



OPEN Mesophotic reefs offer thermal refuge to the 2023 Caribbean mass bleaching event in the Cayman Islands

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Coral reefs are increasingly threatened by marine heatwaves, which drive widespread coral bleaching and mortality. Mesophotic coral ecosystems (MCEs) have been proposed as potential thermal refuges due to their greater depth and relative isolation from surface temperature extremes. Yet their resilience to extreme heat events remains uncertain, with location specific conclusions, thus requiring further studies. Here, we investigate the effects of the 2023 marine heatwave in the Cayman Islands, which resulted in prolonged sea surface temperatures exceeding 31 °C and 17.5 DHW with extensive bleaching across shallow coral reefs. Utilizing vertical transect surveys from 10 m to 50 m, we assessed depth-related variations in bleaching prevalence and temperature profiles. Our results indicate a significant decline in bleaching with increasing depth, with a concurrent reduction in temperature. Depth-generalist species exhibited reduced bleaching at greater depths, whereas shallow-water specialists displayed severe bleaching. These findings suggest that while MCEs may provide thermal refuge for some species, their capacity to buffer against climate-driven reef degradation is species-specific. Given the increasing frequency and intensity of marine heatwaves, understanding the role of deeper reef habitats in mitigating coral loss is critical for informing conservation and management strategies. Our study underscores the importance of protecting MCEs as potential thermal refuges while emphasizing the need for continued research on species-specific thermal resilience with depth.

Keywords Coral bleaching, Marine heatwave, Mesophotic coral ecosystem (MCE), Thermal refuge, Depth-generalist species, Climate change resilience

Over the past several decades, global coral reef ecosystems have experienced a substantial decline in coral cover, with some reefs witnessing reductions from approximately 60% to less than 20%, largely as a consequence of ocean warming^{1–7}. While various local stressors—such as pollution, destructive fishing practices, and coastal tourism—contribute to coral loss, thermal stress induced by marine heatwaves remains the primary driver, leading to bleaching, disease outbreaks, and diminished calcification rates^{5,8,9}. As scleractinian corals exist near their upper thermal limits, even minor temperature elevations can disrupt their symbiotic relationship with dinoflagellates from the family Symbiodiniaceae, a phenomenon known as coral bleaching^{10–14}. Sustained bleaching events can ultimately result in mortality, as many coral species depend on photosynthetic carbon translocated from their symbionts to satisfy their metabolic needs¹⁵. With continued global warming, the frequency, severity, and duration of marine heat waves and subsequent bleaching events are expected to increase⁵.

Beyond the extensively studied shallow coral reef zones, reef ecosystems extend into mesophotic coral ecosystems (MCEs), which occur between approximately 30 m and the lower photic limit (~ 170 m), where light availability no longer supports photosynthesis^{16–20}. A global assessment of 704 scleractinian coral species revealed that while 40% are restricted to depths shallower than 20 m, the remaining 60% of species are capable of inhabiting MCEs^{19,21,22}. Due to their greater depth and relative isolation from direct surface influences, MCEs are hypothesized to experience reduced thermal stress compared to shallow reefs^{17,20,23–25}. Shallow reef temperatures are primarily governed by atmospheric heating and wind-driven processes, leading to substantial thermal accumulation and water column stratification, where prolonged thermal exposure coupled with high light levels can exacerbate extreme thermal anomalies, ultimately triggering coral bleaching^{26–28}. In contrast, increasing depth generally corresponds to reduced thermal accumulation and light driven irradiance, resulting in more stable and cooler temperatures in MCEs^{29,30}. Nevertheless, MCEs are not immune to environmental

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stressors. Observations of coral bleaching at mesophotic depths have been reported in both the Pacific and Caribbean³¹, including multiple bleaching and disease events in MCEs of the U.S. Virgin Islands³². However, recent studies indicate that deeper reefs may provide thermal refuge during extreme heat events^{33–36}. For example, in French Polynesia, Pérez-Rosales et al.³⁶ found that bleaching prevalence declined with increasing depth, suggesting that depth-generalist coral species across multiple genera may benefit from deeper habitats.

In 2023, the Cayman Islands experienced an unprecedented marine heatwave³⁷, with sea surface temperatures exceeding 31 °C for several weeks^{38,39}. This thermal anomaly corresponded to an estimated 17.5 Degree Heating Weeks (DHW), a metric representing accumulated heat stress in an area^{38,40,41}. The prolonged thermal stress resulted in widespread coral bleaching and mortality across the shallow fore-reef zone of Little Cayman and throughout the Caribbean^{39,41,42}. During the peak of this marine heatwave, we conducted three vertical surveys on the highly protected reefs of Little Cayman Island to monitor the impact of the bleaching event on several coral species across their depth distribution and provide documentation of thermal refuge potential in MCEs.

Results

Seawater temperature at the three surveyed sites (Fig. 1) was highest at the surface (31.2 °C) and remained relatively stable between 30.8 °C and 31.0 °C from 10 m to 30 m. At 35 m, temperature declined to an average of 30.6 °C and continued to decrease by approximately 0.2 °C every 5 m, reaching a minimum of 29.9 °C at 50 m.

A GLM with a Gaussian distribution indicated covariance between temperature and depth (Supplementary Table S1). Separate GLMs for each factor showed significant effects on bleaching percentage; however, temperature yielded the lowest AIC value, indicating the best model fit (Fig. 2; Table 1).

Bleaching response across depth differed by species (Fig. 3), where significant correlations of reduced bleaching with increasing depth were found for *Agaricia agaricites* ($R^2 = 0.17$, $P < 0.001$), *Agaricia fragilis* ($R^2 = 0.58$, $P < 0.001$), *Agaricia lamarcki* ($R^2 = 0.66$, $P < 0.001$), *Mycetophyllia lamarckiana* ($R^2 = 0.84$, $P = 0.028$), *Porites astreoides* ($R^2 = 0.25$, $P = 0.002$), *Scolymia cubensis* ($R^2 = 0.72$, $P < 0.001$), *Siderastrea siderea* ($R^2 = 0.22$, $P < 0.001$), and *Stephanocoenia intersepta* ($R^2 = 0.59$, $P < 0.001$). Correlations between bleaching score and depth for other species lacked significance, possibly influenced by the low number of replicates and/or unequal sample sizes across depth for these species (Supplementary Fig. S1, $P < 0.05$; Supplementary Table S2).

Discussion

The occurrence of the extreme Caribbean heatwave in 2023 enabled opportunistic exploration of the impacts of increased temperature on coral bleaching across a vertical gradient during a naturally occurring bleaching event. Our survey results document a significant decline in coral bleaching with increasing depth or decreasing temperatures, where deeper reefs exhibited less bleaching compared to shallow reefs. This decline was found to be driven in part by temperature across the vertical gradient, suggesting that deeper reefs may serve as thermal refuges during extreme heatwave events. However, this pattern differed among species, where not all coral species expressed a uniform decrease in bleaching with increasing depth.

Mesophotic coral ecosystems (MCEs) have been proposed as potential refugia from disturbances affecting shallow-water coral reefs, including storms, sedimentation, habitat fragmentation, and rising sea surface temperatures—a concept known as the Deep Reef Refugia Hypothesis (DRRH)^{17,18,20,24,43–46}. However, several key criteria of this hypothesis have repeatedly failed to be met, most notably the assumption of larval connectivity across depths [e.g.,⁴⁷]. Additionally, MCEs have been documented to experience bleaching, disease, anthropogenic debris accumulation, and storm impacts^{31,32,48}. In fact, in the Indian Ocean, bleaching was found to increase for corals below 60 m compared to shallow corals due to internal waves pushing the thermocline deeper⁴⁹, suggesting that MCEs are vulnerable to temperature anomalies associated with shifting thermoclines. Yet, some studies report reduced bleaching during heatwave events, indicating that while deep reefs may not

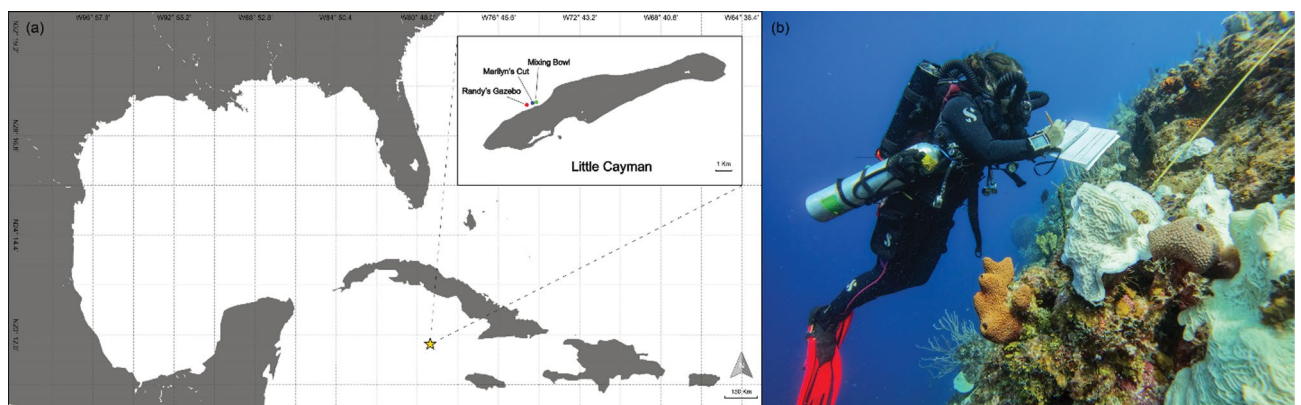


Fig. 1. (a) Map of the Caribbean with Little Cayman inset showing the location of the three survey sites. The base map is from Google Earth (data sources: SIO, NOAA, U.S. Navy, NGA, GEBCO Airbus LDEO-Columbia, NSF; imagery dated 12/14/2015) and was annotated by A. Chequer using Adobe Photoshop v26.5 and Adobe Illustrator v29.4. (b) Image of Goodbody-Gringley conducting a survey on the vertical wall (photo by A. Chequer).

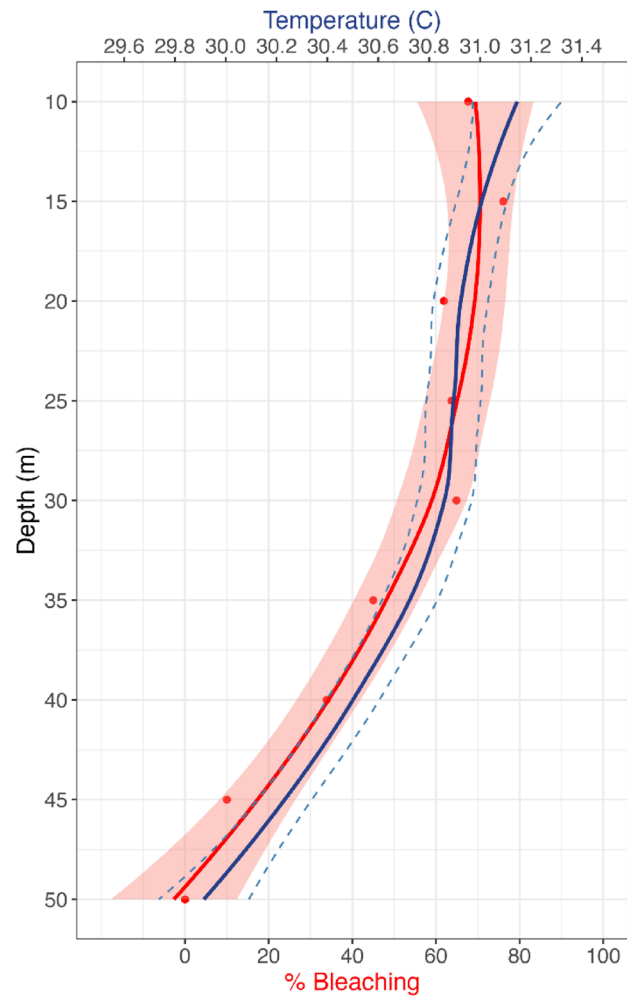


Fig. 2. Bleaching percentage (red; lower x-axis) and seawater temperature (°C; blue; upper x-axis) across depth (m; y-axis). Solid lines indicate the mean values, while areas within shaded sections and dotted lines represent confidence intervals.

Model	df	Coefficient estimate (r)	Std. err	t-value	Pr (> t)	ΔAIC
Temperature	3	0.604	0.077	7.830	1.16e-07	-24.6
Depth	3	-0.017	0.002	-7.281	3.60e-07	-22.2

Table 1. Results of generalized linear models (GLM) with Gaussian distribution with CL for comparisons of bleaching percentage with temperature (°C) and depth (m). Significant relationships are indicated in bold ($p < 0.05$). The difference in Akaike Information Criterion (AIC) from the best fit model is also provided as an indication of model quality.

serve as universal refugia, they may provide thermal refuge for certain species in specific locations^{35,36,50}. For example, during a moderate heatwave in French Polynesia, depth-generalist species exhibited reduced bleaching from shallow to mid-mesophotic depths (60 m), a pattern attributed primarily to changes in light-irradiance attenuation rather than temperatures, which seemed unchanging with depth³⁶. Similarly, Baird et al.³⁵ found a curvilinear decline in bleaching with depth, corresponding with the curvilinear attenuation of light¹⁷, suggesting that light reduction may be a key factor in mitigating bleaching at greater depths. Our model comparisons suggest that temperature, rather than depth, better explained the observed reduction in bleaching indicating that the slight thermocline at 30–35 m in the Cayman Islands during the 2023 bleaching event played a key role in moderating bleaching severity. However, since light was not measured in this study, its relative impact compared to temperature remains unknown.

While bleaching occurrence decreased significantly with increasing depth across all surveyed corals, species-specific variations were observed. Depth-generalist species, including *A. fragilis*, *A. lamarcki*, *M. lamarckiana*, *P. astreoides*, *S. cubensis*, *S. siderea*, and *S. intersepta*, exhibited a marked reduction in bleaching at greater depths.

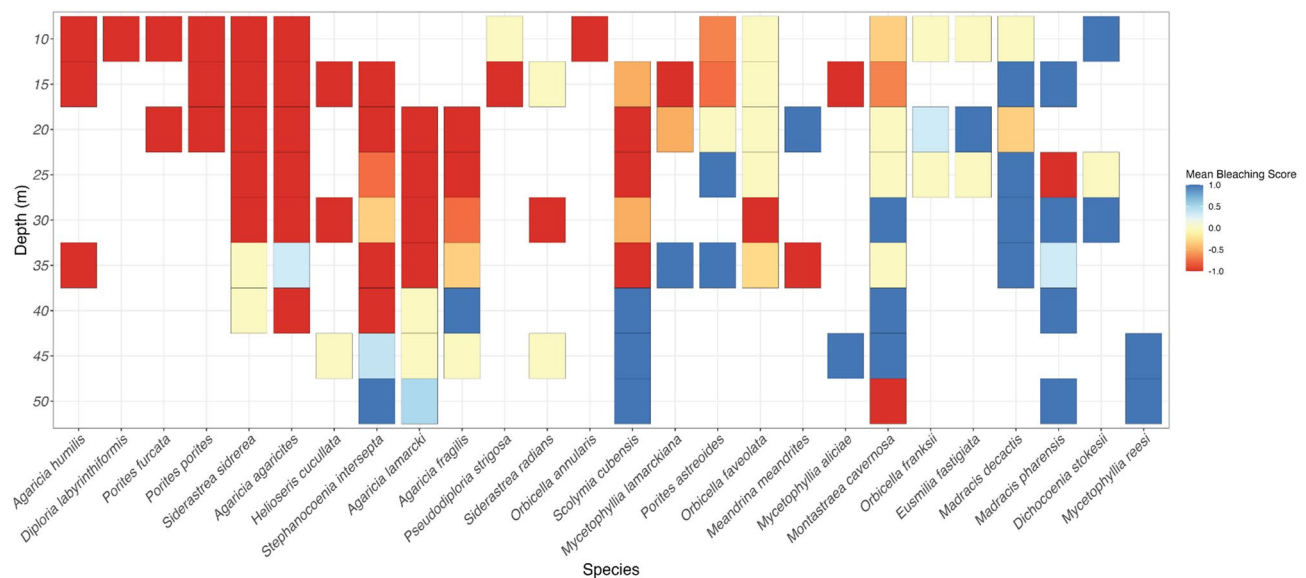


Fig. 3. Mean bleaching response for all species observed across depths, ranging from severely bleached in red to healthy in blue. Bleaching scores were averaged per 5 m depth bin, where bleached = -1 (red), pale = 0 (yellow), and healthy = 1 (blue). The number of colonies per species in each depth bin (n) are available in Supplementary Table S2.

In contrast, MCE-specialists such as *Madracis pharensis* experienced minimal to no bleaching across their depth range, while corals restricted to shallow habitats, including *Agaricia agaricites*, *Pseudodiploria strigosa*, *Diploria labyrinthiformis*, and *Porites porites*, exhibited severe bleaching at all observed depths (Fig. 3; Supplementary Fig. S1). These findings align with those of Pérez-Rosales et al.³⁶, who reported greater depth-related improvements in health status among depth-generalists than depth-specialists. However, not all depth-generalist species in the present study benefited equally. For instance, *Montastraea cavernosa*, *Orbicella faveolata*, and *Madracis decactis* showed no correlation between bleaching prevalence and depth. However, this lack of correlation may have been driven by low and unequal replication across depths, thereby warranting additional assessments across species depth distributions (Fig. 3; Supplementary Fig. S1; Supplementary Table S2).

Species-specific differences in thermal performance may help explain the observed variability in bleaching responses. A study on several common Caribbean coral species in Bermuda found no differences in metabolic responses to a range of temperatures among species⁵¹, yet recent research in the Pacific has identified species-specific variations in thermal performance based on photosynthetic efficiency, growth, and survival^{52,53}. As a result, the extent to which different species will respond at molecular and organismal levels to rising temperatures across their distributions remains uncertain. However, the species-specific responses documented here during a naturally occurring heatwave suggest that depth-generalist and MCE-specialist corals may have a higher likelihood of surviving future marine heatwaves. Evidence of thermal refuge for depth generalist species is particularly important given the wide-scale mortality documented on shallow coral reefs across Little Cayman during the 2023 heatwave⁴¹. At the peak of the event, approximately 80% of corals exhibited bleaching, with 54% experiencing complete colony mortality by its conclusion. Among the most severely affected taxa were *Agaricia* spp., *Porites porites*, and *Mycetophyllia* spp., all of which exhibited bleaching rates exceeding 95% and high mortality. In contrast, corals of the genus *Orbicella*, while displaying visible bleaching, recovered following temperature declines and did not experience significant mortality. These findings underscore the role of marine heatwaves in reshaping coral reef community composition, particularly on shallow regions. As such, future coral reef community composition is likely to shift, with an increasing dominance of thermally resilient depth generalist species and a decline in species restricted to shallow reefs⁵⁰.

Given that 45–54% of Atlantic shallow-water corals are currently at an elevated extinction risk⁵⁴, the identification of thermal refuges is critical for sustaining coral populations. While deep reef communities have the potential to enhance shallow-reef resilience if recovery periods between MHWs are sufficient⁵⁵, the extent to which these ecosystems can mitigate climate-driven coral loss remains unknown. Climate and oceanographic models suggest that most existing shallow-water thermal refuges will not persist under future warming scenarios, with few refuges at $+1.5$ °C and none at $+2.0$ °C above pre-industrial levels⁵⁶. However, if deeper habitats continue to experience reduced thermal stress relative to shallow reefs, they may serve as long-term refuges from climate change, potentially moderating coral species losses⁵⁵. The results presented here add to the growing body of evidence that MCEs can serve as thermal refuges for depth-generalist coral species. Thus, as marine heatwaves increase in frequency and intensity, the conservation and study of MCEs will be essential for informing reef management strategies, underscoring the importance of protecting MCEs as potential thermal refuges while emphasizing the need for continued research on species-specific thermal resilience.

Methods

Study site

The Cayman Islands are located 200 miles northwest of Jamaica and 150 miles south of Cuba in the Caribbean Sea and are comprised of three main islands: Grand Cayman, Cayman Brac, and Little Cayman. Little Cayman, located 80 miles northeast of Grand Cayman, is the smallest and least developed of the three islands with an area of roughly 26 km² and a population of 160 permanent residents. Of the 45 km of shoreline, 74.2% is designated as marine protected areas with roughly 57% under full No-Take protection by the Cayman Islands Government⁵⁷.

Survey methods

Three sites within the Bloody Bay Marine Protected Area considered as replicates, located on the northern side of Little Cayman Island, were surveyed on September 16, 2023: Randy's Gazebo (19.683783; -80.082967), Marylin's Cut (19.684733; -80.079067), and Mixing Bowl (19.684920; -80.078000). Each site features a near-vertical wall that begins at approximately 10 m and extends beyond 1,000 m in depth (Fig. 1).

At each site, a single transect was secured to the substrate at the shallowest point of the vertical wall and extended downward to a maximum depth of 50 m. Corals within 1 m on either side of the transect were identified to species level and categorized by bleaching status: "healthy" (dark in color with no visible bleaching), "pale" (lighter than conspecifics and/or exhibiting white blotching), or "bleached" (completely white).

Seawater temperature was recorded throughout each dive using HOBO ProV temperature loggers attached to the backs of two divers. Depth-specific temperature readings were determined by correlating logger timestamps with depth data from each diver's handheld computer (Shearwater Petrel). All dives were conducted using closed-circuit rebreathers (Hollis Prism 2).

Data analyses

Temperature and bleaching status data were binned into 5 m depth intervals from < 10 m to 50 m. The effects of depth and seawater temperature on the percentage of bleached coral colonies were analyzed using Generalized Linear Models (GLMs) with a Gaussian distribution. Model assumptions were assessed using normal quantile-quantile plots, which confirmed approximate normality (Supplementary Figure S2). Due to collinearity between depth and temperature (Supplementary Table S1), separate GLMs were constructed for each variable. The best-fit model was selected using the Akaike Information Criterion (AIC)⁵⁸.

To compare bleaching responses across species, a bleaching score was assigned to each coral colony: healthy = 1, pale = 0, and bleached = -1. Species-specific bleaching scores were averaged within each depth bin to facilitate visualization. Correlations of bleaching score with depth were then conducted for each species using linear regressions. The number of colonies per species at each depth is provided in Supplementary Table S2.

All statistical analyses and data visualizations were done using R version 4.2.2⁵⁹ and the following R packages: car v. 3.1.2^{59,60}, colorspace v. 2.1.0^{59–62}, feasts v. 0.3.2⁶³, ggcorrplot v. 0.1.4.1⁶⁴, ggfortify v. 0.4.17^{65,66}, ggpmisc v. 0.5.5⁶⁷, hablar v. 0.3.2⁶⁸, janitor v. 2.2.0⁶⁹, knitr v. 1.45^{70–72}, lme4 v. 1.1.34⁷³, RColorBrewer v. 1.1.3⁷⁴, rmarkdown v. 2.25^{74–76}, rstatix v. 0.7.2⁷⁷, tidyverse v. 2.0.0⁷⁸, tsibble v. 1.1.4^{78,79}, vegan v. 2.6.4^{78–80}. Data and code are available on Zenodo (<https://doi.org/10.5281/zenodo.14889221>).

Data availability

The datasets generated and/or analysed during the current study are available in the Zenodo repository, <https://doi.org/10.5281/zenodo.14889221>.

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Author contributions

GG-G and AC developed the project and conducted all data collection. GG-G analyzed the data and wrote the manuscript, AC contributed imagery, and both authors edited the final version.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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