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REPORT

Long-term spatial variations in turbidity and temperature provide new insights into coral-algal states on extreme/marginal reefs

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Abstract Globally, coral reefs are under threat, with many exhibiting degradation or a shift towards algal-dominated regimes following marine heat waves, and other disturbance events. Marginal coral reefs existing under naturally extreme conditions, such as turbid water reefs, may be more resilient than their clear water counterparts as well as offer some insight into how reefs could look in the future under climate change. Here, we surveyed 27 benthic habitats across an environmental stress gradient in the Exmouth Gulf region of north Western Australia immediately following a marine heatwave event. We used multidecadal remotely sensed turbidity (from an in-situ validated dataset) and temperature, to assess how these environmental drivers influence variability in benthic communities and coral morphology. Long-term turbidity and temperature variability were associated with macroalgal colonisation when exceeding a combined threshold. Coral cover was strongly negatively associated with temperature variability, and positively associated with depth, and wave power, while coral morphology diversity was positively associated with turbidity. While moderate turbidity (long-term average ~ 2 mg/L suspended matter) appeared to raise the threshold for coral bleaching and macroalgal dominance, regions with higher temperature variability (> 3.5 °C) appeared to have already reached this threshold. The region with the least turbidity and temperature variability had the highest amount of coral bleaching from a recent heatwave event and moderate levels of both these variables may confer resilience to coral reefs.

Keywords Exmouth Gulf · Marginal reefs · Coral-algal reefs · Turbidity · Macro-algae · Coral bleaching

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Introduction

The global decline in coral reef health (Hughes et al. 2017) greatly threatens the ecological, economic and social services they provide such as shoreline protection (Cuttler et al. 2018; Ferrario et al. 2014), fishing resources (Grafeld et al. 2017), nutrient cycling (Perry and Alvarez-Filip 2019) and tourism (Moberg and Folke 1999; Woodhead et al. 2019). With marine heatwaves and other acute disturbance events (e.g. cyclones) causing mass mortality of corals (Harmelin-Vivien 1994; Zinke et al. 2015), the rate of recovery of these reefs is strongly influenced by chronic disturbance events such as declining water quality from excessive nutrients (Adam et al. 2021; Wiedenmann et al. 2013), suspended sediments (Fisher et al. 2019; Hodgson 1990), and over fishing (Ferrario et al. 2014; Wilson et al. 2010). Under persistent conditions of poor water quality, this can result in 'dead' substratum with algal-dominated reefscapes, and numerous functional and ecological implications (Bruno et al. 2009; Graham et al. 2015; McClanahan et al. 2003).

Ecological effects of dead reef substratum or algal-domination have been documented to include loss of reef rugosity and associated productivity and diversity of reef-associated organisms (Alvarez-Filip et al. 2009; Graham and Nash 2013; Rogers et al. 2014), reduced coral diversity and increased dominance by non-reef building corals (Green et al. 2008; Perry and Alvarez-Filip 2019), decreases in reef 'fisheries' (Pratchett et al. 2018; Wilson et al. 2006) and anoxic conditions inhospitable to other organisms (Gregg et al. 2013; Hauri et al. 2010). Algal growth on reefs can also have long-term implications for reef accretionary potential (Alvarez-Filip et al. 2009), which influences a reef's ability to keep up with current and future sea level rise and the ability to provide shoreline protection (Masselink et al. 2020). While the literature is conflicted over the 'functional' implications of macro-algal growth on reefs (Alvarez-Filip et al. 2013), or what even constitutes a reef 'function' (Bellwood et al. 2019), it is broadly considered that avoiding algal domination of coral reefs is the preferred ecological outcome (Brandl et al. 2019).

Recently, coral reefs existing in naturally marginal environments have become of interest due to their potentially enhanced resilience to climate events as well as being indicators of the fate of other tropical reefs into the future (Burt et al. 2020; Camp et al. 2018). Among these 'extreme' reefs are those that exist under naturally or anthropogenically high turbidity regimes, which are likely to increase in abundance globally due to rising sea levels, changes in rainfall patterns and changing land use practices (Cartwright et al. 2021; Davis et al. 2016; Fisher et al. 2015; Zvifler et al. 2021). The effects of turbidity on coral reefs is multifaceted and include a limitation to light availability for photosynthesis (Kirk 1994), the smothering of coral recruits (Bothner et al. 2006), reduction in the ability of coral larvae to settle (Hodgson 1990) and the import of nutrients that accompany the sediments (Adam et al. 2021). Shifts towards algal-dominated reefs have previously been attributed to turbidity (De'ath & Fabricius 2010); however, there is also evidence of turbidity imparting some resilience to corals facing other environmental pressures such as UV radiation and sea surface temperature variability (Browne et al. 2019; Morgan et al. 2017a, b). In addition, turbidity is thought to impart some control on the dominant coral morphology of reefs, with certain coral types seemingly displaying greater resilience to turbid conditions (Morgan et al. 2017a, b). To assess the vulnerability of turbid coral reefs to coral/algal phase shifts, it is necessary to quantify how turbidity could be interacting synergistically or antagonistically with other key environmental processes (e.g. temperature variability) to effect the 'coral-algal states' of reefs across the gradient of stressors.

While many studies have documented the shift from coral towards algal-dominated reefs (Bruno et al. 2009; Johns et al. 2018; Morais et al. 2020), there has not been sufficient spatial and temporal resolution of environmental data to effectively analyse patterns of environmental drivers that accompany algal domination of benthic habitats. Remote sensing satellite data, now available on multi-decadal timescales, is increasingly being used for many long-term environmental analyses of water quality parameters. For example, it is now possible to quantify average turbidity and temperature variability at a fine scale ($< km^2$) over large coral reef regions, on decadal to multi-decadal timescales, providing a much more thorough assessment of long-term environmental conditions. As such, we can potentially identify important environmental thresholds that support algal domination on coral reefs and which could be used to identify coral reefs at risk in future years.

Here, we have examined the benthic community composition on 27 nearshore reefs within the Exmouth Gulf, in north Western Australia. This region provides an ideal case study for investigating the interactions of environmental variables with the spatial distribution of macro-algae on coral reefs for several reasons: 1. There is very low annual precipitation/cloud cover enabling a more complete remotely sensed satellite dataset. 2. There are extensive coral reefs across the Gulf existing under different long-term environmental conditions and benthic composition. 3. There are no permanent rivers or agricultural runoff into the Gulf, meaning nutrification is not a confounding issue; and 4. The Exmouth Gulf is a high-research-priority marine protected area (EPA 2020) that sits adjacent to the World Heritage listed Ningaloo Reef, but is also subject to a broad range of potential industrial pressures. In this work, we quantify how coral and algal reef assemblages differ across regions within the Gulf that experience differing turbidity, temperature variability, depths, and wave exposure gradients. Specifically, we quantify how long-term spatial trends in turbidity and temperature have influenced the current benthic community states and dominant coral morphology across Exmouth Gulf. This is the first study to use long-term (multi-decadal) remotely sensed turbidity data and SST variability data, and quantified their interaction, to assess assemblages of coral-algal reefs within the same large region but under differing environmental regimes. This work will contribute to the literature on macro-algal colonisation of coral reefs, 'extreme' coral reefs, and provide a baseline against which future regime changes can be detected in an ecologically important marine protected region.

Methods

Study site

The Exmouth Gulf is a large embayment (~ 3000 km^2) in the arid tropical NW of Western Australia (Fig. 1). The region marks the transition zone from the clear, open ocean waters adjacent to the World Heritage Listed Ningaloo Reef (a fringing reef) to the shallow and turbid waters of the North West Shelf. The overlap (Ningaloo Marine Parks northern extent lies within the north-western Exmouth Gulf) means species assemblages in the two regions are similar and coral connectivity between the regions has been shown in models (Bancroft and Long 2008; Feng et al. 2016). However, ambient marine water quality differences between the regions are

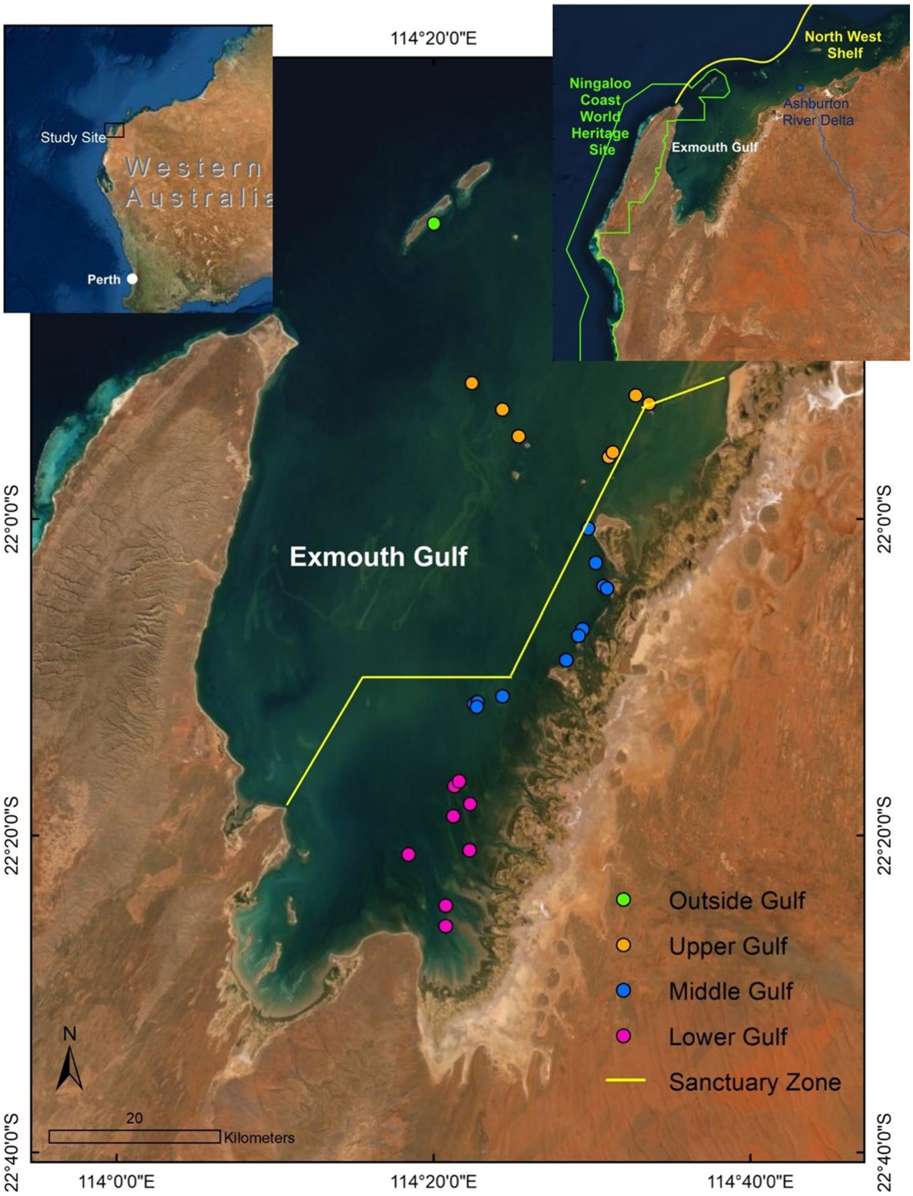

Fig. 1 Location map of 27 sites in the Exmouth Gulf, north Western Australia, where ROV survey transects were conducted. Colour of circles indicate which region of the Gulf the location was allocated to for statistical analysis; yellow line indicates where a fishery sanctuary zone exists (south-east of line). Top left inset map indicates location of study region within Western Australia. Top right inset map indicates the proximity of the World Heritage listed Ninglaoo Reef (green line), North West Shelf (yellow line) and the Ashurton River Delta (blue dot) to the Exmouth Gulf. Basemap images are from ESRI online

distinct, and follow the traditional classifications of Case 1 (Ningaloo) versus Case 2 (Exmouth Gulf) waters, where Case 1 waters are optically clear and high in phytoplankton compared to other substances, and Case 2 waters are dominated by inorganic particles and typically more optically complex/turbid (Mobley et al. 2004.). Turbidity fluctuates in the Gulf over daily/monthly timescales associated with tides, and over seasonal and interannual timescales driven by large-scale climatic drivers (El Niño-Southern Oscillation and Indian Ocean Dipole) that influence regional met-ocean processes, including cyclones and low-pressure systems, wind/waves and mean sea level (Cartwright et al. 2021). Rainfall is very low (~ 300 mm/year) and is mostly associated with tropical low systems and mid-latitude depressions leading to peak falls in Austral Summer to Winter (December–July) and very little rainfall in Austral Spring (September–November). There are no permanent rivers that empty into the Gulf; however, during periods of heavy rainfall, flood plumes from the Ashburton River, located to the north-east of the Gulf can reach parts of the Gulf, particularly when NE winds are dominant. Dust storms from the adjacent desert-like rangelands are known to occur 1–3 times annually during the strong easterly winds that occur ahead of storm fronts (McTainsh et al. 2011) and the dominant sediments (iron rich fines) in the North West Shelf waters are known to be from this terrestrial source (Brunskill et al. 2001; Gingele et al. 2001).

Coral reefs in the Exmouth Gulf have been found mostly along the eastern and northern Gulf and are acclimatised to the varying turbidity conditions of those regions (Cartwright et al. 2021). While turbidity may offer these reefs some protection from bleaching events (Morgan et al. 2017a, b; Zvifler et al. 2021), previous studies found severe bleaching related to marine heatwaves occurred in the region in 2011 (north-west Gulf) (Depczynski et al. 2013) and 2013 (Pilbara coast east of the Gulf) (Lafratta et al. 2017), with post bleaching recovery in some cases involving a strong shift in dominant taxa away from branching/foliose corals to low densities of massive corals and turfing-algae-dominated reefscapes (Depczynski et al. 2013). The Gulfs reefs range from stand-alone shoals to fringing reefs along islands and the mainland coast, mostly in depths of 3–7 m. Since the first known benthic surveys were conducted over 25 years ago, large stands of macroalgae (mostly *Sargassum spp.*) have been apparent in many parts of the Gulf including reef areas (McCook et al. 1995). Primary productivity is disproportionately high for a nutrient-poor arid tropical region, and this could be attributed to the cyanobacterial mats along the eastern coastline as well as iron-rich terrestrial input (Ayukai and Miller 1998; Loneragan et al. 2013; Lovelock et al. 2010; McTainsh and Strong 2007). This productivity has been exploited by a large prawn fishery that has trawled up to 40% of the Gulfs waters for decades (~ 1000 tonnes biomass removed annually, not including bycatch) and the Gulf is also heavily fished recreationally (Department of Fisheries 2017). A fisheries sanctuary zone and newly named Marine Park (extent yet to be finalised) exists in the eastern section of the Gulf, while the rest of the Gulf is used heavily by commercial and recreational fishers (Fig. 1).

Habitat survey

An underwater video survey was conducted in March 2021 (late summer/wet season) along the eastern and northern extent of the Exmouth Gulf. A marine heatwave had occurred during the previous three months, with sea surface temperatures throughout January 2021 up to 3 °C above average (IMOS 2022). Survey locations were chosen haphazardly within (1) habitats that exhibited benthic reef structure above the seabed (identified with vessel echosounder), and (2) habitats situated in water depths of 3–7 m. A total of 27 locations matching this criterion were identified within inshore/offshore locations in the Lower, Middle, Upper and Outside region of Gulf (Fig. 1). All locations were spatially separated from each other and while some locations were close in distance (1–2 km), these were separated by islands, and therefore subject to different environmental conditions. The survey took place over 6 d and consisted of continual line transects (polygonal or spiral) at each of 27 locations throughout the Gulf. The survey was carried out with a GoPro (Hero 7 Silver) attached to a Remotely Operated Vehicle (ROV), Blue Robotics BlueROV2, using the heavy configuration to provide more stability during the survey. The Go Pro was mounted under the ROV and placed facing downward and slightly forward towards the seabed in front of the ROV. The video was captured in high-definition as close as possible to the benthos (< 1.5 m) to capture approximately 5 min of benthic survey (approximately 30 m) at each location. From each transect video, image frames at regular intervals (approximately 10 s) were taken, each capturing approximately 1.5 m^2 of benthos with a resolution of 1920 × 1440 pixels per frame. From these screenshots, randomly allocated point counts (50 per image) were conducted on every third image (approximately, dependent on clarity of image) in the transect to obtain 10 quadrats at each location, giving a total of 500-point counts per transect/sampling location. Benthic point counts were conducted using the Coral Point Count with Excel extensions (CPCe) program using the randomised point allocation (Kohler and Gill 2006). Seven broad benthic categories—hard coral, macroalgae, turfing algae, seagrass, soft coral, sponge and abiotic; and five distinct hard coral morphologies—massive, encrusting, foliose, tabular, and branching, were identified. Bleached coral was also given its own coral category and included all bleached coral points regardless of morphology types or whether the entire colony was bleached or not. Each point count was only given one category, so for example, a point was classified as turf algae regardless of what surface (live coral, dead coral, pavement) the algae was growing on.

Environmental variables

Turbidity data were sourced from Cartwright et al. (2021) which quantified turbidity in the entire Exmouth Gulf region for the time period 2002–2020. This study used daily remote sensing satellite MODIS-aqua data (from first launch in 2002) and the application of a turbidity algorithm that was derived and validated with in-situ measurements in the same North West Shelf region as the study (Dorji et al. 2016). Due to the spatial resolution (pixel size) of the MODIS sensor, the data provided an average turbidity value (in mg/L) for each 250 m^2 of the region. This value was averaged over the entire timespan (2002–2020) for each of the 27 locations to give the mean turbidity at each location used in the analysis.

Temperature data were extracted from MODIS Level 3 SST (sea surface temperature, 4 km spatial resolution) using Google Earth Engine to obtain a ten-year average temperature (2011–2020) and a measure of temperature variability (standard deviation over the record) for each of the 27 surveyed locations. Wave data for each location were extracted from a 20-year regional-scale, fully coupled wave-circulation hindcast (Delft3D-SWAN) that has been extensively validated along the Pilbara coast (Cuttler et al. 2020). Proportional wave power (p) was calculated $p = H^2T$, where H^2 is the squared significant wave height and T is the peak wave period. Depth readings were recorded at each location using the vessel depth sounder.

Statistical analysis

Each of the 27 locations was allocated to one of four regions, (Outside, Upper, Middle and Lower Gulf; Fig. 1), representing regions of different turbidity, and the statistical analysis was conducted between these four regions. A one-way permutational analysis of variance (PERMANOVA (Anderson et al. 2008)) followed by post-hoc pairwise tests in the PRIMER-E statistical software package (Clarke and Gorley 2015) was used to test for differences in (1) benthic habitats, and (2) coral morphologies, among four regions of the Exmouth Gulf. Square root transformed habitat per cent cover data were analysed using a Bray–Curtis distance dissimilarity matrix with 9999 permutations. The variation in habitat per cent cover between locations was illustrated using principal coordinates analysis (PCO) plots. Benthic types that were likely responsible for any of the observed difference were identified using Pearson correlations of their relative abundance with the PCO axes. An arbitrary cut-off of $R \geq 0.30$ was applied to identify benthic types that were driving differences between locations. These relationships were graphically illustrated using vectors superimposed onto the PCO plot.

A multivariate distanced-based linear regression model (DistLM Anderson and Legendre 1999; Legendre and Anderson 1999) was used to assess the relative importance of the environmental variables to the observed differences in benthic cover and coral morphologies. The explanatory variables available for testing were turbidity, temperature, temperature variability, depth and wave power. Models were selected using the Akaike Information Criteria (AIC) (Akaike 1987), where the model with the lowest AIC value was selected. Marginal tests were also carried out to illustrate the contribution of each variable individually. To illustrate the effects of environmental variables on dominant habitat types and coral morphologies, vectors were overlayed on the PCO plots. For these plots, quadrats were relabelled by (1) the dominant habitat type (all quadrats), and (2) the dominant coral morphology (quadrats with no coral were excluded).

Results

Exmouth Gulf benthic habitats

Live benthic cover at the 27 survey sites was dominated by macroalgae (average = 25.6% ± 1.7%), turfing algae (13.3% ± 1.3%) and hard coral (8.4% ± 1.0%). Average soft coral, seagrass and sponge cover together was only 15.0% ± 0.5% of the benthos, while the abiotic substrate, largely composed of sand, mud, pavement and rubble, contributed 33.8% ± 1.8% to the benthos (Fig. 2). There were significant differences in hard coral cover among the regions ($p < 0.05$; Table S1), with hard coral and branching coral cover declining southwards and soft coral cover declining northwards (Figs. 2, 4). Further, macroalgal cover and turfing algal cover, which peaked in the middle and upper regions, differed significantly among most regions ($p < 0.05$; Table S1), with comparable macroalgal cover only observed between the Lower and Outside regions, and comparable turfing algal cover only observed between the Outside and Lower, and Outside and Middle regions (Fig. 3, Table S1).

Specifically, the Outside and Upper regions were characterised by high hard coral (Outside–56.7% ± 7.53%) and high turfing algal cover (Upper–29.8% ± 3.1%%) respectively, as well as low seagrass cover (0% and 6.2%, respectively; Figs. 2a & b, 3). However, the coral community was morphologically diverse in the Upper Gulf region contrasting with the Outside region where massive corals dominated (Fig. 4). The Middle Gulf region had the highest macroalgal cover (36.4% ± 2.7%; Fig. 3) in the Gulf. Coral cover here was low (13% ± 1.8%), but also morphologically diverse (Fig. 4). The most southerly region of

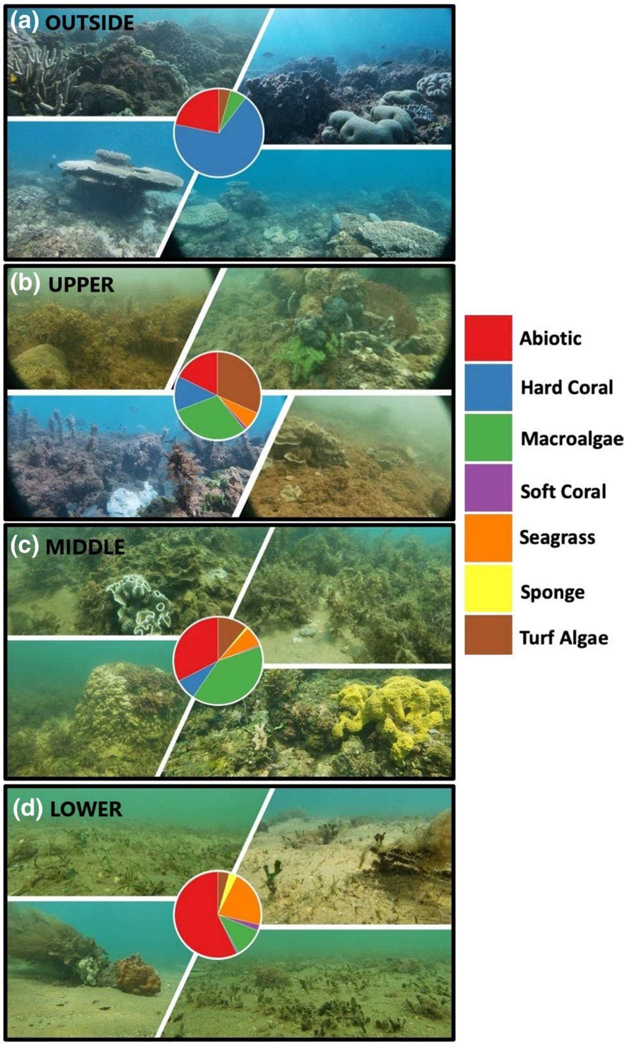

Fig. 2 Examples of benthic habitats from 4 regions of the Exmouth Gulf; **a** Outside **b** Upper **c** Middle and **d** Lower Gulf; pie charts represent the percentage cover of macroalgae, turfing algae, seagrass, sponge, soft coral and hard coral for each region. Abiotic class includes sand, rubble and pavement with no obvious biota attached

the Gulf had the lowest coral cover (5.5% ± 0.1%) with mostly soft, massive or foliose corals observed (Figs. 2 & 4). Macroalgae (10.9% ± 1.8%) and turfing algal cover (4.15% ± 1.1%) were also comparatively low for the Lower Gulf region. Seagrass was also found in the Gulf (average = 10.6% ± 1.1%), primarily *Cymodocea* spp. and *Halodule* spp., and increased in cover southwards. In the Lower Gulf, seagrass represented 20.9% ± 2.4% of the benthic cover, significantly more ($p < 0.0001$) than the Middle and Upper Gulf Regions (6.8% ± 1.3% and 6.2% ± 1.7%, respectively). However, growth was patchy, and blades were usually shorter than 5 cm (Fig. 2d). No seagrass was found in the Outside Gulf region. The calcareous algae *Udotea* spp., was common in the Lower and Middle Gulf and was included in the macroalgae count, (Fig. 3). Coral bleaching was present in all regions with the highest amount in the Outside Gulf (3.4%) and decreasing southward (Fig. 3).

The degree of distinctiveness between regions varied, with a leave-one-out allocation test resulting in low misclassification errors for the Lower and Outside Gulf (85% and 90% correct classifications, respectively), average misclassification for the Upper Gulf (54% correct classification) and the highest misclassification was in the Middle Gulf (29% correct classification). Most commonly, Middle Gulf was incorrectly classified as Lower or Upper Gulf, indicating this region as a transition zone with components of both regions Fig. 5.

Environmental drivers

There were significant differences in environmental conditions throughout all four regions of the Exmouth Gulf ($\text{pseudo-F}_{3,268} = 95.787$, $p < 0.001$). The Lower and Middle Gulf were the shallowest regions (~ 3 m) while the Upper Gulf locations were deeper (~ 5 m) and showed the highest depth variability (Table S2, Fig. 3). Turbidity (18-year mean) was highest in the Middle Gulf (2.44 mg/L) and lowest in the Outside Gulf (1.81 mg/L) and wave power was only high (> 1 *P*) in the Upper and Outside Gulf. While the Outside Gulf had the highest average temperature (26 °C), temperature variability was lowest here. In contrast, the Lower Gulf region had lower average temperatures (25.55 °C) but the highest temperature variability in the Gulf (Table S2, Fig. 3).

Distance-based linear model analysis (DistLM), revealed that all environmental variables (turbidity, temperature, temperature variability, depth and wave power) were included in the best model for describing differences in benthic habitats between the four regions. This model accounted for 29% of the variability in benthic cover among regions (Table S3). All variables except temperature were included in the best model for describing differences in coral morphology types between the four regions of the Gulf (Table S4). This model accounted for 19% of the variability in coral morphology composition.

When all quadrats were reclassified to their dominant benthic habitat type, locations dominated by macroalgal cover were most closely associated with high turbidity and temperature variability. These locations were typically located in the Upper and Middle regions of the Gulf (Fig. 6a). In contrast, locations with high coral and turfing algal cover were most closely associated with higher wave power and depth as well as lower turbidity and temperature variability (Fig. 6a). These locations were typically located outside the Gulf or in the Upper Gulf. Temperature variability was found to explain most of the variation in the coral morphology composition (Table S4), with locations with the highest temperature variability typically

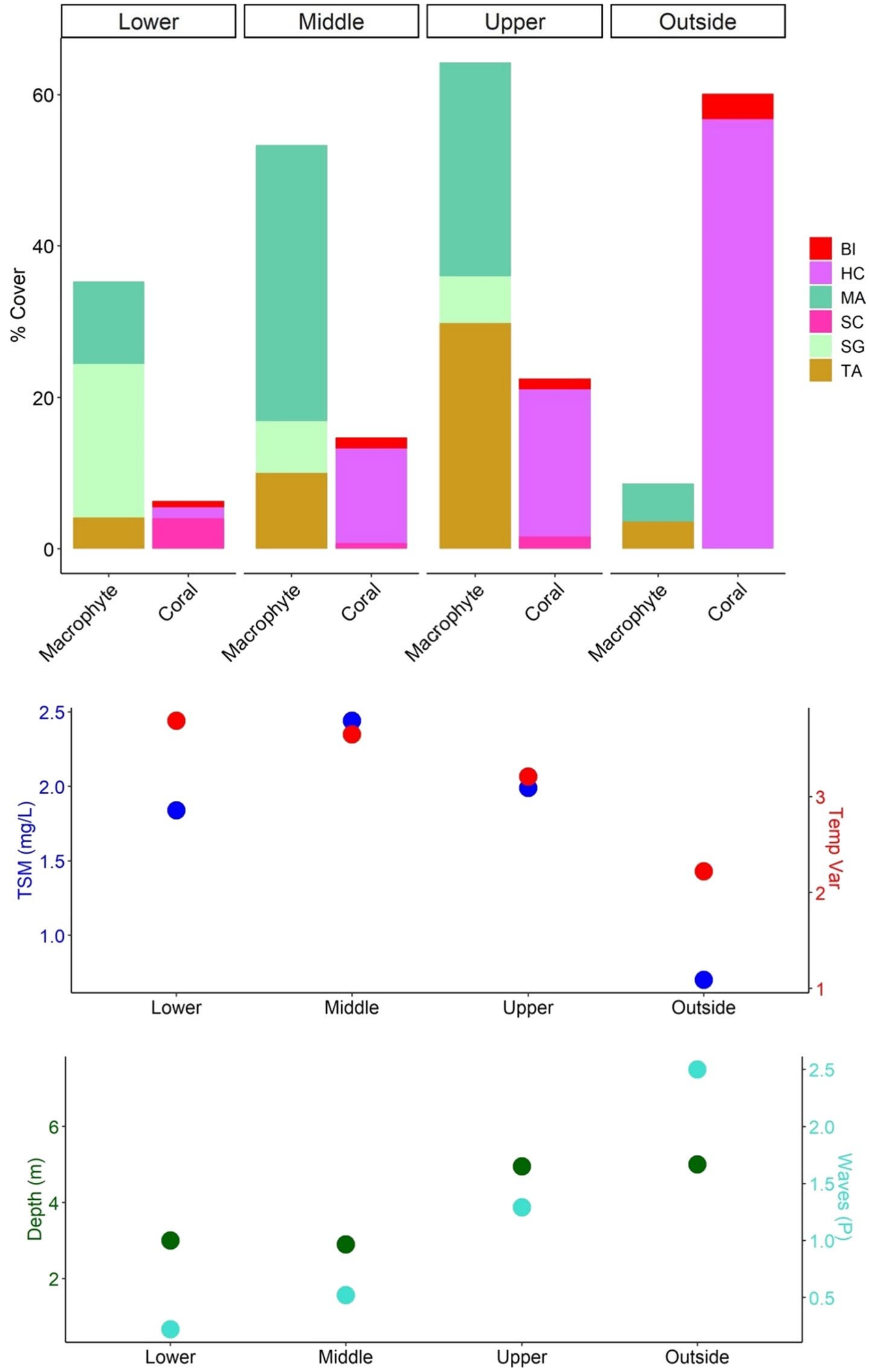

Fig. 3 Percentage cover of macroalgae (MA), turfing algae (TA), seagrass (SG), hard coral (HC), soft coral (SC) and bleached coral (Bl) in four regions of the Exmouth Gulf and the environmental variables–turbidity (TSM), depth (m), wave power and temperature variability (°C) associated with each region

dominated by soft corals (as well as sponges). Depth was also included in the best model for coral morphology (Table S4): as depth increases, there is a trend to more encrusting and foliose species together with a decline in massive species (Fig. 6b). Turbidity was also found to be a significant driver of coral morphological differences between the four regions, having a comparable effect to temperature variability (Fig. 6b).

Discussion

In the Exmouth Gulf, distinct differences in the benthic composition of reefs across relatively small spatial scales (10–100 km) are being influenced by long-term differences in temperature variability, turbidity, and wave power. Coral cover was lower where there was increased temperature variability, and higher where there was increased wave

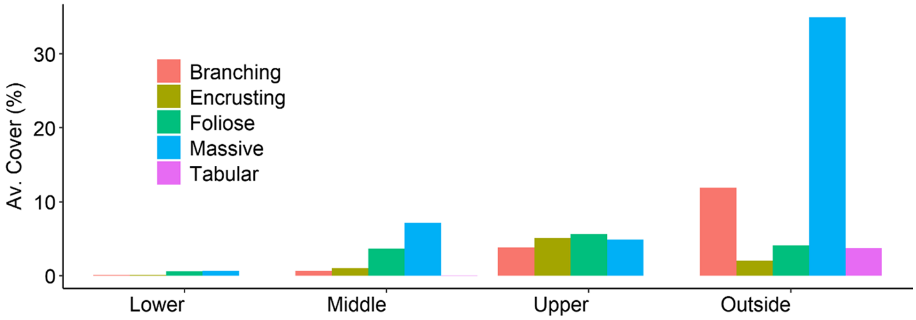

Fig. 4 Percentage cover of five coral morphology types (branching, encrusting, foliose, massive, soft and tabular) in four regions of the Exmouth Gulf

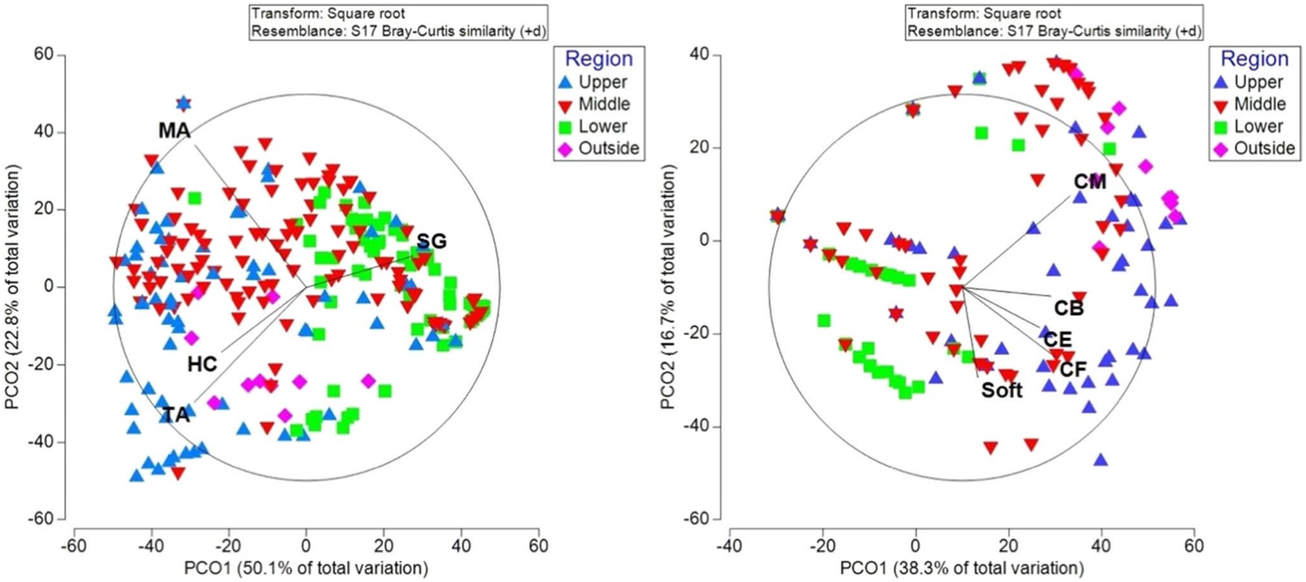

Fig. 5 Principal coordinates analyses showing benthic habitat types with Pearson's R correlations ≥ 0.3 to the first two Principal Components axis describing the differences between 4 regions of Exmouth Gulf; **a** Dominant benthic community–macroalgae (MA), turfing algae (TA), seagrass (SG) and Hard coral (HC); and **b** Coral morphologies associated (Pearson's $R \geq 0.30$) with 4 regions of Exmouth Gulf, massive coral (CM), branching corals (CB), encrusting corals (CE), foliose corals (CF) and soft corals (soft)

power, while macroalgal cover was higher with both higher temperature variability and higher turbidity. Further, coral diversity was lower at both the upper and lower limits of temperature variability and turbidity. There appears to be a threshold level whereby turbidity and temperature variability are high and coral cover and diversity also remain relatively high. However, a further increase in temperature variability despite a small decrease in turbidity is followed by a significant increase in macroalgal cover and decline in coral cover. This demonstrates how the long-term threshold of temperature variability is likely facilitating the spatial differences in coral cover and diversity, with those sites with higher temperature variability typically displaying less coral and more algal growth across their reef environments.

Differences in benthic habitats among coral reefs in Exmouth Gulf are strongly influenced by the long-term interaction of environmental drivers. The Outside Gulf is influenced by the deep offshore ocean, leading to more stable temperatures, lower turbidity, and higher wave power than regions inside the Gulf. These conditions are resulting in a dominance of massive corals, which have increased resilience to wave energy (Baldock et al. 2014) and also provides a suitable habitat for branching corals, as this morphology tends to be less resilient to high turbidity and temperature variability (Humanes et al. 2017; Qin et al. 2020). In contrast the Upper Gulf has higher turbidity and temperature variability, but similar wave power to the Outside Gulf. Here, there is a high turfing algae cover, a parameter that is associated with high coral recruitment and a relatively healthy and diverse coral community (Tebbett and Bellwood 2019). Despite the high turbidity we saw the highest morphological diversity of corals in the Upper Gulf, particularly encrusting and foliose corals that optimise surface area for light capture and are resilient to wave energy. The Middle Gulf, with even

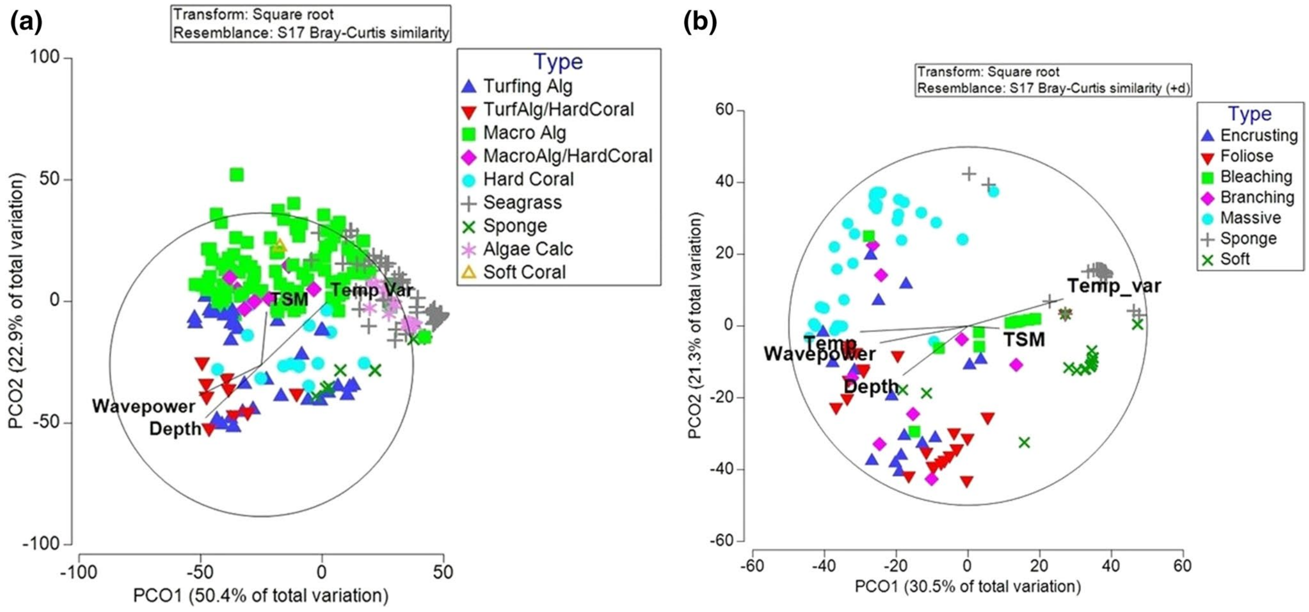

Fig. 6 Principal Components Analyses showing Exmouth Gulf transects relabelled by their dominant habitat type with overlay of environmental drivers (Depth, Temperature, Wave power, Turbidity and Temperature variability) associated with the benthic community differences of **a** Benthic habitat community composition, and **b** Coral morphology types

higher temperature variability and turbidity, but lower wave power, is dominated by macroalgae and has a lower (but still diverse) coral cover. The Lower Gulf has slightly less turbidity than the Middle and Upper Gulf, but the highest temperature variability of all Exmouth Gulf regions. Parts of this low wave-energy region are not conducive to hard coral growth but had comparable levels of macro and turfing algae to the outside Gulf. This suggests that temperature variability and wave power are likely driving the difference in coral cover, while turbidity affects coral cover and macroalgal dominance when these other factors are within a certain range.

Temperature variability was a key environmental driver influencing coral cover and coral morphologies, with coral cover increasing as temperature variability decreased across all regions. However, lower long-term temperature variability has been shown to decrease the resilience of corals to bleaching events (Carilli et al. 2012; Donner 2011; Safaie et al. 2018), meaning the Outside Gulf region (lowest temperature variability) may be less resilient to bleaching than the adjacent regions that have been exposed to higher temperature variability over the past decade. Our findings supported this, and while the rates of coral bleaching from the early 2021 marine heatwave (conditions up to 3 °C warmer than average) were low, bleaching was evident in all regions, with the highest bleaching found in the Outside Gulf (3.4%), where long-term temperature variability is lowest (2.22 °C), and less bleaching in the Upper (1.4%) and Middle Gulf (1.4%) where temperature variability is higher (3.21 °C & 3.65 °C, respectively). In contrast, a meta-analysis of 32 clear water reefs in the western Indian Ocean, found the optimal long-term temperature variability was 2.3 °C, with variability higher and lower than this leading to larger amounts of coral cover loss during a marine heatwave (Ateweberhan and McClanahan 2010). Therefore, turbidity in the Exmouth Gulf may be potentially raising the threshold at which long-term temperature variability can provide resilience to bleaching and adds to the growing evidence that turbidity reduces stress from UV radiation, thereby reducing vulnerability to bleaching, while simultaneously increasing heterotrophy (Browne et al. 2013; Craig and Mangels 2009; Morgan et al. 2017a, b; Zvifler et al. 2021).

The bleaching observed during this study was considered to be related to the marine heat wave event that was ongoing at the time, as there had been no bleaching evident in the gulf on several field trips prior to the event (personal observations). An important point is that the Outside Gulf, where more bleached corals were observed, also had very little algae growing on the reef, whereas the Upper and Middle Gulf had relatively large amounts (Fig. 3). Because the point count survey method only recorded the most superficial species represented at each point, a bleached coral in the Upper or Middle Gulf could have been recorded as algae, not bleached coral, thereby limiting our ability to accurately compare bleaching between these regions.

High turbidity was related to regions with high macroalgal cover. Macroalgae was the dominant benthic cover (36%) in the Middle Gulf, where long-term average turbidity was highest of all regions (Fig. 3). The connection between increased turbidity and increased macroalgal growth has been shown elsewhere, including the Great Barrier Reef (GBR), where macroalgal growth increased fivefold with decreasing water clarity (De'ath and Fabricius 2010). However, the Upper Gulf, also with relatively high turbidity, has significantly less macroalgae than the Middle Gulf, potentially for several reasons.

1. Increased wave energy in the Upper Gulf has removed macroalgae from their holdfasts during the La Niña dominated summer when wave power was at its inter-annual peak (Cartwright et al. 2021; Cuttler et al. 2020; Feng et al. 2003) and before recovery was possible (Loffler and Hoey 2018);
2. Depth, which is significantly increased in the Upper Gulf compared to Middle Gulf (4.95 m & 2.9 m respectively), is limiting light availability that macroalgae require, and
3. Competition from algal turf sediments (dominant in the Upper Gulf) that significantly impede the settlement and survival of macroalgae (Airoldi 1998; Alestra et al. 2014; Goatley et al. 2016).

Further, the turbid Upper Gulf has high coral cover, and high coral morphology diversity, consistent with findings in the GBR (Morgan et al. 2016) and Brazil (Loiola et al. 2019) where significantly more coral cover was found in turbid near shore coral reefs compared to clear water offshore reefs and this may be due to the abundance of coral morphologies here that are photo-acclimated through the long-term turbidity regime (Evans et al. 2020; Loiola et al. 2019). In comparison, the Middle Gulf, with a further increase in turbidity and temperature variability, has significantly less coral and appears to have reached a threshold of combined stressors that are making conditions here optimal for algal colonisation.

It is worth noting that excessive nutrification can contribute to macroalgal overgrowth (De'ath and Fabricius 2010; Morrison et al. 2013; Raven and Taylor 2003) and this mechanism should also be considered in the Exmouth Gulf. While the Gulf does not have a large catchment-derived nutrient input like the GBR (Baird et al. 2021), there is high nutrient input associated with the extensive cyanobacterial mats lining the Gulfs eastern shoreline (Ayukai and Miller 1998; Lovelock et al. 2010). Further, aeolian deposits of iron-rich sediments from the adjacent desert-like rangelands are known to enter the Gulf during dust storms (McTainsh et al. 2011) and iron-rich terrestrial-sourced dust has been linked to primary productivity bursts (algal blooms) in other marine regions (Jickells et al. 2005; McTainsh and Strong 2007). Further, nutrients in coastal waters are often associated with turbidity due to the trapping capabilities of the biogeochemical substances that make up suspended matter flocs (Droppo 2001). Wind-induced resuspension of sediments, which is one of the strongest drivers of turbidity in the shallow regions of Exmouth Gulf (Cartwright et al. 2021), is likely to be simultaneously resuspending nutrients, potentially contributing to the flourishing macroalgal beds. This effect has been shown in several shallow lake and coastal regions where wind-induced resuspension is directly related to primary productivity and algal blooms (Arfi et al. 1993; Schallenberg and Burns 2004; Su et al. 2015).

An important consideration is that some locations in the Exmouth Gulf (particularly in the Middle and Upper Gulf), have shown a significant upward trend in turbidity over the past two decades linked to metocean processes affected by climate change (Cartwright et al. 2021). These same processes (e.g. El Niño-Southern Oscillation) also affect temperature variability (Kumar et al. 2014), and are expected to become more extreme over the coming decades (Cai et al. 2018). If this trend continues there is a risk that coral reef habitats exposed to further increases in temperature variability and turbidity could reach a threshold where irreversible regime shifts occur, as seen in other reefs globally (Graham et al. 2015; Johns et al. 2018).

Algal turfs also have a strong relationship with turbidity and respond to ecological feedbacks. As sediment supply increases due to turbidity, more sediments are trapped in algal turfs (Latrille et al. 2019) creating a positive feedback whereby increased sediment presence in turfs reduces herbivory by fish, allowing the turfs to grow longer and trap even more sediments (Tebbett and Bellwood 2019). Trapped sediments are also subject to resuspension by wind/waves/tides and this contributes to continuing turbidity in a region (Latrille et al. 2019). It has been found that over 80% of all available sediments in some reef systems can be trapped in turfs, though this may be less in turbid regions such as the Exmouth Gulf (Latrille et al. 2019).

It's possible that fishing pressure could further contribute to macro-algal growth on coral reefs. Overfishing has been shown as a major driver of coral reef degradation (Done 1992; Weijerman et al. 2013; Wilson et al. 2010) and contributes to an ecological feedback where less grazing leads to thicker algal stands, and the thicker the algal stands, the more fish and invertebrates avoid grazing there (Hoey and Bellwood 2011; Williams et al. 2001). Whilst herbivore populations (e.g. parrotfish) are sparse in the Exmouth Gulf (Doropolous et al. 2022) some empirical field studies have shown that algal overgrowth and seagrass decline can be a result of removing both the predator fish and the grazing stock (Baden et al. 2012; Bruno and O'Connor 2005) and the catastrophic regime shifts from coral to macroalgal-dominated reefs in the Caribbean was attributed to a synergy of fishing pressure and environmental stressors (Bozec and Mumby 2015). Exmouth Gulf is heavily fished both commercially and recreationally, with biomass removal of up to 1300 tonnes of prawns (with an additional 35 tonnes bycatch) (Kangas et al. 2015), and hundreds of tonnes of demersal fish (Gaughan et al. 2019) annually. However, there is also evidence that excluding fishing, by introducing no-take zones for example, does not improve coral cover and that declining water quality and ocean warming events far outweigh any benefits to coral reefs inferred by marine park protection (Bruno et al. 2019). To better protect the Exmouth Gulf region from degradation into the future, an increased understanding of the interaction between turbidity, nutrient input, algal growth and fishing pressure, such as modelling the ecological balance between primary productivity and biomass removal in this region, is required.

There are some caveats to this study that should be noted. Firstly, there were coral reef islands in the lower Gulf that, while surveyed, were too turbid to analyse from the video images and were therefore excluded from the analysis. Future surveys of these reefs could provide a different insight into the environmental conditions that are conducive to coral-algal growth in the lower Gulf. Further, the lower Gulf sites that were analysed contained less reef availability, and more sand/seagrass, than other Gulf regions (i.e. they were patchy reefs), and this is potentially also why we saw fewer corals in this region.

Secondly, this study does not have a temporal component to its benthic habitat survey and needs to be considered as a study of the environmental stressors that accompany benthic coral-algal states on these marginal reefs rather than an assessment of any phase shifts in those habitats. The field survey was conducted in March 2021 during a marine heatwave and at the end of a La-Nina summer. Both these climatic events could have led to (temporary) seasonal changes to the benthic structure and the analysis should be therefore considered as both a baseline survey of these remote and marginal reefs, and as an analysis of the type of benthic structure that environmental stressors, particularly turbidity, can be associated with.

Thirdly, the point count method has limitations in that it only allows for one benthic category to be recorded. While this is adequate for identifying where there is higher and lower algal growth and to allow for an environmental correlation to these states, it limits how much can be discerned regarding coral cover. At the least, we need to clarify that ‘coral cover’ as defined in this work, is referring to corals that are free from algal growth at the point being recorded. Therefore, while we have included an analysis of coral cover differences across the regions of the Gulf, future work on corals here would benefit from a more comprehensive survey that identifies corals (and other surfaces) that are heavily turfed, and therefore ‘hidden’ in this work.

In conclusion, the Exmouth Gulf currently supports a range of benthic habitats and coral reefs that are existing under various levels of turbidity, wave exposure and temperatures. While moderate levels of turbidity and temperature variability may be lending resilience to coral reefs in moderately turbid regions such as the Upper Gulf, the environmental threshold for which reefs are resilient to macroalgal dominance may have already been reached in others (Lower and Middle Gulf). Top-down pressures such as fishing/trawling could enhance the potential for macroalgal dominance and as turbidity and temperature increase with climate change the threshold could be reached in the Upper Gulf coral reefs as well. With increased marine park protection of this region given recent prioritisation, more research into the effects of turbidity, primary productivity and fishing pressures on the Gulfs benthic habitats is imperative.

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Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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