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Marine heatwave-driven mortality of bleached colonies of the massive coral *Goniopora* is exacerbated by a black band disease epizootic

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During the recent fourth global mass coral bleaching event, the Great Barrier Reef (GBR) experienced the highest temperatures for centuries and widespread bleaching. For massive, long-lived *Goniopora*, bleaching coincided with a black band disease (BBD) epizootic at One Tree Reef (OTR). This necrotic wasting disease, typically rare on the GBR, appeared along the edge of bleached polyps. We tracked 112 *Goniopora* colonies from bleaching onset through winter to summer in seven surveys. In February 2024, 75% of colonies were bleached, and 4% of these had BBD. By April, 61% of bleached colonies had an aggressive black band invading the tissue. For heat stressed and diseased *Goniopora*, winter cooling did not promote substantial recovery with 75% of tagged colonies dead by October. Only 24% of tagged colonies recovered, albeit with partial mortality. Population surveys at two sites showed a similar bleaching-disease pattern with high mortality by October (46% and 66%). Repeated health assessments revealed a link between bleaching, disease and heat in the demise of these normally resilient massive colonies, many of which have been lost at OTR. Understanding the connection between the 'evil twins' of bleaching and disease is important as corals are faced with unprecedented thermal anomalies.

1. Introduction

With increased occurrence of intense and prolonged marine thermal anomalies, as seen in the 2023/2024 fourth global coral bleaching event [1], prospects for the world's coral reefs in a rapidly changing climate are of great concern. The prediction of near-annual mass coral bleaching events made 20 years ago based on climate trajectories [2] is being realized. For the Great Barrier Reef (GBR), bleaching events are now nearly biannual [3,4]. Coral reef ecosystems are foundational in providing key services for a vast diversity of dependent species and for humanity in providing essential food security, prosperity and shoreline protection, with deleterious impacts of climate change for reef-reliant communities around the globe [5]. The existence of coral reefs in the face of Anthropocene heatwaves and how they are transitioning to different species assemblages or states is important to understand because global warming is set for some time to come [6–9]. Heat stress induces coral bleaching as the relationship between corals and the endosymbiotic dinoflagellates that they depend on for nutrition breaks down. In heatwave conditions, mass bleaching can occur at the seascape scale

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as observed in aerial surveys of the GBR [10,11]. Increased temperature is also linked to outbreaks of coral disease [12–14]. Other adverse environmental stressors especially high light levels and decreased salinity also cause bleaching [13,14].

The relationships between heat-driven coral bleaching and disease and their co-occurrence are variable. In some cases, increased temperature caused disease outbreaks, but bleaching was not observed (e.g. *Montipora*, *Diploria*) [15,16]. There are also reports where disease followed bleaching (e.g. *Montastrea*, *Agaricia*) [17,18] while in other cases disease appeared first and bleaching followed (e.g. *Montipora*) [19]. Finally, there are instances where disease and bleaching coincided [20,21] (e.g. *Montastrea*, *Acropora*). Bleached corals are in a weakened state, which increases their susceptibility to disease, and in parallel, warm conditions can increase pathogen virulence [22,23]. Corals can recover from bleaching when water temperature returns to normal but remain susceptible to disease due to their compromised health state [18]. While the relationship between coral bleaching and disease is not clear, the strong relationship between heat stress and disease outbreaks emphasizes the increased risk of coral disease due to climate change [23].

A study that followed tagged *Acropora* colonies showed that disease, in this case white syndrome, exacerbated the mortality of bleached corals [21]. Despite decreasing thermal stress as the water cooled, the health of *Acropora* continued to decline as the colonies infected by the disease succumbed to whole colony mortality [21]. Documenting the interactive effects of bleaching and disease at the population and colony level through *in situ* monitoring provides important insights into the drivers of coral mortality during and following heat stress bleaching events and whether disease is a contributing factor [17,21]. Coral bleaching and coral disease are substantial threats to coral reefs, and links between these stressors are emerging [17,18,20]. Understanding the connections between these 'evil twins' is an imperative as corals are faced with increasing anomalous high temperatures.

During the 2024 El Niño, the GBR experienced the highest sea temperatures on record [24]. These conditions triggered mass coral bleaching across the GBR. This was the seventh such event in this reef system since 1998 and the fifth since 2016 [3,25]. In a review of the history of thermal bleaching on the GBR [26], the first observational record of heatwave bleaching on the GBR appears to be from 1929 [27]. In 2024, the southern GBR had severe and widespread bleaching at levels not previously recorded in the region. At One Tree Reef (OTR) in the Capricorn Bunker Group (Southern GBR) (figure 1), a reef system that has been protected from extractive fishing and tourism for 50 years, diverse coral genera bleached [4]. This bleaching-mortality event impacted many species including heat-sensitive (e.g. *Acropora*, *Isopora*) and heat-tolerant (e.g. *Porites*) coral genera. Being 70 km offshore protects OTR from coastal pollution and development, but not the impact of ocean heating. The bleaching alert level remained high at OTR for months with the degree heating week (DHW) metric based on decades of *in situ* temperature records at the level of the corals peaking at 14.61°C-weeks [4]. This is well beyond the maximum alert levels linked with coral mortality [28].

A tagging study at OTR that followed the fate of corals (bleached and unbleached) over the first 4 months of the 2024 heatwave tracked the initial response of twelve coral genera [4]. This study documented rapid whole colony mortality of *Acropora,* which started to degenerate into rubble as well as mortality of other genera [4]. While bleaching and mortality of heat-sensitive corals such as *Acropora* were expected, mortality of massive *Goniopora*, a generally stress-tolerant coral [29–32], was not. In addition to bleaching, the *Goniopora* colonies became infected with black band disease (BBD), which contributed to poor health [4]. *Goniopora* are long-lived corals that commonly occur in lagoons and turbid reefs [29–31].

BBD is particularly well known in the Caribbean, where it was first reported [33–35]. The appearance of BBD in *Goniopora* at OTR was not expected as decades of studies indicate a very low occurrence of this disease on the GBR [36,37]. This disease is very rare in the southern GBR [38]. There is just one previous report of BBD on a single *Goniopora* colony in a GBR-wide review [36]. BBD is a serious infection of corals caused by a microbial consortium dominated by cyanobacteria that drives polyp necrosis as the band invades and destroys coral tissue [39].

As it appeared that an epizootic in *Goniopora* was emerging at OTR, we followed the fate of tagged *Goniopora* colonies over one year in seven repeat checks (February 2024–2025). We quantified the prevalence of bleaching and BBD in these colonies through the heatwave and winter cooling following their health and the progression of BBD as it drove a wave of tissue necrosis and decimation of this coral. Population surveys of *Goniopora* across two sites were also undertaken to score colony health in May and October. In parallel, we searched the reef for the presence of this disease in other coral genera over the year.

Outbreak of disease together with bleaching was expected to have compounding negative impacts in increasing mortality risk in *Goniopora*. On the other hand, as *Goniopora* is known to be a stress-tolerant coral, we expected to see some recovery of the bleached and infected colonies over time especially as the water cooled. As a BBD epizootic of *Goniopora* has not been seen before on the GBR, our aim was to use the event at OTR to provide insight with respect to the impact of this disease together with bleaching in driving mortality following the extreme heating that these corals experienced in the 2024 event [4].

2. Methods

(a) Location

OTR (23.51° S, 152.09° E) is a platform reef in the Capricorn Bunker Group, southern GBR (figure 1a). We investigated *Goniopora* colonies at two sites in the lagoon (2 m depth): the Gutter, a shallow channel that connects to the open ocean, and Shark Alley, a shallow bay that also connects to the open ocean (figure 1b). Temperatures at the level of the corals were determined from *in situ* temperature loggers (HOBO loggers ± 0.5°C) and the data were used to plot mean, maximum and minimum daily temperatures (electronic supplementary material, figure S1a–c; see [4] for DHW). The temperature data were used to characterize the marine heatwave conditions using *heatwaveR* [40–42] to determine heatwave descriptors (e.g. peak date, intensity, onset rate, category).

The *in situ* logger data, collected with varying periodicity (1–30 min^{-1}) over 25 years, were standardized to daily means. The data compilation comprised data between 6 October 1999 and 4 September 2024 (~25 years). Due to data gaps, there was a total

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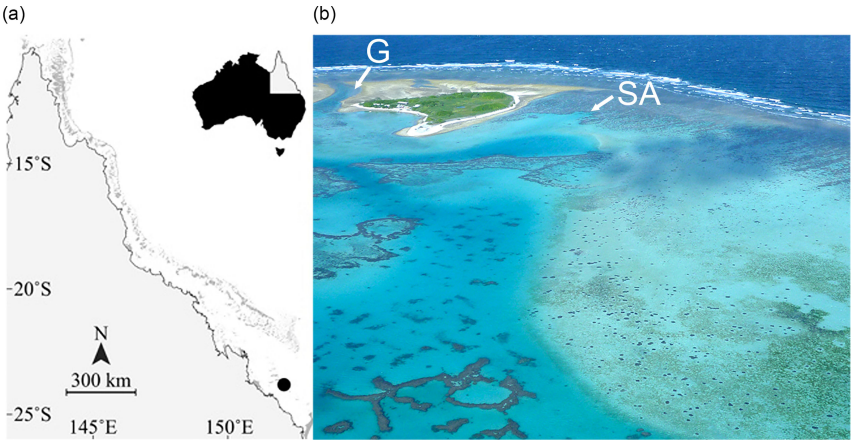


Figure 1. (a) Black circle in lower right shows the location of One Tree Island off the coast of Queensland, Australia. The inset in upper right indicates the main map location within Australia. (b) Photograph of One Tree Island and One Tree Reef with study locations indicated by arrows: Gutter (G) and Shark Alley (SA).

cumulative *in situ* data duration of ~9 years, below the recommended 30 years [41]. Due to this short record, we also used 30 years of satellite-derived data to complement our *in situ* data. Marine heatwave detection was focussed on data for the summer 2023/2024 during which the DHW was highest [4] and classified with respect to the four categories (I–IV) which are based on maximum intensity relative to the difference between the seasonal climatology and threshold temperature: I (moderate), II (strong), III (severe) and IV (extreme) (see [41]).

(b) Colony tracking

At seven timepoints from February 2024 at the start of the bleaching event to 1 year later, we followed the fate of individual colonies to quantify their bleaching status, the presence of BBD and the incidence of mortality and recovery. In seascape images taken along the edge of the reef (50 m distance) at the Gutter and Shark Alley, guided by markers along the lagoon floor and tags near the corals, we identified 112 *Goniopora* colonies (Gutter—109 colonies; Shark Alley—3 colonies). These corals were tracked in repeated health assessments over 12 months. In February 2024, the colonies were photographed with an Olympus Tough TG6 camera and were subsequently rephotographed six times, after 40 (April), 74 (May), 134 (July), 231 (October), 266 (November) and 361 (February 2025) days. Colony colour was checked against the Coral Watch coral health guide, which was in the photographs. Videos were also used to facilitate colony reidentification. Individual colonies in repeated photographs taken over time were categorized as (i) normal colour, (ii) bleached (pale, fluorescent or white), (iii) bleached with BBD, (iv) recovered from bleaching, (v) recovered from bleaching with BBD or (vi) dead. The category 'dead' were colonies that were 100% dead as indicated by the complete absence of living tissue. The category 'recovered' indicates colonies that had polyps that returned to their normal colour. In this category, we considered that the presence of living coral with normal colour to be recovered regardless of the extent of partial mortality (i.e. bare algal-covered skeleton that had died over the year). The percentage of tissue loss was estimated from images with a scale for measurement.

For colonies for which photographs were orientated to allow measurement of disease progression (n = 8), the rate at which BBD invaded the tissue between two time points (April to May, 34 days) was measured using ImageJ (NIH). Note this was a two-dimensional measure and so did not capture the distance with respect to the curvature of the coral. At the last time point (February 2025), surviving *Goniopora* colonies were examined at the interface between the live polyps and the denuded coral skeleton for evidence of regenerative growth of coral tissue over the skeleton.

(c) Population assessment

As it was clear by May that a disease outbreak was underway, we extended our observations to population surveys of *Goniopora* colonies at the Gutter and Shark Alley to assess the relationship between bleaching, BBD and mortality. In May and October, *Goniopora* colonies at the two sites were photographed as they were encountered in a swim along the reef edge. This involved two persons and took 30–40 min per time. The search area (determined using Google Maps) was 12 380 m^2 at the Gutter and 18 076 m^2 at Shark Alley. The photographs were taken away from the tagged coral area. Some of these photographs had more than one *Goniopora* colony, and all colonies in view were assessed. In total, 415 colonies were photographed with the coral health chart in view in May and 305 in October (electronic supplementary material, table S1). By October, algal overgrowth made it difficult to identify some *Goniopora* colonies. Photographs were checked to ensure that no colony was scored twice. Individual colonies in photographs taken in May and October were categorized as (i) normal colour, (ii) normal colour with BBD, (iii) bleached, (iv) bleached with BBD or (v) dead. Note we did not use the recovered category as these colonies were not individually tracked.

For the population data, we addressed the hypothesis that the probability of *Goniopora* colony mortality and health status (e.g. bleaching with or without BBD, or normal appearance) at both sites varied significantly with month (May, October). It was expected that accumulated stress over time would result in higher mortality in the October sample. Therefore, our model for site was no difference at either time point and between time points higher mortality at time two.

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(d) Data analysis

All statistical analyses were conducted using R (v. 4.0.5) [40]. Data on the condition (six categories above) of the 112 *Goniopora* colonies from seven surveys were used to construct a timeline figure of change. Kaplan–Meier survival probability analysis was used to show the trajectory of mortality with 95% CIs [43] using the survival and *survminer* packages [44,45]. The cumulative incidence of BBD (proportion of colonies that developed BBD over time) was also determined.

For the population data, the proportion probability of colonies in the different categories were analysed as a binary (i) dead (1 = perished, 0 = alive), (ii) bleached with BBD (1 = bleached with BBD, 0 = all other alive colonies+dead colonies), (iii) bleached no BBD (1 = bleached no BBD, 0 = all other alive colonies + dead colonies), (iv) normal colour with BBD (1 = normal colour with BBD, 0 = all other alive colonies+dead), or (v) normal colour no BBD (1 = normal colour no BBD, 0 = all other alive colonies+dead colonies). The effect of time (May, October) and site (Shark Alley, Gutter) on these proportional data was modelled as fixed effects with binomial generalized linear models (GLMs) with a logit link function [46] and, where appropriate, bias-reduction (brglmFit, *brglm2* package) to avoid data separation [47]. All combinations of fixed effects and interactions were considered. Model assumptions were assessed with inspection of diagnostic plots using the DHARMa [48] and ggplot2 packages. Interaction terms with $p > 0.25$ were dropped. Wald chi-squared tests (Type II) were used to assess model fit and the significance of fixed effects (*car* package [49]). Tukey's HSD adjusted p-values ($\alpha < 0.05$) were used to identify significant pairwise differences (*emmeans* package [50]).

3. Results

(a) One Tree Lagoon temperature

The mean, minimum and maximum daily temperatures for OTR from December 2023 to February 2025 are shown in electronic supplementary material (electronic supplementary material, figure S1a). The number of days that the mean and maximum daily temperatures were above 28°C, 29°C and 30°C shows the long duration of the warm temperatures in 2024 (electronic supplementary material, figure S1b, c). During the bleaching period, the mean daily temperature was ≥28°C for 74 days consecutively between 28 December 2023 and 11 March 2024 and was ≥29°C for 21 days between 17 January and 7 February 2024. The maximum temperatures recorded in 2024 were 34–35°C.

During the 2023/2024 summer, the main and longest heatwave at One Tree Island occurred from 15 December 2023 to 8 March 2024 and was Category IV (Extreme). This peaked on 29 January 2024 with mean and maximum intensities of 1.4°C and 3.0°C, a cumulative intensity of 119.4°C-days, and onset and decline rates of 0.1°C day^{-1}. Satellite-derived data identified a comparable major event from 29 December 2023 to 10 March 2024 (Category II, Strong) peaking on 29 January 2024 with mean and maximum intensities of 1.3°C and 1.9°C, a cumulative intensity of 93.9°C-days, and onset and decline rates of 0.03°C day^{-1}.

(b) Colony tracking

Bleaching in *Goniopora* started in early February 2024 as indicated by the colonies becoming pale (figure 2a). As bleaching progressed, the colonies varied in colour from fluorescent pink, yellow or green to pale or white (figure 2a–g). In February, 75% of the *Goniopora* colonies were starting to bleach and 4% of these were infected by BBD (figure 3a; electronic supplementary material, table S2). Initially, this was seen as a black line at the edge of the bleached tissue (figure 2d,e). The disease was not present in healthy non-bleached colonies. By April, most colonies were bleached (75%) or dead (24%) (figure 3a; electronic supplementary material, table S2). Most of the bleached colonies (61%) had BBD. BBD caused polyp necrosis and progressed through the coral tissue leaving bare skeleton behind showing the large corallites of *Goniopora* (figure 2e).

The incidence of BBD increased at a steep rate between February and May plateauing by July onwards (figure 3a,b). The proportion of the colonies infected by BBD increased over time in parallel with mortality. Survival plummeted from July (figure 3b). By October, 75% of the *Goniopora* colonies were dead (figure 3a,b) as shown in images of the same colony in April, May and October (figure 4a–c). Across all the tagged corals that died (n = 84), 58% of these were impacted by both bleaching and BBD with the disease appearing after the onset of bleaching. Twenty-three colonies that returned to normal colour in February 2025 had partial mortality with an overall loss of polyp cover of 30%–90% (mean partial mortality ± s.e. = 63.91% ± 3.86). Four colonies were fully recovered (100% normal colour, no partial mortality) at the end of the study; two of these had been infected by BBD. Only one colony did not bleach or develop the disease.

(c) Disease progression

The disease was conspicuous in bleached colonies as an aggressive black band invading the tissue (figure 2f,g). Rapid development of the disease was evident with many corals having recently dead areas of exposed white skeleton and regions that had been dead for a longer time colonized by algae (figure 2d–g). A comparison of colonies photographed in April and May shows black band invasion contributing to the demise of the bleached *Goniopora* (figures 2f,g and 4a–c). Between April and May (34

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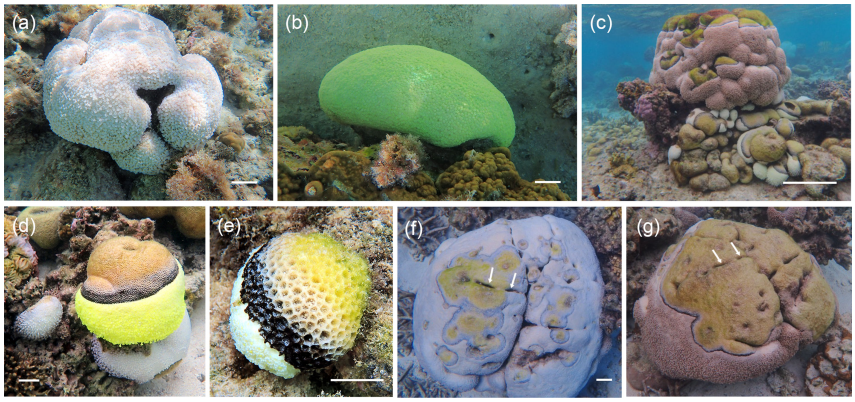


Figure 2. (a–d) Bleached *Goniopora* colonies exhibited a range of colours from pink and white to fluorescent yellow and green. (e) Black band disease forms a black line of invasive bacteria that causes polyp necrosis and colony mortality. Recently dead regions show bare skeleton, which will be colonized by algae. (f, g) Colony photographed in April (f) and May (g) showing progression of the disease. Note the arrows pointing to the same region of the coral in (f) and (g). Scales: (a, b, d) = 5 cm; (c) = 60 cm; (e) = 15 mm; (f, g) = 6 cm.

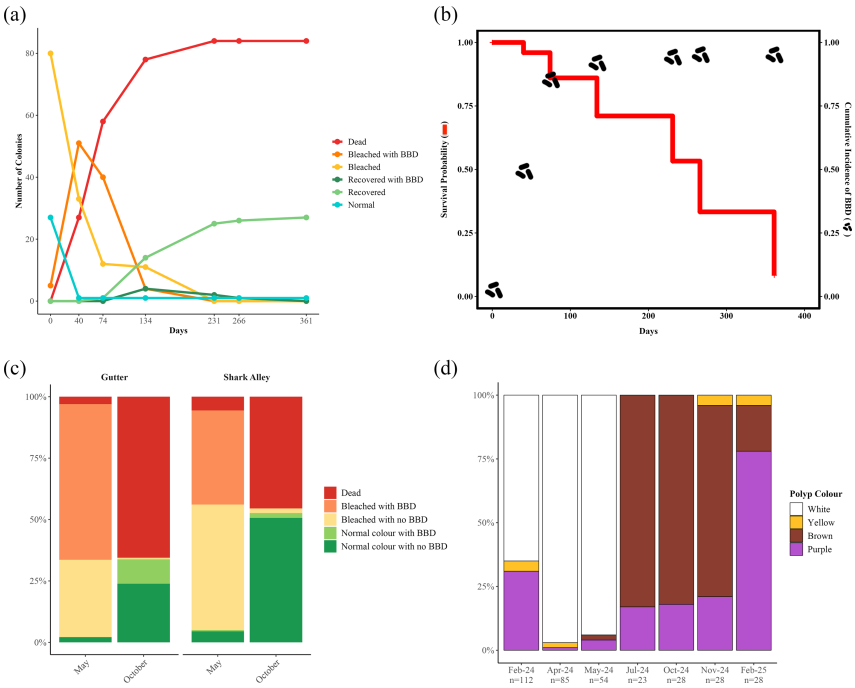


Figure 3. (a) The fate of tracked *Goniopora* colonies ($n = 112$) over seven health assessments over 1 year with the *x*-axis being linear over 361 days. (b) The probability of survival of the tracked colonies and the cumulative incidence of black band disease (BBD). (c) The proportion of colonies from the population surveys at Gutter and Shark Alley that were dead, bleached with and without BBD, and those that had normal coloured polyps with and without BBD in May and October (see electronic supplementary material, table S1 for sample sizes). (d) Polyp colour of tracked *Goniopora* colonies over seven time points from bleaching onset to the following year.

days), the mean rate of progression of disease invasion into the healthy tissue was 1.94 mm day^{-1} (s.e. = 0.362 mm, $n = 8$), and the mean distance moved over the 34 days was 66.11 mm (s.e. = 12.3, $n = 8$).

(d) Population assessment

In May, most of the *Goniopora* colonies in Shark Alley and the Gutter were bleached, 89.4% (n = 180) and 94.9% (n = 235), respectively (figure 3c; electronic supplementary material, table S2). Of the bleached colonies, BBD occurred in 42.8% and 66.8% of the colonies, respectively (figure 3c). Dead colonies were also present at 5.6% and 3%, respectively. By October, there was widespread colony mortality at Shark Alley (45.5%, n = 154) and the Gutter (65.6%, n = 151) (figure 3c; electronic supplementary material, table S2). Some corals were healthy (figure 3c).

Bleaching, disease and mortality impacted some of the largest *Goniopora* colonies (figure 4e,f). A comparison of the seascape in the Gutter area of the population survey pre-bleaching (2022) illustrates the loss of colonies (figure 5).

Analyses of the population data are presented in the electronic supplementary material (electronic supplementary material, table S3). The probability of coral death was significantly affected by both site (GLM: Wald $\chi^2 = 7.13$, df = 1, $p = 0.008$) and month (GLM: Wald $\chi^2 = 267.49$, df = 1, $p < 0.001$) as single factors and by their interaction (GLM: Wald $\chi^2 = 7.15$, df = 1, $p = 0.008$).

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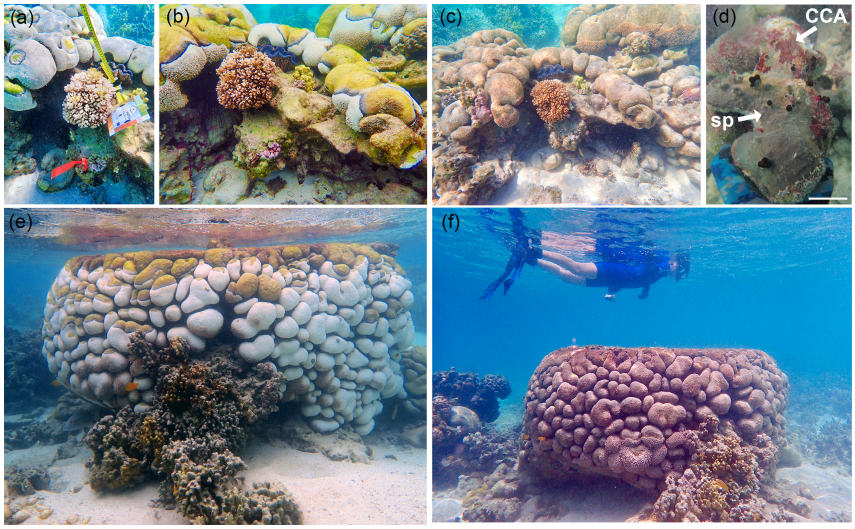


Figure 4. (a–c) Demise of a large *Goniopora* colony from the bleached early disease state in April (a) to invasion of BBD (b) and total colony mortality by October (c). Note tape for scale. (d) One year after the onset of bleaching dead *Goniopora* colony skeletons begin to detach from the reef as they were colonized by sponges (sp), crustose coralline algae (CCA) and other bioeroding organisms (scale = 3 cm). (e, f) Large *Goniopora* colony bleached in April 2024 (e) was largely dead in February 2025 (f). Note swimmer for scale.

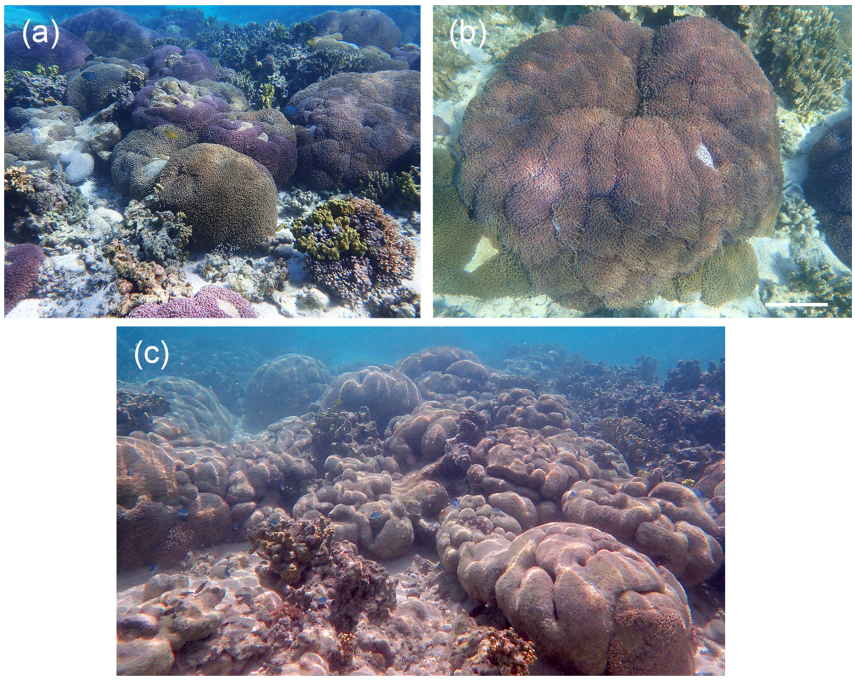


Figure 5. Seascape images of the survey site in the Gutter. (a, b) in 2022 prior to the bleaching event showing *Goniopora* colonies in close proximity (a) and the characteristic long polyps of this coral (b). (c) In February 2025, the colonies were largely dead.

Estimated marginal means indicated the interaction was driven by relatively greater increase in mortality from May to October at the Gutter site compared to Shark Alley.

Site and month influenced the probability of colonies being bleached with BBD (GLM: site: Wald $\chi^2 = 24.92$, df = 1, $p < 0.001$; GLM: month: Wald $\chi^2 = 305.82$, df = 1, $p < 0.001$), with a higher likelihood in the Gutter compared to Shark Alley and in May compared to October. Site and month also influenced the probability of colonies that were bleached without BBD (GLM: site: Wald $\chi^2 = 17.33$, df = 1, $p < 0.001$; month: Wald $\chi^2 = 195.10$, df = 1, $p < 0.001$). Colonies were less likely to be bleached without BBD in the Gutter than Shark Alley, and in October compared to May.

The probability of colonies with BBD that retained normal coloured polyps was significantly influenced by both site (GLM: Wald $\chi^2 = 7.23$, df = 1, $p = 0.007$) and month (GLM: Wald $\chi^2 = 26.57$, df = 1, $p < 0.001$). The frequency of colonies in this category was higher in the Gutter than Shark Alley and in October compared to May. Site and month also affected the probability of colonies with normal coloured polyps without BBD (GLM: site: Wald $\chi^2 = 25.17$, df = 1, $p < 0.001$; month: Wald $\chi^2 = 148.75$, df = 1, $p < 0.001$). Colonies in this category were more likely in Shark Alley than the Gutter and in October compared to May.

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(e) Polyp colour, lack of regeneration and skeletal breakdown

In their normal healthy state, *Goniopora* colonies at OTR can be purple/lavender or a light brown/tan colour with the former being most common as shown in the pre-bleaching image taken in 2022 (figure 5a,b). In February 2024, most of the colonies that were not bleached were purple (figure 3d). By July, the brown colour dominated in the surviving corals and by February 2025 this changed to purple (figure 3d).

To determine the potential for colony regeneration, the interface between polyps that were normal in colour and dead skeleton was examined in 100+colonies in February 2025 a year after bleaching onset. There was no evidence of polyp regeneration along the edge of the bare skeleton. At this time, the skeletal mounds of some of the *Goniopora* colonies that had been dead since October began to become unstable as their structure began to be eroded and undermined by sponges and other fouling species (figure 4d). It became easy to dislodge boulder-sized portions of former live colonies.

4. Discussion

By following tagged corals at OTR, we show the compounding impact of disease in driving substantial loss of large structural corals. In-water tracking of coral colonies is time consuming and resource intensive but is required to understand the relationships between temperature, bleaching, disease and mortality. In Florida, a similar monitoring study observed the co-occurrence of bleaching and BBD from the start of bleaching in the massive coral *Colpophyllia natans*, which was also associated with high mortality [15]. However, the relationship between BBD and bleaching was not clear, highlighting the need for further investigation [15]. For *Acropora* impacted by the 2017 bleaching event on the GBR, white syndrome disease contributed to complete colony mortality [19]. While satellite-based measures can predict large-scale bleaching, local information is needed to understand how coral bleaching, disease epizootics as well as recovery unfold with respect to environmental variation within and across reefs [51–53].

The 2024 event is the first time in decades that OTR has had severe bleaching [4]. In the 2016 mass bleaching event on the GBR, the corals at OTR started to bleach but recovered within a month due to cooling winds from a tropical cyclone [10]. Despite the presence of many species undergoing heat stress bleaching at OTR in 2024 [4], only *Goniopora* was infected by BBD. The disease first appeared in a few colonies in February and by April, 61% of the bleached colonies had BBD. The disease spread quickly in an epizootic-like manner in bleached corals. Survival of the tracked *Goniopora* colonies plummeted from July and mortality was also high in the population-wide surveys. Repeat in-water assessment provided near real-time information on unfolding reef health and for *Goniopora* showed the link between bleaching, disease and intense heat as causative synergistic stressors in the demise of these massive slow-growing colonies. The disease only developed on bleached colonies. Such a destructive epizootic of BBD has not been previously reported for the GBR.

Mass bleaching mortality due to heat stress would not be expected in *Goniopora*, as this coral genus is known to be thermally tolerant [29,30]. *Goniopora* is generally a stress-resilient coral as evidenced by the large stands of this coral in marginal environments with high turbidly, sedimentation and freshwater input [31,32,54]. Rather than recovering from bleaching as the water cooled, as might be expected if temperature was the main stressor, survival plummeted. Clearly, BBD was a major driver of mortality as the aggressive black band invaded the tissue.

Surveys in the northern GBR have shown low background levels of BBD, infecting 1–2% of corals and these were mostly *Acropora* and *Montipora* [15,36,55]. BBD in *Montipora* was linked to increased light levels and temperature [15,56] but coincident bleaching was not observed. That the incidence of BBD is generally low on the GBR and has not been previously reported for the southern GBR [38], the question arises as to why this relatively rare coral disease appeared in the *Goniopora* colonies at OTR. No other coral genera that bleached in the 2024 event at OTR developed the disease. Detailed searches at nearby Heron Island Reef revealed only one case of BBD in the massive coral *Platygyra* (S. Kininmonth, personal communication, 2025). Globally, outbreaks of BBD have been reported from locations prone to anthropogenic disturbances such as from pollution and high nutrient levels [34,35,57]. With its offshore location, OTR is not impacted by such coastal stressors. Due to its ponded nature, the lagoon at OTR can have nutrient levels higher than that for the open ocean [58], but this would seem a marginal source of stress for *Goniopora* considering that this coral is most common on turbid inshore reefs [31].

As shown in the pre-bleaching images, *Goniopora* colonies occurred in close proximity. Observations of spatial clumping of BBD-infected corals within reefs suggest that the disease spreads in a density-dependent manner [36,56]. The clumped distribution of *Goniopora* would have facilitated local dispersal, rapid transmission and spread of BBD. The higher mortality in the Gutter than in Shark Alley (64% and 44%, respectively) in the population surveys may be due to the higher density of *Goniopora* in the Gutter or environmental differences [53]. Although specific transmission mechanisms are not fully understood, it is suggested that BBD spreads through waterborne particles and direct contact between colonies [55,59].

As a serious disease of corals, BBD is associated with rapid polyp necrosis, tissue loss and mortality [15,33,57]. The near-exponential increase in the incidence of BBD in *Goniopora* between February and May over 74 days attests to its virulence. This was followed by a rapid decrease in survival over the following 157 days to October. Total colony mortality occurred in 75% of the tracked colonies. Despite environmental cooling through autumn and winter, mortality continued. The progression (travel distance) of the wave of necrosis in *Goniopora* was 1.94 mm day^{-1}, similar to that reported for BBD in another massive coral, *Diploria strigosa* (1–3 mm day^{-1}) in the Caribbean [18], but slower than that 10 mm day^{-1} also seen in the Caribbean [34]. Other measures of BBD progression report surface area of tissue loss, such as that reported for *Montipora* (57 mm^2 day^{-1} in Hawai'i

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and 38-81 mm^2 day^{-1} in Indonesia) [57,60]. The bare mounds of the *Goniopora* at OTR are testament to the extent of tissue loss in surviving colonies, with a mean partial mortality of 64%. In contrast, most other massive corals such as *Porites* totally recovered from bleaching (M.B., personal observation, 2025). Regenerative growth of tissue over the denuded skeleton has been observed in *Porites* after thermal bleaching and partial colony mortality [61], but we did not see this in the surviving *Goniopora*.

The colour of the *Goniopora* polyps changed from the more common purple to brown over the course of the study. Coral–algal symbioses are dynamic, and this colour change may be due to a change in symbiont composition [62,63]. The change to the brown colour during the bleaching event may indicate a switch to a stress-tolerant symbiont and that reversion to their purple colour may indicate reacquisition of a stress-sensitive symbiont post-bleaching [62]. That these colour varieties may be associated with different symbionts warrants investigation. Shifting to more bleaching-resistant symbionts has been noted not to be stable over time [62].

There have been many studies of the vulnerability of different coral taxa to bleaching mortality in assessments of the 'winners and losers' of mass bleaching events and how coral community composition changes post-bleaching [6,64]. Susceptibility to bleaching varies across taxa, with fast-growing taxa that have complex colony morphologies (e.g. branching or tabular) usually being the most susceptible [6,64]. In general, corals in the families Pocilloporidae and Acroporidae are highly vulnerable to thermal stress, whereas slow-growing massive or encrusting coral taxa tend to bleach less [64]. This pattern was also seen in the 2024 event at OTR [4] except for the high mortality of *Goniopora*, a massive species of coral. Predictions as to the potential outcomes of thermal anomalies with respect to the coral community composition may differ if disease is a combined stressor [20,21]. For the OTR *Goniopora* populations, compounding impacts of bleaching, BBD and the hottest conditions on record have decimated this massive coral. These large structural corals that have survived for 100 s of years are being lost resulting in a potentially permanent change to the ecosystem, as noted for massive *Porities* colonies in mass bleaching events on the GBR [6].

As expected, the denuded surface skeleton of *Goniopora* quickly fouled with algae. In addition, the undersides of large boulder-sized portions of the colonies became colonized by sponges and other bioeroding organisms. It appears that processes that drive skeletal breakdown started soon after complete colony mortality. Portions of the former colony became unstable and started to detach by October. Loss of connection to the reef in *Goniopora* tracked from the outset of bleaching was surprisingly quick. One year post-bleaching, the skeletons of many former *Goniopora* colonies were barely identifiable due to algal overgrowth. It can take months to years for coral skeletons to erode, and this differs between species and location [65–67]. For *Acropora* that died in the 2024 event, large portions of skeleton detached from the colony and algal-covered fragments (rubble) gathered on the benthos [4]. The large boulder-sized portions of dead *Goniopora* would be prone to dislodgement in major storms such as tropical cyclones during which they can be propelled and smash into the reef causing great damage [see [68]. It will be important to determine how long denuded *Goniopora* skeleton remains attached to the reef framework as they form a pavement-like substrate that can be important for coral recruitment [67]. Coral mortality, detachment of skeleton and storms underly the reef-to-rubble phenomenon, a major driver of transformation to tropical ecosystem states that are difficult to recover from [69].

While coral communities that have been previously exposed to warm water have been shown to bleach less in successive bleaching events, a potential adaptive response [70], if other factors such as disease coincide with bleaching, this resilience may be challenged. Corals live in a multistressor world and disentangling the effects of thermally induced bleaching and disease outbreak is increasingly important as coral reefs are being faced with increasingly anomalous high temperatures. Our study was limited to a single reef system and a lagoon environment where sheltered areas can amplify local heating and so the application of our findings to other reefs is not known. It is clear however, as heatwaves become more intense and with longer duration, the incidence of disease in corals weakened by bleaching may increase [23]. While mass mortality of corals is most typically attributed to bleaching, for *Goniopora* tissue loss due to BBD appears to have been the major driver of mortality. Documenting the interactive effects of bleaching and disease at the colony level is important to understand the drivers of coral mortality during and following heatwaves.

The current trajectory of climate change is progressing too quickly for corals to adjust [9]. Coral reefs are in danger, with recurrent anomalous heatwaves and mass coral bleaching being the greatest threat to their survival. These highly significant and diverse ecosystems directly benefit more than a billion people globally providing livelihoods, food security and protection from storms and coastal erosion [5]. Future prospects for coral reefs are of great concern for communities worldwide. The mass mortality of corals on the GBR during the 2024 extreme heatwave [4,11] reinforces the need for urgent global action and for ambitious climate and reduced emissions targets.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data are in the electronic supplementary material or the Dryad Digital Repository [71].

Supplementary material is available online [72].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.B.: conceptualization, data curation, funding acquisition, investigation, project administration, supervision, writing—original draft, writing—review and editing; M.C.: formal analysis, investigation, methodology, writing—original draft, writing—review and editing; M.K.: data curation; S.A.F.: supervision, writing—review and editing; N.R.: formal analysis; A.W.: data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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