



REPORT

Deoxygenation following coral spawning and low-level thermal stress trigger mass coral mortality at Coral Bay, Ningaloo Reef

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Abstract Oxygen depletion is well recognized for its role in the degradation of tropical coral reefs. Extreme acute hypoxic events that lead to localized mass mortality and the formation of ‘dead zones’ (a region where few or no organisms can survive due to a lack of oxygen) are particularly concerning as they can result in wide-ranging losses of biodiversity, ecosystem productivity and functioning, economic prosperity, and wellbeing. In March of 2022, the annual coral spawning event at Bills Bay (Coral Bay, Ningaloo Reef, Western Australia) coincided with elevated seawater temperature, calm weather conditions and a flood tide resulting in coral spawn becoming trapped in Bills Bay. Immediately after, there was a mass fish kill, which is believed to have been caused by local eutrophication resulting in severe oxygen depletion. The impact the deoxygenation and thermal stress event had on benthic communities has not yet been quantified; hence, the principal aim of this study is to document the extent of change that occurred in the benthic

communities before and after the 2022 coral spawning event over a spatial gradient from the nearshore to mid-reef. Percent coral cover in the Bay decreased from $55.62 \pm 2.26\%$ in 2016–2018 and $70.44 \pm 5.24\%$ in 2021 to $1.16 \pm 0.51\%$ in 2022. Over the same period, the percent cover of turf algae increased from $27.40 \pm 2.00\%$ in 2016–2018 and $24.66 \pm 6.67\%$ in 2021 to $78.80 \pm 3.06\%$ in 2022, indicating a dramatic phase shift occurred at Bills Bay. The abundance of healthy coral colonies recorded on replicated belt transects at nine sites declined from 3452 healthy individuals in 2018 to 153 individuals in 2022 and coral generic richness decreased by 84.61%, dropping from 26 genera in 2018 to 4 genera in 2022. Previously dominant genera such as *Acropora*, *Montipora* and *Echinopora*, were extirpated from survey sites. Isolated colonies of massive *Porites* spp. and encrusting *Cyphastrea* sp. survived the event and understanding the mechanisms underpinning their greater survivorship is an important area of future research. Long-term monitoring is recommended to track the community recovery process and improve our understanding of the longer-term implications of this acute mortality event on the ecological, socio-economic and cultural values of Ningaloo Reef.

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Introduction

Environmental disturbances influence the structure and function of ecological communities (Karlson and Hurd 1993; Hughes 2003). On coral reefs, ecological theory predicts that high diversity persists under intermediate levels of natural disturbances (such as cyclones) because space is created

enabling new ecological opportunities that prevent competitive exclusion (Connell 1997). The current situation on coral reefs, however, is that natural disturbances are amplified by climate change meaning that coral reefs are increasingly being exposed to a high disturbance regime. At high levels of disturbance, natural communities do not have sufficient time to reassemble and the inherent capacity for coral reefs to recover after disturbance is eroded leading to biodiversity loss, habitat simplification and losses of productivity and functionality (Sheppard et al. 2002; Graham et al. 2006, 2014; Berumen and Pratchett 2006; Pratchett et al. 2011; Dietzel et al. 2020).

Eutrophication is one of the ten anthropogenic drivers impacting the global biosphere (Sage et al. 2020). One of the possible consequences of eutrophication is lowered oxygen (O_2) saturation and an increase in biological O_2 demands leading to deoxygenation. Hypoxia (detrimental low O_2 , see Hughes et al. 2020) is an increasingly recognized threat to the biodiversity and productivity of marine ecosystems (Diaz and Rosenberg 2008; Altieri et al. 2017; Nelson and Altieri 2019). Oxygen depletion events have been implicated in the mortality of coral reef organisms including fish, invertebrates and coral at many locations around the world including the Cocos Keeling Islands (Hobbs and McDonald 2010; Hobbs and Macrae 2012), the Cook Islands (Manihiki Atoll, Andréfouët et al. 2015), Costa Rica (Cano Island, Guzman et al. 1990), Florida Keys (Lapointe and Matzie 1996), French Polynesia (Hikueru, Manihi, Takopoto, Fangatu, Tatakoto and Ahe Atolls, Andréfouët et al. 2015), Hawaii (Jokiel et al. 1993), Panama (Uva Island and Bahia Almirante, Guzman et al. 1990 and Altieri et al. 2017), Venezuela (Morrocoy National Park, Laboy-Nieves et al. 2001) and Coral Bay, Ningaloo Reef, Australia (Simpson et al. 1993). In the worst cases, localized acute hypoxia events have led to the formation of dead zones (Altieri et al. 2017), which catastrophically impact biodiversity, ecosystem functioning and human wellbeing.

Tropical shallow waters, and their coral reefs, are particularly vulnerable to eutrophication events and extremely low O_2 events, because of anthropogenic pollution (e.g., land-based runoff, oil spills, Baum et al. 2015; Edinger et al. 1998) and natural events such as dinoflagellate blooms (Raj et al. 2020; Gopakumar et al. 2009) and coral spawning (Simpson 1993). At the Cocos (Keeling) Islands for example, coral spawn being trapped in the lagoon has been linked to numerous historical hypoxia-related catastrophic die-offs of fish, coral and benthic invertebrates in 1879, 1961, 1983, 2007–2009 and 2012 (Forbes 1885; Bunce 1988; Blake and Blake 1983; Berry 1989; Hobbs and Macrae 2012). Similarly, in March 1989, a perfect storm of tidal, wind and swell conditions led to coral spawn being trapped in Coral Bay, Ningaloo Reef, Western Australia. Within days, a mass mortality event occurred involving fish, coral and other reef

animals which died as a result of oxygen depletion created initially by the respiratory demand of the coral spawn and maintained by the biological oxygen demand of the decomposing spawn slicks and dead animals (Simpson 1993).

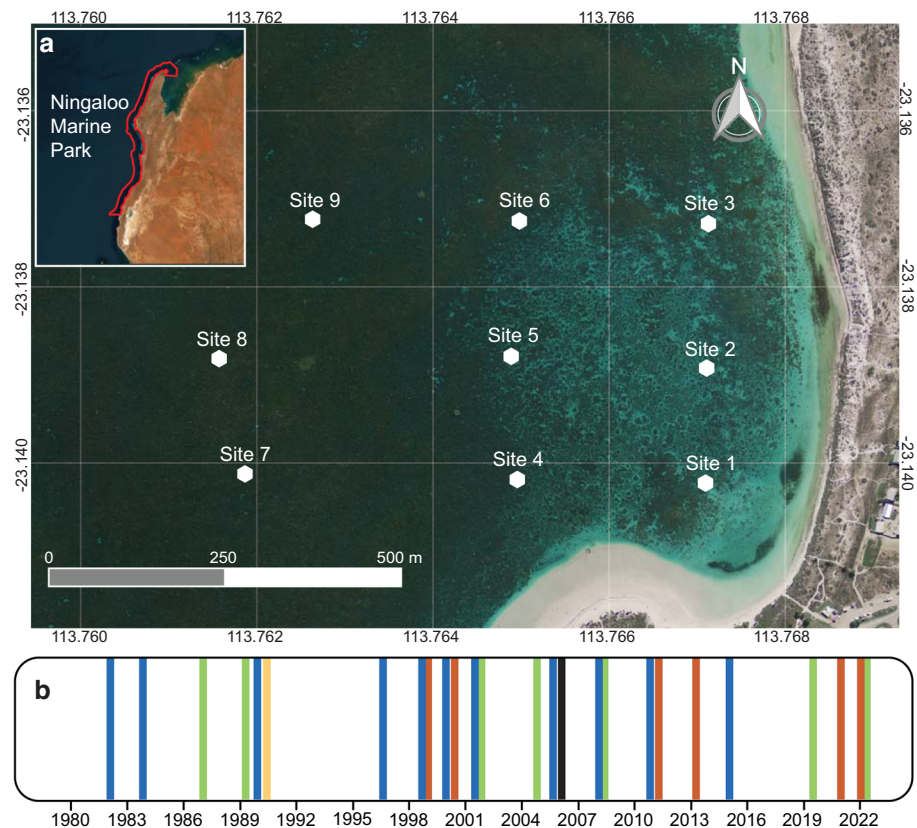
Despite the large local impact deoxygenation events can have, the role of hypoxia as a driver of disturbance on coral reefs is often overlooked (Hughes et al. 2020). Some consider ocean deoxygenation occurring as a result of the interactive effects of ocean warming and nutrient enrichment pose the most immediate threat to coral reef survival (Altieri et al. 2017; Johnson et al. 2018). In March 2022, a widespread deoxygenation event at Bills Bay, Coral Bay, Ningaloo Reef, Western Australia following a coral spawning event. The deoxygenation event was triggered by a combination of weather and oceanographic conditions that led to the prolonged trapping of coral spawn in Bills Bay which led to a massive, localized fish kill, the 7th of its kind at this location in documented history. We compared the spatio-temporal diversity of corals and the structure of the benthic communities in Bills Bay before and after the 2022 coral spawning event to determine the extent of change that had occurred in the benthic community and to test the hypothesis that there is taxonomic variability in scleractinian coral vulnerability to deoxygenation events.

Methods

Study site and disturbance history

Benthic surveys were conducted in Bills Bay at Coral Bay, a partially enclosed inshore lagoon on the eastern boundary of the Maud Sanctuary Zone within the UNESCO World Heritage Ningaloo Marine Park, Western Australia (23.13884° S, 113.76759° E, Fig. 1a). For at least three decades, the benthic community in this area has been dominated by hard coral genera *Acropora*, *Montipora*, *Porites*, *Echinopora* and *Cyphastrea*, however, a diverse array of genera has also been documented to occur in lower abundances (Holmes et al. 2017). Coral Bay has been impacted by several historical environmental disturbances including cyclones, periods of prolonged extreme sea surface temperatures (SSTs), low-temperature bleaching, *Drupella* outbreaks and anoxic events (Simpson et al. 1993; Armstrong 2007; Armstrong et al. 2008; Halford and Perret 2009; Shedrawi et al. 2017) (Fig. 1b, Table S1). From 1990 to 2002, coral cover within Bills Bay declined by as much as 50% as a result of a severe anoxic event in 1989 (Simpson et al. 1993; Shedrawi et al. 2017; Newnham et al. 2020). Despite several tropical cyclones, periods of high Degree Heating Weeks (DHW > 8 usually result in severe coral bleaching; Liu et al. 2003) and anoxic events, coral cover at Bills Bay was in a state of

Fig. 1 Satellite imagery of Bills Bay at Coral Bay within the Ningaloo Marine Park showing **a** the nine survey locations, sites = 1–3 near shore, sites 4–6 = inner mid-reef, sites 7–9 = mid-reef; **b** Environmental disturbances that have occurred at Bills Bay since 1980 (see also Table S1). Disturbances are marked with vertical lines. Blue = cyclones category 1 or above passing within 200 km of Bills Bay, green = deoxygenation event, yellow = *Drupella* outbreak, orange = periods exceeding eight-degree heating weeks (DHW), black = cold water bleaching



expansion from 2002 to 2017 (Newnham et al. 2020). No coral bleaching or very localized bleaching events were observed by the Department of Conservation and Attractions during rapid visual survey assessments from February 2019–February 2022 (Table S2).

Bills Bay, much like the rest of the Ningaloo Reef, has a wave-driven circulation system that flushes nutrients through two reef openings north and south of the bay (Shedrawi et al. 2017). Wave-driven circulation shifts water from outer reef flats into the lagoon, before flushing through passages via hydrodynamic forcing (Zhang et al. 2012). Shoreward sites within the lagoon have greater water residence times (WRT) than sites in closer proximity to outer reef flats, with differences in WRT reaching a few days depending on conditions (Zhang et al. 2012). The high spatial gradient of WRT and the general relationship between modeled DHW and WRT results in shoreward pockets of warm water (equivalent to 30 DHW), or nutrient-enriched water, as seawater can remain stagnant within nearshore Bills Bay for up to 40 h under median offshore wave conditions (Shedrawi et al. 2017). Patterns of water retention in Bills Bay, as modeled by Shedrawi et al. (2017), have influenced the vulnerability of coral communities to past environmental disturbances.

2022 Mass coral spawning event

On March 24, 2022, Bills Bay experienced a mass coral spawning event, seven days after the Full Moon. An unpublished report from the Department of Biodiversity, Conservation and Attractions (DBCA) on March 28 described findings of a fish kill that was estimated to consist of 16,000 individual fish and elasmobranchs washed up on the eastern and southern shorelines of Bills Bay (Fig. 2, Fig. S1). There were also anecdotal reports of fish kills in other parts of Ningaloo Reef including Turquoise Bay, Yardie Creek, Point Billie and Janes Bay although these events were not quantified. A mass coral mortality event was also anecdotally reported (Baird et al. 2023). The exact environmental conditions leading to the mortality event are not known, however, local meteorological reports indicate the bay experienced elevated seawater temperature (NOAA DHW = 3.62) and calm weather conditions exacerbated by a low-pressure system (Cyclone Charlotte) which tracked along the Western Australian coast in the days preceding the event (21st–25th March 2022, Bureau of Meteorology 2022) leading to low barometric conditions offshore. There were also minimal NW to W onshore winds (< 10 km/hr), low swell (< 1 m) and

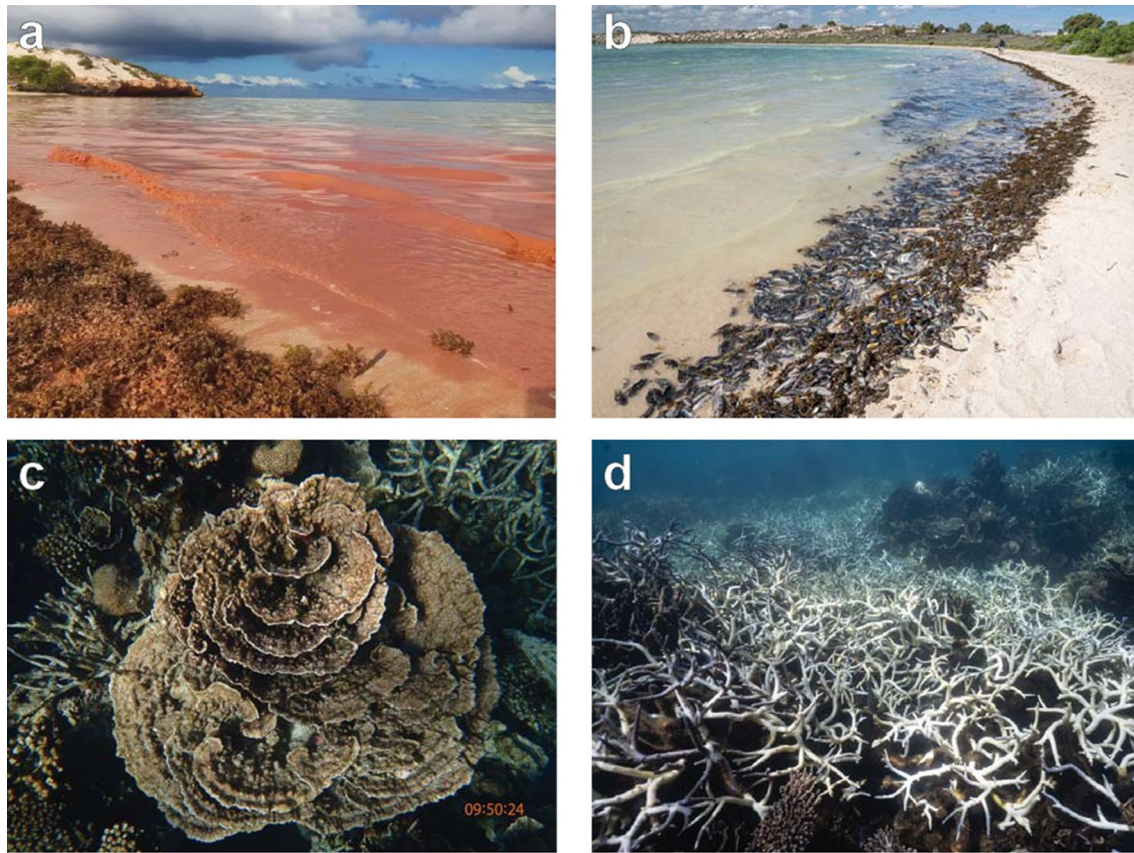


Fig. 2 Imagery obtained during and after the 2022 anoxic event. **a** Coral spawn accumulating at the shoreline on 27th March 2022, photo by Annelies Gevers; **b** Dead fish accumulating on the shoreline,

March 28th, 2022, photo by DBCA/Joel Johnsson; **c** Dead *Montipora* in August 2022, photo by Anthony Terraica, and **d** bleached *Acropora* in Bills Bay, 5th April 2022, photo by DBCA/Joel Johnsson)

limited tidal movement (± 0.5 m) in the days following the coral spawning.

Survey design

Coral diversity and benthic community composition surveys were documented at nine long-term monitoring sites at water depths < 3 m within Bills Bay (Fig. 1a, See Table S3 for site coordinates). Sites were grouped into three zones (sites 1–3 = nearshore, approximately 200 m from shore; sites 4–6 = inner mid-reef, approximately 400 m from shore; sites 7–9 = mid-reef, approximately 700–800 m from shore).

Benthic cover data were collected via snorkel on replicated point intercept transects. Benthic cover was recorded every 25 cm along three replicate 20 m transects (80 points per transect) in 2016–2018, and 2022. The benthos directly below each point were classified into the following categories: live hard coral, soft coral, sponge, turf algae, coralline algae, fleshy algae, rock, sand, rubble, and other invertebrates. Coral abundance and diversity were recorded along three replicate 20 m long, and two-meter-wide belt transects in 2018 and 2022. Every

coral encountered within the belt transect was counted and identified to a genus level. Corals were identified using the Western Australian Coral Compactus Genus Level Identification Guide (Richards 2018). A separate benthic cover survey was conducted in 2021 and benthic cover was estimated on three replicates of point intercept transects ($n = 50$ points per transect) at three sites (See Table S4 for site coordinates). Two of these sites occur in very close proximity (within 50 m) of sites 4 and 8, the third site is located approximately 400 m north of our most northerly survey site.

To investigate thermal stress, we used the NOAA 5 km Coral Reef Watch (CRW) sea surface temperature (SST) measured by satellite and the NOAA degree heating weeks (DHW) (NOAA 2022) at the NOAA 5 km grid point closest to Coral Bay, Ningaloo (-23.125° S, 113.725° E) (See Figs. S2, S3). Continuous measurements of seawater temperature in Coral Bay (-23.1305° S, 113.7532° E) were also made using a HOBO v2 temperature logger ($\pm 0.2^\circ$ C, Onset Computer Corp.) deployed at the benthos at a depth of ~ 3 m (Fig. S3).

Data analysis

Descriptive statistics were calculated for benthic cover data from all years. Relationships between percent benthic cover at the nine long-term monitoring sites in 2016, 2017, 2018 and 2022 were examined using a two-factor PERMANOVA in PRIMER V7 with PERMANOVA + add-on (version 7.0) (Anderson et al. 2008). Factors were ‘Year’ and ‘Zone’ with pairwise comparisons. Multivariate homogeneity of variance was tested using PERMDISP (Anderson et al. 2008) and data did not require transformation. Non-transformed data was converted to a Euclidean distance matrix. Benthic cover was visualized using nonmetric multidimensional scaling (nMDS) with benthic categories overlaid vectors.

Belt transect data from 2018 and 2022 examined via PERMDISP and did not require transformation. The data was converted to a Bray–Curtis similarity matrix and relationships between coral generic abundance at the nine long-term monitoring sites 2018 and 2022 were examined using a two-factor PERMANOVA in PRIMER V7 with PERMANOVA + add-on (version 7.0) (Anderson et al. 2008). Factors were ‘Year’ and ‘Zone’ with pairwise comparisons. Temporal changes to coral generic abundance were visualized using a shade plot.

Results

Benthic composition at Bills Bay lagoon remained relatively stable at all nine sites from 2016 to 2018 (Fig. 3) with no significant difference in benthic cover between years at the three reef zones across this period (Table S5). Generally, the highest level of coral cover across this period was most

consistently recorded in the inner-mid-reef zone (sites 4–6), approximately 400 m from the shoreline where coral cover ranged from 61 to 81% (Table S6). Nearshore (sites 1–3) coral cover ranged from 28 to 58% and on the mid-reef (sites 7–9), approximately 800–900 m from shore, coral cover was highly variable, ranging from 30 to 83%. The overall mean percent coral cover from 2016 to 2018 was $55.62 \pm 2.26\%$ (Fig. 4, Table S6). At the three sites surveyed within Bills Bay in 2021, mean coral cover varied from 63.33 to 80.67% and mean algal cover varied from 11 to 32% (Fig. S4).

When comparative data from 2022 was included in the analysis, there was a significant difference in benthic cover at each reef zone between the years assessed (Table 1). In 2022 the overall mean level of percent coral cover in Bills Bay had dropped to $1.16 \pm 0.51\%$ with a similar extent of decline recorded within all three reef zones (Fig. 3). The mean percent coral cover declined to zero at four sites and was less than 5% at the other five sites (Fig. 3). For example, from 2016 to 2018 mean coral cover at site 6 (inner-mid-reef zone) ranged from 74 to 80%, however in 2022, 0% coral cover was recorded at this site. Similarly, from 2016 to 2018 mean coral cover at site 7 (mid-reef zone) ranged from 44 to 68%, however, in 2022, 0% coral cover was recorded. The site with the highest level of coral cover in 2022 was 4.17% (± 4.17), recorded at site 4 (southern inner-mid-reef zone) followed by 3.75 (± 0.72) recorded at site 8 (central mid-reef).

In 2022, the overall mean percent cover of turf algae increased from 27.40 ($\pm 2.00\%$) in 2016–2018, to $78.80 \pm 3.06\%$ in 2022 (Fig. 4, Table S6). The trend of increasing turf algal cover occurred at all sites (Table S6). For example, at site 6 (northern inner-mid-reef zone) mean turf algal cover ranged from 13 to 24% cover from 2016 to

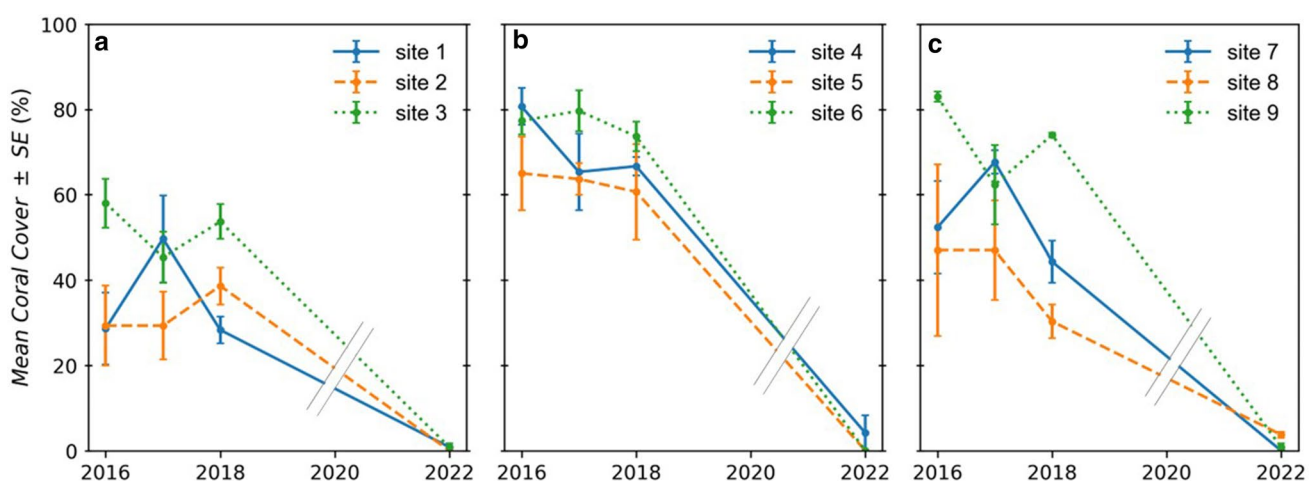


Fig. 3 Temporal change in the mean level of percent coral cover (\pm SE) from 2016 to 2022 at nine long-term monitoring sites in Bills Bay spanning nearshore (sites 1–3), inner-mid-reef (sites 4–6) and mid-reef zones (sites 7–9). Grey diagonal lines indicate the absence

of data for 2019–2021; thus, inferences on the status of the coral community cannot be made over these three years. See Figure S4 for coral cover data collected from three separate sites in 2021

Fig. 4 Pirate plot of turf and hard coral benthic cover per transect for each year assessed. 10th and 90th quantiles are displayed with a 95% confidence interval band

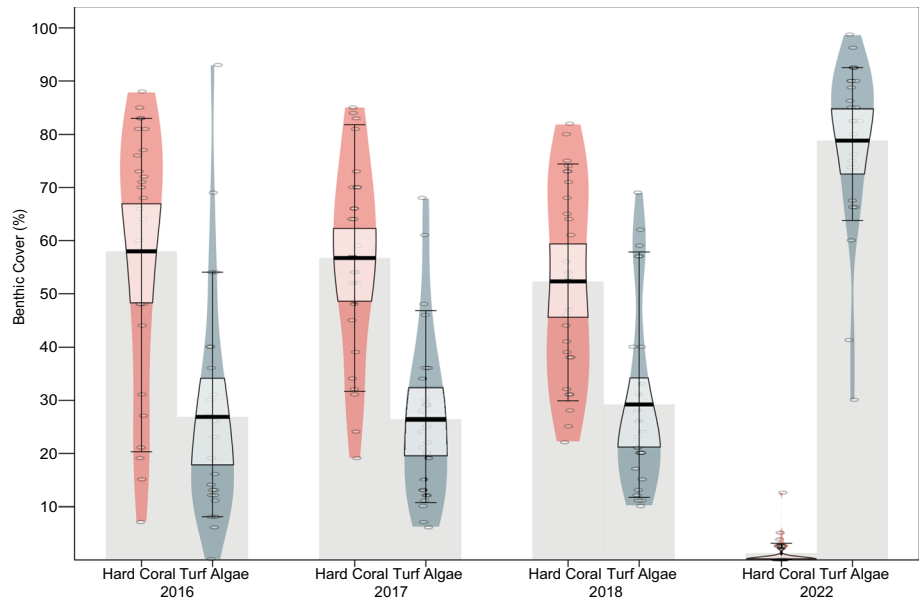


Table 1 Permanova results showing pairwise comparisons of benthic cover (hard coral, turf algae, other algae, abiotic) between years (2016, 2017, 2018, 2022) and zone (nearshore, inner-mid-reef, mid-reef)

Source	df	SS	MS	Pseudo-F	P-value	Unique perms
Year	3	1.1453E+05	38,176	59.387	0.0001	9954
Zone	2	26,832	13,416	20.87	0.0001	9939
Year×Zone	6	11,839	1973.1	3.0694	0.0003	9935
Res	96	61,711	642.83			
Total	107	2.1491E+05				

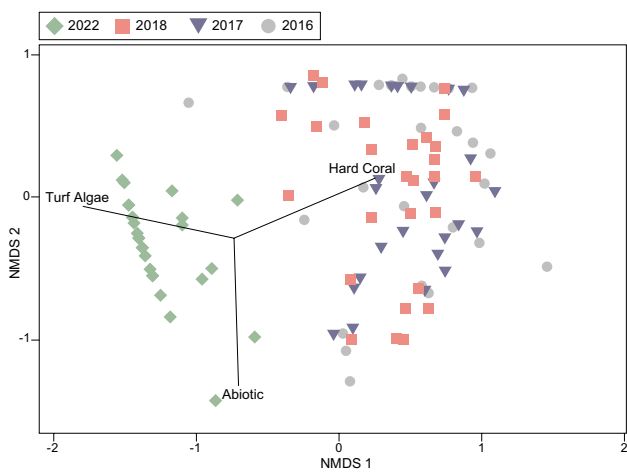


Fig. 5 nMDS ordination of benthic composition. Samples are comprised of 108 transects (27 transects per 4 years). Overlaid vectors include hard coral (healthy, live coral), turf algae (substrate covered in algal turfs), and abiotic (sand, bare rock, rubble)

2018 and increased to 93% in 2022. Similarly, from 2016 to 2018 mean turf algal cover at site 9 (northern mid-reef zone) ranged from 15 to 38%, however, in 2022, 83% turf algal cover was recorded. The consistency of community

composition from 2016 to 2018 and the change in community composition in 2022 is visualized in the nMDS (Fig. 5) and driven by algal turfs replacing hard coral as the dominant benthos in 2022.

In 2018, a total of 3452 healthy individual colonies from 26 genera of scleractinian coral were recorded on belt transects across the nine survey sites (Table S7). 1293 healthy colonies were recorded in the nearshore zone, 1151 healthy colonies from the inner-mid-reef zone and 1008 healthy colonies in the mid-reef zone. The most commonly encountered corals included *Cyphastrea*, *Dipsastraea*, *Montipora*, *Echinopora*, *Galaxea*, *Pocillopora*, *Pachyseris*, *Stylophora* and *Turbinaria* across the three reef zones (Fig. 6). *Cyphastrea*, *Dipsastraea*, *Montipora* and *Echinopora* dominated the nearshore reefs; *Galaxea*, *Turbinaria*, *Montipora*, *Acropora* and *Cyphastrea* dominated the inner-mid reefs; and *Cyphastrea*, *Turbinaria*, *Galaxea* and *Dipsastraea* dominated the mid reefs.

In 2022, the colony abundance was significantly different at all sites (Table 2). When the 2018 sites were resurveyed, a total of 153 live coral colonies were encountered belonging to four genera only (Table S8). This represents an 84.61% decrease in coral generic richness and a 95.57% decline in colony abundance. In 2022, *Cyphastrea* was the

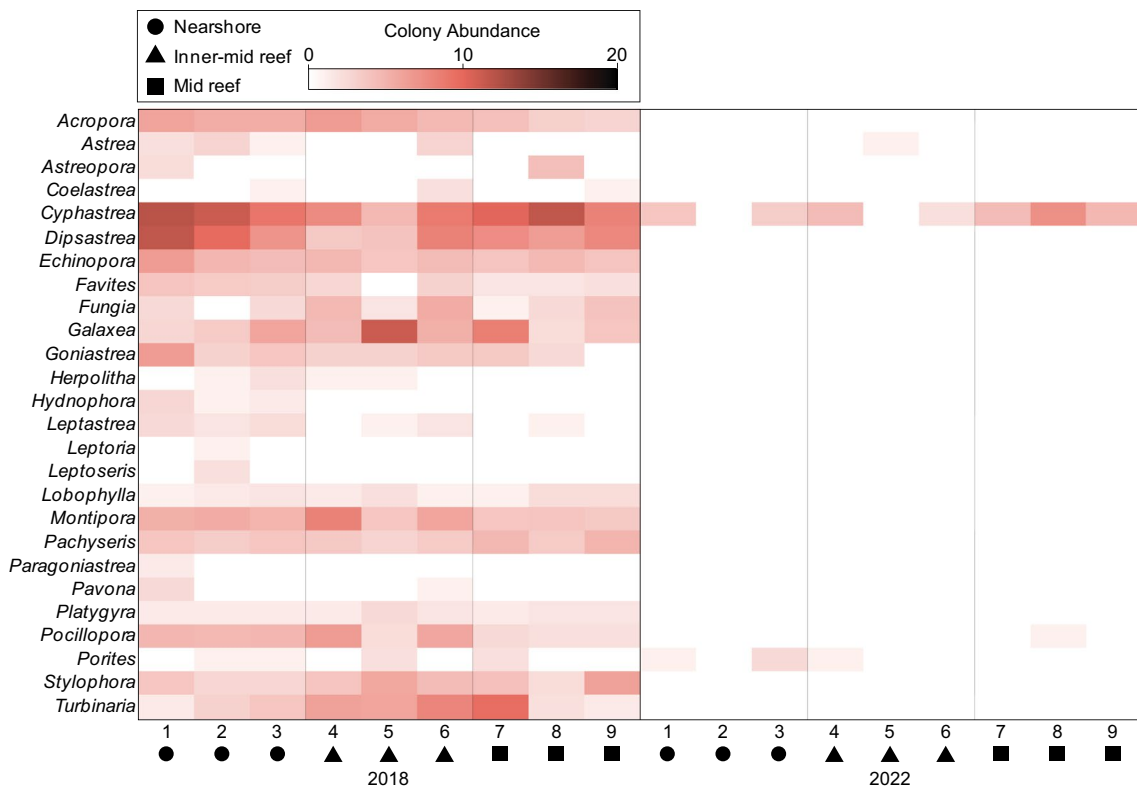


Fig. 6 Shade plot illustrating the change in the abundance of coral genera across sites and reef zones between 2018 and 2022

Table 2 Permanova results showing pairwise comparisons of coral colony abundance between years (2018–2022) at the nine monitoring sites

Source	df	SS	MS	Pseudo-F	P-value	Unique perms
Year	3	41,002	13,667	111.12	0.0001	9940
Site	8	11,818	1477.2	12.01	0.0001	9923
Year × Site	24	7733	322.21	2.6197	0.0003	9897
Res	72	8855.6	122.99			
Total	107	69,408				

most encountered coral and the only coral genera recorded in all reef zones; however, its abundance declined by 82.32% (from 809 colonies in 2018 to 143 colonies in 2022). Isolated colonies of *Porites* ($n = 8$ nearshore and inner-mid-reef) *Astrea* ($n = 1$, inner-mid-reef) and *Pocillopora* ($n = 1$, mid-reef) were also recorded in 2022 (Fig. 6).

Discussion

This study suggests that deoxygenation following the 2022 coral spawning event combined with a mild thermal stress episode is the likely cause of a catastrophic mass bleaching and mortality event that detrimentally impacted the coral communities in the nearshore, inner-mid and mid-reef sections of Bills Bay. Approximately five months after the spawning event, the mean percent cover of live scleractinian

coral dropped from 28 to 83% (recorded from 2016 to 2018) and 63–81% (recorded in 2021) to <5% and the diversity of coral genera encountered on repeat transects dropped from 26 to four. The nearshore and middle sections of the bay experienced a phase shift whereby the dominant benthic cover shifted from a diverse community of hard corals to a depauperate community of dead coral covered in turf algae. The coral community was significantly and detrimentally impacted by the 2022 deoxygenation event and the area of Bills Bay surveyed resembled a temporary ‘dead zone’ akin to that described at other tropical coral reef locations where severe deoxygenation events have occurred (Altieri et al. 2017).

The process by which trapped coral spawn leads to deoxygenation relates largely to the rapid nutrient enrichment that occurs when the coral spawn breaks down. The decomposition of spawn leads to a spike in nutrient levels,

predominantly nitrogen (Guest 2008; Briggs et al. 2013), and the breakdown of nutrient recycling pathways (Falkowski et al. 1993; Bell et al. 2007, 2014). This leads to accelerated growth of phytoplankton (Eyre et al. 2008; Bell et al. 2014) and as the algal blooms rot (along with the coral spawn), microbial biomass increases which in turn, increases net metabolic activity resulting in oxygen depletion (Eyre et al. 2008; Fabricius 2011). While the time frame and tipping point(s) where oxygen depletion becomes catastrophic for resident fauna is not well understood, in this case, it appears to have occurred quickly, given that motile organisms such as fish, rays and eels were unable to escape the low-oxygen water before suffocating (Fig. 1b, S1). It is possible, however, that other causal factors such as the clogging of respiratory surfaces by waxy lipids may help to explain the mortality of motile vertebrates.

Bleaching-induced stress responses in corals are commonly observed after anomalous thermal stress events when seawater temperature exceeds the bleaching threshold, often defined as 1 °C above the local maximum monthly mean (MMM + 1 °C). The major coral spawning at Ningaloo occurs in March or April (Gilmour et al. 2016) and thus coincides with elevated summertime seawater temperatures and an increased chance of thermal stress, with the seasonal maxima typically occurring in February or March (NOAA 2022; Ross et al. 2019). During the coral spawning and deoxygenation event in March 2022, in situ seawater temperature within Bills Bay exceeded the local MMM of 27 °C (Fig. S2) and the NOAA DHW in Bills Bay reached a maximum of 3.62 (Fig. S3). This indicates that the reef communities in Bills Bay were exposed to low-level thermal stress at the time of coral spawning, however, it is unlikely that thermal stress alone resulted in the severe mortality observed here. The calm conditions and slightly elevated seawater temperature may however have further reduced the availability of dissolved oxygen (see Hobbs and McDonald 2010). Hence, we infer that the combination of deoxygenation and mild thermal stress triggered a severe coral bleaching response which led to the high levels of coral mortality documented here.

It is also worth noting that the synergistic effects of environmental disturbances can lower the bleaching threshold by 0.4–1 °C (Alderdice et al. 2022). In *Acropora*, hypoxic stress has been shown to lead to the downregulation of genes responsible for photoreception, hindering photoprotective mechanisms, and prompting heat-induced coral bleaching (Alderdice et al. 2022). Furthermore, when symbiotic zooxanthellae are supplied with increased abundances of N and P (Hallock 2001), the need for a symbiotic nutrient pathway with their coral host is lost (Wooldridge and Done 2009). Hence the breakdown of this fundamental symbiosis in corals within Bill's Bay lagoon may have lowered the thermal bleaching threshold potentially resulting in a more severe

thermal stress response (Wooldridge 2009; Wooldridge and Done 2009). It is therefore possible that the oxygen-starved conditions acted synergistically with elevated sea surface temperatures in a lowered bleaching threshold scenario, which may have further intensified the scale of the coral mortality event.

The 2022 deoxygenation event ultimately led to a benthic phase shift with the Bills Bay community rapidly transitioning from coral to turf algal domination. These impacts spanned the nearshore and mid-reef zones, with the coral death assemblage recorded to extend at least 900 m from shore. Scleractinian corals were not, however, the only casualties of the anoxic conditions. In addition to the wide variety of teleost fishes and elasmobranchs that washed up on the beach (Lyle Shields/DBCA pers. comm., Fig. S1), a range of benthic fauna were asphyxiated as evidenced by the in situ death assemblage of molluscs (e.g., Tridacnid clams, Abalone, Cowrie, *Drupella*) and the absence of sponges, soft corals, anemones and other invertebrates that were observed on and off transects from 2016 to 2018 (Richards pers. comm.).

Our results show that the three previously dominant genera—*Acropora*, *Montipora* and *Echinopora* along with 18 other genera experienced 100% mortality at the survey sites (Fig. 6). *Cyphastrea*, *Porites*, *Pocillopora* and *Astrea* were the only genera with surviving individuals at the survey sites, however, the abundance of colonies within these genera was significantly lower after the anoxic event. It is also worth noting that three species of *Cyphastrea* were present in the community before the event, yet only one encrusting species survived. Understanding the differential susceptibility to deoxygenation and the mechanisms that enable some species to tolerate hypoxia is important (Camp et al. 2017; Johnson et al. 2021). Alderdice et al. (2021) examined how different reef-building corals responded to deoxygenation/reoxygenation stress and found that bleaching-tolerant species of *Acropora* had higher baseline expression of heat shock proteins (*HIFa* and HIF-dependent *hsp90*) enabling them to coordinate cellular activity and to resist bleaching in lowered O₂ conditions. In the present case, however, the *Acropora* corals were overwhelmed by the acute level of stress and unable to resist bleaching. For those corals such as *Cyphastrea* and *Porites* that did survive, it is possible their tendency to grow in shaded areas at the base of other colonies (*Cyphastrea*) or to grow as massive morphologies (*Porites*) beget a degree of protection as has been proposed in other studies (Greenstein and Pandolfi 2008; Camp et al. 2017; Johnson et al. 2021). It is also possible these corals have a lower critical oxygen threshold than other more susceptible corals, or they may have naturally low respiration rates or have other metabolic or molecular mechanisms that limit oxidative stress (see Nelson and Altieri 2019), however further research is needed to investigate these hypotheses.

Bills Bay has previously experienced shifts in community composition due to the accumulation of trapped coral spawn and subsequent hypoxic conditions (Grubba and Carey 2000; Shedrawi et al. 2017). Coral spawning at Ningaloo Reef typically occurs 7–9 nights after a full moon during a neap ebb tide however this varies temporally (Gilmour et al. 2016). In March 1989, the spawning event occurred 7–9 days after the full moon during flood tides and combined with low swell conditions and north-west winds to result in a 3 km² stretch of stagnant putrid water that led to a widespread mortality event causing live coral cover to decline from ~50% to ~7% (Simpson et al. 1993; Newnham et al. 2020). Several deoxygenation events in Bills Bay have also been documented in 2002, 2005, 2008 and 2019 (Fig. 1b, Table S1); however, the impacts of these events appeared to be less severe and widespread than the 1989 event (Shedrawi et al. 2017). Following the 1989 anoxic event in Bills Bay, modeling studies demonstrated that the bay has distinctive local hydrodynamic conditions which culminate under certain conditions (i.e., onshore winds followed by calm conditions) in extended water residence times and a lack of lagoonal flushing (Shedrawi et al. 2017). An examination of coral survivorship after the 1989 hypoxic event demonstrated an interaction between water residence times and coral vulnerability (Simpson et al. 1993) whereby nearshore sites with longer residence times, experienced higher coral mortality than those further offshore (Shedrawi et al. 2017).

Here we show that the environmental conditions in 2022 largely mirrored the patterns reported in 1989 (Simpson et al. 1993). In 2022, spawning occurred 7 days after the full moon during a flood tide, increasing water residence times and trapping spawn material in the southern end of Bills Bay. A low-pressure system passed through the region from the 31st March to 1st April which exacerbated the calm conditions. Our results indicate that at least 1 km² of nearshore shallow, coral-dominated habitat in Bills Bay was impacted, and corals growing in both nearshore, inner-mid and mid-reef habitats succumbed to the mass mortality event. Corals in the family Acroporidae were most affected by the deoxygenation event in 1989 and experienced complete mortality at sites in both the middle and inner zones (Shedrawi et al. 2017). Acroporidae were once again completely decimated from the nearshore and mid-reef zones in 2022. It is postulated that the spatial extent of coral mortality (and the extent of fish mortality) was smaller in 2022 than in 1989, however, the limited spatial extent of quantitative coral (and fish) data from 2022 precludes empirically testing this.

Approximately two decades after the 1989 event, despite multiple other disturbances, the coral community in Bills Bay had fully recovered both in terms of the level of coral cover and the diversity of coral genera present, although shifts in community composition had occurred including the increased cover of *Echinopora* spp. in the inner part of the

Bay. Bills Bay has experienced a variety of disturbances since the 1980's (Fig. 1b) and the coral reef community has shown a remarkable propensity to recover. This is likely due to the health of corals and marine life living on adjacent reefs including the reefs on the outer rim of Bills Bay, which based upon anecdotal observations, do not appear to have been impacted by the March 2022 deoxygenation event. While not surveyed in the current study, these nearby coral communities in the outer sections of Bills Bay (i.e., > 1 km from shore) and, those to the north of Coral Bay will likely promote recovery of the heavily impacted nearshore and middle sections of Bills Bay via local coral larval supply, provided that the substrate and local conditions are conducive for recruitment and survival.

Reefs to the south of Bills Bay, such as Paradise Bay and Five Fingers Reef, also appear to have largely escaped the mortality event and are ideally placed to supply larvae to Bills Bay via the northerly flowing longshore coastal current, however further testing of this hypothesis using coupled population genetic and oceanographic modeling approaches is warranted (see Galindo et al. 2006; Krueck et al. 2020). The local seascape features which culminated in increased WRT in Bills Bay indicate that this location functions as a larval sink; and while, this can be detrimental under certain conditions, this may also help to enhance the rate of community recovery in the absence of further large-scale disturbances such as cyclones, anomalous thermal stress, predator/disease outbreaks or additional deoxygenation events. Overall, this study adds to a growing body of evidence suggesting hypoxia can be a major threat to the diversity, productivity and functionality of coral reefs. Monitoring dissolved oxygen levels in routine monitoring programs is recommended, and further research into the differential responses of corals to oxygen stress is warranted.

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Author contributions ZR conceived the project, supervised students in the field, co-designed the data analysis, undertook descriptive data analyses, wrote the manuscript, and completed the revisions. LH participated in 2022 data collection, conducted data analyses, and wrote the first draft of the manuscript. CR liaised with Ningaloo Reef DBCA staff, collated temperature and DBCA rapid visual assessment

information and edited the original manuscript. SP and YL participated in 2018 fieldwork and edited the manuscript. TM, AT, EB, VM participated in 2022 data collection and assisted with preparing the disturbance timeline. JM, PD participated in 2018 data collection. BS coordinated the ECEV3001 Unit and co-designed the data analysis. All authors approved the version to be published.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

Ethical approval No ethics approvals were required for this study as no samples were collected. Permits to undertake the non-destructive visual monitoring study were obtained from DBCA.

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