1, 18, 28, 34	
<i>Zoanthus</i> spp.	BA	17, 38, 39	
Zoanthidea	BA, NE, RJ, RN, NE	35, 43, 65-69	

^a Abbreviations used for sites along the Brazilian coast: *AL*Alagoas, *BA*Bahia, *CE*Ceará, *ES*Espírito Santo, *MA*Maranhão, *NE*Northeast region, *PB*Paraíba, *PE*Pernambuco, *RJ*Rio de Janeiro, *RN*Rio Grande do Norte, *SC*Santa Catarina, and *SP*São Paulo. Those for oceanic islands are: *ARR*Rocas Atoll, *ASS*Saint Peter and Saint Paul Archipelago, *FN*Fernando de Noronha Archipelago, and *TI*Trindade and Martins Vaz Archipelago

^b The references are numbered according to their order of citation and correspond to: 1 Migotto et al. 1999, 2 Da Silveira and Morandini 2011, 3 Laborel 1970, 4 Pires et al. 1992, 5 Grohman and Peixinho 1995, 6 Rabelo and Matthews-Cascon 2007, 7 Soares et al. 2011, 8 Castro et al. 1999, 9 Amaral et al. 2000, 10 Campos et al. 2005, 11 Bouzon et al. 2012, 12 Swain 2009, 13 Sebens 1977, 14 Kelecom and Solé-Cava 1982, 15 Echeverría et al. 1997, 16 Villaza and Pitombo 1997, 17 De Barros et al. 2000, 18 Acosta 2001, 19 Acosta et al. 2001, 20 MacCord and Duarte 2002, 21 Oigman-Pszczol et al. 2004, 22 Acosta et al. 2005A, 23 Boscolo and Silveira 2005, 24 Pérez et al. 2005, 25 Soares et al. 2006, 26 Acosta and González 2007, 27 Stampar et al. 2007, 28 Chimetto et al. 2008, 29 Correia and Sovierzoski 2008, 30 Mendonça-Neto et al. 2008, 31 Mendonça-Neto and Gama 2008, 32 Souza et al. 2008, 33 Amaral et al. 2009, 34 Chimetto et al. 2010, 35 Francini-Filho and Moura 2010, 36 Francini-Filho et al. 2010, 37 Azevedo et al. 2011, 38 Chimetto et al. 2011, 39 Segal and Castro 2011, 40 Castro et al. 2012, 41 Costa et al. 2011, 42 Almeida et al. 2012, 43 Longo et al. 2012, 44 Martinez et al. 2012, 45 Melo et al. 2012, 46 Rabelo et al. 2013, 47 De Santana et al. 2014, 48 Rabelo et al. 2014, 48 Longo et al. 2000, 50 Kelmo et al. 2003, 51 Metri and Rocha 2008, 52 Wilke et al. 2008, 53 Wilke et al. 2009, 54 Costa et al. 2014, 55 Cruz et al. 2015A, 56 Cruz et al. 2015B, 57 Soares and Souza 2013, 58 Gasparini and Floeter 2001, 59 Teixeira et al. 2008, 60 Villar et al. 2003, 61 Rohlf's and Belém 1994, 62 Sarmento and Correia 2002, 63 Gherardi 2004, 64 Soares and Sousa 2011, 65 Coelho and Ramos-Porto 1980, 66 Costa Jr. et al. 2000, 67 Ferreira et al. 2001, 68 Costa Jr. et al. 2002, 69 Floeter et al. 2007

^c Recorded to BA as *Palythoa* cf. *variabilis*

^d Recorded to SC as *Zoanthus sociatus*; however specimens are *Palythoa grandiflora* (analyses of unpublished images, pers. comm. D. Gherardi)

Within the family Parazoanthidae, *Parazoanthus swiftii* was recorded from Santa Catarina, São Paulo, and Rio de Janeiro states, while *P. catenularis* was reported only from Maranhão state. The literature review also revealed an unidentified *Parazoanthus* sp. from Espírito Santo and Bahia states, as well as from Saint Peter and Saint Paul Archipelago. The genus *Savalia* was recorded only from São Paulo state, and an unidentified specimen belonging to Parazoanthidae (BR01) was found off Santa Catarina state. Lastly, *Epizoanthus* sp. (family Epizoanthidae) was recorded from São Paulo, Rio de Janeiro, Espírito Santo and Bahia states.

Discussion

The literature review and sampling confirmed the presence of at least 13 zoantharian species in Brazilian waters (Fig. 3). Despite the relatively large number of past studies mentioning Zoantharia from Brazil, only one paper has specifically focused on the taxonomy of the group (Rohlf's and Belém 1994). The paucity and plasticity of diagnostic characters utilized in species identification have been a stumbling block in the understanding of both the diversity and biogeography of Zoantharia. In many cases, these problems have led to inexact higher-level taxonomic identification (i.e., order/genera level)

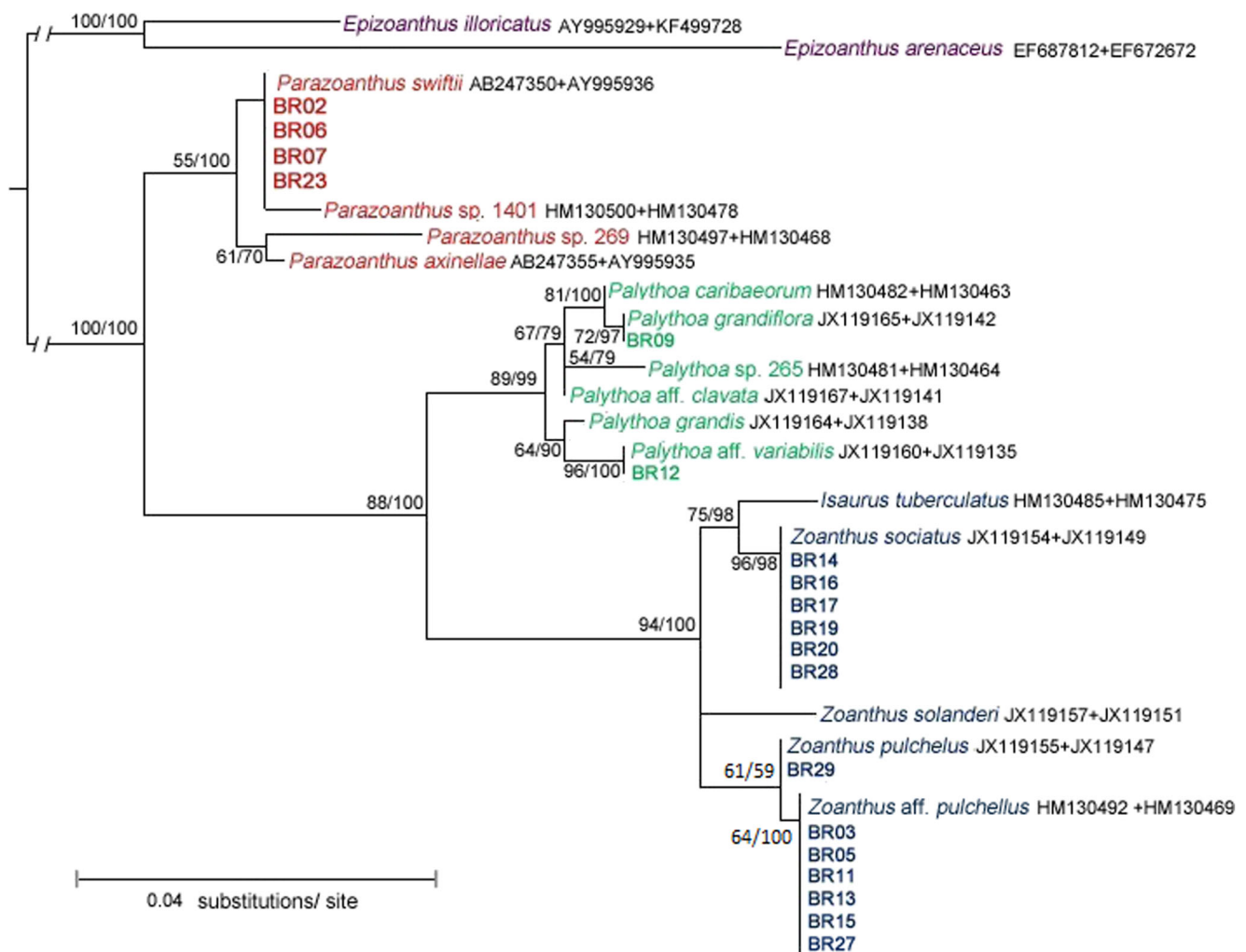


Fig. 2 Maximum likelihood (ML) tree obtained from alignments of mt 16S rDNA+COI sequences. Values at branches represent ML bootstraps and Bayesian posterior probabilities. Sequences from GenBank are

indicated by accession numbers following species name, while sequences of specimens from Brazil collected in this study are shown with same codes as in ESM1. Sequences of *Epizoanthus* spp. were used as outgroup

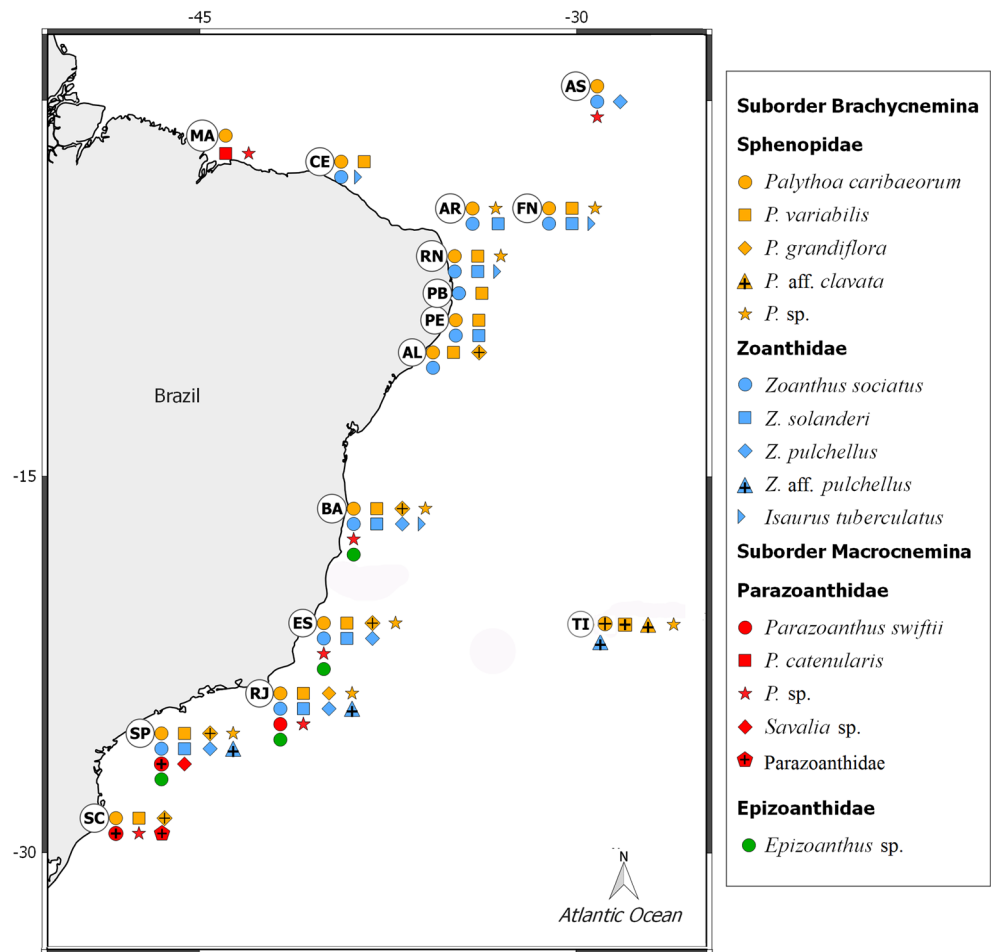
or to mistaken identification (e.g., *Epizoanthus gabrielli* in Cruz et al. 2015b is actually a species of the genus *Palythoa* [Cruz et al. 2015a]). Similarly, *Zoanthus pacificus* has been reported from Espírito Santo state (Rohlf, unpublished), but this record is likely to be *Z. sociatus*. This is because *Z. pacificus* is described from the Pacific Ocean and is most probably a junior synonym of *Z. sansibaricus* (Reimer et al. 2004). In addition, *Z. sansibaricus* is the sister species of *Z. sociatus* (Reimer et al. 2012), which occurs in Atlantic Ocean. Because of such problems, unconfirmed zoantharian distribution data based solely on past literature may be prone to error and should be interpreted carefully.

Phenotypic plasticity has led to the description of numerous synonym species in Zoantharia (see Burnett et al. 1997; Reimer et al. 2004, 2012), as many morphological characteristics used for identification can have high intraspecific variation. For example, Kamezaki et al. (2013) showed that color variation occurs at different depths in *Zoanthus sansibaricus*.

Likewise, sites with low hydrodynamic energy may lead to polyps with longer columns than those from the same species inhabiting sites with stronger currents and wave action (Reimer et al. 2006). Furthermore, polyp size and number of tentacles and mesenteries usually increase during ontogeny (Karlson 1988). Thus, DNA-based analyses are some of the most effective methods of zoantharian species identification as they are independent of intraspecific morphological variability (Shearer and Coffroth 2008). The high morphological plasticity of many zoantharians may be a way to facilitate colonization and adaptation to a wide range of habitats, and may also allow survivorship during environmental changes (Ong et al. 2013).

BLAST results and morphological analyses of specimen BR18 collected in Trindade Island, here identified as *Palythoa* aff. *clavata*, suggest a high similarity to *P. aff. clavata* previously reported from Florida (Reimer et al. 2012). Due to the vague and short original description of *P. clavata*

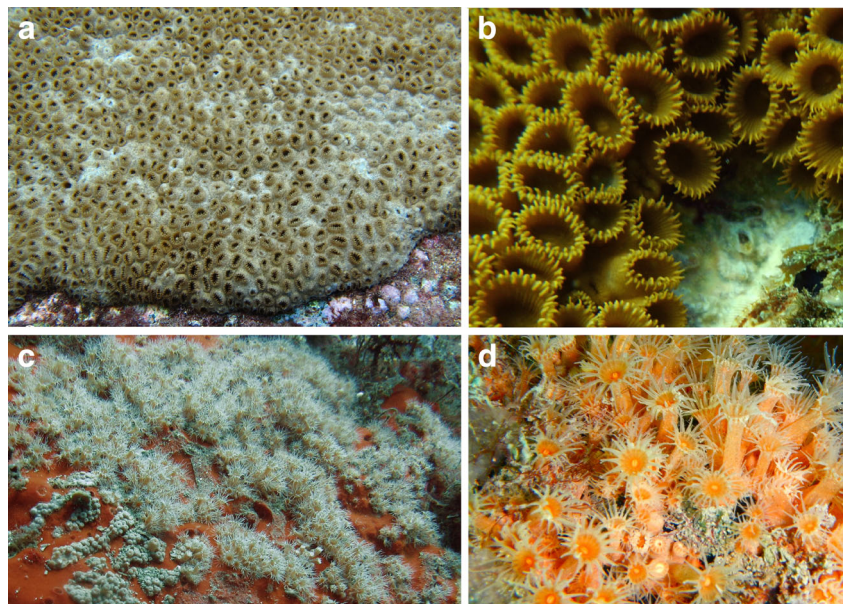
Fig. 3 Distribution of zoantharians in Brazil. Symbols marked with a cross correspond to range extensions presented in this study. The abbreviations used for sites along the Brazilian coast are: *AL* Alagoas, *BA* Bahia, *CE* Ceará, *ES* Espírito Santo, *MA* Maranhão, *PB* Paraíba, *PE* Pernambuco, *RJ* Rio de Janeiro, *RN* Rio Grande do Norte, *SC* Santa Catarina, *SP* São Paulo; those to oceanic islands are *AS* Saint Peter and Saint Paul Archipelago, *ARR* Rocas Atol, *FN* Fernando de Noronha Archipelago, *TT* Trindade and Martins Vaz Archipelago



(Duchassaing 1850), the specimen in Reimer et al. (2012) as well as BR18 may represent an undescribed species. Although there have been no studies on the sexual reproduction of this

putatively undescribed species, it is reasonable to expect that its larval dispersal is similar to other *Palythoa* spp., which can have planktonic larvae living up to 170 days (Polak et al.

Fig. 4 Images of common zoantharian species in Brazil: *Palythoa caribaeorum* (a and b) and *Parazoanthus swiftii* (c and d)



2011). Thus, *Palythoa* aff. *clavata* may have a high dispersal ability, explaining how it has been recorded from Florida and the oceanic islands of Ascension (Reimer et al. 2014b) and Trindade (present study). Further surveys in Brazil should confirm if the distribution of this species is limited to Trindade Island. As well, molecular data from *P.* aff. *clavata* indicate that it is closely related to *P.* sp. *sakurajimensis* from the Pacific Ocean. There are similar records of sister zoantharian species from the Atlantic and Indian/Pacific Oceans with highly similar or identical mtDNA sequences (Reimer et al. 2010a, 2012). This is likely a result of the low mutation rate of mitochondrial DNA in most anthozoans (Shearer et al. 2002; Stampar et al. 2014), and thus only molecular markers with higher resolution can differentiate sister zoantharian species. Because of this, specimens need to have sampling location data included to help improve identification.

Specimen BR12 had identical mitochondrial sequences to *Palythoa* aff. *variabilis* from Florida. Unlike the Florida specimen, BR12 had morphological characters that matched the original description of *P. variabilis* and therefore we identified this specimen as the latter. Specimens of BR12 and BR18 only consisted of a few polyps each. For this reason, collection of more and larger specimens, followed by examination, should help us to understand the morphological variation within these species. Our results indicate the first record in the southwestern Atlantic of *Zoanthus* aff. *pulchellus* (BR03, BR05, BR11, BR13, BR15 and BR27), which was distributed along the southern coast of Brazil (São Paulo and Rio de Janeiro states) as well as Trindade Island. Similar specimens have previously been reported for the Caribbean (Reimer et al. 2012) and Cape Verde (Reimer et al. 2010a).

In Brazil, the suborder Macrocnemina is represented by at least four species belonging to families Parazoanthidae (three species) and Epizoanthidae (one species). It is likely that other macrocnemic zoantharians occur within the Brazilian province, especially considering that these species usually occur in deeper waters, and other understudied or cryptic habitats (e.g., family Microzoanthidae, Fujii and Reimer 2011). Polyps of macrocnemic specimens MNRJ 1590 (*Epizoanthus* sp.), MNRJ 1999 (*Savalia* sp.), and BR01 (Parazoanthidae) were contracted, and besides from a photograph of MNRJ 1999 (A. Migotto, personal communication), in situ images are not available for these specimens. These specimens could not be identified to species level due to the paucity of external morphological information and the failure to extract DNA from them. We have not included specimen BR01 in species list of zoantharians in Brazil, here identified as Parazoanthidae, as it has a scleroprotein layer, and thus may belong to same species as MNRJ 1999 (*Savalia* sp.). Histological examination of these specimens should help in confirming their identification. The macrocnemic species with the widest distribution along the Brazilian coast is *Parazoanthus swiftii*, which has also been reported from the Caribbean (Swain and Wulff 2007)

and Ascension Island (Reimer et al. 2014b). Therefore, the ability to widely disperse appears to be present in both suborders of Zoantharia.

The distribution of zoantharians is at least partly due to their physiological and/or ecological traits, which often act as filters in the establishment of many marine species (Briggs 1974). For instance, environmental factors such as water temperature may act as a barrier in the distribution of zooxanthellate zoantharians (Ryland et al. 2000; Reimer et al. 2008a). In addition, it has been demonstrated that *Zoanthus* spp. are sensitive to variations in salinity (Soares and Sousa 2011). Therefore, the thermohaline properties of water masses in south Brazil (Piola et al. 2000) may be to some extent responsible for the southern distribution limits of *Zoanthus* and *Palythoa* spp. in this region. Moreover, most *Palythoa* species in this study have a wider distribution than *Isaurus tuberculatus*. For example, *Palythoa caribaeorum* is widespread along the Brazilian coast and oceanic islands, whereas *Isaurus tuberculatus* is restricted to northeastern of Brazilian Province. It is conceivable that post-settlement difficulties, such as habitat availability or physiological requirements, may restrict the establishment of *I. tuberculatus*. However, as this species is relatively cryptic (Reimer et al. 2008b), further investigations are needed to confirm the distribution range of this species.

All zoantharian genera recorded in Brazilian waters have previously been reported from the Caribbean (Messing et al. 1990; Acosta et al. 2005b; Swain and Wulff 2007; Reimer et al. 2012), which in turn has a higher zoantharian diversity than Brazil. This pattern has also been observed in other groups of marine animals (Tittensor et al. 2010), and the Caribbean province may act as both a center of origin and a center of accumulation of species through geological time (Rocha et al. 2008; Briggs and Bowen 2013). In addition, the zoantharian diversity recently reported from Ascension Island is relatively low (four spp.; Reimer et al. 2014b), similar to neighboring Brazilian Trindade Island (four spp.). These data also indicate a related pattern of decreasing diversity in oceanic islands, as seen in other common reef animals, such as fishes (Floeter et al. 2008).

Conclusive species-level identifications of some specimens from Brazil in this and previous studies are still required (in Macrocnemina; *Savalia* sp., *Epizoanthus* sp., Parazoanthidae; and in Brachycnemina; *Palythoa* aff. *clavata* and *Zoanthus* aff. *pulchellus*), but for now no zoantharian species endemic to Brazil are known. This situation is different than in other hexacorallian orders—e.g., the endemic Brazilian sea anemone *Bunodosoma caissarum* Correa, 1964 (Russo and Solé-Cava 1991), and the scleractinian coral *Mussismilia brasiliensis* (Verrill, 1868) (Castro and Pires 2001). Similarly, endemism in Brazil is also shown by three species of the hydrozoan fire coral genus *Millepora* (Amaral et al. 2008). The lack of endemic zoantharian species may be due to

exceptionally long-lived zoantharian larvae (Ryland et al. 2000; Polak et al. 2011) as well as their ability to reproduce asexually (Ryland 1997; Acosta et al. 2005a), both of which could lead to higher dispersal in the Atlantic Ocean. In addition, rafting may be an explanation for long-distance dispersal, which could be relevant for zoantharian species that live in shallow waters as the scleractinian coral *Favia fragum* (Hoeksema et al. 2012). Still, it is noteworthy that sympatric processes have also not led to the speciation of zoantharians in the Brazilian province, as has been reported in other animals with long living larvae, such as reef fishes (Rocha 2003). However, as the order Zoantharia has not yet been exhaustively studied in Brazil, more data are needed to make final conclusions on these observations.

Conclusions

Despite many zoantharian species having wide distribution ranges in Brazil, a paucity of morphological diagnostic characters combined with high intraspecific plasticity have historically hampered Zoantharia species identification and overall research on the order. For example, until this study there has only been one previously published record of *Palythoa caribaeorum* from Santa Catarina state (Bouzon et al. 2012), even though this species is widespread and abundant in shallow-water rocky shores, as well as easy to identify in the field. Overall, analyses of zoantharian distributions at a large geographic scale (e.g., thousands of kilometers) still suffer from scarce distribution records. However, recent zoantharian research has started to confirm species distributions in several regions around the globe (e.g., Reimer et al. 2008c in the Galapagos; Sinniger et al. 2013 on Hawaiian seamounts; Koupaei et al. 2014 in the Persian Gulf; Reimer et al. 2014a in the Central Indo-Pacific). It is predicted that additional Zoantharia species will be recorded from Brazil with the advance of research. As well, it will become necessary to study a wide range of biological traits, such as reproduction and interactions with other benthic organisms, in order to better understand species distribution and abundance patterns of the order Zoantharia.

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