

RESEARCH ARTICLE

Bleaching, mortality and lengthy recovery on the coral reefs of Lord Howe Island. The 2019 marine heatwave suggests an uncertain future for high-latitude ecosystems

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Abstract

Oceanic thermal anomalies are increasing in both frequency and strength, causing detrimental impacts to coral reef communities. Water temperatures beyond the corals optimum threshold causing coral bleaching and mass mortality, impacting our global coral reef ecosystems, including marginal high-latitude reefs. Coral bleaching and mortality were observed at the southernmost coral reef, Lord Howe Island Marine Park, during the summer of 2019, coinciding with anomalously high sea surface temperatures across the reef system from January–April. Here we document the extent of coral impacts within the Lord Howe Island lagoonal reef and the recovery from bleaching eight-months later. Significant differences in bleaching prevalence were observed across the lagoonal coral reef, ranging from 16 to 83% across offshore and inshore reef regions and with variable onset timing. Coral mortality of up to 40% was recorded in the reef's most severely impacted near-shore area. The four most dominant species, *Stylophora pistillata*, *Pocillopora damicornis*, *Porites spp.* and *Seriatopora hystrix*, were the most susceptible to bleaching, with all coral colonies found either bleached or dead at the most affected inshore site during and following peak heat stress. Interestingly, during the eight-months following bleaching, there was no evidence of bleaching recovery (i.e., re-establishment of symbiosis) at the offshore lagoonal site. However, there was a significant increase in the abundance of healthy coral colonies at the inshore site, suggesting the recovery of the surviving bleached corals at this site. Importantly, we found no evidence for bleaching or mortality in the *Acropora spp.* and minimal bleaching and no mortality in *Isopora cuneata* during the study period, typically highly susceptible species. Given the isolation of high-latitude reefs such as Lord Howe Island, our results highlight the importance of understanding the impacts of bleaching, mortality and bleaching recovery on coral population structure and resilience of high-latitude coral reefs.

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Introduction

Coral reefs account for less than 1% of the total ocean benthos. Although these ecosystems make up a small proportion of ocean area, they afford habitat and protection for a quarter of all marine species [1]. They also provide numerous ecological goods and services, including food, coastal protection, income, recreational activities, and cultural and aesthetic values [2]. These ecosystems are predominantly located in tropical, shallow, warm waters, where conditions such as; temperature, light, salinity, aragonite saturation, and nutrients are optimal for coral growth [3]. Coral reef ecosystems are experiencing significant disturbances due to the increased frequency and severity of thermal anomalies [4, 5].

Corals exposed to increased water temperatures over an extended period of time cause coral bleaching. Coral bleaching is the breakdown of the partnership between the coral host and the symbiotic algae, Symbiodiniaceae [6], which provides most corals' energy requirements [7]. A decline in the symbiotic algae results in a reduction of pigmentation and, in extreme events, the expulsion of a significant amount of the symbiotic algae resulting in translucent coral tissue, giving the coral a white appearance because of the exposed white endoskeleton [8]. Bleached corals are vulnerable to mortality if energy requirements are not fulfilled either through heterotrophic means or by regaining symbionts [7]. Major coral reef systems have already felt mass mortalities from coral bleaching [9].

Coral reefs have been reported to display varying responses to thermal anomalies through acclimation and local reef dynamics [10–13]. Some sites have been resilient during thermal anomalies, whilst others are highly vulnerable to reported while changes in community composition [5, 14, 15]. There is increased concern for the future of coral reefs and whether these sites exhibiting resiliency to climate change can be identified as places of refuge [16, 17]. High-latitude reefs (reefs higher than 28 degrees north and 28 degrees south) have been identified as potential sources of refuge for corals since corals living in these locations are accustomed to being pushed to their geographical and physiological limits [16, 18–20]. Unlike their low-latitude coral reef counterparts, there is a lack of understanding of the outcomes and responses high-latitude reefs experience during thermal anomalies.

The sub-tropical reef lagoon of Lord Howe Island (LHI) Marine Park is a unique coral reef ecosystem located in the southwestern Pacific Ocean, more than 1,000 km south of the Great Barrier Reef. The island is home to the world's southernmost coral reef and hosts a diverse and abundant reef system of tropical and temperate species [21–25]. The coral reefs of this World Heritage-listed island group have been associated with high endemism and species richness, with many of the 86 described species of coral thought to be endemic [26] and approximately 4% of the 433 shore fish [24, 27] and 15% of the 305 marine algae also endemic.

Species extinctions, loss of habitat structure, ecosystem degradation, declines in coral cover and phase-shifts to algal-dominated systems are common features of coral reefs worldwide [14, 15, 28–30]. Yet high-latitude reefs, such as Lord Howe Island, have previously been hypothesised as refugia for corals in the coming decades [16, 18–20], with some studies suggesting marginal reefs may be protected from the most severe impacts of global warming due to their geographic location (though note the potential opposing effects of ocean acidification; [31]). However, these ecosystems previously thought to be protected from the impacts of climate change are experiencing rapid change [32–38], much like other coral reef ecosystems [6, 9, 28, 39, 40]. High-latitude coral reefs have also been exposed to severe and frequent bleaching events, impacting coral reefs worldwide [32, 37, 41–46].

The first record of bleaching on the reefs of Lord Howe Island was in 1998 [46], coinciding with the most severe global bleaching event at that time [6, 47–49]. Since then, anomalously high seawater temperatures associated with coral bleaching occurred in 2010 and 2011 [45,

[46]. In March 2010, up to 99% of Lord Howe Island's lagoonal corals experienced bleaching, and in deeper reef sites, 17% of corals bleached [45]. The 2011 bleaching event revealed reduced bleaching susceptibility for all coral taxa recorded compared to the 2010 bleaching [45]. The four most common genera *Pocillopora*, *Porites*, *Seriatopora* and *Stylophora*, had high bleaching susceptibility index (BSI) and were the most severely impacted by bleaching [45]. *Acropora* and *Isopora* were reported to have undergone mild bleaching in 2010 and 2011 [45]. The three branching morphology taxa most severely impacted by bleaching (*Seriatopora*, *Stylophora* and *Pocillopora*) also had the highest colony mortality. Coral cover declined by approximately 28% in the most inshore reef areas immediately following the 2010 bleaching event, with coral mortality as high as 69% [45]. Following the 2010/2011 bleaching events surviving plating *Acropora* colonies were outcompeted by ascidians and algae [45].

Severe bleaching and high mortality levels alter community composition, leading to changes in ecological function. Hard coral cover increased in the three years following the 2010/2011 events. However, this was coupled with a reduction in *Acropora* colonies, suggesting complex community-level changes on the Lord Howe Island lagoonal reef [45]. Further changes to coral community structure due to recent thermal anomalies have also been reported, as have changes to coral growth and disease resistance [34, 45, 46]. Taxon-specific annual linear coral growth declines of up to 30% were recorded following the 1998 and 2010/2011 thermal anomalies [34]. Two prominent coral species, *Acropora yongei* and *Pocillopora damicornis*, declined in average annual linear extensions of 15.9 mm and 5.4 mm, respectively. In contrast, no significant difference in linear extension was reported for *Porites* sp. and *Seriatopora hystrix* between 1994/1995 and 2010/2011 [34]. Four coral diseases (growth anomalies, white syndrome, skeletal eroding band and hypermycosis) have also been identified in the lagoon impacting six coral taxa [Moriarty per obs]. The high-latitude coral reefs of the world's southernmost reef system are not isolated from the effects of warming oceans and the impacts of heat stress, including bleaching, mortality, disease and reduction in growth experienced in this ecosystem.

Understanding the impact of increasingly severe and more frequent bleaching events across the biogeographic extent of coral reefs and the capacity for ecosystem recovery and resilience is imperative in determining the long-term sustainability of different reef ecosystems. In 1999, climate model predictions of coral bleaching indicated events would increase in frequency and intensity within the coming decades [6]. These predictions have since been realised regionally (e.g., the Caribbean in 2005; [50]) and globally (in 2010 and 2014–2016; [51–53]). Bleaching events are highly variable, and the magnitude in severity is often mediated by local environmental and physical parameters [5, 10, 13, 14, 54–56]. Including bleaching history, *in-situ* temperature regimes, water flow, nutrients, tropical cyclone-driven cooling, coral taxa, coral taxa morphology and coral taxa abundance [14, 51, 54, 57–63]. For example, coral taxon, tissue thickness and morphology type influenced which coral species had the capacity to be “winners and losers” from the 1998 bleaching event in Okinawa, Japan [14]. Interestingly, subsequent research [64] attributed (1) thermal tolerance of the locally abundant colonies, (2) remnant survivors that rapidly regrew, and (3) regionally abundant colonies characterised as long-term “winning” taxa within the reef ecosystem. “Winners and losers” on coral reefs under climate change reflect complex biophysical factors within each coral reef ecosystem.

Many of the tropical and temperate species of LHI are at their marginal limits [65]. Ongoing periods of increased sea temperatures beyond the thermal tolerance of the diverse community of tropical, temperate and endemic species are likely to lead to significant shifts in community composition and raise questions on the long-term resilience of the World Heritage-listed marine park ecosystem. Here we investigate the heat stress event in early 2019 and the associated coral bleaching on the high latitude reefs of Lord Howe Island Marine Park. We

quantify the extent of bleaching, mortality, and taxonomic variation within the lagoon reef system related to the 2019 bleaching event and the recovery of the reef eight months after bleaching occurred. In doing so, we aim to determine the short- and long-term impacts of heatwave events on the Lord Howe Island lagoon coral species.

Methods

Study sites and bleaching surveys

Lord Howe Island is a remnant volcano located 600 km northeast of Sydney, Australia (Fig 1A). The island has an extensive lagoon to the west with patchy reefs inside, surrounded by a fringing reef (Fig 1). The marine ecosystems are characterised as transitional regions with both sub-tropical and temperate flora and fauna. Coral cover around the island is not dissimilar to that seen in subtropical areas of the Great Barrier Reef [66]. Surveys were conducted within the Lord Howe Island Marine Park lagoonal coral reef system (under Marine Park permit number LHIMP/R/19005/11032019) at three sites: Coral Garden (31° 31'31.768"S159°

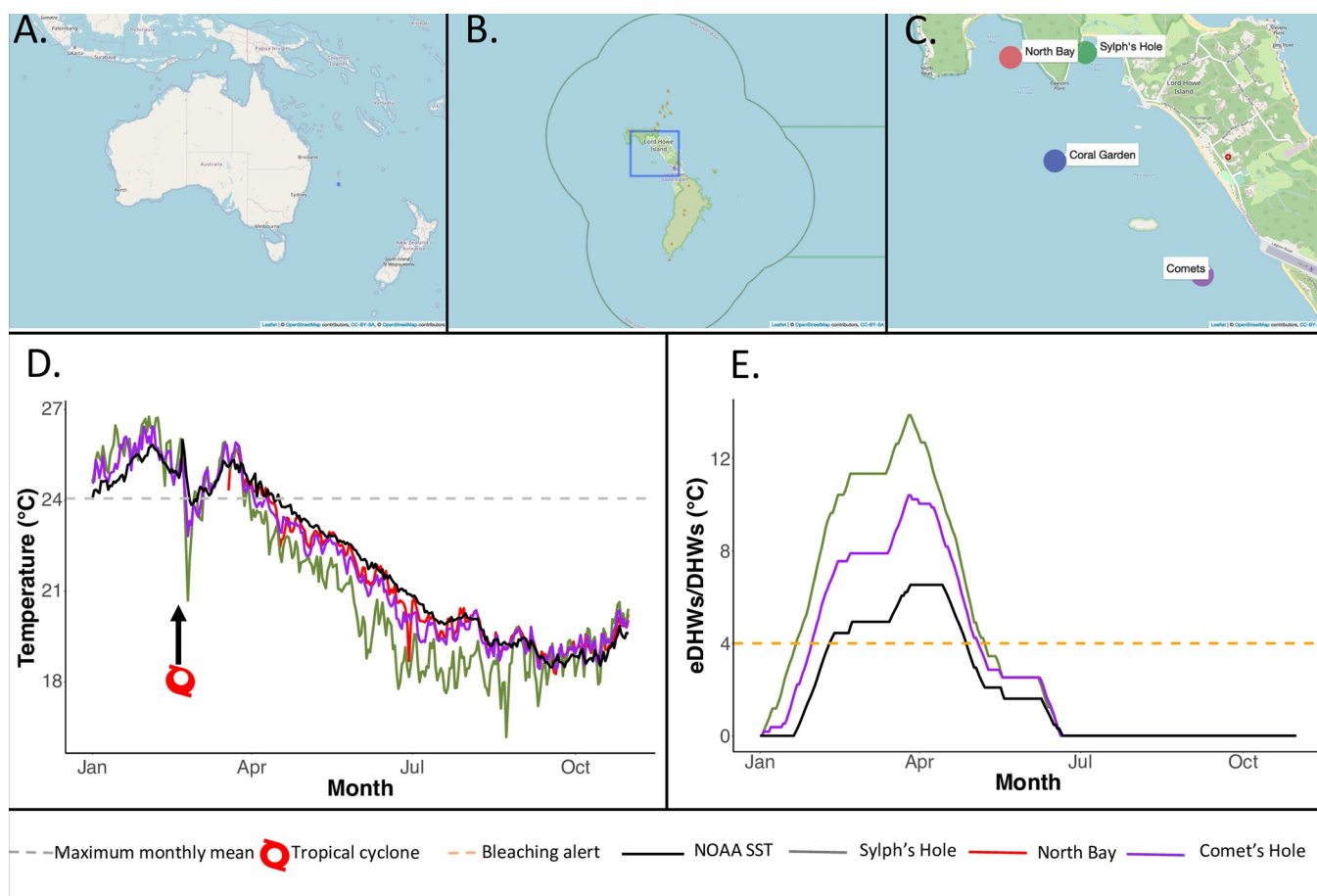


Fig 1. (A) Study site located off the east coast of Australia (B) at Lord Howe Island, (C) with sampling sites located in the north of the lagoon at Sylph's Hole (green), North Bay (red) and Coral Garden (blue); in situ temperature data were recorded at Sylph's Hole, North Bay and Comet's Hole (purple). (D) Satellite sea-surface temperature (SST) and in situ water temperature (IST) at LHI for January to October 2019 –SST (black) from NOAA CoralTemp for the 5-km satellite pixel; IST at Sylph's Hole (green), North Bay (red, from March) and Comet's Hole (purple). The local maximum of the month means SST (MMM; dashed grey) is 24.06°C. Tropical cyclone Oma (red cyclone symbol) passed in late-February 2019. (E) Heat stress from satellite (Degree Heating Week, DHW; black) and in situ (experimental DHW, eDHW) for Sylph's Hole (green) and Comet's Hole (purple), together with the NOAA bleaching alert level threshold (4°C-weeks; orange dashed). The base maps were made with R studio using the "Leaflet" package.

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3.3.106°E North Bay (31° 31'31.257"S 159° 22'2.801"E and Sylph's Hole (31° 31'31.232"S 159° 3.3.272'E (Fig 1A–1C). These three sites were chosen because of their high coral abundance and importance as high-usage snorkelling sites. The three sites vary in proximity to the reef edge and range in depth from 0.5–4 m (Table 1). We measured benthic composition, bleaching severity and coral health at all three study sites from March 14th–26th, April 26th to May 2nd and 16th–October 31st 2019, to evaluate impacts near the peak of stress and post-event recovery.

Snorkelling along three 20 m x 1 m belt transects surveyed each of the three sites. Transects were placed haphazardly at depths from 0.5 to 2 m, where coral communities were observed to be the most abundant, and laid parallel to shore with a minimum of 20 m between transects. All corals within each of the 20 m² belt transects were recorded to species level where possible and assigned to one of the following health categories (S1 Fig) related to coral bleaching severity;

- Healthy 100% of coral tissues look visibly healthy with normal pigmentation. (no signs of bleaching or tissue paling and partial mortality),
- bleached (including 100% bleached, pale, fluorescent, partially bleached, partially bleached with partial mortality),
- recently dead (100% dead, white skeleton, minimal algal growth)

Coral cover and benthic composition were estimated using photo quadrat point count methods. On each belt transect, three 1 m² quadrats were photographed (Nikon Coolpix W300), and images were uploaded to the web-based annotation program CoralNet (coralnet.ucsd.edu) and overlaid with 64 fixed points that were analysed to a benthic group and genus/species level for coral (Table 2).

Temperature data

In situ water temperature (IST) was recorded using HOBO water temperature Pro V2 (U22-001). Loggers were located at North Bay, Sylph's Hole and nearby Comet's Hole (Fig 1C), recording every 30 minutes during January–November 2019 at Comet's Hole and Sylph's Hole and March 18th–November 2019 for North Bay. Satellite sea surface temperature (SST) from NOAA Coral Reef Watch (CRW; CoralTemp, [67]) were extracted for the 0.05° (~5 km) pixel containing the study sites for January–November 2019. Heat stress was determined using the CRW local Maximum of the Monthly Mean (MMM) climatology, 24.06°C. From the satellite data, this followed CRW's standard Degree Heating Weeks (DHW) algorithm (Liu et al. 2014); using IST, a heat stress index was generated for each site (experimental DHW, eDHW; [68]).

Statistical analysis

All statistical analysis was carried out in R version 3.6.2. The benthic composition from the photo quadrats converted the data into counts for each respective benthic category (Table 2).

Table 1. Lord Howe Island site parameters.

Site	Depth (m)	Reef type	Protection zoning	Approximate distance from reef edge (m)	Sheltered or exposed
Sylph's Hole	0.5–3.5	Inshore reef	Sanctuary Zone	1,100	Sheltered
North Bay	0.5–2.5	Patchy reef Offshore	Sanctuary Zone	400	Sheltered
Coral Garden	0.5–3.0	Reef flat Offshore	Habitat Protection Zone	100	Exposed
Comet's Hole	0.5–6.0	Inshore reef	Sanctuary Zone	1,000	Sheltered

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Table 2. Categories used during benthic community structure analysis.

Benthic group	Taxon code	Species description	Benthic group	Taxon code	Species description
Stony coral	Acr_arb	<i>Acropora</i> arborescent	Dead stony coral	D_coral	Dead coral
	Acr_bra	<i>Acropora</i> branching	Soft coral	Soft	Soft coral
	Acr_dig	<i>Acropora</i> digitate	Other invertebrates	Sponge	Sponge
	Arc_tab	<i>Acropora</i> tabular	Algae	CCA	Crustose coralline algae
	Cypha	<i>Cyphastrea</i> sp.		Macro	Macro algae
	Homo	<i>Homophyllia</i> sp.		DeadAlg	Recently dead coral with algae
	Isopora	<i>Isopora</i> cuneata	Seagrass	Seagrass	Seagrass
	Para_austr	<i>Paragoniastrea australis</i>	Abiotic	Silt	Silt
	PocDam	<i>Pocillopora damicornis</i>		Sand	Sand
	Porites	<i>Porites</i> sp.		Rock	Rock
	Seriatop	<i>Seriatopora hystrix</i>	Other	Ascidian	Ascidian
	StPis	<i>Stylophora pistillata</i>			

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The counts from each benthic category were compared between sites and months using generalised linear mixed-effects models (GLMM) in R using the package “glmmTMB” v1.0.1. Once the model was fitted, the emmeans 1.7.1–1 package was used to test benthic composition interactions within sites between months and between sites within months. Transect and quadrat were classified as random and site and month as fixed effects. To compare how similar or dissimilar sites, months, and taxa responded to the bleaching event, a permutational multivariate analysis of variance (PERMANOVA) followed by nMDS plots were made in the R package vegan 2.5–6 and the adonis function.

The belt transect data comparing bleaching severity were also analysed using generalised linear mixed-effects models (GLMM) in R. To check for the best fit, the DHARMA residuals were plotted. To compare bleaching categories, the emmeans 1.7.1–1 package was used to test interactions within sites between months and between sites within months; and within bleaching categories for coral taxa within sites within months and between sites within months. Site and month were fixed variables, and transect was used as a random effect. Poisson and binomial distributions were tested, and the best fitting was selected. Residual plots were visually inspected for appropriate fit regarding dependency structure and deviations from homoscedasticity or normality. P-values were calculated by likelihood-ratio tests and were considered significant when $p \leq 0.05$.

Results

Water temperatures

In January 2019, temperatures within the coral reef lagoon of Lord Howe Island Marine Park exceeded the MMM (24.06°C), as measured by both satellite and *in situ* data loggers (Fig 1D). SST and IST rapidly declined from February 23rd to March 3rd due to cyclone Oma, after which temperature rose above 24.06°C. *In-situ* temperatures were found to have higher maximum and lower minimum temperatures than SST from January to October 2019. The maximum daily-average IST of 26.77°C was recorded at Sylph’s Hole peaking on February 2nd. Accumulated heat stress from satellite (DHW) and *in-situ* loggers (eDHW) exceeded 4°C weeks, the level of stress widely associated with coral bleaching (Fig 1E). Satellite DHW peaked at 6°C-weeks in late March, while the highest eDHW was at Sylph’s Hole, reaching 13.5°C-weeks also in late March.

Lagoonal benthic composition and coral diversity

Each of the three sites reported different dominating benthic compositions. Sylph's Hole and Coral Gardens was dominated by algae (turf and macro) and North Bay by abiotic (Fig 2A). Benthic surveys (photo quadrat data) revealed differences in benthic composition between lagoonal reef sites and between surveys (chi-squared test, $p < 2.0 \times 10^{-6}$, $\chi^2 = 45.2$, d.f. = 10) (Fig 2A). At the beginning of the survey period in March, total coral cover across all sites was $29 \pm 4\%$, which declined to $18 \pm 4\%$ in October (Fig 2A). A significant increase in dead hard coral cover was recorded at Sylph's Hole from March and ($4 \pm 2\%$) May ($4\% \pm 2\%$) to October 2019 ($22\% \pm 5\%$; GLM, $p = 0.0227$ and $p = 0.0118$, respectively; Fig 2A). Coral Gardens significantly increased in algae benthic composition from March ($18 \pm 9\%$) to October ($42 \pm 9\%$, GLM, $p = 0.0150$). No other significant differences in benthic composition were recorded within sites over time. NMDS analysis of benthic composition structure supported the distinction of sites due to their respective benthic composition (Fig 2B).

In terms of coral taxonomic diversity, *Stylophora pistillata*, *Seriatopora hystrix*, *Porites* sp., *Pocillopora damicornis*, and *Isopora cuneata* were the most abundant corals across all sites and survey periods, with other species contributing no more than $12 \pm 6\%$ of the relative abundance (Fig 2C and S1 Table). The relative abundance of coral taxa in the LHI lagoon sites did not change with time during the study (GLM: $p = > 0.05$). Coral taxa relative abundance between sites was significantly different (GLM: $p = < 0.05$). *S. pistillata* had a higher relative abundance of colonies at Sylph's Hole than at North Bay (GLM: $p = 0.015$). *S. hystrix* relative abundance was significantly lower at Coral Garden than at Sylph's Hole (GLM: $p = 0.0095$) and North Bay (GLM: $p = 0.0019$). *Porites* spp was significantly lower at Coral Garden compared to Sylph's hole (GLM: $p = < 0.0001$) and North Bay (GLM: $p = 0.0002$). No difference in relative abundance was found for *P. damicornis*, *I. cuneata* and *Acropora* spp. across the three sites ($p = > 0.05$). The abundance of other coral taxa was significantly greater at North Bay than at Sylph's Hole (GLM: $p = 0.05$), and significant difference in other coral abundance at Coral Garden and North Bay and Sylph's Hole. Significant changes in coral taxa relative abundance within each site over the eight months was only found for *S. pistillata* at Sylph's Hole between March ($27 \pm 2\%$) and October ($13 \pm 4\%$) (GLM: $p = 0.0117$, Fig 2C) and North Bay's *S. hystrix* colonies from March ($16 \pm 7\%$) to April/May ($30 \pm 4\%$) (GLM: $p = 0.048$, Fig 2C).

Hard coral community bleaching responses. A total of 2,102 observations of coral colonies were undertaken across all three sites during March, April/May and October 2019. During the three survey periods, healthy coral colonies were most prevalent at Coral Garden ($51 \pm 13\%$ to $83 \pm 5\%$), and North Bay ($46 \pm 6\%$ to $62 \pm 2\%$) from March to October (Fig 3A), whilst Sylph's Hole consistently had the least amount of healthy coral colonies ($8 \pm 1\%$ to $24 \pm 3\%$) between sites (GLM; $p = < 0.05$) and for each survey time (GLM; $p = < 0.05$) (Fig 3A). There was a significant difference in the abundance of healthy coral colonies by site (chi-squared test, $p = 2.2 \times 10^{-16}$, $\chi^2 = 111.2562$, d.f. = 2). This difference is clearly seen between Sylph's Hole and North Bay (GLM; $p = < 0.0001$) and Sylph's Hole and Coral Garden (GLM; $p = < 0.0001$). During the eight-month bleaching monitoring, no recovery was evident at North Bay and Coral Garden, with no significant increase in the abundance of healthy coral colonies over the 8-month monitoring period (Fig 3A). Healthy coral colonies at Sylph's Hole did not change abundance between March ($8 \pm 1\%$) and April/May ($8 \pm 1\%$). However, healthy coral abundance increased three-fold to $24 \pm 3\%$ in October (March GLM; $p = 0.0053$ and April/May GLM; $p = 0.0054$); however, Sylph's Hole percentage of healthy coral colonies in October was still significantly lower than North Bay ($62 \pm 2\%$ GLM; $p = 0.0024$) and Coral Garden ($51 \pm 13\%$, GLM; $p = 0.0233$) (Fig 3A).

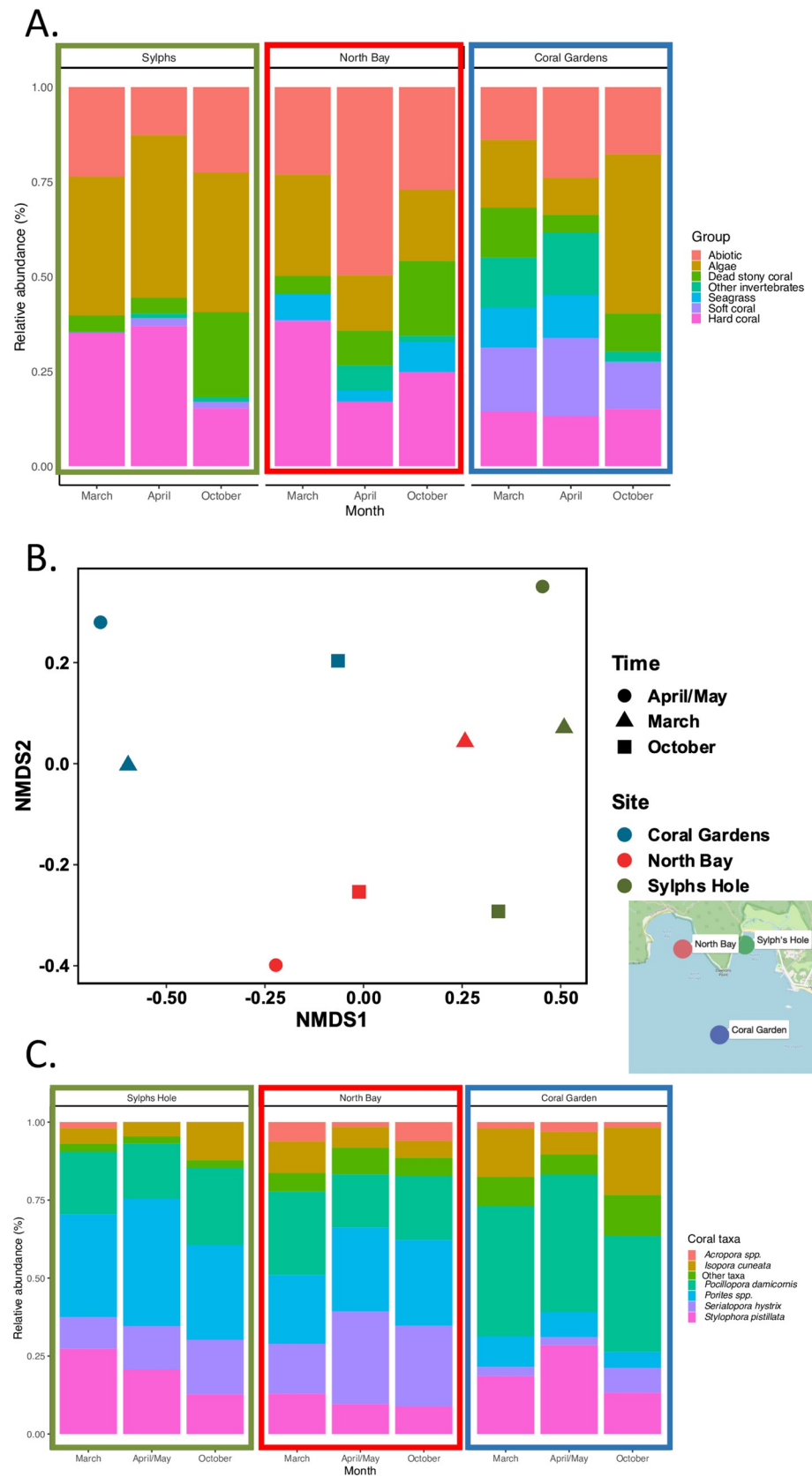


Fig 2. (A) Benthic composition at Sylph's Hole, North Bay and Coral Gardens in March, April/May and October 2019. (B) Ordination (non-metric multidimensional scaling) of benthic composition at Sylph's Hole (green), North Bay (red) and Coral Garden (blue) indicates distinctions between the three sites between March (triangle), April/May (circle), and October (square). ANOSIM analysis resulted in an R-value of 0.58 and $p = 0.008$. (C) Hard coral taxa relative abundance at Sylph's Hole, North Bay and Coral Garden in March, April/May and October 2019. The base maps were made with R studio using the "Leaflet" package.

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Coral bleaching was recorded at all three sites during March, April/May and October 2019 (Fig 3B). The abundance of bleached coral colonies was found to be significantly different between sites (chi-squared test, $p = 1.932e^{-05}$, $\chi^2 = 21.709$, d.f. = 2). The highest incidence of bleaching was recorded during March at Sylph's Hole ($83 \pm 3\%$), compared to North Bay ($46 \pm 10\%$) (GLM; $p = 0.0308$) and Coral Garden ($16 \pm 6\%$) (GLM; $p = 0.0002$) (Fig 3B). The October abundances of bleached colonies at Sylph's Hole ($36 \pm 3\%$) and North Bay ($7 \pm 3\%$) were each significantly lower than in March ($83 \pm 3\%$ and $46 \pm 10\%$ respectively) and April/May ($53 \pm 1\%$ and $46 \pm 6\%$ respectively) (GLM; $p = 0.0074$ and $p = 0.0030$, respectively). We found there was no significant difference in the abundance of bleached coral colonies between all three sites during April/May. However, in October, the percentage of bleached colonies at North Bay was found to be significantly less than at Sylph's Hole (GLM; $p = 0.0073$) and Coral Garden (GLM; $p = 0.0163$) (Fig 3B).

Hard coral mortality responses

Coral mortality was significantly different between sites (chi-squared test, $p = 0.0001243$, $\chi^2 = 17.986$, d.f. = 2) and between months (chi-squared test, $p = 1.232e^{-08}$, $\chi^2 = 36.425$, d.f. = 2) (Fig 3C). Coral mortality at Sylph's Hole significantly increased from $8 \pm 2\%$ in March to $38 \pm 2\%$ and $40 \pm 3\%$ in May and October, respectively (GLM; $p = 0.0001$). In contrast, coral mortality was not detected in North Bay and Coral Garden until October ($28 \pm 3\%$ and $17 \pm 6\%$, respectively). Sylph's Hole was found to have a significantly higher percentage of dead coral colonies ($40 \pm 3\%$) (as a result of bleaching) than Coral Garden ($17 \pm 6\%$) (GLM; $p = 0.0017$) (Fig 3C).

Coral taxa response to heat stress

Bleaching severity differed widely between sites and within coral taxa, with four of the most dominant species, *S. pistillata*, *P. damicornis*, *Porites spp.* and *S. hystris*, most severely affected ($49 \pm 8\%$, $48 \pm 6\%$, $33 \pm 7\%$ and $46 \pm 9\%$ respectively) (Fig 4A, 4C, 4E and 4G). Minimal bleaching was found for *Isopora cuneata* ($8 \pm 4\%$, Fig 4I) and the rarer species (grouped as "Other taxa") ($9 \pm 4\%$; Fig 4K). No bleaching was found for *Acropora spp.* colonies at any sites during March, April/May and October 2019 (Fig 4M). The highest level of taxon-specific bleaching severity across sites and times was at Sylph's Hole during March with $94 \pm 6\%$, $91 \pm 3\%$, $94 \pm 6\%$ and 100% of *Porites sp.*, *P. damicornis*, *S. hystris* and *S. pistillata* coral colonies, respectively, bleached. This was reflected in high mortality in May and October for *Porites sp.*, *P. damicornis* and *S. pistillata*, though only at low-to-moderate levels for *S. hystris* (Fig 4B, 4D, 4F and 4H). In contrast, neither *I. cuneata*, Other taxa or *Acropora spp.* showed any signs of mortality over the study duration (Fig 4J, 4L and 4N). Each of the four coral taxa impacted by mortality displayed different rates and patterns for mortality (Fig 4). Significant bleached coral colonies declined between March and May at Sylph's Hole, coinciding with increased coral mortality found for all four taxa. All colonies of *S. pistillata* (Fig 4A and 4B), *P. damicornis* (Fig 4C and 4D), and *Porites spp.* (Fig 4E and 4F) at Sylph's Hole were either bleached or dead during March (100% and 0% , $91 \pm 3\%$ and $9 \pm 3\%$, and $82 \pm 8\%$ and $18 \pm 8\%$,

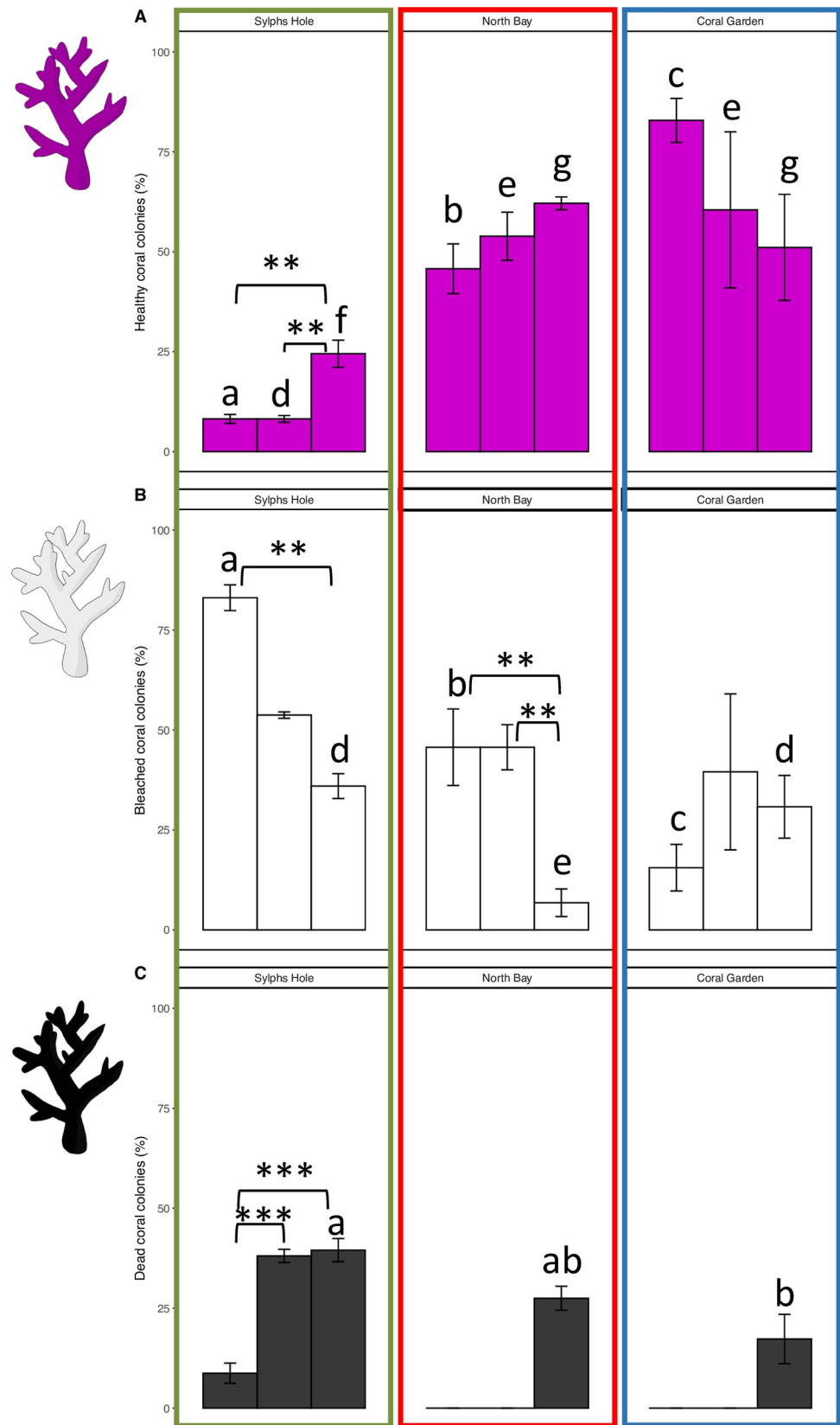


Fig 3. The percentage of (A) healthy (purple), (B) bleached (white), and (C) dead (black) colonies at each of the three sites during March, April/May and October. Letters represent significant differences between sites within surveyed intervals (months). Black bars with stars represent significant differences between surveyed intervals (month) within each site. Significant differences were determined using GLM analysis ($p < 0.05$); the stars indicate significant levels; ^{***} 0.05, ^{**} 0.01, and ^{****} 0.001.

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respectively) and May ($42 \pm 2\%$ and $58 \pm 2\%$, 45 ± 6 and $55 \pm 6\%$, and $80 \pm 5\%$ and $20 \pm 5\%$, respectively). *S. pistillata* (Fig 4A), *P. damicornis* (Fig 4C), and *S. hystrix* (Fig 4G) at Sylph's Hole were all found to have the highest bleaching prevalence in March before significant declines in May (due to coral mortality). For *S. pistillata* (Fig 4A) and *P. damicornis* (Fig 4C), bleaching declines in May coincided with the first record of *S. pistillata* mortality and a significant increase in mortality for *P. damicornis* (GLM; $p = < 0.0001$) (Fig 4D). Notably, mortality of any taxon at Coral Garden and North Bay wasn't observed until October.

Discussion

Higher latitude reefs have been proposed as more resistant to thermal anomalies because there are lower bleaching and mortality rates and faster recovery than those of their low latitude coral reef counterparts [e.g. 16, 19, 58, 59]. Our study finds coral bleaching response to thermal anomalies in the high latitude coral reef system of Lord Howe Island Marine Park is highly variable within and between sites and coral species within the lagoonal reef. A thermal anomaly ($\sim 2^\circ\text{C}$ above the satellite MMM) at the Lord Howe Island reef during February 2019 was associated with severe bleaching, with over 30% of hard coral colonies bleached and substantial coral mortality. Bleaching prevalence was surveyed at three sites within the lagoonal reef, Sylph's Hole, North Bay and Coral Garden, over eight months in 2019, from March, coinciding with peak DHW, to October 2019, following the Austral winter. All sites over the eight months recorded little to no recovery within LHI lagoon reefs (Fig 3). eDHW of over 13°C -weeks was recorded in parts of the reef system, despite the cooling effect of a tropical cyclone (Oma) that reduced sea surface temperatures for approximately 10 days. Without the cooling effects of tropical cyclone Oma we estimate eDHW would have exceeded 16°C -weeks for the reef system. Had tropical cyclone Oma not cooled the coral reef system at Lord Howe Island, our results suggest that the corals across Lord Howe Reef would have experienced more severe bleaching and coral mortality. In 2016 tropical cyclone Winston had similarly cooled the southern GBR, likely saving the area from the severe heat stress and bleaching seen in the northern and central GBR [52]. These examples illustrate how important cooling weather events can be in mitigating bleaching events.

Hard coral composition

Changes in coral cover and taxonomic composition are typical following disturbance events. Given the different bleaching and mortality severities between sites, we expected to see a decline in hard coral cover at Sylph's Hole and increased algae composition. Whilst at the other two sites, we expected to see minimal change as the thermal anomaly had less of an impact on the coral communities at North Bay and Coral Gardens. The LHI lagoon reef sites were relatively high in scleractinian coral cover ($30 \pm 3\%$) compared to other shallow lagoon sites [69–71]. The hard coral cover in the lagoon was similar to the reef crest and reef slopes at LHI [66] and too low latitude reef crest and reef slopes sites on the GBR after the 1998 bleaching [72]. The benthic composition within the LHI lagoon was dominated by algae (turf and macro) ($33 \pm 4\%$). Prior surveys at LHI identified *Caulerpa* (Chlorophyta) and red algae contribute high percentages of algae composition inside and outside of the LHI lagoon [66, 73],

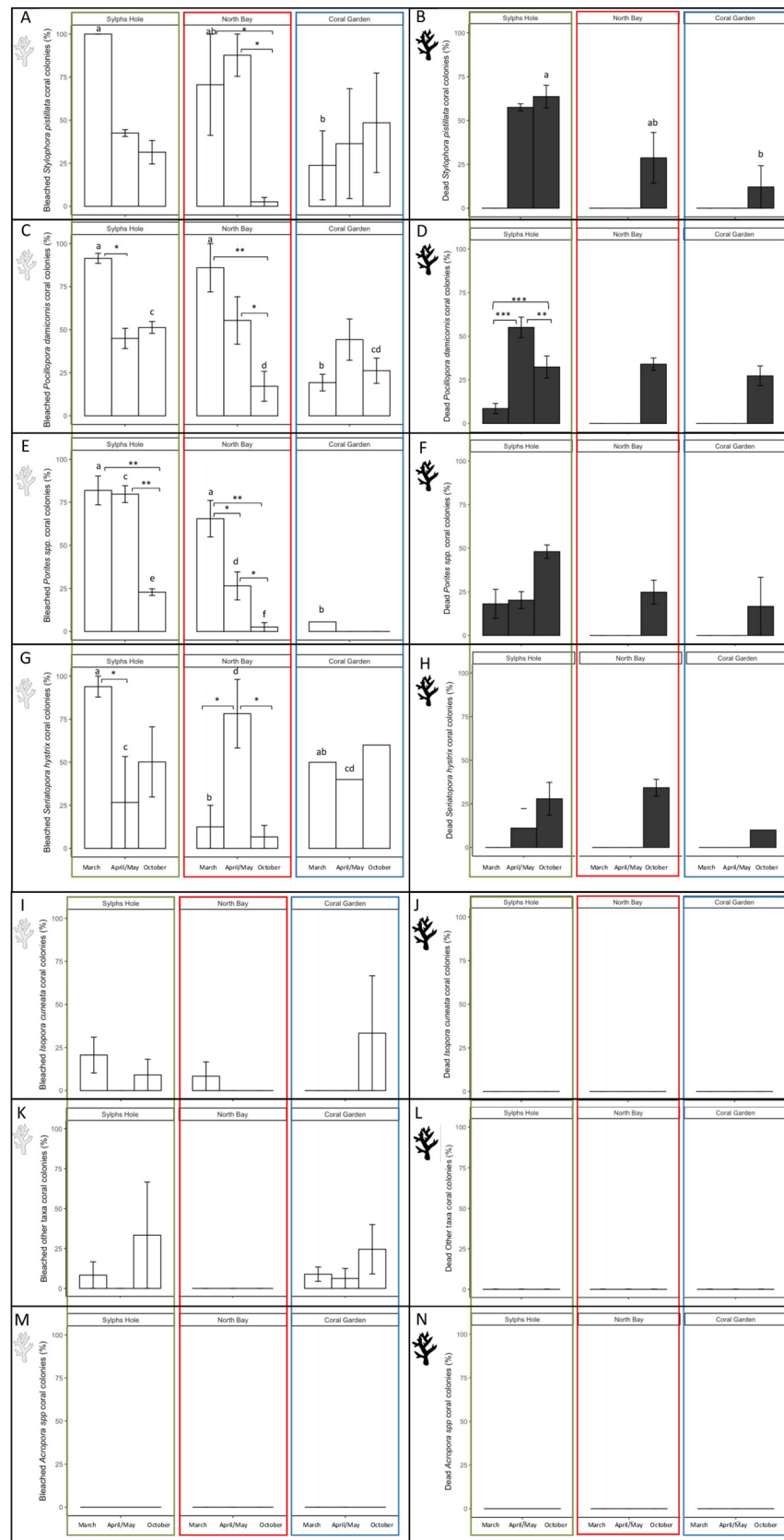


Fig 4. The percentage of bleached (white) and dead (black) colonies at each site during March, April/May, and October for *Stylophora pistillata* (A and B), *Pocillopora damicornis* (C and D), *Porites* spp. (E and F), *Seriatopora hystrix* (G and H), *Isopora cuneata* (I and J), Other taxa (K and L), and *Acropora* spp. (M and N). Letters represent significant differences between sites within surveyed intervals (months). Black bars with stars represent significant differences between surveyed intervals (month) within each site. Significant differences were determined using GLM analysis ($p < 0.05$). The stars indicate significant levels; * 0.05, ** 0.01, and *** 0.001.

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characteristic of temperate and subtropical reefs. Hard coral contributed the second highest benthic composition within the lagoon ($30 \pm 3\%$), consisting of five main taxa, *P. damicornis* ($30 \pm 4\%$), *Porites* spp. ($22 \pm 4\%$), *S. pistillata* ($20 \pm 3\%$), *I. cuneata* ($10 \pm 2\%$), and *S. hystrix* ($10 \pm 3\%$) comprise 90% of the taxa relative abundance (Fig 2C), consistent with previous benthic cover for the LHI lagoon [45]. After the thermal anomaly, benthic and coral taxa composition changed (Fig 2A and 2B). Algae cover increased to $52 \pm 3\%$, and hard coral cover declined by one-third to $19 \pm 3\%$ of total cover. This proportion of the decline in hard coral cover is similar to the shallow sites of the remote Aldabra atoll, Seychelles, after the 2016 mass bleaching event [74].

Lagoonal water and sea surface temperatures

Sea water temperatures were above the maximum monthly mean for almost four months from January to April 2019 (Fig 1D). The maximum *in-situ* and sea surface temperatures reached 26.77°C and 26.0°C , respectively (Fig 1D); these temperatures are lower than that experienced at other high latitude reefs during bleaching events [32, 37]. The use of eDHW provides a way to examine and compare the stress corals experience using *in-situ* temperatures relative to a bleaching threshold; the eDHW for a specific site is typically greater than the corresponding DHW for the co-located 5 km satellite pixel [68]. Sylph's Hole eDHW reached 13.5°C-weeks in late March, coinciding with the satellite DHW peak (10.4°C-weeks) and the highest percentage ($83 \pm 3\%$) of bleached coral colonies (Fig 3B). These DHWs are lower than that experienced at LHI during the 2010 bleaching, where a maximum of 20.1°C-weeks was reached. Notably, bleaching in 2011 occurred when a DHW of 6.5°C-weeks was recorded [60, 64–67, 69–74].

Bleaching variability within the lagoonal reef

Thermal variability within the lagoon leads to divergent impacts of bleaching across small scales in a reef ecosystem. For example, heat stress at the shallow near-shore Sylph's Hole recorded eDHW of 13.5°C-weeks (Fig 1E), resulting in immediate (March) and extensive coral colony mortality and significant declines in hard coral cover from March to October 2019 (Figs 2C and 3C). In comparison, mortality at the more exposed reefs of North Bay and Coral Garden was not observed during the heat stress event but was recorded six months following the most severe heat stress. These two sites showed no signs of post-stress recovery, as shown by the lack of significant increases in healthy (normally pigmented) coral colony abundance between March and October (Fig 3A). This suggests that mortality at these sites was associated with the starvation of the coral host. This is due to the photosynthetically-fixed carbon loss, normally acquired from the intracellular dinoflagellates [6, 7, 75]. This 'traditional' bleaching and mortality contrast the rapid mortality at Sylph's Hole, which was directly caused by the thermal stress event [c.f. 52, 76, 77]. The mortality variability among sites and months was high, ranging from none to a maximum of $40 \pm 3\%$. As all sites were located at similar depths within the lagoon, these large variances in bleaching and mortality are driven by other biophysical factors within the lagoon that influence the corals' physiological response, for

example, light levels, hydrodynamics, nutrients and temperature profiles. *In-situ* temperatures were highest at the near-shore site, Sylph's Hole, while North Bay and Coral Garden were closer to the reef edge, with greater effects of wave and tidal mixing reducing *in-situ* water temperatures leading to less severe impacts. Similar small-scale differences between offshore sites with lower temperatures (and associated lower relative coral mortality) and inshore sites with higher temperatures (and higher relative coral mortality) have been observed in the Indian Ocean [62]. As seen at Sylph's Hole, rapid coral mortality has been observed due to lethal marine heatwave water temperatures [77].

Refuge and bleaching between low and high latitudes

Higher latitude reefs have been considered more resilient to thermal anomalies than their low latitude coral reef counterparts due to lower rates of bleaching and mortality and faster recovery [e.g. 16, 19, 58, 59]. However, we found bleaching was evident at all surveyed sites over the eight months of the study, with an overall prevalence in March of 48%, which is similar to coral bleaching prevalence found on the GBR [51, 78, 79]. Coral bleaching between the three sites was significantly different (Fig 3B), with up to 83% of all coral colonies bleached at Sylph's Hole during the thermal anomaly peak (March), compared with contemporaneous bleaching of 16% of corals at Coral Garden and 46% of corals at North Bay (Fig 3). Our findings of site variability in bleaching severity are consistent with previous studies at low latitudes [51, 80, 81] and high latitudes [32, 37, 43, 82], including previous bleaching events at LHI [45, 46]. Contrary to previous suggestions that remote locations and high latitude reefs, such as LHI, provide refuge from anthropogenically-driven climate change, we have documented a third bleaching event in a decade [see 45, and this paper]. In addition, recovery on high latitude reefs appears to be slower than on low latitude reefs. For example, in the 2002 Great Barrier Reef bleaching event, 70% of corals had recovered after three months [83], in contrast to our observations at LHI. Despite significant differences in thermal stress and bleaching rates at the three LHI sites, recovery was only observed at Sylph's Hole in October, with healthy coral abundance increasing from $8 \pm 1\%$ to $24 \pm 3\%$ (Fig 3A). Since temperature is the major driver of metabolic rates in all organisms, including corals [84], the lower temperatures seen at high latitude reefs may cause the coral host's slow recovery times and symbiont. This slower recovery means that high latitude reefs are likely to be much more susceptible to repeated annual heat stress events (as in 2010–2011) than low latitude reefs, given that they appear slower to replenish their energy reserves and recover.

Hard coral species-specific responses to bleaching

Coral bleaching “losers” have been described as branching coral morphologies and corals with thin tissue thickness [14]. This holds for our findings, with the notable exception of the *Acropora* spp.; however, we also found the massive/sub-massive *Porites* spp. morphologies were heavily impacted by bleaching and mortality—taxa typically with lower bleaching susceptibility [14, 78]. Our study revealed high susceptibility to bleaching and mortality for four of the most common coral species of Lord Howe Island—*P. damicornis*, *Porites* spp., *S. hystrix* and *S. pistillata*—with 64–100% of coral colonies impacted (Fig 4A–4H). Although *I. cuneata* is also among the most prevalent taxa at LHI, minimal bleaching was recorded compared to the other prevalent coral taxa, including no bleaching documented at all sites during April/May 2019 and no whole coral colony mortality throughout the study (Fig 4I and 4J). We found rarer species, classified collectively as “Other taxa”, also experienced minimal bleaching and no mortality during the study (Fig 4K and 4L). Interestingly, no bleaching or mortality was recorded during the duration of the study for *Acropora* spp. (Fig 4M and 4N). Other reef systems have reported

Acropora as one of the first genera to bleach, as observed in the GBR [51, 78, 80, 85] and high latitude reefs at Houtman Abrolhos Islands, Western Australia [41] and South Africa's Sodwana Bay [42]. Further research into the biological and physiological characteristics of LHI's *Acropora* and *Isopora* species to understand their bleaching responses and their observed resistance during the 2019 thermal anomaly.

Comparisons of impacts on the predominant taxa indicate that *S. pistillata* was the most sensitive to the thermal stress with the highest prevalence of mortality (Fig 3B) and a significant decline in relative abundance by 50% at Sylph's Hole between March and October 2019 (Fig 2A). This was despite mortality being recorded earlier for *P. damicornis* and *Porites spp.* in March 2019. Similar findings in coral assemblage declines and bleaching susceptibility have been recorded for *S. pistillata* in the Indian Ocean [86, 87] and the Pacific Ocean [14, 29, 85, 88]. Notably, water flow has been shown to have a positive relationship with *S. pistillata* bleaching susceptibility and recovery potential [63], which may explain the lesser bleaching and mortality at Coral Garden, a site of higher water flow than the other two sites (Fig 4A and 4B). *P. damicornis* and *S. hystrix* are also typically highly susceptible to coral bleaching during thermal anomalies [14, 29, 64, 85, 88–90], consistent with our observations. Massive *Porites* species have shown varying responses during coral bleaching events globally [14, 29, 64, 70, 78, 85, 88, 90, 91]; we observed that the LHI species were highly susceptible to bleaching and mortality (Fig 4E and 4F). No healthy coral colonies of *P. damicornis*, *Porites spp.*, and *S. pistillata* were recorded in March and April/May at Sylph's Hole (Fig 3).

These findings further highlight how coral taxa composition differences affect the coral bleaching response variability. Changes in hard coral composition and relative species abundance in our study occurred in a relatively short time (eight months). Four of the five most common hard coral taxa were impacted. Of these, *S. pistillata* was the overall loser, having significantly declined in relative abundance over the eight-month monitoring period (Fig 2C). Whilst the other three taxa (*Porites spp.*, *P. damicornis* and *S. hystrix*) were short-term losers, as relative abundance didn't change over time. In contrast, *Acropora spp.*, *I. cuneata* and the 'Other' hard coral taxa were long-term winners as bleaching and mortality were low, and no significant differences in relative abundance were found.

Conclusions

This study underlines the ecological impact thermal anomalies have on a pristine, remote, high latitude coral reef on a small spatial scale over a short (eight-month) period. Long-term monitoring programs are important to identify additional stressors to the ecosystem and recovery potential. Reef recovery is interrupted by other acute disturbances such as coral disease outbreaks, additional thermal anomalies, increased coral-algal competition, outbreaks of *Acanthaster planci* or *Drupella spp.*, and losses in recruitment potential and coral growth. Previous recovery rates at LHI from the 2010 and 2011 bleaching events saw the increased coral cover and, in some sites, higher coral cover only two to four years after the event [45]. However, the overall coral composition has changed [45]. We have now documented a third mass bleaching even at LHI in ten years, and further coral community compositional shifts will likely occur as bleaching frequency increases. The bleaching event of 2010 was the most severe with regards to bleaching extent and coral mortality recorded at LHI [45]; however, the impacts in 2019 could be more severe than observed had the island not felt the cooling effect of tropical cyclone Oma.

Globally high-latitude reefs have been increasingly impacted by bleaching events [15, 19, 32, 37, 41, 44, 45, 59, 92–95]. Located at the boundary of temperate and sub-tropical reefs, LHI Marine Park is a model system for observing how corals at the high latitudes will be impacted

by and recover from ongoing thermal stress events. Therefore, we suggest ongoing spatiotemporal monitoring of the LHI coral reefs to provide ongoing trajectories of benthic composition and coral community structure to further our understanding of the impacts of climate change on high-latitude reefs.

Our results show the importance of longitudinal monitoring of coral bleaching events and the potential relationships between site biophysical factors and the severity of coral bleaching and mortality. Our study builds upon previously documented bleaching at LHI to expand the collective understanding of thermal anomaly outcomes and trajectories for benthic assemblages on a remote high latitude reef in Australia. We highlight that high latitude reefs are not a place of refuge for scleractinian corals in an era of ongoing climate change. In fact, given the projected increase in the frequency of climate extremes and the apparent slower recovery time from bleaching compared to low latitude reefs, it is likely that bleaching impacts will be more severe on high latitude reef systems.

Supporting information

S1 Fig. Visual categorical health states of corals during bleaching (a) healthy, (b) partially bleached, (c) pale, (d) fluorescent, (e) bleached, (f & h) dead, and (g) partially dead. Images taken by Tess Moriarty.
(TIF)

S1 Table. Coral taxa abundance from belt transects in each site, month and bleaching category.
(DOCX)

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