Coral Reefs (2022) 41:1537–1548
https://doi.org/10.1007/s00338-022-02303-1

REPORT

Unprecedented erosion of *Mussismilia harttii*, a major reef-building species in the Southwestern Atlantic, after the 2019 bleaching event

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Received: 25 March 2022 / Accepted: 29 August 2022 / Published online: 10 September 2022
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Abstract Reefs are diverse environments because of the structural complexity provided by the tridimensional coral-built framework. However, they are sensitive environments that face multiple stressors including global warming, which triggers bleaching and mortality episodes. After death, coral skeletons are overgrown by a microbial film, which degrades and erodes the reef framework. Although erosive processes have been investigated in the Caribbean and Indo-Pacific, they remain poorly addressed for the unique Southwestern Atlantic reefs. Therefore, we investigated through field surveys of three Brazilian reefs if colonies of the endemic and regionally dominant coral *Mussismilia harttii* underwent erosion after the 2019 bleaching episode. We also collected corallite fragments from healthy, mildly bleached, severely bleached and dead *M. harttii* colonies for microcomputed tomography and densitometry analyses to assess whether microporosity and skeletal mineral density are reduced following bleaching. Our findings show that > 90% of the colonies underwent bleaching and loss of live cover was higher than 60% for all three reefs. All reefs also underwent severe erosion, with an area loss of intact colonies ranging from 33.8 to 85.2%. Furthermore, we detected higher total microporosity for dead skeletons and, together with severely bleached colonies, lower skeletal mineral density. Our results also suggest that bleaching, mortality and erosion processes are connected. These findings show that Southwestern Atlantic reefs are facing unprecedented degradation, although they are often considered climate refugia. In addition, because *M. harttii* is among the most important reef-builders in the region, carbonate budgets and structural complexity may face declines in the Southwestern Atlantic.

Keywords Brazil · Climate change · Habitat complexity · Mortality · Porosity · Skeleton

Introduction

Coral reefs are tridimensional structures produced through the deposition of calcium carbonate mainly by scleractinian corals (Cnidaria, Anthozoa). These organisms may produce more than 10 kg of $CaCO_3$ m^{-2} yr^{-1}, thus engaging in intensive biomineralization and reef-building (Buddemeier and Smith 1988; Hopley et al. 2007; Tambutté et al. 2011). However, reef growth is dynamic in space and time and the carbonate budget is mediated by several processes that may

Topic Editor Lauren T. Toth

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-022-02303-1.

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contribute to either net accretion or erosion. Among the main factors influencing erosion are the local hydrodynamic conditions, physical and chemical properties of seawater and the activity of bioeroding taxa (Tribollet and Golubic 2011; Perry et al. 2012; Bozec et al. 2015; Glynn and Manzello 2015; Januchowski-Hartley et al. 2017).

Although reef environments currently face impacts associated with local-scale stressors including overfishing and pollution (Dubinsky and Stambler 1996; Mumby et al. 2004; Bellwood and Choat 2011; van Dam et al. 2011), global-scale impacts such as ocean acidification and warming often produce stronger deleterious effects on their carbonate budget (see Bruno et al. 2019 and Cornwall et al. 2021). Ocean acidification limits coral calcification and growth by reducing the availability of carbonate ions in the water column (Hoegh-Guldberg et al. 2007; Anthony 2016), while global warming is responsible for the bleaching phenomenon. Under thermal stress, the photosynthetic dinoflagellates (family Symbiodiniaceae—see LaJeunesse et al. 2018) associated with the coral host produce cytotoxic reactive oxygen species (Lesser 2006; Weis 2008; Krueger et al. 2015). The adaptive response of the host is to expel its symbionts, which, together with pigment breakdown, leaves the white skeleton visible under a pale tissue layer (Glynn 1993). Because most shallow-water corals have an obligate mutualistic association with symbiodiniaceans, high mortality often ensues from severe bleaching episodes (Glynn 1993; 1996; Hoegh-Guldberg 1999; Hughes et al. 2018), which in turn prompts the degradation of the reef framework leading to declines in the carbonate budget (Eakin 1996; Roff et al. 2015; Couch et al. 2017; Lange and Perry 2019).

Once corals perish, their bare skeleton is encased by a microbial film composed mainly of turf algae and bacteria (Davey et al. 2008; Leggat et al. 2019). Shortly afterward, the metabolic activity of these microorganisms starts degrading the coral skeleton and rapidly increases its porosity, with a high Ca^{2+} removal rate of approximately 2.0 μmol cm^{-2} h^{-1} (Leggat et al. 2019). This weakens the reef framework and makes it more susceptible to erosion by both wave action and biological activity. The ultimate consequence is the coral skeleton breakdown and crumbling, causing the loss of structural complexity and microhabitats (Wild et al. 2011; Fordyce et al. 2019; Leggat et al. 2019). Numerous feeding, reproduction and shelter sites are therefore lost, thus reducing overall reef fish and invertebrate diversity (Graham and Nash 2012). There are several examples for this process in the Coral Triangle and Great Barrier Reef, where it was shown that after coral mortality and erosion, damselfish (Pomacentridae) no longer took shelter in dead colonies and became more vulnerable to predation (Coker et al. 2012; Boström-Einarsson et al. 2014; 2018—but see Wismer et al. 2019a,b). In the Caribbean, the loss of *Orbicella annularis* has likewise caused a significant reduction in the abundance of the cryptic fauna (Roff et al. 2015). Furthermore, the decay of the reef framework is often associated not only with a decrease in species richness of associated biota, but also in functional diversity (Sano et al. 1987; Bellwood et al. 2003; Garpe et al. 2006; McWilliam et al. 2020).

Erosive processes have been described for reefs in the Caribbean and Indo-Pacific for decades (Edinger et al. 2000; Sheppard et al. 2002; Alvarez-Filip et al. 2009; Perry et al. 2013; Bozec et al. 2015; Alvarado et al. 2016). However, for the unique reef environments found in the Brazilian coast in the Southwestern Atlantic, this topic has only more recently been assessed (Bastos et al. 2018; Dechnik et al. 2019; 2021; Pereira-Filho et al. 2021; Randi et al. 2021). Reef environments in this area and their fauna are biogeographically separated from the Caribbean by the freshwater discharges of the Amazon-Orinoco plume, that is also rich in sediment and nutrients (Leão et al. 2003; Floeter et al. 2008), and from the Eastern Atlantic by more than 3500 km (the mid-Atlantic barrier) (Floeter et al. 2008; Toonen et al. 2016). These oceanographic features led to the establishment of a reef fauna that is characterized by low diversity and high endemism (Castro and Pires 2001; Leão et al. 2003; 2016; Pinheiro et al. 2018). Distributed across nearly 3000 km in latitude, Southwestern Atlantic reef environments are also remarkable because of their higher tolerance to disturbances in general (Leão et al. 2003, 2010). In fact, these reefs are often considered climate change refugia because of their lower mortality associated with global warming (Mies et al. 2020).

Within this context, the present work investigated the erosive process for the endemic scleractinian *Mussismilia harttii* in three Brazilian reefs before, during and after the 2019 bleaching event. This species was chosen because it is a major reef-builder and has a phacelloid morphology, which contributes significantly to structural complexity (Nogueira et al. 2015). Specifically, we (i) assessed bleaching incidence, (ii) quantified loss of live coral cover, (iii) quantified erosion through the loss of area covered by intact colonies (without fallen, broken or tumbled corallites) and (iv) investigated whether skeletal integrity is related to the colony health condition. Investigating these topics allows for the evaluation of the climate change impacts in the Southwestern Atlantic from an unexplored perspective. In addition, monitoring erosion is particularly important because reefs function as underwater barriers that buffer the coast from damage associated with storms and other weather phenomena (Sheppard et al. 2005).

Materials and methods

Field surveys

Surveys of *M. harttii* colonies were performed in three reefs near Porto Seguro (Bahia State, Brazil), located approximately 150 km north of the Abrolhos Bank (which harbors the largest reef complex in Brazil): Araripe, Mucugê and Recife de Fora. Three fixed sites, containing *M. harttii*, at approximately 4 m of depth were randomly chosen within each reef (16°10′55.27″ S, 38°55′15.14″ W; 16°10′56.55″ S, 38°55′13.30″ W; and 16°10′56.80″ S, 38°55′12.86″ W for Araripe; 16°29′41.09″ S, 39°04′01.47″ W; 16°29′40.59″ S, 39°04′01.47″ W; and 16°29′42.45″ S, 39°04′02.10″ W for Mucugê; and 16°24′39.84″ S, 38°59′07.05″ W; 16°24′39.86″ S, 38°59′07.28″ W; and 16°24′39.76″ S, 38°59′07.63″ W for Recife de Fora; Fig. 1) and monitored every two months between October 2018 and February 2020, with the exception of a few occasions on which weather conditions prevented access to the reef and caused for us to skip a survey. At each site, a fixed area of 2.25 m^2 (1.5 × 1.5 m) was delimited and subdivided into nine 0.5 × 0.5 m quadrats, which were photographed at every survey with a fitted PVC frame. A total of 55 colonies were surveyed at the three reefs (13, 15 and 27 colonies for Araripe, Mucugê and Recife de Fora, respectively).

Bleaching, mortality and erosion data

The heat accumulation for the Porto Seguro area (4 × 4 km) was measured with the use of DHW (degree heating weeks), which is defined by the accumulation of temperature anomalies exceeding the maximum monthly mean over a period of 12 weeks (see Liu et al. 2014). Mean and maximum DHW data for the Porto Seguro region were downloaded from the National Oceanic and Atmospheric Administration's Coral Reef Watch database (NOAA 2021).

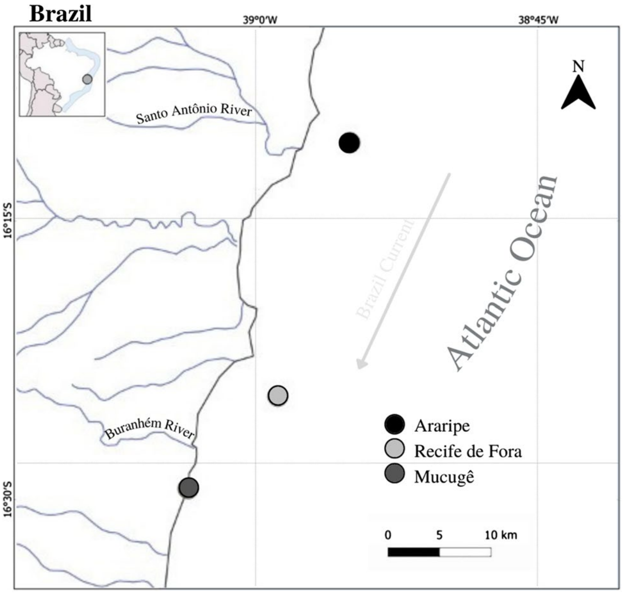


Fig. 1 Location of the three reefs in Porto Seguro (Bahia State, Brazil, Southwestern Atlantic) where the erosive process was investigated for the reef-building coral *Mussismilia harttii* during the 2019 bleaching event

The bleaching condition of each colony was assessed using the Coral Watch Health Chart (see Siebeck et al. 2006; Leiper et al. 2009; Fig. S1), which is a tool that allows for in situ rapid assessment of bleaching intensity. The reference chart was attached to the PVC frame and photographed along with *M. harttii* during surveys. Colonies were considered healthy when matching colors E4–E6 and bleached when matching E1–E3. Mortality was calculated by quantifying the loss of area occupied by live *M. harttii* colonies within each of the 2.25 m^2 sites, with the use of the photoQuad software. This software calculates the area occupied by benthic organisms by comparing its measurements against a metric reference point (in this case, the 0.5 × 0.5-m PVC frame) (Trygonis and Sini 2012). Both the absolute and relative area losses were recorded. Likewise, erosion was calculated by quantifying the loss of area occupied by *M. harttii* colonies that were structurally intact and standing upright, without fallen or tumbled corallites, regardless of being dead or alive.

Skeleton integrity

To evaluate the relationship between colony health and skeleton integrity, we collected corallite samples at one of the Recife de Fora sites in October 2019 in four conditions ($n = 3$ samples per condition, Fig. S2): healthy (E5 in the reference chart), mildly bleached (E3), severely bleached (E1) and recently dead (covered in a microbial film, but less than two weeks after death). The corallite microporosity was analyzed on a SkyScan 1172 high-resolution (2000 × 1332 pixels) microtomograph comprised of a microfocus X-ray tube with voltages 80 kV and a current of 124 mA. A 10 Mp (4000 × 2300 pixels) CCD camera detector and a computer cluster were used to reconstruct the images. Microporosity data were divided into three variables: closed microporosity, which accounts for micropores contained within the skeleton; open microporosity, which assesses micropores that are on the corallite wall; and total microporosity, which is the sum of the two previous parameters with a correction factor.

Skeletal mineral density was investigated with a DXA X-ray densitometer (iDXA-Lunar, enCORETM 2008 software, version 12.30, GE Healthcare®). Image processing was performed with enCORETM 2008 to obtain sections of superficial skeletal density. Several regions of interest were obtained in the samples, measuring 1.51 × 1.78 cm. Skeletal mineral density was calculated for each sample by comparing against the densitometer calcium carbonate internal standard. Both microporosity and skeletal mineral density procedures were performed only in the top 5 cm of the corallite, to guarantee that analyses were performed on corallite regions that were previously in contact with living coral tissue.

Statistical analyses

We performed McNemar's tests (which is a repeated measures variation of a chi-square test) to investigate whether there were differences in the relative live cover for *M. harttii* before and after the bleaching event. Before data points (prior to thermal stress) were considered at Oct 2018, Nov 2018 and Jan 2019 for Araripe, Mucugê and Recife de Fora, respectively. After data points (six months after the end of thermal stress) were Feb 2020, Jan 2020 and Jan 2020, respectively. The same procedures were performed to assess whether there was a reduction in the cover of colonies that were intact and standing upright.

To answer if there is a relationship between colony health condition (healthy, mildly bleached, severely bleached and dead) and skeleton integrity, we ran one-way analyses of variance (ANOVA) with closed microporosity, open microporosity, total porosity and skeletal mineral density as the dependent variable. Whenever statistical differences were detected (at $p < 0.05$) by ANOVA tests, a post hoc Tukey's HSD test was employed to compare difference between category pairs. All data were checked for normality using Shapiro–Wilk's test and for homoscedasticity using Levene's test.

Results

Bleaching and mortality

DHW data show that thermal stress in the Porto Seguro area lasted for approximately 6 months (Fig. 2). Temperature anomalies started in February and increased until May, when the highest value of 15.1 °C-weeks was recorded. Although it decreased afterward, thermal stress only ceased in August. Bleaching incidence (considering both mildly and severely bleached colonies) was high for all three reefs, with 92.2%, 93.3% and 100% of *M. harttii* colonies undergoing bleaching in Araripe, Mucugê and Recife de Fora, respectively. The live cover of *M. harttii* underwent a significant reduction ($\chi^2 = 7.02$, $p < 0.005$) at Araripe, from 25.4 to 2.2% (Fig. 3). At Mucugê and Recife de Fora, live *M. harttii* cover decreased from 8.9 to 2.7% and from 15.8 to 5.6%, respectively, but without significant differences in both cases ($\chi^2 = 0.51$, $p > 0.05$; and $\chi^2 = 1.03$, $p > 0.05$). Compared to the pre-bleaching status, live *M. harttii* cover was proportionally reduced by 91.3%, 69.6% and 64.5% for Araripe, Mucugê and Recife de Fora, respectively. Mortality was apparently higher at the end of the bleaching event, between May and July (Fig. 3).

Erosion

The area covered by intact *M. harttii* colonies also decreased dramatically over time and followed a similar trend to the loss of live cover (Fig. 4). At Araripe,

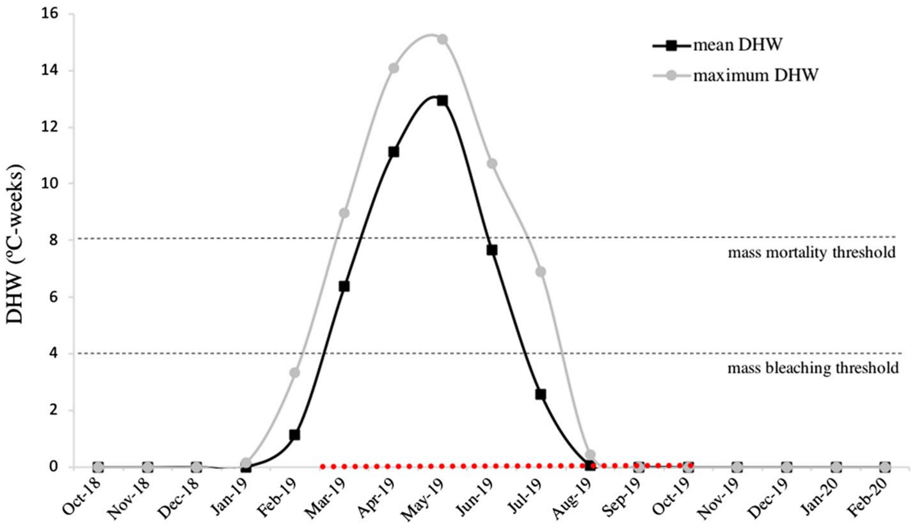


Fig. 2 Mean and maximum heat accumulation (expressed in degree heating weeks, DHW) to which *Mussismilia harttii* colonies were exposed during the 2019 bleaching event in Porto Seguro (Bahia State, Brazil). DHW data were obtained from the National Oceanic and Atmospheric Administration's Coral Reef Watch database (NOAA 2021). Red and dotted line represents time interval during which bleached colonies were observed in the three surveyed reefs (Araripe, Mucugê and Recife de Fora). Mass bleaching and mortality thresholds are depicted according to those described in Kayanne 2017)

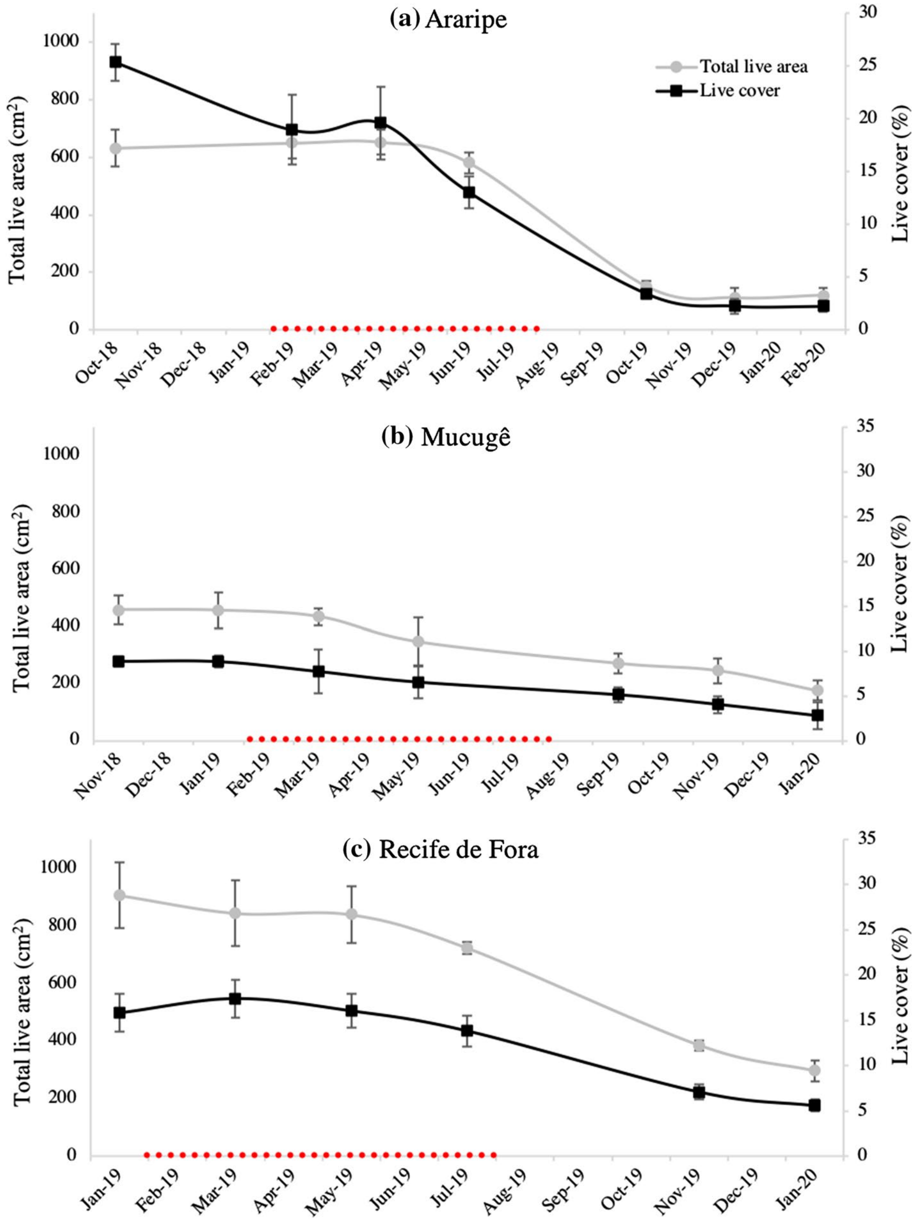


Fig. 3 Total live area (left Y axis and gray line) and relative live cover (right Y axis and black line) for *Mussismilia harttii* during the 2019 bleaching event in three reefs in Porto Seguro (Bahia State, Brazil): **A** Araripe, **B** Mucugê and **C** Recife de Fora. Red and dotted line represents time interval during which colonies underwent thermal stress (DHW > 4.0 °C-weeks). Data are presented as mean ± standard error

intact area was reduced significantly from 29.9 to 4.4% ($\chi^2 = 6.85$; $p < 0.005$). Mucugê and Recife de Fora also underwent reductions in the cover of intact *M. harttii*, from 8.9 to 2.8% and from 20.1 to 13.3%, respectively, albeit not significantly in both cases ($\chi^2 = 0.46$, $p > 0.05$; and $\chi^2 = 0.19$, $p > 0.05$). Compared to the pre-bleaching status, the area occupied by intact *M. harttii* colonies proportionally decreased by 85.2%, 68.5% and 33.8% for Araripe, Mucugê and Recife de Fora, respectively. Erosion was also more intense between May and July, but it continued in the following months (Fig. 4). In general, the data show a succession of events that went from bleaching to mortality to erosion, promoting changes in the local benthos (Figs. 5 and S3).

Health condition and skeleton integrity

The microcomputed tomography analysis showed no significant difference among the four health conditions for both the closed microporosity ($F = 3.30$, $df = 3$, $p = 0.07$; Fig. 6A) and the open microporosity ($F = 1.16$, $df = 3$, $p = 0.38$). However, total microporosity was different among conditions ($F = 5.46$, $df = 3$, $p = 0.024$). Healthy and mildly bleached colonies present significantly lower total microporosity when compared to dead colonies (Tukey's HSD test: $p = 0.042$ and 0.029, respectively). As for skeletal mineral density, it was different across the four health conditions ($F = 6.22$, $df = 3$, $p = 0.017$; Fig. 6B). Healthy coral fragments had significantly higher skeletal mineral density than

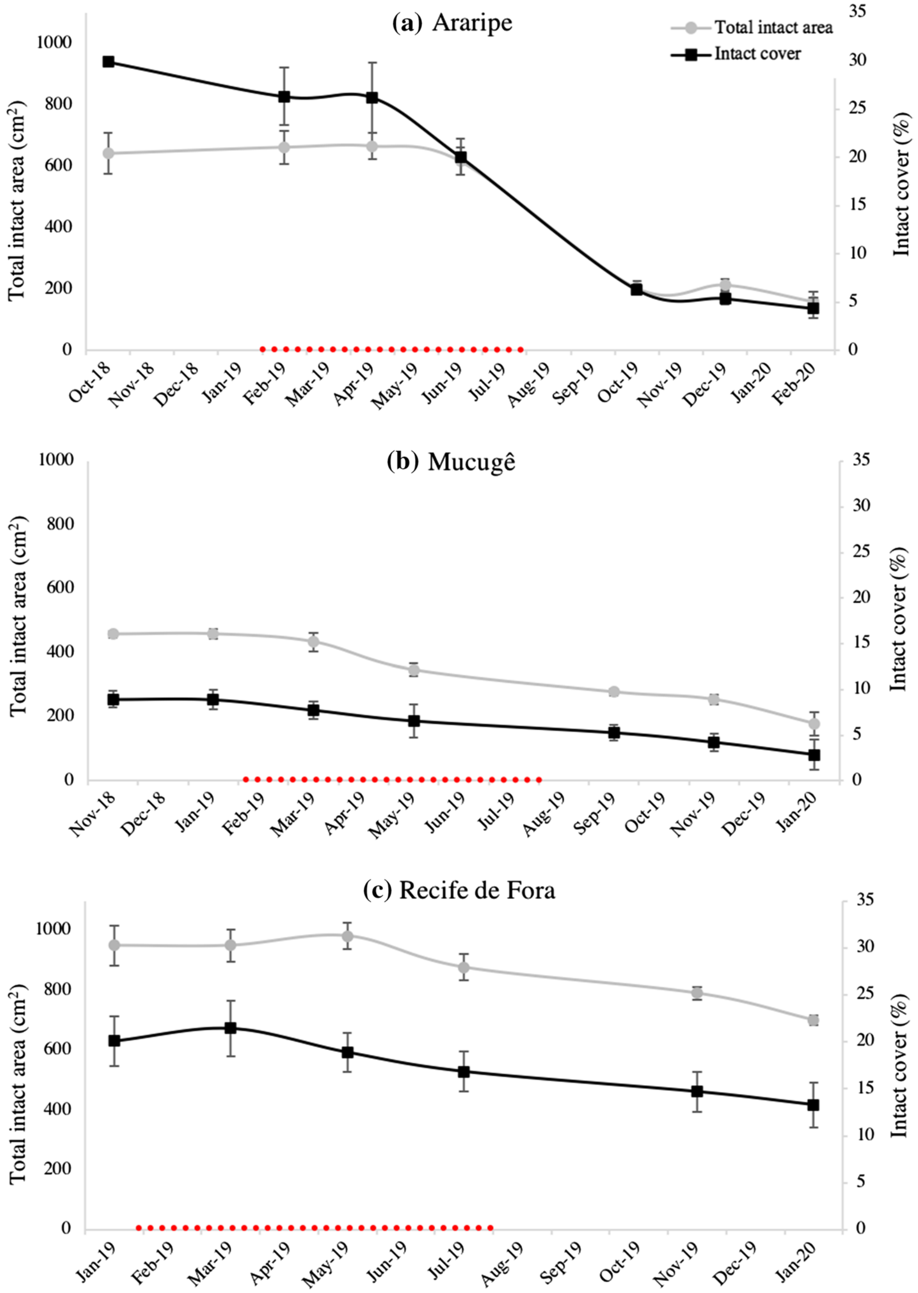


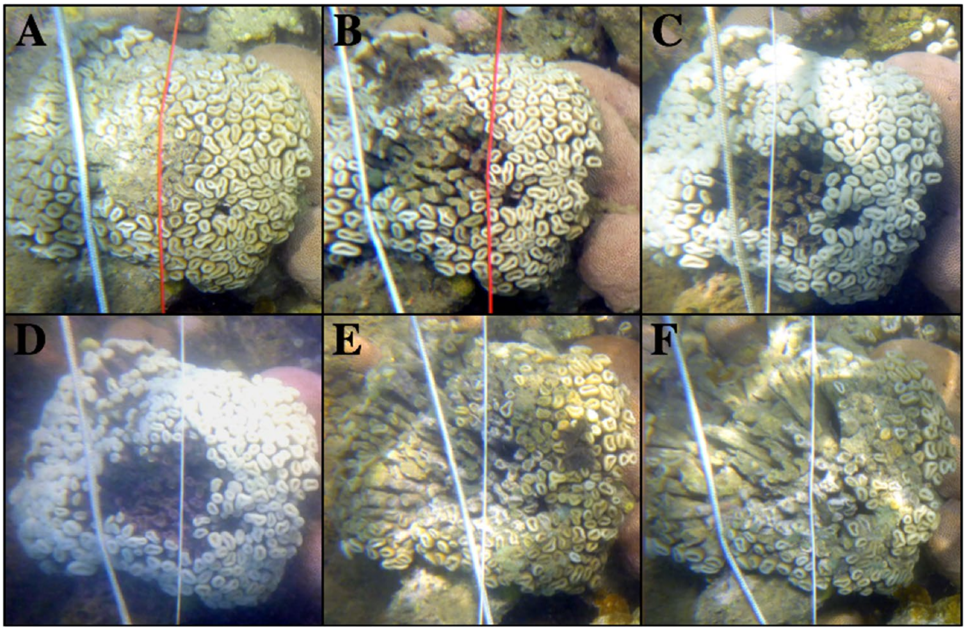
Fig. 4 Total intact area (left Y axis and gray line) and relative intact cover (right Y axis and black line) for *Mussismilia harttii* during the 2019 bleaching event in three reefs in Porto Seguro (Bahia State, Brazil): **A** Araripe, **B** Mucugê and **C** Recife de Fora. Red and dotted line represents time interval during which colonies underwent thermal stress (DHW > 4.0 °C-weeks). Data are presented as mean ± standard error

severely bleached and dead fragments (Tukey's HSD test: $p = 0.032$ and 0.021, respectively).

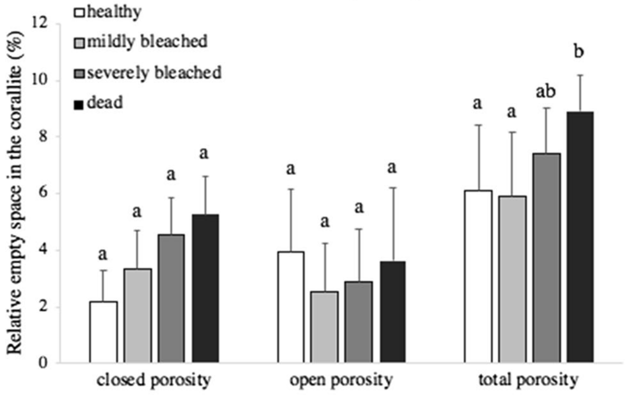
Discussion

The 2019 bleaching event in the Southwestern Atlantic affected nearly the whole Brazilian coast and was largely associated with the warm phase of the El Niño–Southern Oscillation (ENSO). To date, this was the most severe bleaching event in the Southwestern Atlantic, with the highest recorded levels of heat accumulation, bleaching incidence and mortality (Banha et al. 2020; Duarte et al. 2020; Ferreira et al. 2021; Gaspar et al. 2021). Our data show that more than 90% of *M. harttii* colonies bleached in all three reefs monitored in this study. This is the highest bleaching incidence ever recorded for this species, greater than the 55% detected for Abrolhos in 2019 and the 80% for the same region in 2016, during the third global mass bleaching event (Teixeira et al. 2019; Duarte et al. 2020). A DHW value of 4.0 °C-weeks is the threshold for the occurrence of mass bleaching, while more than 8.0 °C-weeks usually triggers mass mortality (Kayanne 2017). Therefore, the elevated degree of bleaching and mortality observed

Fig. 5 The degradation process of a *Mussismilia harttii* colony at Recife de Fora (Porto Seguro, Bahia State, Brazil) during the 2019 bleaching event. **A** intact and healthy colony with only a few dead polyps in the center in January 2019; **B** intact and mildly bleached colony with an increased quantity of dead polyps in the center in March 2019; **C** and **D** intact and severely bleached colony in May and July 2019; **E** partially dead colony undergoing erosion in the top left corner in November 2019; and **F** partially dead colony with the left half eroded in January 2020



(a) Microporosity



(b) Skeletal mineral density

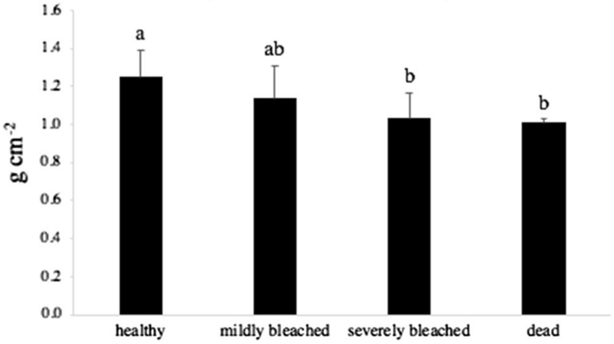


Fig. 6 The skeletal integrity of *Mussismilia harttii* after the 2019 bleaching event was assessed through quantification of **A** microporosity and **B** skeletal mineral density. Four different health conditions were tested: healthy, mildly bleached, severely bleached and dead colonies. Different superscript letters for the same response variable (closed porosity, open porosity or total porosity) denote statistically different groups (*post hoc* Tukey's HSD test)

in this case can be explained by the intense heat stress of 15.1 °C-weeks to which *M. harttii* was subjected to.

The loss of live *M. harttii* cover, greater than 60% for all three reefs investigated, was also the highest ever recorded for the species. Previous losses of 13% and < 1% had been recorded at Abrolhos during the 2019 and 2016 bleaching events, respectively (Teixeira et al. 2019; Duarte et al. 2020). Despite experiencing a heat accumulation of 19.6 °C-weeks in 2019, Abrolhos may have suffered lower mortality because it is a well-preserved marine protected area and much less subject to urban influence than Porto Seguro reefs (Werner et al. 2010; Leão and Kikuchi 2001; Moura et al. 2013). In fact, similar reasons may explain why the Araripe reefs underwent considerably higher mortality than Mucugê and Recife de Fora. They are under the strong influence of the Santo Antônio River, which discharges an elevated quantity of sediment and pollutants (Coral Vivo Institute, unpublished data). In this case, the higher turbidity may not have been enough to buffer the effects from the exceptionally high thermal stress (see Cacciapaglia and van Woesik 2016; Sully and van Woesik 2020). Furthermore, fisheries and tourism are not regulated as in Recife de Fora, which likely increases anthropogenic pressure (de Paula et al. 2018; Lima et al. 2021).

Our data confirm that there was a considerable loss of intact *M. harttii* living cover for all three reefs (Fig. 4). However, statistical differences between pre- and post-bleaching time points were detected only for the Araripe reefs, suggesting that, although cover was reduced in more than 60%, the loss of area occupied by intact *M. harttii* at Mucugê and Recife de Fora may not have been as drastic. Additionally, it was confirmed that the skeleton integrity is directly related to colony health—dead colonies (with fallen, broken and tumbled corallites) displayed higher total microporosity and, together with severely bleached colonies, lower skeletal mineral density. This confirms they were undergoing erosion. It is unclear why no differences were detected among health conditions for closed and open microporosity, but it may be related to the specific circumstances that each colony experienced. For instance, external bioerosion and open microporosity may be associated with fish bites, while internal bioerosion and closed microporosity can be associated with the activity of boring and infaunal organisms (Ong and Holland 2010; Tribollet and Golubic 2011; Bozec et al. 2015). Hydrodynamics likely also play a significant role, although unclear. Nonetheless, the dynamics of the physical and biochemical processes surrounding the increase in porosity in coral skeletons still require more investigation (see Leggat et al. 2019).

The field surveys show that *M. harttii* colonies began eroding shortly after death. This is in accordance with Leggat et al. (2019), where it was demonstrated that coral skeletons may undergo significant ultrastructural changes less than two weeks after death due to microbial activity. In this way, the bleaching, mortality and erosive processes seem to be well connected. It is therefore possible that the Porto Seguro reefs may have suffered a swift decline in their carbonate budgets. It has been reported that reefs may not be able to accrete if coral cover is reduced to less than 10% (Perry et al. 2013). All three reefs investigated in this study had their live *M. harttii* cover reduced to less than 10%, which raises a severe alert. On a Caribbean reef, a coral cover loss of 9%, which is considerably lower than the figures we report, was enough to prevent reef accretion and growth (Roff et al. 2015). The Porto Seguro reefs face additional problems to maintain its structural integrity. Aragonite saturation state (Ω_{AR}) levels below 3.0 have been detected in sections of the nearby Coroa Vermelha reefs (Longhini et al. 2015). However, levels of 3.3 or higher are required for reef development (Kleypas et al. 1999; Hoegh-Gudberg et al. 2007). Therefore, it is possible that reefs in this area may currently be unable to accrete. In addition, the presence of key species such as herbivorous parrotfish is usually lower in Porto Seguro reefs (Chaves et al. 2010). Together with the traditionally low functional redundancy associated with Brazilian reef fishes (Mouillot et al. 2014), herbivorous species, despite also contributing to bioerosion, may not fully control algal overgrowth and thus possibly facilitate phase shifts and reef erosion (see Done 1992; McManus and Polsenberg 2004; Bruno et al. 2009; Hughes et al. 2007a, b). Therefore, because the present work is limited by addressing the eroded area only, investigations on the carbonate budgets, specifically on the loss of carbonate mass, are warranted for Porto Seguro reefs.

In general, the main consequence of our findings is the potential loss of structural complexity in Porto Seguro reefs following the 2019 bleaching event. Branching coral species are usually the main providers of structural complexity, but there are no branching scleractinians in the Southwestern Atlantic. This niche is occupied by *Millepora alcicornis*, a branching and calcifying hydrozoan (Coni et al. 2013) distributed from Maranhão to Rio de Janeiro. However, branching species are usually more susceptible to bleaching (Loya et al. 2001; Pratchett et al. 2020; Morais et al. 2021) and *M. alcicornis* suffered more than 90% mortality during the 2019 bleaching event in the Southwestern Atlantic (Duarte et al. 2020; Ferreira et al. 2021). In the absence of branching corals, the species that provides the highest structural complexity is *M. harttii*, due to its phacelloid morphology and space between corallites (Nogueira et al. 2015; 2021). However, unlike *M. alcicornis*, *M. harttii* is a slow-growing species (Leão et al. 2003) and recovery may take decades. In fact, *M. harttii* populations have been declining in the past 50 yrs (Laborel-Deguen et al. 2019) and high cover is now restricted to a few locations such as Bahia State and the marine protected area Costa dos Corais. Also worrisome is that *M. harttii* populations in that location also suffered high mortality (32.6%) during the 2019 bleaching episode (Pereira et al. 2022). The conservation status for *M. harttii* was listed as "endangered" in 2013 after a major evaluation of the natural stocks (ICMBio 2018). However, our findings suggest that its status may require a careful revision after the recent mortality episodes. Therefore, the two main structural complexity providers in Southwestern Atlantic reefs are currently facing high mortality, and the impacts on overall reef biodiversity need urgent assessment. On the other hand, during field assessments performed few years after the 2019 bleaching episode, we observed that *M. harttii* rubble was colonized by small colonies of faster-growing coral species such as *Favia gravida* and *Agaricia humilis*. Therefore, eroded *M. harttii* skeletons are serving as suitable substrate for coral recruitment.

Current definitions of climate change refugia describe them as areas where impacts from climate change are occurring at a slower pace, providing short-term partial protection against its impacts (Morelli et al. 2020). In that sense, Southwestern Atlantic reefs may be considered climate change refugia because they have historically suffered fewer mass mortality episodes at the community level than other areas such as the Caribbean and Indo-Pacific, especially during the three previous global mass bleaching events (Mies et al. 2020). This is important to clarify, as previous investigations in the Southwestern Atlantic have misinterpreted refugia as immune to climate change, which is certainly not the case (Soares et al. 2021; Pereira et al. 2022). The reasons for this increased resilience in the Southwestern Atlantic include: (i) predominance of massive coral species, (ii) an increased heterotrophic capacity, (iii) protection from heat and irradiance due to highly turbid conditions, (iv) ability to inhabit deeper areas where heat impacts are reduced, (v) symbiosis flexibility and capability of reshuffling symbiont communities, (vi) the framework of local biogenic reefs display a high presence of non-scleractinian and more heat-resistant organisms, such as bryozoans, vermetids and calcareous algae and (vii) a history of lower frequency of severe heatwaves (Gherardi and Bosence 2001; Bastos et al. 2018; Mies et al. 2018, 2020; Marangoni et al. 2019; Skirving et al. 2019; Bleuel et al. 2021). In fact, (ii–v) are directly applicable to *M. harttii* (Marangoni et al. 2019; Mies et al. 2020). However, despite being more tolerant to climate change than other areas of the world, bleaching-associated mortality in the Southwestern Atlantic has been increasing severely in recent years (Duarte et al. 2020; Ferreira et al. 2021; Pereira et al. 2022). Our present findings show that, besides causing high mortality, bleaching may seriously erode the framework of Southwestern Atlantic reefs, mainly when regarding key species that provide high structural complexity.

Although reef environments have alternated between erosive and accretive states in past geological periods, this work documented an unprecedented erosive process during the Anthropocene of a Southwestern Atlantic coral species that contributes significantly to habitat complexity. In addition, we demonstrate that the skeleton of healthy corals displays lower porosity and higher skeletal mineral density when compared to severely bleached and dead ones. Our findings shed light on the dynamics of the erosive process that follows bleaching and may also serve as a red flag for the increasing degradation of Southwestern Atlantic reefs.

Acknowledgements We would like to thank Coral Vivo Project and its sponsors Petrobras (Programa Petrobras Socioambiental) and Arraial d'Ajuda Eco Parque and also Thomás Banha for providing assistance with some of the data.

Author contributions GBB, CHFL, HE, PLD and MM designed the study; CHFL performed fieldwork; AMBR and KCCC provided infrastructure/material/technical support; GBB and AZG analyzed the data; and GBB, HE, AZG, KCCC, PLD and MM contributed to the manuscript.

Declarations

Conflict of interest On behalf of the authors, the corresponding author states that there is no conflict of interest.

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