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Size-dependent spatial variation in bleaching and mortality in massive Porites corals during the extreme thermal stress

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Abstract

In 2024, the fourth global mass coral bleaching event occurred due to strong heat waves. The reefs around Sesoko Island in Okinawa are no exception. Severe heat stress, the highest Degree Heating Weeks (DHWs) on record since the first global bleaching event in 1998, caused bleaching and mortality in many coral species, including heat-tolerant massive colonies of *Porites*. In general, coral bleaching occurs more severely at the top of the colony, which is exposed to stronger sunlight than the bottom parts. However, during the 2024 bleaching event, we found a reversal of the typical bleaching pattern in *Porites*, but not in other coral species, with more bleaching at the bottom of the colony, while the top remained healthy. Bottom-specific bleaching was more pronounced in larger colonies. In smaller colonies, the phenomenon of full bleaching, which involves bleaching at both the top and bottom of colonies, was observed more frequently, resulting in a greater rate of complete mortality within these colonies. Our results suggest that bleaching susceptibility differs between the top and bottom of larger colonies, resulting in a bottom-specific bleaching pattern. One possible hypothesis is that the topsides of larger colonies have acclimatized to bleaching stress, e.g., high temperature and strong light, through frequent bleaching events.

Introduction

Reef-building corals have endosymbiotic dinoflagellates of the family Symbiodiniaceae. Corals rely on symbiont photosynthesis for growth and survival. In return, corals provide inorganic nutrients to algal symbionts to support photosynthesis (Barott et al. 2014). This symbiotic relationship is a cornerstone of coral reef ecosystems, which are among the most biologically diverse ecosystems on Earth. However, under heat stress conditions, corals lose algal symbionts, resulting in coral bleaching. Prolonged bleaching can cause coral mortality due to starvation (Rädecker et al. 2021). Over the past three decades, global coral bleaching has occurred four times: in 1998, 2010, 2014–2017 and 2023–2024 (Reimer et al. 2024). The frequency and severity of mass coral bleaching events have been increasing due to global warming and its associated heat waves (Hughes et al. 2017; Marcos et al. 2025)Over the past three decades, coral cover has declined by 50% worldwide (Eddy et al. 2021). If global warming continues and temperatures rise by 2ºC by the end of this century, most corals are expected to be lost (IPCC 2023; Sweet et al. 2026).

Under heat stress conditions, corals lose algal symbionts and/or algal pigments, resulting in coral bleaching (Rädecker et al. 2021). Heat stress-induced bleaching can be observed in the dark, but its extent is enhanced by an increase in light intensity (Tolleter et al. 2013). Therefore, bleaching extent differs among light environments, even within the same colony. For example, severe bleaching often occurs at the top of coral colonies, which are exposed to direct sunlight (Hoegh-Guldberg 1999). Before coral undergoes bleaching, photoinhibition of photosynthesis often occurs under heat stress (Takahashi et al. 2004, 2009). Because photoinhibition occurs in a light-dependent manner, it is hypothesized that light-dependent bleaching is due to the photoinhibition of algal symbionts (Warner et al. 1999). However, it remains unclear whether photoinhibition causes coral bleaching through the loss of algal symbionts,

although it has been demonstrated that photoinhibition is related to coral bleaching through the loss of algal pigments (Takahashi et al. 2004, 2008).

The sensitivity of corals to bleaching differs among coral species (Loya et al. 2001; Tavakoli-Kolour et al. 2023). In general, massive coral species are more tolerant of heat stress than are branching species (Loya et al. 2001; Tavakoli-Kolour et al. 2023). However, it has been demonstrated that bleaching sensitivity differs between colonies in the same species with different symbionts(Abrego et al. 2008; Sampayo et al. 2008). Symbiodiniaceae includes 11 genera, and each genus includes genetically different types (LaJeunesse et al. 2018; Nitschke et al. 2020; Pochon and LaJeunesse 2021). Previous field and laboratory studies have demonstrated that Symbiodiniaceae types change bleaching sensitivity under heat stress and that corals can acclimatize to increased temperatures by recruiting new algal symbionts from the environment (switching) or by changing the composition of symbiont diversity (shuffling) (Buddemeier and Fautin 1993; Baker et al. 2004; Baskett et al. 2009; Cunning et al. 2015; Thomas et al. 2018). Furthermore, it has been proposed that corals can acclimatize to increased temperatures by modification of phenotypes (van Oppen et al. 2015; Hackerott et al. 2021; Hazraty-Kari et al. 2022) and changing their microbiome composition (Ziegler et al. 2017; Reigel et al. 2021). Thus, thermal sensitivity to bleaching differs in the same coral colony between years, for example, before and after a bleaching event.

Complex coral morphology creates different microenvironments, such as light intensity, water flow, nutrient availability, and oxygen concentration (Drake et al. 2021; Lewis et al. 2022; Dilernia et al. 2024). Therefore, each polyp in the same colony can be exposed to different environments depending on the colony region, for example, the upper and lower portions of the colony. Consequently, each part of the colony sometimes shows differences in symbiont diversity and thermal sensitivity to bleaching ((Rowan et al. 1997; Lewis et al. 2022; Voolstra et al. 2025). However, the difference in microenvironments among colony parts depends on their size, with larger colonies possessing more diverse microenvironments. Therefore, differences in symbiont composition and thermal sensitivity to bleaching among colony parts may depend on colony size.

In this study, we quantified spatial intra-colony bleaching and consequent mortality patterns and evaluated size-dependent susceptibility and mortality in massive *Porites* species during the fourth and most extreme global coral bleaching event, when thermal stress around Okinawa reached record levels of 17°C-weeks (DHWs). We report a reversal of the commonly observed bleaching pattern in large, but not small, *Porites* colonies: while the top part of the colony remained healthy and appeared resistant to bleaching, the bottom part of the colony exhibited pronounced bleaching. We hypothesize that localized acclimatization of upper colony surfaces to repeated thermal and light stress may explain this pattern.

Methods

Study site

Sesoko Island (26° 38’N, 127° 52’E) is located on the central western coast of Okinawa Island in the Ryukyu Archipelago. Fringing reefs surround the island, with the reef edge extending from 70–100 m to 250–400 m on the southern coast (Das et al. 2022). In this study, four sites around Sesoko Island were investigated in September 2024 and May 2025. Two sites, North East and South East, were surveyed on the eastern side of Sesoko Island, while Gorillachop and Yamakawa were surveyed on opposite sides of the island along the Okinawa coastline (Fig. 1A). All sites are characterized by high coral diversity. Surveys at the study sites did not require any special permission. No corals were collected or manipulated in this study, and only digital images of corals were taken.

Temperature and thermal stress accumulation

Temperature data in this study were obtained from the coastal observation dataset of the Sesoko Marine Research Station, Tropical Biosphere Research Center, University of the Ryukyus. Seawater temperature was recorded at hourly intervals using a temperature logger deployed on the inner reef flat in front of the station. To examine the accumulation of heat stress during the summer of 2024 in the study area, we calculated thermal stress using the degree heating weeks (DHW) metric as an indicator of bleaching. The maximum monthly mean (MMM) climatological temperature at the study sites (28.48°C; see (Tavakoli-Kolour et al. 2024)) was obtained from the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch (CRW) satellite products for the Northern Ryukyus Island 5 km Regional Virtual Station (Liu et al. 2014, 2017). The thermal threshold at the study sites was predicted to be 1°C higher than the MMM temperature. All recorded temperatures exceeding this thermal threshold were considered temperature anomalies and were accumulated to calculate DHWs.

Survey methods

At each study site, eight consecutive haphazardly placed 20 × 1 m belt transects were established on the reef flat at depths of 2–6 m in September 2024 for the bleaching survey and in May 2025 for the post-bleaching and consequence mortality survey. Only colonies with at least 50% of their structure within the transect area were recorded. During the bleaching survey, a distinct bleaching pattern was observed in massive *Porites* colonies, where the bases of the colonies were bleached while the tops remained healthy, hereafter referred to as “bottom-specific bleaching”. To record comprehensive data on bleaching patterns and explore possible explanations for this phenomenon, all massive *Porites* within the transects were recorded. Each coral colony was assigned to one of the six bleaching patterns: (1) unbleached (healthy and no signs of bleaching); (2) pale (visibly lighter coloration without complete bleaching); (3) top-specific bleaching (the tops of colonies were bleached while the bases remained healthy); (4) bottom-specific bleaching (the bases were bleached while the tops remained healthy); (5) patchy bleaching (patchy bleaching without a distinct spatial arrangement); and (6) fully bleached (100% of the colony surface was bleached). All massive *Porites* colonies within the transect were photographed from a downward-facing perspective for size measurement using an Olympus TG-5 digital camera, including a ruler for scale. The longest diameter of each colony was measured from the images using ImageJ

software. Coral colonies were classified into five size categories: (1) juveniles (< 5 cm), (2) small (6–20 cm), (3) medium (21–40 cm), (4) large (41–60 cm), and (5) very large (> 60 cm). In the post-bleaching and subsequent mortality survey, different mortality patterns in massive *Porites* colonies were recorded and categorized into five types: (1) healthy (no signs of mortality), (2) patchy dead (patchy dead without a distinct spatial arrangement), (3) top dead (colonies with recent mortality in the top section), (4) bottom-specific dead (colonies with recent mortality in the bottom section) and (5) fully dead (100% mortality). The proportion of bleached or dead tissue on each colony was visually estimated by a single observer across all survey periods to ensure consistency.

Statistical analysis

To assess spatial variation in bleaching and post-mortality, generalized linear models (GLMs) with a binomial error distribution and logit link function were applied. For each colony, bleaching and post-mortality were coded as binary response variables (0 = healthy/alive, 1 = bleached/dead), and site was included as a fixed effect. Post hoc pairwise comparisons were performed using the “emmeans” package with Tukey’s adjustment for multiple comparisons (Lenth, 2019). To examine the influence of colony size on bleaching and mortality patterns in massive *Porites*, Kendall’s rank correlation was used. Colony size was treated as a continuous variable, and individual bleaching and mortality patterns (e.g., fully bleached, bottom-specific bleached, fully dead, bottom-specific dead) were analyzed as binary variables (presence/absence) to test for monotonic relationships with colony size. In addition, the probability of occurrence of bleaching and mortality patterns was modeled as a function of colony size using GLMs with a binomial error structure. For each pattern, the proportion of affected colonies within each size category was modeled using a binomial response (number of colonies exhibiting the pattern versus those not exhibiting it). Predicted probabilities and 95% confidence intervals were obtained from the fitted models on the logit scale and back-transformed to the response scale for visualization. A *p*-value of $p < 0.05$ was considered statistically significant. All analyses were conducted in R v. 2025.05.0 + 496 (R Core Team, 2025).

Results

Sea surface temperature and degree heating weeks (DHWs)

To obtain a comprehensive understanding of the heat stress experienced at the study site during the summer of 2024, we analyzed in situ temperature data recorded throughout the peak thermal period, from mid-June to mid-September. Specifically, we calculated the maximum and mean daily sea surface temperatures (SST), as well as degree heating weeks (DHW). During this period, the maximum recorded temperature reached 32.9°C, and the overall mean daily temperature was 29.9 ± 0.07 (°C ± SE). Based on the in-situ temperature data, the DHW value reached 17°C-weeks. Importantly, DHW values remained

above 16°C-weeks for 22 consecutive days, from September 7 to 29, and above 8°C-weeks for 89 days, indicating prolonged exposure of coral reefs to thermal stress (Fig. 1B).

Coral bleaching and post-mortality patterns in massive Porites

During the peak of the 2024 heatwaves in September, extensive bleaching occurred on reefs around Sesoko Island (Fig. 1C), affecting 18 coral taxa, including massive *Porites*. We observed an unusual bleaching pattern in massive *Porites*, which we term “bottom-specific bleaching,” where the bottom parts of the colonies were bleached while the top remained healthy. Consequently, we investigated bleaching patterns, subsequent mortality, and the relationship with colony size in massive *Porites* colonies.

A total of 481 massive *Porites* colonies were surveyed at four sites. Among colonies, signs of bleaching were observed in 60.9% of the colonies. Of these, 34.9% showed non-directional (patchy) bleaching pattern, 34% were fully bleached, 10.4% exhibited bottom-specific bleaching, and 1.7% displayed top-specific bleaching (Fig. 2A-I). In the post-mortality survey, 446 colonies were assessed, and recent mortality was recorded in 43.9% of the colonies. This included 17% with top mortality, 12.3% with bottom-specific mortality, 10.7% that were fully dead, and 3.5% with no distinct mortality pattern. No significant differences in the bleaching of *Porites* colonies were observed among sites (GLM, $p = 0.346$). In contrast, post-mortality monitoring revealed that Gorillachop had the highest mortality, followed by North East Sesoko, South East Sesoko, and Yamakawa Beach. The difference in post-mortality was statistically significant between Gorillachop and all other sites (GLM, $p \leq 0.005$); however, differences among the other sites were not statistically significant (GLM, $p \geq 0.59$).

Colony Size and bleaching and post-mortality consequence relationship

Bleaching patterns varied across colony size classes, with the relative density of each pattern shifting along the colony size gradient (Fig. 3A, B). A significant positive correlation was found between colony size and the bottom-specific bleaching pattern (Kendall’s rank correlation, $\tau = 0.119$, $p < 0.001$; GLM, $p < 0.001$), suggesting that larger colonies were more likely to exhibit bleaching at the base while the top remained healthy (Fig. 3C). This pattern was mirrored in mortality outcomes, where a significant positive correlation was also observed between colony size and the bottom-specific dead pattern ($\tau = 0.08$, $p = 0.002$; GLM, $p = 0.008$), indicating that larger colonies were more likely to experience bleaching and consequent mortality at the base while maintaining healthy tissue at the top (Fig. 3C). Conversely, a significant negative correlation was found between colony size and both the fully bleached ($\tau = -0.13$, $p < 0.001$; GLM, $p < 0.001$) and fully dead ($\tau = -0.11$, $p < 0.001$; GLM, $p < 0.001$) patterns, suggesting that smaller colonies were more susceptible to complete bleaching and total mortality (Fig. 3D). Colony size did not significantly correlate with other bleaching patterns, such as top-specific bleaching ($\tau = 0.02$, $p = 0.39$) and patchy bleaching ($\tau = -0.01$, $p = 0.64$). However, a significant positive correlation was found between colony size and the top-specific mortality ($\tau = 0.102$, $p < 0.001$).

Discussion

In general, coral bleaching occurs more severely at the top of the colonies, where they are exposed to stronger light (Hoegh-Guldberg 1999). However, in this study, we found an unusual bleaching pattern —“bottom-specific bleaching”—in massive *Porites* during the fourth global coral bleaching event in 2024. Bottom-specific bleaching has also been reported previously in southern Okinawa during the 1998 bleaching events (Nishihira and Higa 1999); however, it has not been observed in our study area despite decades of continuous coral reef monitoring since then (Loya et al. 2001; van Woesik et al. 2011; Afzal et al. 2025). Thus, bottom-specific bleaching appears to be a rarely documented bleaching phenomenon in corals. During our field monitoring, bottom-specific bleaching was observed only in *Porites* but not in other coral species, suggesting that this bleaching pattern is a *Porites*-specific phenomenon, at least so far. Bottom-specific bleaching was not observed in other corals around *Porites*, implying that this bleaching pattern is not due to irregular environments, such as higher seawater temperatures at the bottom of the colony than at the top. Furthermore, the bottom-specific bleaching was not lethal, implying that this bleaching pattern is different from bleaching caused by diseases. It remains uncertain whether bottom-specific bleaching is a transient phenomenon or a recurrent event. Further studies are required to further understand the phenomenon of bottom-specific coral bleaching.

Based on the bleaching patterns, the corals were grouped into six categories: healthy (non-bleached), pale, patchy, top, bottom-specific, and full bleaching. The proportion of each category was consistent among colony sizes, except for bottom-specific and full bleaching. The ratio of bottom-bleaching increased with an increase in the colony size. On the other hand, the proportion of full bleaching increased with a decrease in colony size. It is therefore conceivable that bleaching tolerance at the top of the colony increases with colony size, resulting in less full bleaching and more bottom-specific bleaching in larger colonies. It remains unknown how the top side of the larger colony acquired the bleaching tolerance. In the last decade, mass bleaching events occurred in 2016 and 2017 at the present monitoring sites (Sakai et al. 2019; Singh et al. 2019; Afzal et al. 2025). Thus, larger *Porites* colonies experienced several bleaching stresses, especially on the top side, due to direct sunlight exposure. Because each site of the coral colony separately acclimatizes to bleaching stress, higher bleaching tolerance at the top of the colony might be due to top-side-specific acclimatization to bleaching stress.

After bleaching due to a temporal increase in seawater temperatures during the summer, some corals recover from bleaching by re-establishing algal symbionts (Baker et al. 2004; Berkelmans and Oppen 2006; Silverstein et al. 2014), while others die from starvation (Voolstra 2020; Martinez et al. 2022). An increase in the extent of bleaching decreases the energy supply from algal symbionts to corals, resulting in an increased chance of death in bleached corals. Therefore, the proportion of full mortality is directly related to the proportion of full bleaching among colony sizes. Thus, it is conceivable that the lower proportion of full mortality in large-sized colonies is due to a lower proportion of full bleaching. Our results demonstrated that the decreased full-bleaching in large-sized colonies is due to increase in bottom-specific bleaching. Therefore, it is likely that bottom-specific bleaching helped suppress full

mortality. Further studies are required to understand the ecological significance of bottom-specific coral bleaching in coral reef ecosystems.

Declarations

Supplementary

Data and R scripts are available in an open repository. An anonymized view-only link is provided for peer review:

https://osf.io/82jfg/overview?view_only=3c11914c5ed4413e8bc3045ab3ec5aea

Author Contribution

P.T.-K.: conceptualization, investigation, methodology, project administration, data curation, formal analysis, visualization, writing—original draft, and writing—review and editing; M.B.: investigation and writing—review and editing; S.H.-K.: formal analysis, visualization, and writing—review and editing; S.T.: conceptualization, resources, funding acquisition, writing—review and editing. All authors approved the final version of the manuscript and agreed to be accountable for the work performed therein.

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Figures

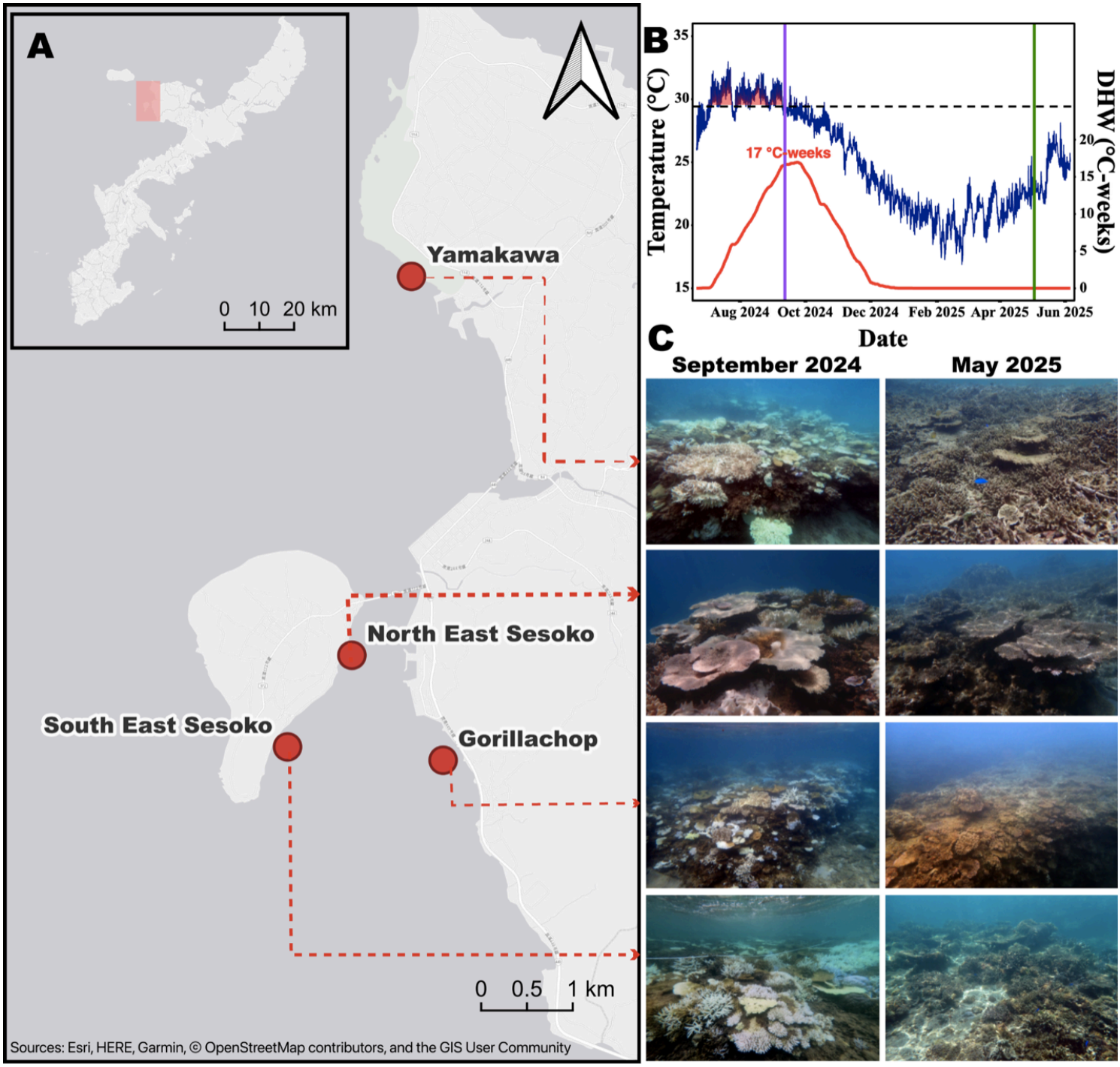


Figure 1

(A) Study sites around Sesoko Island monitored for coral bleaching and post-mortality; (B) Temperature fluctuations and degree heating weeks (red line) at 5 m depth on the eastern side of Sesoko Island from July 2024 to June 2025. The horizontal dashed line indicates the threshold temperature (29.48 °C). The vertical purple and green lines represent the timing of the bleaching survey and post-mortality survey, respectively. (C) Wide-view images of each site were taken during the bleaching and post-mortality surveys.

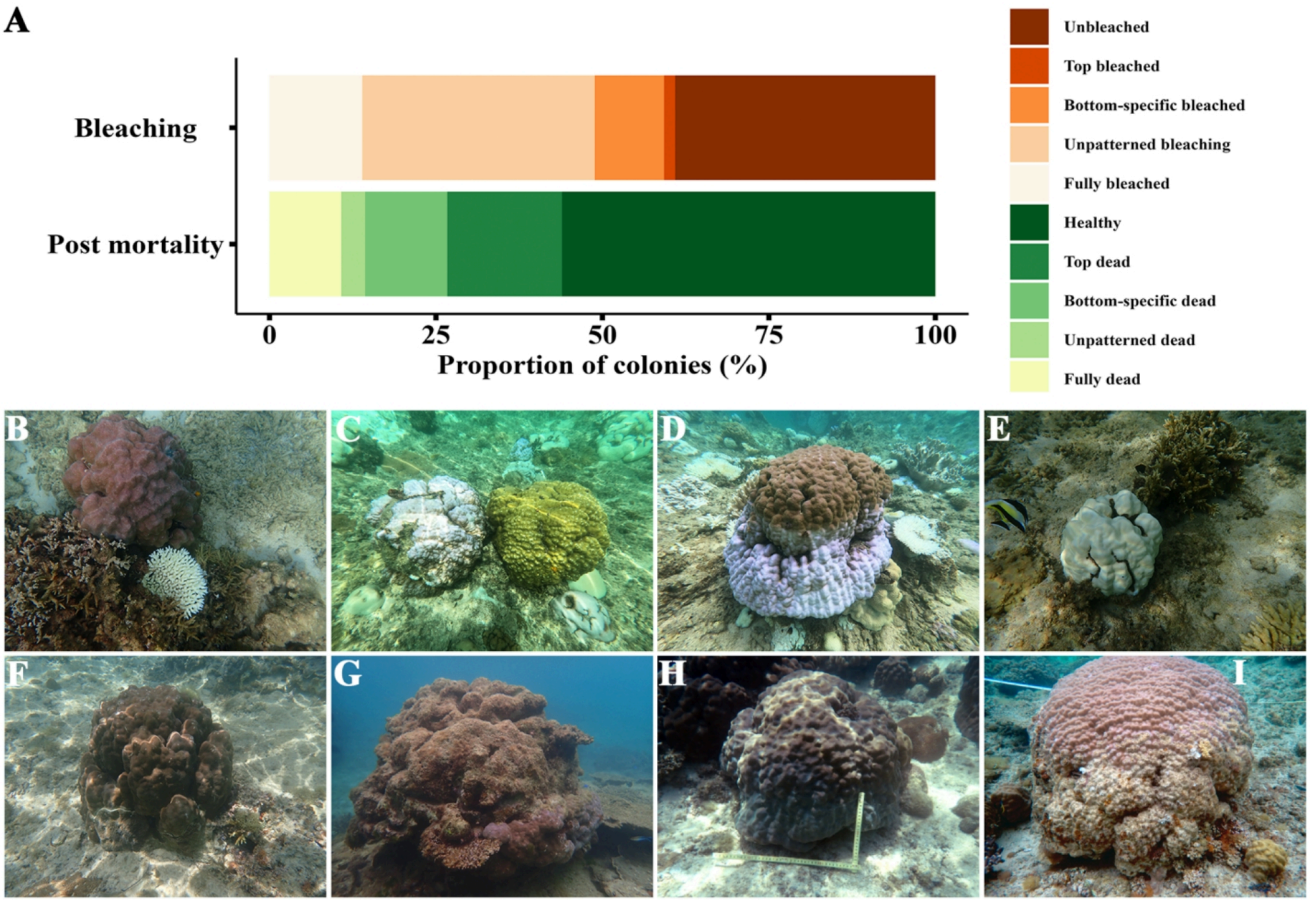


Figure 2

(A) Proportion of colonies exhibiting different bleaching and mortality patterns in massive *Porites*colonies during the bleaching and post-mortality surveys, (B) Healthy *Porites*colony at the peak of heat stress, (C) Top-specific bleaching (left) and a pale colony (right), (D) bottom-specific bleaching in a massive *Porites* colony. (E) Fully bleached colony. (F) Healthy *Porites*colony during the post-mortality survey. (G) Fully dead colony. (H) Recovered colony following bottom-specific bleaching, showing differences in coloration between the base and upper surfaces. (I) Partial mortality associated with bottom-specific bleaching; the basal portion of the colony is dead and overgrown with algae.

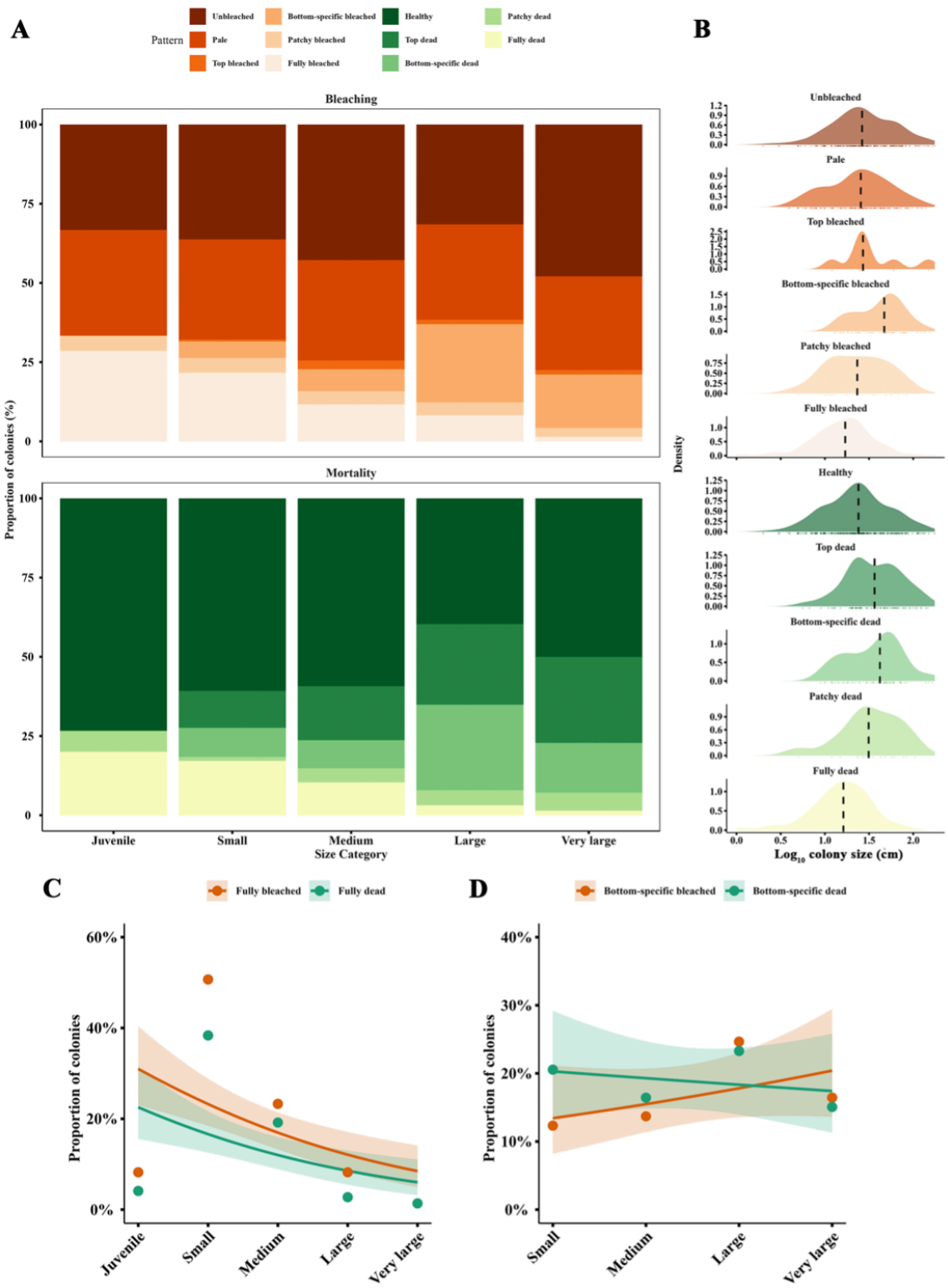


Figure 3

Colony size effects on bleaching and mortality patterns in massive *Porites*. (A) Proportional distribution of bleaching and mortality patterns across different size categories in massive *Porites* colonies. (B) Density distributions of log_{10}-transformed colony size for each bleaching (upper panels) and mortality (lower panels) patterns in massive *Porites* colonies (C) Relationship between colony size and probability of fully bleached/dead in massive *Porites* colonies. (D) Relationship between colony size and the

probability of bottom-specific bleaching/mortality patterns in massive *Porites* colonies. In panels (C-D), points indicate the proportion of colonies exhibiting each pattern within size categories, while solid lines represent predicted probabilities from binomial generalized linear models (GLMs) using continuous colony size with 95% confidence intervals.