Successive bleaching events (2019-2020) in Northeast Peninsular Malaysia revealed selective thermal acclimatization and susceptibility of hard corals at biophysical reef scale

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Abstract:

Based on current greenhouse gas emission trajectories, Malaysian coral reefs are predicted to experience severe annual coral bleaching events by 2043, imminently threatening the survival of Malaysian coral reefs within this century. However, there is no field data on how Malaysian coral reefs respond to successive sequences of coral bleaching. Numerous scleractinian taxa have shown the ability to acclimatize to thermal stress events after previous exposure to heat disturbances. Nonetheless, thermal tolerance and acclimatization potentials might corroborate with accelerating warming rates and increasing frequencies of thermal stress anomalies, necessitating repeated field studies at reef scale to investigate thermal tolerance and acclimatization of scleractinian taxa. Here, we studied two successive thermal stress events during the 2019 El Niño Southern Oscillation (ENSO) and during the onset of the La Niña Oscillation in 2020. We recorded the bleaching susceptibility of scleractinian taxa to document bleaching trajectories across fine temporal and environmental gradients in Northeast Peninsular Malaysia. In addition, we analyzed historic temperature trends to demonstrate rapid warming rates (0.17°C per decade) and high return frequencies of thermal stress anomalies. Despite high maximum temperatures in both years (31.07°C and 31.74°C, respectively), accumulated thermal stress was relatively low during the bleaching episodes (Degree Heating Weeks 1.05°C-weeks and 0.61°C-weeks, respectively) and marginally varied across reef scales (0.94°C-weeks, 0.76°C-weeks, 0.48°C-weeks in 2020), suggesting a widespread thermal sensitivity of most scleractinian taxa (55.21% and 26.63% bleaching incidence in 2019 and 2020, respectively). However, significant discrepancies between satellite and *in-situ* temperature data were found (0.63°C; SD±0.26). Bleaching susceptibility was highly taxon-specific and contrasted historical bleaching patterns (e.g., *Acropora* and *Montipora* showed high thermal tolerance). In 2020, successive heat disturbance moderately increased bleaching susceptibility of three taxa (*Galaxea*, *Leptastrea* and *Platygyra*) despite lower heat stress, while *Heliopora* was highly susceptible in both years. Bleaching analysis of taxa on biophysical reef scales revealed significant difference across depth, wind sites (e.g., leeward and windward), and the combined interactions of wind and depth (e.g., leeward shallow) on bleaching response were significant for numerous taxa. Findings suggest thermal acclimatization of fast-

growing taxa, whereby successive bleaching events and accelerating warming rates selectively pressure scleractinian assemblages.

Keywords: annual coral bleaching, thermal acclimatization, Malaysia, climate change, sea surface temperatures, bleaching resistance index, degree heating weeks.

Introduction

The world's oceans are the largest absorbers of energy derived from anthropogenic carbon-dioxide emissions (Pachauri et al., 2014 (IPCC)), resulting in an increasing rapidity of ocean warming (Stocker et al., 2014). As the oceans warm, abnormally high sea surface temperatures (SST) induce global coral bleaching events with catastrophic consequences for the world's coral reefs (Hughes et al., 2017). Coral bleaching refers to the whitening of coral tissue due to the disruption of its symbiotic relationship with its algae partner (Jaap, 1979; Jokiel and Coles, 1990). This symbiosis is essential for coral colony survival and is highly sensitive to thermal changes (Brown, 1997). Rapid ocean warming has thus been identified as the main threat to coral reefs worldwide (Hoegh-Guldberg, 2011), as the oceans have warmed 1°C over the past century (Hoegh-Guldberg, 1999), continuously exceeding the thermal maximum of scleractinian communities (Skirving et al., 2019; Van Hooidonk et al., 2020 (UNEP)). Consequently, coral reefs are anticipated to decline globally by the end of the 21st century and may not be capable of adapting to the projected increase in frequency and intensity of thermal events (Frieler et al., 2013), resulting in substantial shifts in coral reef assemblages and the baseline structure of these ecosystems (Loya et al., 2001; McClanahan et al., 2004; Hughes et al., 2018a). Nonetheless, several studies indicate high resilience of scleractinian communities to recurrent bleaching events (van Woesik et al., 2012; Fox et al., 2019), and thermal acclimatization might be occurring on broader levels (Sully et al., 2019).

Annual severe bleaching (ASB) is predicted for 99% of the world's coral reefs in this century (van Hooidonk et al., 2013), underscoring a need to understand how consecutive episodes of coral bleaching will impact scleractinian community assemblage on fine spatial scales. In Peninsular Malaysia, ASB is predicted to occur by 2043 (Van Hooidonk et al., 2017 (UNEP)), while regionally the first mass coral bleaching events were reported in 1998 and 2010 (Kushairi, 1998; Tan and Heron, 2011). Annual coral bleaching episodes are still scarce, but adverse in impacts (Donner et al., 2005). The cumulative impact of annual coral bleaching may significantly alter scleractinian community assemblages and counteract thermal acclimatization (Grottoli et al., 2014). Acclimatization responses are not linear and as stress frequencies exceed physiological thresholds, acclimatization potentials might be reduced and / or reversed (Schoepf et al., 2015; McClanahan, 2017). As a result of the increasing frequency of such disturbance events (Hughes et al., 2018b), it is no longer feasible to understand the multifarious impacts of coral bleaching by investigating isolated events, nor to assess ecosystem states without considering the legacy effects of disturbances and resulting ecological memory (Johnstone et al., 2016). Reportedly, the shrinking time-intervals magnify the deleterious impacts by selectively pressuring more susceptible scleractinian taxa (Edmunds, 1994), resulting in winners and losers (van Woesik et al., 2011). In contrast, consecutive events may result in a quick adaptive response based on strengthening interactions of successive episodes (Hughes et al., 2019).

In 2010, a change in the hierarchy of bleaching susceptibility of scleractinian taxa in southern Peninsular Malaysia suggested an increasing capacity of certain taxa to adapt to rising SST based on previous thermal and bleaching exposure (Guest et al., 2012). Acclimatization driven by

thermal susceptibility is highly variable among coral individuals and taxa (Marshall and Baird, 2000; Guest et al., 2016). On the level of coral reef community assemblages, research suggests that high variability in susceptibility to thermal coral bleaching is underlined by the thermal history and variability experienced (Thompson and van Woesik, 2009; Thomas et al., 2018). Thus, adaptive responses such as thermal acclimatization are not uniformly confirmed in scleractinian communities (Hughes et al., 2017). Since previous studies reported on scleractinian bleaching susceptibility in southern Peninsular Malaysia in 2010, ocean warming has accelerated on a global scale (Skirving et al., 2019), culminating in the most prolonged and extensive global coral bleaching event on record between 2014-2017 (Eakin et al., 2019). Thus, as thermal stress and associated bleaching events become more frequent, it is unclear whether higher warming rates reversed or counteracted acclimatization capacities of scleractinian taxa in Northeast Peninsular Malaysia and regionally. Fine-scale assessments, spanning over repeated bleaching episodes, are important to understand mechanisms of thermal acclimatization and to elucidate shifts in scleractinian community assemblages (Harrison et al., 2019). Furthermore, biological stress responses in hard corals are strongly correlated to environmental drivers (Fordyce et al., 2019). The bleaching susceptibility of scleractinian communities is influenced by abiotic-biophysical interactions (Page et al., 2019), including depth-related bleaching incidence (Bridge et al., 2014; Baird et al., 2018; Muñiz-Castillo and Arias-Gonzalez, 2021), and wind exposure (Skirving et al., 2006). Moreover, environmental factors may influence thermal acclimatization in surviving parent colonies and subsequently in their offspring (Wong et al., 2021). Hence, biophysical site characteristics are essential in understanding patterns of susceptibility and thermal acclimatization across environmental gradients. Such information, as well as the current vulnerability of scleractinian taxa in Peninsular Malaysia is unknown.

Under scenarios of continuous selection of bleaching tolerant species, subsequent reorganization of community assemblages and confounding stress factors of human origin that intensify bleaching response and regional reef decline (e.g., sewage outflow) (Wooldridge et al., 2012; Wiedemann et al., 2013), it is becoming important to derive thermal baselines from *in-situ* point measurements in combination with field observations of bleaching response (McClanahan et al., 2007b; Heron et al., 2016a), to better comprehend thermal acclimatization capacities and taxon-specific bleaching susceptibility at reef scale. Therefore, this study investigates the 1.) discrepancies between remotely sensed and *in-situ* temperature measurements to approximate reef-specific thermal bleaching thresholds and to analyse the accuracy of global web-based products (e.g., NOAA Coral Reef Watch) in identifying thermal thresholds at reef scale. In addition, 2.) the historical sea surface temperature trend at local reef scale was determined, as well as historical exposure to thermal anomalies above the upper threshold of scleractinian taxa. Furthermore, we document 3) taxon-specific susceptibility, recovery and mortality of scleractinian communities to thermally induced coral bleaching across the first annual sequence of coral bleaching in Northeast Peninsular Malaysia. During the thermal stress events in 2019 and 2020, 4) this study examined potentially disparate responses in bleaching susceptibility and incidence of scleractinian taxa across these two events. Lastly, to account for environmental co-drivers of thermal coral bleaching, 5) taxon-specific bleaching susceptibility across biophysical environmental gradients such as water depth and reef-specific wind exposure was recorded.

Materials and methods

Study site

The present study investigated four coral reef sites around Pulau Lang Tengah (5°47'N, 102°53'E; Pulau=island) within the Terengganu Marine Park in Northeast Peninsular Malaysia (Figure 1). Two sites on the windward side (Batu Bulan (BB) and Tanjung Telunjuk (TT)) and two sites on the leeward side (House Reef (HR) and Secret Reef (SR)) were selected to explore whether biophysical factors such as depth and wind exposure of reef sites moderate fine-scale differences in the bleaching response of scleractinian taxa. Wind frequency direction was determined using web-based products[1] and data references (Global Wind Atlas 3.0, 2020). Colony sample sizes across sites ranged between 323 and 663 colonies per site (mean 469.25 colonies^{-1}/site). Noteworthy, leeward sites are chronically exposed to high sedimentation rates and sewage outflow from coastal tourism development and nearby resorts. In contrast, windward sites (particularly BB), are not exposed to immediate coastal development and are likely less impacted by sewage outflow from the nearest beach resorts.

Sea surface, *in-situ* and historical sea surface temperature analysis

Temperature records for Pulau Lang Tengah were sourced from remotely sensed sea surface temperature (SST) datasets through the National Oceanic and Atmospheric Administration's (NOAA) next-generation operational daily global 5-km geostationary and polar-orbiting, blended night-only SST analysis, Coral Bleaching Monitoring Products (version 3.1, Coral Reef Watch, 2014), binned to the nearest 5 km^2 satellite pixel (5°46'30.0"N, 102°52'30.0"E) and accessed through the ERDDAP website[2]. The accumulation of heat is expressed using the thermal stress metric "Degree Heating Weeks" (DHW) (Wellington et al., 2001). Additionally, we investigated the spatial extent of thermal stress in 2019 and 2020, by analyzing SST data for five additional locations across the east coast of Peninsular Malaysia, ranging from Pulau Sibu (~420 km south, 2°13'14.7"N, 104°03'16.7"E), to Pulau Perhentian (~35 km north, 5°56'02.5"N, 102°43'51.5"E).

Mean nightly sea surface temperature values between April 1st, 1985 and December 31st, 2020 were averaged for each year and linearly regressed in R Studio version 4.1.0 (R Core Team, 2021) to examine recurrent warming trends of our study location. In further steps, seasonality was eliminated by averaging SST for the six warmest months of the year (April– September). These months experience the least rainfall, cloud cover and storms, factors that significantly reduce bleaching severity (MacKellar and McGowan, 2010; Skirving et al., 2014), and henceforth are referred to as the "bleaching season", as coral bleaching exclusively occurs between April and September. Natural fluctuations leading to variability in SST was estimated by the standard deviation of the mean and temperature ranges were defined as the difference in °C between the lowest and highest temperature measurement. Mean nightly sea surface temperatures were averaged for each decade, and past thermal disturbances were identified based on thermal anomalies that accumulated heat with values of DHW > 1°C-weeks (Liu et al., 2003; Kayanne, 2017). Coral bleaching occurs when SST exceed the climatologically warmest month of an area (MMM), by 1°C to create a coral bleaching hotspot (Glynn and D'Croz, 1990). Cumulatively, hotspots result in DHW (expressed in °C-weeks). DHW > 4°C-weeks induce ecologically significant bleaching, and DHW > 8°C-weeks results in ecologically significant mortality in scleractinian communities (Liu et al., 2006; Heron et al., 2016a; Skirving et al., 2019).

[1] https://globalwindatlas.info/
[2] https://pae-paha.pacioos.hawaii.edu/erddap/griddap/dhw_5km.html

Five automated temperature monitors (HOBO 64K Pendant©, Onset Computer Corporation, USA) were deployed at three locations adjacent to transect sites at 8 meters' depth. Data from TT and Batu Kucing (BK) reef was used to establish windward-site temperature regimes (Figure 1). *In-situ* measurements are not available for the first coral bleaching event in 2019, as monitor deployment was not conducted until the 11th of September, 2019. Thus, the comparative analysis of *in-situ* monitors with remotely sensed data is based on data ranging from the 12th of September 2019 – 30th September of 2020 (19,635 measurements), using mean nightly temperature values (recorded each night between 00:00 – 05:30). A Pearson correlation analysis was used to examine data sets trends over the time period observed. Climatologically, the warmest month of the year in Pulau Lang Tengah is routinely in May, and the remotely sensed MMM is 29.94°C. However, historical *in-situ* temperature data is not available, and the MMM based on *in-situ* measurements is unknown. Therefore, for 2020, the mean monthly temperature difference between remotely sensed and *in-situ* measurements for May 2020 was calculated. The resulting difference was applied to the MMM of 29.94°C to establish an *in-situ* derived MMM of 30.51°C in order to further calculate DHW values. This was repeated individually for each *in-situ* recording site.

Benthic community surveys

We hypothesize that rapid warming rates and more frequent thermal stress selectively influence thermal acclimatization potentials of scleractinian taxa and potentially prevent, counteract and reverse acclimatization potentials. Secondly, we investigated the response of scleractinian taxa to successive heat disturbances to better understand how such frequent heat stress will impact individual stress response in scleractinian taxa. As heat stress was less intensive in the second event, we particularly focus on taxa with equal or higher bleaching response in 2020 as compared to 2019. To differentiate between thermally tolerant and susceptible scleractinian taxa, a fine temporal analysis of the bleaching trajectory between June 2019 and June 2020 was conducted. Immediate bleaching response of scleractinian taxa was surveyed during thermal events in June 2019 and in June 2020, six and four weeks after SST exceeded the MMM by 1°C, respectively. Scleractinian community recovery from the 2019 event was surveyed in October 2019, 22 weeks post thermal stress onset. Surveys in April 2020, 50 weeks post thermal stress onset, were conducted to assess community recovery after the Northeast Monsoon season and before the next bleaching season in 2020. In this fashion, repeated and staggered assessment of the same scleractinian communities was carried out along permanently marked transect sites. A total of seven 10 x 1 m belt transects across the four sites (1,800 + coral colonies surveyed) were laid parallel to the shore on the shallower reef terrace between 5-7 m (mean depth 6 m), and on the reef slope, between 10-14 m (mean depth 12 m), to account for differences in bleaching susceptibility at multiple depths. Each survey transect was marked with rebar stakes or PVC pipes at the start, middle (at 5m) and at the end point, and transect markers were number tagged. Additionally, transects were video recorded during each survey occasion for reference as to ensure the correct repositioning and redeployment of each transect tape during subsequent surveys. The numbers of healthy and bleached colonies encountered along the belt were recorded and identified to genus

level following the Coral Finder 3.0 (Kelley, 2016). Only colonies whose colony centre was within the belt were recorded to avoid belt survey biases (Zvuloni et al., 2008). Bleaching severity categories were assigned for each coral colony: B1 (no bleaching), B2 (pale live and fluorescing colonies), B3 (≤33% of colony surface bleached), B4 (34% - 66%), B5 (67%-90%), B6 (>90% of colony surface bleached), where B5 and B6 are considered very severely bleached (Pratchett et al., 2013). Equally, dead corals were recorded to survey bleaching-associated mortality and colony mortality was separated into these categories: M1 (≤33% of colony surface dead), M2 (34% - 66%), M3 (67%-90%), and M4 (>90%). Percentages of colony surface bleached or dead were visually estimated by the same observer across all survey occasions. Fluorescent bleaching was considered as very mild based on experimental findings (Bollati et al., 2020; Voolstra, 2020). The calcified octocoral *Heliopora coerulea* was included in the analysis, and the genus *Porites* was separated into *Porites sp. 1* (massive and encrusting) and *Porites sp. 2* (*Porites rus*, *Porites monticulosa* and similar species). A complete list of all anthozoan taxa observed bleached, including scleractinian taxa not recorded during belt surveys, is provided in Supplementary S1.

Data and statistical analysis

Generalised Linear Models (GLM) (Nelder et al., 1972) with binomial distribution and a logit-link function were modelled to investigate coral bleaching susceptibilities (B1-B6) of selected scleractinian taxa (with at least ten observations, 11 taxa) in response to the effects of sampling time (June 2019, October 2019, April 2020, June 2020), wind exposure (leeward and windward), water depth (shallow or deep), taxon identity, and morphology. All explanatory variables were checked for multicollinearity prior to analysis. All GLM analyses were performed in R Studio version 4.1.0 (R Studio Team, 2021) using packages modEVA (Barbosa et al. 2014) and car (Fox and Weisberg, 2018). Following general linear model testing, we tested the interactive effects of depth and wind on site- and taxon-specific bleaching response using a Tukey's post-hoc analysis to compare each interaction individually. Interaction were tested at fine biophysical scale (e.g., leeward shallow, leeward deep, windward shallow and windward deep) using emmeans-package v1.6.3 as a post-hoc test (Lenth, 2021). Finally, a Friedman test in R software was used to individually compare bleaching susceptibility (BI) across bleaching years for taxa that increased or maintained their BI in 2020 (four taxa), as well as for taxa who showed markedly higher resistance to thermal stress in 2020 as compared to 2019 (seven taxa).

To compare bleaching susceptibility of scleractinian taxa across annual events and environmental gradients (leeward, windward, shallow, deep), taxa with at least ten observations (n≥10) at each site (e.g., ten colonies at leeward and ten colonies at windward) were selected. A standard Bleaching Index (BI) (McClanahan et al., 2007a) was calculated to express bleaching susceptibility of each taxon at each site (leeward and windward), depth (shallow and deep), and sampling time (June and October 2019, June 2020):

$$Bleaching\ Index\ (BI) = \frac{0B1 + 1B2 + 2B3 + 3B4 + 4B5 + 5B6}{5}$$

The BI weights the proportion of bleached colonies in each taxon by severity and is relative to the total number of observations of each taxon. To express this relationship, a Bleaching Resistance

Index (BRI) was calculated, where N_i is the total number of coral colonies in each taxon, and BI_i is the taxon-specific Bleaching Index:

$$Bleaching\ Resistance\ Index\ (BRI) = \frac{N_i - BI_i}{N_i}$$

The BRI ranges from 0.0-1.0, where BRI=1.0 equals no bleaching. When multiplied by 100, the BRI shows the percentages of unbleached colonies, complementing the Bleaching Response (BR) Index (e.g., McClanahan et al., 2007a). The sum of both indexes, BRI and BR, equals 100%. Furthermore, heat stress does not universally induce whole-colony mortality in all taxa, and partial mortality outweighs whole-colony mortality for numerous taxa (Baird and Marshall, 2002). Thus, heat stress induced mortality was separated from the Bleaching Index (BI) (as opposed to McClanahan et al., 2007a) and the Bleaching Induced Mortality Index (BIMI) was established instead, which accounts for partial- and whole-colony mortality as an immediate result of coral bleaching:

$$Bleaching\ Induced\ Mortality\ Index = \frac{0B1 + 1M1 + 2M2 + 3M3 + 4M5}{4}$$

In order to account for notable differences in the relative density of taxa across environmental gradients (e.g., leeward and windward sites, shallow and deep transects), the site-specific Bleaching Susceptibility Index (McClanahan et al., 2007b) was applied, where BR_i is the taxon-specific bleaching index following McClanahan et al. (2007b) and defined as [(BRI-1) x 100], D_i is the relative density of each taxon, and N the total amount of taxa:

$$\mathrm{BSI} = \sum_{i=1}^{N} \frac{\mathrm{BR_i} \times \mathrm{D_i}}{\mathrm{N}}$$

Summing each taxon's BSI gave a site-specific bleaching index factoring in the relative density and total number of taxa.

Results

Sea surface, *in-situ* and historical sea surface temperature analysis

Linear regression analysis of annual mean SST (R^2 = 0.46; $p<0.001$) and mean SST of the bleaching season (R^2=0.47; $p<0.001$) shows a warming trend since 1985 (Figure 2B and 2C), corresponding to an annual increase of 0.0166°C per year and 0.020°C per bleaching season. Starting in year 2001, minimum nightly SST started to steadily increase to above 27°C, and since 2015, the lower temperature range has not fallen below 27°C (Figure 2A). Mean SST increased rapidly since 2010, as SST during the bleaching seasons between 2010 and 2019 were 0.55±0.95°C (SD) higher as compared to mean bleaching season SST in 1985-1989, and 0.21±0.94°C higher than bleaching SST between 2000-2009 (Table 1). On average, 2020 and 2019 were the second (30.24°C±0.29°C) and fourth (30.12±0.59°C) warmest bleaching seasons since 1985, respectively. In addition to confirmed bleaching events in 1998, 2010, 2014, 2019, and 2020, six bleaching seasons between 1985 -2019 were identified that reached accumulated heat stress values of DHW

> 1°C-weeks. Two of these seasons occurred in 2013 and 2016, respectively, and reached similar or higher DHW values as in reported bleaching years in 1998, 2014, 2019 and 2020 (Table 1). Nine of the ten warmest years, and seven of the ten warmest bleaching seasons occurred between 2010 and 2020 (Supplementary S2).

Heat stress in 2019 and 2020 was observed across the entire extent of the east coast of Peninsular Malaysia, with the highest values being recorded around Pulau Sibu (DHW = 4.61°C-weeks and 1.90°C–weeks, in 2019 and 2020 respectively) in Southeast Peninsular Malaysia (Supplementary S3). At our study location, *in-situ* measurements and remotely sensed measurements followed closely correlated patterns over the recording period from September 2019 to September 2020 ($r=0.97$, $p<0.001$), with a mean difference of 0.53±0.25°C. However, *in-situ* temperature measurements were 0.63±0.26°C warmer when analyzing temperature data for the bleaching season, whereas bleaching season means were less correlated ($r=0.76$, $p<0.001$) (Figure 3). Accumulated heat stress in 2019 measured remotely reached 1.05°C-weeks, and 0°C-weeks in 2020, not predicting levels of coral bleaching observed *in-situ* accurately in either year. Based on the MMM derived from *in-situ* measurements, DHW in 2020 reached 0.61°C-weeks in 2020 when pooling all *in-situ* measurements from all recording sites. At the time of surveying during the second bleaching event in 2020, heat stress accumulated at minor levels at 0.18°C-weeks (equivalent to two days of temperatures 1°C above the MMM). Site-specific analysis revealed fine-scale differences in temperature thresholds and heat stress (Supplementary S4). Heat stress at windward BK (0.94°C-weeks; MMM=30.42°C) were slightly higher than heat stress at the leeward HR (0.76°C-weeks; MMM=30.50°C), and windward facing TT (0.48°C-weeks; MMM=30.60°C) during the 2020 bleaching season. In addition, minimum and maximum temperature ranges (HR 2.63°C; TT 3.23°C; BK 3.65°C) and estimated variability (HR SD±0.40; TT SD±0.47; BK SD±0.52) varied across windward and leeward sites. Nonetheless, observed bleaching levels did not correspond to the bleaching threshold as calculated by the *in-situ* derived MMM.

<u>Annual bleaching severity, recovery, and thermal acclimatization</u>

Taxon-specific differences in bleaching response were chiefly pronounced. In June 2019, 55.21% of colonies surveyed (n=1,882) showed signs of bleaching, with 30.29% (n=570) of recorded colonies beaching severely (Figure 4). Bleaching Index (BI) in June 2019 was 686.4 (BRI=0.64). *Heliopora coerulea* showed the highest susceptibility in June 2019, followed by *Goniastrea*, *Cyphastrea*, *Pavona*, *Echinopora* and *Porites sp. 1* (Table 2, Supplementary S5). In addition, *Porites sp. 2* showed a severe bleaching response (BI=152.8, BRI=0.66) but bleached less severely than *Porites sp. 1*. Of taxa historically considered most susceptible, *Acropora* (BI=44.2 and BRI=0.80) and *Montipora* (BI=9.6, BRI=0.81) demonstrated less thermal susceptibility and higher tolerance, whereas *Pocillopora* bleached more strongly (BI=11.6, BRI=0.60). Taxa with BRI > 0.90 were *Leptastrea*, *Symphyllia*, *Psammocora* and *Galaxea* (Table 2). Recovery rates were high in October 2019 as 91.68% of colonies surveyed (n=1,826) fully recovered and BI decreased significantly to 63.4 (BRI=0.97). The Bleaching Induced Mortality Index (BIMI) was universally low across all taxa (BIMI=31.25, n=1,826), whereas 1.10% of colonies (n=20) recorded full colony mortality, and 1.81% (n=33) experienced partial colony mortality. *Heliopora* showed the highest BIMI (11.25), recording 14.14% colonies with dead tissue, and 10.10% full colony mortality in October 2019. In April 2020, the mortality index recorded was 72.5 (n=128). No bleaching was recorded in April 2020, and thus all taxa recovered fully from the 2019 bleaching event. In June 2020, moderate and frequent bleaching was recorded with a bleaching incidence of 26.63% of

surveyed colonies (n=1,885). Bleaching intensity was significantly lower, as 6.26% of colonies bleached severely. General BI for all taxa was 231.6 (BRI=0.88), whereas *Heliopora coerulea* showed the highest bleaching response (BI=37.6, BRI=0.59). Bleaching susceptibility moderately increased for three taxa in 2020 (*Galaxea*, *Leptastrea* and *Platygyra*) and *Symphyllia* showed the same bleaching response despite lower heat stress in 2020 (Table 2). In contrast, *Cyphastrea*, *Goniastrea* and *Echinopora* doubled their BRI in 2020, and *Favites*, *Fungia*, *Pavona* and *Porites sp. 1* markedly increased their bleaching tolerance by at least 0.30. However, this change in bleaching susceptibility was only significant for *Fungia* (Friedman chi-squared = 4, df = 1, p-value = 0.0455) and *Porites sp. 1* (Friedman chi-squared = 4, df = 1, p-value = 0.0455). Of all *Acropora* morphologies, only corymbose *Acropora* bleached in 2020. Morpho-taxon specific bleaching response is shown in the Supplementary S5.

<u>Bleaching response on biophysical reef scale</u>

Bleaching incidence in 2019 was higher at leeward site (70.82%) compared to windward sites (44.85%). Generalized linear models tested seven taxa (n≥10 at both sites) for significant differences in bleaching response across leeward and windward sites. *Acropora*, *Echinopora*, *Fungia*, *Pavona* and *Porites sp. 2* bleached significantly less at windward sites in 2019 (Table 3), whereas in 2020, *Fungia* and *Porites sp. 1* bleached significantly less at windward sites (Table 3). Pooling data from both years and repeating the analysis revealed that *Acropora*, *Fungia* and *Pavona*, bleached significantly less at windward sites in general (Table 3). Primarily, leeward sites had a markedly higher BSI compared to windward in 2019 but not in 2020 (Table 4). Likewise, bleaching incidence was similar across leeward and windward sites in 2020 (26.96% and 25.63% respectively). Bleaching site susceptibility (BSI) and bleaching incidence was similar across multiple depths and years (56.19% at 6 meters vs. 53.46% at 12 meters in 2019), whereby in 2020 bleaching incidence was higher at greater depth (35.51% against 24.25%). Of the most abundant taxa (n≥10; 13 taxa), seven taxa showed a curvilinear decline in bleaching susceptibility with depth: *Acropora*, *Favia*, *Fungia*, *Galaxea*, *Goniastrea*, *Heliopora* and *Leptastrea*, and six taxa: *Pavona*, *Platygyra*, *Porites sp. 1*, *Porites sp. 2*, *Psammocora* and *Symphyllia* followed a reversed pattern, bleaching more at intermediate depth (Figure 5). This pattern was consistent across years, except for *Acropora* and *Platygyra*, who showed markedly contrasting bleaching patterns at these depths in 2020. Significant differences in bleaching response across depths were found for *Acropora*, *Favia*, *Fungia*, *Pavona*, and *Porites sp. 1* in 2019 (Table 5), and for *Acropora*, *Heliopora*, *Pavona*, *Platygyra*, *Porites sp. 1* and *Porites sp. 2* in 2020 (Table 5). Notably, all *Heliopora* colonies bleached at shallow sites in 2019 (Figure 5).

On genus level, Tukey's post-hoc analysis revealed significant differences between wind and depth interactions for numerous taxa (Table 6). Bleaching response was tested for five taxa with n≥10 (*Acropora*, *Fungia*, *Pavona*, *Porites sp.*1 and *Porites sp. 2*), and all five taxa were substantially less bleached in June 2019 at shallow windward sites as compared to other sites (Table 6). Apart from *Pavona*, this interaction was significant for all taxa in 2019, especially when compared to shallow leeward sites (Table 6). In particular, *Porites sp. 2*, showed markedly less bleaching in both years at shallow windward locations. Furthermore, *Porites sp. 1* was significantly different from shallow leeward sites as well deeper windward sites in 2019, and significantly different from deeper windward sites in 2020. Despite significant difference across depth in general for *Porites sp. 1* (bleaching more at intermediate depth), there was no significant difference between windward deep and leeward shallow in either year for *Porites sp. 1* and *Porites sp. 2*, highlighting

the interactive effect of depth and wind on bleaching susceptibility. Similarly, significant differences across depth were found for *Pavona*, bleaching more at greater depth (Table 5 and Figure 5), whereas differences in bleaching susceptibility of *Pavona* at leeward deep (BRI=0.10) was chiefly more pronounced compared to windward deep (BRI=0.80) (Table 6). At deeper leeward sites, *Pavona* showed a very severe bleaching response, and was significantly more bleached here in both years as compared to shallow leeward sites.

Discussion

Historical sea surface temperature analysis

Linear regression analysis revealed a warming trend since 1985 (Figure 2) of 0.17°C per decade, while this warming trend is more pronounced during the bleaching seasons (0.20°C). Since 1986, the ocean has absorbed up to eight times as much energy-derived heat as previously between 1958 and 1986, resulting in uninterrupted warming (Cheng et al., 2021). Since industrialization, the oceans have warmed by 1°C until the early 2000s (Stocker et al., 2014; Pachauri et al., 2014, (IPCC)). Overall, this analysis found an expeditious and pertinent warming of 0.58°C since 1985. Analogous to globally accelerating warming rates over the past decade (Skirving et al., 2019), warming rates accelerated locally over the last decade with nine of the ten warmest years being recorded since 2010 (Figure 2; Supplementary S2), whereby 2020 was the second warmest bleaching season on average locally, coinciding with the warmest year of mean ocean temperatures globally (Cheng et al., 2021). Bleaching in 2020 occurred outside of an El Niño Southern-Oscillation (ENSO) associated temperature extreme, furthermore underscoring the diminishing relationship between mass bleaching events and extreme temperature anomalies in ENSO years, chiefly highlighting the impacts of globally observed warming patterns on local reef scale (Hughes et al., 2018b). Based on bleaching susceptibilities of taxa reported here and temperature trends at local and global scale, we argue that mild to moderate coral bleaching (particularly of susceptible taxa) is now likely to occur annually in Northeast Peninsular Malaysia during peak seasonal temperatures between April-September (Figure 2 and 3) and irrelevant of ENSO temperature extremes.

Of 11 thermal anomalies with DHW > 1°C-weeks, six anomalies were recorded over the past decade (Table 1). Bleaching occurrence in Northeast Peninsular Malaysia was reported *in-situ* in 1998 (Kushairi, 1998), in 2010 (Tan and Heron, 2011), in 2014 (Reef Check Malaysia, 2014) and during this study in 2019 and 2020. Furthermore, coral bleaching was observed at mild to moderate levels in Southeast Peninsular Malaysia in 2019 and 2020 (Reef Check Malaysia, 2019; Reef Check Malaysia, 2020) at higher levels of thermal stress (Supplementary S3). In 2016, thermal stress reached a maximum of 1.01°C-weeks in mid-July, but bleaching was not observed *in-situ* in Northeast Peninsular Malaysia (Szereday, personal observation) and neither in Southeast Peninsular Malaysia (Affendi, personal observation). In 1998, coral bleaching in Malaysia was reported for the first time reaching moderate levels (≤30% bleaching incidence), and resulting in low level mortality (Kushairi, 1998). Coral bleaching was severest in 2010, with coral bleaching incidence >50%, and severe full colony bleaching was observed for >66% of coral colonies at DHW levels of above 5°C-weeks (Tan and Heron, 2011). Moreover, coral bleaching in 2010 was observed until 25 m of water depth, and mortality levels were significant (Guest et al., 2012). *In-situ* field observations of coral bleaching occurrence in 1987, 1990, 1991, 2001 and 2013, when thermal anomalies exceeded >1°C-weeks, are not available and it is unknown whether bleaching occurred in these years. Observations from 2016 further suggest that bleaching does not occur

universally at DHW > >1°C-weeks, as confounding environmental factors (e.g., irradiance, water flow, vertical mixing and nutrient availability) are likely co-determining thermal stress experienced *in-situ* (Brown, 1997). The Southwest Monsoon starts annually in June and results in strong winds, storms and upwelling (Akhir et al., 2015), and likely plays a factor in cooling seawater temperatures after the annual SST peak in May and June. This may have prevented coral bleaching in 2016 as thermal stress (resulting from extreme ENSO) started to rise during the onset of the Southwest Monsoon, rather than in April and May as in 2010 and 2019, when mass bleaching was observed. Nonetheless, there is reported evidence suggesting that numerous bleaching events and associated mortality have occurred in recent history (1998, 2010 and 2014), possibly influencing thermal tolerance in surviving colonies. The 2014-2016 ENSO events resulted in the most severe and widespread pan-tropical coral bleaching event (Eakin et al., 2019), whereby in 2014 some degree of bleaching induced mortality is plausible (Reef Check Malaysia, 2014). These field observations and studies suggest that DHW >1°C-weeks likely represent a gross underestimation of thermal stress experienced *in-situ* by hard corals in Northeast Peninsular Malaysia, but are a useful indicator to highlights periods of positive thermal anomalies that are commonly induced by global weather extremes such as ENSO. Ultimately, mean seawater temperatures are perpetually rising around Pulau Lang Tengah (Figure 2), in addition to higher frequencies of thermal anomalies that surpass the thermal maxima of scleractinian taxa, causing repeated thermal stress. Regardless of differences in thermal tolerance and low mortality rates post bleaching events as those reported here (Figure 4 and Supplementary S5), such warming trends and resulting bleaching events selectively pressure scleractinian communities by altering scleractinian community assemblages (Loya et al., 2001; Baker et al., 2008, Hughes et al., 2018a), and likely influence demographic processes in surviving colonies who suffer high bleaching severity, such as massive *Porites* (Morais et al., 2021). Thus, severe annual coral bleaching will represent an imminent risk to coral reef survival and integrity (Van Hooidonk et al., 2017 (UNEP)). Immediate action to reduce greenhouse gas emissions is the only effective long-term conservation strategy in order to prevent systematic coral reef collapse (Van Hooidonk et al., 2016; Frieler et al., 2013; Hughes et al., 2017).

<u>Annual bleaching severity, recovery, and thermal acclimatization</u>

We acknowledge that genetic and cellular process are underpinning heat stress response in hard corals and that these can only be investigated on species level (Grottoli et al., 2014; Schoepf et al., 2015; Guzman et al., 2018). However, there is strong evidence that certain functional traits required for establishing thermally tolerant populations after large scale disturbance events, are phylogenetically conserved on genus level (Darling et al., 2012; Morais et al., 2021). Such traits include growth, fecundity and reproductive mode, and further supporting evidence is presented by Alvarez-Noriega et al. (2016), who suggest that fecundity can be predicted by coral colony morphology. In this study, we observed scleractinian taxa that possess these functional prerequisites (such as *Acropora*, and *Montipora*), to have reversed their historical bleaching hierarchy, based on low rates of bleaching severity and low rates of bleaching associated mortality. Supposedly, preceding bleaching events eliminated thermally susceptible individuals from the population. Subsequently, successful reproduction and recruitment of the surviving genotypes and taxa with fast growth and reproduction (Darling et al., 2012), perchance resulted in a directional selection since 1998 and 2010 of thermally tolerant genotypes of taxa historically classified as thermally susceptible (Edmunds, 1994; Thompson and van Woesik, 2009). Dramatic short-term recovery (e.g., <5 years) of depleted *Acropora* populations after bleaching events in 2016 and 2017

has been evidently highlighted on the Great Barrier Reef, whereby genus-wide recovery was facilitated by traits such as quick growth and reproduction (Morais et al., 2021). Furthermore, recent studies suggest that thermal stress does not impede heritability of functional traits responsible for growth and survival (Bairos-Novak et al., 2021), and greater thermal plasticity in surviving offspring has been demonstrated (Wong et al., 2021). Nonetheless, populations of *Acropora* and *Montipora* (as well as other historically susceptible taxa) have likely severely declined compared to pre-2010 levels across the Malaysian Peninsular (Toda et al., 2007), leaving behind large fields of coral rubble unsuitable for coral recruitment (Szereday, unpublished data). Thus, thermal acclimation of these taxa is possibly offset by unfavorable conditions (e.g., substrate availability and monsoon waves) for substrate recolonization and surviving populations will regionally struggle to recover to pre-disturbance levels.

Overall, this study reveals taxon-specific variations in thermal susceptibility and post-bleaching acclimatization similar to those in Southeast Peninsular Malaysia and Singapore during the 2010 mass bleaching event (Guest et al., 2012; Guest et al., 2016). Conferring these last records of taxon-specific bleaching incidence in Peninsular Malaysia, bleaching incidence and intensity was higher in 2019 for numerous major taxa despite more heat stress in 2010 (Supplementary S6). In contrast, mortality rates driven by heat stress were markedly higher in 2010, readily explained by the DHW theory where mortality rates increase with higher DHW. In general, mortality rates observed during this study did not substantially differ from expected levels of mortality due to other natural causes (e.g., predation, disease, physical breakage etc.) (Harriot, 1985). Nevertheless, we report high bleaching incidence and intensity for taxa such as *Porites sp.1*, *Porites sp. 2*, *Goniastrea* and *Cyphastrea*. This may point to worrying trends where certain scleractinian taxa increase their sensitivity after repeated and continuous events of heat disturbance. Of all taxa with $n \geq 10$, *Psammocora*, *Acropora*, *Galaxea*, *Leptastrea* and *Sympyhllia* were the most thermally resistant taxa across both years, whereas *Psammocora* was the only taxa to not bleach in 2020. Despite lower heat stress in 2020, *Galaxea*, *Leptastrea* and *Platygyra* were moderately more susceptible to bleaching in 2020 (higher BI), while the bleaching response of *Symphyllia* remained unchanged, suggesting that annual sequences will selectively pressure community assemblages and counteract thermal tolerance in certain taxa. Experiments on species-specific trends have demonstrated that annual exposure can weaken cellular processes involved in thermal tolerance (Grottoli et al., 2014; Schoepf et al., 2015), turning “winners” into “losers” or vice versa (Van Woesik et al., 2011). Our findings suggest that while fast-growing taxa such as *Acropora* and *Montipora* may adapt to higher thermal stress after directional selection (Figure 4), other taxa possibly do not possess similar life-history strategies and natural capacities due to physiological differences and phenotypic plasticity (Darling et al. 2012; Thomas et al., 2018). Such species-specific differences might explain the diverging responses of taxa seen in this study. For instance, three taxa (*Galaxea*, *Platygyra* and *Leptastrea*) were moderately more susceptible to bleaching in year 2020, whereas *Cyphastrea*, *Echinopora*, and *Goniastrea* were more bleaching tolerant (BRI). *Porites sp. 1*, *Pavona*, *Fungia*, and *Favia* bleached considerably less in 2020 (Table 2), albeit accumulated heat stress was lower in 2020 (Figure 3). *Pocillopora* represented the only major reef-building taxa with fast growth and reproduction not showing higher bleaching tolerance as historically known (Pratchett et al., 2013; Heron et al., 2016a). As high bleaching incidence and susceptibility are reasoned with levels of heat stress experienced (Liu et al., 2003; Liu et al., 2006; Kayanne, 2017), it can be considered that the stronger bleaching response of *Galaxea*, *Platygyra*, and *Leptastrea*, observed in 2020 would further increase to significantly different levels when exposed to heat stress similar to 2019 Likewise, bleaching levels of taxa with lower bleaching susceptibility in 2020 may increase under

slightly higher thermal stress levels as in 2019. However, when conferring *in-situ* models for 2020, differences in thermal stress across both episodes were minimal (1.05°C-weeks vs 0.61°C-weeks).

One notable finding of this study is the high bleaching susceptibility of *Heliopora spp*. (Table 2). In both years, *Heliopora* showed the highest bleaching incidence, severity and mortality of all surveyed taxa, in particular at shallow sites (Table 5, Figure 5 and Supplementary S7). A wide range of field studies conducted in numerous Indo- and Central-Pacific regions (e.g., Palau, Japan, Western Australia, Kiribati) as well as the Indian Ocean (e.g., the Andaman Sea and the Maldives), repeatedly classified this taxon as heat tolerant (Paulay and Benayahu, 1999; Kayanne et al., 2002; Schumacher et al., 2005; Donner et al., 2010; Phongsuwan and Changsang, 2012; Harri et al., 2014; Richards et al., 2018). Supposedly, accretion rates of *Heliopora* increase during positive thermal anomalies, resulting in competitive advantages over scleractinian taxa (Atrigenio et al., 2017; Guzman et al., 2019). Therefore, it has been suggested that species of *Heliopora* may replace scleractinian taxa in the future as dominant reef-builders (Richards et al., 2018). To our knowledge, our findings are the first to report high bleaching susceptibility of *Heliopora sp.*, and further research is warranted to elucidate mechanisms that may have reduced its thermal tolerance in Northeast Peninsular Malaysia. Firstly, environmental factors such as irradiance may play a factor. Bleaching levels of *Heliopora* were severe at both depths surveyed. However, bleaching severity was significantly less in deeper reefs in 2019 and 2020 (Table 5 and Figure 5). This is paradoxical, as *Heliopora* is well-known to inhabit shallow reef areas in living and fossil assemblages (Colgan, 1984; Zann and Bolton, 1985). Secondly, symbiotic partnerships may be a driving factors. In the Andaman Sea, *Heliopora* has thus far been identified to host the thermally tolerant zooxanthellae clade D2 (Lajeunesse et al., 2010), whereas generalist clades of *Symbiodinium sp*. have been identified in association with both *Heliopora* species in Western Australia (Clade C1), and clade C3 is known from the central Pacific and the Philippines (Pochon et al., 2010; Guzman et al., 2018; Richards et al., 2018). Moreover, Guzman et al. (2018) identified an array of genes (e.g., heat shock protein and antioxidants) in *Heliopora coerulea* that are involved in environmental stress response, and mixotrophy is widespread in octocorals to reduce reliance on symbiotic partnerships (Fabricius and Klumpp, 1995). Further research is necessary to understand whether the observed susceptibility of *Heliopora* in Pulau Lang Tengah is associated to any of the above factors, and whether *Heliopora* is generally a bleaching susceptible taxon in Northeast Peninsular Malaysia and the Sunda Shelf ecoregion.

Perchance, high warming rates and more frequent thermal stress may offset mechanisms of thermal tolerance for certain taxa, whilst simultaneously propelling acclimation for species with fast-growth and reproduction. For instance, Guest et al. (2012) argue that faster thermal acclimatization rates of scleractinian taxa in southern Peninsular Malaysia compared to reefs in northern Sumatra were arguably co-facilitated by lower warming rates. In Northeast Peninsular Malaysia, reported warming rates are near equal to reefs in northern Sumatra (0.0166°C vs. 0.0161°C) and higher than those in southern Peninsular Malaysia in 2010 (0.0166°C vs. 0.009°C). Additionally, higher warming rates are increasing the return frequency of high-temperature anomalies resulting in more frequent heat disturbances. Thus, such rapid warming rates may have co-led to the (annual) variations in taxon-specific bleaching susceptibility observed in this study and partially elucidate temporal and spatial variations between Guest et al. (2012) and findings presented here. In summary, bleaching responses of scleractinian taxa vary among time and space (McClanahan 2004), whereby bleaching susceptibility and thermal tolerance are not equivocal across larger spatial scales and may be reversed when primary stressors agents such as frequent heat stress

become overly prevalent. Ultimately, annual coral bleaching results in selective pressure even when thermal stress is not sufficient to trigger mass mortality (Hughes et al., 2019), can counteract and lower the acclimatization potential of taxa based on species-specific traits, and finally ameliorates diverging bleaching responses if heat stress will continue to increase in magnitude and frequency.

Bleaching response on biophysical reef scale

Fine differences in scleractinian bleaching response at marginal differences of thermal stress were observed and may point to a variety of confounding factors that influence and / or induce coral bleaching at low levels of heat stress. For instance, the rapidity of thermal stress onset may influence the severity and incidence of bleaching (Fordyce et al., 2019). Secondly, cloud cover and subsequent irradiance, water flow and vertical mixing may significantly magnify bleaching stress even under low levels of heat stress (Nakamura and van Woesik, 2001; MacKellar and McGowan, 2010; Page et al., 2019), and increasing eutrophication likely reduces bleaching resilience in hard corals (Wooldridge et al., 2012; Wiedemann et al., 2013). Such factors may have acted synergistically with high seawater temperatures in 2019 and 2020, and this study did not investigate such environmental factors directly. Furthermore, it cannot be excluded that the diverging and less severe bleaching response of certain (e.g., fast-growing) taxa is not a result of shifts in species composition post severe bleaching events in 1998 and 2010, where more resistant species have proportionately replaced susceptible species (McClanahan and Maina, 2003; van Woesik et al., 2011; McClanahan, 2017; Hughes et al., 2018a). Mechanism of species-specific bleaching thresholds include genotypic predisposition (Palumbi et al. 2014; Dixon et al. 2015), host-specific physiological traits (Fitt et al., 2009), and symbiotic type (Berkelmans and van Oppen, 2006). However, taxonomically driven susceptibilities may be steered by environmental forces impacting biological stress expressions while determining species distribution along environmental gradients. Shifts in species composition can be found with increasing depth (Roberts et al., 2015), and differentiated bleaching susceptibility of species at multiple depths is common (Bridge et al., 2014; Muir et al., 2017; Muñiz-Castillo and Arias-Gonzalez, 2021). Here, two patterns of bleaching response across multiple depths were found: either a constant decline with increasing depth (seven taxa), or an increase of bleaching severity with increasing depth (six taxa). Baird et al. (2018) found that bleaching incidence declined for most taxa with depth on the Great Barrier Reef in 2016. In contrast, studies on oceanic reefs in Australia found several pronounced non-curvilinear responses of taxa similar to our findings (Crosbie et al., 2019). Particularly the bleaching patterns of *Porites sp. 1* were strikingly similar, bleaching more severely at intermediate depth. Likewise, patterns seen here for *Pavon*a are reflecting patterns seen by Baird et al. (2018), where bleaching response increased at intermediate depth. Such findings highlight both consistencies and dissimilarities across time and space that may be propelled by a complex set of factors such as solar radiation, cloud cover and species acclimation (MacKellar and McGowan, 2010; Muir et al., 2017). Furthermore, vertical mixing of the water column leads to increased water flow and higher light scattering (Fordyce et al., 2019; Page et al., 2019), and thus wind exposure plays an additional role in determining bleaching incidence and severity by modulating light attenuation and water flow at reef scale (Lesser, 1997; Nakamura and van Woesik, 2001). Windward exposure significantly impacted the bleaching responses of *Acropora*, *Echinopora*, *Pavona*, *Porites sp. 1* and *Porites sp. 2* (Table 3), bleaching significantly less at windward sites. Indeed, a differential thermal regime at leeward sites might be a confounding factor, as temperature ranges (HR 2.63°C; TT 3.23°C; BK 3.65°C) and variability (HR SD±0.40;

TT SD±0.47; BK SD±0.52) were narrower during the bleaching season at the leeward sites in 2020 (Supplementary S4). Nonetheless, fine-scale temperature regimes require long-term investigation at multiple depths, not presented here. Additionally, there were large discrepancies in the distribution of taxa across such wind and depth environments (Table 3; Table 5), resulting in few taxa being examined and skewing results due to sample sizes. Taxa that were equally abundant across wind sites are *Echinopora* and *Porites sp. 2* (in 2019), and seven taxa were equally distributed across depth: *Favia*, *Heliopora*, *Leptastrea*, *Platygyra*, *Pavona*, *Porites sp. 1* and *Symphyllia*. Furthermore, we tested the interactive effect of depth and wind on bleaching response for taxa with sufficient observations and compared interactions individually (Table 6). At fine biophysical reef scale, numerous taxa exhibited significant differences in bleaching susceptibility. Notably, *Pavona* was particularly tolerant at shallow windward sites and especially susceptible at deeper leeward sites (Table 6). The latter is chiefly exposed to sedimentation stress, which possibly magnified the bleaching response observed. Additionally, species-specific thermal response may have determined high site susceptibility here, as surveyed *Pavona at* both leeward depths were exclusively *foliose Pavona (e.g., Pavona cactus)*, which dominated the scleractinian assemblage at this scale in both years (n 2019 = 59 of 144, n 2020 = 63 of 155). Moreover, *Acropora* was more susceptible at shallow leeward sites and mostly bleached at mild levels (e.g., fluorescing), whereby this likely represents a species-specific susceptibility as most *Acropora* recorded here are *hispidose Acropora* (e.g., *Acropora longicyathus*, see Supplememtary S5). This morpho-taxon was almost exclusively recorded at shallow leeward sites (140 of 145 colonies recorded). Apart from *foliose Pavona* and *hispidose Acropora*, further significant taxon-specific variations in bleaching susceptibility were found at biophysical scales (Table 4), which are likely not explained by species identity alone. For instance, abundant taxa such as *Fungia, Porites sp.1* and *Porites sp. 2* were significantly more susceptible to bleaching at shallow leeward than at shallow windward sites. Particularly, *Porites sp.1* and *Porites sp. 2* showed significant differences across windward and leeward sites, as well as across depth (Table 3, Table 5 and Figure 5). When comparing individual such interactions at finer scale, bleaching response was consistently lowest at shallow windward sites (Table 6), as the combined effects of wind and depth are possibly overarching the isolated effects of wind and depth on bleaching response of these taxa. For example, comparative Tukey's post-hoc tests of windward deep and windward shallow, as well as leeward shallow and windward shallow were significant for *Porites sp. 1*, whereas leeward shallow and windward deep were not significantly different, indicating similar thermal thresholds of *Porites sp. 1* at leeward shallow and windward dep. This highlights higher bleaching thresholds at shallow windward sites and site-specific factors that over mask bleaching patterns across depth. Similarly, *Porites sp. 2* showed significantly higher bleaching tolerance at shallow windward sites during both bleaching events (Table 6). Although only these five taxa were tested due to sample size, these results strongly suggest that numerous taxa are more prone to coral bleaching at shallow sites with less wind exposure. However, it cannot be ruled out that such contrasting responses are not at least partially due to sewage discharge by nearby beach resorts, as such local pressure may magnify bleaching severity by reducing colony fitness in general (Wooldridge et al., 2012; Wiedemann et al., 2013). This study does not present records of nutrient content across leeward and windward sites, but impacts from sewage discharge are unlikely at windward sites as these are not in close proximity to river estuaries, coastal development or other similar sources of pollution and sedimentation. Additionally, *in-situ* measurements at three sites suggest fine scale differences in thermal thresholds and therefore temperature difference are a likely co-driver of the observed differences in bleaching response (Supplementary S4). We do not present *in-situ* temperature measurements

across multiple depths at these sites and thus our results provide preliminary insights into such biophysical bleaching response dynamics. Further investigations focusing on species-specific susceptibility across a larger sampling area, in combination with environmental data and temperature measurements across multiple depths are required to better understand the interactive effects of wind, depth, temperature and local site pressures (e.g., sewage pollution) on taxon- and species-specific bleaching susceptibility at biophysical reef scale.

Bleaching thresholds at reef scale: *in-situ* vs. satellite temperature monitoring

The 2019 and 2020 thermal events were similar in magnitude and exceeded the thermal maxima of scleractinian communities. Remotely sensed and *in-situ* measurements were closely correlated (annual mean Pearson r=0.97, p<0.001; bleaching season Pearson r=0.76, p<0.001). However, the observed average differences between measurement tools during the 2020 bleaching season (0.63±0.26°C) suggests that remotely sensed measurements are possibly misestimating accumulated heat stress, similar to reports by Guest et al. (2012) in Southeast Peninsular Malaysia. Although satellites measurements are well-suited to determine heat stress, bleaching indices and temperature trends on larger scale (Heron et al., 2014), choosing the best-fit model and most accurate bleaching indices remains a challenge when historical measurements are absent, especially over fine spatial and temporal scales. Degree-heating weeks is an operational web-based product at a global scale. Remotely sensed temperature data is recorded by multiple satellites and sensors and is calculated by an algorithm combining past and present data within and beyond the selected 5 km^2 grid. Consequently, due to changes in algorithm, sensors, and individual satellite accuracy, remotely sensed measurements represent an estimation of the real temperature experienced at any given location (Heron et al., 2014; Liu et al., 2014). However, *in-situ* measurements, are accurate point measurements. In 2019, 55.21% of all surveyed colonies bleached, with 30.29% of colonies bleaching very severely (>66% of colony surface). Such ecologically significant bleaching responses are known for DHW values exceeding at least 4°C-weeks (Eakin et al., 2010; Liu et al., 2014; Heron et al., 2016a). Bleaching thresholds of scleractinian taxa used in this study are based on web-based products, demonstrated to under- and overestimate heat stress experienced *in-situ* (McClanahan et al., 2007b; Kayanne, 2017). Partly, such discrepancies are expected errors of satellites recording near-shore (e.g., reflection from landmasses), requiring measurements to be recorded further out at sea (here 2.5 km from the islands shore), where lateral and vertical movement of water reduces SST, compared to *in-situ* reef measurements in shallower and more stagnant coastal waters. Moreover, selecting a "one size fits all'-model is not feasible when considering the amount of highly localized stressors that may exacerbate coral bleaching by reducing overall community fitness (Brown, 1997; Wooldridge et al., 2012; Wiedemann et al., 2013). Deriving the MMM by interpolating *in-situ* measurements on satellite data did offer a closer explanation of the bleaching incidence in 2020 than satellite derived data. This Model suggests that scleractinian taxa possess a markedly higher temperature threshold (MMM 30.51°C + 1°C), but lower bleaching resistance, as 0.18°C-weeks (equivalent to two days of 1°C above the MMM) sufficed to trigger widespread and moderate coral bleaching in June 2020 (BI=234.2, BRI=0.88), affecting 17 of the 18 most abundant taxa and 20 of 33 taxa overall. In Japan, low levels of heat stress (e.g., <3°C-weeks) resulted in ecologically significant and widespread bleaching (Strong et al., 2002), underscoring that global threshold values (such as DHW 4°C-weeks) do not apply universally at reef scale. As discussed, species assemblages, symbiont identity, environmental, and physical factors co-determine inter-annual and local bleaching response (Baker et al., 2004; Baker et al., 2008), and thus algorithms defining thresholds

need to become more sophisticated. Ultimately, runaway ocean warming may have additionally propelled a higher bleaching sensitivity, as discussed above, since observed bleaching responses do indicate a general sensitivity to above thresholds temperatures.

It cannot be ruled out that thermal thresholds have not been overestimated rather than underestimated. Adding the mean monthly difference of *in-situ* and remote data to satellite measurements for each respective month (e.g., 0.57°C for May 2020 applied to each satellite measurement in May 2020), while keeping the predetermined MMM threshold of 29.94°C +1°C (compared to 31.51°C), would result in DHW of 9.92°C-weeks in 2020 and severe thermal stress. In this scenario, scleractinian taxa demonstrate mechanisms that increase thermal tolerance after experiencing acute thermal stress (Thompson and van Woesik, 2009; Thomas et al., 2018; Fox et al., 2019). Nonetheless, neither model readily explained the bleaching levels observed, whereas immediate impacts from secondary sewage outflow can be ruled out for at least four sites (all windward). In conclusion, longer-term *in-situ* temperature data over environmental gradients combined with field observations of coral bleaching incidence and severity are needed to accurately identify the current thermal baseline and tolerance of scleractinian communities at reef scale in northeastern Peninsular Malaysia. However, based on these findings, a conservative estimate would suggest that bleaching of susceptible taxa starts to occur in Northeast Peninsular Malaysia when temperatures exceed 31.0°C. Ultimately, this study provides a valuable diagnostic for the regional understanding of coral bleaching susceptibility, thermal resilience and highlights the severe future consequences of unchecked global warming for tropical marine ecosystems.

Conflict of interest

The authors declare no conflict of interest.

Author contributions

SS designed and conceived the study, conducted the fieldwork, analyzed the data and wrote the original draft. AYA conceived the study, analyzed the data, and edited the original draft. All authors edited the final draft and granted final approval to submit for publication.

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Table 1| Mean decadal sea surface temperatures (°C) and temperature anomalies exceeding Degree Heating Weeks (DHW) 1°C-weeks are shown for Pulau Lang Tengah, Northeast Peninsular Malaysia. Years with observed and reported coral bleaching events are highlighted in grey and the source of *in-situ* coral bleaching observations is provided. Temperature measurements are sourced from National Oceanic and Atmospheric Association (NOAA), Coral Reef Watch (CRW) product, 2014, version 3.1.

Decade	Mean annual SST °C (±SD)	Mean SST Bleaching Season °C (±SD)
1985-1989	28.86 (0.94)	29.42 (0.95)
1990-1999	28.88 (1.02)	29.55 (1.02)
2000-2009	29.05 (0.97)	29.76 (0.94)
2010-2019	29.30 (0.95)	29.97 (0.95)

Year	Mean SST Bleaching Season (°C)	DHW (°C-weeks)	Field observation
1987	29.76	1.49	-
1990	29.35	1.14	-
1991	29.79	2.10	-
1998	**30.13**	**0.34**	**Kushairi, 1998**
2001	29.79	1.36	-
2010	**30.38**	**5.16**	**Tan & Heron, 2011**
2013	29.97	1.03	-
2014	**30.10**	**1.60**	**Reef Check Malaysia, 2014**
2016	30.09	1.01	No bleaching (Szereday, personal observation)
2019	**30.12**	**1.05**	**This study**
2020	**30.24**	**0.00**	**This study**

Table 2| Bleaching Index (BI) and Bleaching Resistance Index (BRI) of the most abundant scleractinian taxa during two successive bleaching events in June 2019 and June 2020. The Bleaching Induced Mortality Index (BIMI) is shown for surveys conducted in October 2019.

	Jun-19			Oct-19			Jun-20		
Genus	**n**	**BI**	**BRI**	**n**	**BI**	**BIMI**	**n**	**BI**	**BRI**
Acropora	220	44.2	0.80	158	0.0	0.75	171	2.6	0.98
Cyphastrea	19	11.4	0.40	25	0.0	0.00	22	1.8	0.92

Echinopora	34	19	0.44	25	0.0	0.5.0	24	1.0	0.96
Favia	71	12.8	0.82	96	4.6	1.25	114	4.8	0.96
Favites	38	16.4	0.57	35	0.0	0.25	35	2.6	0.93
Fungia	115	45.2	0.61	120	13.2	0.50	137	12.0	0.91
Galaxea	96	1.4	0.98	110	0.0	0.00	101	4.8	0.95
Goniastrea	52	34.2	0.34	61	1.8	0.00	44	6.6	0.85
Heliopora	122	100.4	0.18	99	24	11.25	92	37.6	0.59
Leptastrea	69	4.6	0.93	72	1.0	0.00	80	6.8	0.92
Montipora	51	9.6	0.81	40	0.4	1.25	44	1.8	0.96
Pavona	144	84.4	0.41	125	6.2	2.25	130	33.3	0.74
Platygyra	68	18.6	0.73	95	6.0	1.50	103	19.2	0.81
Pocillopora	29	11.6	0.60	31	1.2	1.50	38	5.6	0.85
Porites sp. 1	202	106.6	0.47	232	1.0	6.25	262	46.4	0.82
Porites sp. 2	447	152.8	0.66	384	1.0	3.00	354	42.4	0.88
Psammocora	42	0.8	0.98	45	0.0	0.00	48	0.0	1.00
Symphyllia	26	1.6	0.94	31	0.0	1.00	34	1.4	0.96
Total	**1,845**	**675.6**	**0.63**	**1,784**	**18.0**	**31.25**	**1,833**	**230.7**	**0.87**

Table 3| Bleaching resistance index (BRI) and generalized linear model analysis of selected scleractinian taxa (n≥10) (*note *Echinopora* at leeward sites in 2020 n<10) at leeward and windward sites during successive bleaching events between 2019 and 2020. ***Pr <0.001, **Pr < 0.01, *Pr < 0.05, ns – not significant.

	leeward 2019		***windward 2019***		***leeward 2020***		***windward 2020***	
Genus	n	BRI	n	BRI	n	BRI	n	BRI
Acropora	164	0.76	56	0.93	130	0.98	41	0.98
*Echinopora**	19	0.14	15	0.72	7*	0.71	17	1.00
Favia	11	0.87	60	0.81	10	1.00	104	0.95
Fungia	95	0.56	20	0.82	107	0.90	30	0.96
Pavona	121	0.32	23	0.91	111	0.68	19	1.00
Porites sp. 1	27	0.45	175	0.48	25	0.72	237	0.83
Porites sp. 2	269	0.58	178	0.78	231	0.87	123	0.88

	leeward (LW) vs. windward (WW) 2019				***leeward (LW) vs. windward (WW) 2020***			
Genus	Estimate	SE	Z value	Pr (>|z|)	Estimate	SE	Z value	Pr (>|z|)
Acropora	(WW) -3.50	0.42	-8.280	***	(WW) -1.20	1.06	-1.131	ns
Echinopora	(WW) -2.83	0.93	-3.057	**	(WW) -20.28	4300.25	-0.005	ns
Favia	(WW) 0.73	0.83	0.886	ns	(WW) 15.71	1251.05	0.013	ns
Fungia	(WW)-3.32	0.63	-5.258	***	(WW) -1.55	0.77	-2.030	*
Pavona	(WW) -3.29	0.77	-4.291	***	(WW) -18.97	1496.40	-0.013	ns
Porites sp. 1	(WW) -0.31	0.45	-0.699	ns	(WW) -0.95	0.43	-2.238	*

Porites sp. 2	(WW) -1.03	0.20	-5.116	***	(WW) 0.30	0.24	1.211	ns

Table 4| Summary of bleaching incidence (percent bleaching of hard coral colonies), Bleaching Resistance Index (BRI), and the Bleaching site susceptibility Index (BSI) at numerous biophysical scales during two successive bleaching events in 2019 and 2020 in Pulau Lang Tengah, Northeast Peninsular Malaysia. Shallow sites range from 5 to 7 meters, and deep sites from 10 to 14 meters of water depth.

Biophysical scale (year)	Colonies	Incidence (%)	BRI	Density (n^{-1}/m^2)	BSI
Leeward (2019)	747	70.82	0.57	24.90	48.21
Windward (2019)	1135	44.85	0.67	28.38	35.56
Leeward (2020)	690	26.96	0.87	23.00	12.78
Windward (2020)	1183	25.63	0.87	29.58	12.23
Shallow (2019)	1203	56.19	0.66	30.08	37.78
Deep (2019)	679	53.46	0.59	22.63	37.12
Shallow (2020)	1138	24.25	0.89	28.45	11.57
Deep (2020)	735	35.51	0.84	24.50	12.76
Leeward Shallow (2019)	592	72.30	0.61	29.60	58.25
Leeward Deep (2019)	155	65.16	0.45	15.50	60.86
Windward Shallow (2019)	611	40.59	0.71	30.55	37.30
Windward Deep (2019)	524	50.00	0.63	26.20	40.38
Leeward Shallow (2020)	546	20.15	0.90	27.30	12.05
Leeward Deep (2020)	144	52.78	0.76	14.40	25.14
Windward Shallow (2020)	592	23.99	0.90	29.60	12.35
Windward Deep (2020)	591	27.41	0.87	29.55	13.47

Table 5| Bleaching Resistance Index (BRI) and generalized linear model analysis of selected scleractinian taxa (n≥10) across multiple depths (shallow 5-7 m; deep 10-14 m) during successive bleaching episodes in June 2019 and June 2020. ***Pr <0.001, **Pr < 0.01, *Pr < 0.05, ns – not significant.

	Shallow 2019		***Deep 2019***		***Shallow 2019***		***Deep2019***	
Genus	n	BRI	n	BRI	n	BRI	n	BRI
Acropora	203	0.80	17	0.85	156	0.99	15	0.88
Favia	28	0.64	43	0.94	61	0.95	53	0.97
Fungia	81	0.59	34	0.66	89	0.92	48	0.90
Galaxea	61	0.97	35	1.00	67	0.94	31	0.97
Goniastrea	36	0.27	16	0.50	27	0.81	17	0.91
Heliopora	58	0.00	64	0.34	31	0.22	57	0.75
Leptastrea	35	0.90	34	0.97	35	0.88	45	0.94
Pavona	71	0.64	73	0.17	63	0.81	67	0.65

Platygyra	35	0.90	35	0.75	56	0.77	47	0.86
Porites sp. 1	103	0.60	99	0.34	123	0.90	139	0.74
Porites sp. 2	317	0.68	130	0.61	247	0.89	107	0.86
Psammocora	13	0.98	9	0.93	20	1.00	28	1.00
Symphyllia	12	0.95	14	0.93	20	0.96	14	0.94

	Shallow (S) vs. Deep (D) 2019				***Shallow (S) vs. Deep (D) 2020***			
Genus	Estimate	SE	Z value	Pr(>|z|)	Estimate	SE	Z value	Pr(>|z|)
Acropora	(S) 1.60	0.53	3.003	**	(S) -3.00	0.70	-4.314	***
Favia	(S) 2.71	0.65	4.160	***	(S) 0.88	0.62	1.403	ns
Fungia	(S) 1.47	0.52	2.820	**	(S) -0.71	0.43	-1.666	ns
Galaxea	(S) 17.68	1817.76	0.010	ns	(S) 0.36	0.85	0.419	ns
Goniastrea	(S) 1.00	0.64	1.555	ns	(S) 0.80	0.69	1.160	ns
Heliopora	(S) 18.78	1412.07	0.013	ns	(S) 3.09	0.67	4.591	***
Leptastrea	(S) 1.71	1.12	1.517	ns	(S) 0.75	0.69	1.090	ns
Pavona	(S) -1.75	0.38	-4.581	***	(S) -1.77	0.39	-4.579	***
Platygyra	(S) 1.07	0.60	1.781	ns	(S) 0.98	0.41	2.394	*
Porites sp. 1	(S) -1.71	0.33	-5.154	***	(S) -1.22	0.28	-4.364	***
Porites sp. 2	(S) -0.29	0.21	-1.373	ns	(S) -0.66	0.25	-2.663	**
Psammocora	(S) -0.33	1.21	-0.270	ns	-7.351e-15	1.043e+05	0.00	ns
Symphyllia	(S) -0.51	0.87	-0.588	ns	(S) -0.41	1.07	-0.380	ns

Table 6| Bleaching resistance Index (BRI) of selected taxa (n≥10) at fine biophysical reef scale (LWS-leeward shallow; LWD-leeward deep; WWS-windward shallow; WWD-windward deep) are shown for two successive bleaching episodes in 2019 and 2020. Tukey's post-hoc test results are shown for significantly different interactions at significance levels of ***p<0.001, **p<0.01 and *p<0.05 (missing entries are due to insufficient sample size).

Bleaching Resistance Index (BRI)					
Genus	**Year**	**LWS**	**LWD**	**WWS**	**WWD**
Acropora	2019	0.76	-	0.93	0.92
	2020	0.99	-	1.00	-
Fungia	2019	0.54	0.63	0.98	0.72
	2020	0.92	0.85	0.93	0.98
Pavona	2019	0.56	0.10	1.00	0.80
	2020	0.77	0.61	1.00	1.00
Porites sp. 1	2019	0.44	-	0.65	0.33
	2020	0.82	-	0.92	0.76
Porites sp. 2	2019	0.58	0.57	0.98	0.62
	2020	0.87	0.85	0.95	0.86

Genus	**Interaction**	**Estimate**	**SE**	**Z-ratio**	**p-value**

Acropora	LWS x WWS x 2019	3.458	0.448	7.7150	***
	LWS x WWD x 2019	-4.241	1.083	-3.915	***
Fungia	LWD x LWS x 2019	-3.050	1.130	-2.706	*
	WWD x LWS x2019	-4.280	1.160	-3.685	**
	LWD x LWS x 2020	1.236	0.472	2.617	*
Pavona	LWD x WWD x 2019	3.640	0.900	4.044	***
	LWD x LWS x 2019	2.180	0.503	4.336	***
	LWD x LWS x 2020	2.030	0.441	4.590	***
Porites sp. 1	WWD x WWS x 2019	2.132	0.363	5.871	***
	LWS x WWS x 2019	1.499	0.527	2.843	*
	WWD X WWS x 2020	1.393	0.312	4.460	***
Porites sp. 2	LWD x WWS x 2019	2.583	0.582	4.437	***
	WWD x WWS x 2019	2.954	0.505	2.853	***
	LWS x WWs x 2019	3.128	0.481	6.508	***
	WWD x WWS x 2020	1.943	0.642	3.026	*

Figure captions

Figure 1| Location of Pulau Lang Tengah (A) within the South China Sea (dashed area), showing survey sites [House Reef (HR), Secret Reef (SR), Tanjung Telunjuk (TJ) and Batu Bulan (BB)] and *in-situ* temperature recording stations [Batu Kucing (BK), House Reef, Tanjung Telunjuk]. The wind frequency rose (B) illustrates wind direction and frequency around Pulau Lang Tengah at island scale.

Figure 2| Nightly satellite measurements of sea surface temperatures (SST°C) around Pulau Lang Tengah between April 1985 and December 2020. The grey dotted line shows the maximum monthly mean (MMM=29.94°C) based on historical satellite measurements by the National Oceanic and Atmospheric Association (NOAA), Coral Reef Watch (CRW) product, version 3.1, and the black line presents the established *in-situ* MMM (30.51°C) after interpolating satellite data with *in-situ* measurements. Linear regressions of mean annual sea surface temperatures (B) and mean bleaching season sea surface temperatures (C) around Pulau Lang Tengah are shown. The regression line illustrates the warming trend since 1985, and the regression equation establishes average warming rates per year.

Figure 3| Comparison of satellite-derived sea surface temperature (grey line) and *in-situ* point measurements (black line) at 8 meters' depth between September 2019 and September 2020. Satellite-derived sea surface temperatures are shown starting in April 2019. Average measurement difference over the time period observed is 0.53°C (SD±0.25). The grey dotted line represents the maximum monthly mean (MMM=29.94°C) based on historical satellite measurements by the National Oceanic and Atmospheric Association (NOAA), Coral Reef Watch (CRW) product, version 3.1, and the black line presents the established *in-situ* MMM (30.51°C) after interpolating satellite data with *in-situ* measurements. Error bars show the standard deviation of the mean to express monthly temperature variability.

Figure 4| Percentage of healthy, fully and partially bleached colonies of scleractinian taxa with at least ten observations during survey occasion in June 2019, October 2019 and June 2020. In October 2019, percentage of bleaching induced mortality is shown, combining complete and partial-colony mortality.

Figure 5| Bleaching Resistance Index (BRI) of scleractinian taxa as a function of depth. Taxa with at least ten observations at each depth are shown. The black lines present the BRI in 2019, and grey lines show the BRI in 2020.

References

Akhir, M. F., Daryabor, F., Husain, M. L., Tangang, F., & Qiao, F. (2015). Evidence of Upwelling along Peninsular Malaysia during Southwest Monsoon. *Open Journal of Marine Science*, *05*(03), 273–279. https://doi.org/10.4236/ojms.2015.53022

Álvarez-Noriega, M., Baird, A. H., Dornelas, M., Madin, J. S., Cumbo, V. R., & Connolly, S. R. (2016). Fecundity and the demographic strategies of coral morphologies. *Ecology*, *97*(12), 3485–3493. https://doi.org/10.1002/ecy.1588

Atrigenio, M., Aliño, P., & Conaco, C. (2017). Influence of the blue coral Heliopora coerulea on scleractinian coral larval recruitment. *Journal of Marine Biology*, *2017*. https://doi.org/10.1155/2017/6015143

Baker, A. C., Starger, C. J., McClanahan, T. R., & Glynn, P. W. (2004). Corals' adaptive response to climate change. *Nature*, *430*(7001), 741-741. https://doi.org/10.1038/430741a

Baker, A. C., Glynn, P. W., & Riegl, B. (2008). Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science*, *80*(4), 435–471. https://doi.org/10.1016/j.ecss.2008.09.003

Barbosa, A. M., Brown, J., Jiménez-Valverde, A., & Real, R. (2014). ModEvA: Model Evaluation and Analysis R Package, Version 1.3

Baird, A. H., Madin, J. S., Álvarez-Noriega, M., Fontoura, L., Kerry, J. T., Kuo, C. Y., et al. (2018). A decline in bleaching suggests that depth can provide a refuge from global warming in most coral taxa. *Marine Ecology Progress Series*, *603*, 257–264. https://doi.org/10.3354/meps12732

Baird, A. H., & Marshall, P. A. (2002). Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series*, *237*, 133-141.

Bairos-Novak, K. R., Hoogenboom, M. O., Oppen, M. J. H., & Connolly, S. R. (2021). Coral adaptation to climate change: Meta-analysis reveals high heritability across multiple traits. *Global Change Biology*, *July*, 1–17. https://doi.org/10.1111/gcb.15829.

Berkelmans, R., & Van Oppen, M. J. H. (2006). The role of zooxanthellae in the thermal tolerance of corals: A "nugget of hope" for coral reefs in an era of climate change. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1599), 2305–2312. https://doi.org/10.1098/rspb.2006.3567

Bollati, E., D'Angelo, C., Alderdice, R., Pratchett, M., Ziegler, M., & Wiedenmann, J. (2020). Optical Feedback Loop Involving Dinoflagellate Symbiont and Scleractinian Host Drives Colorful Coral Bleaching. *Current Biology*, *30*(13), 2433-2445.e3. https://doi.org/10.1016/j.cub.2020.04.055

Bridge, T. C. L., Hoey, A. S., Campbell, S. J., Muttaqin, E., Rudi, E., Fadli, N., et al. (2013). Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. *F1000Research*, *2*, 187. https://doi.org/10.12688/f1000research.2-187.v1

Brown, B. E. (1997). Coral bleaching: causes and consequences. *Coral reefs*, *16*(1), S129-S138. https://doi.org/10.1007/s003380050249

Cheng, L., Abraham, J., Trenberth, K. E., Fasullo, J., Boyer, T., Locarnini, R., et al. (2021). Upper Ocean Temperatures Hit Record High in 2020. *Advances in Atmospheric Sciences*. https://doi.org/10.1007/s00376-021-0447-x

Crosbie, A. J., Bridge, T. C. L., Jones, G., & Baird, A. H. (2019). Response of reef corals and fish at Osprey Reef to a thermal anomaly across a 30 m depth gradient. *Marine Ecology Progress Series*, *622*, 93–102. https://doi.org/10.3354/meps13015

Darling, E. S., Alvarez-Filip, L., Oliver, T. A., Mcclanahan, T. R., & Côté, I. M. (2012). Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*, *15*(12), 1378–1386. https://doi.org/10.1111/j.1461-0248.2012.01861.x

Dixon, G. B., Davies, S. W., Aglyamova, G. V., Meyer, E., Bay, L. K., & Matz, M. V. (2015). Genomic determinants of coral heat tolerance across latitudes. *Science*, *348*(6242), 1460-1462.

Donner, S. D., Kirata, T., & Vieux, C. (2010). Recovery From the 2004 Coral Bleaching Event in the Gilbert Islands , Kiribati. *Atoll Research Bulletin*, *587*.

Donner, S. D., Skirving, W. J., Little, C. M., Oppenheimer, M., & Hoegh-Gulberg, O. (2005). Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology*, *11*(12), 2251–2265. https://doi.org/10.1111/j.1365-2486.2005.01073.x

Eakin, C. M., Morgan, J. A., Heron, S. F., Smith, T. B., Liu, G., Alvarez-Filip, L., Baca, B., Bartels, E., et al. (2010). Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. *PLoS ONE*, *5*(11), e13969. https://doi.org/10.1371/journal.pone.0013969

Eakin, C. M., Sweatman, H. P. A., & Brainard, R. E. (2019). The 2014–2017 global-scale coral bleaching event: insights and impacts. *Coral Reefs*, *38*(4), 539–545. https://doi.org/10.1007/s00338-019-01844-2

Edmunds, P. J. (1994). Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching-susceptible clones. *Marine Biology*, *121*(1), 137-142.

Fabricius, K. E., & Klumpp, D. W. (1995). Widespread mixotrophy in reef-inhabiting soft corals: the influence of depth, and colony expansion and contraction on photosynthesis. *Marine Ecology Progress Series*, *125*(1–3), 195–204. https://doi.org/10.3354/meps125195

Fitt, W. K., Gates, R. D., Hoegh-Guldberg, O., Bythell, J. C., Jatkar, A., Grottoli, A. G., et al. (2009). Response of two species of Indo-Pacific corals, Porites cylindrica and Stylophora pistillata, to short-term thermal stress: The host does matter in determining the tolerance of corals to bleaching. *Journal of Experimental Marine Biology and Ecology*, *373*(2), 102–110. https://doi.org/10.1016/j.jembe.2009.03.011

Fordyce, A. J., Ainsworth, T. D., Heron, S. F., & Leggat, W. (2019). Marine heatwave hotspots in coral reef environments: Physical drivers, ecophysiological outcomes, and impact upon structural complexity. *Frontiers in Marine Science*, *6*, 498. https://doi.org/10.3389/fmars.2019.00498

Fox, J., & Weisberg, S. (2018). *An R companion to applied regression*. Sage publications.

Fox, M. D., Carter, A. L., Edwards, C. B., Takeshita, Y., Johnson, M. D., Petrovic, V., et al. (2019). Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. *Coral Reefs*, *38*(4), 701–712. https://doi.org/10.1007/s00338-019-01796-7

Frieler, K., Meinshausen, M., Golly, A., Mengel, M., Lebek, K., Donner, S. D., et al. (2013). Limiting global warming to 2C is unlikely to save most coral reefs. *Nature Climate Change*, *3*(2), 165–170. https://doi.org/10.1038/nclimate1674

Gintert, B. E., Manzello, D. P., Enochs, I. C., Kolodziej, G., Carlton, R., Gleason, A. C. R., et al. (2018). Marked annual coral bleaching resilience of an inshore patch reef in the Florida Keys: A nugget of hope, aberrance, or last man standing? *Coral Reefs*, *37*(2), 533–547. https://doi.org/10.1007/s00338-018-1678-x

Global Wind Atlas 3.0. (2020). https://globalwindatlas.info/ [Accessed October 24, 2020]

Glynn, P. W., & D'croz, L. (1990). Experimental evidence for high temperature stress as the cause of El Nino-coincident coral mortality. *Coral reefs*, *8*(4), 181-191.

Grottoli, A. G., Warner, M. E., Levas, S. J., Aschaffenburg, M. D., Schoepf, V., Mcginley, M., et al. (2014). The cumulative impact of annual coral bleaching can turn some coral species

winners into losers. *Global Change Biology*, *20*(12), 3823–3833. https://doi.org/10.1111/gcb.12658

Guest, J. R., Low, J., Tun, K., Wilson, B., Ng, C., Raingeard, D., ... & Steinberg, P. D. (2016). Coral community response to bleaching on a highly disturbed reef. *Scientific Reports*, *6*(1), 1-10. https://doi.org/10.1038/srep20717

Guest, J. R., Baird, A. H., Maynard, J. A., Muttaqin, E., Edwards, A. J., Campbell, S. J., et al. (2012). Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS ONE*, *7*(3). https://doi.org/10.1371/journal.pone.0033353

Guzman, C., Atrigenio, M., Shinzato, C., Aliño, P., & Conaco, C. (2019). Warm seawater temperature promotes substrate colonization by the blue coral, Heliopora coerulea. *PeerJ*, *7*, e7785. https://doi.org/10.7717/peerj.7785

Guzman, C., Shinzato, C., Lu, T. M., & Conaco, C. (2018). Transcriptome analysis of the reef-building octocoral, Heliopora coerulea. *Scientific Reports*, *8*(1), 1–11. https://doi.org/10.1038/s41598-018-26718-5

Harii, S., Hongo, C., Ishihara, M., Ide, Y., & Kayanne, H. (2014). Impacts of multiple disturbances on coral communities at Ishigaki Island, Okinawa, Japan, during a 15 year survey. *Marine Ecology Progress Series*, *509*, 171–180. https://doi.org/10.3354/meps10890

Harriott, V. J. (1985). Mortality rates of scleractinian corals before and during a mass bleaching event. *Marine ecology progress series*, *21*(1), 81-88.

Harrison, H. B., Álvarez-Noriega, M., Baird, A. H., Heron, S. F., MacDonald, C., & Hughes, T. P. (2019). Back-to-back coral bleaching events on isolated atolls in the Coral Sea. *Coral Reefs*, *38*(4), 713–719. https://doi.org/10.1007/s00338-018-01749-6

Heron, S. F., Johnston, L., Liu, G., Geiger, E. F., Maynard, J. A., De La Cour, J. L., et al. (2016). Validation of reef-scale thermal stress satellite products for coral bleaching monitoring. *Remote Sensing*, *8*(1), 59. https://doi.org/10.3390/rs8010059

Heron, S. F., Liu, G., Eakin, C. M., Skirving, W. J., Muller-karger, F. E., Vega-Rodriguez, M., et al. (2015). *Climatology Development for NOAA Coral Reef Watch's 5-km Product Suite*. https://doi.org/10.7289/V59C6VBS

Hoegh-Guldberg, O. (2011). Coral reef ecosystems and anthropogenic climate change. *Regional Environmental Change*, *11*(1), 215-227. https://doi.org/10.1007/s10113-010-0189-2

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and freshwater research*, *50*(8), 839-866. https://doi.org/10.1071/MF99078

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., et al. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), 373–377. https://doi.org/10.1038/nature21707

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., et al. (2018)a. Global warming transforms coral reef assemblages. *Nature*, *556*(7702), 492–496. https://doi.org/10.1038/s41586-018-0041-2

Hughes, T. P., Kerry, J. T., Connolly, S. R., Baird, A. H., Eakin, C. M., Heron, S. F., et al. (2019). Ecological memory modifies the cumulative impact of recurrent climate extremes. In *Nature Climate Change*, 9(1), 40-43. https://doi.org/10.1038/s41558-018-0351-2

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., et al. (2018)b. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, *359*(6371), 80–83. https://doi.org/10.1126/science.aan8048

Jaap, W. C. (1979). Observations on zooxanthellae expulsion at Middle Sambo Reef, Florida Keys. *Bulletin of Marine Science*, *29*(3), 414-422.

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., et al. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, *14*(7), 369-378. https://doi.org/10.1002/fee.1311

Jokiel, P. L., & Coles, S. L. (1990). Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral reefs*, *8*(4), 155-162.

Kayanne, H., Harii, S., Ide, Y., & Akimoto, F. (2002). Recovery of coral populations after the 1998 bleaching on Shiraho Reef, in the southern Ryukyus, NW Pacific. *Marine Ecology Progress Series*, *239*, 93–103. https://doi.org/10.3354/meps239093

Kayanne, H. (2017). Validation of degree heating weeks as a coral bleaching index in the northwestern Pacific. *Coral Reefs*, *36*(1), 63–70. https://doi.org/10.1007/s00338-016-1524-y

Kelley, R. (2016). Indo Pacific Coral Finder, 3rd Edition. Townsville: BYOGUIDES.

Kushairi, M. R. M. (1998). The 1998 bleaching catastrophe of corals in the South China Sea. In *Proc. JSPS Joint Seminar on Marine and Fisheries Sciences, Bali, Indonesia, 1998*. http://ci.nii.ac.jp/naid/10018463620/en/

LaJeunesse, T. C., Pettay, D. T., Sampayo, E. M., Phongsuwan, N., Brown, B., Obura, D. O., et al. (2010). Long-standing environmental conditions, geographic isolation and host-symbiont specificity influence the relative ecological dominance and genetic diversification of coral endosymbionts in the genus Symbiodinium. *Journal of Biogeography*, *37*(5), 785–800. https://doi.org/10.1111/j.1365-2699.2010.02273.x

Lenth, R. V. (2021). emmeans: Estimated Marginal Means, aka least-squares means. R package version 1.6.1.

Lesser, M. P. (1997). Oxidative stress causes coral bleaching during exposure to elevated temperatures. *Coral reefs*, *16*(3), 187-192.

Liu, G., Heron, S. F., Mark Eakin, C., Muller-Karger, F. E., Vega-Rodriguez, M., Guild, L. S., et al. (2014). Reef-scale thermal stress monitoring of coral ecosystems: New 5-km global products from NOAA coral reef watch. *Remote Sensing*, *6*(11), 11579–11606. https://doi.org/10.3390/rs61111579

Liu, G., Skirving, W. J., Geiger, E. F., De, J. L., Cour, L., Marsh, B. L., et al. (2017). NOAA Coral Reef Watch's 5km satellite coral bleaching heat stress monitoring product suite version 3 and four-month outlook version 4. *Reef Encounter*, *32*(1), 39-45. https://coralreefwatch.noaa.gov/satellite/bleachingoutlook_cfs/outlook_cfs.php.

Liu, G., Strong, A. E., & Skirving, W. (2003). Remote sensing of sea surface temperatures during 2002 Barrier Reef coral bleaching. *Eos, Transactions American Geophysical Union*, *84*(15), 137-141. https://doi.org/10.1029/2003EO150001

Liu, G., Strong, A. E., Skirving, W., & Arzayus, L. F. (2006, June). Overview of NOAA coral reef watch program's near-real time satellite global coral bleaching monitoring activities. In *Proceedings of the 10th international coral reef symposium* (Vol. 1793, pp. 1783-1793). Gurugram: Okinawa. http://coralreefwatch.noaa.gov/

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., & Van Woesik, R. (2001). Coral bleaching: The winners and the losers. *Ecology Letters*, *4*(2), 122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x

MacKellar, M. C., & McGowan, H. A. (2010). Air-sea energy exchanges measured by eddy covariance during a localised coral bleaching event, Heron Reef, Great Barrier Reef, Australia. *Geophysical Research Letters*, *37*(24). https://doi.org/10.1029/2010GL045291

Marshall, P. A., & Baird, A. H. (2000). Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral reefs*, *19*(2), 155-163.

McClanahan, T. R. (2017). Changes in coral sensitivity to thermal anomalies. *Marine Ecology Progress Series*, *570*, 71–85. https://doi.org/10.3354/meps12150

McClanahan, T. R., Ateweberhan, M., Graham, N. A. J., Wilson, S. K., Ruiz Sebastián, C., Guillaume, M. M. M., & Bruggemann, J. H. (2007)a. Western Indian Ocean coral communities: Bleaching responses and susceptibility to extinction. *Marine Ecology Progress Series*, *337*, 1–13. https://doi.org/10.3354/meps337001

McClanahan, T. R., Ateweberhan, M., Ruiz Sebastián, C., Graham, N. A. J., Wilson, S. K., Bruggemann, J. H., et al. (2007)b. Predictability of coral bleaching from synoptic satellite

and in situ temperature observations. *Coral Reefs*, *26*(3), 695–701. https://doi.org/10.1007/s00338-006-0193-7

McClanahan, T. R., Baird, A. H., Marshall, P. A., & Toscano, M. A. (2004). Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin*, *48*(3–4), 327–335. https://doi.org/10.1016/j.marpolbul.2003.08.024

McClanahan, T. R., & Maina, J. (2003). Response of coral assemblages to the interaction between natural temperature variation and rare warm-water events. *Ecosystems*, *6*(6), 551–56. https://doi.org/10.1007/s10021-002-0104-x

Morais, J., Morais, R. A., Tebbett, S. B., Pratchett, M. S., & Bellwood, D. R. (2021). Dangerous demographics in post-bleach corals reveal boom-bust versus protracted declines. *Scientific Reports*, *11*(1), 1–7. https://doi.org/10.1038/s41598-021-98239-7

Muir, P. R., Marshall, P. A., Abdulla, A., & Aguirre, J. D. (2017). Species identity and depth predict bleaching severity in reef-building corals: Shall the deep inherit the reef? *Proceedings of the Royal Society B: Biological Sciences*, *284*(1864). https://doi.org/10.1098/rspb.2017.1551

Muñiz-Castillo, A. I., & Arias-González, J. E. (2021). Drivers of coral bleaching in a Marine Protected Area of the Southern Gulf of Mexico during the 2015 event. *Marine Pollution Bulletin*, *166*, 112256. https://doi.org/10.1016/j.marpolbul.2021.112256

Nakamura, T. V., & Van Woesik, R. (2001). Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Marine Ecology Progress Series*, *212*, 301-304. https://doi.org/doi:10.3354/meps212301

Nelder, J. A., & Wedderburn, R. W. (1972). Generalized linear models. *Journal of the Royal Statistical Society: Series A (General)*, *135*(3), 370-384.

NOAA Coral Reef Watch Version 3.1 Daily Global 5-km Satellite Coral Bleaching Degree Heating Week Product. (2014). NOAA Coral Reef Watch Daily 5km Satellite Coral Bleaching Heat Stress Monitoring Products (Version 3.1) [Accessed January 3, 2021]

Pachauri, R. K., Myles R. A., Vicente R. B., John B., Wolfgang C., Renate C., et al. (2014). *Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change (p. 151). Ipcc*

Page, C. E., Leggat, W., Heron, S. F., Choukroun, S. M., Lloyd, J., & Ainsworth, T. D. (2019). Seeking resistance in coral reef ecosystems: the interplay of biophysical factors and bleaching resistance under a changing climate: the interplay of a reef's biophysical factors can mitigate the coral bleaching response. *BioEssays*, *41*(7), 1800226. https://doi.org/10.1002/bies.201800226

Palumbi, S. R., Barshis, D. J., Traylor-Knowles, N., & Bay, R. A. (2014). Mechanisms of reef coral resistance to future climate change. *Science*, *344*(6186), 895–898. https://doi.org/10.1126/science.1251336

Pandolfi, J. M., Connolly, S. R., Marshall, D. J., & Cohen, A. L. (2011). Projecting coral reef futures under global warming and ocean acidification. *Science*, *333*(6041), 418-422. http://paleodb.org/cgi-bin/bridge.pl

Paulay, G., & Benayahu, Y. (1999). Patterns and consequences of coral bleaching in Micronesia (Majuro and Guam) in 1992-1994. *Micronesica-Agana*, *32*(1), 109–124. http://octocoralresearch.com/PDF Files/Bleaching in octocorals.pdf

Phongsuwan, N., & Chansang, H. (2012). Repeated coral bleaching in the Andaman Sea, Thailand, during the last two decades. *Phuket Marine Biological Center Research Bulletin*, *71*, 19–41.

Pochon, X., Stat, M., Takabayashi, M., Chasqui, L., Chauka, L. J., Logan, D. D. K., & Gates, R. D. (2010). Comparison of endosymbiotic and free-living Symbiodinium (dinophyceae) diversity in a hawaiian reef environment. *Journal of Phycology*, *46*(1), 53–65. https://doi.org/10.1111/j.1529-8817.2009.00797.x

Pratchett, M. S., McCowan, D., Maynard, J. A., & Heron, S. F. (2013). Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. *PLoS one*, *8*(7), e70443. https://doi.org/10.1371/journal.pone.0070443

Reef Check Malaysia. (2013). *Status of Coral Reefs in Malaysia, 2013*. http://www.reefcheck.org.my/media-information/annual-survey-reports

Reef Check Malaysia. (2019). *Status of Coral Reefs in Malaysia, 2019*. http://www.reefcheck.org.my/media-information/annual-survey-reports

Reef Check Malaysia. (2020). *Status of Coral Reefs in Malaysia, 2020*. http://www.reefcheck.org.my/media-information/annual-survey-reports

Richards, Z. T., Yasuda, N., Kikuchi, T., Foster, T., Mitsuyuki, C., Stat, M., et al. (2018). Integrated evidence reveals a new species in the ancient blue coral genus Heliopora (Octocorallia). *Scientific Reports*, *8*(1), 1–14. https://doi.org/10.1038/s41598-018-32969-z

Roberts, T. E., Moloney, J. M., Sweatman, H. P. A., & Bridge, T. C. L. (2015). Benthic community composition on submerged reefs in the central Great Barrier Reef. *Coral Reefs*, *34*(2), 569–580. https://doi.org/10.1007/s00338-015-1261-7

RStudio Team (2021). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/. [Accessed April 1, 2021]

Schoepf, V., Grottoli, A. G., Levas, S. J., Aschaffenburg, M. D., Baumann, J. H., Matsui, Y., et al. (2015). Annual coral bleaching and the long-term recovery capacity of coral. *Proceedings of the Royal Society B: Biological Sciences*, *282* (1819). https://doi.org/10.1098/rspb.2015.1887

Schuhmacher, H., Loch, K., Loch, W., & See, W. R. (2005). The aftermath of coral bleaching on a Maldivian reef - A quantitative study. *Facies*, *51*(1–4), 80–92. https://doi.org/10.1007/s10347-005-0020-6

Skirving, W. J., Heron, S. F., Marsh, B. L., Liu, G., De La Cour, J. L., Geiger, E. F., et al. (2019). The relentless march of mass coral bleaching: a global perspective of changing heat stress. *Coral Reefs*, *38*(4), 547–557. https://doi.org/10.1007/s00338-019-01799-4

Skirving, W., Heron, M., & Heron, S. (2006). The hydrodynamics of a bleaching event: implications for management and monitoring. *Coral Reefs and Climate Change: Science and Management*, *61*, 145-161.

Stocker, T., Qin, D., Plattner, G., Alexander, L., Allen, S., Bindoff, N., et al (2014). Technical summary. In *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 33-115). Cambridge University Press. https://doi.org/10.1017/cbo9781107415324.005

Strong, A. E., Liu, G., Kimura, T., Yamano, H., Tsuchiya, M., Kakuma, S. I., et al. (2002). Detecting and monitoring 2001 coral reef bleaching events in Ryukyu Islands, Japan using satellite bleaching HotSpot remote sensing technique. In *IEEE International Geoscience and Remote Sensing Symposium* (Vol. 1, pp. 237-239). IEEE. https://doi.org/10.1109/igarss.2002.1024998

Sully, S., Burkepile, D. E., Donovan, M. K., Hodgson, G., & van Woesik, R. (2019). A global analysis of coral bleaching over the past two decades. *Nature Communications*, *10*(1), 1-5. https://doi.org/10.1038/s41467-019-09238-2

Tan, C. H., & SF, H. (2011). First observed severe mass bleaching in Malaysia, Greater Coral Triangle. *Galaxea, Journal of Coral Reef Studies*, *13*(1), 27-28.https://doi.org/10.3755/galaxea.13.27

Thomas, L., Rose, N. H., Bay, R. A., López, E. H., Morikawa, M. K., Ruiz-Jones, L., et al (2018). Mechanisms of thermal tolerance in reef-building corals across a fine-grained environmental mosaic: Lessons from Ofu, American Samoa. *Frontiers in Marine Science*, *4*, 434. https://doi.org/10.3389/fmars.2017.00434

Thompson, D. M., & Van Woesik, R. (2009). Corals escape bleaching in regions that recently and historically experienced frequent thermal stress. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 2893–2901. https://doi.org/10.1098/rspb.2009.0591

Toda, T., Okashita, T., Maekawa, T., Alfian, B. A. A. K., Rajuddin, M. K. M., Nakajima, R., Chen, W., Takahashi, K. T., Othman, B. H. R., & Terazaki, M. (2007). Community structures of coral reefs around peninsular Malaysia. *Journal of Oceanography*, *63*(1), 113–123. https://doi.org/10.1007/s10872-007-0009-6

Van Hooidonk, R., Maynard, J., Grimsditch, G., Williams, G., Tamelander, J., Gove, J., et al. (2020). Projections of future coral bleaching conditions using IPCC CMIP6 models: climate policy implications, management applications, and Regional Seas summaries. United Nation Environmental Programme, Nairobi, Kenya.

Van Hooidonk, R., Maynard, J., & Planes, S. (2013). Temporary refugia for coral reefs in a warming world. *Nature Climate Change*, *3*(5), 508–511. https://doi.org/10.1038/nclimate1829

Van Hooidonk, R., Maynard, J., Tamelander, J., Gove, J., Ahmadia, G., Raymundo, L., et al. (2016). Local-scale projections of coral reef futures and implications of the Paris Agreement. *Scientific Reports*, *6(1)*, 1-8. https://doi.org/10.1038/srep39666

Van Hooidonk, R., Maynard, J., Tamelander, J., Gove, J., Ahmadia, G., Raymundo, L., et al. (2017). *Coral Bleaching Futures: Downscaled Projections of Bleaching Conditions for the World's Coral Reefs, Implications of Climate Policy and Management Responses*. United Nation Environmental Programme, Nairobi, Kenya.

Van Woesik, R., Sakai, K., Ganase, A., & Loya, Y. (2011). Revisiting the winners and the losers a decade after coral bleaching. *Marine Ecology Progress Series*, *434*, 67–76. https://doi.org/10.3354/meps09203

Van Woesik, R., Houk, P., Isechal, A. L., Idechong, J. W., Victor, S., & Golbuu, Y. (2012). Climate-change refugia in the sheltered bays of Palau: Analogs of future reefs. *Ecology and Evolution*, *2*(10), 2474–2484. https://doi.org/10.1002/ece3.363

Voolstra, C. R. (2020). Coral Bleaching: A Colorful Struggle for Survival. *Current Biology*, *30*(13), R768–R770. https://doi.org/10.1016/j.cub.2020.05.008

Wellington, G. M., Glynn, P. W., Strong, A. E., Navarrete, S. A., Wieters, E., & Hubbard, D. (2001). Crisis on coral reefs linked to climate change. *Eos, Transactions American Geophysical Union*, *82*(1), 1-5.

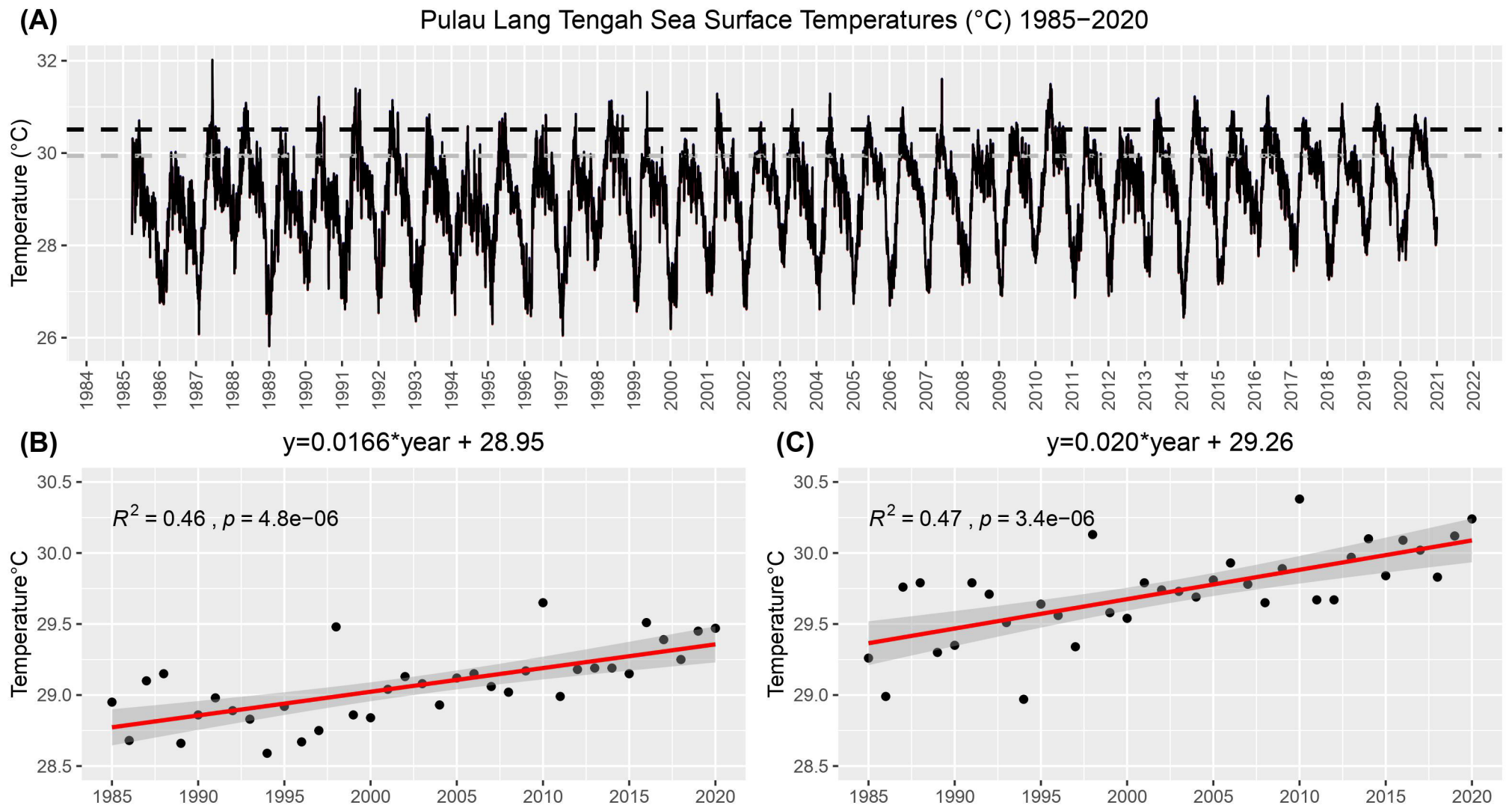
Wiedenmann, J., D'Angelo, C., Smith, E. G., Hunt, A. N., Legiret, F. E., Postle, A. D., et al. (2013). Nutrient enrichment can increase the susceptibility of reef corals to bleaching. *Nature Climate Change*, *3*(2), 160–164. https://doi.org/10.1038/nclimate1661

Wong, K. H., Goodbody-Gringley, G., de Putron, S. J., Becker, D. M., Chequer, A., & Putnam, H. M. (2021). Brooded coral offspring physiology depends on the combined effects of parental press and pulse thermal history. *Global Change Biology*, *27*(13), 3179–3195. https://doi.org/10.1111/gcb.15629

Wooldridge, S. A., Done, T. J., Thomas, C. R., Gordon, I. I., Marshall, P. A., & Jones, R. N. (2012). Safeguarding coastal coral communities on the central Great Barrier Reef (Australia) against climate change: Realizable local and global actions. *Climatic Change*, *112*(3–4), 945–961. https://doi.org/10.1007/s10584-011-0229-z

Zann, L. P., & Bolton, L. (1985). The distribution, abundance and ecology of the blue coral Heliopora coerulea (Pallas) in the Pacific. *Coral Reefs*, *4*(2), 125–134. https://doi.org/10.1007/BF0030087

Zvuloni, A., Artzy-Randrup, Y., Stone, L., van Woesik, R., & Loya, Y. (2008). Ecological size-frequency distributions: how to prevent and correct biases in spatial sampling. *Limnology and Oceanography: Methods*, *6*(3), 144-153.


(A)
Pulau Lang Tengah Sea Surface Temperatures (°C) 1985−2020
Temperature (°C)
32
30
28
26
1984
1985
1986
1987
1988
1989
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1991
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1993
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2008
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2012
2013
2014
2015
2016
2017
2018
2019
2020
2021
2022
(B)
y=0.0166*year + 28.95
R^2 = 0.46 , p = 4.8e−06
Temperature°C
30.5
30.0
29.5
29.0
28.5
1985
1990
1995
2000
2005
2010
2015
2020
(C)
y=0.020*year + 29.26
R^2 = 0.47 , p = 3.4e−06
Temperature°C
30.5
30.0
29.5
29.0
28.5
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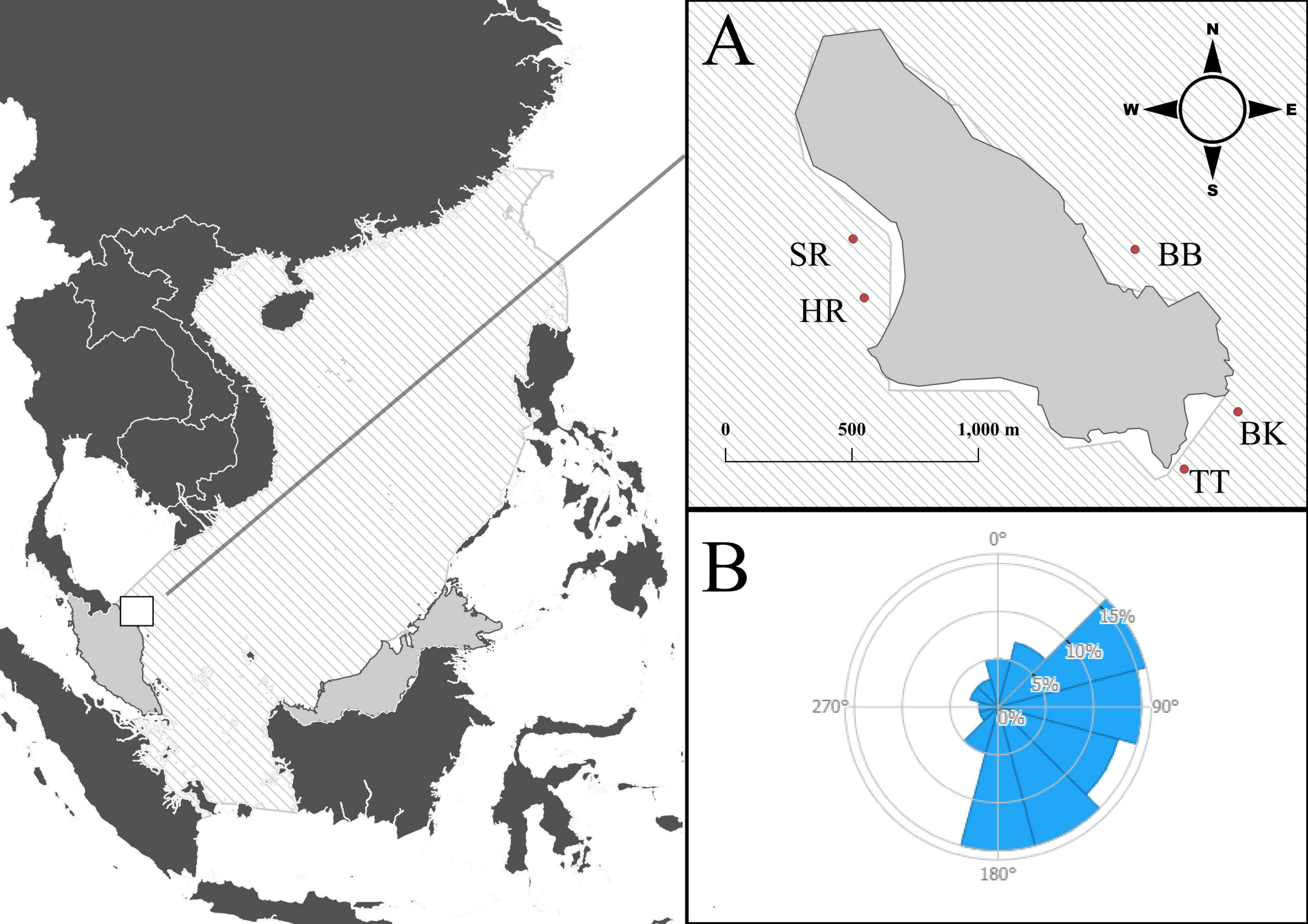
2010
2015
2020


A
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180°
270°
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5%
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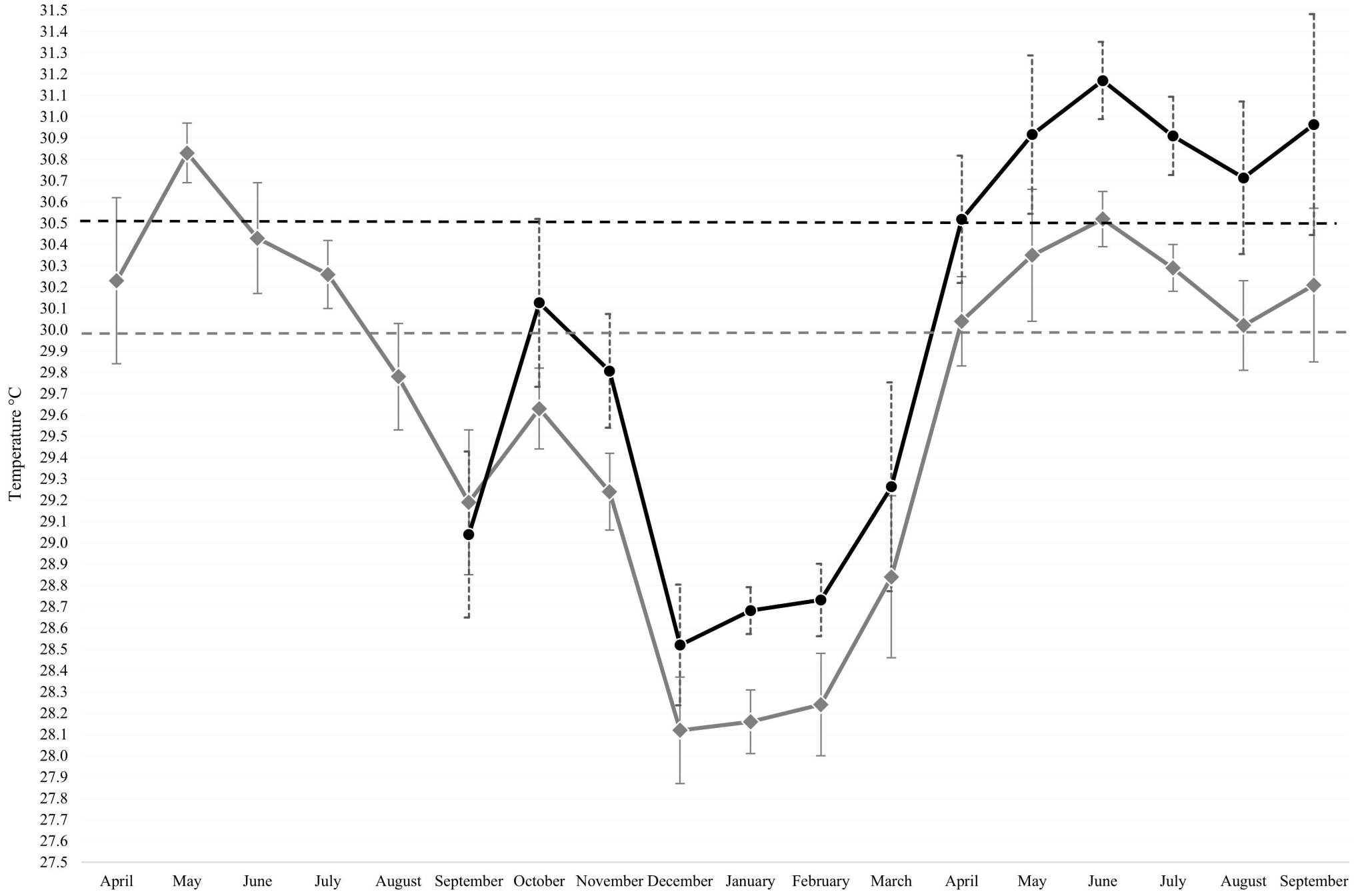
15%


Temperature °C
31.5
31.4
31.3
31.2
31.1
31.0
30.9
30.8
30.7
30.6
30.5
30.4
30.3
30.2
30.1
30.0
29.9
29.8
29.7
29.6
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29.4
29.3
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29.1
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28.9
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28.7
28.6
28.5
28.4
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28.1
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April
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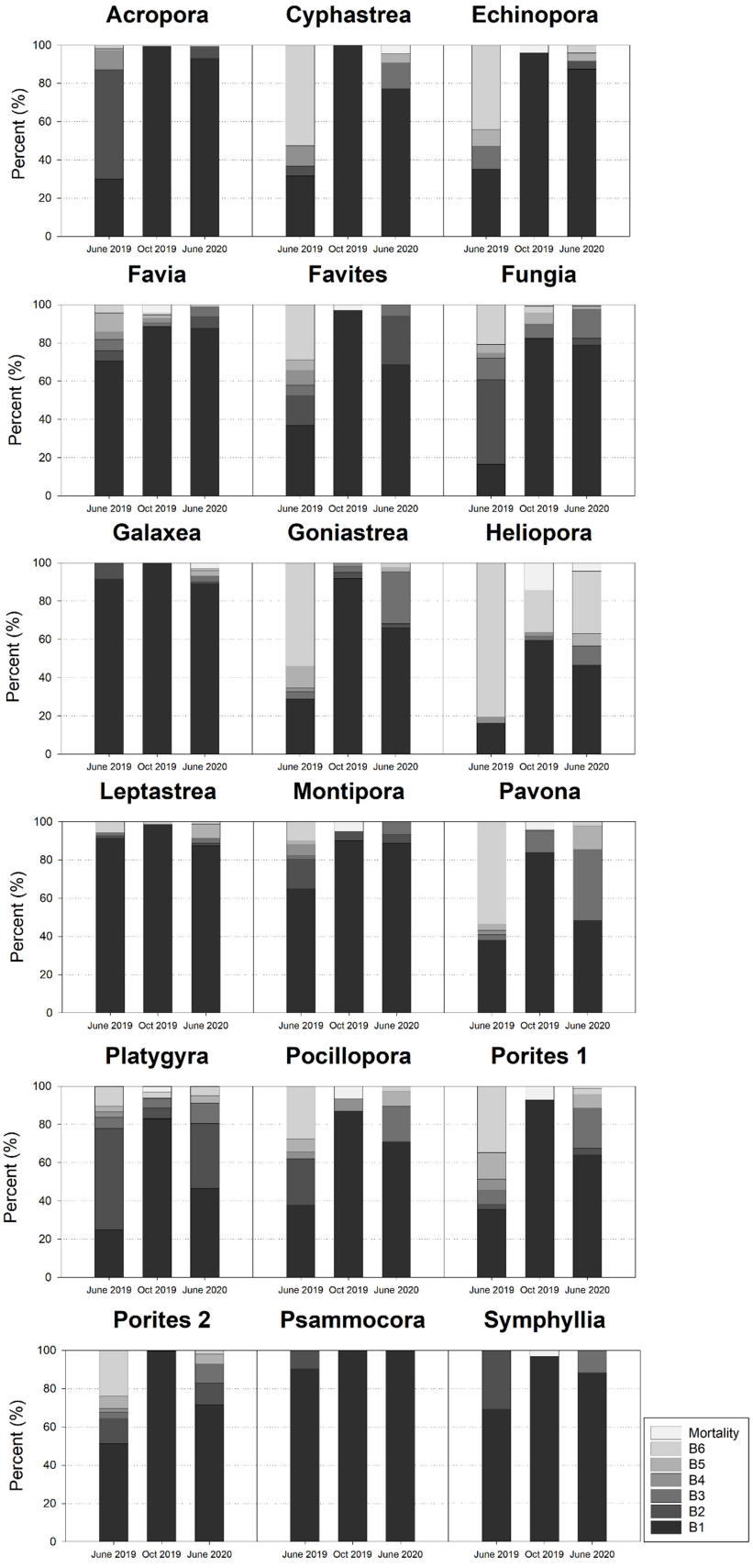
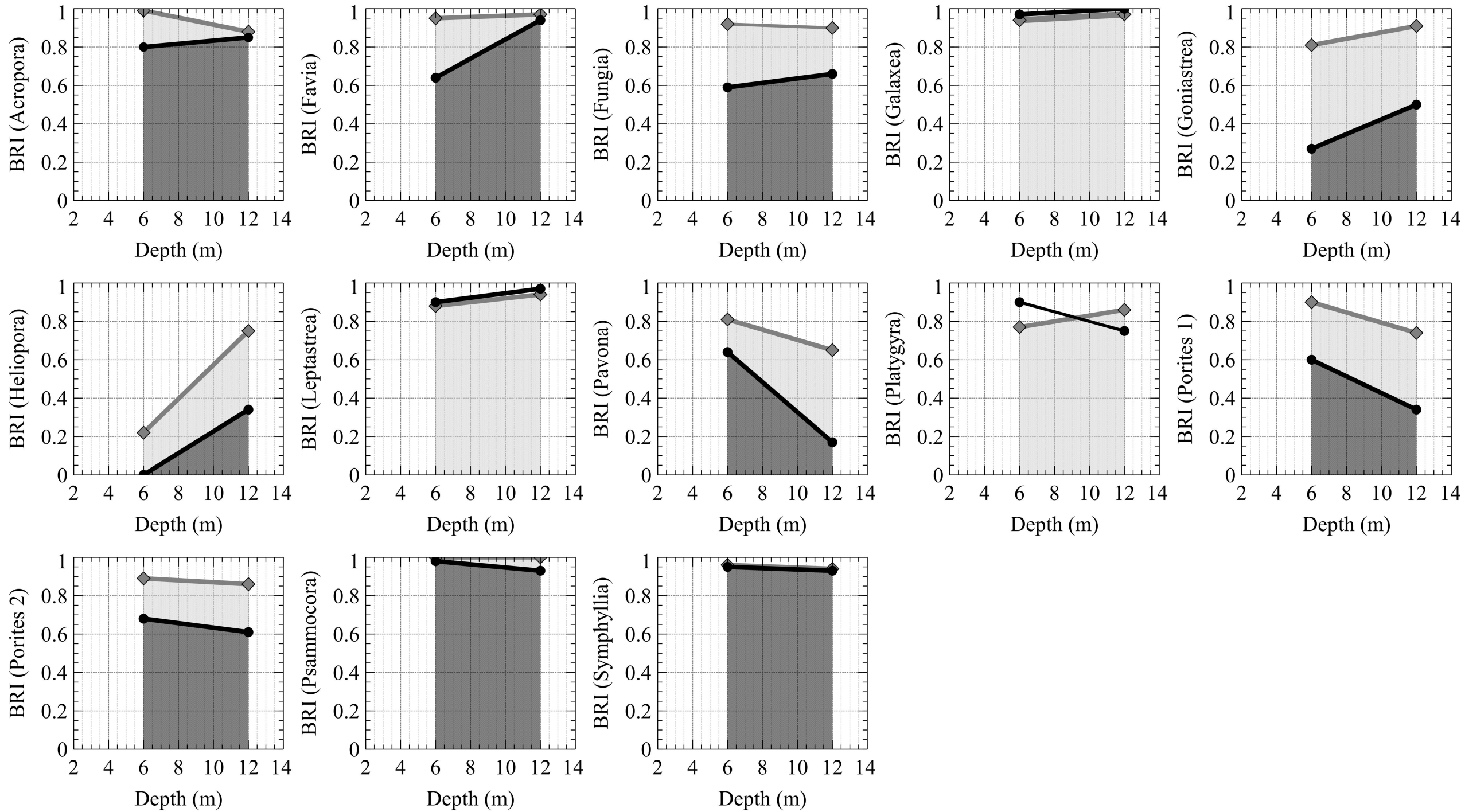
September


Acropora
Cyphastrea
Echinopora
Favia
Favites
Fungia
Galaxea
Goniastrea
Heliopora
Leptastrea
Montipora
Pavona
Platygyra
Pocillopora
Porites 1
Porites 2
Psammocora
Symphyllia
Percent (%)
0
20
40
60
80
100
June 2019
Oct 2019
June 2020
Mortality
B6
B5
B4
B3
B2
B1


BRI (Acropora)
BRI (Favia)
BRI (Fungia)
BRI (Galaxea)
BRI (Goniastrea)
BRI (Heliopora)
BRI (Leptastrea)
BRI (Pavona)
BRI (Platygyra)
BRI (Porites 1)
BRI (Porites 2)
BRI (Psammocora)
BRI (Symphyllia)
Depth (m)
0
0.2
0.4
0.6
0.8
1
2
4
6
8
10
12
14