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REPORT

Resilience of turbid coral communities to marine heatwave

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Abstract High sea surface temperatures recorded in summer 2021 introduced a unique opportunity for 'real-time' assessment of Exmouth Gulf turbid reef's resilience to a marine heatwave event. Four sites along a turbidity and temperature gradient were surveyed during (March 2021) and after (October 2021) the event to assess bleaching rates (Bleaching Index = BI), differences in coral morphological responses to the heat wave, and post-event changes in benthic and coral community structure. Despite experiencing higher temperatures (> 30 °C) and Degree Heating Weeks (DHW = 8), the most turbid reef site, Somerville, displayed greater resilience to heat stress (BI = 14) compared to the "clear water" site, Bundegi (BI = 19.3), where temperatures never exceeded 30 °C (3 DHW). Our results also reveal that encrusting and massive corals, often considered more resilient to bleaching, displayed increased bleaching susceptibility at the turbid sites, potentially due to the synergistic effects of sedimentation and heat stress. In contrast, branching and foliose corals showed greater resilience to the heat wave in turbid water settings, while encrusting and branching corals exhibited lower resilience in the clear-water site. These findings highlight complex interactions between heat and reduced UV stress on turbid reefs potentially increasing resilience to bleaching but likely only for those coral morphologies that are not heavily impacted by sedimentation.

Keywords Coral bleaching · Marine heat wave · Coral morphology · Bleaching · Resilience · Turbid reef

Introduction

Increased sea surface temperature (SST) events pose a significant threat to coral reefs globally, leading to extensive coral bleaching (Heron et al. 2017; Hughes et al. 2017 and 2018). The intensity of bleaching at the coral holobiont level can vary greatly depending on the severity of the thermal stress (Kleypas et al. 2008), local environmental factors (e.g. turbidity, thermal history) (Dunne and Brown 2001; Thompson and Van Woesik 2009), the symbiont algae clade assemblages found in the coral tissue (Baker et al. 2004; Berkelmans and Van Oppen 2006) and the taxonomic structure of the coral community (Marshall and Baird 2000; Loya et al. 2001). Bleaching induced coral mortality can alter coral community composition and their symbionts (Perry and Morgan 2017a), and reduce calcification rates (Dove et al. 2020). This may result in a decrease in coral cover and reef structural complexity (Perry and Morgan 2017b), thereby having critical long-term implications for coral reef ecosystems (Hoegh-Guldberg et al. 2007; Gilmour et al. 2013).

Resilience encompasses two key components: "Resistance", which signifies the immediate effect of external disturbances on the system state, and "recovery", which include the internal processes that restore the disturbed system to

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equilibrium (Hodgson et al. 2015). Certain coral taxa may exhibit enhanced resistance to coral bleaching through key physiological mechanisms (Guest et al. 2016; Fisher et al. 2019). These mechanisms include metabolic responses such as high protein turnover rate to promote growth (Gates and Eomund 1999) and heterotrophic feeding, which provides corals with an alternative energy source (Grottoli et al. 2006; Bessell-Browne et al. 2014). Furthermore, coral colony morphology is likely a significant factor in determining resistance to bleaching (Burn et al. 2023). For example, branching corals such as *Acropora* and *Pocillopora* typically possess thinner tissue and are generally regarded as more susceptible (Harrison et al. 2019). In contrast, massive and encrusting corals such as *Porites* have thicker tissue, enabling them to self-shade their symbiotic algal cells and enhancing their resistance to bleaching (Marshall and Baird 2000; Loya et al. 2001; McClanahan et al. 2004; Van Woesik et al. 2011).

While in clearwater tropical reefs, large-scale bleaching events and susceptibility among taxonomic groups to these events have been widely reported (Wilkinson 1998; Maynard et al. 2008; Pratchett et al. 2013; Hughes et al. 2017; Lough et al. 2018; Edgar et al. 2023), fewer studies have examined the resilience of extreme reef systems. Extreme reefs are characterised by their ability to persist under environmental conditions (e.g., temperature, light, pH, dissolved oxygen, salinity and water quality) that significantly deviate from the average "optimal" levels for Scleractinia coral. These conditions may appear as daily variations or seasonal fluctuations and include a range of environments such as high latitude reefs, hot reefs and turbid reefs (Schoepf et al. 2023). Given that turbid reefs are likely to increase in their global distribution in future years due to both local (e.g. coastal development) and global stressors (e.g. sea level rise) (Oppenheimer et al. 2019; Cartwright et al. 2021; Zweifler et al. 2021), it is critical that we improve our current understanding on how these extreme reef types are responding to marine heat wave events (Guest et al. 2016). Further, recent studies have proposed that turbid reefs may provide a refuge during extreme heat stress events (Potts and Jacobs 2000; Van Woesik et al. 2012; Cacciapaglia and van Woesik 2015; Morgan et al. 2017; Sully and van Woesik 2020). On clearwater reefs, the synergetic effect of high SST and increased UV irradiance has likely contributed to the most severe bleaching events (Brown et al. 1995; Brown 1997; Hoegh-Guldberg 1999). In contrast, the interaction between heat and UV on turbid reefs is potentially reduced due to the high concentrations of suspended sediment that reduces light penetration through the water column (Storlazzi et al. 2015). In addition, turbid water corals may have a higher capacity of heterotrophic feeding promoting their survival during bleaching events (Wooldridge 2014; Fox et al. 2018).

This study aimed to investigate the response of turbid water coral communities in Exmouth Gulf, Western Australia, to a marine heat wave (MHW) event in March 2021 where reefs were exposed to between three to eight Degree Heating Weeks (DHW). Four sites along a turbidity gradient (high to low, east to west) were surveyed during the MHW in March, and after the event in October 2021. In situ data on benthic cover, coral community structure and bleaching were collected to assess total bleaching rates, differences in bleaching between coral morphologies and genera, and changes in benthic and community structure following the MHW. This research provides the first assessment of Exmouth Gulf's turbid reefs resilience to heat stress conditions. The four sites investigated within this study are located approximately 40 km from each other and differ primarily in turbidity and temperature. As such, Exmouth Gulf provides an exceptional setting for exploring the impact of turbidity and its interaction with temperature on coral bleaching. Additionally, the study investigates differences in bleaching response rates between coral genera and morphologies when exposed to diverse turbidity regimes, thereby providing new insights into turbid water coral resilience to heat stress.

Materials and methods

Study site

Exmouth Gulf, located at the southern edge of the Pilbara region of Western Australia (Fig. 1), is a vast subtropical inverse estuarine embayment covering approximately 3000 km^2. The Gulf is shallow (mean depth of 11.9 m) and features fluctuating turbid reefs along its eastern and southern coastlines (Cartwright et al. 2021; Zweifler et al. 2021). The soft-bottom substratum surrounding these reefs consists mainly of fine sands, silts, or clay-sized fractions (Gilmour et al. 2006; Bonesso et al. 2022). These fine sediments are resuspended due to: (1) wind-driven waves and strong tidal currents cycle (Twiggs and Collins 2010), (2) oceanic swells from the gap between North West Cape and South Murion Island, and (3) cyclones that occur approximately five times a year, with wind speeds reaching 90 km h^{-1} (Australian Bureau of Meteorology 2022). The region's continental shelf is highly influenced by the Leeuwin Current, an oligotrophic eastern boundary current that flows strongest during autumn–winter and La Niña years (Feng et al. 2003). The current carries tropical water poleward resulting in warm, low salinity, low-nutrient water entering Exmouth Gulf, leading to large-scale downwelling along the northwest cape (Smith et al. 1991; Hanson et al. 2005; Twiggs and Collins 2010). While sites within the gulf are not directly affected by the Leeuwin current, they are influenced by nearshore currents such as the Holloway current (M. Feng and G. Cresswell pers comm).

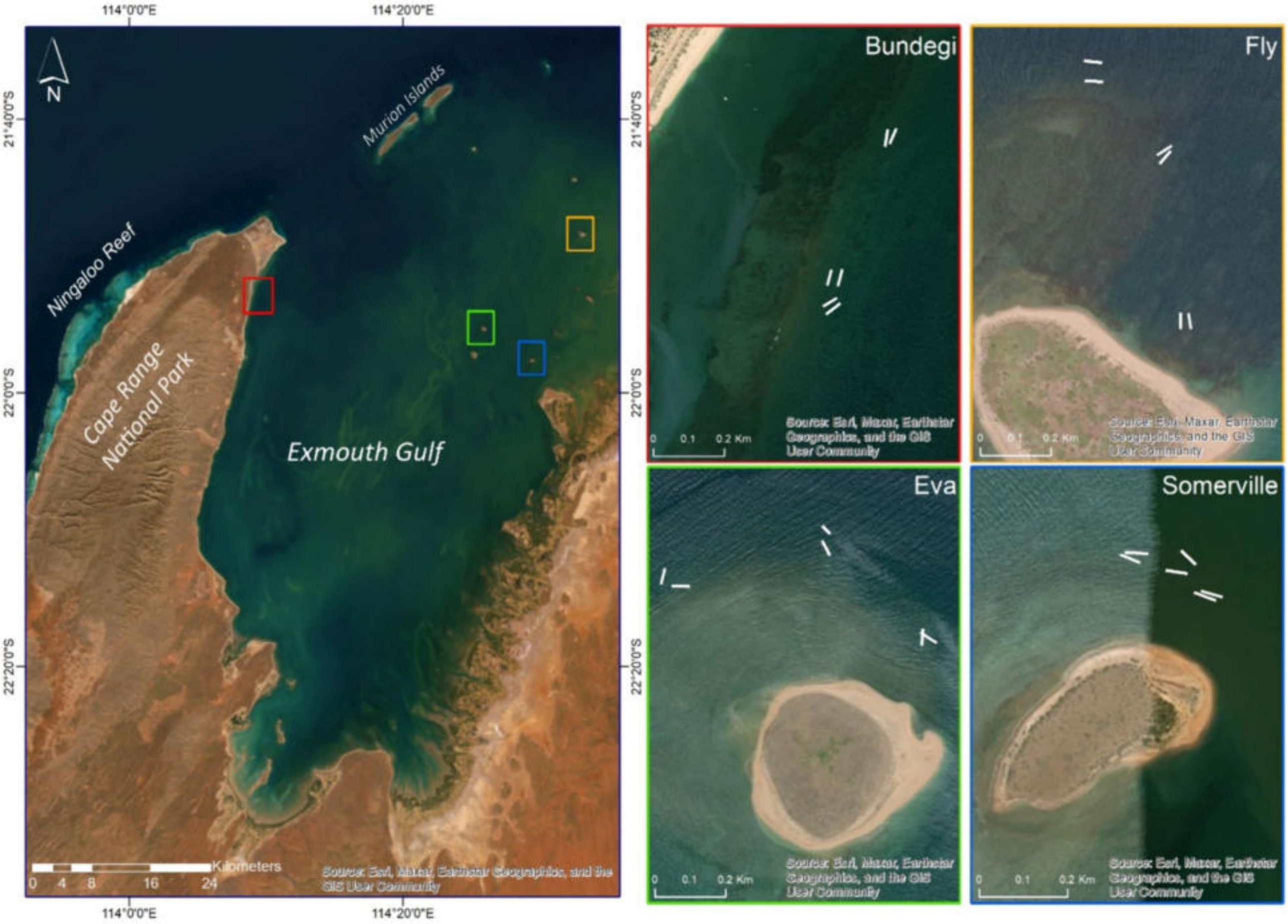


Fig. 1 Site location of Bundegi (red), Fly (yellow), Eva (green), and Somerville (blue) reefs, as well as bleaching survey transects at each site shown in white (imagery from Esri 2023)

Field surveys were conducted in March and October 2021 at four shallow (2–6 m, Table S1) sites across the Gulf (Fig. 1). Sites on the eastern side of the Gulf include Somerville (21°57′27.9″S 114°29′35.3″E), Eva (21°55′02.1″S 114°25′56.9″E) and Fly (21°48′02.74″S 114°33′13.14″E). These reefs surround low lying carbonate islands (Bonesso et al. 2022), with shallow fringing coral reef flats along the northern to eastern sides of the islands, and macroalgae beds along the southern to western margins (Dee et al. 2020). Coral cover at Eva and Fly reefs range from 8 to 10% (with maximum cover reaching 63% per transect), and with coral diversity indices of 0.73 and 0.76, respectively (Shannon-Weiner index) (Dee et al. 2020). Additionally, a video survey conducted by (Cartwright et al. 2023), which covered a larger area of the Gulf (~ 1100 km^2), found coral cover at the upper eastern side of the Gulf to be ~ 29%. Dominant coral genera include sediment tolerant *Turbinaria* sp., *Porites* sp. and *Pavona* sp. While coral bleaching and recovery have been documented on turbid Pilbara reefs located north-east of the Gulf in recent years (Lafratta et al. 2017; Evans et al. 2020), there have been no reported incidents of bleaching events on the eastern side of Exmouth Gulf.

The fourth study site, Bundegi Reef, lies on the northwestern tip of the Gulf (21°50′07.7″S 114°10′40.8″E). This patchy fringing reef serves as a transition zone from the shallow turbid waters of the northwest shelf to the clear, open ocean waters of the World Heritage Listed Ningaloo Marine Park (Fig. 1). Here, sediments are generally coarser, have a higher calcium carbonate content, and are less prone to resuspension or remaining in the water column for extended periods of time (Forde 1985). A bleaching event in 2011 (4 DHW, 32 °C, 5 °C SST anomaly) was the first recorded across the Ningaloo Marine Park. Followed by a cyclone, the two events led to a significant decrease in coral cover at Bundegi, falling from 40 to 60% to approximately 10% (Depczynski et al. 2013; Doropoulos et al. 2022). The region has experienced extensive damage from cyclone activity, further contributing to the low coral cover and slow recovery rates (Speed et al. 2013). Consequently, parts of the reef have undergone a transition to low coral densities with greater cover of rubble and macroalgae beds (Depczynski et al. 2013). Still, the dominant coral genera here are of the family Acroporidae (Doropoulos et al. 2022), providing potential for increased reef structural complexity and ecosystem functions in the future.

Environmental drivers

Records of one year long environmental conditions at the study sites, were obtained from remotely sensed one day composite datasets. These included multi scale ultra-high resolution (MUR) sea surface temperatures (SST), degree heating weeks (DHW) (5 km) and diffuse attenuation (Kd490, used as a proxy for turbidity) (4 km, Aqua MODIS) (NOAA 2022). Elevated Kd490 values typically indicate increased turbidity, reduced water clarity, and quicker light attenuation with depth. However, it is important to note that in shallow water, Kd490 values may be prone to overestimation. Monthly mean was calculated for Kd490, DHW and SST anomaly for data visualisation (Fig. 2).

Bleaching surveys

Coral community photo-quadrat surveys were conducted in March 2021 (peak of the heat wave) and in October 2021 (post heat wave). At each site, six 50 m transects were laid parallel to the reef at 2–6 m depth (Fig. 1; Table S1.). In March, the start and end point of the transects were marked and the GPS coordinates were taken in order to return to the same location in October. Using SCUBA, two divers swam along the transect line with the first diver laying a 50 cm^2 quadrat every 2 m ($n = 25$ quadrats per transect) and the second diver taking stills photos of the quadrat from ~ 50 cm above the quadrat. Quadrats were only laid on the left-hand side of the transect line.

Data and statistical analysis

Photo-quadrat data was analysed using the web application, Marine Ecological Research Management Aid (Mermaid 2022). All coral colonies between ~ 5 cm and ~ 30 cm in diameter were classified to genera level and categorised as (1) normal, (2) pale, (3) 0–20% bleached, (4) 20–50% bleached, (5) 50–80% bleached, (6) 80–100% bleached (Gleason 1993; Marshall and Baird 2000; Edmunds et al. 2003; McClanahan 2004). Since the photos only captured the 50 × 50 cm quadrat and its contents, we lacked information about the condition of the rest of the colony beyond the quadrat. Consequently, we treated each colony as if the entire colony were within the quadrat. For each transect, the total number of colonies, coral genera and number of colonies per genera in each category was calculated as well as the per cent (%) of colonies considered normal, pale, and bleached. Further, coral colonies were categorised into four distinct groups based on their morphology type: branching, encrusting, foliose, and massive. This classification was determined by the genera typical morphology and its appearance in the photographs.

For each quadrat ($n = 25$), per cent (%) cover of hard coral, soft coral and macroalgae cover was estimated and the total average (% cover) of each category was calculated per transect in each survey. In addition, per cent (%) cover was also calculated for each of the coral morphology types at each site and at each survey. To evaluate the impact of the heat wave event, bleaching index (BI) values were calculated for the different coral morphology types (e.g. branching,

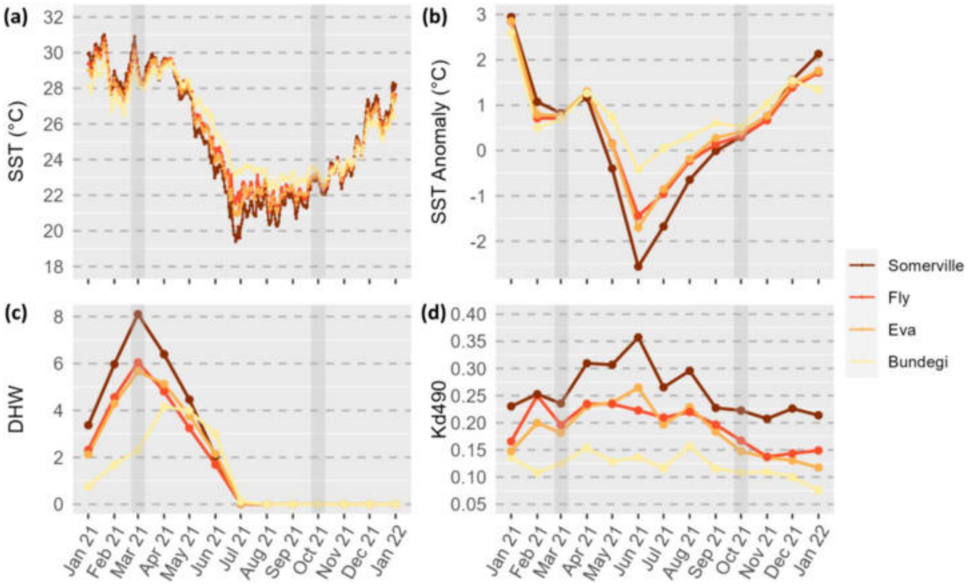


Fig. 2 **a** Daily mean SST (MUR), **b** monthly mean SST anomaly, **c** monthly DHW (5 km) and **d** monthly mean Kd490 (4 km, Aqua MODIS) at the four surveyed sites across the year 2021. Vertical dark grey lines represent survey times, March and October 2021. Data retrieved from https://coastwatch.pfeg.noaa.gov/erddap/griddap

encrusting, foliose and massive) from the percentage of observations in each of the above six bleaching categories in each of the surveys using the following equation (McClanahan 2004):

$$\mathrm{BI} = \left(0c_1 + 1c_2 + 2c_3 + 3c_4 + 4c_5 + 5c_6\right)/5 \tag{1}$$

All statistical analysis was conducted in R software version 4.1.1 (R Core Team 2021). Data were tested for normality using the Shapiro–Wilk test with QQ-plots and homogeneity of variance with Levene's test. Statistical test assumptions were not met when analysing environmental parameter data (i.e. SST, SST anomaly, DHW and Kd490). Therefore, a non-parametric Kruskal-Wallis test was conducted followed by a pairwise Wilcoxon test with Bonferroni correction method to identify differences among sites. Two-way ANOVA was used to explore the differences in benthic cover (%) (e.g. hard coral, soft coral and macroalgae) and in hard coral morphology (e.g. branching, encrusting, foliose and massive) between the study sites and between the survey dates at each site. BI data did not meet test assumptions and was log transformed. A three-way ANOVA was used to determine if there was significant difference in BI values between sites, survey date and coral morphology as well as interactions among the three factors. A pairwise Tukey's post-hoc test was performed where appropriate, using the package emmeans (Lenth et al. 2022).

We also carried a multivariate linear regression model (Legendre and Anderson 1999) to assess the influence of the environmental variables (mean monthly SST, maximum monthly SSTs, DHW, kd490 and depth) and coral morphology on BI. DHW was removed from the model due to multicollinearity. Model residuals met parametric assumptions. To visualise the model, a PCA analysis was conducted using ggbiplot package (Vu et al. 2015).

Results

Environmental drivers

All eastern sites experienced SST anomalies averaging 3 °C for seven or more consecutive days in January 2021, which resulted in a maximum of 6.5 DHW at Eva, 6.6 at Fly and 9 at Somerville during the first bleaching survey in March 2021 (Fig. 2a,b,c). In contrast, Bundegi experienced 3 DHW during the same period and no SST above 30 °C. Daily DHW, SST and SST anomalies were significantly lower at Bundegi compared to the eastern sites (Table S2 and S3). SST anomaly displayed the greatest variation at Somerville ranging from −2.5 ± 1.1 (in June) to 2.9 ± 1.1 (in January) (Fig. 2b).

Daily turbidity, represented by Kd490, differed significantly among all sites ($p < 0.0001$; Table S2) with values increasing from west to east. Throughout the year, Somerville consistently experienced the highest turbidity levels with a mean of 0.25 ± 0.06 (Kd490 ± sd) (Fig. 2d). In contrast, Bundegi displayed the clearest waters among the sites, with a mean of 0.12 ± 0.04 (Kd490 ± sd). As with temperature, turbidity (Kd490) was most variable at Somerville with mean recordings ranging from 0.35 ± 0.05 (in June) to 0.2 ± 0.04 (in November), and least variable at Bundegi with mean recordings ranging from 0.07 ± 0.02 (in January) to 0.15 ± 0.04 (± sd) (in August).

Community structure

In March 2021, mean hard coral cover ranged from 20.8% ± 13.8% (at Fly) to 29.5% ± 7.7% (at Eva) whereas soft coral cover was consistently low at all sites (0–0.5%; Fig. 3). As such, no significant difference was found in hard and soft coral cover (%) between sites (Table S4). In contrast, macro-algal cover was variable ranging from 8% ± 6.4% (at Eva) to 31% ± 15% (at Somerville) ($p = 0.02$, Fig. 3, Tables S4, S5.). By October 2021, total hard coral cover remained relatively stable at Bundegi and Somerville but dropped from 29.5 ± 7.7% to 20.5 ± 11.7% at Eva and from 20.8 ± 13.8% to 12 ± 5% at Fly (mean ± sd; Fig. 3). At all sites, there was no significant difference in soft coral and macroalgae cover over time (Table S4; Fig. 3) although there was an increase in soft corals at Fly (0.25–1.3%) and Somerville (0.58–1.7%), and macro-algae at Eva (7.9–15.4%).

The coral morphology composition in March 2021, varied among sites with Bundegi containing significantly more branching corals (68% ± 13.6%; $p < 0.0001$) and significantly less massive (15% ± 8.8%, $p < 0.0001$) than all three eastern sites (Fig. 4, Tables S6 and S7.). Encrusting corals were significantly higher at Eva (23.4% ± 6.9%) compared to Somerville (14% ± 6%, $p = 0.006$), whereas foliose corals increased significantly ($p < 0.0001$) from west (0.3% ± 0.1%; at Bundegi) to east (30.5% ± 10%; at Somerville; Table S7). In October 2021, the encrusting coral community had the greatest declines ($p < 0.006$, Table S6), with mean cover dropping to 17 ± 6.8% at Eva (March = 23.4 ± 6.8%), 10.2 ± 5% at Fly (March = 17.3 ± 8.7%) and 8.6 ± 5.2% at Somerville (March = 14 ± 6%; Fig. 4). Similarly, the cover of massive coral colonies decreased at Eva, Fly, and Somerville from March to October ($p < 0.014$). In contrast, Bundegi showed a relatively stable coral community, with very little difference in coral morphological composition between March and October (Fig. 4). Furthermore, the increase in foliose coral cover was significant only at Eva ($p < 0.01$; Fig. 4), due to the percentage cover of Pavona coral colonies rising from 2.7% in March to 12.5% in October.

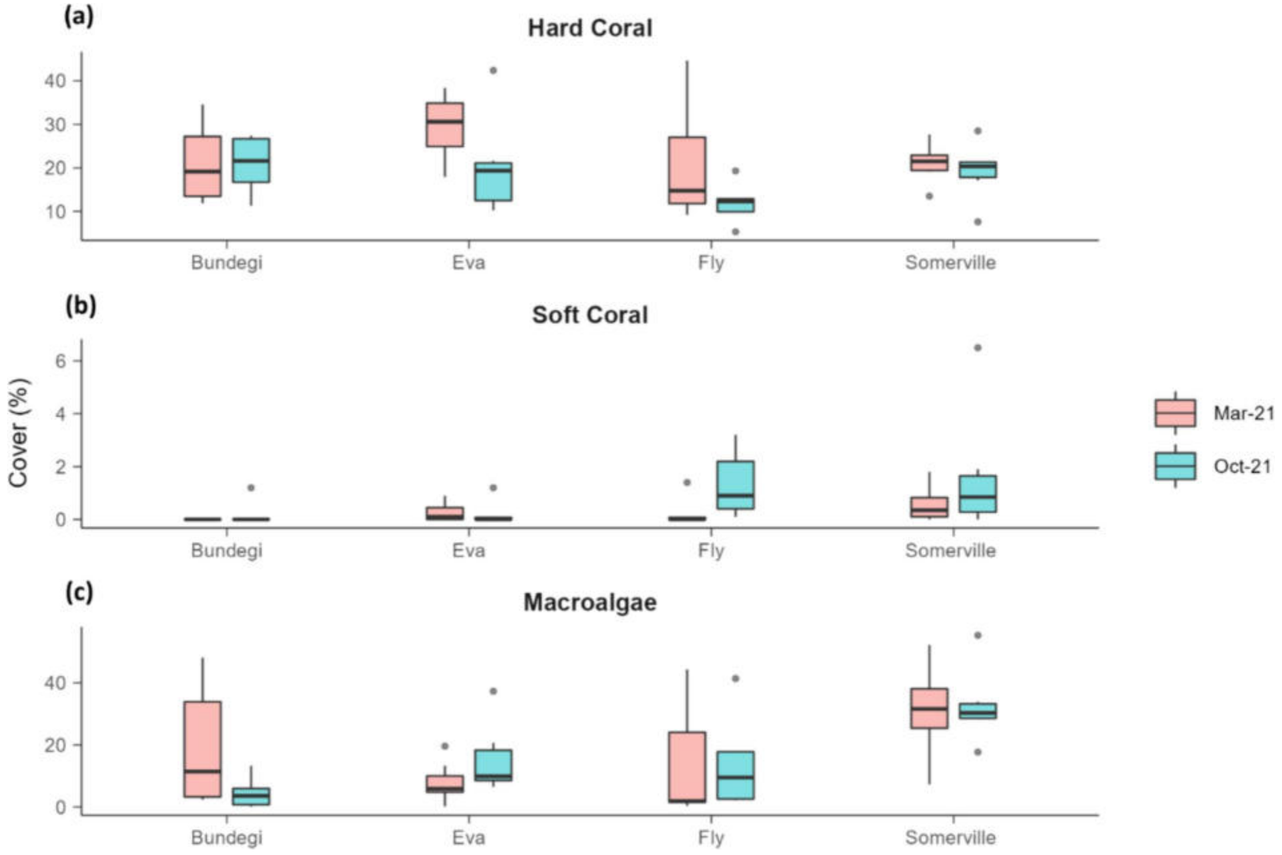


Fig. 3 Per cent cover of **a** hard coral, **b** soft coral and **c** macroalgae at the four survey sites in March and October 2021. Line in box represents median, whiskers represent minimum and maximum values, dots represent outliers

37 coral genera were recorded across all sites in March 2021 (Table S8). Eva had the highest number of coral genera (31) and Bundegi had the lowest (14). The eight most abundant coral genera (*Acropora, Cyphastrea, Goniastrea, Montipora, Pavona, Pocillopora, Porites* and *Turbinaria*) resulted in over 70% of coral cover across the four sites (Fig. 5). At Bundegi, coral cover was dominated by branching *Acropora* (55%) followed by *Pocillopora* (13%) and *Cyphastrea* (8.7%). In contrast, the three eastern sites were dominated by *Porites* and/or *Turbinaria*. *Goniastrea* and *Pocillopora* cover was also comparatively high ranging from 11 to 14% and 3–18%, respectively.

In October 2021, the total number of coral genera decreased at all sites except at Bundegi. Declines were mainly observed in less common coral genera (e.g. *Alveopora, Cosinaraea*, *Leptastrea* and Fungiidae; Table S8), however, some more common coral genera also recorded declines. Specifically, *Echinopora* (1.1% in March) and *Favites* (3.5% in March) at Eva, *Leptoseris* at Eva and Fly (1.5% and 1.3% in March, respectively), and *Galaxea* at Eva (1.2% in March) and Somerville (2.2% in March), were not documented in October. In addition, between three to five new rare coral genera were observed at all sites in October (Table S8). A comparison in cover of the eight most abundant coral genera at each site, found limited change at Bundegi (Fig. 5). At the more turbid sites, cover of *Turbinaria* and *Pocillopora* increased, whereas *Porites* and *Goniastrea* cover declined (Fig. 5).

Bleaching index

In March 2021, the mean BI index was significantly higher at Bundegi (19.3 ± 12.6) compared to all three eastern sites (Eva = 14.7 ± 12, Fly = 7.4 ± 6.5, Somerville = 14 ± 14; $p < 0.001$, Table S9, S10). Across all sites, foliose coral were the least impacted by bleaching ($p < 0.01$) with a BI ranging from 1 ± 1 and 1.9 ± 1.5 at Eva and Somerville, respectively, to 3.0 ± 3.0 at Fly (Fig. 6, 7, Table S11). No foliose corals were recorded at Bundegi. Branching coral mean BI values declined from west to east of the Gulf, decreasing from 11.8 ± 5.5 at Bundegi to 0.3 ± 0 at Somerville. Encrusting and massive coral were equally the most impacted by bleaching ($p < 0.0001$; Table S11) with encrusting coral BI ranging from 24.3 ± 10.4 (Bundegi) to 9.6 ± 7.9 (Fly) and massives BI ranging from 31.1 ± 4.3 (Somerville) to 11.8 ± 5.2 (Fly). By October 2021, BI values had dropped significantly to

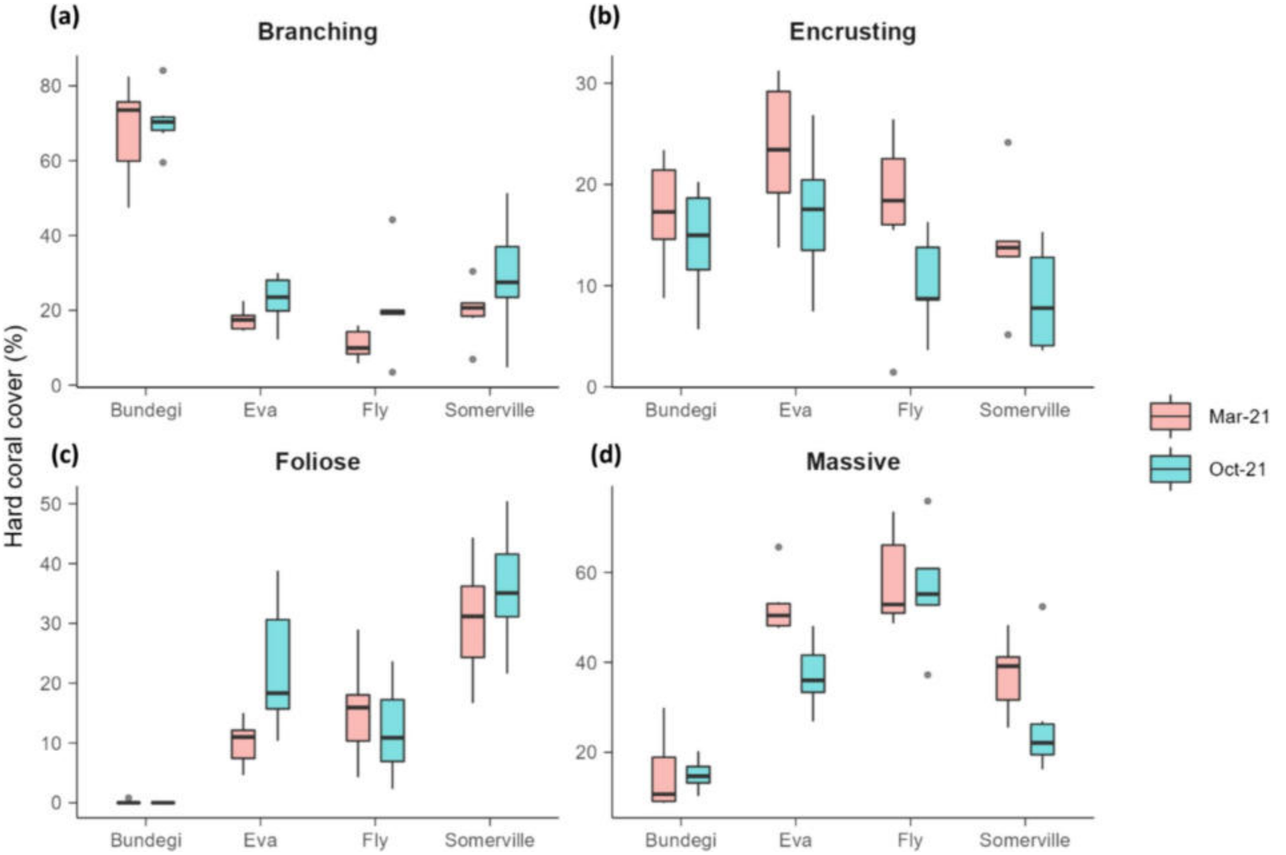
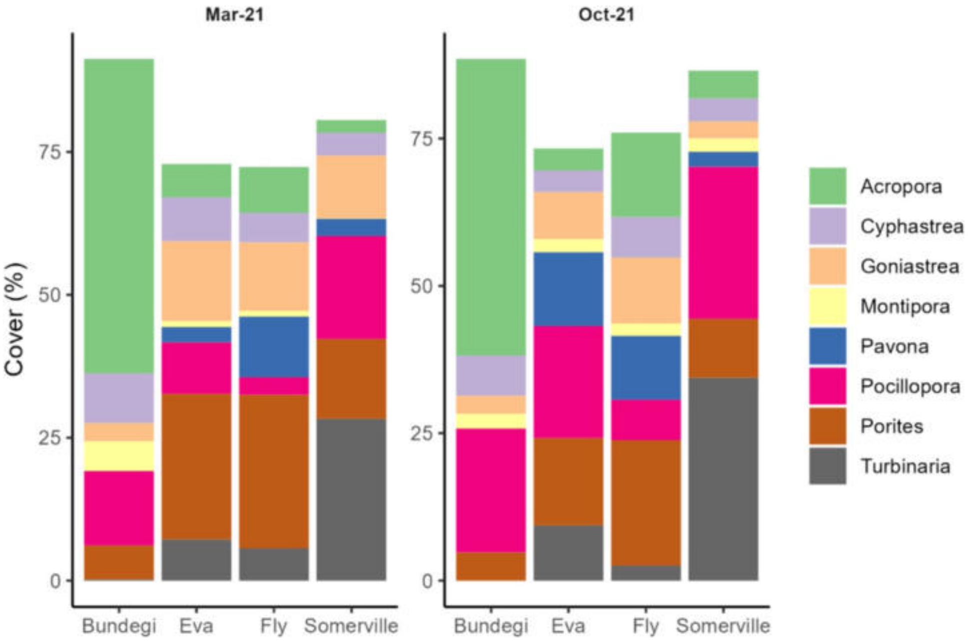


Fig. 4 Per cent cover of **a** branching, **b** encrusting **c** foliose and **d** massive hard coral colonies at the four survey sites in March and October 2021. Line in box represents median, whiskers represent minimum and maximum values, dots represent outliers

Fig. 5 Per cent cover (% out of total number of colonies) of the eight most common coral genera at each site in March and October 2021



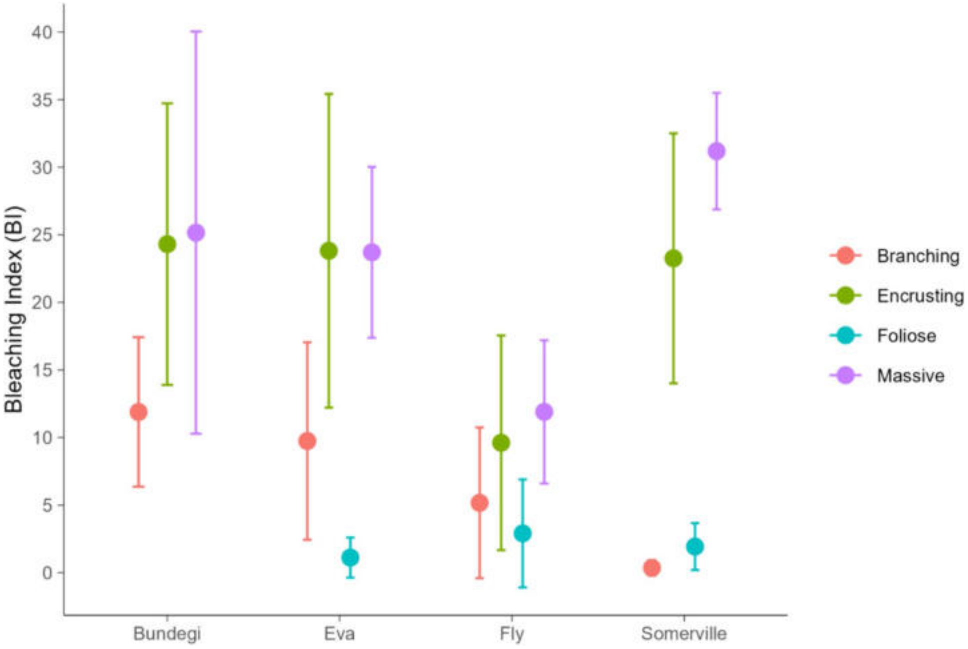


Fig. 6 Bleaching index (BI) (mean ± sd) of branching, encrusting, foliose and massive coral colonies at the four survey sites in March 2021

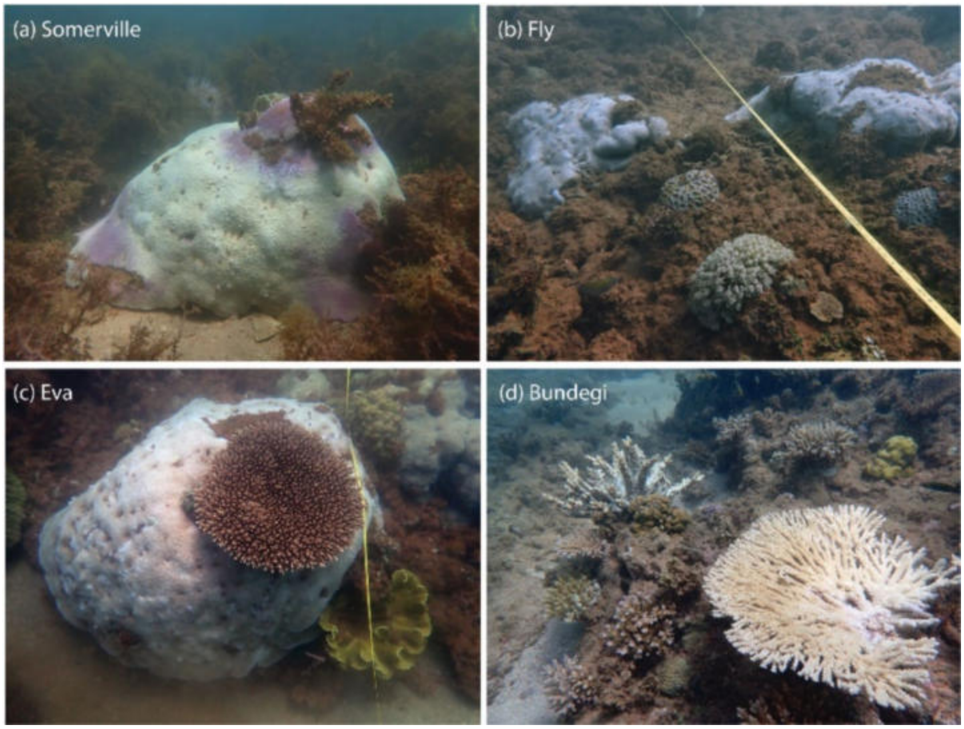


Fig. 7 Coral bleaching examples at Exmouth Gulf in March 2021. **a** At Somerville, massive *Cyphastrea* severely bleached surrounded by macroalgae, **b** at Fly, two severely bleached encrusting *Goniastrea* colonies next to two partially bleached *Favia* colonies and a healthy *Goniopora* colony, **c** at Eva, massive *Astreopora* severely bleached next to a healthy colony of *Acropora* (branching) and *Turbinaria* (foliose), **d** at Bundegi, partially and fully bleached branching *Acropora* colonies next to other healthy *Acropora, Pocillopora* and *Favites* colonies

a 7.6 ± 8 (mean ± sd) across all sites ($p < 0.001$; Tables S9, S10).

Principal component analysis revealed distinct site groupings based on the mean transect BI values (Fig. 8). Moreover, shallow transects exhibited higher BI values across all four sites. However, a multivariate linear regression model, which explained 56% of the variation in the BI values ($r^2 = 0.52$, $p < 0.0001$), found morphological community composition to be the main influence on the BI values (Table S12). Notably, BI values of branching corals were significantly lower than both encrusting and massive coral ($p < 0.0001$) yet higher than those of foliose corals. While both SST and turbidity improved model performance, with BI decreasing as the two factors predominantly increased, these parameters individually did not have significant influence on BI values.

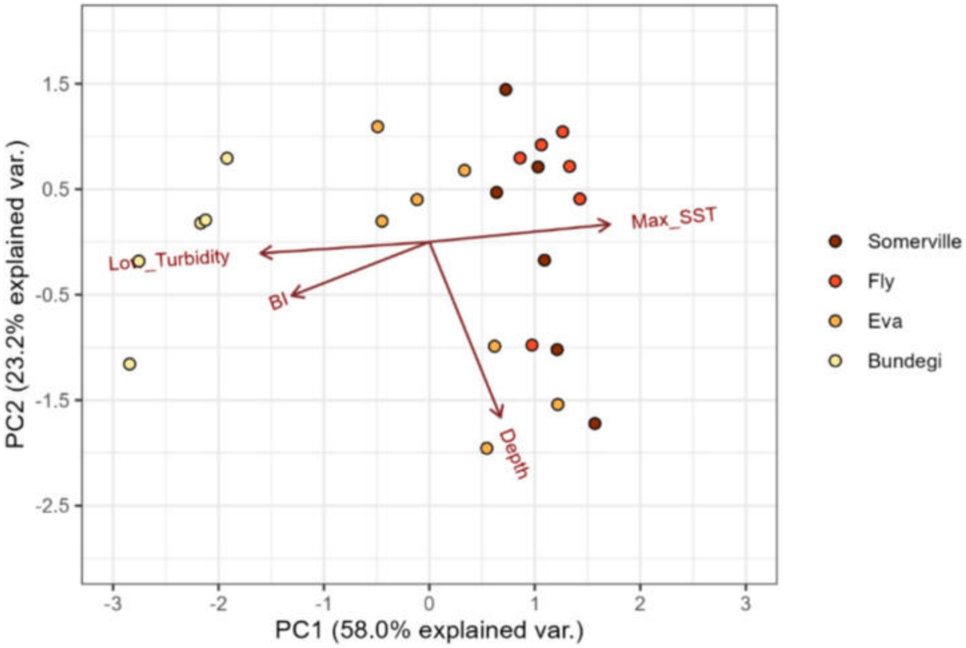


Fig. 8 Principal component analysis (PCA) showing the effect of Turbidity (Kd490), depth and DHW on BI at (a) the four survey sites (points represent mean transect BI at each site)

Discussion

In this study, we conducted a comprehensive examination of coral community response to a MHW across a turbidity and temperature gradient in Exmouth Gulf. Our results provide valuable insights into the resilience and sensitivity of these ecosystems to the heat wave in March 2021, while also emphasising the interplay between turbidity, temperature and coral community morphological structure. We also provide insight into the subsequent recovery and potential changes in community structure following the MHW event. These findings suggest that the turbid reefs of Exmouth Gulf experienced higher temperatures and DHW but also displayed greater resilience to this heat stress event.

There were significant differences in environmental conditions across Exmouth Gulf. Daily SST and SST anomalies were significantly lower at Bundegi compared to the eastern sites, whereas turbidity, represented by Kd490, declined significantly from east to west. Therefore, the most western site Bundegi and the most eastern site Somerville represented the two extremes for these two key environmental parameters. And yet, hard coral cover at these sites did not change, but did decline at the two intermediate sites, Eva and Fly. The decline in hard coral cover at Eva and Fly was accompanied by increases in macro-algal cover suggesting that the conditions at these sites following the acute disturbance event favoured macro-algal growth. Previous studies have highlighted the potential role of macroalgae competition in shaping coral loss or recovery following a heat wave (Brown et al. 2020; Donovan et al. 2021). However, the spatial differences in coral community responses across the Gulf also emphasize the importance of local conditions (e.g., nutrient availability and hydrodynamics) in modulating coral bleaching (Xie et al. 2020; Good and Bahr 2021) as well as the potential of local coral adaptations to environmental conditions (Tisthammer et al. 2019). For example, in turbid environments, the increase in available particulate nutrient sources can enhance coral heterotrophy, compensating for the reduction in autotrophy by the photosymbionts and allowing corals to maintain a positive energy budget (Anthony 2000; Travaglione et al. 2023; Zweifler et al. 2024). It is important to acknowledge that significant changes in coral community structure, particularly concerning less common coral genera, are likely attributed to subtle shifts in the transect location during surveys rather than genuine changes in community structure.

Despite experiencing relatively low DHW, Bundegi reef, dominated by branching coral, exhibited the highest overall BI, suggesting lower resistance to elevated SST. In contrast, BI decreased along the turbidity gradient with Fly reef, dominated by massive coral, showing the lowest overall BI. The variation in BI is therefore attributed to differences in coral community structure between the sites. It is important to note that this heat stress event was milder in comparison to those previous events in 2011 and 2013. During those events, Bundegi corals experienced significant bleaching and widespread mortality (Moore et al. 2012; Depczynski et al. 2013; Speed et al. 2013; Lafratta et al. 2017). Consequently, the current event resulted in comparatively less extensive coral bleaching and mortality at Bundegi. Nevertheless, the fact that it did bleach under the lowest DHW measured between the sites, suggests that it is still recovering from these previous events. It is likely that these events also impacted Exmouth Gulf's eastern coral reefs, but there were no observations conducted on these remote reefs at the time. Regardless, these data suggest that Bundegi was less resilient to the 2021 heating event when compared to the turbid coral community.

Bleaching index data revealed significant differences in susceptibility across coral morphologies to the March 2021 heating event. Encrusting and massive corals had the highest mean BI values suggesting that they were more susceptible to the heat wave. In addition, we found that the BI of branching corals decreased with increased thermal stress (i.e. from Bundegi with 3 DHW to Somerville with 8 DHW), indicating branching and foliose morphologies are more advantageous in turbid water settings. This finding contrasts with previous studies on clearwater reefs, where branching corals were found to be more susceptible to thermal stress (Loya et al. 2001; Van Woesik et al. 2011). However, other reports indicate that branching *Acropora* corals exhibit relatively lower susceptibility to bleaching in turbid reef environments such as those in Malaysia (Guest et al. 2012), Singapore (Guest et al. 2016) and the Great Barrier Reef (Morgan et al. 2017). It is probable that this reduced susceptibility to thermal stress is associated with a concurrent increase in turbidity (Sully and van Woesik 2020), as well as acclimatisation to local temperature regimes (Oliver and Palumbi 2011), with the eastern sites having larger seasonal amplitude and higher summer means. Foliose coral had the lowest BI at all three eastern sites, likely because it consisted mainly of the coral *Turbinaria*, a widespread genus known for its high sediment tolerance and dominance in various marginal reefs (Sofonia and Anthony 2008; Ross et al. 2018). Together, these findings support the expanding body of in situ observations that suggest that turbid reefs are more resilient to bleaching events, demonstrated by both the reduced rates of bleaching and rapid recovery following a thermal stress event (Guest et al. 2016; Morgan et al. 2017; Evans et al. 2020). Studies have highlighted that the symbiont type (Ng and Ang 2016), shading due to turbidity (Cacciapaglia and van Woesik 2016) and heterotrophy (Anthony and Fabricius 2000; Travaglione et al. 2023) are important factors influencing turbid water coral resilience to high temperatures.

Interestingly, unlike branching corals, encrusting and massive coral morphologies did not exhibit any clear spatial pattern of BI with turbidity or thermal stress. This is most likely because these are slower growing genera with lower respiration rates, characteristics that have been strongly correlated to thermal stress susceptibility (Jokiel and Coles 1990). Thus, these taxa behaved normally, i.e., they bleached moderately and recovered relatively slowly (Baird and Marshall 2002). However, coral loss as a result of high BI within these morphologies was only recorded at turbid sites. This is expected to be a result of the synergistic effects of heat stress with increased sedimentation stress as sediments can settle directly on the flatter coral surface and block corallites (Fabricius 2005). In contrast, branching and foliose corals are less vulnerable to sedimentation due to their more vertical and complex structure (Rogers 1990). These findings emphasize the multitude of variables influencing the impact of stress events on reef systems across different settings, as well as their ability to recover.

This study represents the first assessment of the status of turbid reefs in Exmouth Gulf under heat stress conditions. Importantly, the data provides evidence of greater resilience of turbid water corals to bleaching events compared to their clear water counterparts, likely due to a combination of different coral morphologies found at the more turbid sites as well as the shading and nutrition influence of suspended sediments. A deeper understanding of how these factors interact and contribute to reef resilience to thermal events will be central to improving future coral management as well as highlighting the value of turbid reefs in coral reef conservation efforts. Further, the recovery and subsequent changes in the coral community structure highlight that environmental disturbances have long-term effects on coral ecosystems. Management strategies that consider both the short-term response to bleaching events and the longer-term dynamics of recovery and community shifts are essential for the conservation of coral reefs. These findings underscore the need for localised conservation and management efforts that consider the unique characteristics and stressors of individual reef systems to ensure the long-term survival and health of coral reefs in the face of ongoing environmental challenges.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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