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Severe Heat Stress Resulted in High Coral Mortality on Maldivian Reefs following the 2015–2016 El Niño Event

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Abstract: Coral cover worldwide has been declining due to heat stress caused by climate change. Here we report the impacts of the 2015–2016 El Niño mass coral bleaching event on the coral cover of reefs located on central and northern atolls of the Maldives. We surveyed six reef sites in the Alifu Alifu (Ari) and Baa (South Maalhosmadulu) Atolls using replicate 20 m benthic photo transects at two depths per reef site. Live and recently dead coral cover identified from images differed between reef sites and depth. Recently dead corals on average made up 33% of the coral assemblage at shallow sites and 24% at deep sites. This mortality was significantly lower in massive corals than in branching corals, reaching an average of only 6% compared to 41%, respectively. The best predictors of live coral cover were depth and morphology, with a greater percentage of live coral at deep sites and in massive corals. The same predictors best described the prevalence of recently dead coral, but showed inverse trends to live coral. However, there was high variability among reef sites, which could be attributed to additional local stressors. Coral bleaching and resulting coral mortalities, such as the ones reported here, are of particular concern for small island nations like the Maldives, which are reliant on coral reefs.

Keywords: Maldives; Indian Ocean; El Niño; mass coral bleaching; coral mortality; benthic cover

1. Introduction

Elevated seawater temperatures resulting from climate change are causing widespread coral bleaching events across tropical regions of the world [1–3]. Over the past 30 years the frequency and severity of these bleaching events have increased and they are now occurring on an unprecedented scale [1,4]. In 2015–2016, a severe El Niño event led to widespread coral bleaching across the Pacific and Indian Oceans [1,2,4–8], with some regions experiencing repeated heat stress events throughout this period (e.g., Chagos Archipelago [9], Great Barrier Reef (GBR) [2,10]). During the El Niño, some areas of the Pacific experienced extreme heat stress, reaching over 20 degree heating weeks (DHWs) [5], a metric representing accumulated heat stress over a 90-day window in comparison to historical maximum monthly means (MMMs) [10]. Although not quite as extreme, DHWs from the Western and Eastern Indian Ocean during the same period still greatly exceeded the bleaching threshold, with records ranging from four to 11 [11–13].

Coral bleaching occurs when corals expel their photosynthetic endosymbiotic algae (Symbiodiniaceae), often as a result of temperature stress, leaving a white skeleton visible through translucent tissue [14]. Corals may recover over time or coral mortality may occur

if the algae cells are not regained and temperature stress conditions persist. Susceptibility to bleaching and mortality can vary among coral species due to a variety of factors, which include coral morphology [15,16], history of stress or temperature exposure [17,18], associated algal symbiont type [19–21], and the coral microbiome [22]. This variability in susceptibility can cause not only a loss in overall coral cover, but also a reduction in both the biodiversity and functional diversity of coral assemblages [23]. In severe cases bleaching and subsequent mass mortality events result in decreased larval supply and connectivity, which can result in phase shifts that are often from coral to macroalgal dominated reefs [24]. Other alternate states include sponge- or urchin-dominated reefs [25,26]. It becomes difficult for corals to re-populate reefs and reverse such phase shifts (reviewed in [27]), resulting in obvious changes to benthic and reef-associated pelagic assemblages across the reef ecosystem.

Mass coral bleaching events impact not only the health of the coral reef ecosystem, but also the human populations that may rely on artisanal fisheries, coastal protection, and ecotourism. Coral mortality can be particularly concerning for small island nations because reefs represent a lifeline that provides food and livelihood. Loss of coral in the ecosystem can decrease catches of artisanal reef fisheries and discourage tourism, ultimately impacting the food security and economy of local communities [28,29].

One such small island nation is the Republic of Maldives, located in the central equatorial Indian Ocean. The Maldives is made up of over 1000 islets situated within 26 atolls. It is the largest group of coral reefs in the Indian Ocean, hosting approximately 1100 reef-associated fish species and 250 species of coral [30]. The economy of the Maldives benefits from marine resources through tourism and ecosystem services such as coastal protection, food, and construction materials [31]. Thus, changes to the state of Maldivian reef health is of concern to the nation. During the 2015–2016 El Niño event, reefs in the Maldives experienced between four and 11 DHWs, suggesting considerable heat stress [32]. This resulted in widespread bleaching across the region [7,33–35], with bleaching observed in 73% of corals from 0–13 m depth [12]. Here we document the effects of the 2015–2016 global bleaching event on the survival and mortality of coral communities in the northern atolls of the Maldives.

2. Results

Six coral reef sites were monitored in the Alifu Alifu and Baa Atolls in the Republic of Maldives (Figure 1) to assess post-bleaching coral mortality. The percentage of live coral cover at each coral reef site ($n = 6$) and depth was variable and ranged between 3% and 26% of substrate cover in December 2016, following the peak of the heating event that occurred in May of the same year (Figure 2). Of all the sites, live coral cover was lowest at Hurasdhoo, with an average of $3 \pm 4\%$ (mean $\pm$ standard error, $n = 51$) at deep sites (Figure 2). No records were available for this site at shallow depths. All other sites had similar live coral cover at shallow depths, ranging from $13 \pm 8\%$ ($n = 34$) at Rasdhoo to $26 \pm 13\%$ ($n = 51$) at Dhonfanu (Figure 2). Live coral cover at depth had a similar range, from $13 \pm 14\%$ ($n = 51$) at Nika Point to $27 \pm 12\%$ ($n = 51$) at Dhonfanu (Figures 2 and 3).
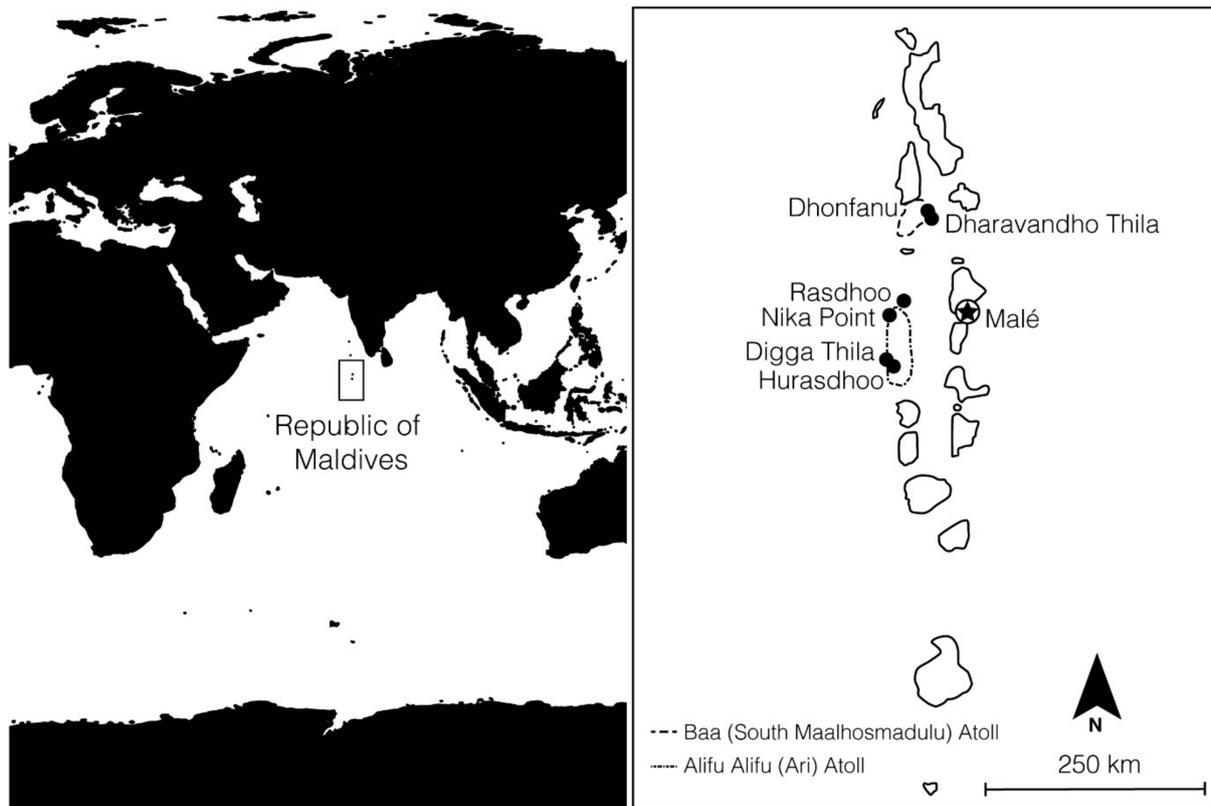
Figure 1. Reef site locations within the northern atolls (Baa and Alifu Alifu Atolls) of the Republic of Maldives. Sampling locations are marked with a black dot on the map.

Recently dead coral, classified as coral skeletons covered with turf algae but with the skeleton still intact, was also abundant at each of the sites surveyed (Figure 2). At shallow depths, this was as high as 54 ± 19% (*n* = 52) of the substrate cover at Digga Thila (Figure 2). The percentage of recently dead coral at shallow transects at all other sites ranged from 12 ± 8% (*n* = 50) at Nika Point to 40 ± 14% (*n* = 51) at Dhonfanu (Figure 2). Of the deep transects, the percentage of recently dead coral was highest at Hurasdhoo, averaging 41 ± 25% (*n* = 51), although this was highly variable between transects and replicates (Figure 2).

Very few coral colonies were still bleached, with translucent live tissue covering the skeleton, at the time of data collection seven months after peak heat stress. The total substrate covered by bleached corals ranged from 0.1 ± 0.7% (*n* = 54) to 2.9 ± 7.6% (*n* = 54) across all reef sites and depths.

Modelling of variables influencing the percentage cover of live coral suggested that the best model fit was obtained when including additive effects of reef site, depth, and morphology (Table 1). When accounting for these variables, live coral cover was estimated to be considerably lower at Hurasdhoo (3% live cover, with confidence intervals (CI) of 2–5%), compared with all other reef sites, over which coral cover ranged from 18% (15–22% CI) to 29% (25–34% CI) (Figure 4a). Mean live coral cover was found to be higher at deep rather than shallow sites, estimated to be 23% (19–27% CI) and 16% (13–19% CI), respectively (Figure 4b). In addition, mean live coral cover was found to be greater in massive corals than branching corals, estimated to be 33% (27–39% CI) in massive corals and 6% (5–7% CI) in branching corals (Figure 4c).
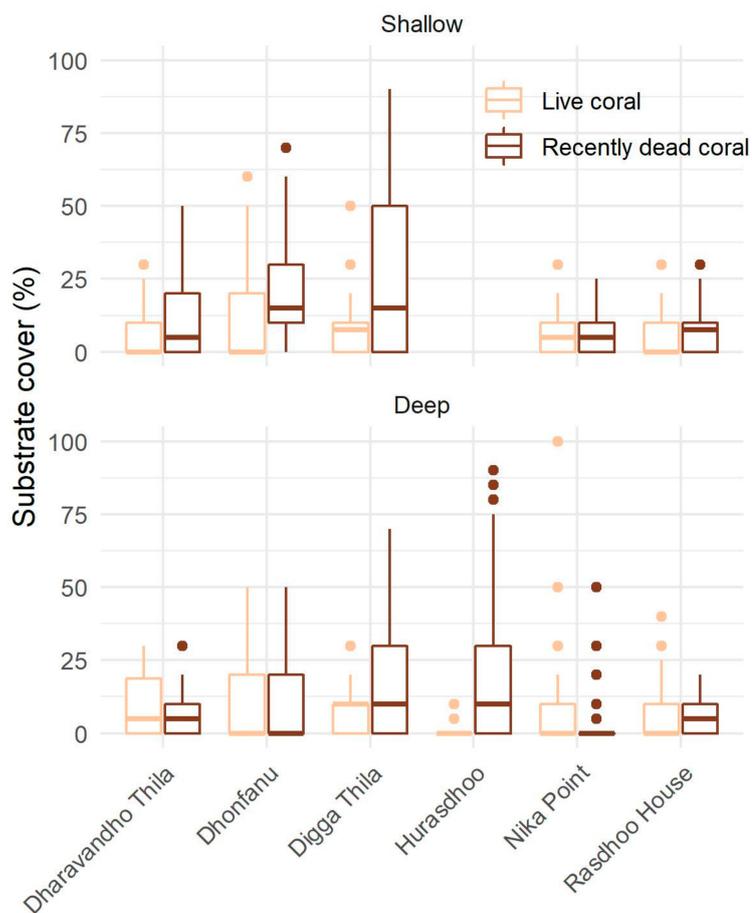
Figure 2. Box and whisper plot showing the percentage of substrate cover of live corals and recently dead corals at both shallow and deep transects at each of the six reef sites surveyed.
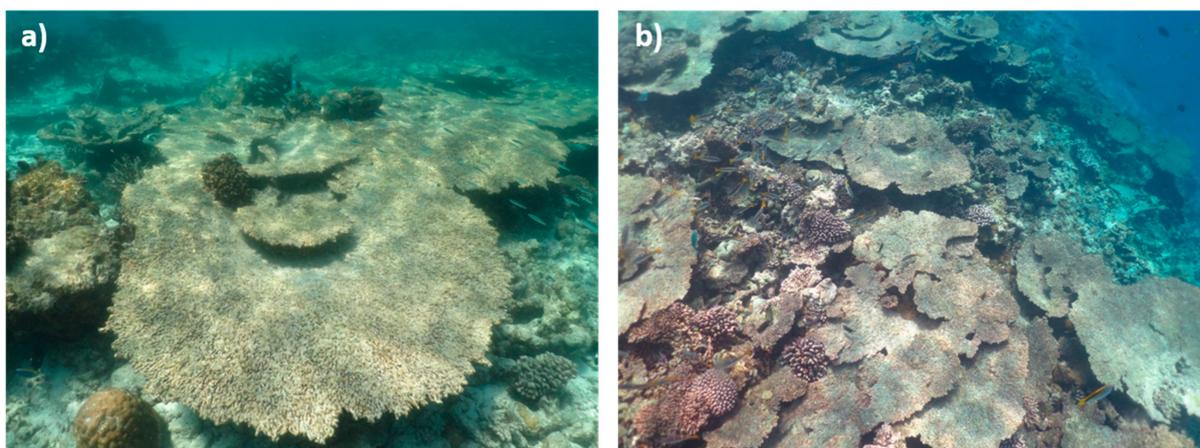

Figure 3. Extensive stands of dead corals (*Acropora* spp.) in the Maldives, where reefs exhibited high levels of coral mortality in December 2016 following the 2015–2016 El Niño mass coral bleaching event ((**a**) and (**b**)).

Table 1. Generalised linear mixed effect model (GLMM) fit statistics investigating the most important variables influencing both (**a**) live coral and (**b**) recently dead coral. Shown are the number of parameters (*n*), Akaike information criteria (AICc), δ AICc, and AICc weight (*ω*$_i$). The best fitting model is highlighted in bold.

| Coral Cover	Model	*n*	AICc	δ AICc	*ω*$_i$
(a) Live coral	**Reef site + depth + morphology**	**11**	**1013.3**	**0**	**1**
	Reef site + morphology	10	1036.7	23.31	0
	Depth + morphology	6	1153	139.64	0
	Morphology	5	1156.4	143.05	0
	Reef site + depth	10	1523.5	510.12	0
	Reef site	9	1537.7	524.31	0
	Depth	5	1635.1	621.79	0
	Null	4	1637	623.64	0
(b) Recently dead coral	**Reef site + depth + morphology**	**11**	**1034.7**	**0**	**1**
	Reef site + morphology	10	1056.2	21.53	0
	Depth + morphology	6	1093	58.25	0
	Morphology	5	1096.5	61.81	0
	Reef site + depth	10	1177.8	143.12	0
	Reef site	9	1193.5	158.75	0
	Depth	5	1236.9	202.18	0
	Null	4	1238.1	203.41	0
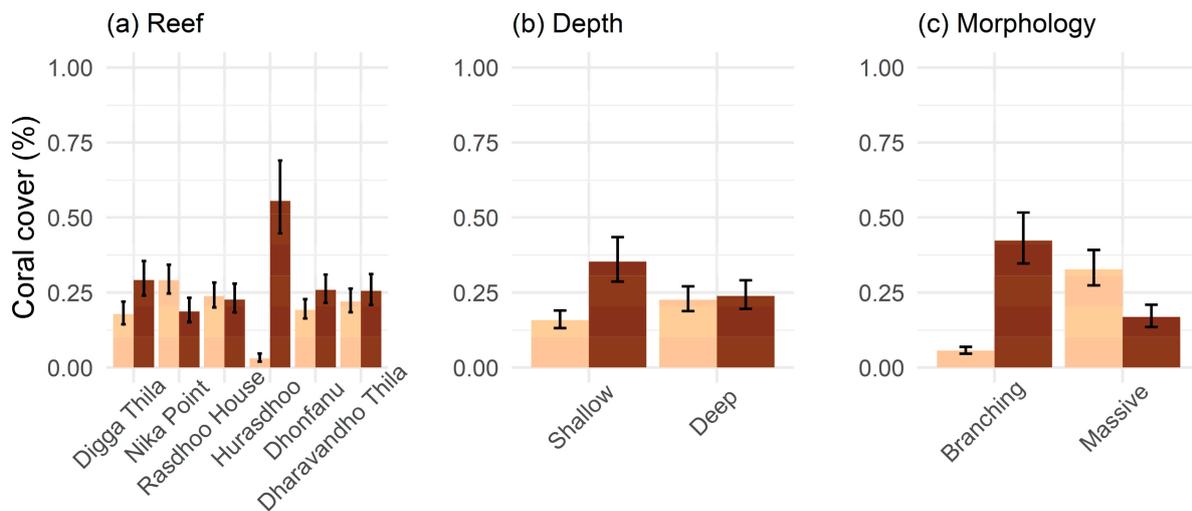
Figure 4. Predicted percentage of substrate cover of both live coral and recently dead coral by (**a**) reef, (**b**) depth, and (**c**) morphology, with 95% confidence intervals.

Modelling the cover of recently dead coral also suggested the best fitting model included additive effects of reef site, depth, and morphology (Table 1b). The percentage of dead coral cover at each reef site varied. The highest percentage was found at Hurasdhoo, with 56% (±45–69%) recently dead coral cover, whereas the remainder of the reef sites ranged from 19% (±15–23%) to 29% (±24–36%) (Figure 4a). Overall, there were more recently dead corals at shallow depths, with estimates of 35% (±28–43%) compared to 24% (±20–29%) at deep sites (Figure 4b). Estimates of recently dead massive corals were also lower than those for branching corals, with massive estimates of 17% (±14–21%) and branching estimates of 42% (±34–52%) (Figure 4c). The percentage of cover of recently dead corals was inverse to the trends observed for live coral cover (Figure 4).

3. Discussion

3.1. Bleaching and Mortality

During the 2016 El Niño the Maldives experienced a severe bleaching event with the overall mean percentage of bleached corals (across 71 sites and depths ranging from 0–13 m) reaching 73%, with some sites exhibiting close to 100% bleaching [12]. Although the peak of the bleaching event occurred between mid-April and mid-June 2016 and some mortality was seen at this time, many colonies remained bleached for several months. Live mean coral cover was reduced to approximately 6–20% across the central and southern Maldives [33–35], with both lagoonal and oceanic reefs impacted [35]. Higher mortality was observed at reef sites in proximity to higher local population sizes, suggesting that these sites were more strongly impacted by human pressures (e.g., North and South Malé Atolls [35]). Coral reef sites investigated in the present study were exposed to comparatively lower human pressures (Baa and Alifu Alifu Atolls), but still exhibited extensive mortality (Figures 3 and 4), with mean live coral cover reduced to 3–27%. The observed bleaching-induced mortality followed similar patterns as previously recorded bleaching severity in the area (see [7,12,34]); mortality was highest in shallow depths (~30% mortality) and among branching corals (~40% mortality), especially *Acropora* spp.

Bleaching severity is considered to vary spatially (e.g., [36,37]) and to be influenced by microhabitat features [38]. Additionally, coral morphology is a factor and branching corals are more susceptible to bleaching and mortality during heat stress in comparison to massive corals [15,39,40]. Branching structures can help optimize light dispersion and reflection that may be important for maintaining colony health at depth or in normal light conditions. However, for colonies in shallow habitats where irradiance is naturally higher, this structure may cause supra-optimal irradiance conditions during heatwaves, accelerating or intensifying bleaching [15,39,40]. In contrast, massive corals have less structural complexity and have been found to have a higher resistance to bleaching, taking longer to bleach and experiencing less mortality [41]. Although branching corals did experience higher bleaching-induced mortality than massive corals in the present study, these mortality levels (approximately 40%) were comparably lower than branching coral mortality in other areas of the Maldives in the aftermath of the 2016 El Niño event. North Malé (Kaafu) Atoll experienced 80% mortality of *Acropora* spp., the dominant branching coral genus in the Maldives [12], and southern sheltered reefs exhibited 75% mortality in branching corals [33]. In a similar pattern, the Chagos Archipelago, situated south of the Maldives, lost 86% of *Acropora* spp. cover (from 2–14%) during the 2015–2016 thermal anomalies, shifting to a community dominated by *Porites* spp. post bleaching [9].

Interestingly, although branching corals are generally considered more susceptible than massive corals on mildly bleaching reefs, this pattern breaks down when reefs are exposed to severe bleaching: Some corals that are normally classified as thermotolerant (e.g., many massive species) can nevertheless become bleached under severe heat stress (e.g., [1]). This may suggest that the Maldives was not hit as hard by this El Niño event as some reefs in other areas around the globe. In support of this, although DHWs in the Maldives reached 11, which exceeds the proposed eight DHW mass bleaching threshold, other reefs around the globe reached much higher DHWs: up to 16 on the GBR and over 20 in the central Pacific [1,5]. Mortality in some of these areas was nearly 100% [42]. The mortality recorded here on Maldivian reef sites still exceeded 50%, and although this is less than what some of the hardest hit reefs globally experienced during the 2015–2016 El Niño, this remains a mass mortality event that can have major consequences for reef recovery.

3.2. Potential for Recovery of Maldivian Reefs

Maldivian coral reefs experienced severe bleaching in 1998 [43,44] and again in 2016 [12], and between these dates also endured a series of mild bleaching events in 2003, 2005, 2007, and 2010 [45–47]. During this recovery period, Maldivian reefs faced other disturbances, such as a tsunami in 2004 [48] and outbreaks of crown-of-thorns starfish (*Acanthaster planci*), both of which contributed to further coral mortality and influenced

recovery capacity in the impacted localized areas [49]. Following the 1998 bleaching event, which resulted in mass mortality (90%) of hard corals [50] and a near total disappearance of tabular coral [51], Maldivian reefs underwent a recovery trajectory that spanned the next 18 years. Initial mortality of acroporids (up to 90% [51]) led to a shift in assemblage composition of coral cover, from *Acropora*-dominated to *Porites*-dominated, for the first eight-plus years of recovery [43,49,52,53]. By 2014, 15 years post bleaching, reefs in the region resembled pre-1998 bleaching assemblages, however, with an absence of species that had yet to recover [46,49]. After the 1998 bleaching event the constructional capacity (i.e., bioconstruction potential, carbonate deposition, and reef accretion) of Maldivian reefs was severely affected, with two to three years required for renewed carbonate deposition and 14–16 years required before accretion rates were high enough to ensure constratal (low-relief) growth [54].

Recovery of Maldivian reefs post 1998 bleaching event was slower than rates reported in the neighbouring Chagos Archipelago [49,55,56], which lacks local human threats and recovered in 10 years [9]. Slower recovery was likely related to the increased level of human pressures that Maldivian reefs experience (e.g., overexploitation of resources, pollution, and coastal development) that influence the success of coral reef recovery, overall coral reef health, and resilience (e.g., [57,58]). Environmental degradation associated with human-induced pressures have increased in the Maldives, particularly related to local population growth, coastal development, land reclamation works, and tourism [59–62]. Whereas local populations reached 344,023 in 2014, increases in the numbers of tourists grew by 400% between 1997 and 2019, reaching 1.5 million visitors in 2019 [35].

Following the 2016 bleaching event, coral mortality was greater at coral reefs exposed to increased human pressures (e.g., North and South Malé [35]). For example, reefs in proximity to land reclamation projects experienced four-fold increases in sedimentation loads and exhibited significant reductions in live coral cover post bleaching event in comparison to reefs not impacted by both land reclamation activities and bleaching [62]. Land reclamation and associated dredging (Figure 5a) and dumping activities contribute to increased suspended sediments and deposited sediment loads (i.e., sedimentation). Increased suspended sediments reduce light levels required by corals to photosynthesize [63–65], but even low levels of sediment or other particulate deposition reduces suitable reef substrate for coral recruitment [66,67]. Bleached corals are less capable of removing sediments from their tissue surface [68], resulting in prolonged smothering and increased energy expenditure to clear sediments [69,70]. Recent investigations into cumulative impacts of increased suspended sediments and bleaching events indicate that these impacts can be synergistic when suspended sediments are at high concentrations, resulting in greater mortality than would be observed with either individual event [71].
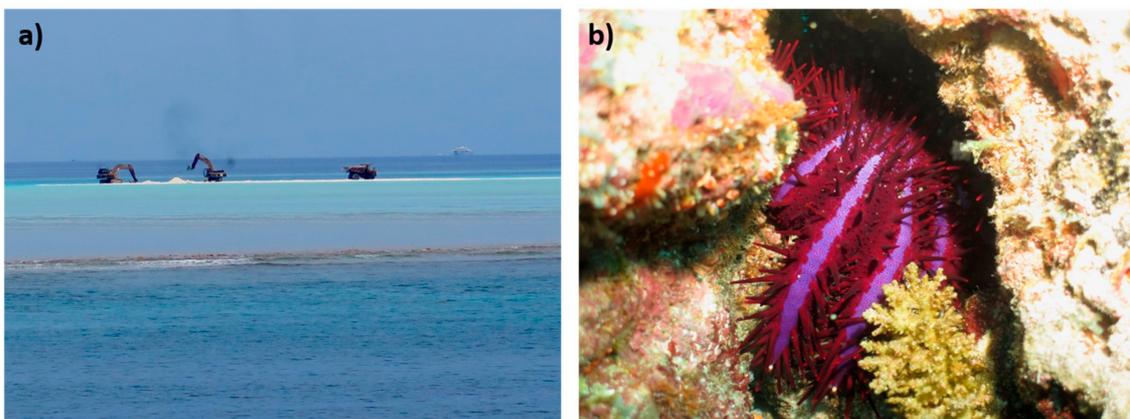

Figure 5. Maldivian coral reefs are exposed to local disturbances such as coastal development and land reclamation projects (**a**) and crown-of-thorns starfish that prey on corals (**b**). These additional pressures and thermal stress events may contribute to cumulative pressures on coral reef health and influence reef resilience and recovery.

Although land reclamation activities were not taking place near the coral reef sites surveyed in the present study, two crown-of-thorns starfish (Figure 5b) were observed at Hurasdhoo, which exhibited the highest coral mortality. Coral mortality caused by bleaching can be compounded and/or exacerbated by crown-of-thorns starfish, which favor branching corals as prey [34], and likely contributed to the higher reported mortality at this reef site.

The 2016 bleaching event resulted in lower coral mortality than the 1998 event and initial recovery has been faster [54]. By May 2017 hard coral cover had increased to a mean of approximately 30% (at eight reef sites surveyed across the atolls of Ari Felidhoo, Gaafu Alifu (Suvadiva), North Malé, South Malé, Rasdhoo, and Thoddoo), however, *Acropora* spp. had yet to show evidence of recovery at that time [54]. Current research shows that recovery trajectories are following different trends post 1998 and post 2016 bleaching events [54]. These differences are not surprising given that local human pressures have increased while pre-bleaching coral assemblage and reef health differed. Though faster recovery rates are positive for these reefs, the projected increases in both the frequency and intensity of bleaching events, lengthy recovery timeframes, and local disturbances suggest that Maldivian reefs may not have time to recover before the next severe bleaching event [35,54]. It is therefore critical that policies and management actions are created and implemented that focus on reducing local and regional stressors. Effective management initiatives will be crucial in facilitating the future resilience of both Maldivian reefs and the livelihoods of those that depend on them.

4. Materials and Methods

4.1. Field Surveys

Coral mortality surveys were conducted from 2–8 December, 2016, approximately 7 months after the peak thermal stress occurred [7]. Six coral reef sites were monitored in the Alifu Alifu and Baa Atolls (Figure 1) in the Republic of Maldives using modified Reef Check International protocols [72]. In brief, within each reef, coral cover was surveyed on both the reef crest and reef slope of lagoon reefs. Three 20 m transect lines were surveyed at each depth, with 5 m between each transect (for a total of *n* = 6 transects per reef site, 60 m length per depth). Shallow transects were placed along a 4–5.5 m contour (average depth = 4.9 m ± 0.2), and deep transects were placed at a 9–11 m contour (average depth = 10.7 m ± 0.3). Photos were taken at 1 m interval points along each transect from approximately 1 m above the substrate and 0.5 m in each direction from the interval point. The shallow transect of one reef, Hurasdhoo House Reef, was omitted from analysis due to poor image quality.

4.2. Image Analyses

Photographs taken along each transect were assessed to determine the percentage of cover of benthic organisms and substrate. Each photograph contained approximately one square meter of the substrate. A grid was placed over each image to aid in the calculation of substrate proportions. In every photograph each component of the benthic substrate was recorded as a percentage of the total area and rounded to the nearest 5%. The categories that were used to determine benthic substrate included the 10 Reef Check International substrate categories, including hard coral, soft coral, recently dead coral, nutrient indicator algae, sponge, rock, rubble, sand, silt, and other [72].

Only data in the hard coral category were analysed for the purpose of this study. Insufficient numbers of some growth forms in the photographs limited the morphological categories to two: branching and massive, within the first of which corymbrose corals were grouped with branching and within the second of which sub-massive corals were grouped with massive (see Table 2).

Table 2. Categories used to characterize benthic substrate during image analysis.

Category	Description
Live hard coral	Live coral that is pigmented. Split into three morphology categories.
Bleached hard coral	Live coral that appears white or fluorescent in color and has lost normal pigment. Tissue has not been colonised by any algae and is therefore considered to still be alive.
Recently dead hard coral	Coral colonies that have recently died. Skeletons had a light covering of turf algae that distinguish them from translucent tissue in bleached coral and pigmented tissue in live coral. Algae cover was not well established and there was no breakdown of skeletal structure, suggesting coral mortality was recent.

Each of the hard coral categories were grouped by growth form and health status, including live branching hard coral (BC), massive hard coral (MC), and hard coral of other growth forms (HC). Those corals that were visibly bleached with translucent tissue covering their skeleton were classified as bleached branching corals (BBC), bleached massive corals (BBM), and bleached corals of other growth forms (BHC). Those corals that were recently dead were also classified into their respective growth forms, including recently dead branching corals (RDBC), recently dead massive corals (RDMC), and other recently dead corals (RDHC).

Each of the hard coral categories used in the analysis are illustrated in Figure 6. These photographs illustrate the specification of recently dead coral in both massive and branching colonies as opposed to coral that has been dead for an extended period that has since turned to rock or rubble (Figure 6). Examples are included from both shallow and deep transects across various reef sites (Figure 6).

4.3. Statistical Analyses

To assess the impact of reef site, depth, and morphology on the percentage of cover of live and recently dead coral, data were analysed using generalised linear mixed models (GLMM, R version 3.6.3 [73]). The influence of reef, morphology, and depth was investigated using a full subsets model selection approach [74]. Following convention, the simplest model with the lowest Akaike information criterion was considered optimal [74]. A null model with only the intercept and random effect was included to determine whether any of the included variables were useful predictors of coral cover. The percentage of live or recently dead hard coral was modelled in relation to reef site, coral morphology, and transect depth, with transect included as a random effect. The model used a Tweedie distribution with a log link and was modelled using the glmmTMB function within the glmmTMB package [75].
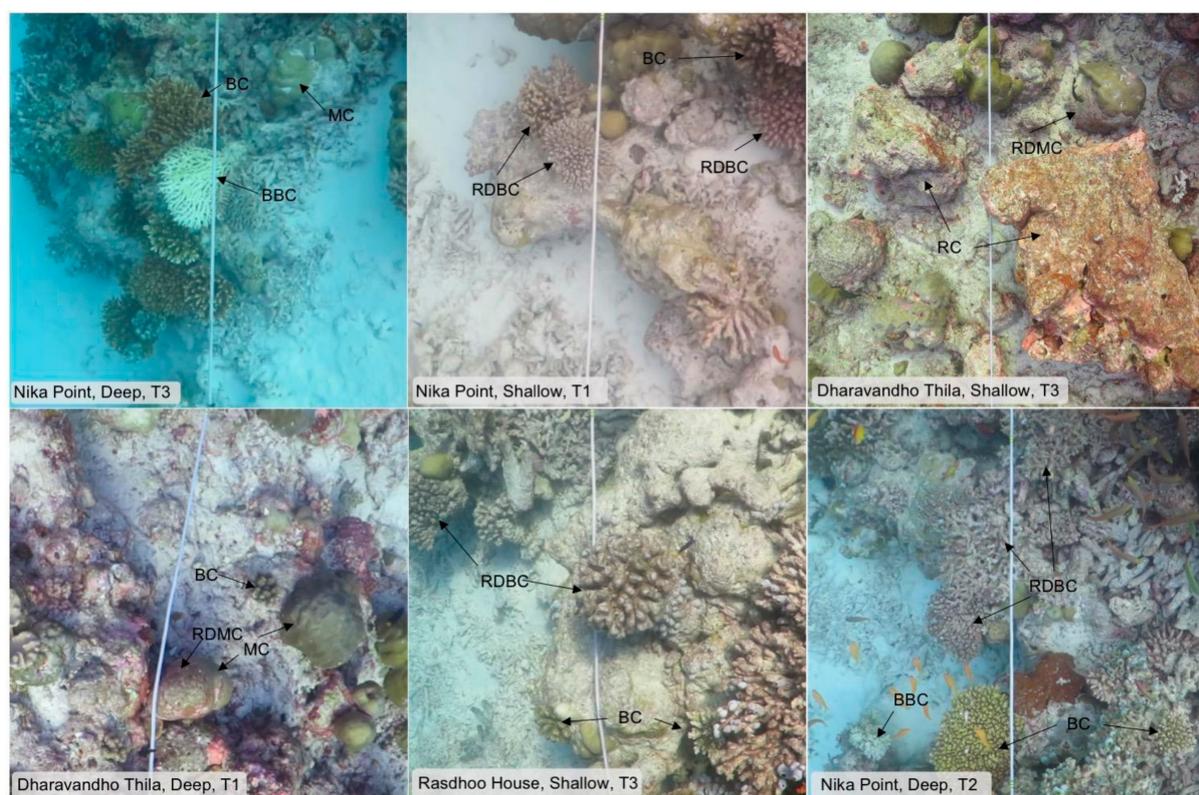
Figure 6. Examples of different coral health categories. The legend on each image indicates the site name (see Figure 1), transect depth (either deep or shallow), and number (T1, T2, or T3), along with the recorded coral health category. Coral health abbreviations include live branching coral (BC), bleached branching coral (BBC), recently dead branching coral (RDBC), live massive coral (MC), and recently dead massive coral (RDMC).

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