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SHORT COMMUNICATION

Marine heatwaves lead to bleaching and mass mortality in a key zoantharian

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Abstract

The increased frequency of severe marine heatwaves (MHWs) is a major contributing factor contributing to mass bleaching and large-scale mortality in reef-building corals. However, the effects of MHWs on other major reef organisms (e.g., zoantharians) are poorly studied. In this study, we demonstrate the vulnerability of the key habitat-forming zoantharian *Zoanthus sociatus* to severe MHWs. Temporal image analysis from 2019 to 2022 on intertidal South Atlantic reefs shows extensive healthy colonies (2019), bleaching (2020), and mass mortality of *Z. sociatus* with the occupation of the entire space by filamentous algae (2022). We calculated a loss of 99.6% of total area of the colonies due to mass mortality after the bleaching event. Thermal stress was identified during mass bleaching in *Z. sociatus* in 2020 by indicators such as MHWs and degree heating weeks (DHWs). In the first 6 months of 2020, this low-latitude region underwent three MHWs at 1.5, 2.0, and 1.3°C above the mean temperature. Moreover, the most intense (2°C) and longest (76 days) MHW occurred near the detected mass bleaching. Furthermore, DHWs (14.5 to 17.6) showed that 2020 had the highest and longest heat stress recorded in this century (since 2001) in this extreme reef. Despite its adaptation to this harsh intertidal habitat, our results showed the vulnerability of *Z. sociatus* to high heat-light stress on these reefs when exposed to high desiccation, elevated temperatures (>30°C), higher salinities, and solar irradiation at low tides. We suggest that *Z. sociatus* is most vulnerable to severe and repetitive bleaching due to its higher dependence on autotrophy. In this regard, these marginal reef specialists are near the bleaching threshold limit that increases their vulnerability to environmental changes, such as MHWs, especially in intertidal reefs. Our study highlights the vulnerability of symbiotic zoantharians to heat-light stress and the need to include these organisms in long-term monitoring to assess their recovery potential and resilience to climate change in reefs worldwide.

Keywords Climate change · *Zoanthus sociatus* · Autotrophy · Coral reefs · Heat stress

Introduction

Shallow-water reefs are undergoing a global transformation due to local disturbances (e.g., pollution) and climate change-related phenomena, such as marine heatwaves (MHWs) (Duarte et al. 2020; Smale et al. 2019). The increased frequency of severe MHWs has been one of the main factors contributing to mass bleaching and large-scale mortality in reef-building corals (Hughes et al. 2017). However, the effects of MHWs on other major reef organisms (e.g., zoantharians) are poorly studied (Reimer et al. 2021; Soares et al. 2022).

Zoantharians are colonial cnidarians that are key components of tropical reefs (Santos et al. 2016; Reimer et al. 2021; Soares et al. 2022). In some tropical and subtropical reefs, non-reef-building zoantharians have shown persistence and resilience in the face of climate change (Reimer et al. 2021), such as on South Atlantic phase-shifting reefs where *Palythoa* has increased in abundance (Cruz et al. 2016). However, some zoantharian species (e.g., *Palythoa* and *Zoanthus sansibaricus*) are vulnerable to MHWs (Goreau 1964; Reimer et al. 2021; Singh et al. 2022; Soares et al. 2022); a topic that needs further study to investigate species-specific effects. In this study, we demonstrate the vulnerability of the key habitat-forming zoantharian *Zoanthus sociatus* to severe and repeated MHWs.

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Material and methods

The study area was the Paracuru Beach, located in the tropical Southwestern Atlantic (Ceará coast, Brazil), with a 3 km stretch of intertidal reef, which is fully exposed at low tide. There is a great abundance of zoantharians (e.g., *Zoanthus sociatus, Palythoa caribaeorum*, and *P.* cf. *variabilis*), which form large colonies on sandstone reefs (Rabelo et al. 2013; Portugal et al. 2016). This reef is under the influence of the mesotidal regime (tidal range is 2–4 m) which generates a daily period of about 12 h (usually 6 h during the day and 6 hours at night) where the reefs and zoantharians are exposed at low tide. In the study area, normal temperature (30.3 to 33.5 °C), and salinity (35.2 to 43.2) values at low tides characterized an extreme reef habitat (Barros et al. 2021).

Our sampling covered the area where the species occurs on this intertidal reef. This occurrence zone of *Z. sociatus* is a small and restricted reef zone and is at the limit between the intertidal and subtidal zone (outer mid-littoral with 20 m zone) (Rabelo et al. 2015), which increases the risk of local disappearance. In this narrow zone, isolated colonies of *Z. sociatus* colonized more exposed areas such as the top of elevated and exposed sandstone rocks (Rabelo et al. 2015). We calculated the area of *Zoanthus sociatus* colonies before (2019), during (2020) and after (2022) the mass bleaching event from photos taken at low tide. Area calculations (in cm^2) of each colony were made using the Image J program.

Thermal stress was evaluated from oceanographic factors such as DHW (degree heating weeks) and MHW for 2019 and 2020. The DHW is calculated by accumulating temperature readings that are more than one degree Celsius over the historical maximum temperature for a given location (e.g., study area). Thus if the temperature is 2 °C above the summer maximum for 4 weeks then the corresponding DHW indicator is (2 °C × 4 weeks) 8 DHW. The DHW was extracted from the Global Coral Reef Watch (NOAA) at a resolution of 5 km, and corresponds to the accumulation of heat over the previous 3 months. MHW is an indicator produced from NOAA's daily Optimally Interpolated Sea Surface Temperature data and is available at http://www.marineheatwaves.org/tracker.html (Schlegel and Smit 2018). In this regard, we used MHW, a recent product for marine heatwaves analysis that qualitatively observes periods of thermal anomalies lasting at least 5 days in a given location.

Results and discussion

Temporal image analysis from 2019 to 2022 (Fig. 1) on intertidal South Atlantic reefs shows extensive healthy colonies in 2019 (Fig. 1a), bleaching in 2020 (Fig. 1b), and mass mortality of *Z. sociatus* with the occupation of the entire space by filamentous algae in 2022 (Fig. 1c). In 2019, the area occupied by each *Z. sociatus* colony ranged from 1,007 and 3,232 cm^2 (Supplementary Material 1). Even though *Z. sociatus* an accelerated growth in the study area (Rabelo et al. 2013), we detected only residual colonies in 2022 (0.4% of the total area occupied before), even after 2 years of the severe bleaching event in 2020.

Currently (2022) and previously abundant (Rabelo et al. 2013, 2015) *Z. sociatus* persists in the studied reef as small colonies (e.g., 33.6 cm^2) (Fig. 2c; Supplementary Material 1) on lateral or shaded reef surfaces. Thus, we calculated a loss of 99.6% of total area occupied by all colonies due to mass mortality after the bleaching event.

Record-breaking thermal stress was identified during mass bleaching in *Z. sociatus* in 2020 by indicators such as MHWs, DHWs, and sea surface temperature (SST). In the first 6 months of 2020, this low-latitude region underwent three MHWs at 1.5 (03/01/2020 to 17/02/2020), 2.0 (29/02/2020 to 14/05/2020),

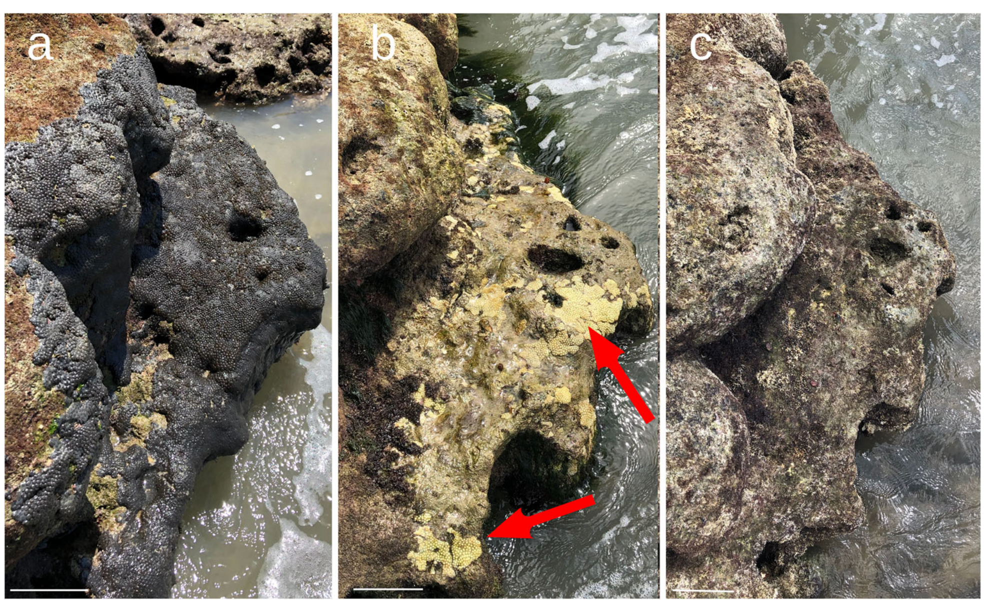

Fig. 1 Bleaching process and mass mortality of the habitat-forming zoantharian *Zoanthus sociatus* on an intertidal reef in the Tropical Southwestern Atlantic (Paracuru, coast of Ceará state, Brazil, 3° 25′ 31″ S, 39° 1′ 29″ W). **a** To the left are healthy colonies of 3232 cm^2 (09/27/2019); **b** in the center are bleached colonies (arrows) (06/23/2020); **c** to the right is mass mortality with occupation by filamentous algae (07/16/2022). Scale: 10 cm

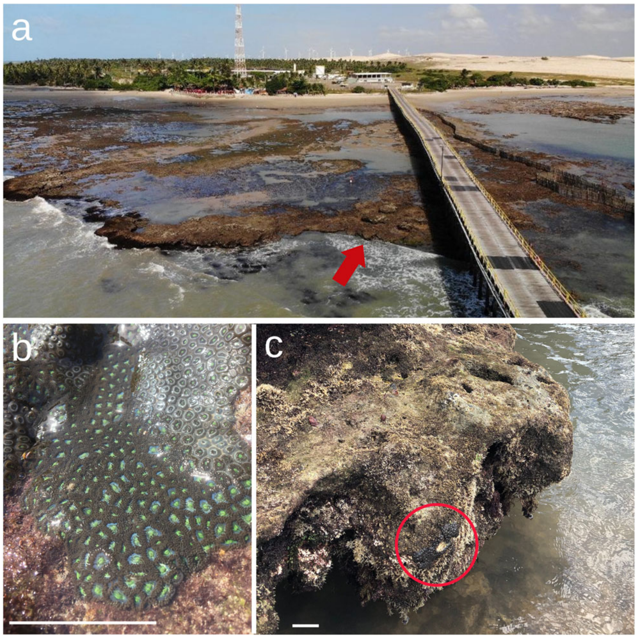

Fig. 2 **a** Drone image showing the reef under study, with locality (arrow) shown in b; **b** Healthy *Zoanthus sociatus* colonies (09/27/2019) on an exposed rock at low tide; **c** *Z. sociatus* (circle) persists in the studied intertidal reef after mass bleaching and mortality as small colonies on lateral or shaded reef surfaces (07/16/2022, Tropical Southwestern Atlantic, Paracuru, Ceará coast, Brazil, 3°25′31″ S, 39°1′29″ W)

and 1.3 °C (22/05/2020 to 25/06/2020) above the mean temperature. Moreover, the most intense (2.0 °C) and longest (76 days) MHW occurred near the detected mass bleaching (Fig. 1b). Furthermore, degree heating weeks (DHW) showed that 2020 had the highest and longest heat stress recorded in this century in this marginal reef, with May at 17.6 °C/week (Table 1). In the same month in 2019 (with healthy *Z. sociatus* colonies) (Fig. 1a), the DHW was ~ 3 times lower (5.2 °C/week). The highest values of 2020 DHW were observed in April (14.8 °C/week), May (17.6 °C/week), and June (14.5 °C/week). Accordingly, the highest MHWs in these months of 2020, corroborating severe thermal stress (Table 1)

To our knowledge, this is the first temporal record of the impact of MHW on mass bleaching and mortality in this major and widespread species. No diseases were detected in the field surveys and no other events that could generate bleaching (e.g., pollution) due to it being an area (Fig. 2a) with low anthropogenic pressure (Portugal et al. 2016). In 2019/2020, degree heating weeks (DHW) of 19.65 coincided with catastrophic declines in coral cover in Southwestern Atlantic reefs, especially in the major reef building hydrocoral *Millepora alcicornis* (Duarte et al. 2020). Interestingly, in this recent and severe marine heatwave, healthy colonies and absence of mass mortality were detected in *Z. sociatus* (Duarte et al. 2020) a result which is different from ours. However, the study of Duarte et al. (2020) was conducted in a subtidal environment (4 to 8m depth) while our research was in intertidal reef habitat. The subtidal zone is inherently more stable than the intertidal zone (Reimer et al.

Table 1 Heat stress showing monthly Degree Heating Week (DHW) values between 2019 and 2020 in the Equatorial Southwestern Atlantic (Ceará coast, Brazil). Color changes with 2 °C/week variation, with minimum values shown in pink and maximum values shown in red color

	2019	**2020**
January	0.0	0.2
February	0.0	2.8
March	0.2	7.5
April	1.8	14.8
May	5.2	17.6
June	5.3	14.5
July	2.8	7.0
August	0.0	1.8
September	0.0	0.0
October	0.0	0.0
November	0.0	0.0
December	0.0	0.0

2021; Soares et al. 2022), so differences in resistance in *Z. sociatus* may be misinterpreted (Fig. 3).

Zoanthus sociatus is an abundant zoantharian species on West Atlantic reefs, which is essentially autotrophic, with a high photosynthesis rate (Goreau 1964; Graham et al. 2015; Santos et al. 2016; Leal et al. 2017a; Rosa et al. 2018; Montenegro et al. 2020). In the South Atlantic, the intertidal habitat (emerged and in tidal pools) showed C isotopes ($\delta^{13}C$) ranging from 10.68 to 13.96 ‰ and significant photochemical efficiency and

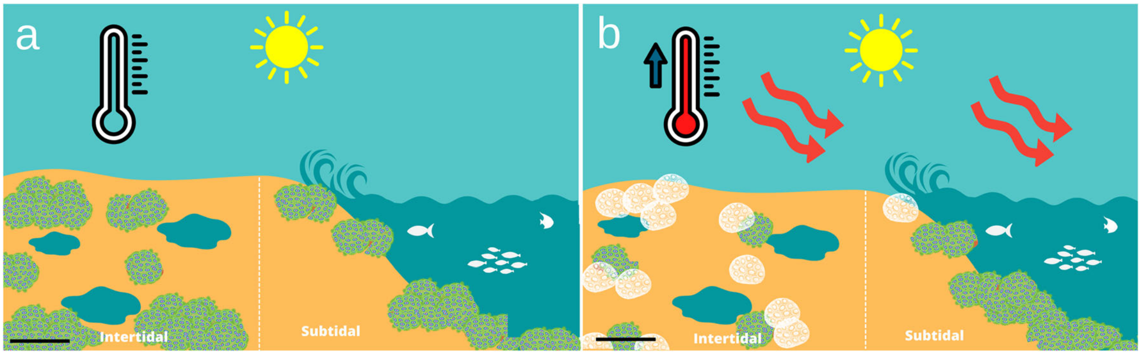

Fig. 3 Heat-light stress in *Zoanthus sociatus* in intertidal and subtidal habitats. Scenario **a**: Under normal conditions of sea surface temperature and without the occurrence of marine heatwaves (or other stressors), the colonies of *Zoanthus sociatus* in the intertidal and subtidal reefs remain healthy. Scenario **b**: With the increase of severe MHWs, the colonies of *Zoanthus sociatus* in the intertidal region are more vulnerable to bleaching and mass mortality, compared to those in the subtidal reef habitat

Symbiodinium density, showing major autotrophic input (Leal et al. 2017a, 2017b). Despite its adaptation to this harsh intertidal habitat (Rabelo et al. 2014, 2015), our results showed its vulnerability to high heat and light stress on these intertidal reefs when exposed to high desiccation, elevated sea temperatures (>30 °C), higher salinities, solar irradiation, and air temperature exposure at low tides. The aerial exposure conditions in intertidal reefs induce reversible downregulation of photochemical processes but no photophysiological impairment or bleaching in *Z. sociatus* (Leal et al. 2017b).

We suggest that *Z. sociatus* is most vulnerable to severe and repetitive bleaching due to its higher dependence on autotrophy, unlike *Palythoa*, which is mainly heterotrophic according to Sorokin (1991) and Rosa et al. (2016), it has shown resilience in coral reefs worldwide (Cruz et al. 2016; Reimer et al. 2021; Soares et al. 2022). Zoantharian bleaching events of *Z. sociatus* and *Palythoa* spp. have been detected at intertidal and subtidal habitats (Soares et al. 2022) over the last 60 years in West Atlantic reefs, especially in 1963 (Goreau 1964), in 2002–2003 (Ferreira and Maida 2006), in 2010 (Soares and Rabelo 2014), and during the most intense marine heatwave ever recorded on the Brazilian coast in 2019–2020 (Duarte et al. 2020). In this recent event, between 29.9% and 46.3% of *P. caribaeorum* colonies were bleached however with low mortality rates (0 to 2.1% of colonies) (Duarte et al. 2020). *Palythoa caribaeorum* populations appear to be resilient and able to survive and recover after episodic bleaching events with a high heterotrophic input (Rosa et al. 2016, 2018). In this regard, heterotrophy plays a major role in the trophic ecology content of *P. caribaeorum*, particularly because two of the prevailing fatty acids are common biomarkers of phyto- and zooplankton (Rosa et al. 2016). Moreover, in addition to its morphological plasticity, *P. caribaeorum* seems to display a trophic plasticity when facing exposure to air (common on intertidal reefs) by changing the bulk of energy with autotrophic and heterotrophic origin in such intertidal reefs (Rosa et al. 2016).

Zoantharians are now thought to be expanding their populations and may be dominant species in a future scenario of human impacts and global climate change over coastal and marine ecosystems (Cruz et al. 2016; Reimer et al. 2021). We demonstrate that not all species are resilient and can actually be affected, for example, by severe heat-light stress especially in marginal intertidal reefs. In this regard, these marginal reef specialists are near the bleaching threshold limit (Singh et al. 2022; Soares et al. 2022), which increases their vulnerability to environmental changes, such as MHWs, especially in intertidal reefs. Thus, marginal reefs are ecologically distinct ecosystems and represent limited potential as climate-change refugia (Soares 2020). In this regard, our study highlights the vulnerability of autotrophic-dependent zoantharians to MHWs and the need to include these organisms in long-term monitoring to assess their recovery potential and resilience to climate change in reefs worldwide.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval No animal testing was performed during this study.

Sampling and field studies The study does not contain sampling material or data from field studies.

Data availability Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

Author contribution MOS conceptualized and wrote the paper. EFR reviewed and edited the manuscript. ALG obtained pictures, reviewed and edited the manuscript.

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