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SHORT NOTES

Different responses of massive and branching corals to a major heatwave at the largest and richest reef complex in South Atlantic

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Abstract

In 2019, a major coral bleaching event affected reefs worldwide, including marginal reefs within the Abrolhos Bank (16°40′–19°40′S, 39°10′–37°20′W), the largest and richest coral reefs in the South Atlantic. Between March and May 2019, this area was affected by the strongest heatwave since 1985. The health trajectories of the branching hydrocoral *Millepora alcicornis* and the endemic reef-building coral *Mussismilia braziliensis* were recorded during this thermal stress event. The degree heating week value reached its historical maximum (DHW 19.65), causing bleaching in 100% of *Millepora alcicornis* and 80% of *Mussismilia braziliensis* colonies. Bleached *Millepora alcicornis* were rapidly covered by cyanobacteria, followed by algal turfs and calcareous algae, leading to 90% mortality. Conversely, 90% of *Mussismilia braziliensis* colonies recovered to a healthy state after bleaching. The high post-bleaching recovery capacity and resistance to mortality of this massive reef-building coral suggests these marginal reefs can be resilient to thermal stress events, despite losing structural complexity due to high mortality of branching and less abundant hydrocorals.

Introduction

Marine ecosystems have been affected globally by thermal stress events, leading to alterations in biological compositions and ecological functions (Hughes et al. 2018). Increases in oceanic temperatures during the last 40 years have affected coral reefs worldwide, resulting in global-scale coral bleaching events (GCBE). The effects of the last GCBE, triggered by severe heat stress during the 2014–2017 El Niño event, are still visible and degrading reef communities (Hughes et al. 2017; Eakin et al. 2019).

In the Southwestern Atlantic, Brazilian marginal reefs comprise the only coralline structures, mostly found in the eastern and northeastern coast (Leão et al. 2003). Brazilian reefs comprise low coral diversity and high endemism (~ 30%), being mostly composed by massive and encrusting forms (Leão et al. 2003, 2019; Mies et al. 2020). Corals in marginal reefs of the Southwestern Atlantic have a wider depth distribution, are more tolerant to high sedimentation, turbidity, and nutrient levels, and suffered less from mass bleaching events in comparison to the Indo-Pacific and the Caribbean, attributes that can help corals be more resilient to thermal–stress events (Mies et al. 2020).

Most recent bleaching events in the Brazilian coast have resulted in low coral mortality, such as the 2016–2017 event in the Abrolhos region, in Eastern Brazil, where mortality was estimated to be less than 3% (Teixeira et al. 2019), and the 2019 event that affected reefs in Southeast Brazil, where coral mortality was estimated 2% (Banha et al. 2019). In contrast, high mortality of one branching species (*Millepora alcicornis*) was reported in the 2019 event that reached the Abrolhos reefs (Duarte et al. 2020). Understanding how different species respond to thermal stress events in the largest and richest marginal reefs in South Atlantic, the Abrolhos

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Bank (Leão et al. 2003), is critical to estimate their susceptibility to predicted global climate change and the potential role of these environments as refugia (Mies et al. 2020).

The Abrolhos Bank comprises most Brazilian reef types and coral species (Laborel 1970; Moura et al. 2013; Ferreira et al. 2020) and is partially protected by the Abrolhos Marine National Park (AMNP). Among the endemic coral species in the Abrolhos Bank, *Mussismilia braziliensis* has a restricted distribution, mostly within the state of Bahia, and is considered the major reef builder (Leão et al. 2003), reaching more than 1 m in diameter. In comparison to the Indo-Pacific and the Caribbean, there is a paucity of branching corals in Brazilian reefs (Mies et al. 2020), so hydrocorals of the genus *Millepora*, such as *Millepora alcicornis*, are critical to add structural complexity to these reefs despite being more common in reef crests and less abundant than massive corals (Coni et al. 2013; Francini-Filho et al. 2013; Teixeira et al. 2019; Duarte et al. 2020).

In the summer of 2018–2019, bleaching alerts were repeatedly disclosed by the National Oceanic and Atmospheric Administration (NOAA) for Brazilian reefs, including those within the Abrolhos Bank. As a response, Park authorities implemented a monitoring protocol focused on two distinct reefs within the AMNP. In this study, we report the bleaching and post-bleaching trajectories of two important coral species in the Abrolhos reefs, the branching hydrocoral *Millepora alcicornis* and the reef-building *Mussismilia braziliensis*, assessed through monthly transects. We evaluated whether the health condition of each species differed between the monitored months, and if the mortality of *Millepora alcicornis* was influenced by the distinct reef habitats. We also present a weekly photographic monitoring of the health progression and post-mortality succession of marked colonies of both species throughout the bleaching event.

Materials and methods

The Abrolhos Bank is located in the South Atlantic Ocean (16°40′–19°40′S, 39°10′–37°20′W), on the wider extension of the Brazilian continental shelf (approx. 200 km), off the states of Bahia and Espírito Santo (Fig. 1). This area comprises the largest and richest coral reefs in the South Atlantic Ocean (Leão et al. 2003). The AMNP protects about 2% of the Abrolhos Bank, including a large reef complex and the Abrolhos Archipelago (60 km from the coast), a no-take area, where tourism activities are regulated (Francini-Filho et al. 2013; Moura et al. 2013). Different reef formations occur within this region, including fringing reefs surrounding the five islands of the Archipelago, formed mainly by the cementation of coralline algae (Leão et al. 2003). Moreover, the AMNP also protects unique mushroom-shaped reef pinnacles typical of this region, the "chapeirões", which can reach up to 20 m high and are built by bryozoans, coralline algae, and corals (Leão et al. 2016; Bastos et al. 2018).

The most abundant corals in Abrolhos are the endemic *Mussismilia braziliensis* and *Mussismilia hartii*, the broadly distributed *Montastraea cavernosa, Siderastrea* spp., and *Porites astreoides*, in addition to the hydrocoral *Millepora alcicornis*, which is less abundant than massive scleractinians but occurs on shallower areas of the reefs and crests (Francini-Filho et al. 2013). Corals in this area suffered massive bleaching in the 2016–2017 events, but experienced low mortality (Teixeira et al. 2019) until the 2019 heatwave that caused major mortality of the hydrocoral *Millepora alcicornis* (Duarte et al. 2020). Anticipating the 2019 heatwave in the Southwestern Atlantic, we monitored corals in two distinct sites within the AMNP: a fringing shallow reef (~5 m deep) around the Archipelago (Mato Verde) and the top of a pinnacle reef (~9 m deep) located ~2 km from the Archipelago (Jean Pierre; Fig. 1).

To characterize the 2019 thermal–stress event, data on sea surface temperature (SST) and degree heating week (DHW) were obtained weekly at a 5 km resolution from the NOAA database using the Abrolhos Reefs Virtual Station (NOAA Coral Reef Watch 2019). Degree heating week is a standardized measure of the accumulated heat stress exceeding the monthly maximum mean SST for a given region (Kayanne 2017). The relationship between DHW values and coral bleaching has been established in a way that corals submitted to DHW higher than 8.0 are expected to experience severe bleaching (> 70%; Kayanne 2017).

We conducted surveys between February and August 2019 to monitor the health status of two species of corals: *Mussismilia braziliensis* and *Millepora alcicornis*. We chose these species based on their contribution to reef construction and structural complexity, respectively (Coni et al. 2013; Francini-Filho et al. 2013). Colonies of *Mussismilia braziliensis* are abundant at the top of coral pinnacles and in fringing reefs, while colonies of *Millepora alcicornis* are found in the shallowest areas of Abrolhos' fringing reefs and in the borders of the coral pinnacles (Laborel 1970; Leão et al. 2003).

We assessed the health status of *Mussismilia braziliensis* in both the fringing and the pinnacle reef, which are about 2 km apart, and of *Millepora alcicornis* in the pinnacle reef, through four replicated 20 m line intercept transects (LIT) conducted monthly. We conducted a health evaluation on every colony intercepted by each transect. Health conditions were assigned to the following categories: healthy, when the colony had no bleaching signs and held its natural color; slightly bleached, when up to 30% of the colony was bleached; partially bleached, when 30–90% of the colony was bleached; severely bleached, when more than 90% of the colony was bleached; and dead, when the skeleton was

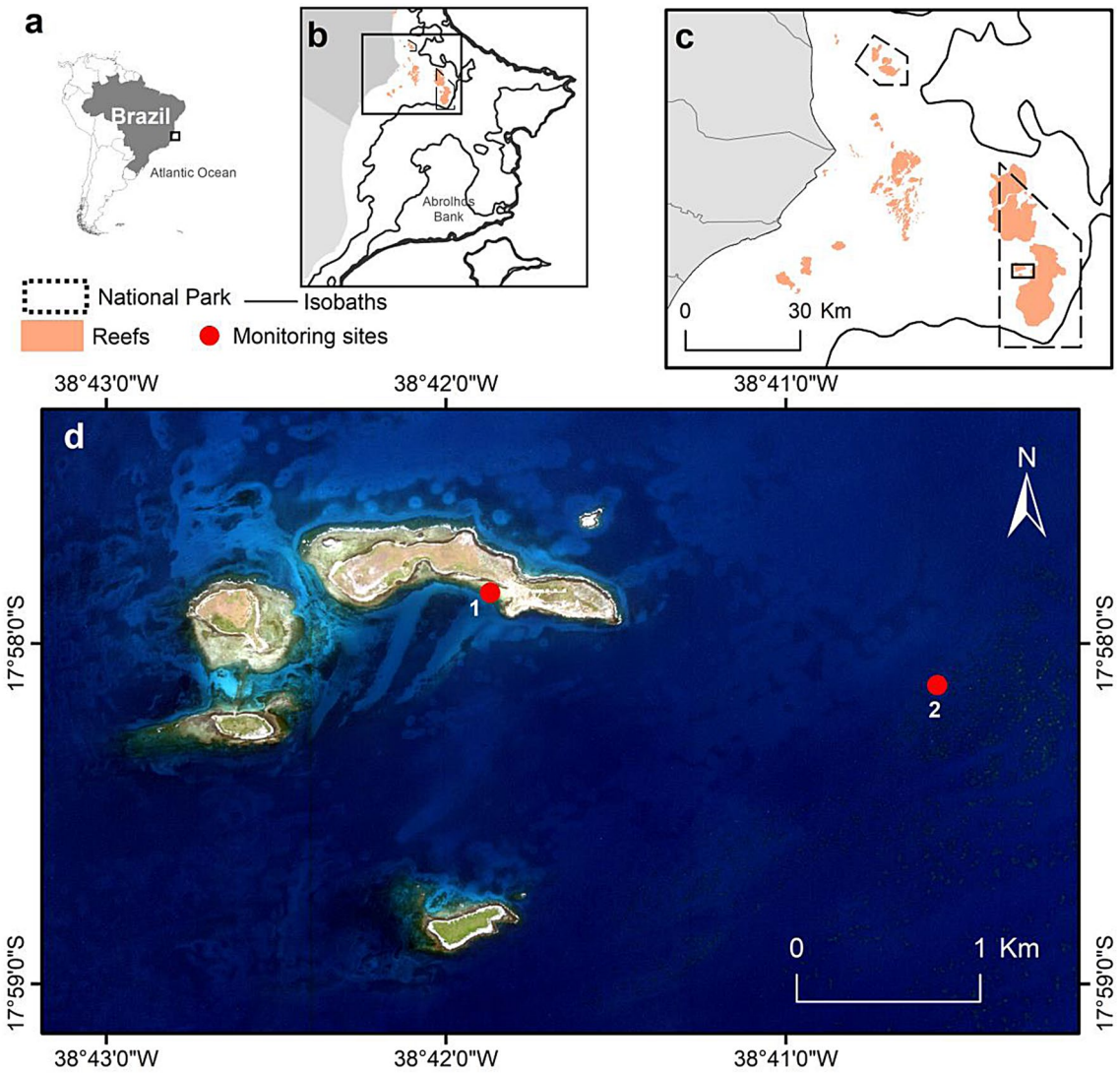


Fig. 1 Abrolhos Bank in Southwestern Atlantic and monitoring sites. **a** Location of the Abrolhos Bank in Eastern Brazil; **b** Abrolhos Bank; **c** protected area of Abrolhos Marine National Park (dashed lines) and Abrolhos Archipelago (solid lines); **d** Abrolhos Archipelago and monitoring sites: Mato Verde fringing reef (1) and Jean Pierre pinnacle reef (2). Image: Satellite Ikonos (4 m resolution), Conservation International

apparent or overgrown by other organisms. Because the LIT method may underestimate the abundance of the branching hydrocoral *Millepora alcicornis*, we additionally assessed the health of 30 colonies of *Millepora alcicornis* in August 2019 haphazardly selected in each site and quantified the maximum length and proportion of mortality of each colony. We also marked six colonies of *Mussismilia braziliensis* and six of *Millepora alcicornis* in the fringing reef and photographed them weekly between February and August 2019. Through a visual analysis of the photographs, we obtained the percentage area of each colony on the following conditions: healthy, bleached, and overgrown by cyanobacteria, algal turfs, and crustose coralline algae. To visualize the coral health trajectories for each species we calculated the mean percentage area of their health conditions on each monitoring week through the bleaching event.

To investigate differences in the proportion of health conditions (response variable) between the monitored months (independent variable) we conducted separate pairwise Kolmogorov–Smirnov tests for each species. We also conducted a Pearson's Chi-squared test with Yates' continuity correction to evaluate the influence of reef habitat (fringing and pinnacle reef, independent variable) on mortality (response variable) of the 60 surveyed colonies of *Millepora alcicornis* . Statistical tests were run using R in RStudio (R Core Team 2018, v. 1.2.5001).

Results and discussion

In 2019, the Abrolhos reefs were affected by the strongest heatwave since 1985, causing massive bleaching in most coral species. However, the two monitored species had different responses. The hydrocoral *Millepora alcicornis*, critical for reef complexity (Coni et al. 2013; Teixeira et al. 2019), experienced great mortality (> 90%), while the endemic brain coral *Mussismilia braziliensis*, one of the main reef builders in the region, showed greater resistance to mortality and higher post-bleaching recovery capacity.

The 2019 thermal–stress event

In the beginning of 2019, several bleaching warnings and alerts were disclosed for the Abrolhos region (NOAA Coral Reef Watch 2019), resulting from an unprecedented heatwave in the region, in both magnitude and duration. According to the time-series data (1985–2019) of the Abrolhos virtual station (Fig. 2), by the end of January, the SST reached the regional coral bleaching threshold of 27.9 °C (NOAA Coral Reef Watch 2019). The SST kept increasing and peaked in February when it reached 29.33 °C. Similarly, the DHW reached its maximum historical value (19.65 DHW) in May 2019, the highest value ever recorded for the Abrolhos virtual station since 1985 (Fig. 2).

Coral response to the thermal–stress event

Colonies of *Millepora alcicornis* and *Mussismilia braziliensis* responded differently to the thermal stress event in the pinnacle reef (Jean Pierre; Fig. 3). All colonies of both species were healthy when we started monitoring in February. In March, colonies of *Millepora alcicornis* presented the first signs of bleaching (distributed in three categories: slightly, partially, and severely bleached), and only 6% of the colonies remained healthy, whereas all *Mussismilia braziliensis* were healthy during this month. In April and May when DHW peaked (19.65 DHW), all surveyed colonies

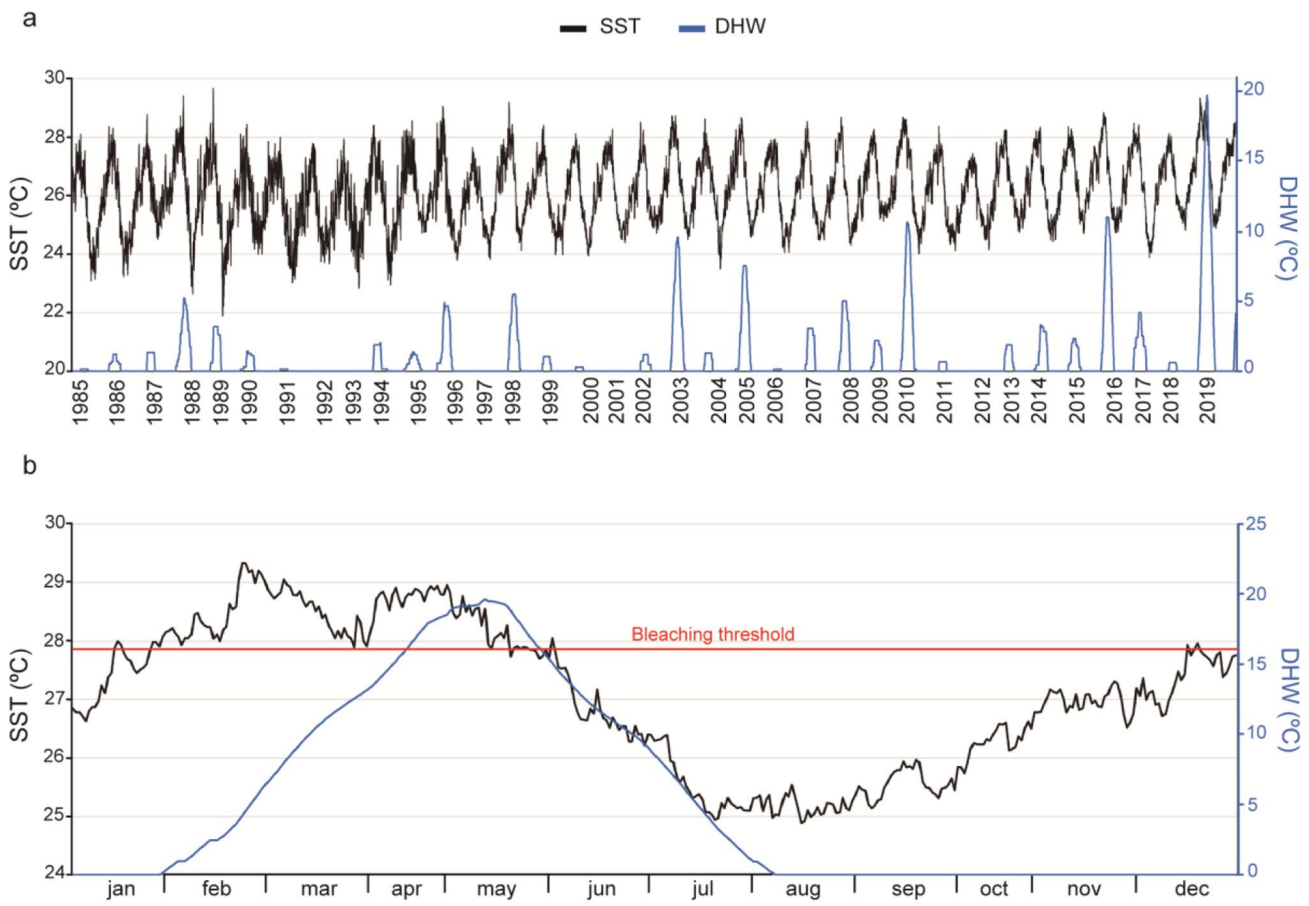


Fig. 2 Temporal variation in sea surface temperatures (SST) and degree heating weeks (DHW) in the Abrolhos Reefs Virtual Station according to the NOAA Coral Reef Watch database. **a** Historical time-series (1985–2019); **b** monthly variation in 2019 showing SST regional bleaching threshold of 27.9ºC (sensu Teixeira et al. 2019)

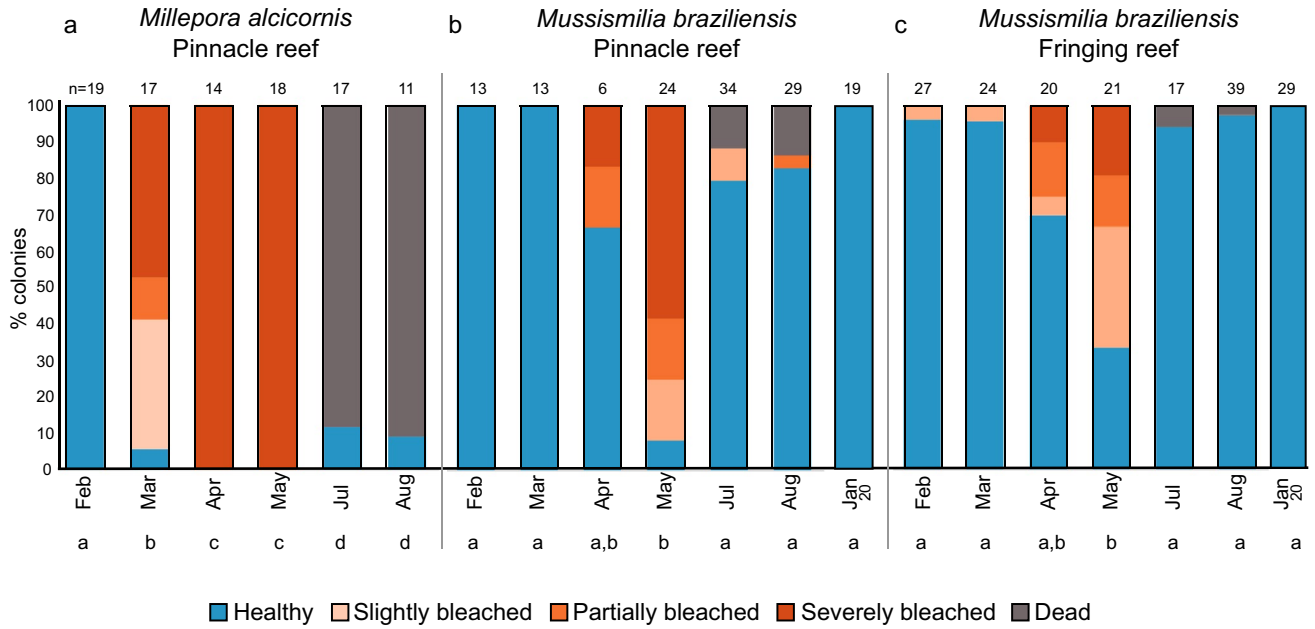


Fig. 3 Health status of *Millepora alcicornis* and *Mussismilia braziliensis* colonies surveyed in the pinnacle reef (Jean Pierre) and fringing reef (Mato Verde) through the bleaching event, from February to August 2019 and January 2020. Letters indicate statistical differences between months for each species ($p < 0.05$) using Kolmogorov–Smirnov tests

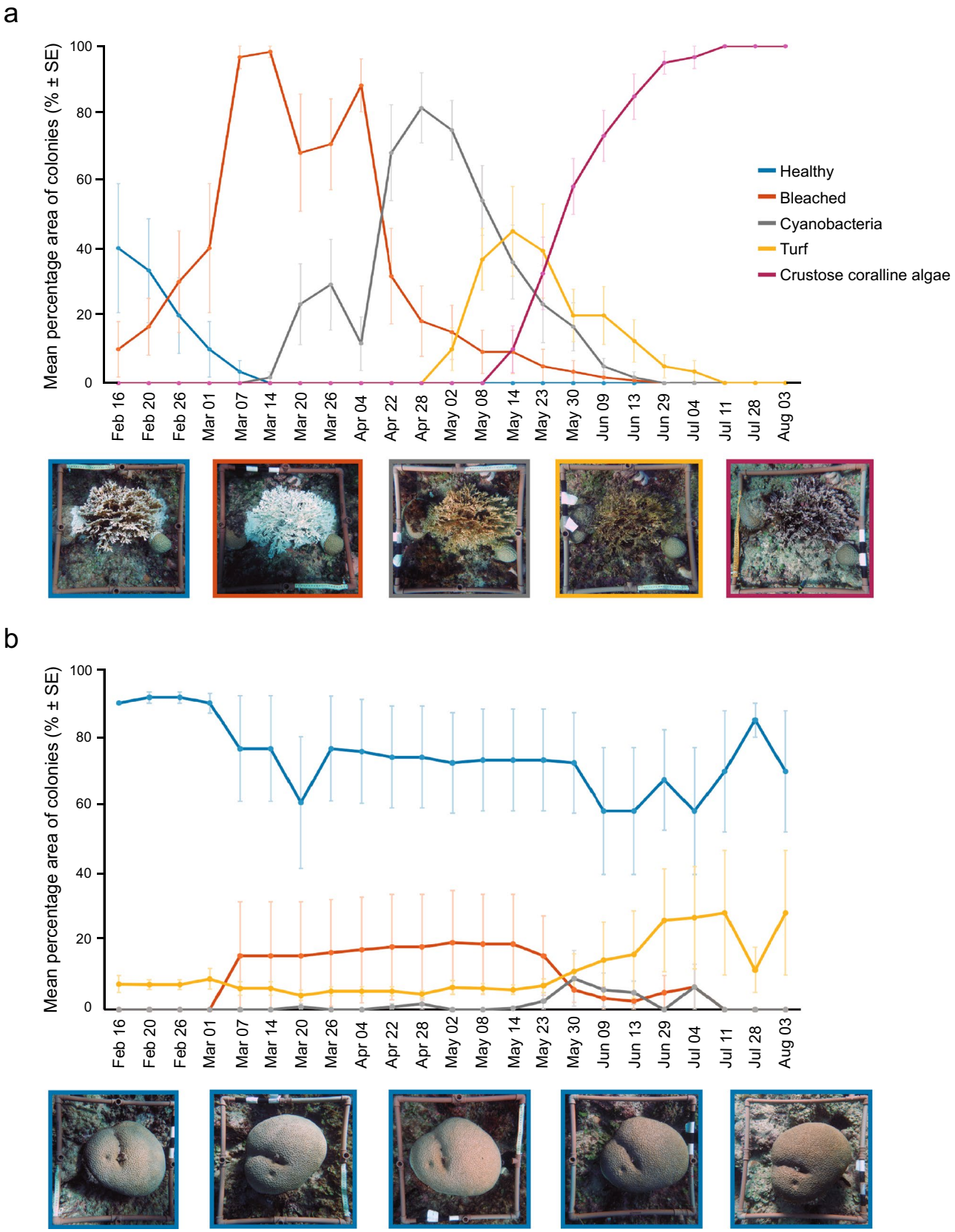
of *Millepora alcicornis* were severely bleached, and ~ 90% were dead and overgrown by crustose coralline algae by July (Fig. 3a). Health conditions of *Millepora alcicornis* were variable between months (Kolmogorov–Smirnov test, $p < 0.03$), except for April–May and July–August when conditions were similar (Kolmogorov–Smirnov test, $p = 1$).

Colonies of *Mussismilia braziliensis* showed the first signs of bleaching in April and bleaching peaked in May when only 8% of the colonies were healthy. In contrast to *Millepora alcicornis*, most colonies of *Mussismilia braziliensis* recovered by July and August, when 80% of the colonies were healthy and ~ 13% partially dead (Fig. 3b). Health status of *Mussismilia braziliensis* was less variable between the monitored months and only significantly different in May (Kolmogorov–Smirnov test, $p < 0.01$). Colonies of *Mussismilia braziliensis* in the fringing reef (Mato Verde) followed a similar pattern as on the pinnacle reef (Fig. 3b, c). In January 2020, 6 months after the event, both reefs were revisited and all colonies of *Mussismilia braziliensis* were healthy, demonstrating full recovery and resistance to mortality (Fig. 3b, c).

The 30 colonies of *Millepora alcicornis* surveyed on each reef in August 2019 confirmed the high mortality of this species in response to thermal stress. All colonies presented signs of mortality regardless of their maximum length, which ranged between 10 and 600 cm. In the pinnacle reef, 27 colonies presented over 85% of mortality and overgrowth by algal turf and crustose coralline algae, and 3 presented less than 40% of mortality. Similarly, in the fringing reef, 29 colonies were completely dead and only one presented 5% of mortality. Therefore, the mortality of *Millepora alcicornis* on both reefs ranged between 90 and 97%. Such high mortality of *Millepora alcicornis* occurred regardless of reef type (Chi-square test $X^2 = 0.27$, df = 1, $p = 0.60$), a pattern also observed in other sites monitored by the AMNP (87% mortality; AMNP, unpublished data) and in adjacent reefs within the Abrolhos Bank (Itacolomis; see Duarte et al. 2020).

Colony-based progression of coral health and post-mortality succession

The weekly photographs evidenced the differences in health progression and succession of overgrowth on *Millepora alcicornis* and *Mussismilia braziliensis* through the bleaching event in the fringing reef (Online Resource 1). The six colonies of *Millepora alcicornis* were completely bleached in the beginning of March and were gradually covered by cyanobacteria between April–May, turf algae in May, and completely dead and overgrown by crustose coralline algae in June–July (Fig. 4a). In contrast, among the six colonies of *Mussismilia braziliensis*, three maintained more than 90% of their surface healthy through the entire monitoring period, one presented 30% of its surface bleached and overgrown by turf algae, and one was completely bleached, overgrown by cyanobacteria and turf algae, and thus dead by the end of the monitoring. The sixth colony was healthy until ripped out by a storm, killing almost half of it. None of the colonies of


a
Mean percentage area of colonies (% ± SE)
100
80
60
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0
Feb 16
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Apr 04
Apr 22
Apr 28
May 02
May 08
May 14
May 23
May 30
Jun 09
Jun 13
Jun 29
Jul 04
Jul 11
Jul 28
Aug 03
Healthy
Bleached
Cyanobacteria
Turf
Crustose coralline algae
b
Mean percentage area of colonies (% ± SE)
100
80
60
40
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0
Feb 16
Feb 20
Feb 26
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◂**Fig. 4** Weekly mean percentage area of each health condition among colonies (% ± SE, $n = 6$ colonies of each species) of *Millepora alcicornis* (**a**) and *Mussismilia braziliensis* (**b**) photographed through the bleaching event in the fringing reef (Mato Verde) between February and March 2019

Mussismilia braziliensis were overgrown by crustose coralline algae (Fig. 4b).

Our findings indicate that massive corals, that are dominant in marginal reefs, such as those in the Southwestern Atlantic, have high post-bleaching recovery capacity and resistance to mortality, contributing to potential higher resilience of marginal reefs to thermal stress events (e.g., Bento et al. 2016; Mies et al. 2020). Because marginal reefs are environmentally and ecologically distinct from tropical coral reefs, coral species in these areas can cope with non-optimal conditions, so these habitats present unique opportunities to study potential refuges for reef-building corals under climate change scenarios (Camp et al. 2018; Mies et al. 2020).

Even though the dominant corals in Brazilian reefs are massive and have experienced low mortality in heating events (Banha et al. 2019; Teixeira et al. 2019; present study), the branching hydrocoral *Millepora alcicornis* seem highly vulnerable (Duarte et al. 2020; present study). The coral *Mussismilia braziliensis* has large polyps (Leão et al. 2003), favoring a more heterotrophic strategy and recovery capacity (van Woesik et al. 2011; Mies et al. 2018, 2020). On the other hand, the hydrocoral *Millepora alcicornis* is fast-growing and highly autotrophic, occurring in areas with high light incidence (Oliveira et al. 2008), and is one of the first species to bleach in Brazilian reefs (Duarte et al. 2020). It is also the main branching species that adds structural complexity to Brazilian reefs and is used as a nursery by many species of fish and invertebrates (Coni et al. 2013). Therefore, mass mortality of *Millepora alcicornis* caused by more frequent and intense thermal–stress events could have strong negative impacts on reef biodiversity. A follow-up survey conducted in January 2020 showed an increase in living tissue of *Millepora alcicornis*, but it still remains to be investigated if this is due to recolonization by recruits or regeneration of existing surviving polyps ('Phoenix effect'; e.g., Roff et al. 2014; Sheppard and Sheppard 2020). Despite the significant loss of branching hydrocorals in Abrolhos, our results support the hypothesis that marginal reefs dominated by massive coral species, such as those in the Abrolhos Bank, may be more resilient to heat stress due to high resistance to mortality and high post-bleaching recovery capacity of massive corals. This should be particularly true, where local stressors are minimized by protected areas, which is the case of the Abrolhos Marine National Park.

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Author contributions All authors designed the study; LCLF, ACG, FN, FPMRF performed fieldwork; LCLF, FPMRF, and GOL contributed to infrastructure/material/technical support; LCLF, ACG, and GOL analyzed the data; LCLF, ACG, and GOL wrote the paper and all authors contributed to the manuscript.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest LCLF, ACG, FN, FPMRF, and GOL declare no conflicts of interest.

Ethical approval This work was conducted with non-destructive methods under the permit SISBIO-ICMBio #70541 in accordance with all ethical guidelines authorized by the Brazilian Ministry of Environment and did not involve collection of animal tissue, individuals or experimentation

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