Multi-scale observations during the 2024 mass coral bleaching event on Heron Reef, Australia

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Abstract

In the Austral summer of 2023–2024, the Great Barrier Reef, Australia, experienced a significant mass coral bleaching event, driven by record-setting sea surface temperature anomalies. This occurrence was part of the fourth recorded global coral bleaching event. A collaborative effort was initiated between researchers from different disciplines on Heron Reef (23°27'S, 151°55'E), to fill critical gaps in our understanding of how marine heatwaves influence corals across varied ecological and spatial scales. Coral bleaching was quantified using environmental and ecological data captured across three spatial scales: the reef, community, and individual colony level. Data were collected using satellite imagery, in situ ecological surveys, temperature loggers and manipulative experiments, conducted across multiple reef zones and depths. Bleaching responses were quantified primarily from 15 January to 31 May 2024. At the reef scale, satellite remote sensing revealed that 65% of the live coral area on the reef slope presented some level of bleaching. Both reef and community-scale analyses, including citizen science surveys, indicated that the windward east reef slope had the greatest bleaching impacts. Colony-scale investigations revealed finer-scale bleaching responses, such as overall reductions in growth rates across all sites and taxa, higher bleaching prevalence in hard carbonate substrate as opposed to rubble habitats, higher bleaching susceptibility in juvenile plate corals compared to branching and massive morphologies, and intra-specific variation in thermal stress response within a population of *Stylophora pistillata*. This multi-scale, cross-disciplinary approach provides insights into the variability of coral bleaching at different spatial scales and underscores the importance of collaboration and scale-appropriate monitoring to accurately quantify impacts and effectively inform reef managers.

Key words: coral bleaching, monitoring, thermal stress, ecological scales, spatial scales, collaboration

1. Introduction

Ocean warming due to anthropogenic climate change has significantly impacted marine ecosystems, especially coral reefs. In recent decades, an increasing frequency of heatwaves has resulted in widespread coral bleaching and mortality (Glynn 1996; Heron et al. 2016b; Sully et al. 2019; Hoegh-Guldberg et al. 2023; Reimer et al. 2024). Coral bleaching most often occurs when the relationship between coral hosts and their photosymbionts breaks down, leading to mortality if heat stress is severe and persistent (Hoegh-Guldberg 1999; Hughes et al. 2018a). The bleaching response varies depending on the duration and severity of temperature stress above the local thermal threshold (Liu et al. 2014b). The susceptibility and survival of corals are species-specific, influenced by factors including the identity of photosynthetic symbionts (Ulstrup et al. 2006; Sampayo et al. 2008), microbial communities (Ziegler et al. 2017; Peixoto et al. 2021), and host genetic factors (DeSalvo et al. 2010; Meyer et al. 2011; Fuller et al. 2020). Local environmental conditions and bleaching history also play a role (Oliver and Palumbi 2009; Guest et al. 2012; Brown et al. 2023b), whereby communities previously exposed to significant heat stress might develop 'ecological memory' which can mitigate or exacerbate future bleaching impacts (Hughes et al. 2019; Brown et al. 2023b). However, the degree to which corals can adapt to rapidly warming conditions is unknown. Furthermore, after degradation of coral reefs there is an increased generation of coral rubble that can further complicate recovery prospects depending on many biophysical drivers (Kenyon et al. 2024). While there will almost certainly be a general decline in coral cover under climate change, the future composition of coral reefs is difficult to predict, owing to the complex and variable nature of bleaching susceptibility and responses shaped by both biotic (e.g., community composition) and abiotic (e.g., temperature, salinity, UV exposure, depth, hydrodynamics) factors.

Coral bleaching responses are documented using various techniques, ranging from field surveys to aerial imaging across different spatial scales, from the polyp to ecosystem level (Hickey et al. 2020; Lutzenkirchen et al. 2024; Rivera-Sosa et al. 2025). Field studies often use in water surveys to track changes in benthic cover or bleaching severity in coral species or communities (Siebeck et al. 2006; Done et al. 2017; Knipp et al. 2020; Roelfsema et al. 2021b; Edmunds 2024). While field studies consider community- or colony-scale patterns, remote sensing provides broader reef-scale observations by detecting changes in sea surface temperature (Henson et al. 2010; Heron et al. 2016a) or visual signs of bleaching (Hughes et al. 2018c; Cantin et al. 2024). The Degree Heating Weeks (DHW) metric, derived from satellites, is often used to detect large-scale temperature anomalies (Berkelmans et al. 2004; Liu et al. 2014a; Skirving et al. 2020). Remote methods can also distinguish species-specific responses and potential acclimatisation (Hughes et al. 2018b; Drury et al. 2022). Both reef- and community-scale approaches help to clarify local reef conditions and health trends (Palandro et al. 2003; Hughes et al. 2018b). Data collected at various scales can improve predictive models that track bleaching risk (Liu et al. 2014b), predict the likelihood of future events (Teneva et al. 2012; Langlais et al. 2017; Mason et al. 2020) and identify bleaching refugia (Cheung et al. 2021; Bozec et al. 2025). Understanding coral reef responses and variations across spatial scales is crucial for developing effective conservation and intervention strategies (Morri et al. 2015; Cinner et al. 2018; Gouezo et al. 2021; Edmunds 2024).

Coral bleaching severity and extent varies across time and space, influenced by factors beyond DHW. Local conditions such as storm regimes, light availability, hydrodynamics, and turbidity can affect thermal stress and recovery dynamics (Brown et al. 2002; McClanahan et al. 2005; Brown et al. 2023c). It is challenging to disentangle these environmental and biotic influences and their relative contributions when monitoring bleaching events (Lesser and Slattery 2021). This is driven partly by the fact that studies usually focus on a specific scale (e.g., individual colonies, local communities, or regional ecosystems) which limits overlap among scales due to resource constraints. There is usually a trade-off between resolution and extent covered (Madin and Madin 2015). For instance, large reef systems like the Great Barrier Reef (GBR) have been monitored with substantial resources over long-term periods (Mellin et al. 2020; Emslie et al. 2024), yet less than 1% of the GBR is assessed at the community scale. During recent mass bleaching events (MBEs) on the GBR, reef-scale approaches were needed to rapidly determine bleaching extent over a wider area. While understanding finer-scale responses (e.g., identifying thermally tolerant or sensitive species) is critical to conservation and restoration decisions, reef-scale insights can inform larger scale predictive models that in turn scale up interventions. Integrating colony-scale processes with reef-scale patterns can therefore enhance our comprehension of a reef system's resilience and vulnerability.

In November 2023, the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch forecasted a potential MBE on the GBR. This fourth global bleaching event was confirmed in April 2024, following widespread bleaching in the Northern Hemisphere during the Boreal summer of 2023 and in the Southern Hemisphere during the Austral summer of 2023–2024 (Reimer et al. 2024). Like the MBEs on the GBR in 2016, 2017, 2020, and 2022, this event coincided with widespread above-average sea surface temperature (SST) anomalies, with average SST in 2024 setting a record for the GBR (Henley et al. 2024).

The November 2023 event triggered various scientists, each engaged in distinct, ongoing research on Heron Reef, to initiate a collaborative effort to share resources and monitor the 2024 bleaching event within the scope of their existing projects and resources. The aim was to investigate the bleaching response at different scales, from reef-scale (m-km resolution) to in-situ community- (cm-m resolution) and colony- (mm-cm resolution) scale surveys. Our specific objectives were to: 1) quantify and compare bleaching impacts across Heron Reef spatially and at varying ecological resolutions, and 2) examine the contribution of different resolutions to our understanding of coral bleaching responses. Our findings provide insights into the variability in reported bleaching outcomes at different spatial scales and underscores the importance of scale-appropriate monitoring and collaboration to accurately quantify impacts and effectively inform reef managers.

2. Methods

2.1 Study site

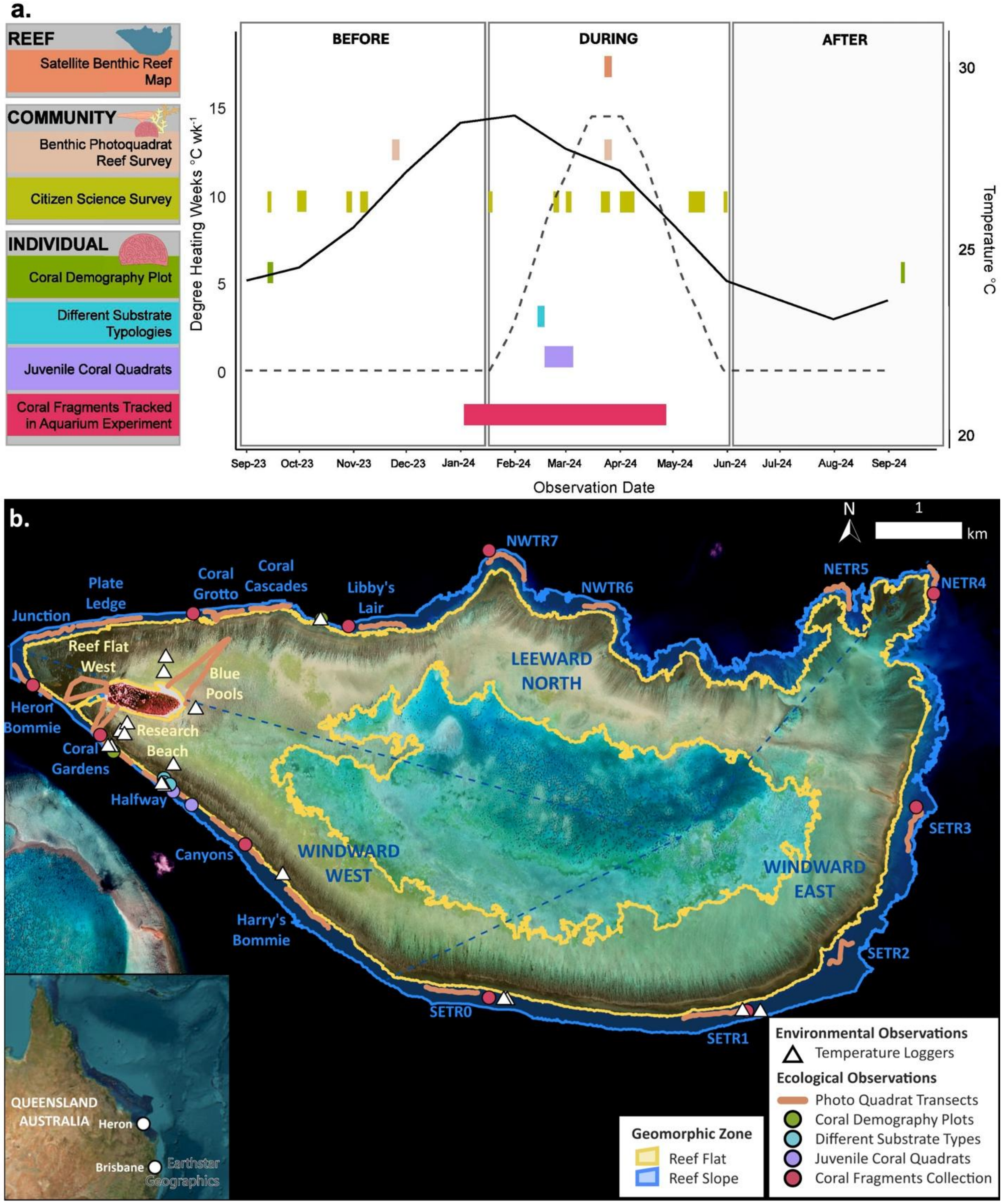
Heron Reef is an offshore platform reef in the Capricorn Bunker group of the Southern GBR (23°27'S, 151°55'E) located within the Sea Country of the Gooreng Gooreng, Gurang, Bailai, and Taribelang Bunda peoples. The reef covers approximately 27 km^2 and features a well-developed reef flat, crest, and slope with a relatively wide, shallow lagoon (Ahmad and Neil 1994). Heron Reef was chosen for this study as it has a history of various research projects and long-term monitoring by both scientists and citizen science organisations. Long-term monitoring has assessed the benthic composition annually at the reef scale since 2002, by combining satellite imagery and benthic photo quadrats (Roelfsema et al. 2018; Roelfsema et al. 2021b; Carrasco Rivera et al. 2025). For example, Brown et al. (2018, 2023a) has surveyed six sites along the reef slope since 2015, and Connell et al. (1997) has surveyed reef flat sites since 1964. Citizen science programs, Reef Check Australia (Salmond and Schubert 2023) and CoralWatch (Siebeck et al. 2006), have monitored Heron Reef since 2009, providing annual benthic composition and impact assessments across 16 sites.

The bleaching event in 2024, which included Heron Reef, impacted large parts of the GBR. The 2024 event marked the eighth mass coral bleaching event documented for the GBR since such occurrences were first recorded in the 1980s. Five MBEs have occurred in recent years: 2016, 2017, 2020, 2022 and 2024 (Berkelmans et al. 2004; Henley et al. 2024). During the 2016 and 2017 MBEs, Heron Reef experienced minimal bleaching (less than 10%; Hughes et al. 2017), since the region is typically cooled by the southeasterly trade winds and cyclonic activity (Hughes et al.

2019). In 2020, however, the region did not escape heat stress, with over 80% of branching *Acropora* colonies on the Heron Reef flat bleached because of a site-specific DHW value of 7.84 °C-wk (Ainsworth et al. 2021; Brown et al. 2023b). On the reef slope, the impact of the 2020 heatwave was comparatively lower, with an accumulation of DHW of 5.60 °C-wk, resulting in only 9% of branching *Acropora* colonies bleaching (Ainsworth et al. 2021; Brown et al. 2023b; Wasim et al. 2024). In 2022, 54% of monitored reefs in the southern GBR experienced bleaching (Emslie et al. 2024), but Heron Reef was not one of them.

2.2 Data collection overview

This study reports on bleaching-related observations from research conducted at different spatial scales and resolutions on Heron Reef (Figure 1). Coral bleaching datasets were collected and allocated to one of four geomorphic zones on Heron Reef, delineated by depth and wind exposure: leeward north slope, windward east slope, windward west slope (all 4–15 m depth) or the reef flat (1–2 m) (Figure 1b). These zones experience different predominant wind and tidal current directions and strengths and temperature regimes (Roelfsema et al. 2021a; Vercelloni et al. 2024). In this paper we predominantly report on observations made during the bleaching event, defined as beginning when thermal stress started to accumulate (i.e., DHWs >0 °C-wk) and ending when that thermal stress returned to 0, from 15 January to 31 May 2024. The few datasets that use data outside of this temporal range are temporally delineated as being collected either before or after the bleaching event.



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185 **Figure 1** Overview of data collection activities. Ecological scale and corresponding temporal range of activities
186 undertaken on Heron Reef across the 2024 mass bleaching event. Panel (a) shows a timeline of the seven studies
187 included in this paper, including the dates when each study was undertaken along with the corresponding mean daily
188 in-situ sea surface temperature (solid line) and degree heating weeks (dashed line; from NOAA Coral Reef Watch

2024). Panel (b) shows a map of Heron Reef and the locations of environmental and ecological observations for this paper within the leeward north slope, windward east slope, windward west slope (all 4–15 m depth) or the reef flat (1–2 m) geomorphic zones. Photo quadrat survey site names are also listed. The inset map indicates the position of Heron Reef within Queensland, Australia. Citizen science surveys conducted at sites across the western reef flat surrounding Heron Island and the reef slope are not depicted in the above figure. For data collection site coordinates and dates see Tables S1 and S2. Data collection sites are overlaid on a Planet Dove satellite image from 2 March 2024.

The analyses presented here are an opportunistic compilation of multiple datasets collected by different research teams who were already conducting various research projects at Heron Island Research Station (HIRS) prior to the 2024 bleaching event (Figure 1; Tables S1 and S2). Together, these datasets span three ecological scales: the reef, community, and colony (Figure 1a) and include environmental and ecological data. At the reef scale, bleaching observations were derived by integrating field data and Planet Dove satellite imagery to create a bleaching presence-absence map (Carrasco Rivera et al. 2025). At the community scale, benthic composition was assessed using geolocated photo quadrats (Roelfsema et al. 2018) and coral bleaching colour scores collected within all reef zones (Siebeck et al. 2006). Finally, at the colony scale we recorded growth of coral colonies, bleaching incidence of adult and juvenile colonies on varied substrates, and bleaching and survival of fragments collected for an aquaria-based experiment. This study focused on the observations at various scales during the bleaching event from January to May 2024, not on the before and after bleaching observations, which will be presented in subsequent works. In doing so, we centered the scope of this study on the importance of scale-appropriate monitoring and collaboration, supporting a streamlined and focused narrative. The two exceptions to this approach are the community-level CoralWatch study (Section 2.4.2), which requires before bleaching observations to provide context for the baseline coral colour score distributions on Heron Reef, as well as the colony-level coral demographics study (Section 2.4.3), which necessitated inclusion of data from 2022 to 2024 to demonstrate changes in colony growth and mortality over time. Soft corals were excluded from all analyses due to differing tolerances and physiological responses to thermal stress (Steinberg et al. 2022).

2.3 Temperature Data Collection and Evaluation

We recorded seawater temperatures at 10-to-60-minute intervals across multiple depth ranges (reef flat: 1–2 m, reef slope shallow: 4–8 m, and reef slope deep: 9–15 m) and the three exposure zones (windward east, windward west, and leeward north; Figure 1b). Data were collected between August 2023 and June 2024 using temperature loggers (ElectricBlue EnvLogger (version T7.3), Onset HOBO 64K Pendant (UA-001-64), Onset HOBO TidbiT MX (MX2203), and Dataflow Systems Odyssey loggers; Table S1). After retrieval, logger accuracy was validated by comparing logger-recorded temperature to a reference temperature for a 30-minute period, at 1-minute intervals. Data were adjusted to account for fine-scale variation between loggers (± 0.91 °C accuracy).

Coral reef temperature anomalies, or 'hotspots' (HS), are commonly determined using climatological baselines (i.e., the Maximum Monthly Mean - MMM) to identify periods of thermal stress (Liu et al. 2014a). The climatological MMM for Heron Reef is 27.3 °C (Weeks et al. 2008). Temperature anomalies were calculated from the collected temperature data using the U.S. NOAA Coral Reef Watch (CRW) methodology (Eakin et al. 2010); if T, representing the daily mean temperature, exceeded the region's coral bleaching threshold (MMM + 1 °C; 28.3 °C), then the MMM was subtracted from T:

$$HS_i = (T_i \geq MMM + 1° C) - MMM, HS_i \geq 0$$

Importantly, we did not use nighttime-only temperatures, as is done with NOAA CRW, and instead used 24 h mean temperatures, due to the diel variability across sites (Brown et al. 2023b). Thermal anomalies were then summed across a rolling 12-week (84-day) period to determine the extent of thermal stress in DHW (°C-wk):

$$DHW_i = \sum_{n=i-84}^{i} \left(\frac{HS_n}{7}\right), where\ HS_n \geq 1$$

Regional SST data from August 2023 to June 2024 were plotted against collected temperature data from Heron Reef using the NOAA CRW Virtual Stations product for the Southern GBR (v3.1), which includes the region from Hervey Bay to Mackay (NOAA Coral Reef Watch 2024).

2.4 Ecological data collection

As the resolution of collected data varies with scale, the bleaching metrics we present exhibit minor variability among scales. While we aim to utilise the metrics of 'bleached', 'partially bleached,' or 'not bleached' across scales, any differences in the definitions of these metrics between datasets are clarified below.

2.4.1 Reef scale

Bleaching extent at the reef scale was derived by integration of benthic composition field data with satellite imagery, using machine learning and object-based contextual editing. Benthic composition data were derived from georeferenced photo quadrats sampled in March 2024 using an established monitoring protocol (Roelfsema et al. 2021a; Carrasco Rivera et al. 2025). Our surveys were conducted along 21 transects on the reef flat (~2 m depth) and slope (~5 m depth) of Heron Reef. These included 8 sites on the leeward north slope, 5 on both the windward east and west slopes, and 3 sites on the reef flat. Each transect was between 100 and 600 m in length (Figure 1b) and was surveyed while snorkelling on the reef flat and on SCUBA on the reef slope, while towing a GPS to log the position. Each photo quadrat captured approximately 1 m^2 of the seabed and was spaced roughly 2–4 m apart. Benthic composition was derived from the photo quadrats using a trained machine learning model in ReefCloud (AIMS 2024; see Table S3). Within ReefCloud, 50 random points were overlaid onto each photo quadrat, which were assigned a benthic classification by the machine (see Table S3; Roelfsema et al. 2021). The machine was trained manually until a high model validation score was achieved (F1 > 0.8). Training points were only annotated as bleached if the coral was distinctly white or fluorescent, to avoid model confusion between bleaching and healthy pale morphs.

The benthic composition from each photo was used to derive mapping classes that include 'Coral', 'Algae', 'Algae/Coral', 'Rock', 'Rock/Coral', 'Sand', 'Sand/Coral', and 'Mixed' benthic types. The 'Coral' class (where live coral cover is ≥30%) was further classified into three levels of bleaching: >50% of coral bleached, 10-50% of coral bleached, and <10% of coral bleached. Calibration (80%) and validation (20%) datasets were derived from the field dataset and resampled to ensure representation across the benthic classes.

A cloud free, atmospherically corrected, and multispectral Planet Dove satellite image with a 3 x 3 m pixel resolution was acquired from the 2nd of March 2024. The calibration dataset was used to train a Random Forest classifier on the overlaid satellite image, and this was followed by an automated contextual editing routine (Lyons et al. 2020; Lyons et al. 2024; Carrasco Rivera et al. 2025). The benthic classes were mapped for the reef slope of Heron Reef limited to 10 m depth. Classes cannot be accurately differentiated at deeper depths. Finally, using the validation dataset, a confusion matrix was created to determine the accuracy of the mapped distribution of 'Coral' and respective bleaching levels (Congalton and Green 2008). We did not map the entire extent of the reef because there was no consistent field data for other geomorphic zones such as the lagoon, reef flat, and forereef.

2.4.2 Community scale

Bleaching response within benthic communities on the reef flat and slope

Bleaching was investigated at the community scale using benthic composition determined from the same photo quadrats taken along 21 transects (Figure 1b) in March 2024 (Section 2.4.1) and analysed within R Statistical Software (v4.4.2; R Core Team 2024) using the 'tidyverse' (v2.0.0; Wickham et al. 2019) and 'ggplot2' R packages (v3.5.1; Wickham 2016). For each site, we calculated both the mean total live hard coral cover (%) and relative percentage of live hard coral cover that was bleached and not bleached (%) from each quadrat and associated standard error.

The coral bleaching data were further aggregated into three morphotype classifications: 'branching', 'massive', and 'plate/encrusting' (Table S3). Corals exhibiting plate or encrusting morphologies could not be categorised separately within our dataset as some genera often display both traits concurrently. Solitary corals were excluded from this comparison of morphotypes as they did not fall into one of these categories and had low occurrence. We calculated both the mean total live hard coral cover (%) and relative percentage of live hard coral cover that was bleached and not bleached (%) and associated standard error for each of these morphotypes in each zone (averaged across all quadrats in a site, and then for all sites in a zone). As we did not model the data, we are not able to account for spatial autocorrelation of our nested sample design when pooling multiple sites across a zone. To test whether bleaching prevalence differed significantly among coral morphologies, chi-squared tests were applied separately for each zone using the ‘stats’ package in R (v4.3.2; R Core Team 2024).

Bleaching indicated by CoralWatch colour scores in different reef zones

The CoralWatch Coral Health Chart (Siebeck et al. 2006) was used to quantify bleaching severity during random surveys conducted on the leeward north, windward west, windward east, and reef flat zones. The chart employs a standardised six-point colour saturation scale to measure coral health, where lower colour scores indicate reduced symbiont density and chlorophyll *a* content, representing a potentially bleached state (Siebeck et al. 2006). This method has been used to collect 17% of all globally accessible bleaching field data (Carrasco Rivera et al. 2025). From 1 September 2023 to 31 May 2024, a total of 167 surveys were conducted at 30 sites on Heron Reef to monitor changes in coral colour before and during the 2024 bleaching event. Observations were recorded from 12 sites in both the leeward north and reef flat zones, 4 sites in the windward east, and 6 sites in the windward west (Figure 1b). Each survey included an average of 20 observations (1 observation = 1 individual coral colony measured), resulting in the assessment of 3,343 coral colonies throughout the survey period. The surveys followed a random transect protocol and were carried out by CoralWatch ambassadors, citizen scientists, school groups, and researchers. Observations were collected during surveys via reef walks (number of colonies observed = 1,196), by SCUBA at depths of 5–7 m (n = 1,051), and by snorkelling at depths of <5 m (n = 1,096). Due to differing susceptibility to bleaching, 217 observations of soft corals were excluded from the analysis. A chi-squared test was employed to assess the differences in the frequency distribution of colour scores across the four zones before and during the bleaching event using the ‘stats’ package in R.

2.4.3 Colony scale

Growth and survival of colonies in coral demography plots

Data were collected in September 2022, 2023, and 2024 at two sites (Coral Gardens, on the windward west slope, and Libby’s Lair, on the leeward north slope; Figure 1b) to assess changes in coral demography rates (growth, survival, and recruitment) due to the bleaching event. Whilst we were unable to demonstrate the effect of bleaching experienced by individual colonies during the bleaching event, we measured the size (2D planar area of live tissue) of tracked colonies and recorded total mortality across our permanent coral plots (at 6–8 m water depth) before (September 2022 to September 2023) and after (September 2023 to September 2024) the MBE. We had 9 permanent plots at Libby’s Lair and 5 at Coral Gardens (Table S7). Our methods for assessing coral demography are shown in Figure S1, but briefly, we took scaled photographs of all living individuals (following Cant et al. 2023) to measure coral size. Any new colonies that recruited into the permanent plots were assigned an ID and photographed. From the scaled images, we manually outlined the area of living coral tissue on each coral colony, following the SizeExtractR protocol (Lachs et al. 2022) on ImageJ (Schneider et al. 2012). Where partial mortality occurred, parts of a tracked colony might have no live coral tissue or were overgrown by other organisms. In these instances, only parts of the colony with live coral tissue were outlined and the area measured. Tracked coral colonies that were either missing or had no living tissue were considered dead and contributed to total mortality.

Changes in 2D planar live tissue area between 2022-2023 and 2023-2024 demonstrated the growth or shrinkage (partial mortality) of coral colonies before and after bleaching, respectively. For all living corals, growth was defined as the change in 2D planar area from one survey year to the next. Specifically, we calculated ratios of coral size for both time periods (the period after bleaching and the period before), to determine growth by dividing the new size (colony size at current year) by the old size (colony size at previous year). We then took $\log_2$ of each ratio: $\log_2(\frac{new\ size}{old\ size})$. Log_2 of the size ratio is intuitive: no change in coral size gives 0 (i.e., $\log_2(1) = 0$), doubling in coral size gives 1 (i.e., $\log_2(2) = 1$), and halving in size gives -1 (i.e., $\log_2\left(\frac{1}{2}\right) = -1$). We performed the Wilcoxon rank sum test to assess whether growth (the $\log_2$ size ratio) differed before and after the bleaching event for all corals pooled across Coral Gardens and Libby's Lair. We further investigated if the $\log_2$ size ratio between the two sites, and among the most abundant taxa (*Acropora, Montipora,* Merulinidae, and Pocilloporidae; Table S4), differed before and after the bleaching event using the Kruskal-Wallis rank sum test and the post-hoc Dunn's test. For each site or taxon, we also examined the mortality rates before (number of dead coral colonies in September 2023) and after (number of dead colonies in September 2024) the bleaching event. We tested if mortality was different before or after bleaching for both sites and across the four common taxa using the Cochran-Mantel-Haenszel test and then calculated the conditional odds ratios for each site and taxon using the R package 'samplesizeCMH' (Egeler 2023).

Bleaching incidence of adult colonies in different substrate typologies

Various rubble bed types were assessed because rubble is predicted to increase in cover in the future (Kenyon et al. 2023a), and rubble of different typologies can lead to varying levels of coral recovery (Kenyon et al. 2024). This project originally aimed to assess how coral survival differs between rubble beds of varying levels of stability and stable hard carbonate reef, based on the fact that rubble instability can increase coral mortality (Brown and Dunne 1988; Fox and Caldwell 2006). Since little research exists on coral responses to bleaching within rubble bed environments, especially under varying substrate conditions, this was an opportunity to examine how corals across different substrate types respond to thermal stress, particularly as climate change increases both the frequency of bleaching events and production of rubble.

In February 2023, on the windward west slope of Heron Reef, at a site known as Halfway, we established 8 experimental plots, each within a boundary of 5 m x 5 m, across three substrate typologies: loose rubble beds (n = 3 plots), interlocked rubble beds (n = 3 plots), and hard carbonate reef (n = 2 plots). All these plots were situated at a depth of 8–10 m and on the same aspect of the reef within a 400 m range (Figure 1b). Therefore, we assume that corals present in each substrate experience similar hydrodynamic activity, temperatures, and light, limiting confounding factors. Temperature data were also collected from one plot per substrate type as per the methods outlined in Section 2.3 (Figure S2). Within each plot, 1 m^2 permanent quadrats were established and every hard coral colony within each quadrat was tagged with a unique ID tag, photographed, and measured in situ via SCUBA, for a total of 400 tagged colonies. For each coral present, we noted the percentage of living, dead, and bleached tissue per colony during the in situ visual assessments. Colonies were then classified as either living (100% unbleached tissue), dead (100% mortality), or bleached (any proportion of bleached tissue). Tagged corals were re-measured in November 2023, February 2024, and June 2024, but only data from the bleaching event (February 2024) is presented here.

While coral species composition is unlikely to change dramatically within a 400 m range (Salmond et al. 2019), we used a PERMANOVA with log+1 transformed data and a Bray-Curtis resemblance matrix to assess differences in coral morphologies (branching, encrusting, massive, and plating) between substrates, thus accounting for bleaching susceptibility driven by community differences. To determine how the proportion of bleached corals (part or all bleached) and unbleached corals differed between substrate types, a generalised mixed-effects model ('glmmTMB' package in R) was used with a binomial error structure and 'site' as a random effect (Brooks et al. 2017). Dead colonies were excluded from this analysis.

Bleaching incidence of juvenile colonies of different coral morphologies

In February 2023, two sites were selected at depths of 8-–0 m on the windward west slope in hard carbonate dominated areas, to track the natural survival of juvenile corals (defined as coral colonies <10 cm maximum diameter) in situ (Figure 1b). Permanent benthic quadrats (0.5 x 0.5 m, n = 10) were established at each site and given a unique ID tag. Every three months from February 2023 to June 2024, all juvenile corals present within each quadrat were mapped and measured using SCUBA, noting the coral's morphology (based on classifications in Roelfsema et al. 2021a) and tissue condition (percentage of tissue alive, dead, or bleached). We present the number of bleached (either fully or partially bleached), dead, unbleached, and missing individuals (those that could not be located within the quadrat at the time of the assessment) for each morphological type. Only data from the bleaching event (February 2024) are presented here. The difference in bleaching incidence between coral morphologies was assessed using a Pearson's chi-squared test with the 'stats' R package.

Survival and bleaching of coral fragments tracked during a common garden experiment

A common garden experiment was conducted at the HIRS to assess thermal susceptibility differences within a coral species during a bleaching event. Eighty colonies of *Stylophora pistillata* corals from 10 reef slope sites (Figure 1b) were fragmented into 5 cm² nubbins (total of 240 nubbins) between 3 February to 5 February 2024. Sampling followed depth transects (5–12 m) and colonies were selected irrespective of their bleaching status, at least 3 meters apart. Within two hours of collection, coral nubbins were glued onto labelled aragonite substrates and placed in experimental tanks. The experimental setup consisted of a semi-flow-through system with two outdoor aquarium tables shaded with neutral density shade cloth. Heron Island Research Station maintains a continuous seawater flow-through system, pumping seawater (from a depth of ~15 m in the Heron-Wistari channel at a rate of ~11 L/s) throughout the HIRS experimental facilities. We placed three sumps onto each table, which were continuously fed seawater (flow rate of 0.2 L/s), filtered for large particles, and each contained a 1500 L/hour pump. Each sump fed into two 70 L aquarium tanks (flow rate of 0.04 L/s) and each tank included a 2500 L/h wave maker. The tanks drained back into the sump, and the sumps drained onto the holding tables and back to the reef. We did not control the temperature, such that the temperature profile reflected the conditions where the seawater was sourced from, including diel fluctuations (Figure S3). We monitored temperature in the tanks using HOBO loggers (HOBO Pendant MX Temperature/Light Data Logger MX2202) and found no significant differences in temperature profiles among tanks over the course of the experiment. The experiment lasted 12 weeks, between 3 February to 27 April 2024. Once a week, we measured the survival, bleaching status, percentage of bleaching, and colour score for each fragment. Survival was categorised as 'alive', 'dead' (no polyp visible and/or fragment covered by algae), or 'partially dead' (only parts of the coral fragment dead). Bleaching status was recorded as 'not bleached', 'partially bleached' (only part of the fragment was completely bleached), or 'fully bleached' (entire fragment was completely bleached). The percentage of bleaching was visually quantified as the area of the fragment that was completely bleached. The colour score was visually selected based on the closest match to the CoralWatch Coral Health Chart (Siebeck et al. 2006).

3. Results

3.1 Temperature observations

Mean daily (24-hour) seawater temperatures began to rise in October 2023 and peaked toward the end of the Austral summer in February 2024. The highest mean daily temperatures were recorded in this month at the windward east shallow (28.82 °C) and deep slopes (29.03 °C), and on the reef flat (30.18 °C). Mean daily temperatures on the leeward north deep slopes peaked in January at 28.78 °C, as did temperatures on the windward west shallow (28.77 °C) and deep (28.99 °C) slopes (Figure 2). Regional SSTs for the Southern GBR tended to be slightly higher (by 0.9–1.2 °C on average) than the mean daily temperatures recorded in situ at Heron Reef, likely due to spatial differences and/or their greater depth below the sea surface. Mean daily temperature obscures tidal fluctuations, which are greater on the reef flat than the reef slope. On the reef flat, the maximum mean hourly temperature of 32.3 °C, and highest temperature record of 35.2 °C were both recorded in February. The maximum hourly temperature recorded on the reef slope was 29.6 °C, at the windward west deep slope in the same month.

Heat stress began to accumulate at Heron Reef in mid-January 2024. The lowest maximum DHW value was recorded for the leeward north slope deep sites at 5.23 °C-wk. These leeward north deep sites experienced lower heat stress than the deep sites on the windward west slope (8.69 °C-wk) and the windward east slope (9.66 °C-wk). The shallow slope sites on the windward side experienced less heat stress than their deeper counterparts (shallow west: 5.42 °C-wk; shallow east: 6.9 °C-wk). The highest heat stress was experienced on the reef flat at 12.13 °C-wk. Additionally, the heat stress associated with regional SSTs peaked at 14.57 °C-wk, which is slightly higher than the DHW reported for any specific Heron Reef sites (Figure 2).

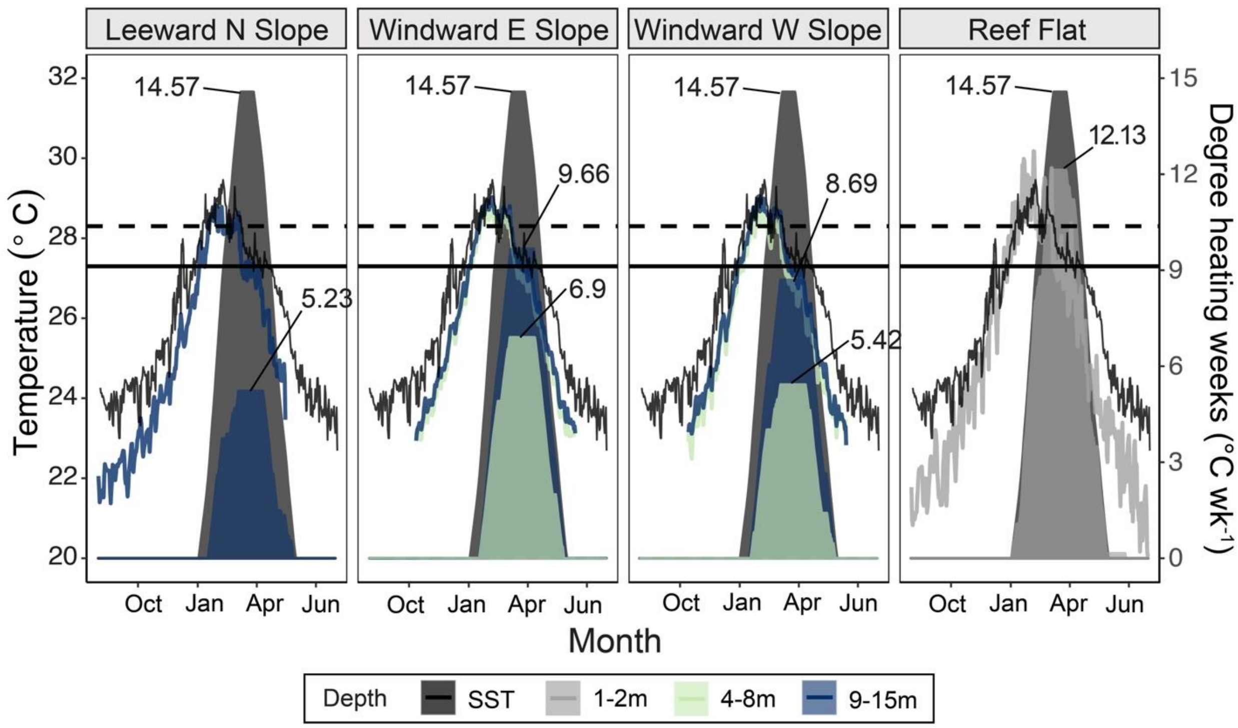


Figure 2 Seawater temperature and degree heating weeks (DHW) across Heron Reef (August 2023 - July 2024) during the 2024 marine heatwave. From left to right, seawater temperatures (°C) and DHW (°C-wk) for the leeward north reef slope, windward east slope, windward west slope, and the reef flat. Solid lines represent mean daily (24-hour) temperatures, where DHW profiles are indicated by shading and DHW maximums are labelled. The solid horizontal line indicates the region's climatological maximum monthly mean (MMM; 27.3 °C), and the dashed horizontal line indicates the region's coral bleaching threshold (MMM+1 °C; 28.3 °C). Satellite derived sea surface temperature (SST) data are from the NOAA CRW Virtual Stations, southern GBR region v3.1.

3.2 Ecological observations

3.2.1 Reef scale

Significant bleaching responses from the 2024 bleaching event were observed on the reef slope through the analysis of satellite imagery. The total mapped area was 3.6 km², of which 1.61 km² (44%) was classified as live coral (Figure 3). Of the live coral pixels (defined as pixels where live coral cover ≥30%), 43% (0.69 km²) presented over 50% bleaching, 22% (0.36 km²) displayed 10–50% bleaching, while the remaining 35% (0.56 km²) showed less than 10% bleaching. Thus, a total of 65% (1.05 km²) of the living coral pixels were bleached to some degree. At the within-geomorphic zone level, the windward east slope displayed the highest level of living coral pixels with bleaching, where 74% of the living coral pixels presented some level of bleaching, compared to the windward west and leeward north slopes with 70% and 58%, respectively. The mapped accuracy of the living coral class area was

68%, and for the bleaching levels of >50%, 10-50%, and <10%, the accuracies were 54%, 62%, and 51%, respectively.

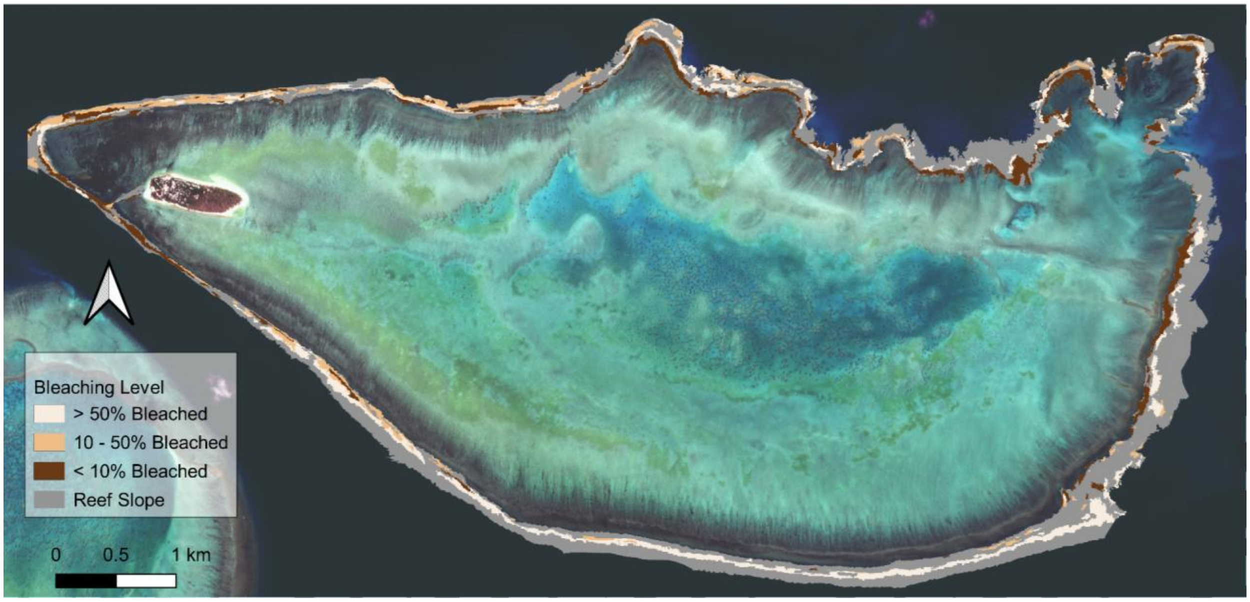


Figure 3 Distribution of live coral (where live coral cover is ≥30%) on the Heron reef slope. Mapped classes display the level of bleaching (>50% bleached; 10-50% bleached; <10% bleached) during the bleaching event in March 2024. The grey area represents the extent of the reef slope geomorphic zone. The classified live coral area is overlaid on the Planet Dove satellite image from 2 March 2024, used for the mapping via remote sensing.

3.2.2 Community scale

Bleaching response within benthic communities on the reef flat and slope

Varied coral bleaching responses across sites and morphologies were revealed by the geolocated photo quadrat surveys. Across the entire study area, hard corals made up an average of 35.4% (± 3.21 SE) of the total benthic cover. A mean of 37.9% (± 2.85 SE) of this hard coral was bleached. Hard coral cover was higher on all sides of the reef slope (40.8% ± 4.76, 26.6% ± 2.33, and 46.0% ± 5.41 for leeward north, windward east, and windward west zones, respectively) than on the reef flat (17.9% ± 6.56). The relative percentage of bleaching was also higher on the reef slope (40.0% ± 2.53, 49.2% ± 6.2, and 37.4% ± 4.76 for leeward north, windward east, and windward west zones, respectively) compared to the reef flat (17.2% ± 5.75).

While the mean hard coral cover on the slope generally decreased toward the windward east corner of the reef platform, the relative percentage of bleaching increased (Figure 4). The percentage of bleached coral cover was high across the entire windward east slope, peaking at Southeast Transect 1 (SETR1; 60.8% ± 1.88) and Southeast Transect 0 (SETR0; 58.8% ± 1.73), which were also the highest values across all sites. Coral Gardens had the lowest percentage of bleached coral cover of any site on the reef slope (22.2% ± 1.75), while the lowest bleaching percentage on the reef flat was observed at Reef Flat West (RFWest; 5.99% ± 0.76).

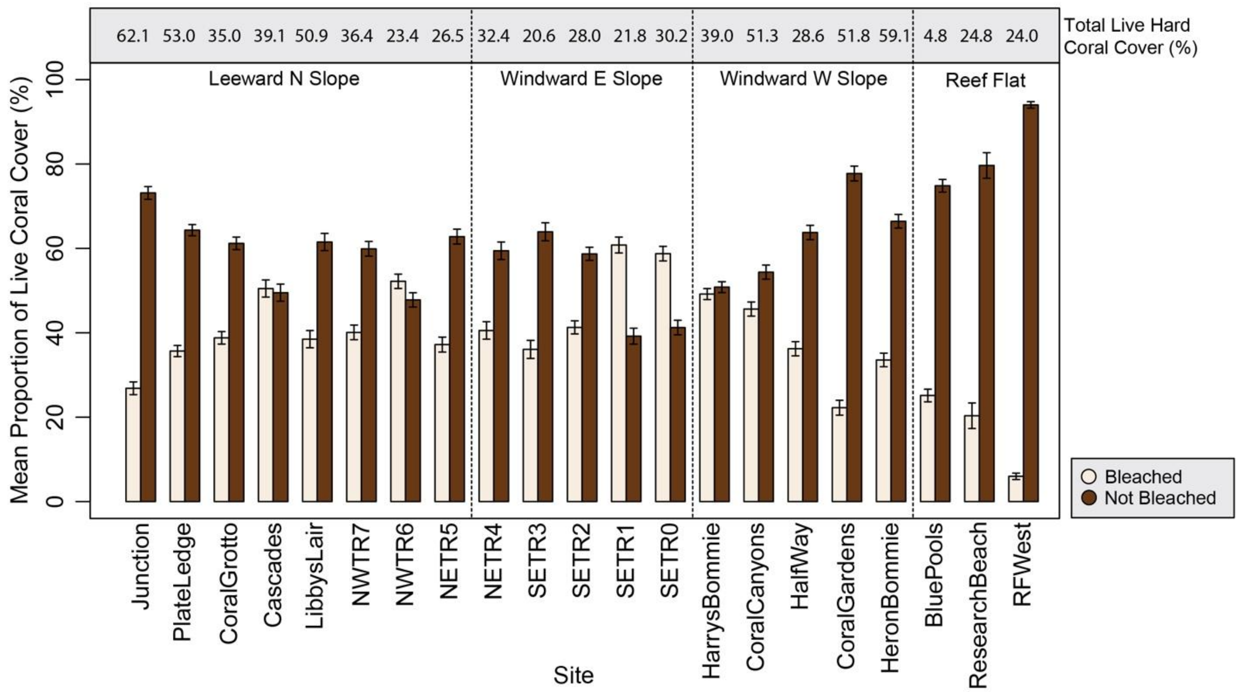


Figure 4 Mean relative percentage of live hard coral cover (% ± standard error) that was bleached (beige) and not bleached (brown) per photo quadrat transect/site on Heron Reef in March 2024. The total live hard coral cover for each site is noted in the grey box across the top of the plot and further detailed in Figure S4. Sites are organised by geomorphic zone, where sites on the slope were surveyed at ~5 m depth and on the reef flat at 1–2 m depth. Refer to Figure 1b and Table S2 for the location of each site.

Prior to the bleaching event, branching corals were the dominant morphology in all zones (31.19% ± 3.90, 26.27% ± 3.90, and 13.31% ± 3.90 for the windward west slope, leeward north slope, and reef flat, respectively) except the windward east slope, which consisted of relatively low cover of both plate/encrusting and branching morphotypes (12.30% ± 3.20 and 10.81% ± 3.90, respectively; Figure S4). Bleaching prevalence differed significantly among morphologies within each zone (Leeward N Slope: $\chi^2 = 5553.0$, df = 3, p-value < 0.001; Reef Flat: $\chi^2 = 86.5$, df = 3, p-value < 0.001; Windward E Slope: $\chi^2 = 5415.7$, df = 3, p-value < 0.001; Windward W Slope: $\chi^2 = 5751.4$, df = 3, p-value < 0.001). The lowest percentage of bleaching for any morphotype was observed for branching corals on the reef flat (11.15% ± 1.55; Figure 5). Massive corals were most affected by bleaching on the leeward north slope, windward east slope, and reef flat (58.10% ± 0.64, 63.14% ± 0.62, and 12.19% ± 0.66 bleaching, respectively; Figure 5). On the windward west slope, plate/encrusting corals experienced the highest percentage of bleaching (54.69% ± 1.57; Figure 5c).

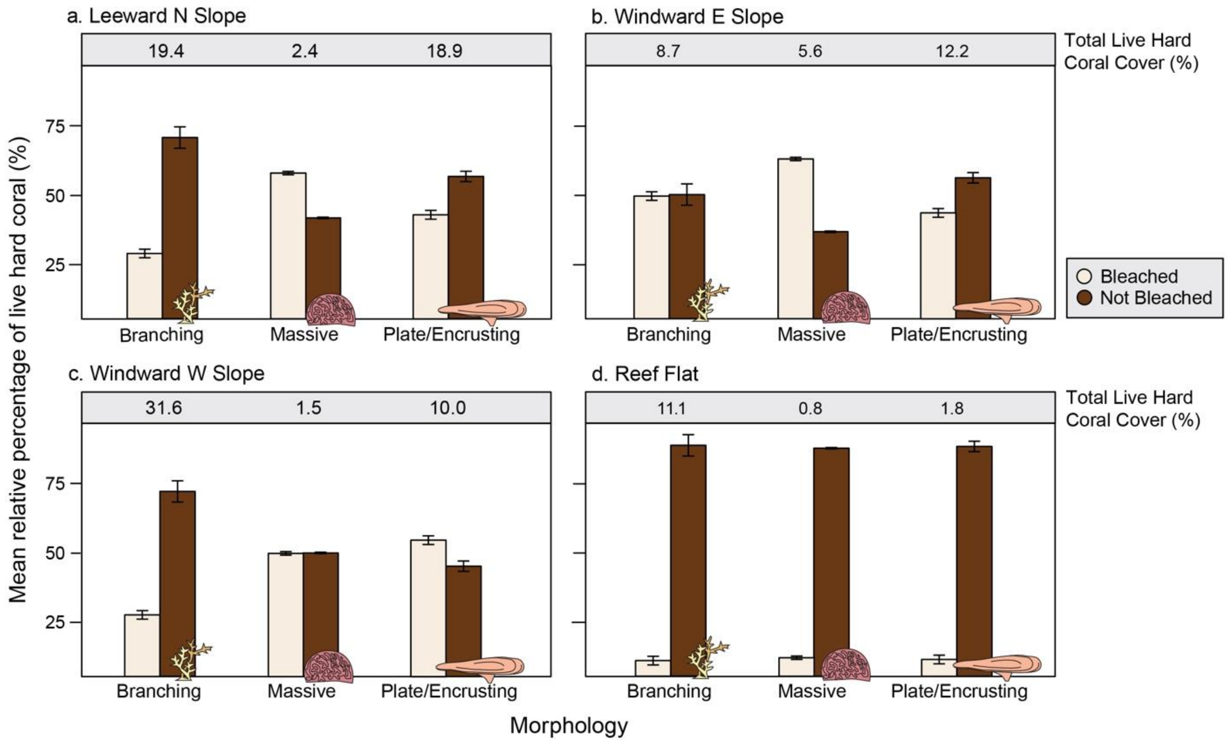


Figure 5 Mean relative percentage of live hard corals (% ± standard error) that were bleached (beige) and not bleached (brown) for three hard coral morphotypes (branching, massive, plate/encrusting), within each of four geomorphic zones (panels a-d) on Heron Reef in March 2024. The total live hard coral cover for each morphotype is noted in the grey box across the top of each plot. The slope was surveyed at ~5 m depth and the reef flat at 1–2 m depth. Refer to Figure 1b for the location of each zone.

Bleaching indicated by CoralWatch colour scores in different reef zones

During the bleaching event, bleaching was observed in 49 of the 93 surveys (52% of surveys), in which >20% of the hard corals surveyed had a colour score of 1 (Figure 6). Whilst a statistically significant difference was found in the frequency distribution of colour scores before and during the bleaching event across all zones (p-value <0.001; Table S6), the magnitude of this difference varied between zones. The most dramatic increase in bleaching was observed in the windward east, where there was a 36% increase in the number of colonies that were bleached (colour score of 1). The leeward north and windward west zones experienced similar increases in bleached corals with an increase of 22% and 21%, respectively.

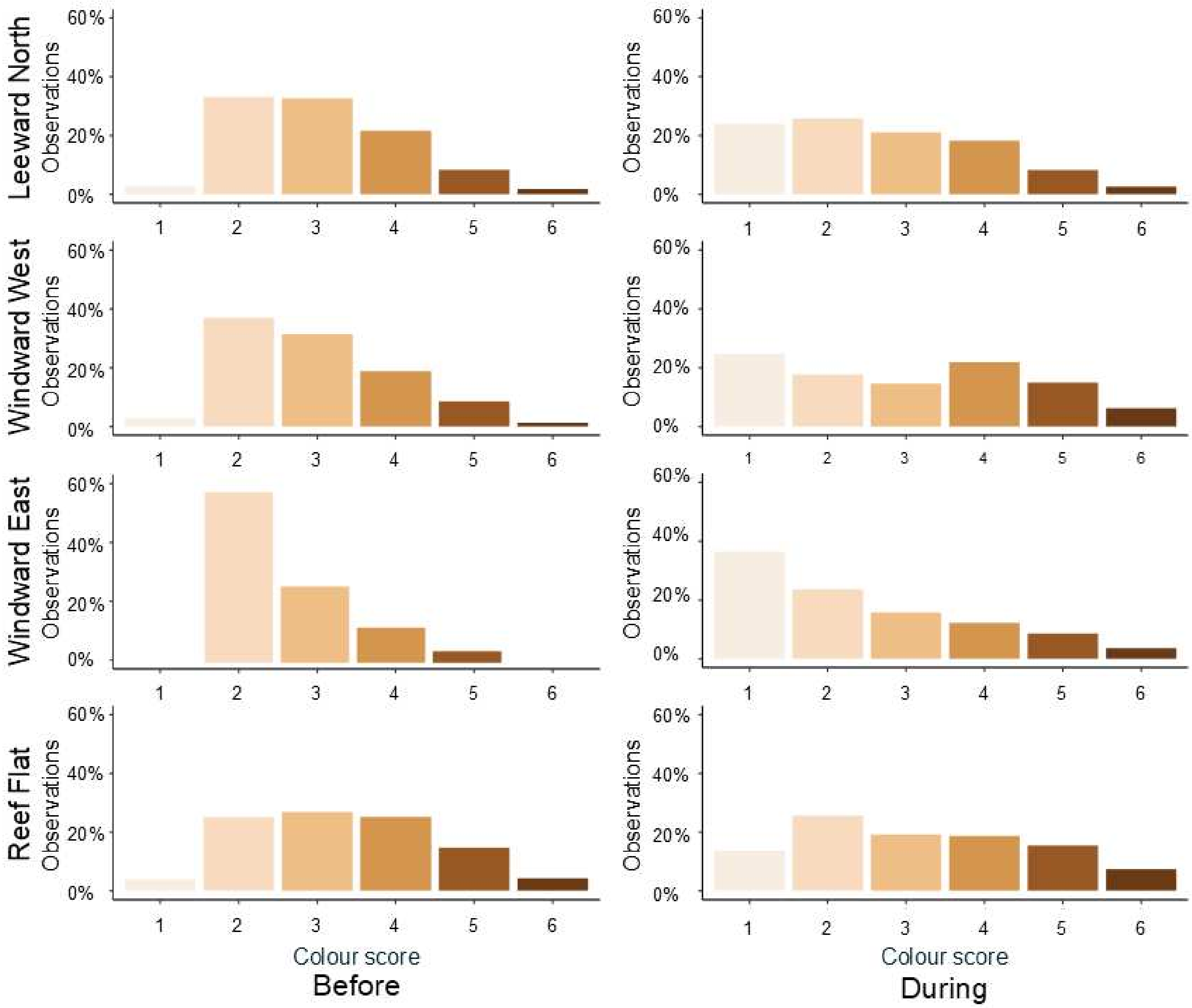


Figure 6 Frequency distribution of CoralWatch coral colour scores from surveys conducted before (1 September 2023 - 14 January 2024) and during (15 January 2024 - 31 May 2024) the 2024 bleaching event across four geomorphic zones of Heron Reef.

3.2.3 Colony scale

Growth and survival of colonies in coral demography plots pre- and post-bleaching

Colony growth ($\log_2$ coral size ratio) differed before and after bleaching, but there was no difference between the two sites nor among the four taxa. Before the 2024 bleaching event (2022-2023), most corals across Coral Gardens (windward west slope) and Libby's Lair (leeward north slope) grew (positive $\log_2$ coral size ratio), with median $\log_2$ size ratio greater than 0 (Figure 7a; Coral Gardens = 0.135 and Libby's Lair = 0.068). However, these changes in size were not significantly different between the two sites (K-W $\chi^2 = 0.42$, df = 1, p-value = 0.52). After the bleaching event (2023-2024), corals reduced in 2D planar area or experienced partial mortality, evidenced by a general decrease in $\log_2$ size ratio. The median $\log_2$ size ratios for both sites were negative (Figure 7a; Coral Gardens = -0.237 and Libby's Lair = -0.399), and not significantly different across the two sites (K-W $\chi^2 = 0.0013$, df = 1, p-value = 0.97). The overall reduction in $\log_2$ coral size ratio after bleaching, however, meant that growth rates were significantly different to those before bleaching (Wilcoxon W = 20842, p-value < 0.001). All four focal taxa except for Merulinids grew before bleaching (Figure 7b; Table S7). Taxa did not differ significantly in their growth rates before bleaching (K-W $\chi^2 = 6.91$, df = 3, p-value = 0.08; Table S8). After the bleaching event, all taxa decreased in size, as exhibited by negative median $\log_2$ size ratios, and there were no significant differences across taxa (Figure 7b, Table S7; K-W $\chi^2 = 1.70$, df = 3, p-value = 0.64).

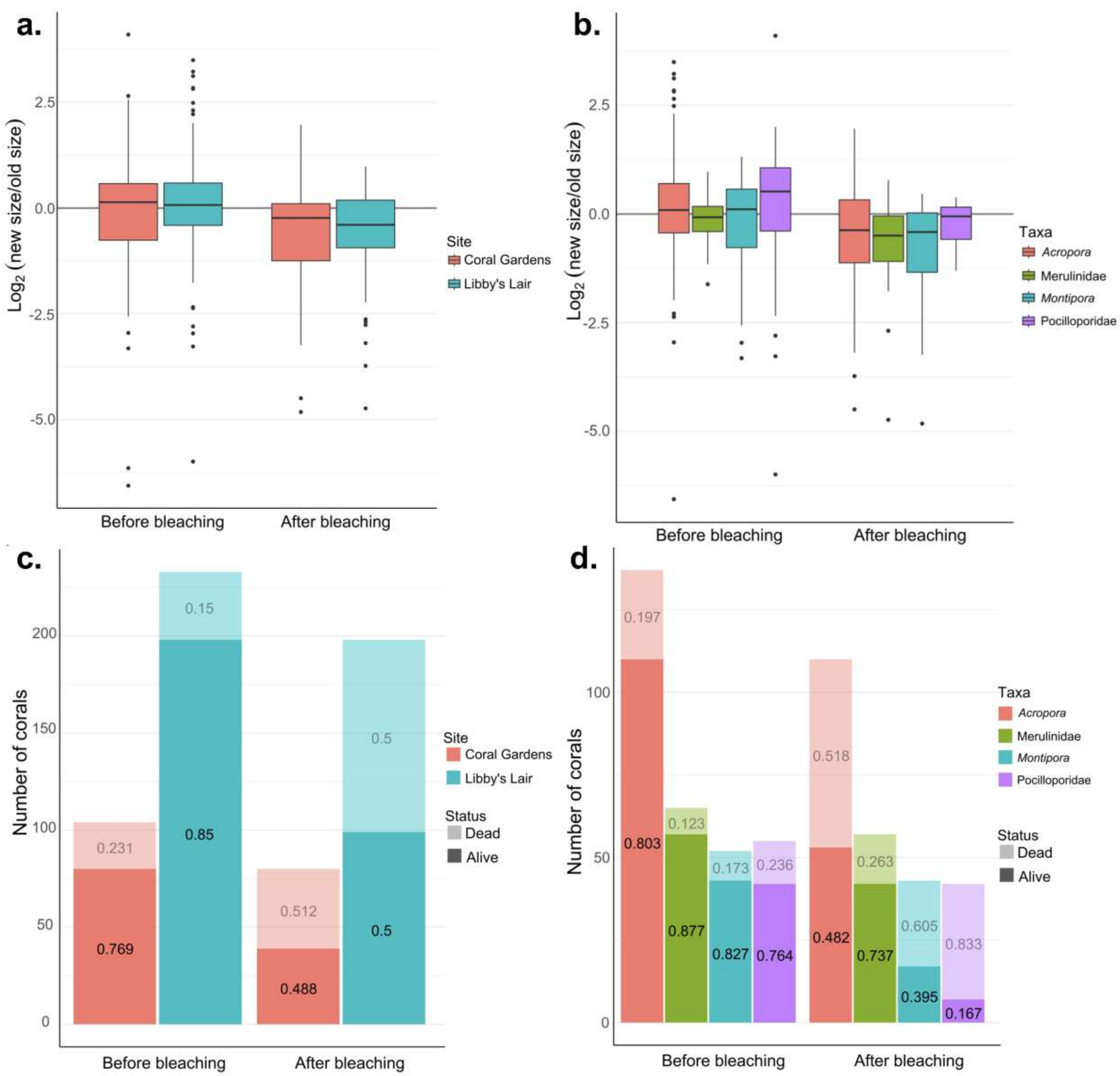


Figure 7 $\log_2$ coral size ratio (a and b) and numbers of corals that were dead or alive (c and d) before (September 2022-2023) and after bleaching (September 2023-2024). Panels (a) and (b): coral growth was calculated by taking the $\log_2$ of the coral size ratio. A $\log_2$ size ratio of 0 indicates no change in coral size ($\log_2(1) = 0$), a 1 demonstrates doubling in size ($\log_2(2) = 1$), and -1 indicates halving in size ($\log_2(1/2) = -1$). Boxplots show Q1, median, and Q3. The length of the whiskers are 1.5 times the interquartile range and the dots indicate outliers. Data were averaged

across sites: Coral Gardens (windward west slope) and Libby's Lair (leeward north slope. Panels (c) and (d): the number of corals that were alive (solid fill) and dead (transparent fill) at each sampling period. The numbers within each bar are the proportion of the total number of corals that were either alive or dead. Data are grouped by the four main taxa: *Acropora*, Merulinidae, *Montipora,* and Pocilloporidae.

Mortality increased dramatically across sites and for all taxa after the bleaching event. Across both sites, the odds ratio (OR) of a coral being dead after the bleaching event was 4.82 (Figure 7c; Mantel-Haenszel $\chi^2 = 74.0$, df = 1, p-value < 0.001, common odds ratio estimate = 4.82 [95% CI: 3.34–6.97]; Table S10). An OR greater than 1 indicated a positive association between mortality and the bleaching event and the larger the number, the stronger the association. Increased mortality after bleaching also occurred across taxa, where the OR of a coral from the four main taxa being dead after the bleaching event was 5.35 between the 2022-2023 and 2023-2024 sampling periods (Figure 7d; Mantel-Haenszel $\chi^2 = 75.9$, df = 1, p-value < 0.001, common odds ratio estimate = 5.35 [95% CI: 3.62–7.90]; Table S10). Pocilloporidae and *Montipora* spp. had the highest proportions of mortality after bleaching (83% and 60%, respectively; Figure 7d).

Bleaching incidence of adult colonies in different substrate typologies

A total of 2% and 11% of corals died in the loose and interlocked rubble beds, respectively, while 6% died in the hard carbonate (Figure 8a). The likelihood of coral bleaching—for corals that were still alive—varied significantly across substrates (p-value = 0.007; Figure 8b). The probability of bleaching was lower in the loose rubble bed than in the hard carbonate (53% ± 0.09 and 85% ± 0.05, respectively; p-value = 0.01; Figure 8b). Corals were also less likely to bleach in the interlocked rubble bed (58% ± 0.07) than in the hard carbonate (p-value = 0.01; Figure 8b). However, the likelihood of bleaching in the two rubble beds was statistically similar (p-value = 0.9; Figure 8b).

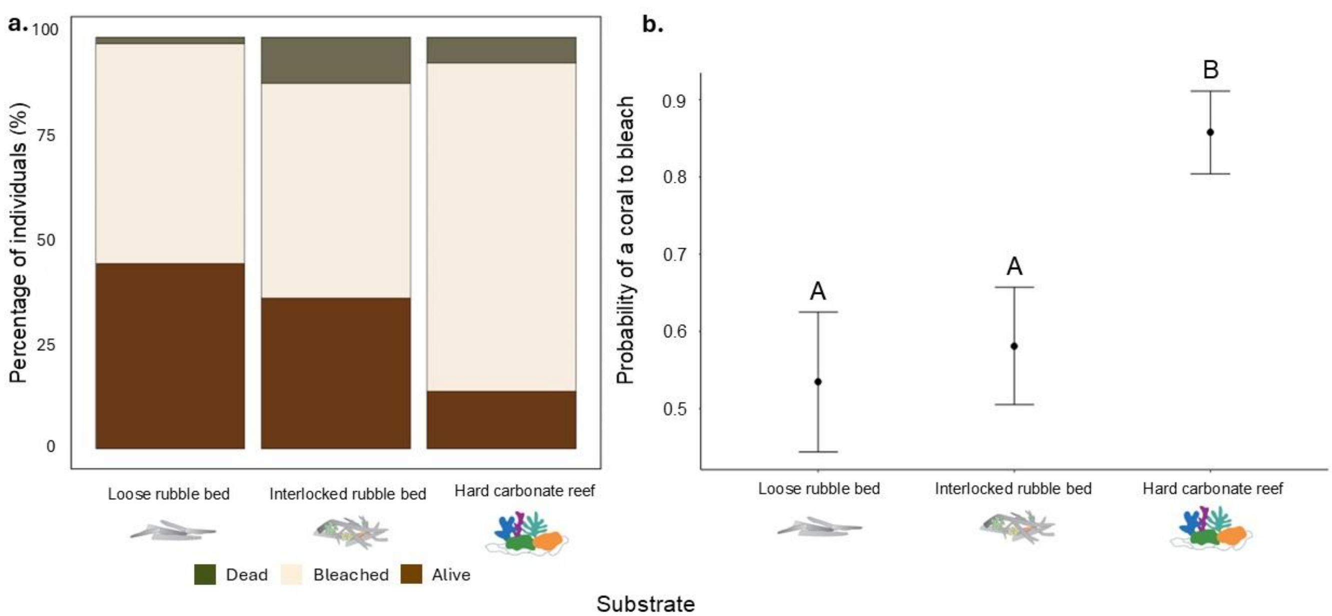


Figure 8 The (a) proportion of bleached, unbleached, or dead corals across substrate types and the (b) average probability (mean ± SE) of bleaching per substrate type for live corals. Differing letters (i.e., A and B) indicate a significant difference in the probability of bleaching between substrate types.

The composition of coral morphologies was similar across all substrates (p-value = 0.07; Table S11; Figure S5). Temperatures were also similar between the loose and interlocked rubble bed substrates into which loggers were deployed (Figure S2). The mean daily temperature peaked in February at 28.7 °C and 28.9 °C in the interlocked and loose beds, respectively (Figure S2), like other nearby windward west sites at the same depth (windward west deep: 28.99 °C; Figure 2). Unfortunately, the flooding of both loggers in the hard carbonate resulted in no data for the substrate.

Bleaching incidence of juvenile colonies of different coral morphologies

A total of 148 juvenile corals were recorded in February 2023 at the windward west slope site, with 56% of them being branching morphotypes, predominantly *Acropora* spp. During the bleaching event in February 2024, 116 of these corals were still present, with bleaching impacts (individual colonies either fully or partially bleached) observed in 43% of these remaining corals (Figure 9). Bleaching incidence was significantly different between coral morphologies ($\chi^2 = 80.108$, df = 3, p-value < 0.05), with bleaching observed for 90% of plate corals, 40% of branching corals, 34% of massive corals, and 42% of the other hard coral colonies (Figure 9).

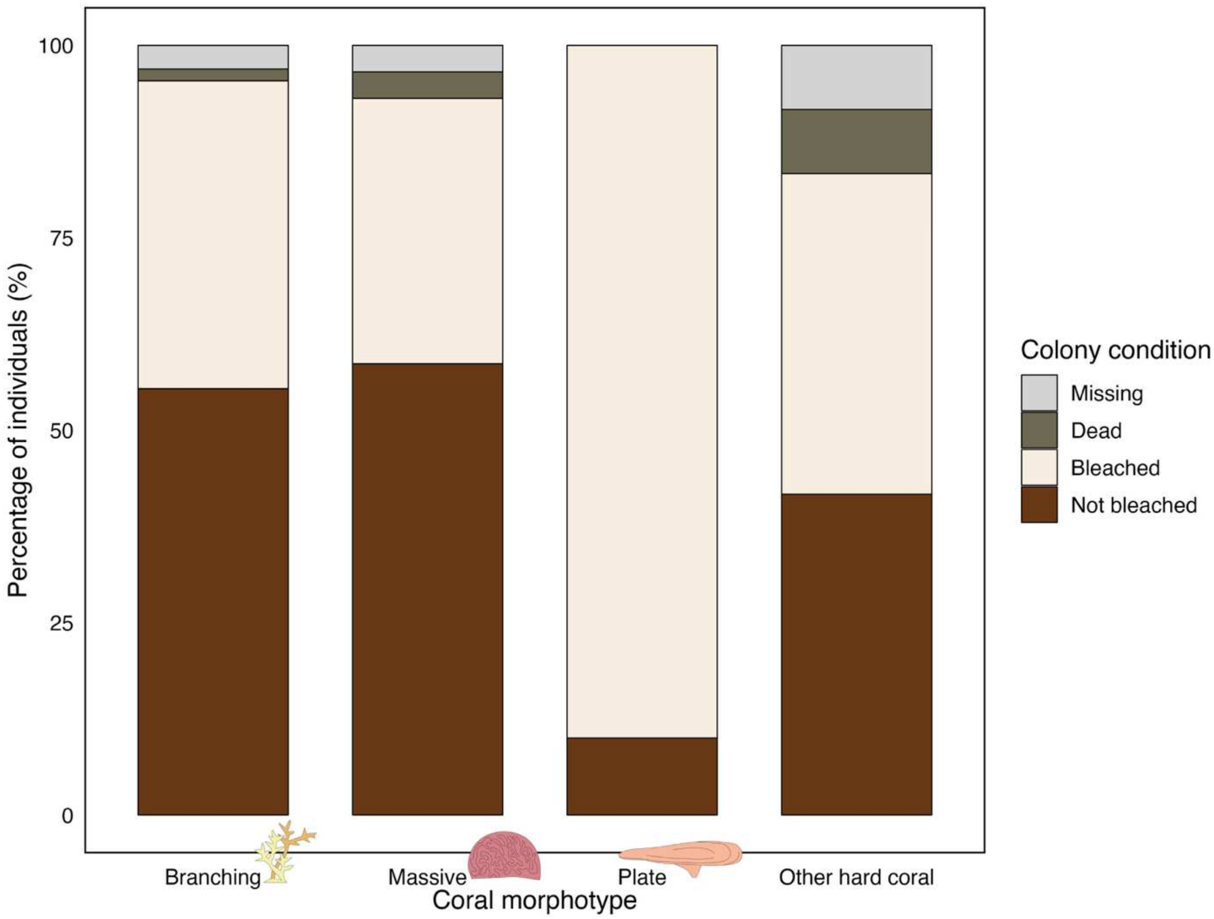


Figure 9 Percentage of juvenile coral colonies (%) by colony condition observed during the bleaching event (February 2024) per each coral morphotype on the windward west slope.

Survival and bleaching of coral fragments tracked during a common garden experiment

The 12-week common garden experiment resulted in substantial variation in survival and bleaching response among the 240 *S. pistillata* fragments. At the end of the experiment, 68% (164/240) of fragments had died and all observed cases of mortality had bleached prior to death. We observed an increasing number of bleached fragments over the twelve weeks: the proportion of partially bleached fragments reached 35% (86/240) at week three and the proportion of fully bleached fragments reached 13% (32/240) at week five (Figure 10a). Bleaching area for each fragment also increased, reaching an average of 40% at week six (Figure 10b) along with a decrease in overall fragment colour (i.e., paling) (Figure 10c). For those fragments that were still alive, a recovery stage appeared to be reached in the last three weeks, as the bleaching area per fragment reduced and the fragments regained a darker colour. The temperature in the experimental tanks showed concurrence with the temperatures observed on the reef during the heat stress (Figure S3).

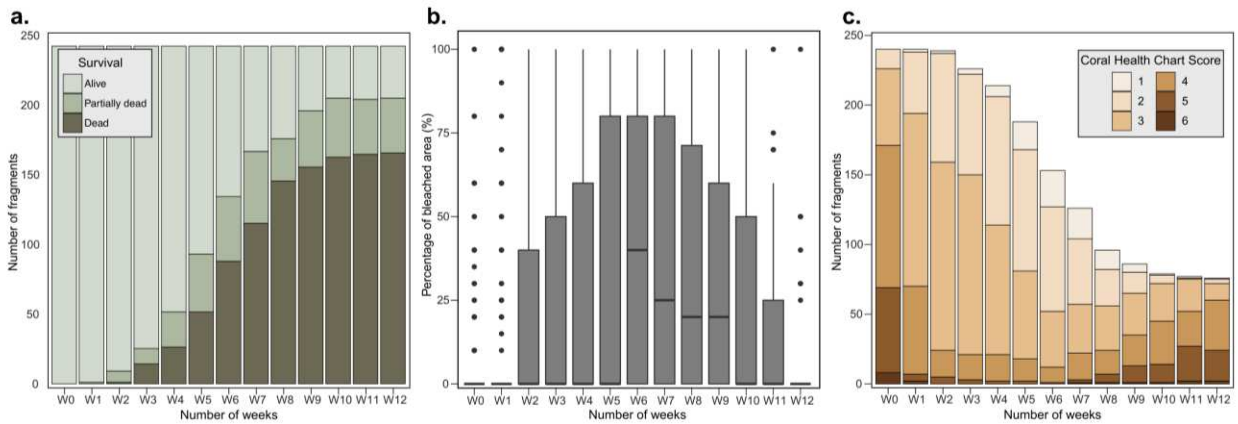
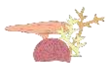


Figure 10 Variability in bleaching response of 240 *Stylophora pistillata* fragments held in common garden conditions at Heron Island Research Station, subject to 2024 heat wave temperatures for 12 weeks (W1-W12). Panel (a) presents changes in fragments' survival over time ('Alive' = no tissue was dead and 0% was bleached, 'Partially dead' = more than 0% and less than 100% of tissue surface was dead, 'Dead' = all tissue was dead). Panel (b) shows changes in the fragments' percentage of bleached area over time. Panel (c) shows the changes in fragments' colour score over time.

Table 1 Summary of bleaching responses observed across all spatial scales.

Ecological scale	Sampling method	Key bleaching results
Reef 	Environmental (temperature & DHW)	• The greatest accumulation of heat stress (DHW) was within the reef flat (12.12 °C-wk). • Northern, eastern, and western slopes accumulated between 5.23–9.66 °C-wk. • Heat stress on the reef flat in 2024 was 155% higher than the 2020 event (7.84 °C-wk).
	Bleaching observations based on satellite derived data Depth: <10 m	• 43% (0.69 km²) of live coral pixels on the reef slope presented >50% bleaching, 22% (0.36 km²) presented 10–50% bleaching, 35% (0.56 km²) exhibited <10% bleaching. • Overall, 65% (1.05 km²) of living coral pixels were affected by bleaching (to any level), with bleaching being most prevalent on the windward east slope.
Community 	Bleaching response within benthic communities on the reef flat and slope Depth: 1–5 m	• Across the entire reef, 38% of hard coral cover was bleached, with massive and plate/encrusting morphotypes being the most affected. • There was more bleaching on the reef slope than the flat, with the most bleaching on the windward east slope.
	Bleaching indicated by CoralWatch colour scores in different reef zones Depth: 0–7 m	• Coral colour score changes were most pronounced in the windward east zone.
Colony 	Growth and survival of colonies in coral demography plots pre- and post-bleaching Depth: 6–8 m	• The bleaching event was associated with reduced coral growth rates (indicated by $\log_2$ coral size ratios) and heightened mortality at both sites. • Mortality rates were the highest for Pocilloporidae followed by *Montipora* spp. Merulinidae corals showed greater resilience with the smallest increases in mortality.
	Bleaching incidence of adult colonies in different substrate typologies Depth: 8–10 m	• Bleaching was most probable in the hard carbonate substrate plots (85% probability of bleaching), compared to the interlocked rubble bed (58%) and the loose rubble substrate (53%).
	Bleaching incidence of juvenile colonies of different coral morphologies Depth: 8–10 m	• Bleaching incidence was observed in 43% of remaining tagged juveniles. • Juvenile bleaching incidence was observed in 90% of the plate corals, 40% of branching corals, 34% of massive corals, and 42% of other hard coral morphotypes.
	Survival and bleaching of coral fragments tracked during a common garden experiment Depth: 5–12 m	• 68% of *S. pistillata* fragments died over the 12-week period and survivors appeared to recover in the last 3 weeks. • Different fragments of *S. pistillata* exposed to the same thermal stress environment for three months showed different bleaching responses and survival.

4. Discussion

By quantifying bleaching effects across multiple spatial scales, we documented severe and extensive coral bleaching in response to the 2024 thermal stress at Heron Reef. Heat stress reached levels never recorded before at Heron Reef, with 12.13 °C-wk on the reef flat and up to 9.66 °C-wk on the reef slopes. This led to a total of 43% of coral area on the reef slope considered bleached and 65% affected by bleaching to some degree, when observed at a reef-scale. At the community level, photo quadrats aligned with remotely sensed patterns, revealing that between 37% and 49% of corals across the reef slope zones were bleached, whereas only 17% were bleached on the reef flat. At both reef and community-scales, bleaching was more prevalent on the windward east reef slope, where heat stress was slightly higher. At the colony-scale, bleaching affected adults and juveniles similarly. Observations from both methods of data collection detected bleaching in branching and plating corals, with Pocilloporidae and plating/foliose *Montipora* corals suffering the highest mortality. Finally, bleaching responses varied at the finest-scale, among individual colonies of the same species. A summarised description of the key results at each scale are presented in Table 1. Future studies will ascertain how these bleaching impacts have affected post-bleaching mortality rates across exposures and depths.

4.1 Temperature observations

Unprecedented thermal stress was experienced across Heron Reef during the 2024 MBE on the GBR. Thermal stress, as measured by DHW, varied by zone and depth, with the highest heat stress recorded on the reef flat, followed by windward deep sites, windward shallow sites, and finally leeward north deep sites. Our results revealed greater heat stress on the reef flat compared to the reef slope, aligning with patterns observed during the 2020 marine heatwave (Ainsworth et al. 2021; Brown et al. 2023b). However, reef flat heat stress in 2024 was 155% higher (12.13 °C-wk) than in 2020 (7.84 °C-wk). Regarding the reef slope, heat stress was slightly higher at windward eastern compared to western sites. We expected higher stress in the west, owing to reduced hydrodynamic energy there compared to eastern sites (Dechnik et al. 2017; Duce et al. 2020). Lower energy can result in longer seawater residence times which can exacerbate temperature stress. While this link between lower energy and higher temperature stress was not apparent with respect to aspect, it could explain observed patterns of heat stress across depth. Heat stress was slightly higher at deeper sites (lower wave energy) as compared to shallow sites (higher wave energy). Depth is often considered a refuge due to reduced seawater temperatures and/or light levels. However, in other areas of the GBR during the 2016 bleaching event, a subsidence of upwelling led to very similar temperatures and heat stress between depths of 10 m and 40 m (Frade et al. 2018). Our results with respect to heat stress on the reef slope highlight the complexity of coral bleaching and underscore the need for comprehensive monitoring of seawater temperatures and coral community health across fine-scale spatial resolutions.

4.2 Ecological observations: Reef scale

Monitoring coral bleaching at the reef-scale has only recently gained attention, highlighting an important shift toward understanding bleaching impacts across an entire reef system (Hickey et al. 2020; Lutzenkirchen et al. 2024).

Our remotely sensed results provide valuable insights into the extent and severity of bleaching across the Heron Reef slope down to 10 m in depth. Within the area of reef slope mapped as live coral, approximately 43% (0.69 km²) exhibited >50% bleaching and 65% (1.05 km²) exhibited some degree of bleaching (>10% bleaching). Bleaching predominantly affected the windward east slope, which coincided with the highest accumulation of DHW on the reef slope. The accuracy of these maps aligns with those reported in other remote sensing coral reef studies (Andréfouët 2008; Roelfsema et al. 2018), and the March 2024 live coral cover and bleaching map showed patterns consistent with previous field-based studies at Heron Reef (Roelfsema et al. 2021a). These reef-wide snapshot estimates facilitate a broad quantification of disturbance impacts, allowing for the extraction of surface area metrics per bleaching level (i.e., >50% bleached, 10-50% bleached, and <10% bleached; Naumann et al. 2009; Foo and Asner 2019).

4.2 Ecological observations: Community scale

4.2.1 Bleaching response within benthic communities on the reef flat and slope

Community-scale assessments are a common approach for monitoring coral bleaching and offer insights into the spatial variability of coral health, resilience, and deterioration. On Heron Reef, analysis of 21 geolocated photo quadrat transects revealed the average percentage of bleached coral cover was 38% across the entire reef, with variability in bleaching responses between geomorphic zones and coral morphotypes. Corals on the reef slope exhibited more bleaching, particularly on the windward east side, with southeast transects SETR1 and SETR0 having bleaching percentages of 61% and 59% respectively. These findings corresponded with high DHW on the windward east slope. Bleaching, and subsequent mortality on the reef flat, was very high in 2020 (60-70% of total coral cover bleached and/or dead) (Ainsworth et al. 2021; Brown et al. 2023b). In contrast, only 17% of corals on the reef flat experienced bleaching in 2024, with a currently unknown survival rate. This suggests that coral mortality in 2020 could have resulted in strong selection for robust coral hosts and Symbiodiniaceae genotypes and/or that the colonies which survived the 2020 event experienced beneficial acclimatisation or stress hardening via environmental memory (Hughes et al. 2019; Brown et al. 2023a; Brown et al. 2023b). In comparison, the reef slope on Heron Reef experienced very little bleaching during the 2020 event (approximately 10% bleached; Ainsworth et al. 2021) as compared to the 37-49% bleaching exhibited across the reef slope in 2024. Such spatial and temporal variability in bleaching responses can arise from interactions between extrinsic factors like hydrodynamics and intrinsic factors such as adaptations (Penin et al. 2007). This differential response in bleaching across zones may be related to preexisting coral community composition (Carrasco Rivera et al. 2025; Vercelloni et al. 2024; Darling et al. 2012).

Unlike ex situ reef-scale observations, in situ surveys can discern coral community bleaching responses at finer scales, such as by morphotype, providing insights into community shifts following disturbances (Hughes et al. 2018b). During the 2024 event, the massive and plate/encrusting morphotype categories experienced the highest proportion of bleaching, while branching morphotypes experienced the least. This pattern reflects trends from the

2016 event, where Hughes et al. (2018b) noted corals in the now revised Faviidae family, which typically exhibit massive morphologies, experienced the most bleaching. Despite this, corals within the Acroporidae and Pocilloporidae families faced higher mortality, suggesting that bleaching is not always a reliable predictor of mortality (Hughes et al. 2018b). However, the colony-scale results in our study showed that bleaching in juvenile corals was highest for plating morphologies, and that plating adult *Montipora* corals also had the highest rates of mortality post-bleaching, showing that mortality can mirror bleaching in some cases. Future research will investigate the post-bleaching survival of bleached corals observed in this study.

4.2.2 Citizen science bleaching observations

Citizen science initiatives like CoralWatch significantly broaden the scope of participation in observing and documenting bleaching events as they unfold. Our incorporation of CoralWatch surveys conducted during the March 2024 event revealed that 52% of surveys indicated bleaching. Reductions in coral colour scores were most pronounced in the windward east zone, reflective of the other community- and reef-scale observations. Previously, the average colour score from CoralWatch health charts has been used to identify bleached reefs. However, supplementary analysis (see Figure S6 and Table S5) revealed that this metric is not a sufficiently informative indicator of changes to colony health. Coral species vary in their susceptibility and resilience to thermal stress, therefore there is significant variation in coral colour when enduring or recovering from a bleaching event. Averaging colour scores across a survey can therefore generate a deceptively high overall score, masking fine-scale heterogeneity in coral colour as bleaching progresses. This limitation meant that bleaching events were only identifiable after widespread and severe bleaching had already occurred. As a result of these findings, the approach to recording and reporting bleaching events in the CoralWatch global coral health database has been updated and now also incorporates changes in the frequency distribution of colony colour scores to assist in the early detection and communication of bleaching events.

4.3 Ecological observations: Colony scale

4.3.1 Growth and survival of colonies in coral demography plots pre- and post-bleaching

At Libby's Lair (leeward north slope) and Coral Gardens (windward west slope), we observed trends in growth and mortality rates reflective of the community- and reef-scale findings. Many corals across the most abundant taxa (*Acropora,* Merulinidae, *Montipora*, and Pocilloporidae) suffered losses of live coral tissue (i.e., partial mortality) between 2023 and 2024. Since coral bleaching is physiologically stressful, the observed net reduction in coral colony size could hinder future reproductive output (Ainsworth and Brown 2021). Although our findings show that all coral taxa were negatively affected, bleaching mortality appears to vary among taxa and growth forms, consistent with previous findings (Darling et al. 2012; Morais et al. 2021). Merulinidae corals (massive and sub-massive morphologies), for example, were least affected by the bleaching event, having the lowest mortality. On the other hand, Pocilloporidae and *Montipora* corals, which were mostly of branching or plating/foliose morphologies, had the highest mortality post-bleaching. Taxa-specific variation in bleaching and mortality response might lead to shifts in coral community composition if low growth and recruitment persist. Such shifts can impact the delivery of key ecosystem services reliant on habitat complexity (e.g., Beese et al. 2023). Under climate change, recurrent marine heatwaves leading to increased frequency and intensity of bleaching events will likely lead to further partial and total mortality. Where corals have died, open substrate becomes available for the recruitment of new individuals into the demographic plots, provided there is sufficient brood stock to replenish the local populations (Dietzel et al. 2020). However, it is unclear whether local populations will persist into the future under the current community structure (e.g., Cant et al. 2021), especially if MBEs negatively affect coral growth indiscriminately, as shown in this study. For example, we demonstrated that although Merulinidae had the least mortality relative to other taxa, the taxon's growth had been negative even before the MBE. Further monitoring and research are needed to determine the recovery of Heron Reef coral populations.

4.3.2 Bleaching incidence of adult colonies in different substrate typologies

Loose rubble creates a hostile environment for coral recruitment due to its instability and tendency for mobilisation (Kenyon et al. 2023b). No studies have specifically explored how different rubble bed typologies affect coral bleaching. Filling these knowledge gaps through further investigation into rubble bed dynamics could provide insights into the characteristics that influence coral susceptibility to bleaching. Our results indicate significant variation in the probability of bleached corals between the substrates. The highest proportion of bleached corals was found on hard carbonate, while fewer bleached corals were found in loose and interlocked rubble beds. Despite the sites having similar coral community compositions, temperatures, and water depths, small-scale environmental differences may have influenced the extent of coral bleaching between hard carbonate and rubble bed plots. Structural complexity can affect water flow, which can affect warm water residence times during a bleaching event (Lenihan et al. 2008; Green et al. 2019; Grimaldi et al. 2023). Rubble beds, which are less structurally complex than living reefs, can experience higher free-stream flow than hard carbonate habitats (Guihen et al. 2013). Increased water flow in the rubble beds could reduce thermal stress and may explain the lower levels of bleaching. Morais et al. (2024) found severe bleaching in more sheltered lagoonal habitats compared to exposed reef habitats, supporting other studies that have also shown an influence of water movement and substrate composition on bleaching responses (Lenihan et al. 2008; DeCarlo et al. 2017; Grimaldi et al. 2023). Differences in coral sizes between substrates might also have contributed to bleaching discrepancies and should be considered in future investigations. Although determining the exact drivers of the bleaching differences between substrates is challenging, this kind of investigation is important given the scarcity of existing data on bleaching within these habitats. As climate change worsens and rubble bed production increases due to more frequent and intense storms and MBEs (Ceccarelli et al. 2020), research on coral bleaching responses in these habitats will become ever more important.

4.3.3 Bleaching incidence among juvenile colonies of different coral morphotypes

Morphological variation in bleaching incidence was observed in our study of juvenile corals, with plating corals being the most impacted. This was reflective of the previous demographic results that revealed Pocilloporidae and plating/foliose *Montipora* spp. had the highest mortality post-bleaching (Figure 7d). Coral morphological differences are known to mediate stress responses as a function of colony growth form and tissue thickness (Loya et al. 2001), as thicker tissue provides better protection from intense solar irradiance and increases the mass transfer of toxic radicals within a colony (Hoegh-Guldberg 1999). Our results suggest the disadvantages from thinner tissue could explain why 90% of plating and 40% of branching morphologies bleached as these morphologies have thinner tissue and lower mass transfer rates than massive morphologies making them less able to protect the underlying symbionts from severe light intensities and higher than average SSTs (Loya et al. 2001). Coral size can also influence bleaching susceptibility (Hughes and Jackson 1985; Shenkar et al. 2005; Wagner et al. 2010; Pratchett et al. 2013). Interestingly, smaller branching *Acropora* colonies have been observed to be less affected by thermal stress than larger colonies (Loya et al. 2001; Nakamura and van Woesik 2001) suggesting juvenile corals may have an advantage over larger adult colonies during thermal stress events. However, Alvarez-Noriega et al. (2018) observed contrasting patterns of bleaching susceptibility between taxa, with juveniles of *Acropora* spp. and *Goniastrea* spp. less susceptible to bleaching than adults but the opposite trend for *Pocillopora* spp. and Merulinidae. In this study we observed adult and juvenile colonies to have similar incidences of bleaching, which was likely a result of the extended duration of thermal stress from the accumulation of DHWs (mid-January – June 2024) during this bleaching event overriding any taxon-dependent tolerances. This reinforces the need for continued assessments of coral community population structure to understand the vulnerability of juvenile corals to future disturbance events and their post-disturbance recovery capacity (Alvarez-Noriega et al. 2018; Burn et al. 2024; Speare et al. 2025).

4.3.4 Survival and bleaching of coral fragments tracked during a common garden experiment

Intraspecific response variation might be an important component of coral persistence during and following mass mortality events. The common garden experiment conducted here revealed high variation in bleaching response and survival among *Stylophora pistillata* fragments exposed to the heat stress that matches the temperature and duration of the concurrent heatwave. While many fragments bleached and died within a few weeks, others remained healthy until the end of the heat stress period. Our results suggest that extensive fitness variation can evolve at fine spatial scales. However, further investigations are needed to evaluate the relative importance of genetic diversity, symbiont community composition and micro-environmental conditions (e.g., depth, wave exposure) in explaining the observed phenotypic variation. Within-reef intraspecific variation in heat tolerance might be critical in determining coral population persistence following heatwaves, yet it is often overlooked (but see Thomas et al. 2018; Humanes et al. 2022). These findings add nuance to the classification of "winner" and "loser" coral species facing climate change by suggesting the existence of substantial adaptive potential *within* species, the genetic basis of which could be evaluated.

4.4 Strengths and limitations of data collection methods across scales

Monitoring coral bleaching across different spatial scales revealed unique strengths and limitations for each data collection method. At the reef-scale, remote sensing techniques offer snapshot assessments over extensive areas, enabling the detection of large-scale bleaching events and helping to prioritise locations for finer-scale surveys to evaluate impacts and reef health (Hickey et al. 2020). Remote sensing provides an upscaled and rapid quantification of bleaching extent beyond what field surveys can (Edmunds and Bruno 1996), while also measuring surface area metrics (i.e., area in km^2). These metrics are crucial for management efforts as they quantify the spatial extent of coral area that exhibited bleaching stress (Naumann et al. 2009; Foo and Asner 2019). However, the non-uniformity of bleaching responses highlights the heterogeneity of reef habitats. Our remote sensing model categorises corals as a single group, lacking the ability to differentiate between morphotypes (e.g., branching, massive, encrusting) or genera/family, which can only be assessed through complementary in situ surveys. Additionally, remote sensing can sometimes overestimate bleaching responses due to pixel resolution and spectral mixing of different benthic types (Andréfouët et al. 2002). Conversely, despite their limited spatial coverage and need for greater resources, bleaching surveys at the community-scale offer more precise quantification of bleaching, specific to each geomorphic zone, morphotype, and/or finer taxonomic resolution. The fine-scale differences between reef- and community-scale estimates in their resolution for discerning bleaching responses was evident within our data. On the reef slope, community-scale estimates of bleaching ranged from 37% to 49%, while remote sensing estimates indicated that 43% of living coral pixels had >50% bleaching and 65% had >10% bleaching. This variability highlights the differences detected regarding bleaching severity as a result of different scales and emphasises the importance of integrating various scales of analysis in discerning bleaching responses.

Colony-scale data collection offers several strengths and limitations when assessing coral bleaching impacts. One strength is the ability to capture fine-scale ecological dynamics that broader-scale assessments might overlook. These assessments reveal bleaching susceptibility trends across different morphologies or species, life-history stages (i.e., juvenile and adult), locations, and microhabitats (i.e., rubble vs. hard carbonate). This scale provides critical insights for inferring resilience or deterioration of coral communities. However, it is essential to integrate these local findings with broader reef and community-scale data to develop comprehensive bleaching management strategies that can span much wider spatial scales (Rivera-Sosa et al. 2025).

Our study revealed that bleaching responses do not need to be solely quantified by scientists. Initiatives like CoralWatch engage communities and expand data collection and interpretation. Many other citizen science programs monitor coral reefs and their responses to disturbances across the GBR and around the world (e.g., Reef Check Australia, Reef Life Survey, Eye on the Reef). Such engagement fosters a deeper appreciation for coral reefs among participants, potentially enhancing their commitment to conservation efforts and generating a sense of stewardship (e.g., Hesley et al. 2023). These initiatives also create a wealth of additional data points that enhance our understanding of how bleaching responses manifest across reef systems. However, the accuracy of bleaching estimates gathered by non-scientists and non-specialists can vary. Yet, in our study and in previous work (Siebeck et al. 2006), analyses using CoralWatch data revealed comparable levels of bleaching to those measured by researchers. This suggests that with proper training and guidance citizen scientists can provide valuable contributions to reef monitoring efforts, ultimately enriching the data landscape and facilitating more comprehensive ecological insights.

4.5 Implications for reef managers - The need for collaboration

Our multi-scale, interdisciplinary approach highlighted the critical need for collaboration among researchers to effectively monitor the reef during bleaching events and to provide valuable information for managers. Remote sensing offers significant advantages in mapping coral bleaching responses across large areas, but understanding intricate variations within coral communities requires combining reef-scale and community-scale assessments. Further, community-scale surveys can be supported by citizen science data. Cooperation between researchers and citizen scientists can enrich the data landscape and provide additional insights into bleaching responses. Colony-scale investigations, despite having limited spatial focus, provide insights into species' susceptibility and survival likelihoods to thermal stress and elucidate the factors which modulate those responses. These analyses can be used to prioritise species or genotypes for restoration, as well as specific locations on the reef where restoration will be most effective. The integration of multiple spatial scales through collaboration between scientists and citizen scientists facilitates more informed estimates of bleaching responses, enhancing our understanding of ecological trajectories over vast scales. Owing to the complexity of bleaching responses and increasing intensity of events, strategies that incorporate data from various platforms, as well as across various spatial and ecological resolutions, will become crucial for informing management and applied interventions.

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Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

Ethics approval

We declare that all applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study have been followed, and all necessary approvals have been obtained. RPH data and TK temperature loggers were deployed, and data was collected under GBRMPA Research permit G21/45534.1. DAR and ZM data were collected under GBRMPA Research permit G21/44774.1 and granted Free, Prior and Informed Consent from Port Curtis Coral Coast Traditional Use Marine Resource Agreement. KTB data was collected under GBRMPA Research permits G19/42845.1 and G24/50387.1. DC, KG, FD, KM, CR data was collected under Limited Impact Accreditation No. UQ003/2021. MB, FC, WCH, GD, and AD's coral demographics data comes under GBRMPA permits G19/42221.1 and G23/49031.1. CoralWatch data comes under GBRMPA permit G19/41922.2.

Data availability

The CoralWatch dataset generated and analysed during the current study is available from the Atlas of Living Australia (ALA) Biocollect platform, https://biocollect.ala.org.au/coralwatch/bioActivity/allRecords#mapVis?hub=coralwatch&hub=coralwatch. All other datasets generated during and/or analysed during the current study will be made available upon reasonable request to the corresponding author.

Authors' contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by DAR, KMG, TMK, ZM, CM, KTB, FFD, DECR, KE, RPH, MB, FC, GD, AD, WVH, CAL, HM, GE and CR. The first draft of the manuscript was written by DAR, NMH, KMG, TMK, ZM, CM, KTB, FFD, DECR, RPH, MB, FC, and CR and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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