



Short communication

Thermal refugia support the long-term survival and growth of giant coral colonies

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ABSTRACT

Coral reefs face global threats, primarily from ocean warming, acidification, diseases and pollution. Mass coral mortality events due to severe thermal stress are becoming increasingly frequent, intense, and widespread. Models predict a loss of over 90 % of coral cover by the century's end, while historical records document widespread coral mortality in recent decades. Despite this, some coral colonies have survived and grown for centuries, reaching remarkable sizes. Focusing on 85 large coral colonies with sizes varying between 5 and > 20 m in their maximum dimension, we investigated whether their extended survival is due to intrinsic resilience to thermal stress or to their occurrence in thermal refugia characterized by reduced exposure to heatwaves. For that, we used historical data to assess the exposure of giant coral colonies to bleaching-triggering conditions in the last 4 decades. Most colonies (85 %) never experienced such conditions within the observational time window. However, 13 giant colonies were exposed to severe heat stress multiple times (experiencing between 2 and 22 events, with a median of 13), and six of them significantly more often than in control localities. These results support both hypotheses. On the one hand, environmental protection emerges as a major factor favoring the survival of giant corals. On the other hand, the few giant coral colonies that survived through high thermal stress might have exceptional features worth further, in-depth investigation. However, future climate projections indicate that most giant corals might soon face unprecedented thermal stress, which begs the question of whether giant corals will withstand the looming "coralgeddon" by the end of the century.

1. Introduction

Corals are slow growing and long living organisms capable of building massive colonies that are hundreds or even thousands of years old (Bythell et al., 2018; Coward et al., 2020). However, old and large coral colonies are extremely rare, with reefs dominated by young and small coral colonies, partly due to recurring mass mortality events triggered by ocean warming in combination with other, mostly anthropogenic, synergistic stressors (Ban et al., 2014; Riegl and Purkis, 2015). A recent initiative named "Map the Giants" (Montano et al., 2024; Siena et al., 2025) has been launched to map these last remarkable colonies before they disappear. The goals of

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the initiative are multiple. On the one hand, it aims at making giant corals (coral colonies > 5 m in their largest dimension, Fig. 1) a symbol for nature conservation in the oceans, akin to the role played by monumental trees in the terrestrial environment (Piovesan et al., 2022), and to enhance their protection by mapping their exact location (which could be used as a basis to inform, for instance, protected area planning). On the other hand, it aims to explore whether the exceptional survival of the giant colonies hides potential secrets of coral resilience which might provide essential information and possibly new avenues to mitigate global coral loss (D'Olivo et al., 2024; Montano et al., 2024; Siena et al., 2025). In that context, a fundamental question is whether standing giant corals have survived because of an inherent resistance to stressors, or because they benefited from environmental protection, inhabiting localities such as thermal refugia where thermal stress is relatively low. The two hypotheses are not mutually exclusive and might be simultaneously or alternatively valid for different colonies and locations. Here, we tested the latter by looking at the historical exposure to thermal stress for 85 giant colonies identified by in-situ observations, with sizes ranging from 5 to > 20 m along their maximum dimension (Fig. 2a). We also looked into the expected fate of the colonies by looking at future climate projections. Our results reveal a dichotomous thermal history among coral colonies: while most experienced minimal stress over the past decades, a subset faced exceptional thermal events — yet future projections indicate a challenging road ahead for all of them.

2. Methods

We collated information on the exact geographical location, depth, size and taxonomy of 85 coral colonies larger than 5 m in their maximum dimension from Map the Giants website (<https://www.mapthegiants.com/>). All the colonies included in the study were identified by in-situ observation, and were alive at the time of the observation. For 83 out of 85 colonies, information on health status was available. Nearly all of these (93 %) had more than 50 % of live tissue, and 78 % with a percentage of live tissue ranging from 76 % to 100 %. Only three colonies had less than 50 % of their tissue alive (see supplementary figure S1). The most represented genus was *Porites* (51 giant colonies), followed by *Pavona* and *Diploastrea* (7 colonies each); *Psammocora* and *Goniopora* (5 colonies each); *Heliopora* (3); *Turbinaria*, *Galaxea* and *Acropora* (2 colonies each); and *Montipora* (1 colony).

We obtained historical maximum DHW monthly data from 1985 to 2024 matching the locations of the giant corals (at a spatial resolution of $0.05^\circ \times 0.05^\circ$) from NOAA Coral Reef Watch (data accessible at <https://coralreefwatch.noaa.gov>, (Skirving et al., 2020)). We computed the number of times a giant colony was exposed to severe bleaching risk conditions (which we identified as $DHW \geq 8$, (Mellin et al., 2024)) within the study period. We replicated the same computation in 1000 randomly sampled reef localities for each giant colony, having the same depth of the target colony (within ± 5 m, to ensure habitat consistency between the target and the reference points) and located between 20 and 200 km from it, to obtain a null expectation against which comparing the observed exposure of the 85 colonies under study. We then computed a set of Z scores (one per each giant coral) as $(x-\mu)/\sigma$ where x is the number of months with $DHW \geq 8$ for the target colony, μ and σ are the mean and standard deviation of the number of months with $DHW \geq 8$ in the 1000 randomly sampled reef locations. We paired each Z score to an empirical p value, computed as the fraction of null sites for which the number of severe bleaching risk events was lower or equal (if $x > \mu$; alternatively, higher or equal) than that observed in the target coral giant site. We tested the sensitivity of these results to the distance criteria used for selecting random sites by replicating the procedure described above. Null sites were sampled in two alternative ways: first, by increasing the radius of the sampling area around the target localities (0–50 km, 0–100 km, ..., 0–250 km); and second, by sampling in discrete rings at increasing distances from the target localities (0–50 km, 50–100 km, ..., 200–250 km).

We obtained future projections of DHW to quantify future exposure of giant colonies to accumulated thermal stress. For that, we used data from (Mellin et al., 2024) in the form of degree heating weeks (DHW, °C-week), calculated over a rolling 12-week (84-day) window. We focused on an intermediate climate projection (SSP2–4.5, ‘middle of the road’), and used the model-ensemble product (combining 5 different models) provided by the authors. Note that these data are provided at a lower spatial resolution than the historical data (0.5° latitude \times 0.5° longitude). For this reason, we did not look at the maximum DHW as a bleaching triggering condition for the giant colonies, as these might still be located in cooler spots within the $0.5^\circ \times 0.5^\circ$ cell. Instead, we looked at how the thermal stress will change in the future relative to the average monthly conditions in the last decade (2015–2024). Again to avoid



Fig. 1. Colony of a massive *Porites* sp. measuring 23.5 m in circumference, at 5.5 m depth reported at Goidhoo, Republic of Maldives, discovered in the context of Map the Giants initiative. Photo by F. Siena (2024).

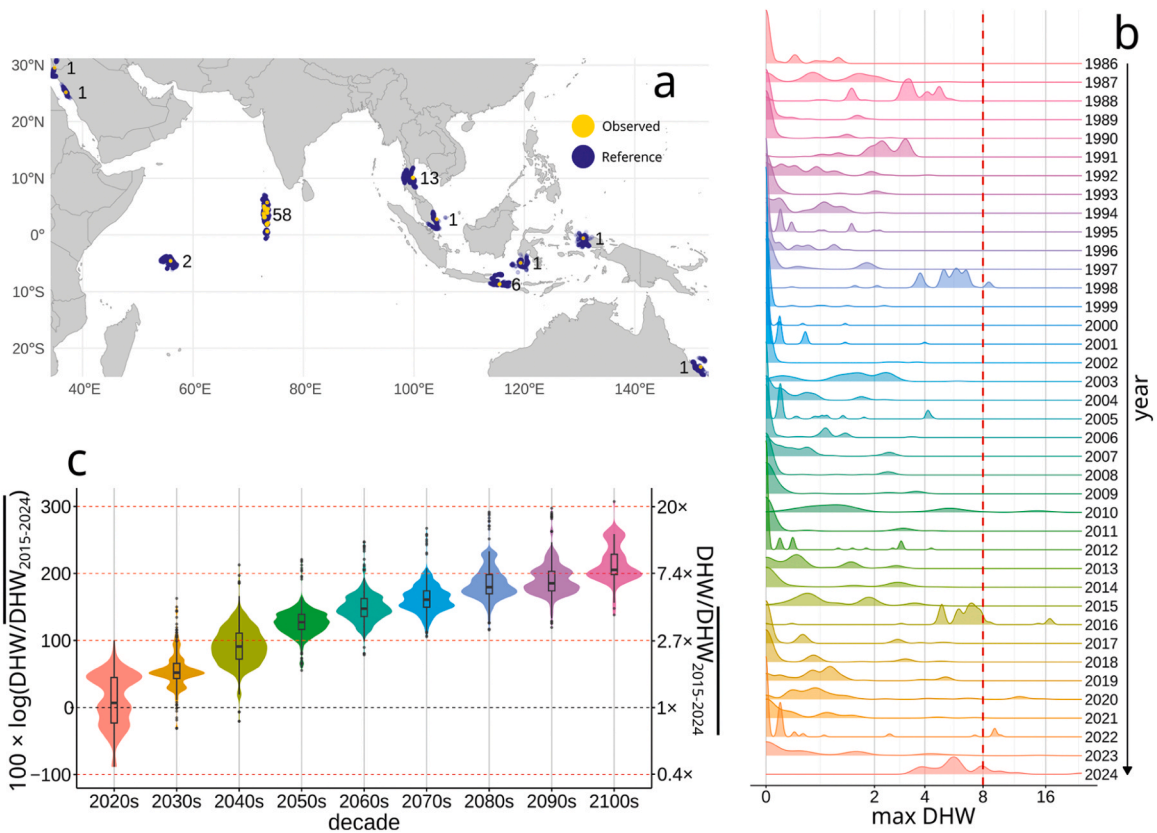


Fig. 2. (a) Map of locations of the giant colonies (yellow dots) and of the reference locations (blue dots). Numbers indicate the total number of observed giant colonies within each cluster of points. (b) Density plots showing the distribution of yearly maximum DHW recorded in all of the giant colonies' locations. (c) Future changes in accumulated thermal stress (DHW) for all giant colonies. Changes are expressed as the log-percentage difference between the maximum yearly DHW at each colony's location and the corresponding mean DHW during the reference period (2015–2024). The secondary y-axis shows the corresponding multiplicative increase relative to the reference period (e.g., $1 \times$ = baseline, $7.4 \times \approx 200\%$ log difference).

potential biases due to discrepancies between the modeled and actual temperature, we computed the reference based on the historical modeled scenario.

3. Results

Within the study time windows, out of 85 giant corals, 72 never experienced severe bleaching risk conditions, defined as local records of maximum monthly degree heating weeks (DHW) $\geq 8^\circ\text{C}/\text{week}$ (Mellin et al., 2024) (Fig. 2b). However, in the remaining 13 colonies, DHW exceeded $8^\circ\text{C}/\text{week}$ between 2 and 22 times in the last decades (on average, 12.3 ± 9.4 SD times). Of all colonies, 75 were less (66) or equally (9) exposed compared to the average of 1000 reference sites within a radius of 200 km. The difference in exposure between the giant colonies and their respective sets of reference sites was never statistically significant ($p > 0.05$ in all cases). The lack of a significant difference suggests that giant colonies with low exposure to thermal stress were located within larger thermal refugia that were only sparsely affected by heatwaves. Ten out of the 13 colonies that experienced thermal stress were exposed to a higher number of severe coral bleaching risk events compared to reference localities, with the difference being significant in 6 cases ($Z > 1.96$, empirical p value < 0.001). These 6 colonies belonged to 3 different genera (*Acropora*, *Porites* and *Galaxea*, 2 colonies per genus), and were all found off the coast of Bali, Indonesia. These results were robust to the choice of the distance range for the selection of the reference localities (see supplementary Table S1). The frequency of severe bleaching risk events experienced by individual colonies did not differ significantly among coral health categories (Kruskal–Wallis $\chi^2 = 0.98$, $df = 3$, $p = 0.81$). This suggests that variation in coral health cannot be explained by differential exposure to high thermal stress during the observation period.

We then looked at how the exposure to thermal anomalies will change for the giant colonies, by considering DHW projections based on an intermediate socio-economic pathway (CMIP6 SSP2–4.5). We found that, during the remainder of the century, most of the monitored giant coral colonies might no longer benefit from environmental protection, and could be exposed to severe bleaching risk, with the accumulated thermal stress exposure per colony per year increasing on average by more than 7.4 times (i.e. $> 200\%$ log percentage difference) compared to the average conditions recorded in the last decade (Fig. 2c).

4. Discussion

Our results suggest that low exposure to thermal stress might have played an essential role in the exceptional growth and long-term survival of giant coral colonies. This finding could be instrumental in speeding up the discovery of the last standing giant colonies, which might be facilitated by focusing search efforts in areas with low historical exposure to thermal stress, while excluding areas that have been heavily impacted by bleaching in recent decades. Combining this information with future climate projections might also help identify priority areas, as thermal refugia where giant colonies might be present and simultaneously at imminent risk of future bleaching.

The fact that, so far, most giant colonies have been found localities that benefited from low levels of thermal stress in the recent past does not rule out the possibility that other inherent properties of the individual giant colonies might also contribute to their survival. In fact, given that giant colonies might be several hundred years old, we cannot exclude the possibility that they were hit by heatwaves before the time window of our assessment. Furthermore, a non-negligible proportion of the giant colonies investigated (15 %) has been exposed to severe bleaching risk conditions multiple times. Various hypotheses can be advanced—and hopefully explored in future studies—to explain these colonies' endurance in the face of the dramatic transformation the oceans have witnessed over the last 50 years.

A conservative one is the existence of highly localized microhabitat features, either offering environmental protection to the colonies despite the overall temperature patterns in the area, or providing them with superior resilience. This hypothesis is supported by the fact that the colonies which apparently survived the highest levels of stress in our dataset all come from the same small area.

However, an alternative (or complementary) explanation would be that such giant colonies have an exceptional thermal tolerance, either on a genetic basis (Dixon et al., 2015) or on an ecological one, possibly due to ecological interactions with thermally resistant symbionts (Howells et al., 2012), or both. This hypothesis might stem from the consideration that the oldest coral colonies alive have been subjected to a few centuries of environmental selection, which might have resulted in the survival of the most thermally tolerant specimens. If that proves to be the case, then the study of giants' DNA might advance our understanding of potential coral adaptation to warming and open new avenues for coral reef rehabilitation.

This last aspect might be crucial for the future of giant colonies worldwide. End-of-century projections leave little hope for their long-term survival, with exposure to thermal stress expected to increase severalfold in the coming decades (Fig. 1c). Although the relatively coarse resolution of future temperature projections (0.5°) may overlook small-scale local refugia that could enable the persistence of individual colonies, the global and pervasive reach of ocean warming makes the existence of truly "safe" reef locations unlikely (Strona et al., 2021). Under this gloomy scenario, the possibility that at least some giant colonies might persist offers a faint—but meaningful—glimmer of hope for the future of coral reefs.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03992](https://doi.org/10.1016/j.gecco.2025.e03992).

Data availability

Research Link Provided

[Code and data associated to the paper "Thermal refugia support the long-term survival and growth of giant coral colonies" \(Zenodo\)](#)

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