



Back-to-back bleaching events in Peninsular Malaysia (2019–2020) selectively affect hard coral taxa across- and within-reef scales

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Abstract

The impacts of (repeat) bleaching events and the differential heat stress susceptibility of hard coral taxa are largely unknown in Malaysia, although it is part of the greater coral triangle. Here we determined bleaching trajectories of 46 hard coral taxa across- and within-reef scales based on data recorded during the first reported back-to-back coral bleaching occurrences in Malaysia between May 2019 and September 2020. Although the severity of coral bleaching in both years did not correspond to the rather small magnitude of heat stress observed, i.e., Degree Heating Weeks (DHW) of 1.05 °C-weeks and 0 °C-weeks in 2019 and 2020 respectively, we observed high levels of bleaching (55.21% and 26.63% of all surveyed colonies in 2019 and 2020, respectively). Notably, the bleaching response for both consecutive years was highly taxon-specific and significantly varied across- and within-reef scales. Mortality rates overall were low following the 2019 event, likely due to a rapid decrease in heat stress. Five of the 46 surveyed hard coral taxa exhibited more severe bleaching in 2020, despite a lower heat stress load. Interestingly, we observed low bleaching of ascribed susceptible taxa such as *Acropora* and *Montipora*, while we found taxa considered to be resilient, e.g. *Heliopora* and *Porites*, to exhibit severe bleaching, suggesting a reversal of bleaching hierarchies of taxa over time. Our findings provide a foundation for further coral bleaching studies in a region with few published records to enable more accurate regional assessments and to follow the trajectory of future coral bleaching events.

Keywords Coral bleaching · Malaysia · Climate change · Ocean warming · Coral reef · Mortality

Introduction

Coral bleaching refers to the whitening of coral tissue due to the disruption of the coral-Symbiodiniaceae relationship under heat stress. Although several stressors can induce bleaching (Jaap 1979; Lesser 2011; Rådecker et al. 2021), the association between the coral host and its specific algal endosymbiont assemblage is considered to contribute

to bleaching susceptibilities of coral taxa (Baker et al. 2004; Hume et al. 2020). Under non-stressful conditions, photosynthetic Symbiodiniaceae algae provide the coral's energy requirements to build calcium carbonate skeletons, which in turn provide the backbone of the three-dimensional structure of coral reefs and habitat for one third of all described marine species (Muscatine 1990; LaJeunesse et al. 2018).

The spatial and temporal extent of thermal stress events are increasing in all ocean basins (Skirving et al. 2019; Eakin et al. 2022; Reimer et al. 2024), making the understanding of the cumulative and interactive impacts of repeat (i.e., back-to-back) bleaching events a critical component for accurately projecting the future of reef ecosystems and to implement active interventions (Hughes et al. 2021; Voolstra et al. 2021). It is no longer feasible to fully understand the impacts of coral bleaching by investigating isolated events, nor to assess ecosystem states without considering the legacy effects of previous disturbances (Hughes et al. 2019; Slattery et al. 2019; Johnston et al. 2020; Evensen et al. 2022; Lachs et al. 2023). In particular, because coral species exhibit differential susceptibility to

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heat stress, forecasting the trajectories of tropical coral reefs is not possible without knowledge on the response of various hard coral taxa to repeat thermal stress events (Hackerott et al. 2021; Hughes et al. 2021; Wall et al. 2021; Evensen et al. 2022). Furthermore, it is critical to understand coral bleaching by considering within-reef heterogeneity (Pineda et al. 2013; Fordyce et al. 2019; Voolstra et al. 2020). Such knowledge contributes to understanding how environments drive bleaching outcomes and stipulate adaptive responses (Thomas et al. 2023). Ultimately, dynamic physico-chemical and environmental reef settings (Oliver and Palumbi 2011) in combination with coral holobiont genotypes drive bleaching outcomes (van Woessik et al. 2022), which makes it necessary to assess bleaching responses within and between coral taxa and across environmentally distinct reef sites (Safaie et al. 2018; Suggett and Smith 2020).

In Peninsular Malaysia, a region with over 4000 km² of coral reef cover and over 500 hard coral species (Huang et al. 2015), severe heat stress exposure is predicted to result in annual severe coral bleaching by as soon as 2035 (van Hooijdonk et al. 2020). However, detailed surveys of coral bleaching severity, associated mortality, and recovery are not yet available for Malaysian reefs. The first general mass bleaching observations in Malaysia were made during the severe pan-tropical coral bleaching event in 1998 (Kushairi 1998). In 2010, partial investigations of taxon-specific bleaching responses identified a putative change in bleaching susceptibilities of taxa (Guest et al. 2012), and severe bleaching was observed across the east coast of Peninsular Malaysia in 2010 (Tan and Heron 2011; Guest et al. 2012). Nonetheless, these observations were based on a single survey at each site, and neither differences between reef sites and environments (e.g., across depth), nor bleaching outcomes (e.g., bleaching driven mortality) were investigated (Claar and Baum 2019).

Here, we report on the spatial and temporal bleaching trajectories of 46 hard coral taxa across the first observed back-to-back coral bleaching events in Peninsular Malaysia. These findings are contextualized to previous mass bleaching events in this region (Tan and Heron 2011; Kimura et al. 2014) to provide a brief historical context of previous thermal stress events and assessment of putative changes in taxon-specific bleaching susceptibility. The differential bleaching susceptibility of taxa as a function of wind and water depth is also explored.

Methods

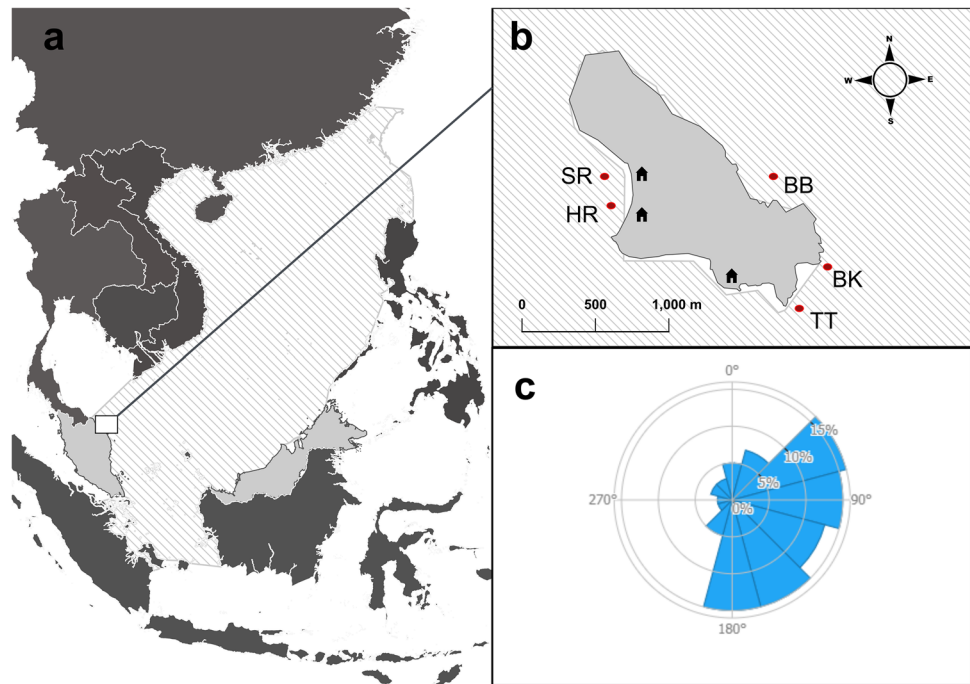
Reef sites

The eastern coast of Peninsular Malaysia is a dynamic environment with significant seasonal fluctuations in rainfall, wind force, and sea temperatures predominantly influenced

by the region's monsoon cycle (Moten et al. 2014). As such, intra-annual sea surface temperature (SST) varies between 26 °C during the northeast monsoon (from November to February) when rainfall, wind forcing, and turbidity are highest and 31 °C between May and June, when sea conditions are calmest (Supplementary Material, ESM 1). Therefore, historically, heat stress induced coral bleaching in Malaysia exclusively occurred between the months of April and October (Tan and Heron 2011; Guest et al. 2012; Kimura et al. 2014). We investigated four reef sites around Pulau Lang Tengah (5°47'N, 102°53'E) within the Redang Marine Park (a declared no-take fishing zone) in Northeast Peninsular Malaysia (Fig. 1). Although there is no permanent human population on the island, there are three tourist beach resorts operating seasonally between March and October. In general, tourist numbers and activities (e.g., snorkeling and SCUBA diving) are low in comparison to other Malaysian islands and are not considered a significant driver of coral reef degradation at present. Tidal ranges at the study location are approximately 2 m between April and October (<https://www.worldtides.info>), and there are no freshwater streams discharging into the sea.

Two windward sites, Batu Bulan and Tanjung Telunjuk, and two leeward sites, House Reef and Secret Reef, were chosen to assess how individual coral taxa respond to the interactions between thermal stress, water depth (sensu Baird et al. 2018; Frade et al. 2018), and differential wind exposure (McClanahan and Maina 2003; Pineda et al. 2013). Wind frequency direction was determined using web-based products from historical data recorded between 2008–2017 (Global Wind Atlas 3.0 2021). Based on a 2019 survey (Bernard et al. 2023), the selected reef sites range from 'coral-dominated' to 'rubble-dominated', due to marked differences in live hard coral cover, coral density, diversity, and benthic substrate composition. For example, the average live hard coral cover at Batu Bulan is 43.37% with the extent of coral rubble (11.82% benthic substrate cover) and sand (14.37% benthic substrate cover) being substantially lower than at the leeward sites (i.e., 39.61% coral rubble and 48.11% sand cover at House Reef). The hard coral assemblage at Batu Bulan is composed of 66 morpho-taxa with an average coral colony density of 25.7 colonies m⁻². Morphologically, this reef site is dominated by massive taxa (31.90% of measured live hard coral cover), encrusting taxa (30.75%), and encrusting taxa with up-growths (25.09%). In contrast, at the leeward sites, the reefs are presently dominated by branching (69.00% of measured live hard coral cover) and encrusting taxa with up-growths (14.39%), whereas live hard coral cover (8.78%), the number of morpho-taxa ($n = 38$), and the average coral density (9.2 colonies m⁻²) are notably lower. Of note, live hard coral cover and colony density decline at all reef sites with depth. A survey in 2018 measured high live hard coral cover (i.e., > 45%) at Tanjung Telunjuk

Fig. 1 Study location and survey sites. **a** South China Sea (dashed area) with **b** Location of Pulau Lang Tengah (5°47'43.2"N, 102°53'39.7"E) in Northeast Peninsular Malaysia (light grey), showing survey sites House Reef (HR), Secret Reef (SR), Tanjung Telunjuk (TT), and Batu Bulan (BB) as well as the in situ temperature recording stations at Batu Kucing (BK), House Reef (HR), and Tanjung Telunjuk (TT). House icons in panel **b** show the location of tourist beach resorts. **c** The wind rose illustrates wind direction and frequency around Pulau Lang Tengah at island scale based on historical data recorded between 2008 and 2017



(Szereday, unpublished data), similar to surveys conducted in 2000 (41.3% live hard coral cover; Harborne et al. 2000).

Thermal stress metrics

Sea surface temperature (SST) data for Pulau Lang Tengah were sourced from the National Oceanic and Atmospheric Administration's (NOAA) Coral Reef Watch (CRW) version 3.1 (NOAA, Coral Reef Watch 2014), binned to the nearest 5 km² satellite pixel (5°46'30.0"N, 102°52'30.0"E), and accessed through the ERDDAP website (https://pae-paha.pacioos.hawaii.edu/erddap/griddap/dhw_5km.html) (Liu et al. 2014). Thermal stress accumulation is expressed in Degree Heating Weeks (DHW described in °C-weeks) (Wellington et al. 2001) with ecologically impactful coral bleaching generally being observed at ≥ 4 °C-weeks, corresponding to a temperature of ≥ 1 °C above the long-term maximum monthly mean (MMM) for 4 weeks. Central to the DHW metric is the universal bleaching threshold concept of MMM + 1 °C (Glynn and D'croz 1990), below which thermal stress is not considered. However, this universally fixed threshold concept has been challenged previously, positing that more fine-scale temporal heat stress metrics may be more representative in certain cases (Whitaker and DeCarlo 2024; Neo et al. 2023; McClanahan et al. 2019; McClanahan 2022). For instance, periods of heat stress can be expressed as daily SSTs exceeding the MMM, irrespective of the + 1 °C threshold (Gleeson and Strong 1995; van Hooijdonk and Huber 2009; van Hooijdonk et al. 2013). Following this, we calculated nDHW (Eq. 1) as described

by DeCarlo (2020) as the cumulative thermal stress over 9 weeks considering any instance where the average daily SST exceeded the local MMM.

$$\text{Degree Heating Weeks (nDHW)} = \sum_{j=1}^i \left(\frac{HS_j}{7} \right), \text{ if } HS_j \geq \text{MMM} \quad (1)$$

The nDHW metric was calculated based on satellite temperature data for 2019 and 2020, and for 2020 the nDHW was additionally calculated using in situ temperature data at a reef site scale.

In situ reef temperature data, bleaching thresholds, and diel temperature profiles

Temperature loggers (HOBO 64 K Pendant, Onset Computer Corporation, USA) were deployed at 8 m depth adjacent to the transect sites at House Reef and Tanjung Telunjuk. Due to a loss of loggers at Batu Bulan, we used additional data from the nearest temperature logging site at Batu Kucing (Fig. 1) to establish reef scale temperature profiles. The comparative temperature data analysis between in situ loggers and satellite data is based on data ranging from 12 September 2019 to 30 September 2020 (19,635 measurements) using mean nightly temperature values, as satellite monitoring is only available for nightly measurements.

To further assess the interaction of site-specific temperature variability and bleaching responses (Safaie et al. 2018), we examined site-specific diel temperature ranges (DTRs), defined as the difference between the minimum and maximum

temperature values across a 24 h period, a co-variate shown to impact hard coral bleaching response (Barshis et al. 2018; Safaie et al. 2018). DTRs were calculated for each reef site. Reef-specific DTRs were summed over the following time spans to investigate seasonal differences of DTRs across sites: (i) DTR_{Total} from 12 September 2019 to 30 September 2020, (ii) $DTR_{BleachingSeason}$ from 1 April 2020 to 30 September 2020, (iii) $DTR_{PeakSummerSeason}$ from 1 May to 31 July 2020, (iv) $DTR_{Monsoon}$ from 31 October 2019 to 31 March 2020, and (v) DTR_{60} and DTR_{90} to indicate the 60- and 90-day period preceding the first bleaching observation in 2020 (20 June 2020). We used a non-parametric Kruskal–Wallis test, followed by a Nemenyi's test with a Bonferroni correction, to examine pairwise differences of reef site DTRs.

Benthic surveys

Bleaching of hard coral taxa was surveyed over two consecutive years in 2019 and 2020. To account for the possible impact of survey timing on taxon-specific bleaching outcomes (Claar and Baum 2019), surveys were conducted during the peak of the heat stress events in 2019 and 2020, i.e., 6 and 9 days after the first observations of widespread bleaching, respectively. In addition, putative recovery and mortality from the June 2019 bleaching event was surveyed in October 2019 at the end of the 2019 heat stress event and in April 2020 between heat stress events. Since transect surveys were not repeated in September 2020, assessment of putative bleaching-associated mortality following the 2020 bleaching episode are not available. Site-specific survey dates and time of max nDHW are available in the Supplement (ESM 2). Benthic surveys were conducted along marked transects. A total of seven 10×1 m belt transects for each of the four sites were laid parallel to the shore on the shallow reef between 5 to 7 m (mean depth = 6 m) and on the deeper reef slope between 10 to 14 m (mean depth = 12 m). Each transect was marked with rebar stakes at the start, middle, and end point. Transects were video recorded during each survey occasion for reference to ensure correct repositioning and redeployment of the transect tape during subsequent surveys. A total of > 1,800 coral colonies were surveyed, ranging from 323 to 663 colonies per site (mean = 469.25 colonies/site).

Colonies encountered along the belt transects were recorded and identified to the genus level in addition to their respective growth morphology (e.g., massive *Porites*, encrusting *Porites*). The octocoral *Heliopora coerulea* was included in these surveys due to its reef-building importance on Indo-Pacific coral reefs (Colgan 1984) and its putative superior heat stress tolerance (Phongsuwan and Changsang 2012; Harri et al., 2014; Raymundo et al. 2019). Bleaching categories were assigned for each coral colony as follows: B1 (no bleaching), B2 (pale live), B3 ($\leq 33\%$ of colony surface bleached), B4 (34–66% bleaching), B5 (67–90%

bleaching), B6 (> 90% of colony surface bleached). Bleaching-associated mortality was also recorded. Bleaching-associated mortality was differentiated from previous mortality based on the integrity of dead coral skeleton (i.e., uneroded corallites and skeletal features) and was distinguished from predation-inflicted mortality based on the absence/presence of distinctive predation markings of typical coral predators such as Crown-of-thorns starfish and *Drupella* snails (Beeden et al. 2008). Colony mortality was separated into the following categories to account for partial colony mortality: M1 ($\leq 33\%$ of colony surface dead), M2 (34–66% dead), M3 (67–90% dead), and M4 (> 90% dead). Percentages of colony surface bleached or dead, were visually estimated by the same observer across all survey occasions. To determine the severity of bleaching for each morpho-taxon, the percentage of colonies per morpho-taxon in each bleaching category (B1–B6) was determined to calculate the Bleaching Response Index (BRI) (McClanahan et al. 2007a) based on Eq. (2).

$$\text{Bleaching Response (BRI)} = \frac{0B1 + 1B2 + 2B3 + 3B4 + 4B5 + 5B6}{5} \quad (2)$$

The BRI Index is a normalized and weighted measure on a 0–100 scale, whereby higher values indicate more severe bleaching. In addition, a bleaching mortality index (BMI) was determined (Eq. 3) to account for partial- and whole-colony mortality following bleaching:

$$\text{Bleaching Mortality Index (BMI)} = \frac{0B1 + 1M1 + 2M2 + 3M3 + 4M4}{4} \quad (3)$$

The combined bleaching response of all taxa across depth, reef sites (e.g., leeward and windward), and within-reef scales (wind condition and depth combined per site) was determined with the scale-specific bleaching susceptibility index (BSI) (McClanahan et al. 2007b), where BR_i is the taxon-specific bleaching response index, D_i is the relative density of each taxon, and N is the total number of coral taxa recorded at each reef scale (Eq. 4). Summing each morpho-taxon's BSI gave a site-specific bleaching index factoring in the relative density and total number of taxa. Taxa with less than five observations were excluded, given that rare taxa can significantly bias the BSI.

$$BSI = \sum_{i=1}^N \frac{BR_i \times D_i}{N} \quad (4)$$

Statistical analysis

Coral bleaching is influenced by the interaction of environmental variables and taxon-specific susceptibility. To investigate drivers of coral bleaching at the reef scale, a generalized linear model ('glm') (Nelder and Wedderburn

1972) with binomial distribution of bleaching categories [0-unbleached (B1); 1-bleached (B2–B6)], and a logit-link function was modelled to investigate the bleaching response of hard coral taxa. We tested the severity of coral bleaching in response to: ‘wind’ (leeward vs. windward), ‘depth’ (shallow vs deep), ‘site’ (four sites), ‘habitat’ (i.e., leeward shallow, leeward deep, windward shallow, windward deep), ‘genus’, ‘morpho-taxon’, and ‘max nDHW’ (corresponding to the maximum nDHW value recorded during each event). The variable ‘year’ was excluded since it is colinear with the variable ‘max nDHW’. Thus, any significant correlations between ‘max nDHW’ and bleaching response reflect significant differences in bleaching response across the two bleaching years. Explanatory variables were examined for multicollinearity prior to analysis, and the variance inflation factor (VIF) was determined using the package ‘car’ (Fox and Weisberg 2018). Any covariate with a VIF value > 5 was rejected. The ‘drop1’ function with a ‘chisq’ test for logistic regression was used to remove redundant explanatory variables. To obtain the ‘best fit model’, all models were tested for best-fit with the Akaike Information Criterion (AIC) (package ‘AICcmodavg’) and were compared based on the information score adjusted for small sample size (AICc) and Akaike weights to compare the relative predictive power of each model. The distribution of the model’s residuals was visually examined for normality by graphing Q-Q plots. According to the ‘best fit model’, bleaching response of 15 hard coral morpho-taxa (with at least ten observations) was significant and this model was selected to re-test each explanatory variable for each morpho-taxon independently, further adjusting the model with the ‘drop1’ function (but refraining from adding new variables). Finally, we used hierarchical partitioning to calculate the relative importance of each explanatory variable (i.e., percent of explained variation) using the ‘hier.part’ package (Walsh and MacNally 2013). All *glm* analyses were performed in R Studio version 4.1.0 (R Core Team 2021) using the packages ‘modEVA’ (Barbosa et al. 2014) and ‘car’ (Fox and Weisberg 2018). Furthermore, general linear models were used to compare bleaching responses of individual morpho-taxa across depth and wind conditions for each bleaching event. To determine drivers of mortality, we correlated mortality data recorded in October 2019 with the variables ‘morpho-taxon’, ‘depth’, and ‘wind’, considering that the observed mortality was due to excessive thermal stress in the months prior. Following generalized linear model testing, we conducted post hoc tests to compare bleaching responses at the within-reef scale (e.g., leeward shallow vs. leeward deep) and between reef sites (e.g., leeward shallow vs. windward shallow). Here, individual taxa with at least 10 observations at three of the four within-reef scales were considered using the ‘emmeans’ package v1.6.3 to conduct a Tukey’s HSD post hoc test for unequal sample size (Lenth 2021) and a Dunn’s correction

of p-values. Finally, Tukey’s HSD post hoc tests were conducted for morpho-taxa whose bleaching response increased in 2020, despite lower thermal stress.

Results

Thermal stress and in situ thermal regimes

Based on NOAA CRW data, accumulated thermal stress reached a maximum of 1.05 °C-weeks in 2019 and 0 °C-weeks in 2020. This contrasts with the nDHW metric, which determined 6.68 °C-weeks in 2019 and 4.47 °C-weeks in 2020, respectively (Fig. 2), in line with the expected widespread bleaching response at > 6 °C-weeks in 2019 and the less prevalent bleaching at ~ 4 °C-weeks in 2020. Thus, the nDHW metric provided a more accurate indication than the DHW metric considering the level of bleaching observed.

In situ temperature measurements closely correlated with satellite measurements over the monitored period from September 2019 to September 2020 ($r=0.97$, $p<0.001$). However, a discrepancy with a mean difference of 0.53 ± 0.25 °C (SD) (Fig. 2) was observed, which further increased to 0.63 ± 0.26 °C when analyzing temperature data for the 2020 bleaching season (i.e., April–September), reducing correlation between datasets during this period ($r=0.76$, $p<0.001$) (ESM 3). Reef-scale MMMs varied slightly (30.28–30.39 °C), accounting for differences in accumulated thermal stress at the reef-scale (ESM 4). Average diel temperature variations (DTR) of each time series were significantly more variable at leeward sites compared to windward sites, except for DTR_{MS} (ESM 5), indicating that each reef site experienced distinct thermal regimes during the period in which coral bleaching occurred (ESM 5, ESM 6).

Predictors of bleaching severity

To identify predictors of bleaching, we constructed a best fit model based on abiotic and coral bleaching data (see Methods, ESM 7). Analyzing the bleaching response of all coral taxa combined, the variables ‘max nDHW’, ‘morpho-taxon’, ‘depth’, and ‘wind’ were significant predictors of the bleaching response (Table 1), whereby bleaching was significantly less at windward sites, at shallow depths, and during the second bleaching event in 2020 (at 4.43 °C-weeks nDHWs). However, not all coral taxa bleached less at windward sites and at shallow depths (ESM 8, ESM 9). Certain abundant taxa, such as foliose *Pavona*, submassive *Platygyra*, and massive *Porites*, bleached significantly more with increasing depth (ESM 8). In general, bleaching was significant for 12 morpho-taxa (Table 2, ESM 7), and ‘max nDHW’ accounted for most of the explained variance for seven taxa, while the

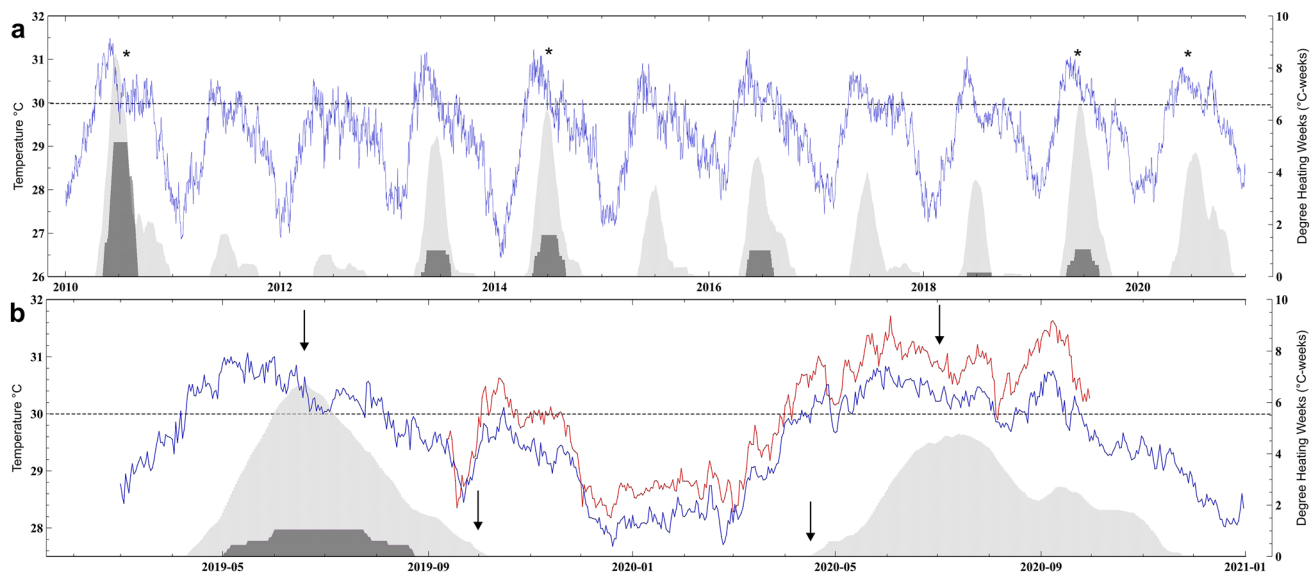


Fig. 2 Sea surface temperature (SST) and degree heating weeks (DHW). The blue line shows the satellite-based nightly sea surface temperatures (SST °C) between 1 March 2019 and 31 December 2020 around Pulau Lang Tengah, recorded by the National Oceanic and Atmospheric Association (NOAA) Coral Reef Watch (CRW) product version 3.1. Time series are plotted against the standard DHW metric (dark-grey area), the adjusted nDHW metric (light-grey area), and the maximum monthly mean (MMM) temperature (black

dotted line, 29.94 °C) based on CRW satellite data. Panel **a** shows heat stress events since 2010 with observed coral bleaching events (identified by available literature and author observations) highlighted by an asterisk (*). Panel **b** shows average nightly satellite-based (blue line) and in situ (red line) sea temperature measurements from three sites at 8 m water depth, recorded between 12 September 2019 and 30 September 2020. The black arrows indicate the time of in situ bleaching surveys and data collection

bleaching response of five taxa was more dynamic and varied across environmental reef-scales considering ‘wind’ and ‘depth’ (Table 2, ESM 8, ESM 9).

Coral taxon-specific variability in bleaching response, recovery, and mortality

Taxon-specific differences in bleaching were pronounced (Table 3). In June 2019, 55.21% of surveyed colonies ($n=1,882$) were bleached, of which 30.29% ($n=570$) were severely bleached (i.e., >66% of colony surface) (Fig. 3). The general bleaching response index (BRI) in June 2019 was 36 out of 100, suggesting a moderate bleaching intensity on the population level. Importantly, however, the BRI

varied greatly across morpho-taxa (Table 3). For instance, of the more abundant morpho-taxa (i.e., $n > 10$ colonies; 27 morpho-taxa total), seven morpho-taxa showed a severe BRI above 50. Notably, branching *Echinopora* (BRI=86) and *Heliopora coreluea* (BRI=82) showed the highest bleaching susceptibility in June 2019, followed by encrusting *Goniastrea*, foliose *Pavona*, encrusting *Cyphastrea*, massive *Porites*, and encrusting *Porites* (all BRI > 50, Table 3). In addition, three morpho-taxa had a higher BRI than the average population BRI of 36: encrusting *Dipsastraea*, *Pocillopora*, and solitary *Fungia*. The most abundant taxa *Porites* spp. bleached moderately (BRI=34). By contrast, bleaching levels of *Acropora* and *Montipora* morpho-taxa, which were historically considered most susceptible, were

Table 1 Results of the ‘best fit’ generalized linear model for bleaching response of the hard coral assemblage across successive bleaching events in 2019 and 2020.

Variable	Estimate	SE	z value	Pr(> z)	VIF	IE (%)
(Intercept Best Model)	-1.85594	0.41931	-4.426	9.59E-06	–	–
Wind (windward)	-0.77409	0.11469	-6.749	1.49E-11	2.19	19.86
Depth (shallow)	-0.37350	0.08895	-4.199	2.68E-05	1.25	3.16
max nDHW (6.68)	1.47082	0.08007	18.370	<2e-16	1.08	76.98
Morpho-taxon (15 morpho-taxa)	–	–	–	–	2.43	–

Note: IE for morpho-taxa was tested separately for each taxon

VIF variance inflator factor, IE (%) independent effect value that accounts for the explained variance by each explanatory variable, nDHW Degree Heating Weeks

Table 2 ‘Best fit’ generalized linear model for the 12 morpho-taxa with a significant bleaching response and a sample size \geq ten observations.

Morpho-taxon	Variable	Estimate	SE	z value	Pr(> z)	IE (%)
<i>Cyphastrea</i> encrusting	(Intercept)	-1.4469	0.5557	-2.604	0.00922	-
AICc - 48.15	max nDHW (6.68)	2.2201	0.7432	2.987	0.00282	100.00
<i>Echinopora</i> branching	(Intercept)	-21.55	4432.59	-0.005	0.996	-
AICc - 26.35	max nDHW (6.68)	20.85	4432.59	0.005	0.0231	100.00
<i>Favites</i> encrusting	(Intercept)	-0.7802	0.3641	-2.143	0.03214	-
AICc - 97.59	max nDHW (6.68)	1.3192	0.4957	2.661	0.00778	100.00
<i>Fungia</i> solitary	(Intercept)	-1.0198	0.2164	-4.713	2.44E-06	-
AICc - 214.91	Wind windward	-2.8078	0.539	-5.209	1.90E-07	0.60
	max nDHW (6.68)	3.4969	0.4197	8.331	< 2e-16	99.40
<i>Goniastrea</i> encrusting	(Intercept)	-0.6592	0.318	-2.073	0.038187	-
AICc - 114.45	max nDHW (6.68)	1.7579	0.4607	3.815	0.000136	100.00
<i>Heliopora coerulea</i>	(Intercept)	-0.9204	0.287	-3.207	0.00134	-
AICc - 176.56	Depth shallow	3.4741	0.6358	5.464	4.65E-08	71.42
	max nDHW (6.68)	1.7649	0.3839	4.597	4.28E-06	28.58
<i>Pavona</i> foliose	(Intercept)	1.6393	0.3030	5.410	6.29E-08	-
AICc - 253.74	Depth shallow	-2.2950	0.3414	-6.722	1.798E-11	57.63
	Wind windward	-3.5291	0.8037	-4.392	1.12E-05	37.61
	max nDHW (6.68)	0.7761	0.3198	2.427	0.0152	4.76
<i>Platygyra</i> submassive	(Intercept)	-0.1793	0.294	-0.61	0.54196	-
AICc - 165.7	Depth shallow	0.8861	0.3862	2.295	0.02175	37.51
	max nDHW (6.68)	1.1886	0.4135	2.875	0.00405	62.49
<i>Pocillopora</i> spp.	(Intercept)	-1.9496	0.5578	-3.495	0.000474	-
AICc - 79.00	Wind windward	1.9222	0.6122	3.14	0.00169	70.22
	max nDHW (6.68)	1.0924	0.5747	1.901	0.057298	29.78
<i>Porites</i> encrusting	(Intercept)	-0.9753	0.3799	-2.567	0.01025	-
AICc - 127.28	Depth shallow	-1.3351	0.4775	-2.796	0.00517	80.04
	max nDHW (6.68)	2.266	0.4725	4.796	1.62E-06	19.96
<i>Porites</i> massive	(Intercept)	1.2536	0.385	3.256	0.00113	-
AICc - 418.33	Wind windward	-1.0881	0.3605	-3.018	0.00254	9.26
	Depth shallow	-1.6124	0.2651	-6.082	1.19E-09	57.01
	max nDHW (6.68)	1.157	0.2478	4.669	3.02E-06	33.73
<i>Porites</i> spp.	(Intercept)	-1.2241	0.3236	-3.783	0.000155	-
AICc - 1007.1	Wind windward	0.5951	0.3394	1.753	1.49e-08	28.13
	Depth shallow	0.391	0.3188	1.227	5.49e-08	24.45
	max nDHW (6.68)	1.1162	0.1596	6.995	4.53e-10	47.42

IE (%) independent effect value that accounts for the explained variance by each explanatory variable, nDHW Degree Heating Weeks

low or mild (ESM 10). Notably, eight abundant coral taxa had a $BRI \leq 10$. Thus, although overall bleaching levels were severe in 2019, substantial differences across morpho-taxa were observed.

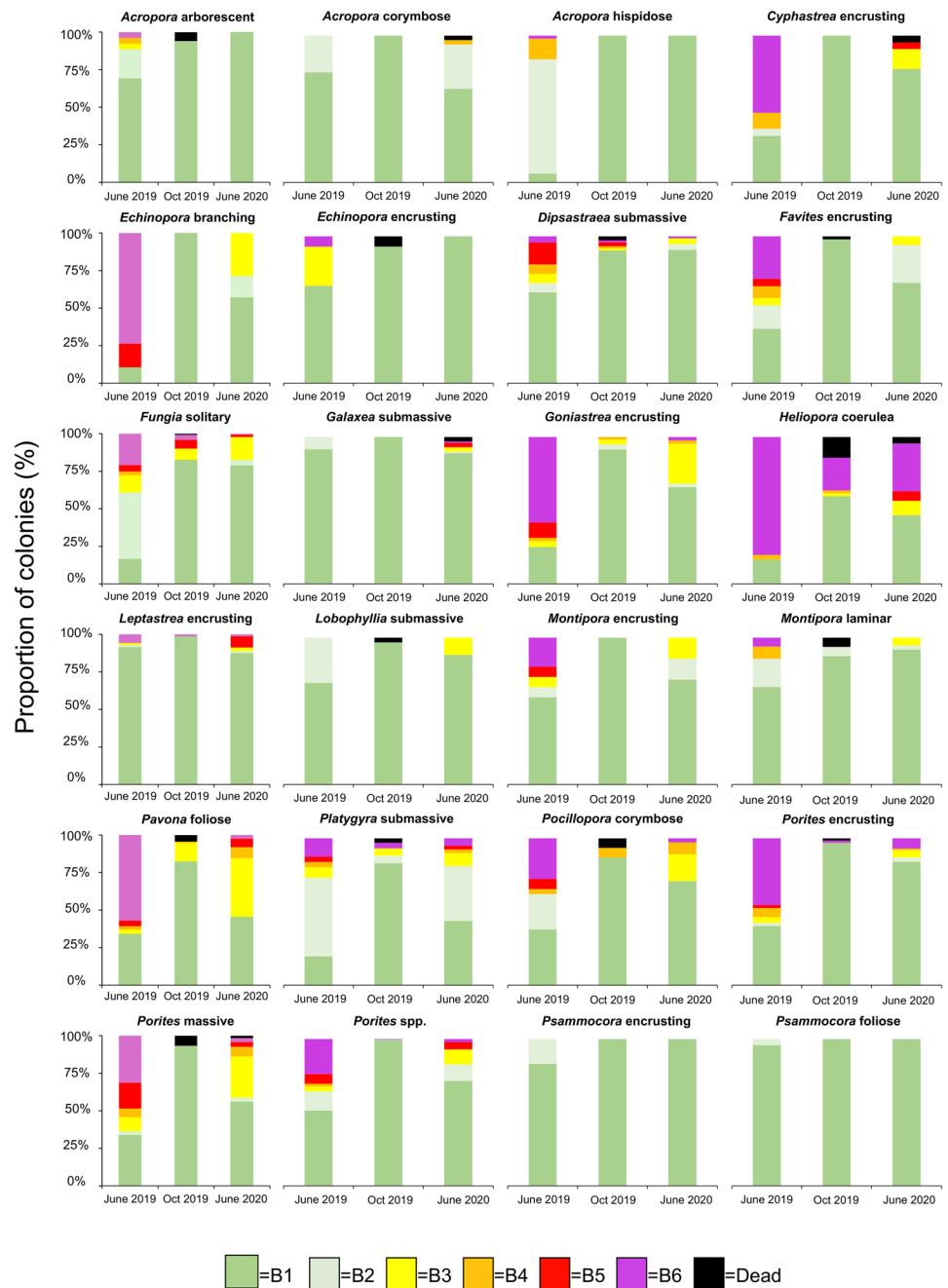
Based on transect surveys in October 2019, 91.68% of surveyed colonies ($n = 1,826$) appeared fully recovered with an overall low BRI ($BRI = 3$) (Table 3, Fig. 3, ESM 11). Concurrently, the BMI was relatively low across all taxa ($BMI = 1.71$, $n = 1,826$). We observed full colony mortality for only 1.10% of colonies surveyed ($n = 20$), while 1.81% ($n = 33$) experienced partial colony mortality. Notably,

Heliopora coerulea showed the highest BMI (11.36), with 14.14% of surveyed colonies exhibiting patches of dead tissue and 10.10% suffering full mortality in October 2019 (ESM 12). Importantly, mortality was significantly correlated with windward sites, as 86.79% of all colonies with dead tissue ($n = 46$) and 90.48% of fully dead colonies ($n = 19$) were recorded at windward sites (ESM 13). In line with this, no bleaching was observed during April 2020, suggesting that coral taxa recovered from the 2019 bleaching event.

Table 3 Taxon-specific bleaching response (BRI) and bleaching-induced mortality index (BMI) of hard coral taxa (n =number of colonies) during successive coral bleaching events in June 2019 and June 2020 in Pulau Lang Tengah. The percentage of partial and whole-colony mortality combined is shown for October 2019 and highlights post-bleaching mortality after heat disturbance in June 2019

Genus	Morphology	June 2019		October 2019			June 2020	
		n	BRI	n	Dead (%)	BMI	n	BRI
<i>Acropora</i>	Arborescent	26	12	17	5.9	1.47	15	0
	Corymbose	32	5	25	0.0	0.00	33	8
	Digitate	9	9	12	0.0	0.00	11	0
	Hispidose	143	26	100	0.0	0.00	102	0
	Tabular	10	14	4	25.0	12.50	11	0
<i>Astreopora</i>	Massive	1	40	1	0.0	0.00	1	40
	Encrusting	1	100	1	0.0	0.00	0	0
<i>Blasstomussa</i>	Encrusting	0	0	1	0.0	0.00	3	0
<i>Cyphastrea</i>	Encrusting	19	60	25	0.0	0.00	22	8
<i>Diploastrea</i>	Encrusting	2	10	2	0.0	0.00	2	10
<i>Dipsastraea</i>	Encrusting	11	0	17	0.0	0.00	31	3
	Submassive	47	24	74	2.7	0.68	76	4
	Massive	3	53	5	40.0	15.00	7	17
<i>Echinopora</i>	Branching	19	86	11	0.0	0.00	7	14
	Encrusting	15	17	14	7.1	3.57	17	0
<i>Favites</i>	Encrusting	48	43	35	2.9	0.71	35	7
<i>Fungia</i>	Solitary	115	39	120	0.8	0.42	137	9
<i>Galaxea</i>	Encrusting	96	2	110	0.0	0.00	101	5
<i>Goniastrea</i>	Encrusting	48	70	58	0.0	0.00	11	15
	Submassive	4	20	3	0.0	0.00	44	0
<i>Goniopora</i>	Submassive	0	0	4	0.0	0.00	3	0
<i>Herpolitha</i>	Solitary	2	60	4	0.0	0.00	1	0
<i>Heliopora</i>	Columnar	122	82	99	14.1	11.36	92	41
<i>Hydnophora</i>	Branching	1	40	1	0.0	0.00	1	0
	Encrusting	6	40	7	0.0	0.00	6	10
<i>Leptastrea</i>	Encrusting	69	7	72	0.0	0.00	80	9
<i>Leptoria</i>	Submassive	2	0	1	0.0	0.00	1	0
<i>Lobophyllia</i>	Submassive	26	6	31	3.2	3.23	34	4
<i>Merulina</i>	Encrusting	7	31	6	0.0	0.00	5	0
<i>Montipora</i>	Encrusting	15	29	8	0.0	0.00	7	9
	Laminar	36	14	32	6.3	3.91	37	3
<i>Oulophyllia</i>	Massive	5	12	2	0.0	0.00	3	0
<i>Pachyseris</i>	Encrusting	3	67	2	0.0	0.00	1	0
<i>Pavona</i>	Encrusting	9	0	11	0.0	0.00	7	0
	Foliose	135	63	114	4.4	1.97	123	27
<i>Physogyra</i>	Submassive	1	0	7	0.0	0.00	5	0
<i>Platygyra</i>	Encrusting	12	10	17	5.9	1.47	23	16
	Submassive	56	31	78	2.6	1.60	80	20
<i>Pocillopora</i>	Corymbose	29	40	31	6.5	4.84	38	15
<i>Porites</i>	Encrusting	47	52	68	1.5	1.47	76	10
<i>Porites spp.</i>	Encrusting	447	34	384	1.3	3.20	354	12
<i>Porites</i>	Massive	155	53	164	6.7	0.78	189	21
	Encrusting	18	3	16	0.0	0.00	22	0
<i>Psammocora</i>	Foliose	24	1	29	0.0	0.00	26	0
	Solitary	1	20	3	0.0	0.00	3	0
<i>Sandolitha</i>	Solitary	1	20	3	0.0	0.00	3	0
<i>Stylocoenellia</i>	Cryptic	5	0	0	0.0	0.00	6	0
Total		1882	36	1826	2.90	1.71	1884	12

Fig. 3 Percentage of healthy, fully, and partially bleached hard coral colonies for all morpho-taxa with at least 15 observations during surveys in June 2019, October 2019, and June 2020. In October 2019, percentage of bleaching-induced mortality is shown, combining complete and partial-colony mortality



For the consecutive back-to-back bleaching event in June 2020, we recorded moderate and frequent bleaching with a bleaching prevalence of 26.63% of surveyed colonies ($n = 1,884$). Bleaching intensity was lower compared to 2019, as only 6.26% of colonies exhibited severe bleaching. Average population-level BRI of all taxa was 12, and *Heliopora coerulea* showed the highest individual bleaching response (BRI = 41), exhibiting high thermal susceptibility

for both consecutive years. Notably, despite the overall lower thermal stress in 2020, bleaching prevalence moderately increased for five taxa: corymbose *Acropora*, *Dipsastraea*, *Galaxea*, *Leptastrea*, and *Platygyra* (all encrusting). However, these BRI increases over successive bleaching occurrences were insignificant following Tukey’s HSD post hoc testing (ESM 14).

Bleaching response across- and within-reef scales

When accounting for the relative abundance of morpho-taxa (i.e., BSI), leeward deep reef sites were the most bleaching susceptible during both consecutive bleaching events (Table 4). At windward sites, deeper sites exhibited a higher bleaching prevalence and response than shallow sites. Ultimately, bleaching prevalence and response across wind conditions and depth were driven by the susceptibility and abundance of morpho-taxa, as corroborated by the site-susceptibility bleaching index (Table 4, Fig. 4). For instance, leeward deep was significantly more bleached in both years (Fig. 5, ESM 15) as a result of the higher bleaching susceptibility and dominant abundance of foliose *Pavona* (Fig. 5). Foliose *Pavona* colonies bleached severely at leeward deep, strongly at leeward shallow, and did not bleach at windward shallow. Depth and wind combined accounted for 95.26% of the observed variance for foliose *Pavona* (Table 2). Solitary *Fungia* bleached similarly across all reef sites. In contrast, massive *Porites* bleached significantly less at shallow windward sites in both years, while the BRI of massive *Porites* at windward deep was substantially more severe compared to windward shallow, demonstrating clear within-reef scale differences in BRI as a function of depth. Similarly, *Porites* spp. showed a strong bleaching response at all scales, but not at windward shallow sites in 2019. Combined, these abundant taxa were representative of bleaching responses at across- and within-reef scales, as leeward deep and windward shallow were overall the most and least bleached reef scales in 2019, respectively (Fig. 5). In 2020, bleaching

response at leeward deep was significantly higher compared to all other reefs.

Discussion

Regional thermal stress levels inducing bleaching

The nDHW metric better reflected coral bleaching observed in situ for both bleaching events than the broadly used DHW metric. Such local adjustments of common thermal stress metrics can improve predictive power for thermal stress analysis (van Hooidonk and Huber 2009; Hooidonk et al. 2013; McClanahan 2022; Whitaker and DeCarlo 2024). This is not unexpected, as previous studies have noted such discrepancies, specifically across annual temperature peaks (Strong et al., 2002; Venegas et al. 2019; Klepac and Barshis 2022). Field observations in the Red Sea (Monroe et al. 2018) and in several Indian Ocean locations (McClanahan et al. 2007b) have reported widespread coral bleaching at below DHW threshold levels (i.e., <4 °C-weeks) and in the Caribbean ~30% of coral bleaching occurred at DHW of 0 °C-weeks (Eakin et al. 2010), highlighting regional differences that may necessitate updating commonly used universal thresholds to better predict and reflect bleaching outcomes (Whitaker and DeCarlo 2024).

During the 2010 mass bleaching event in southeast Peninsular Malaysia, Guest et al. (2012) concluded that NOAA CRW was underestimating experienced thermal stress, likely due to the underestimation of the importance of daily SST peaks. In line with this, thermal stress based on nDHW corresponded to the expected occurrence of widespread

Table 4 Summary of number of coral colonies assessed, bleaching prevalence, bleaching response index (BRI), hard coral density, and the site-specific bleaching susceptibility index (BSI) across- and within-reef scales during successive bleaching events in 2019 and 2020 in Pulau Lang Tengah, Northeast Peninsular Malaysia.

Reef scale (year)	Colonies	Prevalence (%)	BRI	Density (n/m ²)	BSI
Leeward (2019)	747	70.82	43	24.90	39.28
Windward (2019)	1135	44.85	32	28.38	23.00
Leeward (2020)	690	26.96	13	23.00	10.89
Windward (2020)	1183	25.63	13	29.58	8.81
Shallow (2019)	1203	56.19	34	30.08	26.15
Deep (2019)	679	53.46	41	22.63	25.08
Shallow (2020)	1138	24.25	11	28.45	8.01
Deep (2020)	735	35.51	16	24.50	9.57
Leeward Shallow (2019)	592	72.30	40	28.50	125.79
Leeward Deep (2019)	155	65.16	64	12.50	200.00
Windward Shallow (2019)	611	40.59	29	29.20	38.37
Windward Deep (2019)	524	50.00	37	24.70	45.60
Leeward Shallow (2020)	546	20.15	10	26.00	23.82
Leeward Deep (2020)	144	52.78	28	12.60	58.67
Windward Shallow (2020)	592	23.99	12	28.95	13.73
Windward Deep (2020)	591	27.41	14	27.15	20.79

Shallow sites range from 5 to 7 m water depth and deep sites from 10 to 14 m water depth

Fig. 4 Examples of coral bleaching in 2019 at **a** leeward shallow, **b** leeward deep, **c** windward shallow, **d** windward deep reef sites in Pulau Lang Tengah, Northeast Peninsular Malaysia

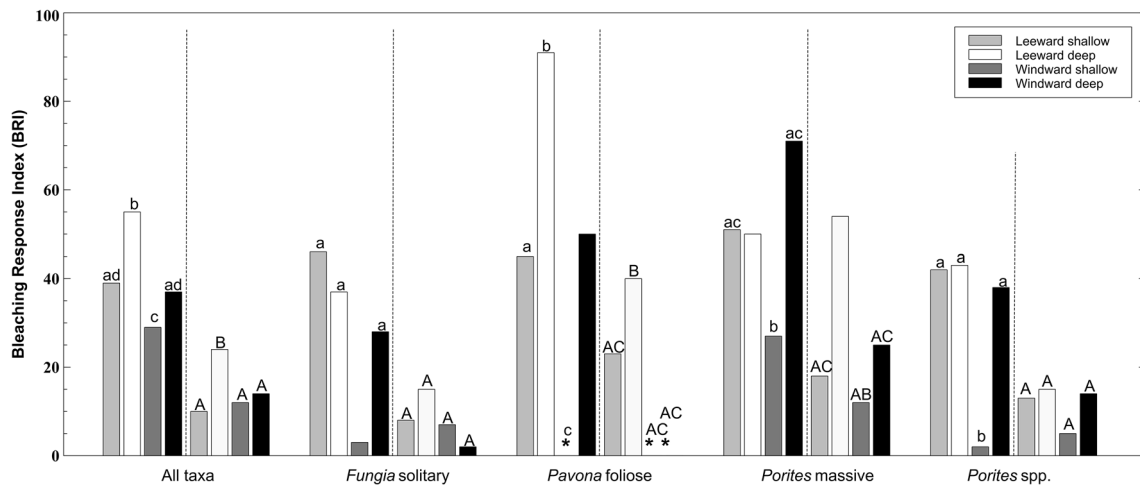
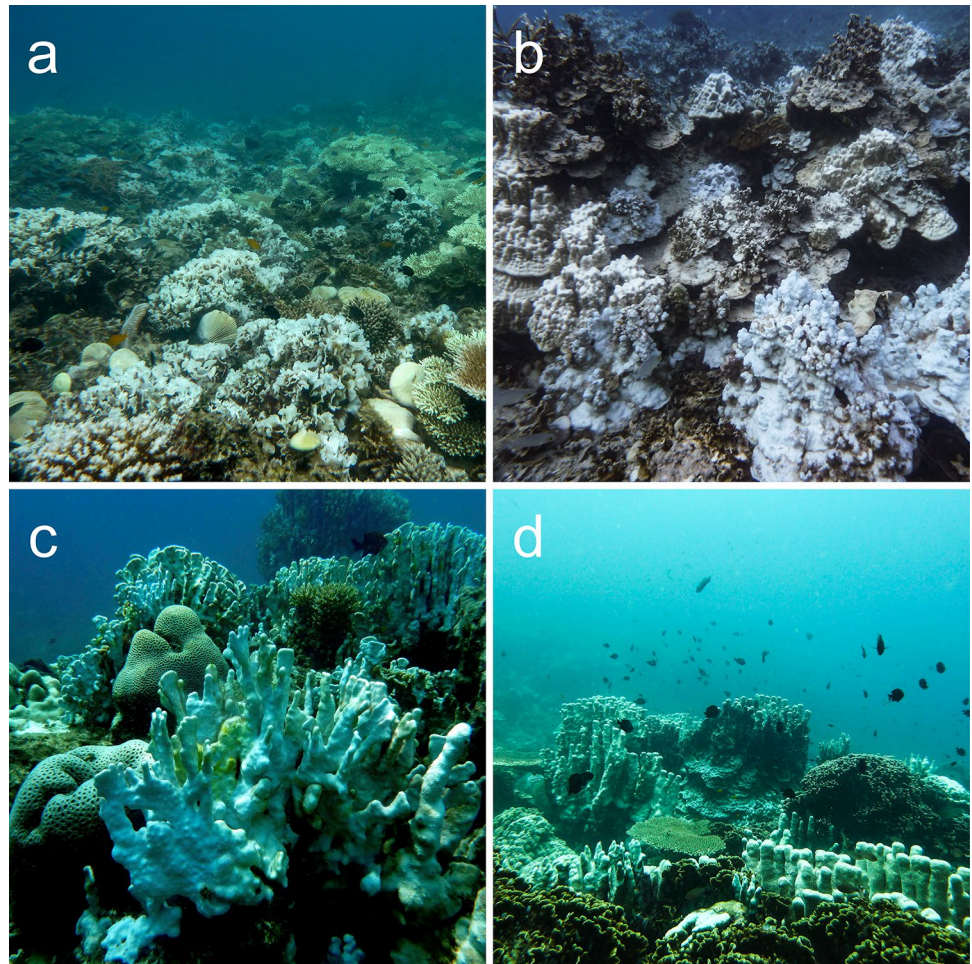


Fig. 5 Bleaching response of hard coral taxa during successive bleaching events in 2019 and 2020 in Pulau Lang Tengah across and within reefs. The dotted lines separate the bars based on bleaching events (left 2019, right 2020). Letter annotations indicate significant differences between taxa based on Tukey’s HSD post hoc comparisons tested for each year individually. For clarity, letters alternate

between lowercase (2019) and uppercase (2020). The absence of letters indicates insufficient samples size (i.e., less than ten observations) and were not statistically tested; ‘*’ highlights morpho-taxa with no bleaching response (i.e., BRI=0). Only morpho-taxa with data from at least three sites for each year were tested

bleaching at 4–8 °C-weeks (Heron et al. 2016; Kayanne 2017; Hughes et al. 2018a). The levels of thermal stress determined by means of nDHW are in line with the level of bleaching observed in 2019, when coral bleaching was significantly more severe at 6.77 °C-weeks compared to 4.43 °C-weeks in 2020. Notably, mortality associated with the 2019 bleaching was minor, further denoting the putative mortality threshold of > 8 °C-weeks (Wellington et al. 2001; Eakin et al. 2010; Hughes et al. 2018a). Based on the available literature, bleaching was observed regionally in 2010 and 2014 (Tan and Heron 2011; Kimura et al. 2014) at nDHW 8.54 °C-weeks and 6.39 °C-weeks respectively, but not in 2013 (5.44 °C-weeks) or 2016 (4.62 °C-weeks). Therefore, based on the published and collected data, a regional bleaching threshold of nDHW ≥ 6 °C-weeks emerges, at which ecologically significant bleaching occurs. Further regional adjustment based on diel in situ data is poised to further refine bleaching thresholds and taxon-specific sensitivities (McClanahan et al. 2020a) across Peninsular Malaysia.

Back-to-back bleaching provides insight to coral resilience

The back-to-back successive bleaching events in 2019 and 2020 represented a decadal local climax of rapid ocean warming (Cheng et al. 2021) (ESM 1). This study is the first to report back-to-back coral bleaching in this region and elaborates on taxon-specific bleaching response and recovery trajectories. One of the key insights gained is the substantial difference in bleaching response across morpho-taxa and between bleaching events. Bleaching-induced mortality in 2019 was very low. Only five morpho-taxa bleached at higher levels in 2020, despite lower levels of thermal stress, suggesting potential legacy effects (Hughes et al. 2019). Although these differences were insignificant, thermal stress in 2020 was below the proposed regional bleaching threshold (see above).

A common observation of in situ bleaching studies is lower bleaching levels during the second (and typically more severe) of back-to-back thermal events (Gintert et al. 2018; Fisch et al. 2019; Harrison et al., 2019). Notably, these studies often report considerably higher bleaching-associated mortality during the first bleaching episode (Head et al. 2019; Hughes et al. 2019; Dalton et al. 2020), suggesting that thermally susceptible colonies may be removed from the population (Loya et al. 2001; van Woesik et al. 2011; Stuart-Smith et al. 2018). Consequentially, the cumulative impacts of repeat back-to-back thermal bleaching on coral communities depends on the composition of species and their relative susceptibility to the magnitude and amplitude of prior thermal stress experienced (Ritson-Williams and Gates 2020). Here, the locally most abundant morpho-taxa (i.e., encrusting and massive *Porites*, *Heliopora coerulea*,

foliose *Pavona*, submassive and encrusting *Platygyra*, and *Pocillopora* spp.; see Bernard et al. 2023 for a 2019 census) exhibited bleaching in both years, whereas the majority of other taxa (of which some are equally abundant) showed remarkably low levels of bleaching. Specifically, taxa such as *Acropora* and *Montipora* that are typically considered thermally susceptible (Pratchett et al. 2013) bleached less in 2020, while the opposite was observed for some taxa that are generally considered thermally resilient (e.g., *Heliopora coerulea*, massive *Porites*, etc.). This ‘reversal’ of bleaching hierarchies has been documented in southeast Peninsular Malaysia in 2010 (Guest et al. 2012) and more recently on larger geographical scales and across diverse eco-regions (McClanahan et al. 2020a, 2020b), suggesting that some degree of adaptation to heat stress is occurring across geographic regions and populations (Sully et al. 2019; Lachs et al. 2023). Whether the low bleaching response of these taxa at significant levels of thermal stress in 2019 and 2020 is the result of ‘thermal weeding’ of thermally susceptible colonies or due to an increase in resilience from prior exposure to thermal stress (sensu Guest et al. 2012) is unclear due to the lack of sufficient data on bleaching response and mortality in this region.

While the overarchingly low to mild bleaching response of most taxa across the 2019 and 2020 bleaching events suggests high thermal tolerance relative to the levels of thermal stress (in line with very low bleaching associated mortality rates), it should be noted that we observed a rapid and acute onset of thermal stress in 2019 that resolved equally quickly (Fig. 2). Extended duration of excess thermal stress is increasingly recognized as one decisive factor in determining severity, mortality, and recovery from bleaching (Eakin et al. 2019, 2022; Skirving et al. 2019), in contrast to the short-term and acute heat stress observed for the 2019 coral bleaching event. Thus, we suggest that bleaching and mortality rates were mitigated by the rapid decline of thermal stress in 2019 (Wellington 2001; Eakin et al. 2010; Hughes et al. 2018a).

By comparison, the 2020 bleaching event is the first observation of thermal coral bleaching in Malaysia during a La Niña year, and mild to moderate coral bleaching was reported across the extent of the Malaysian east coast (Reef Check Malaysia 2020). Thermal stress accumulated to a maximum of 4.77 °C-weeks (nDHW) based on satellite data, although interpolating satellite and diel in situ data, a maximum of 5.08 °C-weeks could be determined. This is still below the suggested regional threshold of ≥ 6.0 °C-weeks (nDHW).

Taken together, bleaching responses of taxa were consistent with thermal stress levels observed across events, noting a significant dissimilarity of taxon-specific bleaching thresholds. One notable finding is the high bleaching susceptibility of *Heliopora coerulea* (Table 3). In both years,

H. coerulea showed the highest bleaching prevalence, severity, and mortality of all surveyed taxa, particularly at shallow sites (Table 4 and 5, ESM 12). A wide range of field studies across the Indo- and Central-Pacific regions (e.g., Palau, Japan, Western Australia, Kiribati, Guam) as well as the Indian Ocean (e.g., the Andaman Sea and the Maldives) classified this taxon as bleaching tolerant (Paulay and Benayahu 1999; Kayanne et al. 2002; Schumacher et al. 2005; Phongsuwan and Changsang 2012; Harri et al., 2014; Raymundo et al. 2019). Therefore, it has been suggested that *H. coerulea* may replace scleractinian taxa in the future as dominant reef-builders (Courtney et al. 2021). Counter to this, our findings suggest severe bleaching susceptibility of *H. coerulea*, and further research is warranted.

It is important to note that the symbiotic associations between coral hosts and their algal symbionts may contribute to the observed taxon-specific differences in bleaching response (Hume et al. 2020; Baker et al. 2004). Presently, data on species-specific coral host-algal symbiont associations are limited in Peninsular Malaysia (Lee et al. 2022) and require urgent investigation to identify heat tolerant taxa and associated holobiont compositions. Shifts in Symbiodiniaceae composition to heat tolerant algal species have been observed after periods of heat stress (Grottoli et al. 2014) and supposedly co-facilitate changes in bleaching hierarchies over time (Baker et al. 2004; Silverstein et al. 2015). However, novel associations do not universally persist (LaJeunesse et al. 2009; Hume et al. 2020), as fine-scale differences in thermal and depth regime on individual reef sites are also important determinants impacting the persistence of stress-induced changes in the Symbiodiniaceae composition (Baker et al. 2013; de Souza et al. 2023). Ultimately, quantifying such associations with reference to reef heterogeneity is required to understand mechanisms of heat tolerance of the coral host.

Bleaching response across- and within-reef scales

At the across-reef scale, our analysis of reef-specific diel temperature variations (DTR) shows that DTRs were significantly more variable at leeward sites for all seasonal time series of the bleaching period (ESM 5). Further, generalized linear model analysis revealed significant differences across depth and wind exposure overall (Table 1 and 2, ESM 8–9) resulting in the lowest bleaching response at shallow windward sites. This contrasts with previous studies that found that leeward coral reef sites harbor more thermally tolerant corals (McClanahan and Maina 2003; Pineda et al. 2013; Woolstra et al. 2020), putatively due to greater diel variability in thermal regimes (Oliver and Palumbi 2011; Barshis et al. 2018; Thomas et al. 2018).

With regard to depth differences, we found higher bleaching prevalence and response at 10–14 m depth than at 5–7 m

depth, echoing conclusions from previous studies that depth does not necessarily provide refuge from thermal coral bleaching (Frade et al. 2018; Venegas et al. 2019). However, in this study the observed pattern is the result of the relatively higher abundance of specific taxa that bleached less at shallow depth (e.g., massive *Porites*, *Porites* spp.). Ultimately, bleaching response as a function of depth is highly taxon-specific and varies across regions and local reef environments (Muir et al. 2017; Baird et al. 2018; Crosbie et al. 2019; Raymundo et al. 2019).

We found the bleaching response of *Porites* spp. to be significantly different at windward shallow compared to all other sites, irrespective of depth. Further, foliose *Pavona* did not bleach at windward shallow in either year, in contrast to leeward shallow sites (albeit sample sizes differed among sites). As coral taxa were distributed unequally across these spatial scales, it was not possible to compare more taxa across all sites. Thus, increasing the overall sampling area would be beneficial for future investigations. Additionally, environmental covariates such as in situ wind, temperature, and light measurements would be needed to establish corroborative relationships between taxon-specific bleaching response and across- or within-reef scales. Our data highlights that across- and within-reef scale phenomena are interconnected. The combined effects of wind and depth influence taxon-specific bleaching responses, implying that dynamic reef environments contribute to the differential bleaching response of hard coral taxa. Ultimately, known stressors that reduce coral fitness and potentially exacerbate the bleaching response, such as nutrient enrichment due to wastewater discharge (Donovan et al. 2021), are unlikely to have influenced the observed bleaching response, as windward sites are not near wastewater effluents (e.g., river estuaries, coastal resorts) and septic tanks are installed at leeward sites to prevent nutrient input to coral reefs.

Conclusions

The increasing spatial and temporal extent of thermal stress events is projected to result in more severe annual coral bleaching events on a global scale. However, detailed data are typically only available for a few regions, hampering the forecasting of bleaching trajectories under climate change. Here, we determined bleaching trajectories of 46 hard coral taxa across- and within-reef scales based on data recorded during the first reported back-to-back coral bleaching events in Malaysia between May 2019 and September 2020. We observed high levels of bleaching (55.21% and 26.63% of all surveyed colonies in 2019 and 2020, respectively) associated with high thermal stress levels when considering an nDHW metric that better explained observed in situ bleaching levels than the

common DHW metric (6.68 °C-weeks and 4.77 °C-weeks in 2019 and 2020, respectively, for the nDHW metric in contrast to 1.05 °C-weeks and 0.00 °C-weeks in 2019 and 2020, respectively, for the DHW metric). We found broad dispersion of taxon-specific bleaching prevalence, whereby susceptible taxa were found to exhibit bleaching at ~4.5 °C-weeks, while widespread and severe bleaching occurred at ≥ 6 °C-weeks (nDHW). The data gathered here provides a baseline to monitor and project bleaching prevalence and severity in Peninsular Malaysia as oceans continue to warm. To support field observations of differential bleaching of coral taxa, future studies should identify Symbiodiniaceae assemblages associated with heat stress susceptible and tolerant coral taxa.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-024-04495-2>.

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Author contributions SS designed and conceived the study, conducted the fieldwork, analyzed the data, and wrote the original draft. AYA analyzed the data, supported scientific framework development, and edited the original draft. CRV supported scientific framework development, data interpretation, and edited the original draft. All authors edited the final draft and granted approval to submit for publication.

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Data availability The datasets analyzed are available on the Github repository: <https://github.com/Coralku/Bleaching-Data-2019-2020>

Declarations

Competing interest. Author CRV is an associate editor at 'Marine Biology'. The authors have no further financial or non-financial interest to declare that are relevant to the content of this article.

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