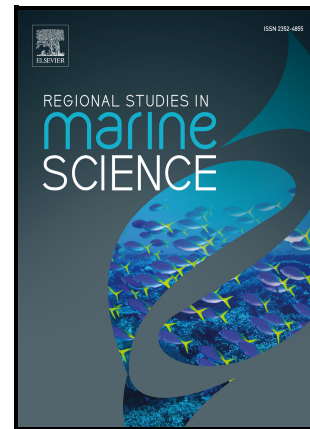


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## Turbid reefs experience lower coral bleaching effects in NE Borneo (Sabah, Malaysia)

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### ABSTRACT

The impacts of climate change are becoming more evident in recent years. Future projections suggest that heat stress events will likely be more frequent and severe over the next century, threatening the high diversity of the Coral Triangle. Shallow turbid reefs may help dampen some of these effects as several studies have shown their inherent resilience to heat stress events. Therefore, our main goal was to test this hypothesis by assessing the response of corals to the heat stress event of 2020. We conducted bleaching surveys in two contrasting habitats in Darvel Bay, Sabah: the turbid reef of Sakar, and the clear-water reef of Blue Lagoon. Relatively high coral cover (40-43%) was observed on both reefs in 2019. Underwater data loggers were used to monitor temperature and light. Coral colonies were scored from video transects of 100 m at 5 m and 10 m depth in both localities, with an additional transect at 15 m depth in Blue Lagoon. A total of 1,326 coral colonies were evaluated for bleaching presence and bleaching severity based on the six-point scoring method. Bleaching severity varied significantly between both reefs. Low bleaching impacts were observed in the high turbid reef, with an average of 9.6% of colonies having bleached. Meanwhile, the clear-water of Blue Lagoon had an average of 37.1% of coral colonies affected by bleaching. Bleaching severity also varied significantly among depth, where corals in deeper depths bleached less in Blue Lagoon. Foliose coral forms were most affected in Blue Lagoon, while massive coral forms suffered the most in Sakar reef. Bleaching responses were also significantly different among coral genera. While *Ctenactis* and *Herpolitha* were consistently resistant in both reefs, *Leptoseris*, *Fungia* and *Goniopora* were most affected in the 5 m of Blue Lagoon. Meanwhile, *Pachyseris* was notably more affected in Sakar reef at 10 m than in Blue Lagoon. Overall, bleaching indices within these two reefs are lower than most that were assessed around the globe during heat stress events in 2020. These outcomes support the hypothesis of turbid reefs hosting resilient coral communities in the face of climate change.

**Keywords:** Thermal stress; Reef refugia; Coral Triangle; Marginal reef; Coral bleaching

## 1. Introduction

Tropical coral reefs represent some of the most biodiverse and productive ecosystems on Earth and as such, they provide valuable ecological, social, and economical importance to millions of people around the world (Burke et al., 2012). Coral reefs are highly dynamic ecosystems with the capacity for recovery following a distressing event (e.g. storms, bleaching, etc.), which undoubtedly have contributed to their success in shallow tropical waters (Bellwood et al., 2006). However, their perceived resilience has progressively been tested in the past few decades, with the effects of climate change in the form of increasingly frequent extreme marine heat-wave events that are slowly reconfiguring the world's coral reef ecosystems (Hughes et al., 2017). Today, approximately a third of the world's corals face an elevated risk of extinction due to climate change induced heat stress, with the Coral Triangle in the Indo-Pacific hosting most of these high-risk coral species (Carpenter et al., 2008). This threat is alarming as the Coral Triangle region hosts the highest diversity of coral species in the world (Hoeksema, 2007).

Extreme heat stress breaks down the coral-algal endosymbiosis (Lesser, 2011). Corals may expel their algal endosymbionts during these stress events in a process called coral bleaching, leaving the host coral to secure alternate sources of energy (Lesser and Farrell, 2004). Failure to do so would lead to starvation and the eventual death of bleached corals (Douglas, 2003; McClanahan, 2004). At the community level, coral bleaching has driven catastrophic loss of coral cover and structural complexity of a reef, as well as causing shifts in reef community structure that reduce local coral diversity in favour of the most resilient taxa (Graham and Nash, 2013; Wismer et al., 2019; Bauman et al., 2022). On a more global scale, mass coral bleaching events have caused the collapse of ecosystem functions and reduced ecosystem service provision from coral reefs (Suggett and Smith, 2020; Tebbett et al., 2021). Coral bleaching events have been increasing in frequency and magnitude over the past two decades (Manzello et al., 2007; Buglass et al., 2016; Xie et al., 2017; van Woesik and Kratochwill, 2022). In particular, the year 2016 saw one of the worst mass-coral-bleaching events in recent years, where regions across the world observed extensive coral bleaching (Hughes et al., 2018; Ranith and Kripa, 2019; Quimpo et al., 2020).

While the main triggers to coral bleaching are associated with increased temperatures and light intensity, coral bleaching is rarely uniform (Lesser and Farrell, 2004; Rosic et al., 2020). There are a multitude of factors underpinning the various response patterns of corals to heat stress, ranging from local-scale environmental factors (Jiang et al., 2022) to the minute details of the coral microbiome (Fordyce et al., 2021; Sun et al., 2022). The physical architecture of corals reflected by the growth forms and coral skeletal density influence bleaching severity by altering the surface area and skeletal-tissue interface (Loya et al., 2001; Walsh et al., 2012). Other morphological characteristics of corals may play a role in the varying patterns of bleaching observed, such as their colony size, whereby smaller colonies are more likely to survive periods of heat stress (Bena and Van Woesik, 2004; Feliciano et al., 2018) and tissue thickness that regulates the level of photoprotection by buffering light intensity within the coral tissue (Hoegh-Guldberg and Salvat, 1995; Baker et al., 2008).

Climate projections continue to show that marine heatwave events are expected to increase in frequency and magnitude over the coming century, putting existing corals at a higher risk of

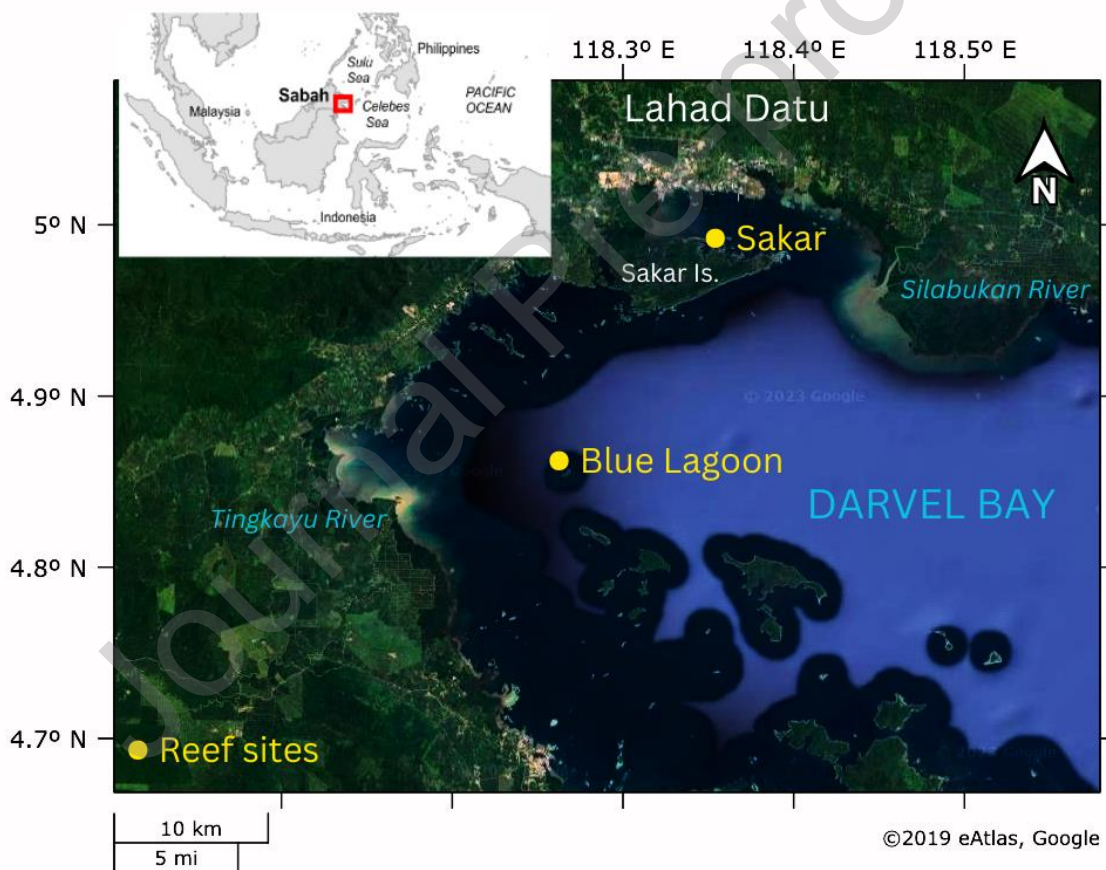
extinction (IPCC, 2022). Therefore, there has been renewed interest in identifying potential climate change refugia for corals in recent years in an effort to increase coral survivability over repeated stressful events. The “deep reef refugia” hypothesis proposed by Glynn (2006), argues that corals inhabiting the mesophotic zone (> 30 m depth) are protected from increased sea surface temperature during heat stress events and may provide a viable source of recruits for affected reefs following a disturbance (Bongaerts et al., 2010). Other potential refugia come in the form of shallow mesophotic reef environments, so-called turbid reefs. Although turbidity is often considered detrimental to corals due their light-reducing and smothering effect of sediments on coral polyps (Erftemeijer et al., 2012), turbid reefs may be able to support coral populations that withstand thermal stress events more efficiently than their counterparts in clear waters (Sully and van Woesik, 2020). Several coral species have the ability to shift between autotrophy and heterotrophy feeding modes in response to environmental disturbance (Anthony, 2000). Heterotrophic feeding relies on actively feeding on plankton and suspended organic matter to gain energy, rather than on the algal endosymbionts to photosynthesise. Corals living in naturally turbid environments have acclimated to low-light, highly sedimented conditions in the long-term, allowing them to fully utilise energy gained via heterotrophy into coral growth, maintenance, and reproduction (Borell et al., 2008; Seemann et al., 2013). Meanwhile, corals that have not acclimated to such conditions are unlikely to utilise this feeding strategy as most energy gained would be expended towards survival (Anthony and Fabricius, 2000).

Some studies of fossil reefs suggest that shallow turbid reefs were common during the early origins of the Coral Triangle and throughout the Cenozoic, suggesting that they may have played an important role as cradles of coral diversity while hosting resilient communities over the past 30 million years (Santodomingo et al., 2016). Interestingly, it seems that the Coral Triangle in the present day may provide environmental conditions in which coral reefs mainly occur under relatively higher levels of turbidity (Sully and van Woesik, 2020). However, turbid reefs remain poorly explored coral habitats. Although there are growing interests in studying turbid reefs (Zweifler et al., 2021), existing approaches such as large-scale visual censuses and remote sensing methods are often more challenging or inapplicable in turbid settings. Hence, the spatial extent of turbid reefs remains largely uncharted. Even more rare is research on the ecological functioning and importance of these reefs. Therefore, the main objective of this study is to assess the extent of coral bleaching by comparing a turbid reef to a clear-water reef in Darvel Bay (East coast of Sabah, Malaysia) following the recent onset of the 2020 bleaching event in the region. This study also specifically aims to examine variations in bleaching response of corals between the two reefs along a depth gradient, and among different coral growth forms and coral taxa. These local surveys are important because in addition to global heating, the Coral Triangle is a region heavily affected by a number of local anthropogenic stressors caused by coastal development, deforestation and watershed-based pollution, all of which affect mostly these shallow marginal reef ecosystems (Burke et al., 2012). In addition, by shedding light on the potential refugia nature of shallow mesophotic reefs in Darvel Bay, informed decisions can be made by policy-makers that may prioritise the conservation of these often-overlooked reef ecosystems.

## 2. Material and methods

### 2.1 Study site

This study was conducted in Darvel Bay, located on the east coast of Sabah, Malaysian Borneo (Fig. 1), at the northwest border of the Coral Triangle. This region has the highest concentration of Malaysian coral reefs (Burke et al., 2012) and one of the highest species richness compared to other regions within the Coral Triangle, as is the case for mushroom corals of the family Fungiidae (Waheed and Hoeksema, 2013). Coral reefs within the greater Semporna - Darvel Bay region primarily consist of fringing reefs and small patch reefs, including several rare and endemic coral reef species, contributing to its high biological diversity (Jakobsen et al., 2007) that accounts for about 225 species of hard corals (Ditlev, 2003).



**Fig. 1.** Map showing the locations of studied reefs, Sakar and Blue Lagoon, in Darvel Bay (Sabah, Malaysian Borneo).

Darvel Bay is a semi-enclosed bight, and its oceanography is influenced by two monsoon seasons that are regulated by winds from the northeast from November to March, and from the southeast from May to September (Saleh et al., 2007). Darvel Bay seawater ranges from very turbid to clear water. Brown turbid waters with low pH values and high humic content are dominant in the innermost part of the bay (Ditlev, 2003). For this study, two



contrasting habitats were surveyed, the clear-water reef of Blue Lagoon (4°51'N, 118°15'E) and the turbid reef of Sakar (4°58'N, 118°21'E). The Blue Lagoon is an offshore semi-atoll reef located approximately 11 km away from the mainland (Table 1). Surveys in Blue Lagoon were performed on the outer reef that extends to over 30 m in depth. On the other hand, Sakar is an urban reef that lies on the leeward side at 150 m off Sakar Island, hence protected from storms and wave action. Sakar reef extends down to 11 m in depth with a gentle slope surrounded by particularly fluffy, muddy, and silty substrate (Ditlev, 2003). An ongoing study of these reefs indicated that both have high live coral cover, relatively high cover of turf and coralline crustose algae, low macroalgal cover, and no apparent diseases (Santodomingo et al., 2022).

**Table 1.** Environmental conditions and habitat characterisation of Blue Lagoon and Sakar reefs.

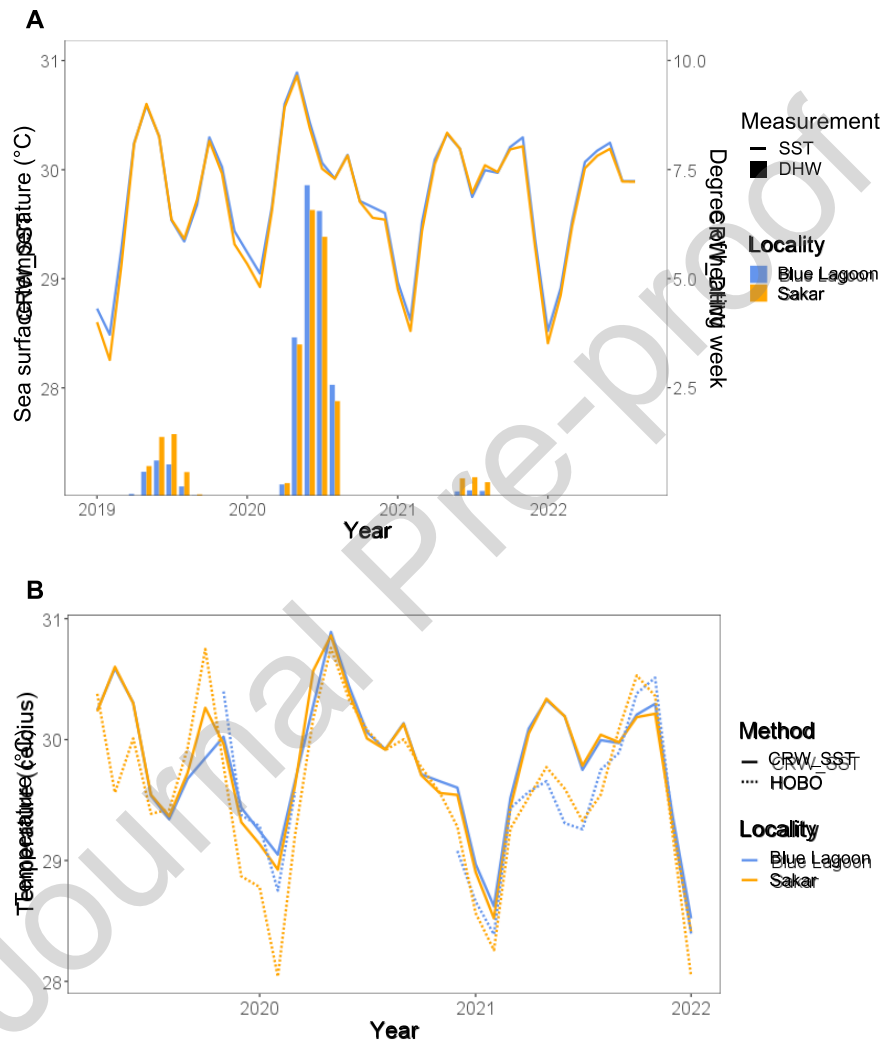
Parameters	Blue Lagoon	Sakar
Sedimentation*	1.0 ± 0.4 mg cm <sup>-2</sup> d <sup>-1</sup>	6.2 ± 1.1 mg cm <sup>-2</sup> d <sup>-1</sup>
Sediment composition	Gravel + Sand: 94%; Silt + Mud: 6%	Gravel + Sand: 21% Silt + Mud: 79%
Distance to coast	11 km	0.2 km
Distance to Lahad Datu	20 km	4 km
Reef extension	> 30 m depth	Up to 11 m depth
Benthic cover	Live coral: 26-61%; Turf algae: 32-40%; Macroalgae: 0-21%	Live coral: 39-40%; Turf algae: 24-25%; Macroalgae: 0%

\*Average sedimentation rate between October 2019 and January 2022 at 10 m depth of each reef station.

Water samples from each reef were collected to assess their turbidity levels. The first batch was taken on-site at only 10 m depth in January 2022 during the wet season. Meanwhile, the second batch of turbidity data was collected during the dry season in July 2022 at 5 m, 10 m and 15 m depths in Blue Lagoon, and at 5 m and 10 m depths in Sakar reef. Two replicates of water samples were collected at each depth. Turbidity measurements were taken using the Thermo Scientific™ Orion™ AQ4500 turbidity metre. Although Darvel Bay is affected by two monsoon seasons, strong winds and rainfall are significantly higher during the northeast monsoon season, a period categorised as the wet season (Saleh et al., 2007). High water movements plus an increase on sediment inputs from run-off and river outflow during this period could explain the increase in turbidity levels on both reefs during the wet seasons compared to what was observed during the dry season. Light and temperature data were collected by placing HOBO Pendant® MX2202 loggers at 5 m and 10 m depths in both reefs from 2019 to 2022, with additional loggers at 15 m of Blue Lagoon. Unfortunately, data from 5 m of Blue Lagoon was lost due to flooded and unrecovered loggers. Light intensity (in Lux or lumens/ft<sup>2</sup>) data was extracted to show the daily averages from 10 am to 3 pm throughout 2020.

## 2.2 Environmental monitoring of bleaching progression

Records of sea surface temperature (SST) and the degree of heating weeks (DHW) within the Blue Lagoon and Sakar reef regions were compiled from the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch dataset available at ([https://coastwatch.pfeg.noaa.gov/erddap/griddap/NOAA\\_DHW.html](https://coastwatch.pfeg.noaa.gov/erddap/griddap/NOAA_DHW.html)). Daily averages of SST and DHW were then extracted from January 2019 to August 2022 to determine temperature peaks and identify the start of the bleaching event (Fig. 2A). Daily averages of SST were compared with *in-situ* temperature loggers to determine variations in temperature at 10 m depth (Fig. 2B).



**Fig. 2.** (A) Sea surface temperature (SST) and the degree of heating weeks (DHW) of Blue Lagoon and Sakar stations from 2019 to 2022 gathered from NOAA's Coral Reef Watch (CRW); and (B) Comparison between NOAA's CRW SST and *in-situ* temperature measurements at 10 m depth of Blue Lagoon and Sakar stations from Hobo data loggers. Gaps indicate missing data records from lost or broken loggers.

### 2.3 Coral bleaching survey and measurements

Bleaching surveys were conducted in July 2020, two weeks following a coral bleaching alert within this region released by NOAA. Assessments were done on 100 m x 1 m video transects along the reef of Blue Lagoon at 5 m, 10 m, and 15 m, while video transects on the reef of Sakar were only conducted at 5 m and 10 m due to the shallow nature of this particular reef. One hundred still images were extracted from each of the video transects using the OpenCV Python library (Bradski, 2000) and of these images, 20 were randomly selected for analysis (approximately 1 still image every 5 m along the transect). Each still image or frame covers an area of approximately 1 m<sup>2</sup>. Therefore, a total of 20 m<sup>2</sup> area was analysed for bleaching at each depth and locality. All coral colonies larger than 5 cm across were assessed using ImageJ (Schneider et al., 2012). Colonies were identified to the genus level, along with their growth forms (massive, encrusting, foliose, branching, free-living) recorded, bleaching prevalence (occurrence of bleaching or not), and bleaching severity. Bleaching severity was analysed using the six-point scoring system by categorising each colony into the following six categories: (1) unbleached (normal colouration), (2) pale (lighter colour than the usual), (3) 0-20 % of the surface bleached, (4) 20-50 % bleached, (5) 50-80 % bleached, and (6) 80-100 % bleached (McClanahan, 2004). A taxon-specific bleaching index (BI) was then calculated from the percentage of observations in each of the above categories as below:

$$BI = \frac{(0c_1 + 1c_2 + 2c_3 + 3c_4 + 4c_5 + 5c_6)}{5}$$

where  $c_i$  is the percentage of observations in each of the above six categories. A total of 1,326 coral colonies were evaluated in order to assess their response to the 2020 bleaching event. The dominant coral genera across both reefs were identified and chosen to be the focus in the BI analysis. The BI scale runs from 0 if no colonies were bleached to 1, where all colonies of that particular taxon were fully bleached.

### 2.4 Statistical analyses

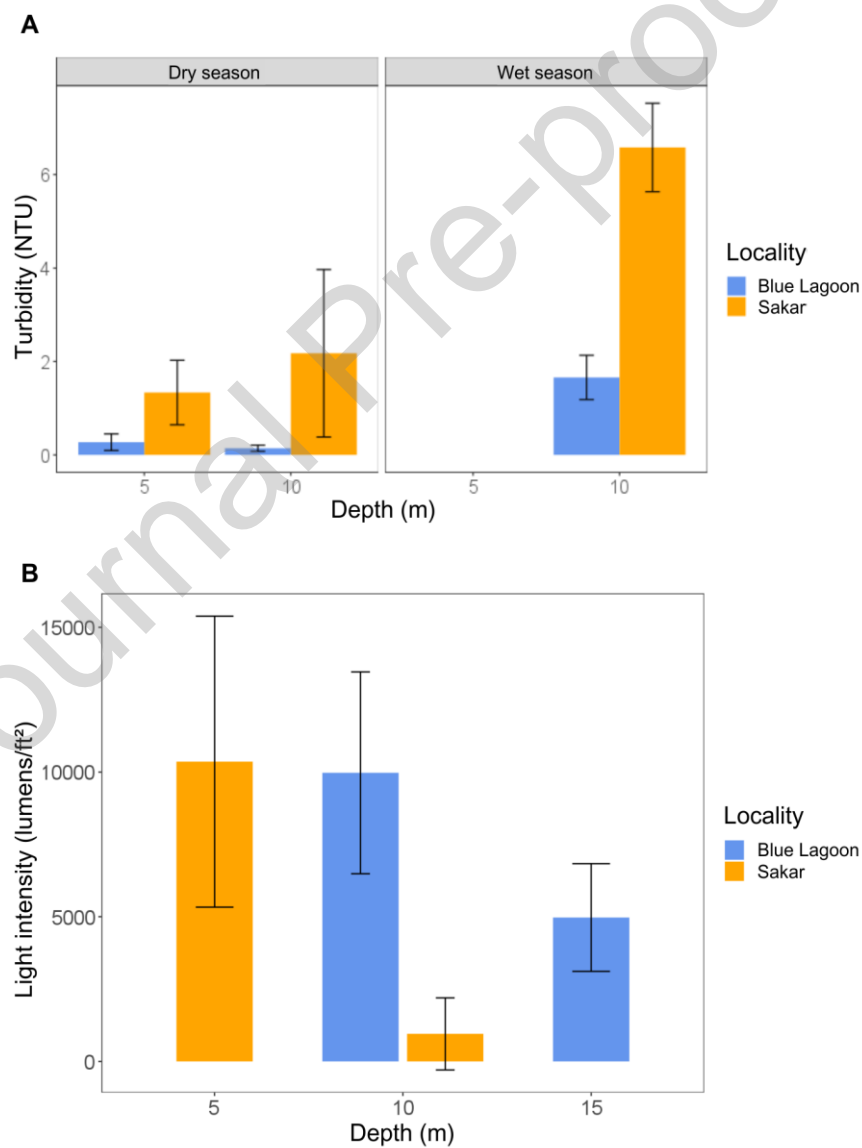
Differences in the percentage of coral bleaching among Blue Lagoon and Sakar reef were examined using a generalised linear model (GLM) in the form of a two-way ANOVA and the post-hoc Tukey's test were used to detect any significant changes in the bleaching prevalence between the two stations. All prerequisite assumptions of the parametric tests were met prior to the analyses of variance. The relationship between most bleached genera with their respective abundance was investigated using a linear regression. Correlations were performed for taxa for which more than 20 colonies were present across both reefs.



### 3. Results

#### 3.1 Environmental characterisation

Turbidity levels in Blue Lagoon remained lower with respect to the values of Sakar throughout both seasons, where turbidity levels during the wet season were up to three-fold higher (Fig. 3A). Light levels at 5 m in Sakar are similar to light levels in Blue Lagoon at 10 m depth, while at 10 m depth in Sakar is only 950 Lux on average (Fig. 3B). Meanwhile, light levels at 15 m depth in Blue Lagoon are on average 4,970 Lux, which is half the amount of light in that locality at 10 m, but still five times higher than at 10 m depth in Sakar. No light data was successfully recovered at 5 m of Blue Lagoon during this period.

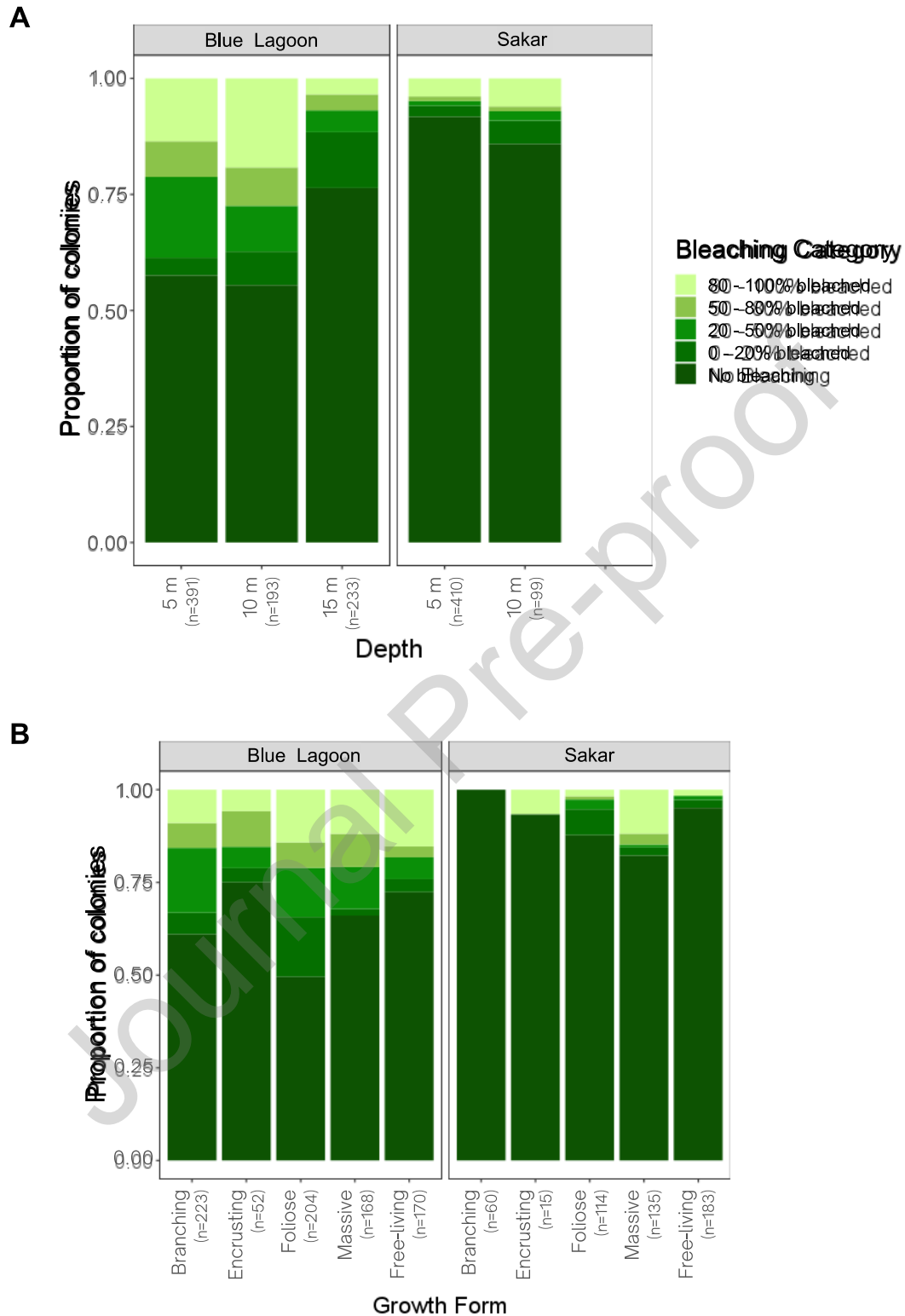


**Fig. 3.** (A) Turbidity levels at Blue Lagoon and Sakar reef at 5 m and 10 m depth between the dry and wet seasons in 2022; and (B) Light intensity at 5 m, 10 m and 15 m depth of Blue Lagoon and Sakar reefs in 2020.

### 3.2 Bleaching prevalence and severity

The response of corals to the heat stress in July 2020 were substantially different between reefs and growth forms (Fig. 4). Of the 1,326 coral colonies surveyed in July 2020, 26.5% were partially or severely bleached. Corals in Blue Lagoon reef were more affected by bleaching, with an average of 37.1% of colonies having bleached compared to the average of 9.6% coral colonies affected by bleaching in Sakar reef (ST1;  $F = 92.0$ ,  $P < 0.001$ ). Bleaching prevalence also varied significantly across depths, whereby corals were more impacted by bleaching at 5 m and 10 m of Blue Lagoon (41.2% and 44.6% of colonies bleached respectively), compared to colonies at the deeper depth of 15 m (Fig. 4A; 24% of colonies bleached ( $F = 31.5$ ,  $P < 0.001$ )). Interestingly, corals in Blue Lagoon were most severely impacted by bleaching at 10 m, where 14.5% of colonies showed very severe to full bleaching. Meanwhile, corals in Sakar reef showed much less bleaching severity across both depths, albeit a slightly higher proportion of colonies having bleached at 10 m with 14.1% of colonies bleached, compared to 8.5% of bleached colonies at 5 m.

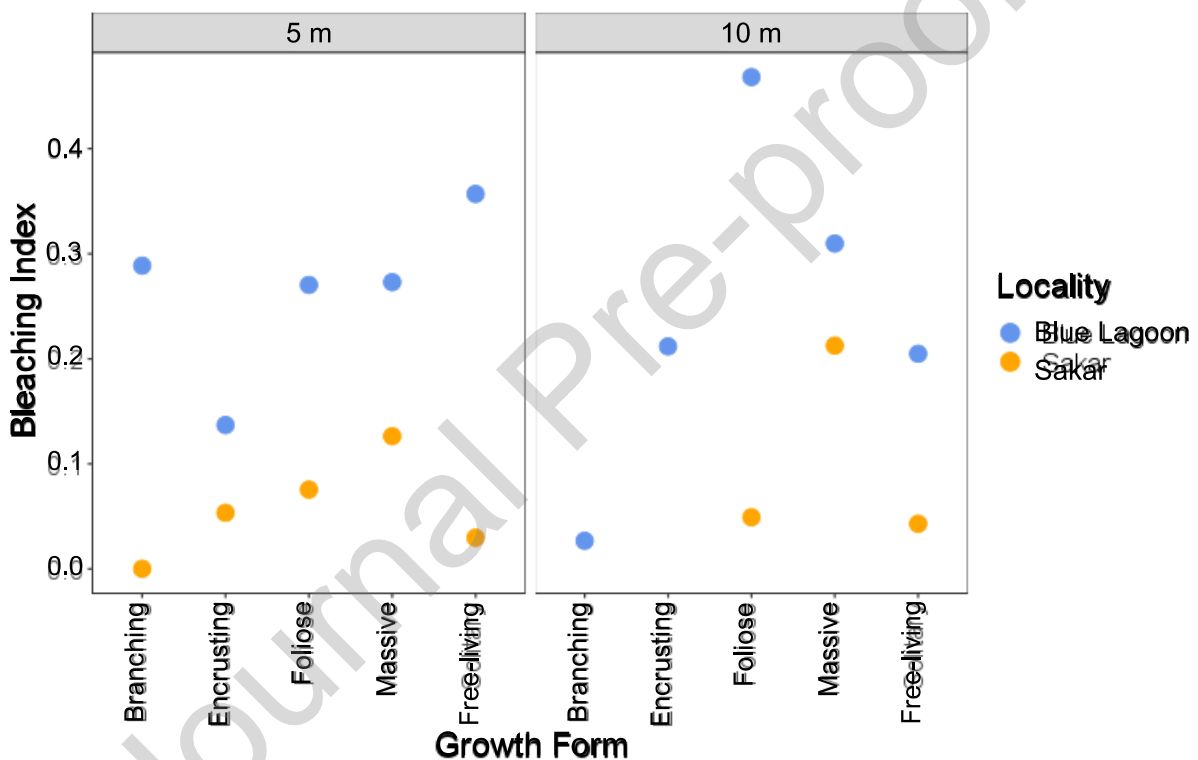
Corals also showed varying responses to heat stress across different growth morphologies (Fig. 4B). The differing responses were significant, although to a lesser degree ( $F = 3.8$ ,  $P < 0.01$ ). In Blue Lagoon, foliose or foliaceous coral growth forms were most impacted by bleaching, whereby half of the assessed colonies were bleached (50.5% of colonies bleached). This is followed by the abundant branching coral forms where 39% of colonies were found to have bleached. Encrusting coral forms were the least affected, with only 25% of colonies affected in this reef. Meanwhile for corals in Sakar reef, branching coral forms seemed unaffected by the heat stress accounting for the lack of apparent bleaching in these colonies. Compared to the other growth morphologies in Sakar, massive coral forms were the most impacted by coral bleaching, with 17.8% of colonies showing signs of bleaching, while the common foliaceous forms show a 12.3% of colonies bleached.



**Fig. 4.** Proportion of coral colonies in different classes of bleaching severity across: (A) depth gradient; (B) coral growth morphologies in reefs of Blue Lagoon and Sakar. The number of colonies assessed are indicated within the parenthesis.

### 3.3 Bleaching indices of corals

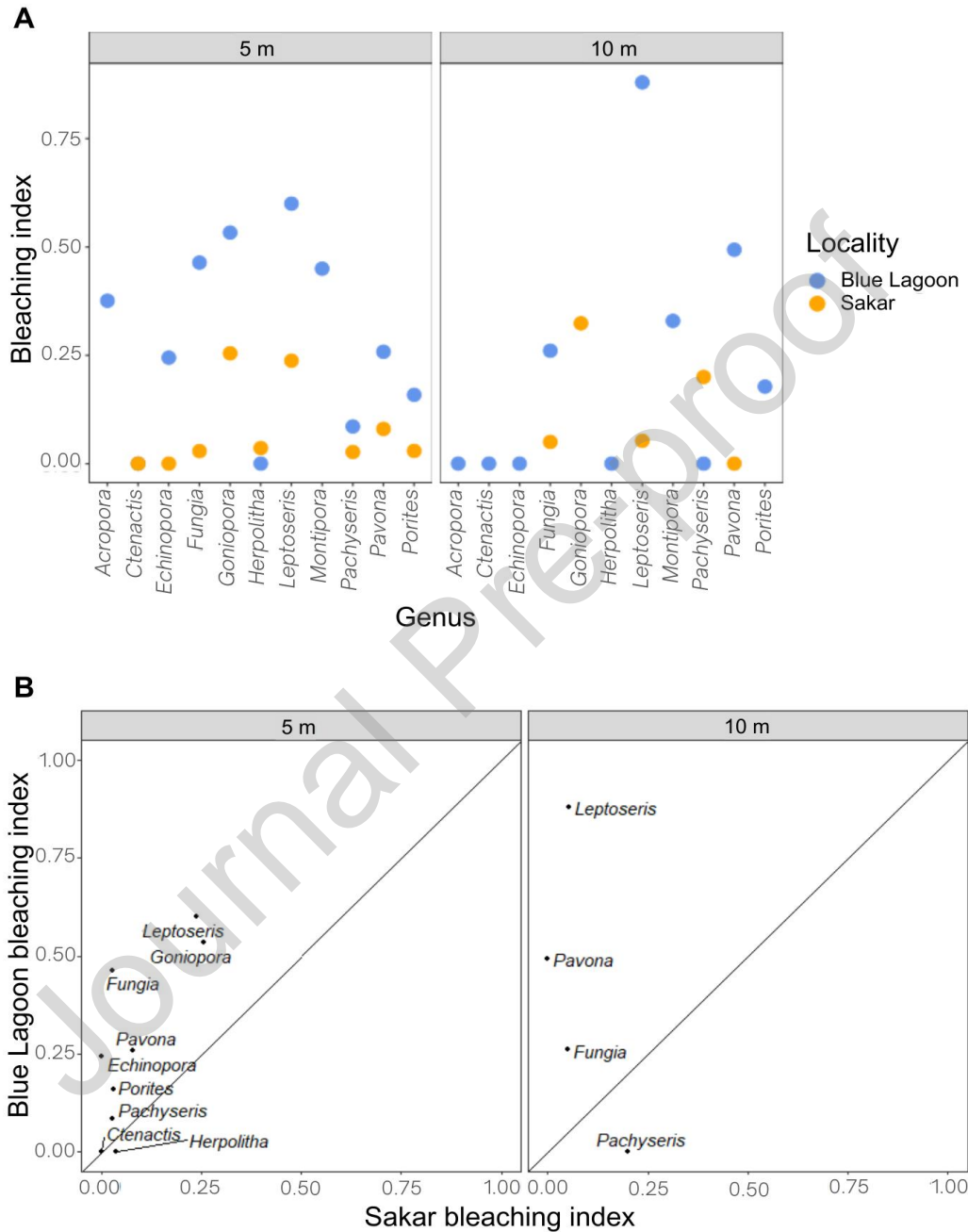
In addition to looking at the prevalence of bleached corals, the bleaching index provides an enhanced view to any interspecific variations as different observations may vary among species and could be related to other factors such as species composition (McClanahan, 2004). Varied responses to bleaching were evident between coral growth forms (Fig. 5). At 5 m depth, free-living (BI = 0.36) and branching corals (BI = 0.29) in Blue Lagoon reef were the most affected by bleaching. This is in contrast to those found in Sakar reef, whereby branching (BI = 0) and free-living corals (BI = 0.03) remained unaffected or minimally affected by bleaching. Foliose or foliaceous corals were the most affected by bleaching at Blue Lagoon reef (BI = 0.47), while massive coral forms were the most affected in Sakar reef (BI = 0.21).



**Fig. 5.** Bleaching indices showing different coral growth forms in Blue Lagoon and Sakar at 5 m and 10 m depths. Missing Sakar data at 10 m depth is due to the absence of both branching and encrusting coral forms in the survey.

The BI indicates marked variation in the severity of bleaching among the most abundant coral genera across depths at both reefs (Fig. 6;  $F = 3.42$ ,  $P < 0.001$ ). As previously stated, coral colonies in Sakar (BI = 0.07) were substantially less affected by bleaching compared to that of Blue Lagoon (BI = 0.26), especially at 5 m (Fig. 6A). At 5 m depth, *Ctenactis* and *Herpolitha* were consistently resistant on both reefs, while *Leptoseris*, *Goniopora* and *Fungia* were notably the most affected in Blue Lagoon in comparison to Sakar reef (Fig. 6B). On the other hand, there are several instances whereby coral taxa in Sakar showed a slightly higher bleaching severity compared to those in Blue Lagoon. *Herpolitha* was more affected in Sakar (BI = 0.04) than in Blue Lagoon (BI = 0.00) at 5 m depth, while *Pachyseris* showed a similar trend at 10 m in both reefs with BI = 0.20 at Sakar and no bleaching at Blue Lagoon. Even though there

are marked differences in the bleaching response of coral taxa between the two studied reefs, the overall bleaching index accounting for all coral colonies evaluated within Darvel Bay in this study is relatively low with a BI = 0.19.



**Fig. 6.** Bleaching indices of (A) the most abundant coral genera (>20 colonies across both reefs), and (B) scatterplots of the bleaching indices of corals in Blue Lagoon and Sakar reefs at 5 m and 10 m depths. The diagonal line represents a 1:1 correlation, which denotes an equal bleaching response between the two reefs.



## 4. Discussion

### 4.1 Effects of turbidity on coral bleaching

Our bleaching observations are consistent with other studies that show corals living in turbid environments seem to be less susceptible to bleaching compared to their clear-water counterparts (Van Woesik et al., 2012; Morgan et al., 2017; Teixeira et al., 2019; Valino et al., 2021). Even though coral communities in the turbid reef of Sakar experienced similar levels of heating during the peak SST event in July 2020, they show low incidences of bleaching observed in 9.6% of corals suggesting that they were significantly more resistant to heat stress. This finding supports the idea that suspended sediments in high turbid settings can reduce solar irradiance by buffering UV light rays and helping to alleviate radiative stress of the corals to some extent (Anthony et al., 2007). Similar examples of turbidity being favourable for corals during bleaching events have been reported in the nearshore turbid reefs of the Great Barrier Reef in Australia (Morgan et al., 2017), Singapore (Guest et al., 2016), Palau (Van Woesik et al. 2012), and Hawaii (Carlson et al. 2022). However, in some cases turbidity alone cannot fully counteract the effects of high temperatures, especially in highly degraded turbid reefs near urban areas (Bauman et al., 2022; Carlson et al., 2022) in which generalist coral taxa (such as *Merulina*, *Pachyseris* and *Pectinia*) that have survived continuous bleaching events may eventually show higher bleaching prevalence and post bleaching mortality. If local anthropogenic impacts may diminish the effect of turbidity to alleviate thermal stress, then it is recommended to monitor further bleaching events in the turbid reefs of Darvel Bay. In particular, the resilience observed in the urban reef of Sakar may be compromised in the near future as a result of the continuous environmental degradation in this locality due to pollution (Santodomingo et al., 2021).

### 4.2 Drivers of spatial variation of coral bleaching in Darvel Bay reefs

Although gradual reduction in light intensity with increasing depth is typical in clear-water reefs, in turbid reefs there is consistent rapid reduction in light over short depth intervals (Morgan et al., 2017). Indeed, light availability in the clear-water of Blue Lagoon declined by 50% from 10 m to 15 m, while light in the turbid reef of Sakar was reduced by a staggering 91% from 5 m to 10 m depth. Depth seems to be a more important factor in attenuating coral bleaching in the clear-water reef, as even small reductions in light intensity from 10 m to 15 m ostensibly lowered bleaching responses of corals in Blue Lagoon. Meanwhile within the turbid reef of Sakar, variation in depth did not affect the bleaching response of corals, even though there is a greater light reduction between the two depth intervals compared to the light reduction seen in the clear-water reef. This generalised low bleaching effect in corals at the Sakar reef can be related to the already high turbidity and low-light conditions at 5 m depth, as turbidity and light are lower than those of the deeper regions in the clear-water reef. Our observations show that the same principles used in the depth refugia hypothesis, whereby low-light conditions at depth may help corals alleviate heat stress (Eyal et al., 2022), can also be applied to shallow mesophotic reefs. On the other hand, some studies have found the opposite effect of

depth on coral bleaching. For instance, during the 2015 bleaching event in Mexico, the most severely affected clear-water reefs were those with depths greater than 5 m (Muñiz-Castillo and Arias-González, 2021). The argument was made that depth may not provide refuge from bleaching, as it lacks complete protection from heat stress. Instead, adaptation of corals living in shallower reefs may play a bigger role because these corals may have acclimated due to the regular exposure to sublethal stress and with time, would become less sensitive to bleaching.

This study showed that in the clear-water reef, corals with higher complexity in the form of foliose and branching coral forms were more susceptible to bleaching. This is consistent with other findings that show branching coral forms generally suffer more devastating effects of bleaching and mortality than corals with massive and encrusting morphologies (Hoegh-Guldberg and Salvat, 1995; Baker et al., 2008; Xie et al., 2020). In the long term, the reduction of branching and foliose coral forms can have negative functional consequences in a reef, as these growth forms increase the rugosity and structural complexity supporting a high diversity of fish and other reef-dwelling organisms (Bellwood et al., 2006; Wismer et al., 2019). On the other hand, massive and encrusting corals typically have thicker tissues that enable them to retract their polyps hence reducing the effect of heat stress, and they are more efficient at removing oxidative radicals that are produced during different stress events (Loya et al., 2001; Putnam et al., 2017). Conversely, massive coral forms in the turbid reef of Sakar were observed to be most affected during this bleaching event. Although, it is important to note that many of the massive coral forms in this reef, particularly at 10 m were represented by small colonies of *Goniopora* that were mostly found loosely lying on the extremely silty, muddy substrate. Hence, it could be argued that these colonies, albeit massive or sub-massive in growth form, may have bleached due to the compounding factors of high heat stress and extremely high sedimentation and smothering.

#### 4.3 Species response to bleaching

In the clear-water of Blue Lagoon reef, acroporiids of the genera *Acropora* and *Montipora* were the most affected, followed by *Pavona*, *Goniopora* and *Leptoseris*. This is consistent with the evidence observed in the Great Barrier Reef (GBR) where *Acropora* was identified to be the genus that is most susceptible to thermal stress (Loya et al., 2001), bleaching extensively in clear-water sites (Hughes et al., 2018), while being minimally affected in turbid sites (Morgan et al., 2017). Throughout our study, *Acropora* and *Montipora* colonies were absent in the turbid reef of Sakar, demonstrating their specialist nature brought about by life-history strategies that favour high-light environments (Darling et al., 2012), but impairing direct comparisons of their response under high turbidity. At a global scale, the genus *Acropora* seems to present a more complex response to bleaching (Hoegh-Guldberg and Salvat, 1995; Rosic et al., 2020). Indeed, some studies have found low to moderate bleaching in the two *Acropora* species occurring in Caribbean reefs (Muniz-Castillo & Arias-Gonzalez 2021). Furthermore, the varying responses of coral taxa to bleaching may be due to heterotrophy. The ability to gain energy by ingesting organic particles allows corals to compensate for the reduction in autotrophic feeding activity in low-light environments or during bleaching events

(Baird et al., 2008). Subsequently, corals with higher heterotrophic capacity have been associated with lower susceptibility to heat stress (Price et al., 2021; Sturaro et al 2021). This is consistent with our findings where the primarily autotrophic *Acropora* and *Goniopora* (Conti-Jerpe et al., 2020) colonies within the high-light environment of Blue Lagoon were some of the most affected by bleaching. Furthermore, *Porites* colonies that were only moderately affected by this bleaching event, may owe their successes to their mixotrophic nature by utilising both autotrophic and heterotrophic feeding modes (Price et al., 2021).

Response to bleaching by other coral taxa was also different between the two localities. While *Leptoseris* colonies in the Blue Lagoon had a high bleaching index (BI = 0.68), they were less affected in Sakar. *Leptoseris* in the clear-water of Blue Lagoon reef were predominantly found in small clumps of foliose colonies within large stands of *Pavona cactus* and both taxa were overgrown by extensive fleshy patches of *Padina* macroalgae. Competition with macroalgae may be another evidence of multiple compounding factors resulting in bleaching of *Leptoseris* colonies not often regarded as susceptible to bleaching. On the contrary, large foliose colonies of *Leptoseris* in the turbid reef of Sakar were less affected by bleaching, showing only focal bleaching limited to the colony margins. Corals of the family Fungiidae exhibit relatively high recovery from bleaching compared to many other taxa. Indeed, their remarkable recovery was demonstrated directly in the Gulf of Thailand in 2011 where extensive bleaching occurred in an assemblage of Fungiidae just a year prior (Hoeksema et al., 2012). Additionally, many studies have reported colonies of this family to have high heterotrophic capacity (Houlbrèque and Ferrier-Pagès, 2009; Pogoreutz et al., 2017) and are likely to be bleaching-resistant (Feliciano et al., 2018). In this study, *Ctenactis* and *Herpolitha* were consistently resistant to bleaching in both reefs, especially in the shallower depth. Resistance to bleaching by the genus *Ctenactis* has been previously recorded during a bleaching event in 1983 in the Java Sea (Hoeksema, 1991), as well as in 2010 in the Gulf of Thailand (Hoeksema and Matthews, 2011). At species level, Fungiidae may display different bleaching patterns as a response to thermal stress depending on their life stage and disturbance history (Hoeksema, 1991), thus individual responses to heat stress and therefore their bleaching susceptibility can vary greatly even within one species (Borell et al., 2008). This high variation on bleaching response by Fungiidae was observed in this study, as *Fungia* colonies show a high bleaching severity in the clear-water reef of Blue Lagoon, while *Fungia* colonies that dominate the shallow turbid reef remained minimally affected by thermal stress. Despite the varying heat stress responses between the clear-water and turbid reefs, the large overlap of coral taxa occurring in both reefs observed in this study could prove to be beneficial for adjacent reefs damaged by heat stress events.

#### 4.4 Response of corals in other regions during bleaching events in 2020

The temporal onset and bleaching percentage of coral reefs in Darvel Bay to the 2020 bleaching event was compared to other studies across the Indopacific region during the same year (Table 2). The majority of these studies show that coral bleaching in 2020 was more severe elsewhere than within Darvel Bay. For instance, in the GBR, the onset of bleaching started

during the austral summer months of February and March (Benthuisen et al., 2021; Fordyce et al., 2021; Smith et al., 2022; Tebbett et al., 2022), which is much earlier than when bleaching started in Darvel Bay; data from such bleaching events show that corals of Heron Island were moderately affected (Ainsworth et al., 2021) while in One Tree Island bleaching occurred in more than half of the corals surveyed, although no measure of bleaching severity was conducted (Nolan et al., 2021). The South China Sea was hit by severe marine heatwaves between July to October 2020 (Liu et al., 2021; Chen et al., 2022; Feng et al., 2022), resulting in multiple reports of severe coral bleaching such as in the Hainan Island where more than 80% of the colonies were affected (Zhu et al., 2021; Lyu et al., 2022; Mo et al., 2022). These events in particular coincided with the bleaching occurrence we observed within Darvel Bay, yet the impact in our study area was much lower. Across the Indopacific, it was reported that coral bleaching was also occurring in the Red Sea between September and October 2020, whereby the corals were low to moderately affected by bleaching (Dosoky et al., 2021). Additionally, there were also records of observed bleaching between 50 to 65 m depths during this period and region, albeit unquantified (Eyal et al., 2022). In summary, corals in Darvel Bay, especially those occurring in turbid reef environments, have responded better to the 2020 heat stress event compared to many coral reefs around the globe. This highlights the importance of protecting the marine ecosystem of Darvel Bay, be it clear-water or turbid, to continue providing safe havens for corals during periods of heat stress.

**Table 2.** Coral responses to heat stress events in 2020 in different regions around the world.

Country	Site	Locality	Season	Survey period	Local threats	Methods	Bleaching indices	Paper
Malaysia	Darvel Bay	Northern Sakar Island	Dry season	July 2020	Overfishing, pollution	1m x 1m photo-quadrats; 6-point scoring method (McClanahan, 2004)	0.07	Present study
Malaysia	Darvel Bay	Blue Lagoon (outer wall)	Dry season	July 2020	Overfishing, pollution	1m x 1m photo-quadrats; 6-point scoring method (McClanahan, 2004)	0.26	Present study
Australia	Southern GBR	One Tree Island	Austral summer	February 2020	Crown-Of-Thorns Starfish outbreaks	Video transects; Coral Watch colour chart (Siebeck et al., 2006)	0.31 – 0.66	Nolan et al. (2021)
Australia	Southern GBR	Heron Island	Austral summer	March 2020	Coastal development	1m x 1m photo-quadrats; CoralNet (coralnet.ecsd.edu)	0.35 – 0.50	Ainsworth et al. (2021)
China	Northwest Hainan Island	Meixia, Huanglong, and Paipu	Summer	September – October 2020	Coastal development, aquaculture	Line Intercept transect (Huang et al., 2020)	0.80	Zhu et al. (2021)
China	Hainan Island	Weizhou, Xuwen, and Sanya	Summer	September 2020	Coastal development, pollution	1m x 1m belt transect; 3-category bleaching severity	0.81 – 0.88	Mo et al. (2022)

China	Hainan Island	Paipu	Summer	August–September 2020	Coastal development	10m x10m quadrats	0.56	Liu et al. (2021)
Egypt	Northern Red Sea	Hurghada, Safaga, Al-Quseir, Port Ghaleb, Marsa Alam, and Wadi El-Gemal	Summer	September – October 2020	Coastal development, destructive fishing practices	Line Intercept transect; Bleaching severity ranking (Baird and Marshall, 2002)	0.14 – 0.66	Dosoky et al. (2021)

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## 5. Conclusion

While many regions across the world showed high coral bleaching occurrences during the 2020 bleaching event, our data show the overall impacts of coral bleaching was comparatively low in the reefs within Darvel Bay. This is further emphasised by minimal coral bleaching found in the marginal reef of Sakar during this period of usually high temperatures. With climate projections showing upward trends of sea surface temperatures globally, more marine heatwaves and subsequent coral bleaching events are expected to hit coral reefs worldwide (Knutson et al., 2019; Johnson and Lumpkin, 2021). Shallow turbid reefs of Darvel Bay may provide a safe haven for corals during heat stress events. Furthermore, following these events, corals in these reefs may even act as diversity reservoirs for coral taxa within Darvel Bay and for nearby reefs that may have been negatively affected by coral bleaching events. In fact, Darvel Bay is the third locality in which the bleaching-resistant *Ctenactis* appears to be recorded, further driving the importance of protecting this region. However, due to the absence of some important reef taxa such as *Acropora* and *Montipora* within the turbid reef in this study, it remains unclear if they would benefit from the buffering effect of turbidity.

This study only captured the short-term response to heat stress of corals in Darvel Bay, so further monitoring efforts need to be carried out in the long term to explore recovery rates of corals and additional responses of these corals to the repeated heat stress events expected in the near future. Furthermore, it is also important to note that although our results show that shallow mesophotic environments may alleviate heat stress and thus, acting as refugia for many coral taxa in the wild, their role may be constrained by a conjunction of other environmental factors such as higher sedimentation (Evans et al., 2020). Turbidity in shallow mesophotic reefs can be caused by different sources from coastal runoff, to humic content from mangrove forests, to sediment inputs from river mouths, among others. Due to the inherent proximity to coastal areas, turbid environments are often heavily subjected to local anthropogenic activities in addition to global stressors (Heery et al., 2018; Mo et al., 2022). The main urban centre in Darvel Bay, which is adjacent to Lahad Datu, is affected by commercial fishing activities, urban development, oil palm plantations, and marine pollution (Santodomingo et al. 2021). If not managed properly, these compounding local stressors may ultimately result in the collapse of reef ecosystems in the area. It is therefore imperative that policy-makers and managers focus their attention on the conservation of these overlooked, yet important marginal reefs in this region to ensure they continue to provide refuge for corals as the oceans warm.

### Credit authorship contribution statement

**Allia Rosedy:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft. **Isabel Ives:** Methodology, Formal analysis, Writing – review & editing. **Zarinah Waheed:** Supervision, Validation, Writing – review & editing. **Muhammad Ali Syed Hussein:** Validation, Writing – review & editing. **Sindia Sosdian:** Writing – review & editing. **Kenneth Johnson:** Conceptualization, Formal analysis, Validation, Writing –

review & editing. **Nadiezhdha Santodomingo:** Conceptualization, Methodology, Formal analysis, Supervision, Validation, Writing – review & editing.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Figure captions

**Fig. 1.** Map showing the locations of studied reefs, Sakar and Blue Lagoon, in Darvel Bay (Sabah, Malaysian Borneo).

**Fig. 2.** (A) Sea surface temperature (SST) and the degree of heating weeks (DHW) of Blue Lagoon and Sakar stations from 2019 to 2022 gathered from NOAA's Coral Reef Watch (CRW); and (B) Comparison between NOAA's CRW SST and *in-situ* temperature measurements at 10 m depth of Blue Lagoon and Sakar stations from Hobo data loggers. Gaps indicate missing data records from lost or broken loggers.

**Fig. 3.** (A) Turbidity levels at Blue Lagoon and Sakar reef at 5 m and 10 m depth between the dry and wet seasons in 2022; and (B) Light intensity at 5 m, 10 m and 15 m depth of Blue Lagoon and Sakar reefs in 2020.

**Fig. 4.** Proportion of coral colonies in different classes of bleaching severity across: (A) depth gradient; (B) coral growth morphologies in reefs of Blue Lagoon and Sakar. The number of colonies assessed are indicated within the parenthesis.

**Fig. 5.** Bleaching indices showing different coral growth forms in Blue Lagoon and Sakar at 5 m and 10 m depths. Missing Sakar data at 10 m depth is due to the absence of both branching and encrusting coral forms in the survey.

**Fig. 6.** Bleaching indices of (A) the most abundant coral genera (>20 colonies across both reefs), and (B) scatterplots of the bleaching indices of corals in Blue Lagoon and Sakar reefs at 5 m and 10 m depths. The diagonal line represents a 1:1 correlation, which denotes an equal bleaching response between the two reefs.

### Table captions

**Table 1.** Environmental conditions and habitat characterisation of Blue Lagoon and Sakar reefs.

**Table 2.** Coral responses to heat stress events in 2020 in different regions around the world.

### Appendix A. Supplementary data

The environmental and coral bleaching data, as well as their corresponding R scripts are included in the supplementary material for this article.

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### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Credit authorship contribution statement

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