

The flourishing and vulnerabilities of zoantharians on Southwestern Atlantic reefs

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ABSTRACT

In the Southwestern Atlantic reefs (SWA), some species of massive scleractinians and zoantharians are adapted to turbid waters, periodic desiccation, and sediment resuspension events. Moreover, phase shifts in this region have mostly been characterized by the emergence of algae and, less typically, zoantharians. However, nutrient excess and organic pollution are key drivers of the hard coral habitat degradation and may, thus, favor the emergence of novel zoantharian-dominated habitats. Many zoantharian species, particularly those from the genera *Palythoa* and *Zoanthus*, have traits that could help them thrive under conditions detrimental to reef-building corals, including rapid growth, several asexual reproduction strategies, high morphological plasticity, and generalist nutrient acquisition strategies. Thus, in a near future, stress-tolerant zoantharians may thrive in nutrient-enriched subtidal SWA locations under low heat stress, such as, upwelling. Overall, coral-zoantharian phase shifts in the SWA may decrease the species richness of reef communities, ultimately influencing ecosystem functioning and services, such as the provision of nursery habitats, fish biomass production, and coastline protection. However, zoantharians will also be threatened at intertidal zones, which are expected to experience higher heat stress, solar radiation, and sea-level rise. Although zoantharians appear to cope well with some local stressors (e.g., decreasing water quality), they are vulnerable to climate change (e.g., heatwaves), invasive species (*Tubastraea* spp.), microplastics, diseases, and mostly restricted to a narrow depth range (0–15 m depth) in SWA reefs. This shallow zone is particularly affected by climate change, compressing the three-dimensional habitat and limiting depth refugia in deeper SWA reefs. As mesophotic ecosystems have been hypothesized as short-term refuges to disturbances for some species, the narrow depth limit of zoantharians seems to be a potential factor that might increase their vulnerability to growing climate change pressures in SWA shallow-water reefs. Together, these could lead to both range expansions in some locations and loss of suitable reef habitats in other sites. Additional research is needed to better understand the systemic responses of these novel SWA reefs to the concert of increasing and interactive local and global stressors, and their implications for ecosystem functioning and service provisions.

1. Introduction: Southwestern Atlantic reefs (SWA)

Coral reefs are undergoing major and rapid transformations in their structure and function (Hughes et al., 2017). Recently, these processes have been largely driven by local (e.g., eutrophication) and global (e.g., marine heatwaves) impacts, which tend to be exacerbated by climate

change (Hughes et al., 2018). On some formerly hard-coral-dominated reefs, non-reef-building organisms such as algae, sponges, octocorals, and zoantharians have established and become dominant (Norström et al., 2009; Rossi, 2013; Lesser and Slattery, 2020; Reimer et al., 2021). These phase shifts may be temporary or long-lasting. For instance, if an alternative state is unstable, removing the stressor that causes the shift

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(e.g., sewage pollution) may allow the system to return to its original state (e.g., reef-building coral dominance) (Stimson, 2018).

Phase shifts and their stability have been extensively studied in the Caribbean, where they typically involve transitions from coral-to either algal-, sponge-, or octocoral-dominance (Mumby, 2009; Bell et al., 2013; McCauley and Goulet, 2019; Lasker et al., 2020a,b). Phase shifts in the SWA reefs are much less frequently monitored or studied (Cruz et al., 2015a, 2015b, 2016, 2018), compared to those in the Caribbean and Indo-Pacific ecosystems (Mumby, 2009; Lasker et al., 2020a,b), although it could be more common than recorded in scientific literature until now (Reimer et al., 2021).

SWA reefs off the Brazilian coast are the richest and largest reef complexes in the South Atlantic (Leão et al., 2016; Bastos et al., 2018; Mies et al., 2020). Overall, SWA reefs are characterized by a relatively low richness (19 species) but high endemism (>20%) of shallow-water zooxanthellate scleractinians, and a significant cover of coralline algae (Nunes et al., 2011; Leão et al., 2016) and benthic suspension feeders such as bryozoans (Bastos et al., 2018) and zoantharians (Santos et al., 2016, 2019; Teixeira et al., 2021). In these reef ecosystems, massive scleractinians (Leão et al., 2016; Mies et al., 2020) and zoantharians (Acosta and González, 2007; Rabelo et al., 2013) have adapted to the turbid local environmental conditions (Soares et al., 2021).

Unlike in neighboring Caribbean reefs, phase shifts in the SWA are characterized by the emergence of algae and zoantharians (Cruz et al., 2018). Reimer et al. (2021), in a review on phase shifts and dominance of *Zoanthus* and *Palythoa* species, classified the substrate cover by species of these genera worldwide in three categories: 1) 'dominance', in which these zoantharians are dominant but no information on past ecosystem states is available from published studies; 2) 'barrens', in which these genera have replaced another benthic community but no information is available on this state's persistence over time; and 3) 'phase shifts', in which the zoantharians have replaced other benthic groups and have persisted for five years or more. Based on these classification, only one case of zoantharian phase shift has been reported (Todos os Santos Bay, Brazil, South Atlantic) (Cruz et al., 2015a), whereas eight barrens and eight dominant cases have been reported worldwide (Reimer et al., 2021). The same study highlights that these numbers are probably underestimated due to a lack of long-term monitoring initiatives that consider zoantharians.

Zoantharian barren habitats may arise due to ongoing environmental changes (González-Delgado et al., 2018; Reimer et al., 2021), highlighting their importance in future studies. However, it is currently not clear which environmental conditions or zoantharian traits promote or impede the establishment and the emergence of these novel communities. In fact, we understand even less how biodiverse these systems are/will be, how they will function, and how vulnerable they may be to the ever increasing local and global pressures. Thus, a better understanding of the dominance of zoantharians in present-day and future reef scenarios is necessary. These encrusting soft corals have long been neglected in research, despite being an emergent and dominant reef group under certain environmental conditions that are not fully understood especially in marginal reefs (Camp et al., 2018; Burt et al., 2020) such as those from the SWA (Mies et al., 2020).

Marginal reefs have been recently defined as communities developed in hard bottoms that survive under suboptimal or extreme conditions (Burt et al., 2020; Soares 2020). Knowledge on the impacts, phase shift and ecological state of tropical reefs stem mainly from scientific studies conducted in the Caribbean Sea and Indo-Pacific (Morais et al., 2018), places where many reefs have optimal conditions for coral growth and development (e.g., narrow sea temperature variability and clear waters) (Soares et al., 2021). Nonetheless, information on zoantharian responses to water quality, heatwaves, invasive species, pollution, and climate change, particularly in ecoregions outside the Indo-Pacific and Caribbean (Morais et al., 2018) are still scarce. Moreover, such geographic biases in research undermine the potential for understanding the resistance and environmental changes of all tropical coral reefs (Soares et al.,

2021), which must include ecosystems under suboptimal conditions (Camp et al., 2018; Burt et al., 2020; Soares, 2020) such as SWA turbid-zone reefs.

In order to address these important knowledge gaps, this perspective article aims to discuss the: 1) potential adaptations and dominance of zoantharians on SWA marginal reefs; 2) environmental drivers promoting the regional success of zoantharians and phase shifts in SWA; 3) vulnerability of zoantharians to climate change, invasive species, microplastics, diseases, and narrow depth range in SWA reefs; and 4) how the dominance (or decline) of these zoantharians will impact the structure and functioning, as well the composition of habitats and geo-ecological functions, of future SWA reefs. Finally, we discussed important questions to guide future research on poorly known SWA reefs. To address these aims, a qualitative analysis of literature on dominant zoantharians and SWA was performed (Supplementary Material I).

2. Zoantharian adaptations that promote dominance on intertidal and shallow-water reefs SWA

To date, 14 zoantharian species belonging to the genera *Palythoa*, *Isaurus*, *Zoanthus*, *Epizoanthus*, *Bergia*, *Terrazoanthus*, *Savalia*, and *Parazoanthus* have been identified in the shallow waters from SWA (Santos et al., 2016, 2019; Vaga et al., 2021, Fig. 1). Unlike some scleractinians (e.g., *Mussismilia* spp.), no Zoantharia endemic species were reported to SWA. Brazilian zoantharian species are important components of intertidal and shallow-water (<15 m) reefs on both tropical and subtropical Atlantic coasts, as well as on the oceanic islands (Santos et al., 2016, 2019) (Fig. 1). *Palythoa* species are especially abundant within a narrow depth range in SWA (i.e., 1–7 m; Aued et al., 2018) and occur in marginal reef habitats that are generally unsuitable for many stress-sensitive scleractinians, such as tide pools (e.g., sandstone reefs or crystalline outcrops), shallow highly wave-exposed (e.g., mesotidal), and moderately turbid biogenic reefs (Aued et al., 2018; Mies et al., 2020; Soares et al., 2021).

Compared to scleractinian corals, some zoantharian species, particularly those belonging to *Palythoa* and *Zoanthus*, have morphological and physiological traits that enhance their ability to thrive and persist in shallow-disturbed habitats (Cooke, 1976; Sebens, 1982; Karlson, 1983; Ong et al., 2013; Reimer et al., 2021). First, the polyp morphology of some *Palythoa* species may present advantages under stress situations, such as sediment inputs, which are generally common in marginal SWA reefs (Leão et al., 2016). For example, *P. variabilis* and *P. grandiflora* have long expandable column-shaped polyps that enable their survival in high sedimentation localities (Rabelo et al., 2015). Moreover, *P. caribaeorum* and *Z. sociatus* can colonize areas subjected to strong wave action, and endure desiccation and solar radiation exposure during low tides, such as in intertidal sandstone reefs (Sebens, 1982; Rabelo et al., 2013, 2014, 2015) (Fig. 2).

Regarding their dispersal modes, species have strategies such as: fast growth rates (*P. caribaeorum* [11.0 cm²/month] and *Z. sociatus* [10.6 cm²/month] in the northeastern coast of Brazil [Rabelo et al., 2013; Silva et al., 2015]) that allow them to spread rapidly over large portions of the benthos following disturbances; and differential reproductive strategies (colonies of *P. caribaeorum*, *P. variabilis*, and *Z. sociatus* are hermaphrodite (Fadlallah et al., 1984; Boscolo and Silveira, 2005), *P. variabilis* and *P. caribaeorum* have a high frequency of fertile polyps [83% and 72%, respectively], high frequency of female colonies in reproductive condition (65.3% and 41.7%, respectively), and apparently continuous gametogenesis (Boscolo and Silveira, 2005). Also, *Palythoa* and *Zoanthus* can expand via several asexual reproductive modes (Acosta et al., 2001, 2005; González-Muñoz et al., 2019), and some species produce large amounts of mucus that allow them to occupy marginal habitats (e.g., tide pools and shallow areas) subjected to periodic desiccation and intense sunlight stress (Fig. 2).

In the SWA, the mucus of *P. caribaeorum*, *P. variabilis*, and *Z. solanderi* are characterized by high microbial diversity (Chimetto et al., 2009).

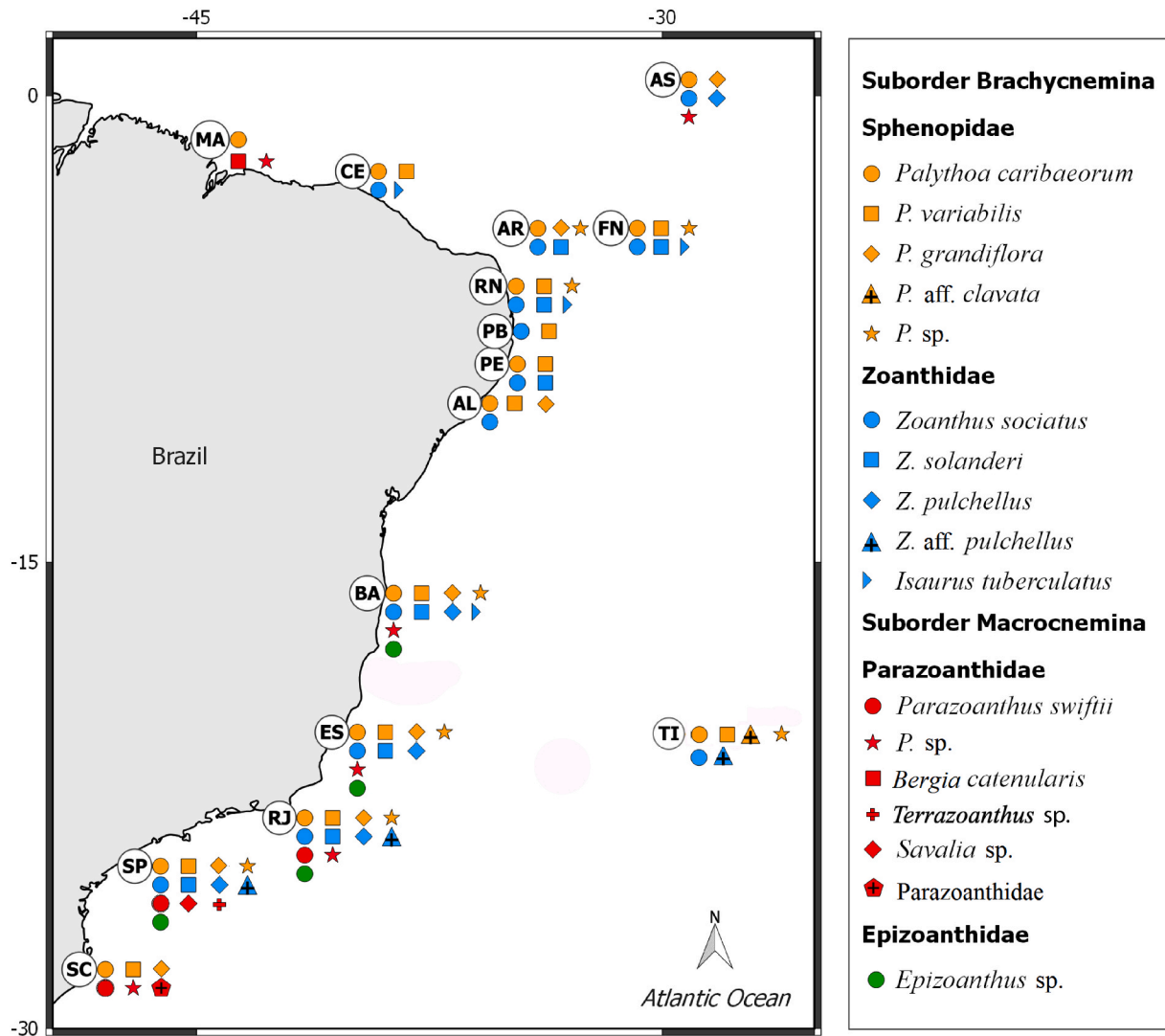


Fig. 1. Shallow water Zoantharia distribution along the Southwestern Atlantic reefs (the Brazilian coast; Santos et al., 2016, 2019; Vaga et al., 2021). The abbreviations used for sites along the SWA coast (Brazil) are: MA Maranhão CE Ceará, RN Rio Grande do Norte, PB Paraíba, PE Pernambuco, AL Alagoas, BA Bahia, ES Espírito Santo, RJ Rio de Janeiro, SP São Paulo, SC Santa Catarina; those to oceanic islands are AS Saint Peter and Saint Paul Archipelago, AR Rocas Atoll, FN Fernando de Noronha Archipelago, TI Trindade and Martim Vaz Archipelago.

These bacteria may play a key physiological role in their health status, such as the provision of essential nutrients or the metabolism of waste products (Chimetto et al., 2009). Furthermore, the selection of different zooxanthellae genera (photosynthetic endosymbionts of the family Symbiodiniaceae; Muscatine and Hand, 1958; LaJeunesse et al., 2018) could be advantageous. For example, the greater flexibility in the selection of some *Cladocopium* and *Symbiodinium* lineages by the zoantharian *Z. sociatus* could allow the host persistence in different environments (LaJeunesse, 2002; Rabelo et al., 2014). Similarly, its sibling species from the Indo-Pacific region, *Z. sansibaricus*, can also associate with *Cladocopium* spp. or *Symbiodinium* spp. symbionts (Reimer et al., 2016; Kamezaki et al., 2013). On the other hand, *Palythoa* spp. from the SWA associated with species of *Cladocopium*, *Symbiodinium* and *Durusdinium* (LaJeunesse, 2002; Reimer et al., 2010), while species of *Palythoa* from the Indo-Pacific are reported to be associated with different lineages of *Cladocopium* and *Durusdinium* endosymbionts (Burnett 2002; Wee et al., 2021). The flexible association with distinct Symbiodiniaceae lineages by the same zoantharian species may be related to environmental factors that differ among depths or geographical locations (Burnett, 2002; Kamezaki et al., 2013).

Some of the most common SWA zooxanthellate zoantharians (e.g.,

Z. sociatus, *P. caribaeorum*, and *P. grandiflora* - Fig. 1) are mixotrophic (Leal et al., 2017; Rosa et al., 2016, 2018), and appear to be stress-tolerant (Fig. 2). Overall, these species are highly tolerant to temperature and salinity extremes, and high levels of siliciclastic sedimentation, such as those currently found in tide pools (Rabelo et al., 2014, 2015). Moreover, they are effective space competitors on marginal reefs and quickly cover available regions due to their rapid growth (Rabelo et al., 2013). Among them, *P. caribaeorum* has the largest spatial distribution in the SWA (Santos et al., 2016, 2019) (Fig. 1), and is the dominant species in several reef locations; for instance, covering up to 34% of the benthos in the shallow, nearshore, and well-illuminated pinnacles atop Abrolhos bank (Teixeira et al., 2021).

Zoanthus sociatus is also widely distributed throughout the Brazilian coastal reefs in the exposed areas of intertidal and subtidal reefs, with considerable resistance to desiccation during low tides (Sebens, 1982; Rabelo et al., 2014) (Figs. 1 and 2). *Palythoa* cf. *grandiflora* occur on shallow-water reefs with high sedimentation rates (Rabelo et al., 2014), and reach high densities especially in areas where other zoantharians are absent. Thus, these traits enhance their ability to thrive in marginal conditions (Soares, 2020) that are unsuitable for many strongly dependent autotrophic scleractinians. For example, *P. tuberculosa*, which is



Fig. 2. Zoantharians (*Palythoa* spp. and *Zoanthus sociatus* in the middle zone) in an intertidal sandstone reef in northeastern Brazil (Ceará coast) subjected to periodic desiccation (two times per day), strong waves under mesotidal regimen, and intense sunlight stress. Scale 5 cm.

distributed across the Indian and Pacific oceans and is the sibling species of *P. caribaeorum*, has a high heterotrophic performance and low reliance on the endosymbionts for nutrition (Santos et al., 2021), compared to many highly dependent autotrophic scleractinian species (Conti-Jerpe et al., 2020). Nevertheless, the interaction of *P. tuberculosa* with its endosymbionts is very plastic and varies according to environmental conditions (Santos et al., 2021). *P. tuberculosa* is also a voracious feeder which in a tank experiment, was found to prey more effectively on planktonic larvae than scleractinian corals (Fabricius and Metzner 2004). The flexible nutrition strategy of *P. tuberculosa* likely explains its resistance to mass mortality after severe bleaching events (Hibino et al., 2013; Santos et al., 2021). In this regard, some dominant zoantharians (e.g., *Zoanthus sociatus* and *Palythoa* spp.) from SWA have important physiological functional traits that promote their abundance, such as: 1) significant levels of heterotrophy in shallow and intertidal environments (Leal et al., 2017; Rosa et al., 2018); 2) endosymbiont diversity that provides autotrophic nutrition (Costa et al., 2013); and 3) endosymbionts with the plasticity to cope with suboptimal environmental conditions (Rabelo et al., 2014).

3. Factors promoting the success of zoantharians and driving coral-zoantharians phase shifts in the SWA

Coral-zoantharian phase shifts in some Brazilian shallow-water reefs have occurred due to the increase in the abundance of *P. cf. variabilis* (>25% substrate cover) (Fig. 3) (Cruz et al., 2018). Positive correlations have been found between zoantharian dominance (i.e., *P. cf. variabilis* and *P. caribaeorum*) and local impacts, such as proximity to human populations with over 100,000 inhabitants, urbanized nearshore surfaces, and dredged ports (Cruz et al., 2018). Consequently, the increased nutrients (soluble reactive phosphorus, reactive silica, and total oxidized nitrogen) observed in such localities may be a key driver of the dominance of zoantharians at such reefs. Moreover, a negative correlation has been found between these factors and scleractinian coral cover (Costa et al., 2008). In this regard, fast-growing zoantharians (e.g., *Palythoa* and *Zoanthus*) can be superior competitors to reef-building corals when nutrient supplies increase (Costa et al., 2002; Cruz et al., 2016). Nitrate concentrations in the SWA are about 2.5 times higher than those from the Indo-Pacific and Caribbean reefs, with some coastal habitats presenting concentrations higher than $5.0 \mu\text{M.L}^{-1}$ (Mies et al., 2020). An analogous process is occurring in the Caribbean reefs, where some

gorgonians cope better with short-term nutrient enrichment than scleractinian corals (Rossi et al., 2018; McCauley and Goulet, 2019).

Therefore, changes in local environmental conditions that decrease water quality are important drivers of zoantharian dominance not only in the SWA, but also worldwide (Reimer et al., 2021). Some nearshore SWA reefs are already experiencing substantial nutrient loading from land-based sources, such as surface runoff, submarine groundwater discharge, and untreated sewage (Costa et al., 2002, 2008). Nonetheless, most locations lack historical baselines to shed light on the factors driving these potential zoantharian phase shifts (Cruz et al., 2018; Reimer et al., 2021).

Coral-zoantharian phase shifts may be facilitated by the interspecific competitive advantages of zoantharians over reef-building corals in shallow reefs (Cruz et al., 2016), especially under high nutrient input (Cruz et al., 2015a; Reimer et al., 2021) such as SWA marginal reefs. In this regard, Cruz et al. (2015a) identified the high cover of *P. cf. variabilis* on two reefs (52% and 70%) in Todos os Santos Bay (Bahia, Brazil), confirming a decrease in hard coral cover. Such dominance has persisted for over nine years, characterizing a true phase shift (Cruz et al., 2016). Manipulative *in situ* experiments and surveys have found that 78% of the scleractinian coral colonies in contact with zoantharians experienced tissue necrosis over 118 days (Cruz et al., 2015a). Furthermore, an increase of 5.5% in *P. cf. variabilis* cover could be enough to bring 50% of the coral colonies in contact with this zoantharian, increasing partial mortality in key reef-building species in the SWA (i.e., *Montastraea cavernosa*, *Mussismilia hispida*, and *Siderastrea stellata*) (Cruz et al., 2016).

4. Zoantharian vulnerabilities in SWA reefs: climate change, invasive species, microplastics, diseases, and narrow depth range

Zoantharians are vulnerable to the stressors associated with climate change, invasive species, microplastics, diseases, and have a narrow depth range in SWA reefs. A negative relationship between zoantharian dominance (e.g., *P. caribaeorum*, *P. cf. variabilis*, and *Z. sociatus*) and prolonged sea surface temperatures $>1^\circ\text{C}$ above normal was found in SWA reefs (Cruz et al., 2018). Such a relationship indicates the vulnerability of zooxanthellate zoantharians to long-term warming and severe and repeated marine heatwaves in the turbid-zone reefs of the SWA (Bleuel et al., 2021; Soares et al., 2021). This intrinsic sensibility lies mainly in mixotrophic zoantharians, which have of their nutrition from the autotrophy of Symbiodiniaceae. For example, Leal et al. (2017) demonstrated that in intertidal reefs in northeast Brazil, 90% of *Z. sociatus* carbon comes from Symbiodiniaceae photosynthesis. Moreover, Steen and Muscatine (1984) showed that *Z. sociatus* in the Caribbean received >40% of their translocated carbon from endosymbionts, while *P. variabilis* received 13%. Unlike algae and various non-photo symbiotic sponges, zoantharians are susceptible to severe and repeated bleaching (Figs. 4 and 5). Thus, zoantharian and scleractinian species that rely less on endosymbionts for nutrition will likely have a higher chance of survival during bleaching events (Conti-Jerpe et al., 2020; Santos et al., 2021).

Bleaching events of *Z. sociatus*, *Palythoa cf. variabilis*, and *P. caribaeorum* (Figs. 4 and 5) have been detected at intertidal and subtidal reefs over the last 20 years, especially in 2002–2003 (Ferreira and Maida, 2006), 2010 (Soares and Rabelo, 2014) and during the most intense marine heatwave ever recorded on the SWA coast (2019/2020) (Duarte et al., 2020). In this recent event, between 29.9% and 46.3% of *P. caribaeorum* colonies were bleached (Duarte et al., 2020). However, *P. caribaeorum* populations appear to be highly resilient and able to survive (low mortality rates) episodic bleaching events with a high heterotrophic performance, similar to their sibling species, *P. tuberculosa* (Santos et al., 2021). For example, *P. caribaeorum* feeds mainly on small phytoplankton, but also on copepods, invertebrate eggs, and nematodes (Sebens and DeRiemer, 1977; Santana et al., 2015). However, its

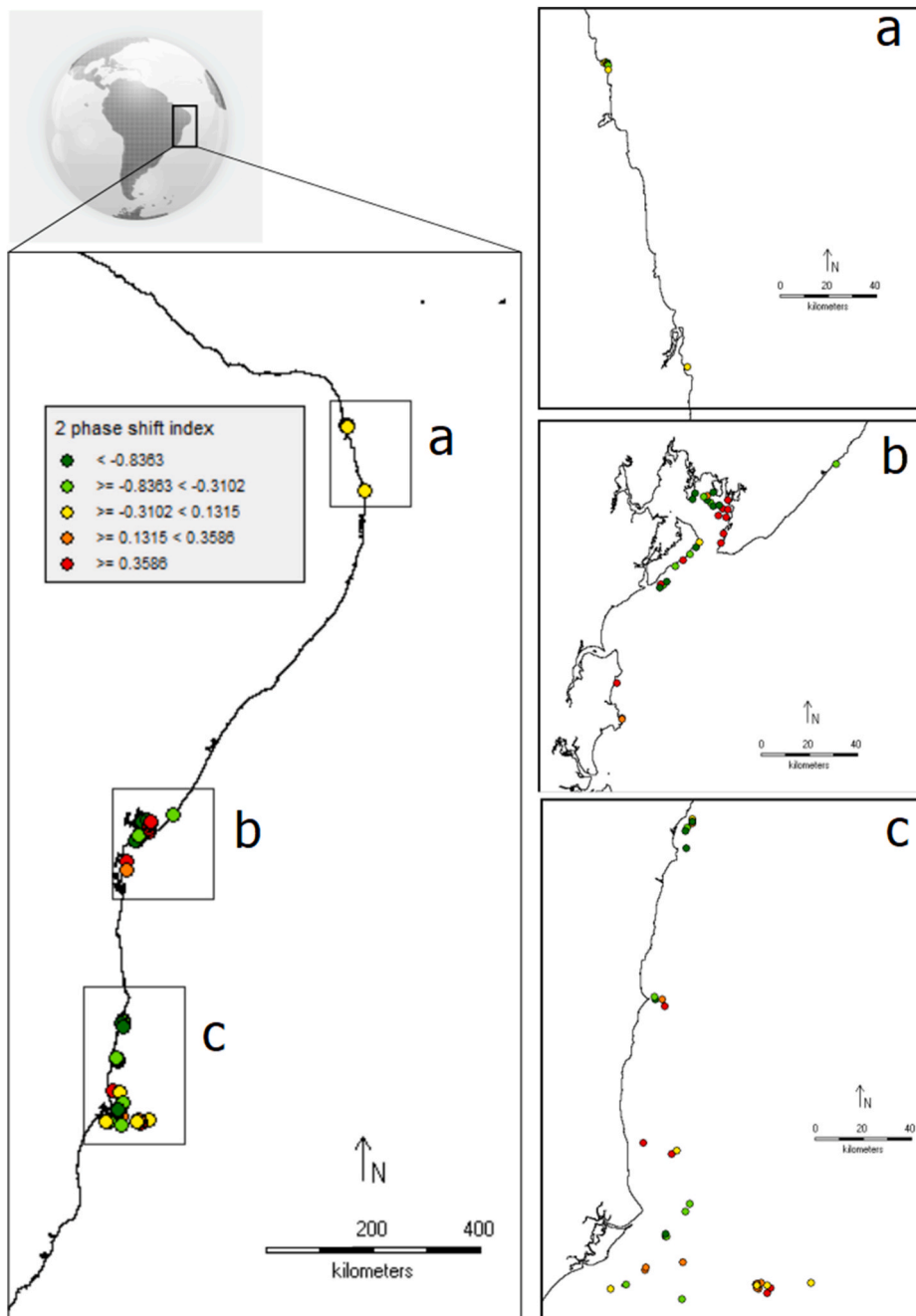


Fig. 3. Zoantharian-dominated reefs in the Southwestern Atlantic (Cruz et al., 2018) and phase shift index. A) Costa dos Corais Marine Protected Area, Pernambuco State (Brazil); B) Todos os Santos Bay (Bahia state, Brazil); C) Abrolhos Bank (southern coast of the state of Bahia, Brazil). The purpose of the Phase-shift index (PSI) is to facilitate graphical representation and statistical comparison, simplifying contrasts between marginal SWA reefs and between different types of studies. Each PSI corresponds to the first axis of a Principal Component Analysis (PCA) produced with two variables, for each PSI, the first variable was assigned to the non-reef-building organism (i.e., zoantharian) coverage and the second to scleractinian coral cover to simplify interpretation, so that coral cover decreased with increasing PSI. All calculated PSIs ranged from < -0.83 to > 0.35 . A negative PSI indicates a reef in “near pristine” condition, with high coral cover and low zoantharia coverage. A positive value indicates low coral cover and high zoantharia coverage (Cruz et al., 2018).

capacity to weather the chronic and increased intensities and frequencies of thermal stressors predicted to occur at the intertidal reefs of SWA under RCP 8.5 (Bleuel et al., 2021) may be lower; when zoantharians are already reaching their adaptive limit to increased stress factors such as solar irradiation, salinity, and temperature (Soares 2020). In this regard, few zoantharians will cope with or sustain the large environmental variability of these intertidal habitats in the worst climate change scenarios (Durante et al., 2018). On the other hand, the significant levels of heterotrophy and sessile lifestyles of zoantharians may expose them to other emergent threats, such as contamination by suspended solids (e.g., microplastics) (Soares et al., 2020). For example, microplastics such as polyvinyl chloride (at 10 mg L^{-1}) alter photobiology and induce oxidative stress in *Zoanthus sociatus* (Rocha et al., 2020).

Additionally, zoantharians are vulnerable to invasive species and diseases. Several SWA reefs are already affected by invasive species,

such as the scleractinian corals, *Tubastraea coccinea* and *T. tagusensis* (Creed et al., 2017). Although bearing palytoxins (Gleibs and Mebs, 1995), *P. caribaeorum* has been impacted by these invasive corals in SWA, and colonies of this zoantharian have receded or necrosed (Luz and Kitahara, 2017). Contact between the zoantharian *P. caribaeorum* and the invasive coral *T. coccinea* was evaluated by laboratory experiments that detected physiological and growth effects in both species. The zoantharian exhibited an increase in metabolic costs after contact with the invasive coral (e.g., respiration rates) and *Tubastraea* demonstrated accelerated growth that could lead to eventual overgrowth (Saá et al., 2020).

Other stressors such as diseases were detected in *P. caribaeorum* colonies from shallow-water SWA reefs ($< 4 \text{ m}$ depth) (Fig. 4D) and were linked with high levels of sedimentation, increased turbidity, and low levels of incident light (Acosta et al., 2001). Diseases also induce partial mortality, loss of colony area, and reduced reproduction rates in these

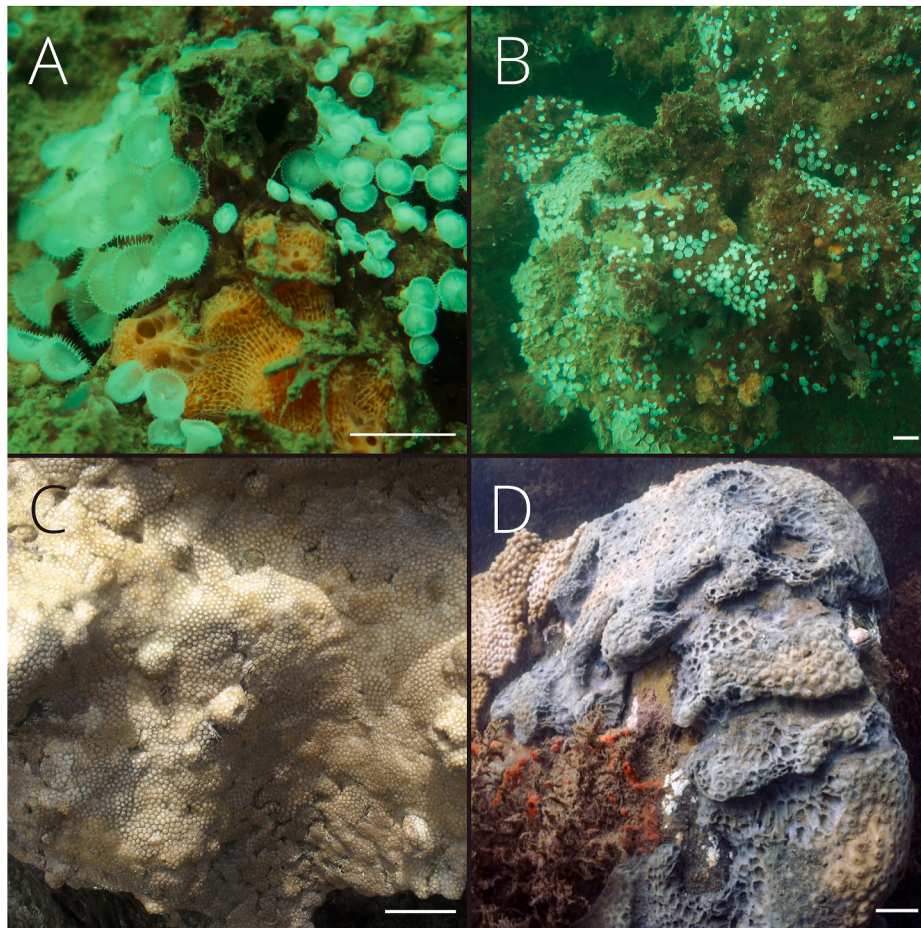


Fig. 4. Bleaching of zoantharian species in Southwestern Atlantic reefs (Brazil). (A) and (B) Bleaching of *Palythoa* cf. *variabilis* in Todos os Santos Bay (Salvador, Brazil) in May 2019. (C) Bleached *Zoanthus sociatus* in an intertidal sandstone reef in northeastern Brazil (Ceará coast, Brazil) in 2014. (D) Diseased *Palythoa caribaeorum* colonies in subtropical reefs after severe bleaching (São Paulo coast, Brazil). Scale: 5 cm.



Fig. 5. Severe bleaching in the dominant zoantharia *Palythoa caribaeorum* in the subtropical Southwestern Atlantic (São Paulo coast, Brazil). Scale 10 cm.

anthozoans (Acosta et al., 2001). However, although understudied in the SWA, this topic is a key research area for understanding the vulnerability of zoantharian populations and the resilience of zoantharian-dominated reefs to ongoing environmental changes.

Another potential vulnerability of SWA zoantharians is related to their depth distribution. Key zoantharians such as *P. caribaeorum*, *P. grandiflora*, *P. variabilis*, and *Z. sociatus* (Figs. 1 and 2) normally occur at 0–15 m and dominate in a narrow depth range (0–7 m) on Brazilian reefs (Aued et al., 2018). This shallow zone is particularly affected by climate change, compressing the three-dimensional habitat (Jorda et al.,

2020; Reimer et al., 2021) and limiting depth refugia in deeper SWA reefs (Soares et al., 2018). Forecasts indicate that common major species such as the *P. caribaeorum* could be vulnerable to more severe IPCC scenarios such as RCP 4.5 and 8.5 (Durante et al., 2018). Its restricted depth distribution contrasts with that of some SWA massive scleractinians and hydrocorals that possess extended depth distributions (Mies et al., 2020). Excluding mesophotic reef species, the bathymetric limit for coral species from the Indo-Pacific, Caribbean Sea, and SWA is 30.6 ± 0.7 (mean \pm standard error), 59.5 ± 3.9 , and 70.1 ± 9.0 m, respectively (Mies et al., 2020). As deep reefs (e.g., mesophotic coral ecosystems) have been hypothesized as short-term refuges to disturbances (e.g., heatwaves and extreme sedimentation levels) for some species (Bongaerts et al., 2017), the narrow depth limit of zoantharians seems to be a potential factor that might increase their vulnerability to growing climate change pressures in SWA shallow-water reefs. These include long-term warming and severe and repeated marine heatwaves under moderate and high-emission scenarios (RCP 4.5, 8.5) (Duarte et al., 2020; Bleuel et al., 2021; Soares et al., 2021), and therefore, the loss of suitable habitat in the coming decades.

Finally, the deforestation of estuarine mangrove habitats and coastal urbanization on the SWA has increased sedimentation rates and negatively impacted the cover of scleractinian corals (Leão et al., 2016). Hence, a crucial topic for future research is the influence of sedimentation on the dominance and vulnerability of different zoantharian species. Except for species of the family Zoanthidae (i.e., genera *Isaurus*, *Neozoanthus*, and *Zoanthus*) and genus *Kulamanamana*, which have sediment-free polyps, zoantharians can incorporate sediment into body

tissues to varying extents (sediment can account for up to 45% of the wet tissue weight in some *Palythoa* species; Haywick and Mueller, 1997). However, the effects of increased sedimentation on nearshore shallow-water reefs and zoantharian phase shifts in SWA still need to be clarified. Increasing knowledge about the impact of sedimentation levels (Acosta and González, 2007; Rabelo et al., 2013; Teixeira et al., 2021) on key zoantharian/scleractinian species will aid more accurate predictions for future turbid-zone reef seascapes.

5. Zoantharians in the SWA: scenarios and future studies

Tropical and subtropical marine ecosystems are expected to restructure in response to ongoing local and global environmental changes (Burt et al., 2020; Soares 2020). This may result in increased zoantharian abundance in some regions around the world. Records of zoantharian dominance in shallow-water habitats span from the late 19th century to the present day (Reimer et al., 2021). For example, a population increase of *P. canariensis* and *Zoanthus* sp. is projected for the Canary Islands (Macaronesia, Spain) (i.e., tropicalization effect) (González-Delgado et al., 2018). In addition, most global records of Zoantharia dominance have been linked to human impacts, with the large majority of them associated with decreasing water quality. The historical records from before the 1990s largely report Zoantharia intertidal dominance, while more recent records point to the subtidal flourishing of these soft corals (Reimer et al., 2021). Moreover, future scenarios of higher CO₂ levels may increase Zoantharia abundance in formerly scleractinian coral-dominated habitats. Besides supporting endosymbionts that can benefit from an increase in pCO₂ under ocean acidification and nutrient enrichment, non-scleractinian cnidarians are unaffected or, at least, less affected by changes in the aragonite saturation state under projected acidic waters. Nonetheless, projected lower pH levels can also negatively affect soft corals, such as zoantharians. For instance, decreases in the growth rate, weight, and size of *P. caribaeorum* colonies have been observed under low pH conditions (López et al., 2021).

Thus, in the ongoing Anthropocene, Reimer et al. (2021) predicted a rise in the number of shallow-water habitats experiencing Zoantharia barrens (i.e., substrate major covered by zoantharians), particularly in reef areas exposed to rising seawater temperatures and decreasing water quality. These are the exact conditions currently occurring in the SWA (Leão et al., 2016; Cruz et al., 2018; Mies et al., 2020; Soares et al., 2021), which highlights the potential for reef biota reorganization in the foreseeable future due to the expansion and retraction of species habitats and distributions (Durante et al., 2018), as well as the fast growth of

zoantharians under nutrient enrichment episodes (Costa et al., 2002, 2008). For example, higher phosphorus and nitrogen inputs promoted *Palythoa* and *Zoanthus* population outbreaks in SWA (Costa et al., 2002, 2008; Cruz et al., 2018).

The rise of zoantharian-dominated reefs may provide as novel habitats for reproduction, feeding, and habitats for some microcrustaceans, invertebrate larvae, and small fish, as well as food for polychaetes, reef fishes, and turtles in the SWA (Stampar et al., 2007; Mendonça-Neto et al., 2008; Francini-Filho and Moura, 2010). However, the low-relief marine animal forests (Rossi, 2013) formed by them (Fig. 6) have lower three-dimensional rugosity complexity (Alvarez-Filip et al., 2009) than reef-building species such as scleractinian corals. Although no difference in fish abundance has been observed between normal and zoantharian-dominated SWA reefs, fish species richness differs significantly between normal (48 species) and phase-shift reefs (38 species) in Todos os Santos Bay (Brazil). Reefs with high coral cover display higher abundance of carnivorous fishes, while mobile invertivores dominate zoantharian-dominated reefs (Cruz et al., 2015b).

In this context, coral-zoantharian phase shifts may decrease the richness of fish and benthic species, ultimately influencing ecosystem functioning and services, such as the provision of nursery habitats, fish biomass production, and coastline protection (Cruz et al., 2015b). Geo-ecological functions such as carbonate sediment production, wave energy reduction, carbonate accretion, and shoreline protection are significantly displaced by encrusting morphologies, a shortage of hard carbonate structures, and low bottom rugosities (Perry and Alvarez-Filip, 2019). Thus, SWA reefs with a higher dominance of zoantharians provide less protection against wave action and energy dissipation (Elliff and Kikuchi, 2017; Elliff et al., 2019), leading to beach erosion and shoreline destabilization in a process analogous to conditions in algal- and octocoral-dominated Caribbean reefs (Sheppard et al., 2005; Rossi et al., 2018; Lasker et al., 2020a,b).

Overall, zoantharians have always been abundant in the SWA (Leão et al., 2016; Teixeira et al., 2021), but increases in their abundance over the last few decades suggest that these encrusting soft corals have the potential to expand in the coming decades, where their reef populations have hitherto been dominated by massive scleractinian corals (Cruz et al., 2015a,b, 2018; Reimer et al., 2021; Soares et al., 2021). Modeling indicates that over the next 80 years, key zoantharian species will disappear in some SWA reef habitats and expand into new areas due to increasing stressors (Durante et al., 2018). In the climate scenario with the most severe changes (RCP 8.5), *P. caribaeorum* would lose half of its suitable SWA habitats, including its northernmost and southernmost ranges (Durante et al., 2018). This may occur because of drastic

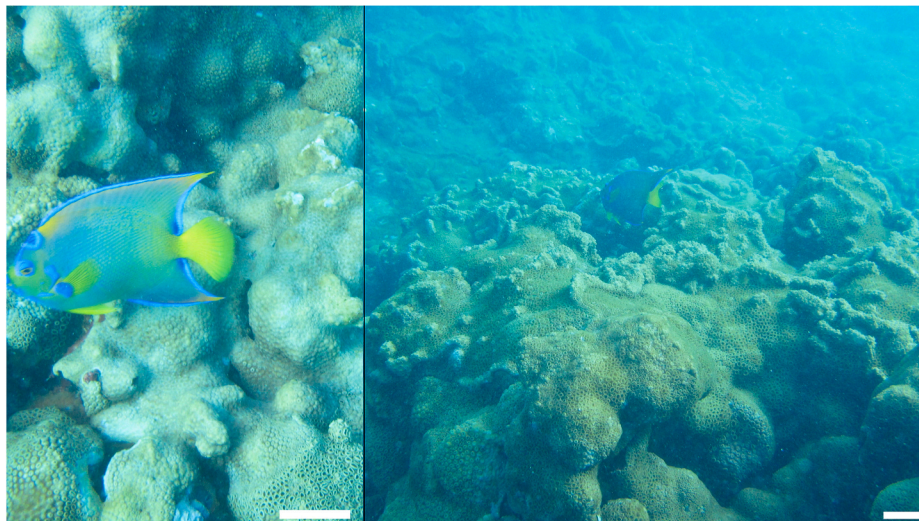


Fig. 6. Tropical reef João da Cunha (Rio Grande do Norte state, Brazil) with high monospecific dominance of *Palythoa caribaeorum*. Scale 10 cm.

decreases in salinity and pH (Durante et al., 2018). However, the Caribbean Sea (a hotspot of species diversity) and northeastern Brazil, as well as other places under the influence of coastal upwellings (e.g., Cabo Frio in Brazil and northern Colombia), may serve as potential mid-term refugia for these species until the end of the present century (Durante et al., 2018).

In conclusion, we summarize the biological and ecological features predisposing zoantharians to short- and mid-term success under the environmental conditions of SWA reefs. Moreover, we focus on those features that could have generated vulnerability and resilience of zoantharian populations to local (eutrophication and sedimentation) vs. global (warming and heatwaves) changes. Local and short-term impacts (e.g., nutrient pollution) might generate current and future outbreaks of zoantharians in SWA reefs. Considering future scenarios, zoantharians may thrive in nutrient-enriched subtidal locations with low heat stress (e.g., under upwelling influence). On the other hand, they are highly threatened in intertidal reefs, which are expected to be strongly affected by increases in factors such as temperature, solar irradiation, and sea level.

The persistence of zoantharians (e.g., *Zoanthus sociatus* and *Palythoa* spp.), to continue as potential “winners,” in future SWA reefs relies on the sustenance of sufficient genetic diversity within benthic populations in intertidal and subtidal reefs to support acclimatization and adaptation to future changes predicted in the South Atlantic. Without high genetic diversity and gene flow (Gallery et al., 2021) within the zoantharian populations, they would have limited capacity for adaptation, and the competitive advantages of the species in the marginal reefs analyzed in this study could be short-lived. Therefore, although human-induced alterations (e.g., eutrophication) may initially increase zoantharian cover on reefs, cumulative anthropogenic pressures (e.g., heatwaves, long-term warming, sedimentation inputs) will most likely negatively affect the zoantharian composition of most SWA reefs.

There is a broad range of research opportunities for advancing our knowledge on the key factors driving the success of zoantharians on SWA reefs, but we highlight the specific following lines of future research: 1) the functional implications of algae- and zoantharian-dominated reefs (intertidal and subtidal) in associated communities; 2) whether the genetic diversity of zoantharian populations allows them to cope with current and future environmental changes in SWA; and 3) the emergent properties associated with novel emerging zoantharian-dominated subtidal ecosystems, such as the provision of geo-ecological and nursery functions. More research is needed to fully understand the systemic responses of these novel seascapes to the concert of increasing and interactive stressors and the implications for ecosystem function and service provision.

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All data generated or analyzed during this study are included in this published article [and its supplementary information files].

Authors' contributions

MOS: Conceptualization, Writing - Original Draft, Writing - Review & Editing, Methodology, Formal analysis. **MVK:** Writing - Original Draft, Writing - Review & Editing, Formal analysis. **MEAS:** Writing - Original Draft, Writing - Review & Editing, Formal analysis. **SB:** Writing - Original Draft, Writing - Review & Editing, Formal analysis. **EFR:** Writing - Original Draft, Writing - Review & Editing, Formal analysis. **ICSC:** Writing - Original Draft, Writing - Review & Editing, Formal analysis. All authors read and approved the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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