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SHORT COMMUNICATION

Thermal stress and tropical reefs: mass coral bleaching in a stable temperature environment?

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Abstract
This study reports on the deepest records (~24 m depth) of coral bleaching in a naturally temperature-stable environment (> 26 °C with an intra-annual variability of ~2 °C), which was recorded during a mass bleaching event in the locally dominant, massive scleractinian coral *Siderastrea stellata* in equatorial waters of Brazil (SW Atlantic). An inter-annual analysis (2002–2017) indicated that this bleaching event was related to anomalies in sea surface temperature (SST) that led to the warmest year (2010) in this century (1 to 1.7 °C above average). Such anomalies caused heat stress (28.5–29.5 °C) in this equatorial environment that resulted in a bleaching event. Our results suggest that the increase in SST, low turbidity, and weak winds may have acted together to affect these stress-tolerant corals in marginal reefs. The equatorial coastline of Brazil is characterized by low intra-annual and inter-annual variations in SST, which suggests that the *S. stellata* corals here may be acclimatized to these stable conditions and, consequently, have a lower bleaching threshold because of lower historical heat stress.

Keywords ENSO · Coral reef · Temperature · Climate change · *Siderastrea stellata* · Brazil

Introduction

The El Niño climate phenomenon is linked to abnormally warm sea surface temperatures (SSTs) in the Indo-Pacific region. Furthermore, El Niño is connected to major changes in the atmosphere through another process, known as the southern oscillation (SO). Together these two processes are commonly known as the El Niño Southern Oscillation (ENSO) (Enfield and Mayer 1997; Rossi and Soares 2017), which has many ecological impacts on reefs worldwide, depending on their geographic location, including mass coral bleaching events (Hughes et al. 2017).

High SST anomalies were observed during the thermal stress events of 1997–1998, 2009–2010, and 2015–2016, which had visible impacts on tropical reefs in various regions of the world (Guest et al. 2012; Hughes et al. 2017). Evidence connecting the health of reefs to thermal stress is commonly reported from the Indo-Pacific and the Caribbean Sea and represents a direct ecosystem response to El Niño events (i.e., coral bleaching due to warmer waters) (Hughes et al. 2017; Nohaïc et al. 2017). Bleaching events have increased in frequency and intensity and can lead to reductions in coral cover and diversity, mainly in stress-sensitive species (Hughes et al. 2018). In the tropical southwestern Atlantic, changes in SST and lower wind speeds during El Niño warm events have been linked indirectly to coral bleaching (Ferreira et al. 2013; Dias and Gondim 2016).

Reefs in the southwest Atlantic are predominantly restricted to the Brazilian coastline (Leão et al. 2016). These reefs are considered a marginal ecosystem, with scleractinian corals living at the limit of their turbidity and sedimentation

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tolerance (Suggett et al. 2012). Tropical reefs in Brazil stretch from the Amazon River to the Cape of São Roque (0° 30′ S to 5° 29′ S) in the equatorial margin of the southwest Atlantic, representing a transition between Caribbean and Brazilian reefs (Leão et al. 2016). Coral bleaching is well documented in shallow-water Brazilian reefs; however, there are few published records of bleaching at low latitudes in the Atlantic (Ferreira et al. 2013). Despite the socioeconomic and ecological importance of reefs, there is a knowledge gap in terms of their response to environmental stress and bleaching in the equatorial Atlantic (Leão et al. 2016). Naturally temperature-stable environments (e.g., near-equatorial reefs) can provide insights into the underlying thermal tolerance responses of corals (Schoepf et al. 2015).

The aim of the present study was to provide a record of mass coral bleaching on a reef located in a naturally temperature-stable environment (> 26 °C with intra-annual variability of ~ 2 °C) in equatorial waters of Brazil (SW Atlantic). Considering the scarce evidence for ENSO effects on equatorial Atlantic reefs, the ENSO 3.4 SST index was used to analyze the correlation between SST anomalies and ENSO.

Material and methods

Study area

This equatorial continental shelf margin (northern region of Brazilian reefs sensu Leão et al. 2016) is the least studied region of the Brazilian coast (Soares et al. 2019). These equatorial waters hold poorly studied turbid-water reefs of great scientific interest, including shallow-water coral assemblages on sandstone (Soares et al. 2017) and the mesophotic ecosystem underneath the Amazon River plume (Francini-Filho et al. 2018).

The research was conducted in the Parque Estadual Marinho da Pedra da Risca do Meio, a marine protected area (MPA) located 23 km off Fortaleza city (Fig. 1). It covers an area of 33.20 km^2 and shelters submerged tropical reefs between 18 and 25 m depth. The study site is located in a low-enforcement MPA (Andrade and Soares 2017).

A high coverage of macroalgae (including filamentous algae) and sponges has previously been reported from these coral assemblages on sandstone rock (Soares et al. 2017). The coral community is dominated by the scleractinian coral *Siderastrea stellata*, with low abundances of *Montastraea cavernosa* and *Mussismilia hispida* (Online resource 1). These corals do not form biogenic reef structures, in the face of turbidity and sediment resuspension, but can occur as coral assemblages visible as isolated colonies on sandstone substrate (Soares et al. 2017). These marginal coral assemblages offer a "natural laboratory," in which the impact of environmental conditions (i.e., high and stable SST) on coral bleaching of stress-tolerant taxa (i.e., *S. stellata*) can be studied. The SST in the study area is considered to be high (> 26 °C) with low inter- and intra-annual variability (< 2 °C). The intra-annual variability is associated with the seasonal heating/cooling of the seawater surface in the region and explains approximately 60% of the total SST variability (Teixeira and Machado 2013).

Data sampling

The occurrence of bleaching in the scleractinian corals *S. stellata* and *M. cavernosa* was recorded in March and July 2010 by digital videos and photographic images taken and a $50 \times 50\text{-cm}^2$ quadrat along five 60-m^2 belt transects (BT) was randomly distributed across the reef site at depths between 22 and 24 m. Photoquadrats were also used on the same study area during an oceanographic survey conducted in the summer (May) of 2013 using similar methods (i.e., BT).

Bleaching of *S. stellata* was assessed from videos and images in March 2010, July 2010, and May 2013 along belt transects (30 × 2 m). The variation in bleaching intensity (healthy bleaching, weak bleaching, or strong bleaching) per transect was determined by the combined fractions (%) of colony colors (normal brown, yellowish brown, pale yellow to white, respectively) as applied earlier in the Java Sea (Hoeksema 1991) and in Brazil (Miranda et al. 2013; Leão et al. 2016).

Remote sensing data analysis

Sea surface temperature (SST), SST anomaly (SSTA), and diffuse light attenuation coefficient at 490 nm (K_{490}) values were obtained from the Giovanni NASA platform (https://giovanni.gsfc.nasa.gov/giovanni/). We used monthly values of SST and K_{490} from the MODIS Aqua sensor with a 4-km spatial resolution covering the period from 2002 to 2017. The K_{490} provides a measure of water transparency. The SSTA values of a given month were estimated by subtracting the monthly average SST value for 2010 from the long-term average for that month from 2002 to 2017 climatology data. The SSTA values were correlated with the ENSO 3.4 SST index (https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/) for lead-lag times ranging from minus 12 months to plus 12 months. This methodology was used to reveal correlation coefficients between the anomalies in SST and the occurrence of ENSO in 2010.

Coral Bleaching Alert Area and Degree Heating Weeks (DHWs) were obtained from the NOAA Coral Reef Watch website (https://coralreefwatch.noaa.gov/satellite/index.php). Coral Bleaching Alert Area has two levels: Alert Level 1 (heat stress indicates significant coral bleaching) and Alert Level 2 (heat stress indicates widespread coral bleaching and significant mortality). We also used monthly wind speed data

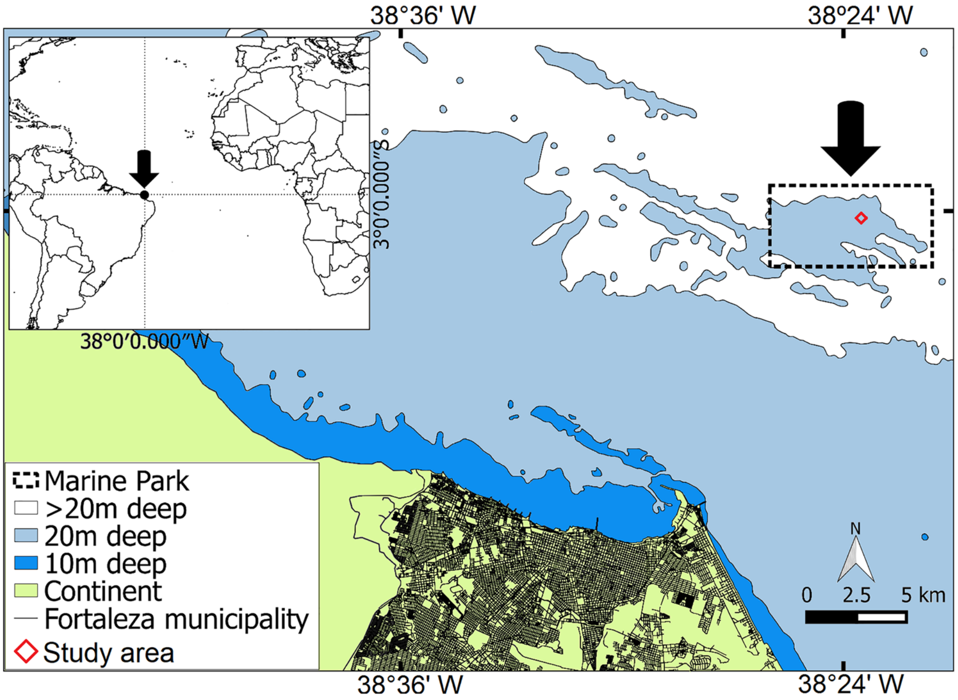

Fig. 1 Location of offshore MPA "Parque Estadual Marinho da Pedra da Risca do Meio" (equatorial southwestern Atlantic, Brazil). Source: Andrade and Soares (2017)

from the BDMET (Brazilian Meteorological Database) using the nearest meteorological station from Fortaleza (Ceará, Brazil). Analyses and visualizations concerning maximum satellite sea surface temperature, wind speed, and K_{490} used in this paper were produced with the Giovanni online data system, developed and maintained by the NASA GES DISC.

Results and discussion

SST results, thermal stress, and coral bleaching

We observed strong bleaching in most of the *S. stellata* colonies (90.9%) in July 2010. Weak bleaching was detected in 7.9% of the colonies, while the fraction of colonies characterized as normal was low (1.1%). This extensive bleaching was not detected during the earlier dives in March 2010 (< 10% colonies bleached). We also detected strong bleaching in a few colonies (10.9%) of the same species in May 2013. This low bleaching rate in 2013 was explained by sedimentation and other factors, and not the temperature, which was close to the average value (Fig. 2c).

Throughout 2010, variation in SST in Brazil ranged from 26.7 to 29.6 °C, with the maximum values occurring between March and June 2010 (Fig. 2a). A comparison of the SST annual mean values from 2003 to 2017 indicated that the mass bleaching observed in 2010 was correlated with the warmest year during this period for the quarters March to May (Fig. 2b) and for June to August (Fig. 2c).

Thermal stress in the equatorial SW Atlantic reached Alert Level 1 in May 2010 between latitudes 0° and 8° S, where the MPA is located (Online resource 1). This alert was nonexistent until May but persisted through July and disappeared by October. Overall, in July 2010, the equatorial margin region of the SW Atlantic was subjected to 8–16 DHWs (Online resource 1) and the study site between 8 and 9 DHWs in July 2010.

This mass coral bleaching event was related to higher SST, mainly between May and July of 2010, which led to SST anomalies that ranged from 1 to 1.7 °C (SI 1 and Fig. 3a). The SST anomaly in the study site in 2010 was not correlated with the ENSO 3.4 SST index (Table 1). During the episode, lower wind speeds (2 to 3 m s^{-1}) (Fig. 3b) and lower turbidity values, which could be inferred from the low K_{490} values (Fig. 3c), were detected up to the end of the first semester of 2010.

We hypothesized that ENSO is not the main driver of SST anomalies in the equatorial Atlantic. Other anomalies such as the Atlantic Meridional Mode (AMM) (tropical Atlantic SST dipole) could be a major driver of these temperature anomalies, but this hypothesis needs to be tested in further studies using long-term data. The study area off the Brazilian equatorial margin is one of the major regions affected by the AMM (Bourles et al. 1999). An anomalous displacement of the intertropical convergence zone (ITCZ) toward the north leads to significant drying across the region (low precipitation), and this phenomenon is also associated with a pattern of anomalous warm SST in the northern tropical Atlantic (Marengo et al. 2017).

In the study area, the temperature is relatively homogeneous in the top 70 m of the water column due to strong wind and tidal mixing (Bourles et al. 1999; Dias et al. 2013;

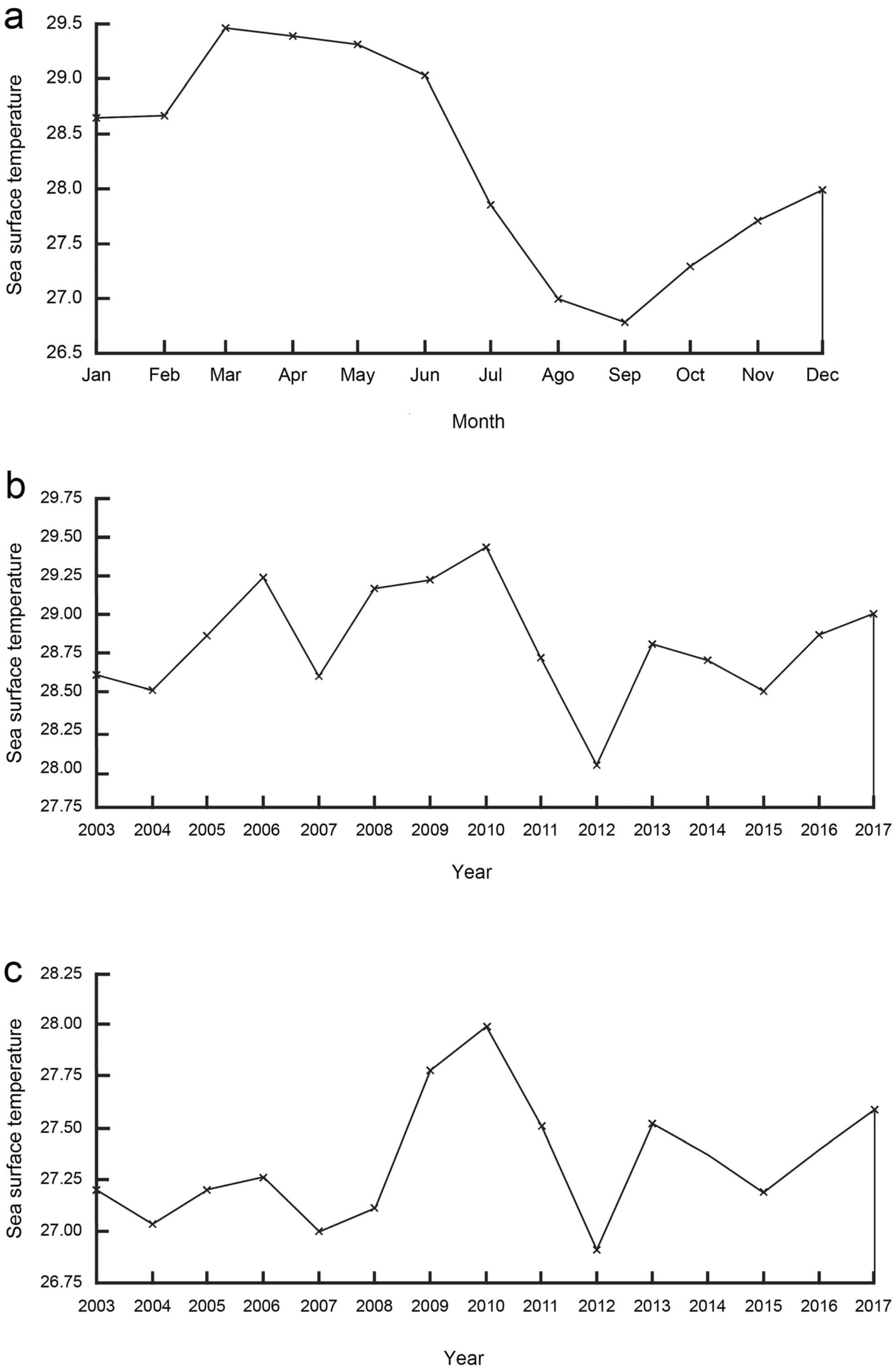

Fig. 2 Sea surface temperature (SST) within the mass coral bleaching region. **a** Monthly mean SST throughout 2010; **b** yearly mean SST (2003–2017) for the quarter March–May; and **c** yearly mean SST (2003–2017) for the quarter June–August

Teixeira and Machado 2013), likely accounting for the unusually deep bleaching recorded. These oceanographic conditions allow sea surface temperature anomalies to reach ~ 24 m depth and enabled us to use satellite-based SST measurements to study the impacts of anomalously high temperatures on these marginal reefs. This mixing (Online resource 1) also precludes the possibility for deep thermal refugia (Muir et al. 2017; Frade et al. 2018) in the equatorial Atlantic. We hypothesized that these corals are acclimatized to stable environmental conditions and have lower bleaching thresholds than corals from more variable thermal conditions (Magris et al. 2015) because of lower historical heat stress. The 2010 event presented SST

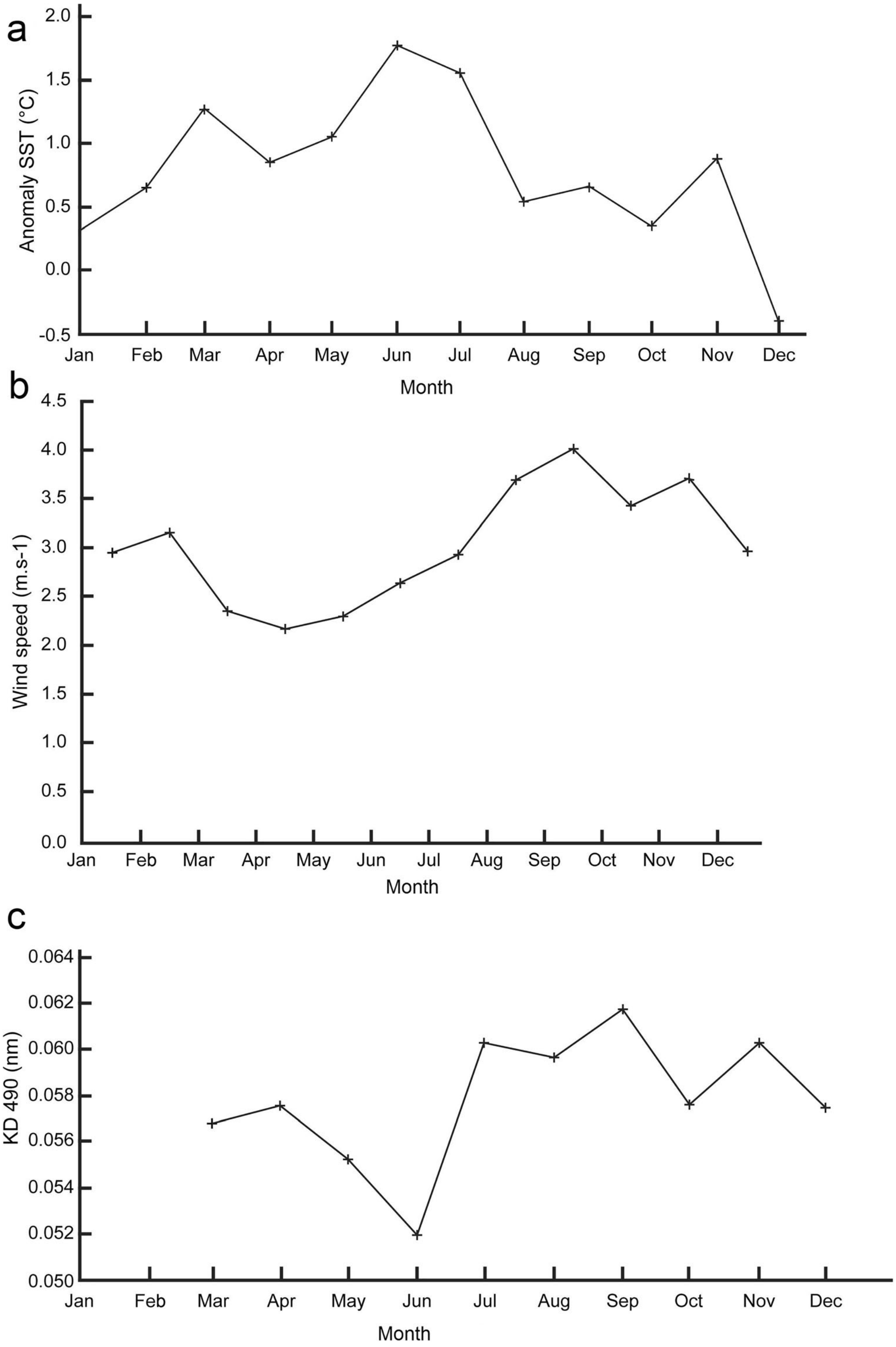

Fig. 3 Environmental conditions during 2010. **a** Sea surface temperature anomaly (SSTA) showing the highest positive anomalies during the period May to July; **b** wind speed showing low wind speed in the first semester; **c** diffuse attenuation coefficient for downwelling irradiance at 490 nm (K_{490}) showing lower turbidity during the first 6-month period of the year

anomalies above these values and consequently led to the mass bleaching event.

In such high temperature, but stable environments, coral species in the equatorial SW Atlantic may be very resistant to high temperatures but have little tolerance for anomalies. However, in another study conducted in a near-equatorial reef in the Pacific Ocean, Carili et al. (2012) suggested that warm events affect corals even in areas with lower historical heat stress (1–2 °C). In the Pacific, the equatorial waveguide causes strong inter-annual variability of temperature associated with El Niño. The 2015–2016 El Niño caused 95% coral mortality at Jarvis Island located only ~ 15 km from the equator (Barkley et al. 2018). This difference could occur given the significant latitudinal differences in thermal variability across

Table 1 Non-significant correlations ($p > 0.05$) between SSTA (sea surface temperature anomaly) and ENSO 3.4 SST index in 2010, including the lags of the months

Lags	Correlation
−12	0.04
−11	0.04
−10	0.03
−9	0.01
−8	0.04
−7	0.06
−6	0.06
−5	0.07
−4	0.07
−3	0.03
−2	0.02
−1	0.00
0	−0.02
1	−0.06
2	−0.08
3	−0.10
4	−0.12
5	−0.12
6	−0.08
7	−0.03
8	0.01
9	0.02
10	−0.03
11	−0.06
12	−0.08

each of the ocean basins and in the composition of stress-tolerant corals between the SW Atlantic and the Central Pacific.

Coral resilience and contributing factors

This study also identified that the mass bleaching occurrence at the end of the first half of 2010 was concurrent with low wind speeds and low turbidity waters. Together, SST and low turbidity may have acted synergistically to affect corals in these marginal reefs, which also occurred in other tropical reefs in clear shallow waters (Hughes et al. 2017, 2018). The winds, which were stronger at the beginning of the second half of 2010, increase turbidity due to vertical mixing. Winds increase surface gravity waves and the waves cause internal mixing and potential particle suspension (Knoppers et al. 1999). Turbidity is favorable for stress-tolerant corals (i.e., *S. stellata*) because it acts as a physical barrier preventing the penetration of UV radiation (Baker et al. 2008). However, during the detected critical event, the water mass was more stable due to the lower wind speeds. In this scenario, the turbidity and cloudiness (beginning of dry season in the studied tropical semi-arid coast) were low, which allowed solar radiation to penetrate. We hypothesize that increases in the wind speed and turbidity (e.g., shading) protect the corals from insolation effects. Low turbidity could indeed cause deeper penetration of UV light. In this case, turbidity probably reduces the impact of bleaching by light-heat stress because *S. stellata* corals are resilient to turbidity and sedimentation (Leão et al. 2016).

This is one of the deepest records of coral bleaching in SW Atlantic reefs related to the 2010 bleaching event (Table 2). These results are dissimilar to depth patterns of bleaching in other Brazilian reefs and elsewhere (Monroe et al. 2018) in that shallow-water corals and inshore reefs are generally the most susceptible to bleaching. Previously, extensive bleaching was reported mainly for depths at 0–15 m in oceanic (Ferreira et al. 2013) and coastal (Miranda et al. 2013; Soares and Rabelo 2014; Dias and Gondim 2016) Brazilian reefs. The event reported here occurred before the mass bleaching detected in Caribbean coral reefs (October–December 2010) (Alemu and Clement 2014) (Online Resource 1). Our results indicate that after the bleaching event on SW Atlantic reefs, there was a northward migration of the heat stress toward the Caribbean Sea when the North Atlantic warmings were reported (Enfield and Mayer 1997).

In this region, the temperature anomaly in 2009–2010 was similar to that in 1997–1998 (Ferreira et al. 2013; Teixeira and

Table 2 Mass coral bleaching and ENSO 2010 in Southwestern Atlantic reefs

Reef/region (region in Brazilian coral reefs sensu Leão et al. 2016)	Depth	Scleractinian species affected	Reference
Pedra da Risca do Meio reef/northern region	24 m	*Siderastrea stellata*	This study
Pecém and Paracuru reefs/northern region	0–2 m	*Siderastrea stellata*, *Favia gravida*	Soares and Rabelo (2014)
Rocas Atoll/northeastern region	2–9.5 m	*Siderastrea* spp.	Ferreira et al. (2013)
Fernando de Noronha/northeastern region	8.5–22 m	*Siderastrea* spp., *Montastraea cavernosa*	
Ponta dos Seixas reef/northeastern region	1–6.5 m	*Siderastrea stellata*, *Porites astreoides*, *Agaricia agaricites*, *Mussismilia hartii*	Dias and Gondim (2016)
Caramuanas reef/eastern region	1–6 m	*Siderastrea* spp., *Montastraea cavernosa*, *Mussismilia* spp.	Miranda et al. (2013)

Machado 2013). Both events were related to positive SST anomalies, including several weeks of above-average temperatures and positive hot spot values (Ferreira et al. 2013; Pereira et al. 2015). Considering our results and previous reports (Miranda et al. 2013; Ferreira et al. 2013; Soares and Rabelo 2014; Dias and Gondim 2016), we hypothesize that the 2010 event had a regional-scale (> 1000 km) (Hughes et al. 2018) impact at latitudes of 2–13° S on the SW Atlantic reefs.

An important factor in understanding the bleaching thresholds in scleractinian corals in this region is adaptation to suboptimal conditions (Woesik et al. 2011; Guest et al. 2016). Soares et al. (2017) suggested that the study area sustains turbid-water reef assemblages, characterizing it as a tropical marginal area, which may explain the low coral diversity and dominance of a single stress-tolerant coral species (*S. stellata*). Despite the low river runoff in this semi-arid coast (dominated by short, shallow, and low-inflow estuaries), the scleractinian corals here are subjected to fast-flowing currents and large–swell wave events (Knoppers et al. 1999). Soares et al. (2017) found a high percentage of sand (19.6% of total coverage) under the sandstone coral assemblage in 2013 at 22 m depth and suggested that this was due to the large amount of carbonate sands and constant resuspension of bottom sediments. Indeed, sedimentation and turbidity affect reefs considerably (Erftemeijer et al. 2012) and present a selective pressure for species more adapted to stressful conditions (Guest et al. 2016).

Siderastrea stellata is the major reef-building coral in Brazilian reefs (Leão et al. 2016) with an extensive depth range (intertidal to mesophotic zone) (Soares et al. 2019). *Siderastrea* spp. are also very resistant to chronic factors (e.g., thermal stress) and are considered to be indicators of environmental stress in coral communities (Oigman-Pszczol and Creed 2011; Monteiro et al. 2013). Highlighting this viewpoint on the flattened reef tops in Brazilian coastline, which are subaerially exposed during low tides, living corals of *S. stellata* occur within tidal pools (Portugal et al. 2016). In these environments, variations in water temperature, salinity, and solar radiation are stress environmental factors. Colonies of the endemic *S. stellata* and the amphi-Atlantic *Favia gravida* are the only corals that can inhabit this kind of marginal reef environment, where they may occur in large densities (Correia 2011; Hoeksema and Wirtz 2013; Leão et al. 2016). Moreover, Costa et al. (2008) demonstrated that the stress-tolerant *S. stellata* is associated with zooxanthellae clade C (genus *Symbiodinium*), which is considered to be one of the most bleaching-resistant microalgal groups. In addition, Monteiro et al. (2013) found a high specificity between *Siderastrea* and *Symbiodinium* type C in Cape Verde (Africa). They suggested that these symbioses in the Caribbean, Brazil, and Africa exhibit some flexibility under different oceanographic conditions, as these corals occupy a wide range of ecological niches (Monteiro et al. 2013).

In addition to host-symbiont adaptations in marginal reefs, the mixotrophic (autotrophic and heterotrophic balance) strategies of this major reef-building coral may help to explain its resilience. Rosa et al. (2018) detected a higher percentage of zooplankton-associated fatty acids in colonies of *S. stellata* from a subtidal environment. This potential for heterotrophy and the host-symbiont association drive the capacity of *S. stellata* to recover from bleaching after severe SST anomalies and also promote recovery from environmental and human disturbances.

We assessed the bleaching rate and not the mortality rate, which depends on the recovery of species in a certain area (Sutthacheep et al. 2012). On the other hand, Soares et al. (2017) observed that most of the colonies of *S. stellata* in the same study site (in 2013, after a mass bleaching event) belonged to small-diameter classes, with 83.7% exhibiting a diameter < 20 cm. They have also found that this species remained the dominant coral in these marginal reefs, which clearly indicates a recovery after the mass bleaching. Other factors that explain this recovery of *S. stellata* are its population structure and reproductive strategies. Oigman-Pszczol and Creed (2011) suggested that the large number of small-diameter colonies is an adaptive reproductive strategy developed in reefs subject to environmental stress. Another important factor is that this species tends to reproduce early and incubate larva (Barros and Pires 2006). This phenomenon may be the consequence of a survival strategy under turbid conditions, temperature anomalies, and resuspension of sediments, all of which were present in our study site, which was characterized by high mortality rates and short life spans (Soares et al. 2017).

Marginal coral reefs in turbid waters have been considered potential thermal refugia (Woesik et al. 2011; Cacciapaglia and Woesik 2015). However, the waters in this equatorial region were unusually clear during the mass bleaching event. These results indicate that the thermal refugia in marginal turbid reefs are not universal and depend on local seasonal conditions (temperature, solar radiation, wind speed, waves, and currents) during thermal stress. All these environmental variables (SSTA, SST, turbidity, and wind speed) were selected and calculated to cover selected major environmental drivers that have been reported to be relevant for coral bleaching, in an attempt to understand the oceanographic and atmospheric conditions in this equatorial coast. The results are also important to provide limited evidence of mass coral bleaching in equatorial SW Atlantic reefs with low intra- and inter-annual temperature oscillations.

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Authors' contributions MOS and TT conceived and coordinated the study, analyzed coral species and remote sensing data, participated in its design, and helped to write and revise the manuscript. MD, SF, BP, MM, and AG executed the study and revised the manuscript. CEPT helped to write and revise the manuscript. All authors read and approved the final manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval No animal testing was performed during this study.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgments, if applicable. The study is compliant with the Convention on Biological Diversity (CBD) and Nagoya Protocol.

Data availability The datasets generated during and/or analyzed during the current study are available as supplementary material.

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