



No coral recovery three years after a major bleaching event in reefs in the Southwestern Atlantic refugium

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Abstract

Mass bleaching events are growing in duration and intensity. Besides causing extensive mortality, the progressively shorter time between events disrupts the ability of reefs to recover. The unique reefs of the Southwestern Atlantic are often considered climate refugia as they have suffered less bleaching-related mortality when compared to Indo–Pacific and Caribbean reefs. However, their recovery capacity still requires investigation. In 2019, an unprecedented heatwave triggered the most severe bleaching episode recorded for Southwestern Atlantic reefs. Therefore, this study aimed to (i) document the bleaching incidence and mortality during the heatwave, and (ii) assess coral recovery over 3 years. We measured bleaching incidence and monitored coral cover through surveys in three Southern Bahia (central Brazilian coast) reefs before, during and after thermal stress. Our findings show that coral assemblages were exposed to a 5-month-long thermal anomaly, experiencing thermal stress peaking at 14.1 °C-weeks. Roughly 70% of the coral cover was bleached, resulting in a decline of ~40%. *Millepora alcicornis*, *Mussismilia braziliensis*, and *Mussismilia hartii* were among species that mortality exceeded 50%. After 3 years, corals showed no increase in cover neither at assemblage nor species levels. This constrained recovery capacity may indicate the breakdown of the refugium, and also trade-off for resistance. Typical features of the region, such as high turbidity and the dominance of massive corals, provide these reefs with bleaching resistance, but likely also limit their recovery. With the anticipated effects of the 2023–24 El Niño–Southern Oscillation in the southern hemisphere, still unrecovered Southwestern Atlantic reefs face a substantial challenge.

Keywords Brazil · Climate change · Coral cover · Mortality · Resilience · Thermal stress

Introduction

The emission of greenhouse gases has raised the atmospheric CO₂ concentration by approximately 140 ppm since the Industrial Revolution, resulting in an increase of more than 1 °C in average ocean sea surface temperatures (IPCC 2021). Acute and sustained ocean warming triggers coral bleaching, as these organisms usually develop close to their upper thermal threshold (Hoegh-Guldberg 1999; Fitt et al. 2001). Bleaching results from the disruption of the

coral–dinoflagellate symbiosis and is defined by the loss of symbiotic dinoflagellates (family Symbiodiniaceae) and/or photosynthetic pigments by the coral host (Glynn 1993). Under thermal stress, the symbiotic dinoflagellates living within the cells of their coral hosts produce cytotoxic reactive oxygen species (Lesser 2006; Weis 2008; Krueger et al. 2015). Consequently, the coral releases its symbionts and the white calcareous skeleton becomes visible under a translucent living tissue layer. Depending on the duration and intensity of the thermal stress, the loss of symbionts and the build-up of reactive oxygen species may produce elevated coral mortality (Glynn 1993; Douglas 2003; Lesser 2006; Jones 2008; but see Schlottheuber et al. 2024).

Global Mass-Bleaching Events (GMBEs) refer to episodes in which extensive reef areas in the Atlantic, Indian, and Pacific oceans undergo bleaching roughly over the

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same period. In recent decades, three GMBEs have been confirmed in 1997–98, 2009–10, and 2014–17, all closely related to the El Niño–Southern Oscillation (ENSO) warm phase (Eakin et al. 2016; Hughes et al. 2018; Oliver et al. 2018). The duration and intensity of the ENSO warm phase have increased over time, exacerbating coral bleaching and mortality globally (Hughes et al. 2018; Oliver et al. 2018; Skirving et al. 2019). Consequently, important reef areas such as the Great Barrier Reef and the Caribbean underwent severe coral mortality episodes (Eakin et al. 2010; De'ath et al. 2012; Jackson et al. 2014; Dietzel et al. 2020), and global estimates show that approximately 50% of coral benthic cover has been lost since the first GMBE (Tebbett et al. 2023). This has produced several reported episodes of regime shifts (*sensu* DeYoung et al. 2008) where opportunistic turf algae outcompete corals, making it challenging to revert to the original coral-dominated scenario due to hysteresis (Done et al. 1992; Hughes et al. 2007; Steneck et al. 2019).

The extent and speed of coral recovery after a mortality episode is a metric often used to determine how well a reef might handle subsequent bleaching events. When a reef recovers more quickly and effectively, the corals may acclimatize and exhibit enhanced resilience during future disturbances (Connell et al. 1997; West and Salm 2003; Roff and Mumby 2012; Mcleod et al. 2019). This has been well documented for reefs in the Western Indian Ocean, where swift coral recovery translated into increased resistance (McClanahan et al. 2007). The effectiveness of the recovery process, however, is a consequence of multiple intrinsic biological and oceanographic factors (McClanahan 2000; Graham et al. 2011), including coral morphology, functional diversity of fish assemblages, nutrient concentration, reef depth and physiological plasticity (Marshall and Baird 2000; Graham et al. 2015; Ortiz et al. 2018). This highlights the importance of monitoring the reef recovery process to better understand the impacts of upcoming disturbances.

Although bleaching recovery processes have been investigated in coral reefs from the Indo–Pacific and Caribbean (Mumby et al. 2007; Roth et al. 2018; McManus et al. 2021), they remain largely unaddressed in the Southwestern Atlantic. The unique reefs in this area, mainly restricted to Brazilian waters, are known for their reduced diversity and high degree of endemism (Leão et al. 2016; Pinheiro et al. 2018). This is primarily a consequence of the discharge of several large rivers into the South American Atlantic continental shelf, including the Amazon–Orinoco plume, which serves as a major biogeographic filter between the Caribbean and Southwestern Atlantic (Castro and Pires 2001; Leão et al. 2003; Floeter et al. 2008; Moura et al. 2016). Bleaching investigations in the region started only in 1994 (Castro and Pires 1999), and mass bleaching was not detected until 1998, during the first GMBE, with incidence below 50% (Leão

et al. 2010; Kelmo and Attrill 2013). At that time, widespread mass mortality was not observed (Leão et al. 2010), but significant coral mortality was described in northern Bahia State (Kelmo and Attrill 2013). The second GMBE produced little bleaching and minimal mortality for Brazilian reefs (Ferreira et al. 2013; Miranda et al. 2013). However, during the third GMBE, extensive bleaching occurred with several species experiencing over 75% bleaching but little to no mortality (Teixeira et al. 2019). Compared to the Caribbean and Indo–Pacific, this positive bleaching record prompted the Southwestern Atlantic to be identified as a relevant climate refugium (Mies et al. 2020). However, the recovery process was not assessed at any given point, despite lengthy periods between GMBEs.

In 2019, a regional-scale heatwave, unconnected to the ENSO, was caused by the blocking of advancing cold fronts by the South Atlantic Subtropical Anticyclone (Cheng et al. 2020; Vieira and Cupolilo 2021). This blocking induced an intense atmospheric subsidence, resulting in low humidity and high temperatures. This heatwave caused the strongest observed bleaching episode to date for several Southwestern Atlantic reef sites (Banha et al. 2020; Duarte et al. 2020; Ferreira et al. 2021; Gaspar et al. 2021; Braz et al. 2022; Pereira et al. 2022). In this context, for reefs in Southern Bahia (Brazil), the present study aimed to (i) document the incidence of bleaching and mortality during the 2019 bleaching event, and (ii) describe the coral cover recovery process over the period of 3 years. Considering the typically slow growth rates of most Brazilian corals (Suggett et al. 2012), we aimed to assess whether post-bleaching coral recovery is also slow.

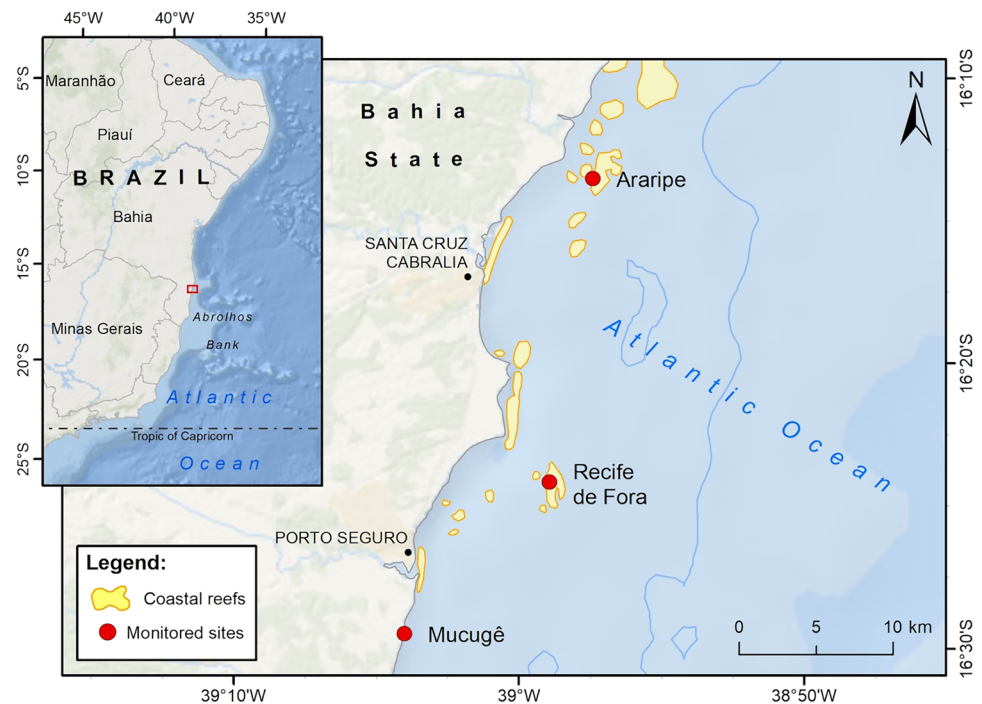
Investigating the response of Southwestern Atlantic marginal coral reefs to bleaching is critical because they offer ecosystem services to millions of people along more than 5000 km of coastline (Elliff and Kikuchi 2017; Waechter et al. 2023). In addition, because of the expected arrival of a massive 2023–24 ENSO heatwave in the Southwestern Atlantic (see Lian et al. 2023; Ludescher et al. 2023), it is critical to understand how these unique reef systems may respond in longer terms.

Materials and methods

Study area

The reefs selected for investigation are situated in Southern Bahia State (eastern coast of Brazil, ~ 16°S). This region hosts the most extensive, diverse and representative coral reefs of the Southwestern Atlantic, harboring nearly all photosymbiotic scleractinian coral species found in the South Atlantic (Francini-Filho et al. 2013; Leão et al. 2016). Three reefs from this region were assessed (Fig. 1): Araripe

Fig. 1 The three reef sites of Araripe, Mucugê and Recife de Fora (Southern Bahia State, Brazil, Southwestern Atlantic—red rectangle in the inner picture, expanded in the outer picture) where bleaching, mortality and recovery were recorded before, during and after the 2019 thermal stress episode



(located at the Coroa Alta Municipal Marine Park, $-16.225517, -38.956702$); Mucugê ($-16.491478, -39.066782$); and Recife de Fora (located at the Recife de Fora Municipal Marine Park, $-16.402901, -38.982132$). These reefs may be considered representative of the South Atlantic because of their historically high coral cover and presence of all the coral species found in the Southern Bahia area, which harbors the richest reef formations in the South Atlantic Ocean (Castro and Pires 2001; Leão et al. 2016). Furthermore, these reefs are considered model reefs that have been subject to multiple investigations and monitoring since 1997 (M. Mies et al., *in prep.*).

Thermal stress data

To determine cumulative heat stress to which reefs were exposed, the monthly mean and maximum Degree Heating Week (DHW) for the specific region (5×5 km) encompassing the three reefs were calculated using remote sensing data provided by the National Oceanic and Atmospheric Administration (NOAA Coral Reef Watch version 3.1; NOAA, 2018). DHW is a measure that accumulates thermal anomalies relative to the maximum monthly average sea surface temperature over 12 weeks (Liu et al. 2014). Values above 4 °C-weeks typically trigger mass bleaching, and those above 8 °C-weeks usually result in widespread coral mortality (Kayanne 2017). These thresholds are consistent with the bleaching trends witnessed in Brazil during 2019–20 (Duarte et al. 2020; Ferreira et al. 2021; Braz et al. 2022; Pereira et al. 2022; but see DeCarlo 2020). The DHW

data were gathered for the period between August 2018 and November 2022.

Field assessments and data processing

The coral assemblages (comprised of scleractinian, octocoral, zoantharian and milleporid species) from each of the three reefs were evaluated approximately every 2 months. The evaluation period was divided into four different stages: before thermal stress (September 2018 to February 2019), during thermal stress (March 2019 to August 2019), during the first year of recovery (September 2019 to August 2020), and a final single assessment after 3 years of recovery (between October and November 2022). Underwater photographic surveys were taken to assess the health status of the coral assemblages in the region. The studied reefs are located between 3 and 7 m in depth, and three fixed areas of 2.25 m² were selected haphazardly and sampled for each analyzed reef. Each fixed area was photographed in its entirety using a 50×50 cm PVC frame attached to a GoPro Hero 7 digital camera.

To assess the incidence of bleaching and estimate the bleached area of each reef, the following approaches were employed based on the photos collected in situ: (i) the establishment of three categories indicating hue (adjusted through normalization of brightness and hue patterns according to recommendations in Mantiuk et al. 2009) of the corals—“healthy” for colonies where discoloration was not evident; “mildly bleached” for colonies with noticeable color changes; and “severely bleached” for colonies with

significant color loss and predominantly pale white; and (ii) the evaluation of the percentage of bleached coral cover relative to the total living coral cover, using the photoQuad software and calculating the perimeter of live coral cover (Trygonis and Sini 2012). Mortality was assessed by calculating the loss of coral cover, which is the percentage area occupied by live corals relative to the total sampled area, also using photoQuad to calculate absolute and relative covers.

Statistical analyses

Coral cover data from four distinct time points were used, to specifically examine the process of recovery in comparison to the observed mortality: (i) pre-thermal stress, (January/February 2019, depending on the reef's sampling month), served as the baseline for assessing coral health just before the onset of thermal stress; (ii) post-thermal stress (October/November 2019), indicating coral mortality immediately after the end of the thermal stress period; (iii) 1 year post-thermal stress (August/October 2020), representing the short-term recovery; and (iv) 3 years post-thermal stress (October/November 2022), indicative of medium-term recovery. Repeated measures one-way analyses of variance (ANOVA) using Geissner–Greenhouse correction (for adjustments of lack of sphericity) were conducted to test differences in coral cover considering the periods as a fixed factor. The nine fixed areas (three sites for each of the three reefs) were used as replicates, to get a regional characterization of bleaching and recovery across the Southern Bahia area. Time points in (i–iv) served as the independent variable (factor) and live coral cover as the response variable. Post-hoc Tukey's HSD tests were conducted for ANOVA

significant results. All data were previously checked for normality and homoscedasticity using Shapiro–Wilk and Levene's tests, respectively. Given the normal and homoscedastic nature of the data, we kept the parametric approach without transformations. Lastly, a Spearman correlation analysis was performed between the log data of coral cover loss and coral recovery after 1-year and 3-year post-thermal events to test for the existence of a trade-off between tolerance to acute thermal stress and growth capacity. Statistical significance was considered at $p < 0.05$.

Results

Thermal stress and bleaching incidence

The 2019 thermal stress episode in Southern Bahia intensified in March when DHW values first exceeded 4 °C-weeks. This degree of stress or higher persisted for 5 consecutive months, with DHW values remaining above 4 °C-weeks until July 2019 (Fig. 2). During this period, the coral assemblages endured DHW values exceeding 8 °C-weeks for 3 consecutive months—April, May, and June, peaking in May 2019 (14.1 °C-weeks). Thermal stress beyond 4 °C-weeks was not recorded again until March–June of 2022, in the third year of recovery. In this instance, a less intense thermal anomaly was recorded with monthly mean DHW values not surpassing 8 °C-weeks at any moment (Fig. 2).

At the assemblage level, corals in the three Southern Bahia reefs experienced less than 8% bleaching incidence before thermal stress based on visual assessment. By the peak of thermal stress in April–July 2019, 69% of the

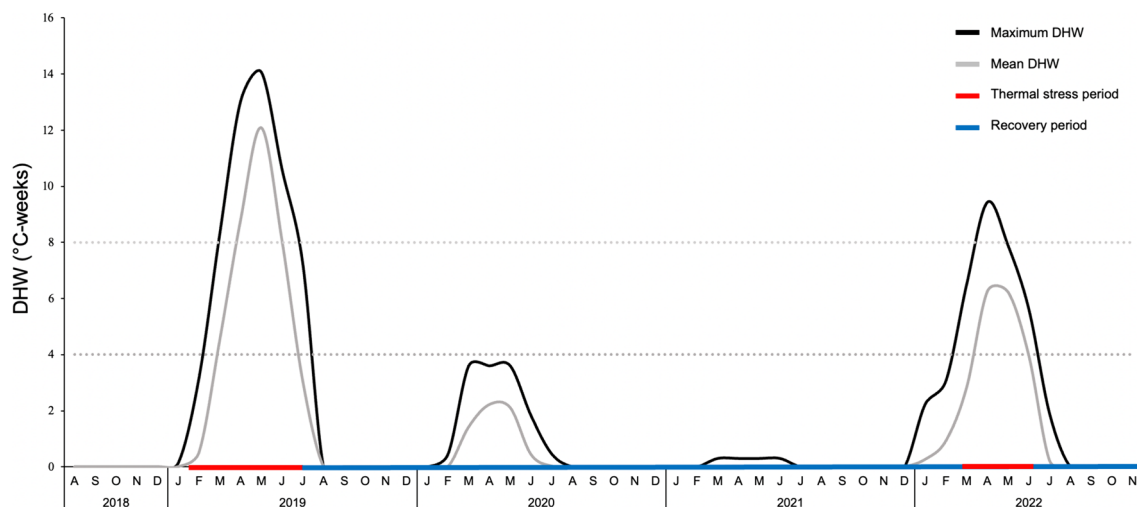


Fig. 2 Monthly maximum and mean Degree Heating Week (DHW) values for the Southern Bahia area encompassing the Araripe, Mucugê and Recife de Fora reefs (Brazil, Southwestern Atlantic) during the 2019 thermal stress episode and subsequent 3-year recovery

period. Dotted lines account for 4 and 8 °C-weeks, which represent thresholds for mass bleaching and mass mortality of corals, respectively (see Kayanne 2017). The thermal stress period is defined by the time interval when DHW values intensified and surpassed 4 °C-weeks

coral cover showed signs of bleaching (Table 1). Individually, reefs of Araripe, Mucugê and Recife de Fora displayed bleached cover levels of 58.7, 74.4 and 54.5%, respectively (Supplementary Information Table S1). One year after the thermal stress, bleaching incidence reduced to less than 1% and increased to 4.6% in 2022 during the second and smaller thermal anomaly (Table 1). During the second heatwave, bleaching primarily affected *Favia gravida*, a small-sized coral species, leading to a reduced bleached coral cover.

Fourteen different species (nine scleractinians—*Agaricia humilis*, *Favia gravida*, *Mu. braziliensis*, *Mu. harttii*, *Mu. hispida*, *Mu. leptophylla*, *Porites astreoides*, *Po. branneri*, and *Siderastrea* sp.; a milleporid hydrocoral—*Mi. alcicornis*; three octocorals—*Muriceopsis sulphurea*, *Phyllogorgia dilatata*, and *Plexaurella grandiflora*; and a zoantharian—*Palythoa caribaeorum*) were found in the reef areas assessed. All species but *Pl. grandiflora* and *Po. branneri* experienced some degree of visual bleaching during the first thermal stress episode (Table 1). However, for both species, bleaching may have gone undetected as they are light brown to white in coloration and usually display a lower density of Symbiodiniaceae cells in their tissues (B. M. Corazza et al., in prep.). Several species experienced bleaching in more than 50% of their cover, including *A. humilis*, *F. gravida*, *Mi. alcicornis*, *Mu. braziliensis*, *Mu. harttii* and *Mu. hispida*. Remarkably, between 2019 and 2020, some colonies of the most abundant *Mussismilia* species (*Mu. braziliensis*, *Mu. harttii* and *Mu. hispida*) remained fully bleached for a period of 13 months, before recovering to a healthy coloration.

Coral cover loss and recovery

During the 2019 thermal stress episode, total live coral cover on Southern Bahia reefs declined considerably, from 16.9 to 10.6% (Fig. 3; Tables 2 and 3). Cover was further reduced after the end of the thermal stress, since bleaching took 6–8 months to fade and colonies of several species were still in poor health and died during the first year of recovery. Coral cover declined for all three reefs investigated, mainly between April and August of 2019. During the thermal stress period, Araripe, Mucugê and Recife de Fora reefs underwent a loss of coral cover of 47.0, 76.0 and 25.7%, respectively (Supplementary Information Table S2). Araripe and Recife de Fora suffered less coral cover loss during thermal stress, but suffered coral mortality after thermal stress had ceased. Recife de Fora lost an additional 22.4% of coral cover during the first 6 months after the end of the thermal stress. Mucugê, however, underwent the most severe loss but suffered no relevant mortality after thermal stress had ended.

Species that underwent most coral cover reduction post-thermal stress were *Mi. alcicornis* (93%), *Po. astreoides* (64%) and *Mu. harttii* (65%) (Tables 2 and 3). In the case of *Mu. braziliensis* there was a significant reduction in cover detected between post-thermal stress and 1 year post-thermal stress (Tables 2 and 3). For *Mi. alcicornis*, dead colonies underwent significant erosion, and tumbled branches fell to the reef bottom (Fig. 4). The same erosive process was also detected for dead *Mu. harttii*. In 2022, during the thermal anomaly in the third year of recovery, while bleaching occurred, there was no significant change in coral cover for any species (Tables 1 and 2).

No significant recovery was detected for the overall coral assemblages in Southern Bahia reefs at both the

Table 1 Bleaching incidence (mean \pm standard error) detected for coral species in nine fixed sites in three Southern Bahia reefs before (pre-thermal stress), during (highest bleaching incidence detected between april and july 2019), and one and 3 years after the 2019 thermal stress episode. Bleaching incidence is expressed as the proportion of bleached coral cover to the overall live coral cover

Coral species	Pre-thermal stress	Highest bleaching incidence	1 year post-thermal stress	3 years post-thermal stress
<i>Agaricia humilis</i>	27.10 \pm 0.22	87.35 \pm 12.66	0.99 \pm 0.01	0.00 \pm 0.00
<i>Favia gravida</i>	16.20 \pm 0.07	53.51 \pm 14.02	0.20 \pm 0.00	17.97 \pm 0.16
<i>Millepora alcicornis</i>	12.44 \pm 0.06	79.62 \pm 10.77	0.00 \pm 0.00	3.73 \pm 0.02
<i>Muriceopsis sulphurea</i>	18.73 \pm 0.12	29.00 \pm 15.53	0.00 \pm 0.00	7.28 \pm 0.03
<i>Mussismilia braziliensis</i>	7.91 \pm 0.08	57.89 \pm 5.44	1.98 \pm 0.01	1.20 \pm 0.01
<i>Mussismilia harttii</i>	15.11 \pm 0.13	74.82 \pm 16.78	0.00 \pm 0.00	7.36 \pm 0.02
<i>Mussismilia hispida</i>	4.18 \pm 0.03	53.75 \pm 20.42	0.00 \pm 0.00	9.68 \pm 0.10
<i>Mussismilia leptophylla</i>	0.00 \pm 0.00	2.83 \pm 2.83	0.00 \pm 0.00	3.30 \pm 0.00
<i>Palythoa caribaeorum</i>	0.00 \pm 0.00	33.33 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
<i>Phyllogorgia dilatata</i>	5.98 \pm 0.06	36.42 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
<i>Plexaurella grandiflora</i>	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
<i>Porites astreoides</i>	0.00 \pm 0.00	38.21 \pm 14.41	0.00 \pm 0.00	0.00 \pm 0.00
<i>Porites branneri</i>	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
<i>Siderastrea</i> sp.	6.40 \pm 0.03	31.65 \pm 7.94	0.01 \pm 0.00	3.52 \pm 0.01
Overall coral assemblage	7.81 \pm 0.06	69.09 \pm 9.81	0.44 \pm 0.01	4.60 \pm 0.41

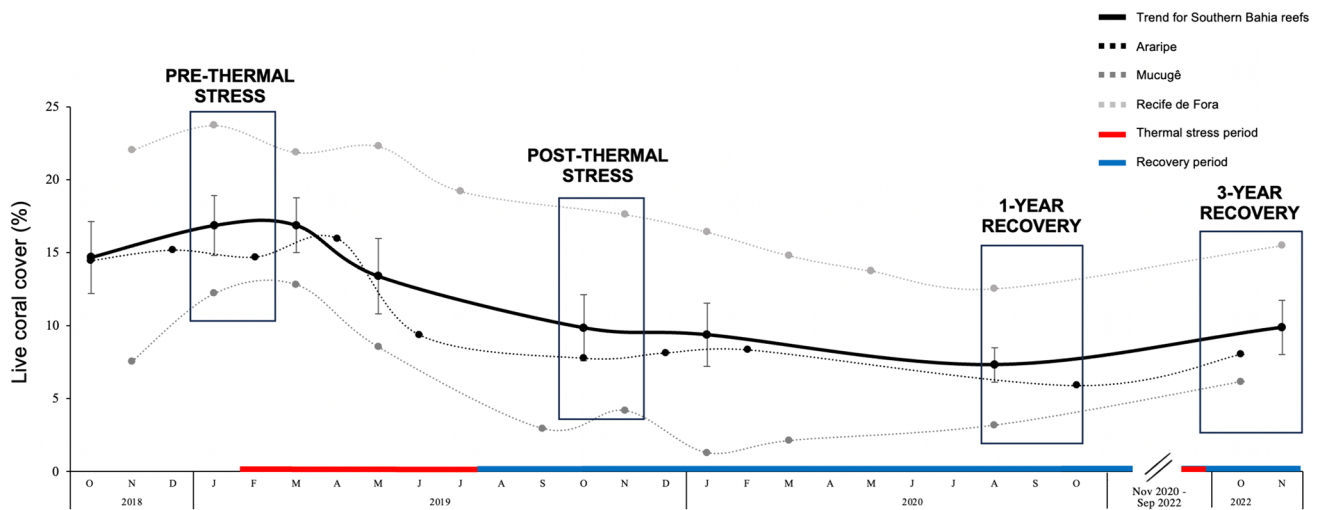


Fig. 3 Change in coral cover for Southern Bahia reefs (thick black line) during the 2019 thermal stress episode and subsequent 3-year recovery period. Trends for individual reefs (Araripe, Mucugê and Recife de Fora) are presented in thin dotted lines. The thermal stress

period is defined by the time interval when DHW values intensified and surpassed 4 °C-weeks. Error bars indicate standard error and were removed from individual reefs data for proper visualization

Table 2 Relative benthic cover (mean ± standard error) for coral species in Southern Bahia reefs before (pre-thermal stress), immediately after (post-thermal stress), and one and 3 years after the 2019 thermal stress episode. Statistically significant coral cover reductions (after

thermal stress) and cover gains (after 3 years of recovery, compared to post-thermal stress) are displayed. Refer to Table 3 for statistical analyses results

Coral species	Pre-thermal stress	Post-thermal stress	Significant relative cover loss	1 year post-thermal stress	3 years post-thermal stress	Significant relative cover gain in 3 years
<i>Agaricia humilis</i>	0.56 ± 0.37	0.36 ± 0.24	–	0.19 ± 0.11	0.09 ± 0.06	–
<i>Favia gravida</i>	0.18 ± 0.05	0.21 ± 0.04	–	0.10 ± 0.05	0.24 ± 0.12	–
<i>Millepora alcicornis</i>	3.90 ± 1.10	0.27 ± 0.18	–93%	0.38 ± 0.27	0.72 ± 0.54	–
<i>Muriceopsis sulphurea</i>	1.25 ± 0.46	1.08 ± 0.42	–	0.99 ± 0.31	1.55 ± 0.73	–
<i>Mussismilia braziliensis</i>	1.82 ± 0.54	1.64 ± 0.49	–	0.69 ± 0.26	0.63 ± 0.30	–
<i>Mussismilia harttii</i>	2.17 ± 0.69	0.76 ± 0.24	–65%	0.50 ± 0.13	0.87 ± 0.26	–
<i>Mussismilia hispida</i>	0.33 ± 0.09	0.21 ± 0.06	–	0.27 ± 0.04	0.40 ± 0.31	–
<i>Mussismilia leptophylla</i>	0.72 ± 0.63	0.67 ± 0.57	–	0.33 ± 0.29	0.47 ± 0.47	–
<i>Palythoa caribaeorum</i>	0.21 ± 0.21	0.15 ± 0.15	–	0.01 ± 0.01	0.01 ± 0.01	–
<i>Phyllogorgia dilatata</i>	2.15 ± 1.20	1.83 ± 1.30	–	1.52 ± 0.79	1.07 ± 0.43	–
<i>Plexaurella grandiflora</i>	0.10 ± 0.05	0.14 ± 0.07	–	0.08 ± 0.02	0.13 ± 0.08	–
<i>Porites astreoides</i>	1.10 ± 0.28	0.39 ± 0.27	–64%	0.32 ± 0.09	0.55 ± 0.31	–
<i>Porites branneri</i>	0.04 ± 0.02	0.02 ± 0.01	–	0.01 ± 0.00	0.01 ± 0.00	–
<i>Siderastrea</i> sp.	4.96 ± 1.31	4.64 ± 1.60	–	3.69 ± 0.68	4.64 ± 1.13	–
Overall coral assemblage	16.87 ± 2.05	10.62 ± 2.42	–37%	6.39 ± 1.05	7.89 ± 1.85	–

1-year and 3-year marks following the end of the 2019 thermal stress episode (Tables 2 and 3). In fact, some decrease in cover was still detected 1-year after the thermal stress, as indicated by the ANOVA results (Table 3). In addition, a negative Spearman correlation was detected between mortality (coral cover loss) and coral recovery

($-0.58 \leq R \leq -0.56$; $0.03 \leq P \leq 0.04$) for both 1 and 3 years after the first thermal anomaly (Fig. 5). At the individual reef level, no relevant coral recovery was detected for the three studied reefs (Supplementary Information Table S2). At the species level, again, no species displayed significant recovery after 3 years since the end

Table 3 Statistical results from repeated measures one-way analyses of variance (ANOVA) for differences between periods (pre- and post-thermal stress, pre- and 1 year post-thermal stress, and pre- and 3 years post-thermal stress, $df=3$), for each coral species and for the entire coral assemblage in Southern Bahia reefs during the 2019 thermal stress episode and subsequent 3 years of recovery

Species	F	p	Tukey's HSD	Trend
<i>Agaricia humilis</i>	1.454	0.263	n/a	–
<i>Favia gravida</i>	0.704	0.446	n/a	–
<i>Millepora alcicornis</i>	8.758	0.013*	0.027 (pre- and post-thermal stress)	↓
<i>Muriceopsis sulphurea</i>	3.786	0.077	n/a	–
<i>Mussismilia braziliensis</i>	7.609	0.004*	0.045 (pre- and 1 year post-thermal stress)	↓
<i>Mussismilia harttii</i>	5.070	0.043*	0.020 (pre- and post-thermal stress)	↓
<i>Mussismilia hispida</i>	0.684	0.443	n/a	–
<i>Mussismilia leptophylla</i>	1.341	0.283	n/a	–
<i>Phyllogorgia dilatata</i>	1.452	0.266	n/a	–
<i>Plexaurella grandiflora</i>	0.483	0.596	n/a	–
<i>Porites astreoides</i>	3.826	0.035*	0.019 (pre- and post-thermal stress)	↓
<i>Porites branneri</i>	2.273	0.169	n/a	–
<i>Siderastrea</i> sp.	4.811	0.221	n/a	–
Overall coral assemblage	25.38	<0.0001*	0.003 (pre- and post-thermal stress), 0.040 (pre- and 1 year post-thermal stress), and 0.036 (pre- and 3 years post-thermal stress)	↓, ↓, ↓

(*) indicates statistically significant results

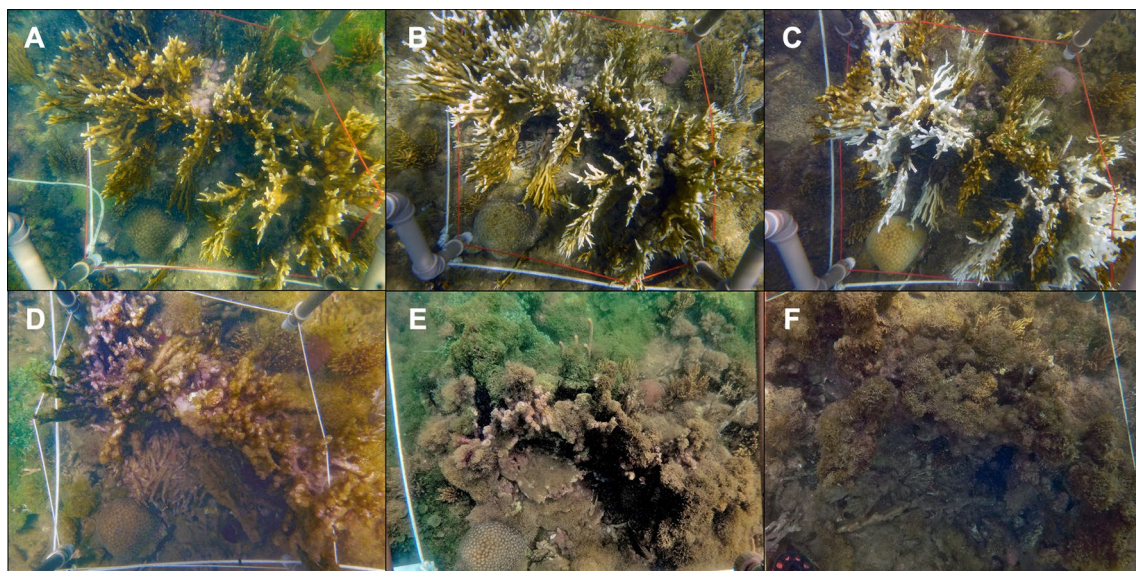


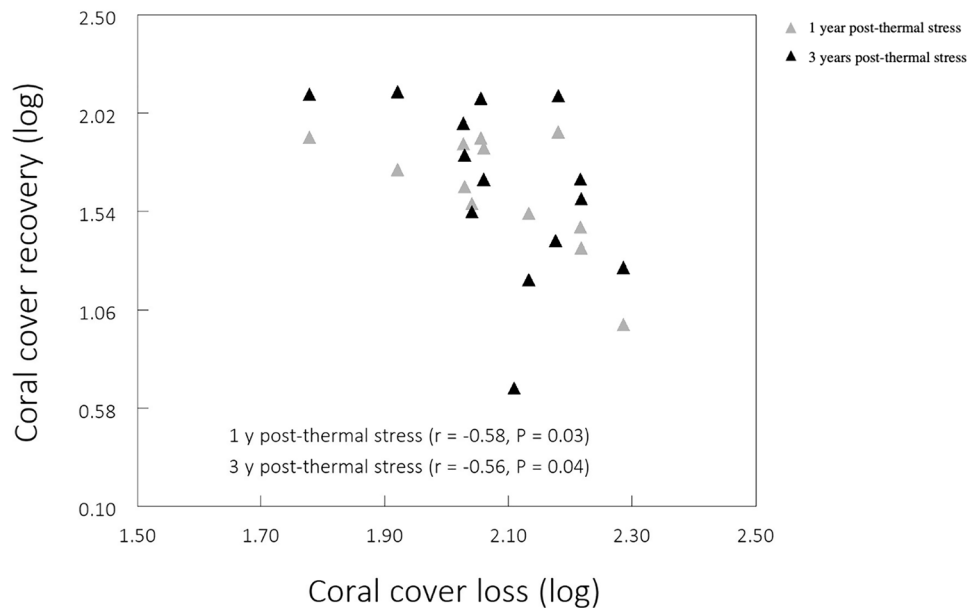
Fig. 4 Bleaching and mortality process of a *Mi. alcicornis* colony at araripe reef (Southern Bahia, Brazil, Southwestern Atlantic) during the 2019 thermal stress episode. **A** healthy colony in October 2018; **B** mildly bleached colony in March 2019; **C** severely bleached colony in April 2019; **D** dead colony covered in turf and crustose coralline

algae (purple and brownish sections, respectively) in October 2019; **E** dead and partially eroded colony covered in turf algae in October 2020; and **F** dead and eroded colony in October 2022—note fallen branching fragments in the bottom left corner

of the 2019 thermal stress episode (Table 3). In the case of *Mi. alcicornis*, the only branching species, we visually observed in the field an early recovery process that, while

not statistically significant, merits acknowledgment due to its upward trend (0.27 to 0.72% in relative cover) and ecological relevance of this species.

Fig. 5 Relationship between coral cover recovery and coral cover loss across 14 photosymbiotic cnidarian species. The logged data for percentage of cover recovery and cover loss after 1 and 3 years of the 2019 Southwestern Atlantic thermal stress episode is provided in comparison to pre-thermal stress levels



Discussion

In 2019, a strong heatwave caused widespread coral bleaching in the Southwestern Atlantic, impacting the entire spectrum of tropical and subtropical reef communities (Banha et al. 2020; Duarte et al. 2020; Ferreira et al. 2021; Gaspar et al. 2021; Braz et al. 2022; Pereira et al. 2022). Our findings show that almost every species in Southern Bahia reefs experienced both intense bleaching and cover loss, including endemic and threatened species like *Mu. braziliensis* and *Mu. harttii*. Three years after the event, there has been no coral cover gain for the local coral assemblage or any individual species. However, a high increase in algal cover has been observed in the area after the 2019 thermal stress episode (C.F.B. Santarém, *in prep.*).

Prior to thermal stress, Southern Bahia coral assemblages displayed background bleaching levels of ~7%, which is typical for the area (Coral Vivo Institute, unpubl. data). However, during thermal stress, bleaching incidence rose to 69% of the coral cover, similar to the elevated levels of 60–80% documented along other segments of the Brazilian coast during the 2019 bleaching event (Banha et al. 2020; Duarte et al. 2020; Ferreira et al. 2021; Gaspar et al. 2021; Braz et al. 2022). Mortality, on the other hand, was notably higher in Southern Bahia reefs compared to the overall trend along the Brazilian coast. In other areas, elevated mortality rates (> 15%) were observed exclusively for *Mi. alcicornis* and *Mu. harttii*, with the other coral species displaying reduced mortality rates despite experiencing maximum DHW values between 13.0 and 20.5 °C-weeks (Banha et al. 2020; Duarte et al. 2020; Pereira et al. 2022). This lower mortality under high thermal stress suggests that Southwestern Atlantic reefs and their unique coral fauna have many traits

that confer higher resilience. These include high turbidity, predominance of massive species, increased heterotrophic capacity, flexible symbiotic associations, and higher aerobic capacity, among others (Mies et al. 2018; 2020; Marangoni et al. 2019; Fonseca et al. 2021; Godoy et al. 2021; Angonese et al. 2022; Garrido et al. 2023; Lucas et al. 2023; Santana et al. 2023). These traits, together with a history of low mortality during past GMBEs have led to the proposition that the Southwestern Atlantic province has acted as a major climate refugium (*sensu* Morelli et al. 2020), in the sense that they have suffered much less global warming impacts compared to Indo-Pacific and Caribbean reefs (Mies et al. 2020). Our findings, however, show that overall coral cover decreased by nearly 40%, and also that four coral species, including some of the main reef-builders, underwent more than 50% loss in Southern Bahia during the 2019 bleaching episode. Thus, at least in this specific case and area, reefs may not have served as refugia and, therefore, it is likely that the Southwestern Atlantic may not be refugia as a whole; rather, some sites within this province may serve as refugia and some may not. For example, subtropical rocky reefs in the Southwestern Atlantic experienced less than 2% coral mortality under extreme DHW values > 20 °C-weeks (Banha et al. 2020). Another potential scenario is that the intensity of the heatwave surpassed the tolerance threshold of that specific site. It is crucial to emphasize that even refugia sites, such as the Southwestern Atlantic, are vulnerable to high mortality events linked to severe heatwaves and are unlikely to survive unless decisive measures are taken to halt global warming (Oliveira et al. 2019; Bleuel et al. 2021; Príncipe et al. 2021). Regardless, there is a need for more detailed and localized investigations to determine the specific reef sites in the Southwestern Atlantic that are most sensitive and

those that are more tolerant, with emphasis on their specific environmental conditions.

An additional concern regarding mortality is that the most significant contributors to reef habitat complexity in the Southwestern Atlantic—*Mi. alcicornis* and *Mu. harttii*—were the species that most experienced cover loss. Branching scleractinians are traditionally the main structural complexity engineers (Graham and Nash 2013; Darling et al. 2017), but are absent in the Southwestern Atlantic. *Mi. alcicornis*, a branching and calcifying hydrozoan, takes up this ecological niche in the region (Coni et al. 2013; Luza et al. 2022). However, like branching scleractinians, milleporids are sensitive to thermal stress, suffer high mortality during intense heatwaves (Loya et al. 2001; Ferreira et al. 2021), and become more susceptible to benthic competition under thermal stress (Lonzetti et al. 2022). *Mu. harttii*, with its phacelloid morphology, features wide spaces between corallites and thus provides shelter for a diverse array of crustaceans, mollusks, and other invertebrates (Nogueira et al. 2015; 2021). However, it may also be a thermally-sensitive species (see Braz et al. 2022; Pereira et al. 2022) and, even after the end of thermal stress, mortality rates were elevated due to colonies remaining bleached and in poor health over several months.

Most surviving bleached colonies returned to their original healthy color approximately 6 months after the end of the thermal stress endured during the 2019 bleaching episode. This agrees with the findings of Ferreira et al. (2021), which show that colonies of *Mi. alcicornis* and *Mu. brazilensis* required a similar amount of time to fully regain their symbionts. However, the scenario is quite different for coral recovery. The term “coral recovery” has a broad range of definitions and, therefore, can be defined and interpreted in several different ways. While some more stringent interpretations equate recovery to the restoration of the original coral cover levels prior to stress, others perceive a return to at least 50% of the initial levels as sufficient for confirming recovery (Connell 1997; Gilmour et al. 2013; Johns et al. 2014). Even if recovery is merely considered as any statistically significant gain in coral cover after suffering mortality, the investigated reefs underwent no significant recovery after 3 years. Although a full return to original coral cover levels is known to take several years to decades (Gardner et al. 2005; Adjeroud et al. 2009; Gouezo et al. 2019), an absence of recovery in 3 years is alarming. Significant recovery has been observed in several cases during the first 3–5 years following mass mortality (Gilmour et al. 2013; González-Barrios et al. 2021; Abesamis et al. 2023; Speelman et al. 2023), but this does not seem to be the case for Southwestern Atlantic reefs. Our findings show clear dynamics: severe heatwaves induce acute coral mortality, succeeded by more gradual and less intense mortality after the heatwave subsides, and 3 years after thermal stress, coral assemblages still display no palpable signs of recovery. These insights

underscore the imperative need for continuous, long-term monitoring of coral cover in Southwestern Atlantic reefs.

The reasons for the absent or slow recovery are possibly the same as those associated with increased resilience. Southwestern Atlantic reefs are widely dominated by massive coral species (Leão et al. 2003; Mies et al. 2020). Although these species are generally thermally tolerant, they are also notoriously slow-growing, which greatly diminishes the recovery capacity of local reefs—full recovery for massive corals may require decades (Gates and Edmunds 1999; Lough and Barnes 2000; Loya et al. 2001; Edmunds and Elahi 2007). Similarly, the elevated turbidity in Southwestern Atlantic reefs (Santana et al. 2023) increases resilience by sheltering corals from heat and photoinhibition (see Cacciapaglia and van Woesik 2016; Skirving et al. 2017), but also hinders growth rates and recovery because of the reduced photosynthetic efficiency (Anthony and Fabricius 2000; Hennige et al. 2008; Bessell-Browne et al. 2017). Thus, a trade-off arises when comparing the biogeographic regions of the Indo-Pacific, Caribbean, and South Atlantic concerning bleaching tolerance and coral recovery. In reefs of the Southwestern Atlantic, coral mortality is notably lower compared to the Indo-Pacific and Caribbean (Mies et al. 2020). Even when specifically considering Southwestern Atlantic coral species, the negative correlation between recovery and cover loss suggests a functional conflict between tolerance and growth. The argument posits that tolerance to acute thermal stress trades off growth capacity, possibly via shifts in physiological functions associated with oxidative status, constraining the amount of energy available for other physiological functions and impacting fitness costs (e.g., Barley et al. 2021).

The occurrence of a smaller-scale thermal anomaly towards the third year after the first thermal stress episode in 2019 may have further impaired recovery. The second thermal anomaly was notably milder than the first, as indicated by its shorter duration, mean DHW values never exceeding 8 °C-weeks, and the absence of detectable coral cover loss during that period. It is also possible that corals may have exhibited increased resistance after enduring the previous instance of thermal stress (see DeCarlo et al. 2019). Regardless, it is a stressful event that likely hindered recovery. In addition, Brazilian reefs suffer from several local impacts such as eutrophication and overfishing (Costa Jr et al. 2008; Francini-Filho and Moura 2008), which may slow or impede coral recovery after severe disturbances (Gove et al. 2023).

In the current context, a lack of significant coral recovery is particularly worrisome because a GMBE is expected in 2023–24 in association with a new and unprecedentedly strong ENSO cycle (see Lian et al. 2023; Ludescher et al. 2023). As GMBEs and regional-scale heatwaves become more frequent, intense and longer-lasting (Hughes et al. 2018), so do bleaching episodes. If reefs face new bleaching episodes

before adequately recuperating from a prior event, not only are recovery processes stopped, but corals become more vulnerable to suffering a higher degree of mortality because of their fragile state (Baker et al. 2008; Schoepf et al. 2015; Brown and Barott 2022). A case in point is the Great Barrier Reef, which grappled with consecutive bleaching episodes in 2016 and 2017, severely hampering its recovery, recruitment and overall health (Dietzel et al. 2020; Mumby et al. 2021). This highlights the causes for concern regarding the state of *Mi. alcicornis* and *Mu. harttii* populations, which faced severe reductions in the Southwestern Atlantic in 2019–20 and may endure additional declines that are likely to further compromise their conservation status. On the other hand, thermal anomalies and resulting bleaching also act as selective filters, most probably decreasing the genetic diversity of affected species. However, those genotypes that survive might further tolerate thermal stress. Although Southwestern Atlantic reefs may be considered large-scale refugia for now (Mies et al. 2020), it is critically important not to misinterpret the concept of refugium and regard them as immune to bleaching (see Pereira et al. 2022). Proper investigations on bleaching dynamics in refugia are relevant as they are considered conservation priorities against local scale stressors, thanks to their ability to partially buffer the effects of climate change (Keppel et al. 2012). Therefore, enhancing local conservation policies and providing protection against pollution, overfishing and tourism is critical to increase their resilience to bleaching (Knowlton and Jackson 2008; MacNeil et al. 2019; Nunes et al. 2023).

The present work shows that Southern Bahia reefs displayed high bleaching incidence, elevated mortality and, most alarmingly, the absence of any significant coral recovery during the 3 years following the 2019 bleaching episode. The limited recovery capacity may indicate the initial breakdown of the refugium, and is likely also a trade-off for resistance. Typical characteristics common in the region, such as high turbidity and the prevalence of massive corals, render these reefs less susceptible to bleaching. However, these same factors could be responsible for diminishing growth and recovery rates. Therefore, given the impending arrival of the 2023–24 ENSO, Southwestern Atlantic reefs face a major challenge for their persistence.

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Data availability The data generated and analyzed during this study are available at the Supplementary Material. Raw data may be supplied by the corresponding author upon request.

Declarations

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

Ethical approval This is an observational study. The Chico Mendes Institute for Biodiversity Conservation (ICMBio) has confirmed that no ethical approval is required.

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