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Evidence of coral bleaching avoidance, resistance and recovery in the Maldives during the 2016 mass-bleaching event

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ABSTRACT: During the third global coral bleaching event in 2016, the Maldives experienced elevated water temperatures, inducing coral bleaching. We recorded the bleaching intensity and mortality of coral communities in different habitats, depths and wave exposure conditions around North Ari Atoll in the central Maldives to investigate the effect of physical and biological factors that may contribute to bleaching avoidance, resistance and recovery. Approximately 50% of coral cover bleached and ~20% died, with significant variation with wave exposure and depth. Deeper wave-exposed reefs were dominated by bleaching resistant massive and encrusting growth forms and experienced less thermal stress than shallow sheltered reefs. Shallow sheltered reefs showed rapid recovery from the previous mass-bleaching event in 1998, regaining high coral cover dominated by branching and tabular growth forms by 2015. However, these bleaching-sensitive growth forms experienced high bleaching and mortality in 2016, causing greater coral loss. Several of the reefs in central Ari Atoll simultaneously experienced a crown-of-thorn starfish (COTS) outbreak, resulting in very degraded reefs that lacked any apparent resilience in 2017. Our findings demonstrate the complex interactions between different components of resilience. In this case, wave exposure and depth appeared to promote avoidance and resistance of corals to bleaching, but reduced their recovery potential, while the reverse was true for shallow sheltered reefs. The resilience of reefs in the Maldives to date appears to be the result of low thermal and anthropogenic stress; therefore, their future condition will depend on the frequency and intensity of bleaching events and the level of human pressures such as construction and fishing.

KEY WORDS: Coral bleaching · Resilience · Thermal stress · Resistance · Recovery · Maldives

1. INTRODUCTION

Severe coral bleaching and mortality have impacted most coral reefs globally during recent decades, often on more than one occasion (Heron et al. 2016). Observations of the ecological impact of these events have identified important factors that help reduce bleaching damage and promote recovery (West & Salm 2003, Obura & Grimsditch 2009). There are numerous factors that can promote reef resilience to coral bleaching: those that reduce exposure to bleaching conditions (e.g. cold water upwelling, physical shading from sunlight, wave exposure); those that increase coral resistance to bleaching (e.g. symbiont clade, coral growth form and taxon); and those that improve recovery from disturbance (e.g. coral recruitment, fish herbivory, water quality) (Loya et al. 2001, Baker 2003, Obura 2005, McClanahan et al. 2012, Darling et al. 2013). In recent years, empirical evidence has demonstrated these principles, but with a wide variety of outcomes that are sometimes contradictory. Some studies have shown that bleaching susceptibility of corals can be reduced with repeated bleaching experience (e.g.

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Guest et al. 2012, Penin et al. 2013, Langlais et al. 2017), whereas others recorded no changes in susceptibility (e.g. Hughes et al. 2017). Long water retention times in sheltered areas are conditions that have been proposed to locally increase thermal stress, leading to higher bleaching levels and more thermally tolerant corals (e.g. Grimsditch et al. 2010, Obura & Mangubhai 2011, Shedrawi et al. 2017). However, observations from elsewhere found higher bleaching in fore reef areas, for which the calm conditions during a bleaching event were more stressful (McClanahan et al. 2007).

One element of coral bleaching that is widely recognised is that protection (i.e. reducing local anthropogenic stressors) does not reduce bleaching response during acute thermal stress, but can improve the recovery potential of these reefs post-bleaching (Wilson et al. 2012, Darling et al. 2013, van Oppen et al. 2017). Hence, an important element of coral reef management includes identifying areas least likely to be affected by bleaching and protecting them against local stressors to maximise resilience (Bellwood et al. 2004, Anthony et al. 2015). A lack of historical baselines hampers our understanding of the ecological impact of past disturbances on reef communities today, and what should represent a natural climax community (Knowlton & Jackson 2008). In addition, the uncertainty around possible synergies and interactions between multiple stressors makes it difficult to ascertain how reefs will respond in different natural and anthropogenic contexts (Ateweberhan et al. 2013, Darling et al. 2013, Fabricius et al. 2013).

In the aftermath of the last global bleaching event in 1998, coral reefs in the Maldives were noted for their resilience and recovery from bleaching impacts. Despite losing extensive (~90%) coral cover in 1998 (Zahir 2000), the reefs quickly became colonised with coral recruits (Edwards et al. 2001). By 2010, reefs around the archipelago had regained high (50–80%) coral cover with a dominance of *Acropora* (Morri et al. 2015, Tkachenko 2015) similar to the historical state of reefs in the Maldives documented by the 1958 'Xafira' Expedition (Scheer 1974) and by an expedition to Addu Atoll in 1964 (Stoddart 1966). Allison (1995) noted that the reefs in the Maldives were hit by bleaching in 1983 and 1987, and by the impacts of resort construction and crown-of-thorns starfish (COTS) *Acanthaster planci* outbreaks in the 1980s and 1990s. During this period, some reefs were also impacted by coral mining, to supply building materials to the growing tourist industry and general economy (Brown & Dunne 1988). Maldivian reefs have recovered from multiple disturbances and remained ecologically resilient, recovering in just 5–10 yr from acute mortality events (Morri et al. 2015, Pisapia et al. 2016).

North Ari Atoll in the central Maldives is an interesting case-study for observing the impact of multiple stressors on a resilient reef system (Pisapia et al. 2016). The central Maldives has detailed historical records of reef condition from over 40 yr ago that provide information about the historical community (Stoddart 1966, Scheer 1974), along with more recent records of reef condition, coral community and anthropogenic stressors (Allison 1996, McClanahan 2000, Zahir 2000, McClanahan & Muthiga 2014, Morri et al. 2015, Tkachenko 2015, Moritz et al. 2017). We present data on the impact of bleaching in the atoll in 2016 under a variety of environmental conditions determined by wave exposure, depth and reef-zone. We document the bleaching of corals on reefs simultaneously impacted by the COTS and examine the mortality and initial recovery 1 yr after bleaching in order to understand the future persistence of coral-dominated reefs in the Maldives.

2. MATERIALS AND METHODS

2.1. Field surveys

Bleaching surveys took place from 17–29 May 2016, between 2 and 4 wk after peak thermal stress occurred. Surveys took place at 2 spatial scales: a local scale around Madivaru (max. site distance: ~2 km), and a regional scale around North Ari (max. site distance: ~40 km) (Fig. 1) using Rapid Health and Impact Surveys (RHIS), which record key indicators of anthropogenic stress on reefs (Beeden et al. 2014). In each RHIS replicate, an observer swam around a circular area with a 5 m radius (80 m^2) and visually estimated the cover of various benthic categories and bleaching cover to the nearest 5%. Major benthic categories (live hard coral, recently killed coral [RKC], soft coral, macroalgae, rock, rubble and sand) were estimated. On COTS-affected reefs, care was taken to inspect white coral colonies to determine whether the coral was recently killed or alive, but bleached. The cover of different coral growth forms (massive, foliose, encrusting, branching, table, corymbose and solitary) were then visually estimated as a percentage of total coral cover. Finally, the percentage cover of bleached coral (completely white tissue) in each growth form was estimated, and bleached coral cover was expressed as percentage of total coral cover.

At Madivaru, 45 replicates were collected from 5 sites: 2 in the lagoon, 2 in channels in the atoll rim

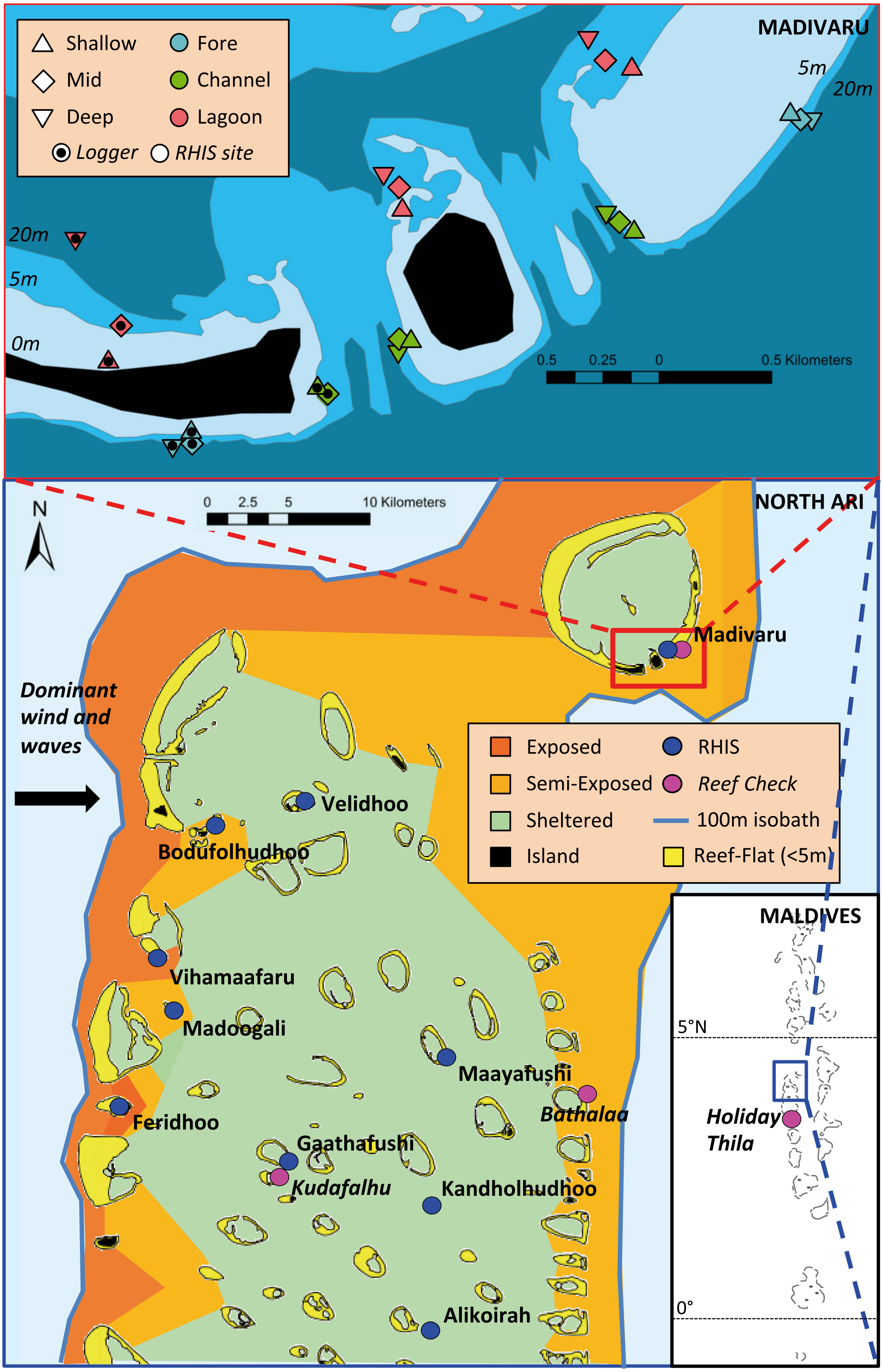

Fig. 1. North Ari Atoll and an inset of Madivaru showing the position of survey sites. Reef Check site Holiday Thila is not displayed and is located at 3° 29′ 41″ N, 72° 49′ 23″ E in the south of the atoll. RHIS: Rapid Health and Impact Surveys

and 1 on the fore reef. At each site, 9 replicates were collected, with 3 replicates at 3 depth zones (deep: 20–25 m, mid: 8–12 m and shallow: 2–5 m). At the scale of North Ari, 74 replicates were collected from 10 islands, all from the fore-reef slope at a mid-depth. Most islands had 3 sites, in which 3 RHIS replicates were conducted, giving 9 replicates per island; but Madivaru, Madoogali and Vihamaafaru had incomplete sampling. Replicates were grouped into 3 levels of wave exposure: exposed (n = 15, island = 2), semi-exposed (n = 15, island = 3), and sheltered (n = 44, island = 5). Exposure was estimated based on the reefs' aspect to dominant wind and waves from the west and the presence of deep water. Exposed sites on the outer western edge of the atoll were exposed daily to large surf and were in close proximity to deep oceanic water; semi-exposed sites were either on the eastern lee-side of North Ari near to deep oceanic water or along channels near the western windward-side; while sheltered sites were found in the centre of the atoll where the maximum depth was 30–40 m. Three sheltered islands surveyed in the central part of the atoll had been affected by a recent COTS outbreak (Gaathafushi, Kandholhudhoo and Alikoirah), giving 26 RHIS replicates affected by COTS and 18 replicates on sheltered reefs unaffected by COTS.

Logistical constraints prevented us from revisiting the same replicates after bleaching occurred, but additional data was provided from the Reef Check Maldives monitoring programme at shallow and mid-depth fore reefs on 2 sheltered and 2 semi-exposed islands. The earliest records of these reefs using Reef Check methods were from 2005 in Madivaru at a site <200 m from the RHIS replicates. This site, along with Kudafalhu (a sheltered island 1 km away from Gaathafushi also affected by COTS), Bathalaa (a semi-exposed island on the lee edge of the atoll) and Holiday Thila (3° 29′ 41″ N, 72° 49′ 23″ E; a sheltered 200 m long patch reef at the south of Ari Atoll), were monitored in 2011, 2013, 2015, 2016 and 2017 (3 and 15 months after thermal stress). Reef Check methods (Hodgson et al. 2006) recorded the benthic cover of major categories (live hard coral, RKC, soft coral, sponge, macroalgae, rock, rubble, sand and 'other') along 100 m long point intercept transects (PITs) at shallow and mid-depths. Each PIT was divided into four 20 m stretches separated by 5 m, with a recording point every 0.5 m interval. In July 2016, photo-quadrats were used to assess recent mortality of corals at the different sites and depths during Reef Check surveys. Photos were taken of 50 × 50 cm (0.25 m^2) quadrats placed near the PIT. Some photos were discarded because of poor quality, resulting in 5 (1.25 m^2) to 21 (5.25 m^2) quadrats at each site–depth giving a total of 94 quadrats (23.5m^2). RKC tissue was identified by the presence of intact corallite and/or distinctive new growth of green and red turf algal filaments on a white coral skeleton, unlike the grey turf mats on older and more eroded coral skeletons. All coral colonies >5 cm in diameter were counted, with their genus and growth form noted and condition defined as either alive (>90% tissue alive), partially killed coral (PKC; 10–90% recently killed tissue) or RKC (>90% recently killed tissue).

2.2. Evaluating thermal stress using satellite and *in situ* loggers

Historical thermal stress in North Ari was evaluated using sea surface temperature (SST) data derived from the advanced very high resolution radiometer (AVHRR) satellite, which has a resolution of 0.25° (~30 km^2) and records daily. The AVHRR pixel used was centred at 4° 7′ 30″ N, 72° 52′ 30″ E and data from 1982–2016 were accessed from the Indian National Centre for Ocean Information Services (http://las.incois.gov.in/las). The Southern Oscillation Index (SOI) for the time series was derived from the Australian Bureau of Meteorology (www.bom.gov.au/climate/influences/timeline/). The mean annual (SST_{ann}), hottest month (SST_{max}) and coolest month (SST_{min}) temperatures were calculated for each year. The maximum monthly mean (MMM) expresses the average summer conditions to which corals are acclimatised (Liu et al. 2003). MMM was calculated as the average of the SST_{max} values during the 9 non-El Niño years (where SOI values were above −10) before 1998. The coral bleaching threshold was assumed to be MMM +1°C (Liu et al. 2003). The severity of thermal stress in each year of the time series was calculated using degree heating weeks (DHWs), where 1 DHW is a +1°C anomaly above MMM lasting for 1 wk (Liu et al. 2003).

Local variations in temperature around Madivaru were recorded using Hobo® U22-001 loggers with ±0.2°C accuracy. Recordings were taken at shallow, mid and deep depths on fore, channel and lagoon reef zones every 2 h from 1 February 2015 until 31 August 2016. The similarity between daily satellite (SST) and logger (LOG) recordings was estimated using Pearson's correlation coefficient. Acute thermal stress in 2016 was expressed as the mean temperature during May, the hottest month (LOG_{max}^{16}), and as the absolute maximum temperature reading during 2016 (LOG_{abmax}^{16}). Chronic thermal stress was estimated using the mean annual range, absolute annual range and daily range in temperatures. Mean annual range was calculated by taking the difference between average temperature in the hottest month of 2015 (LOG_{max}^{15}) and the coolest (LOG_{min}^{15}) and absolute range as the difference between the highest and lowest absolute temperature reading in 2015 ($LOG_{abmax}^{15} – LOG_{abmin}^{15}$). Daily range was calculated by taking the average difference between the daily highest and lowest temperature recordings for the entire time series.

2.3. Data analysis

The variation in percentage cover of bleached coral in RHIS replicates was explored using linear mixed models (LMMs). At both spatial scales (Madivaru and North Ari) the explanatory variable 'resistant coral cover' was used, by taking the percentage cover of bleaching-resistant massive and encrusting growth forms, assuming that branching, corymbose, table and solitary growth forms were bleaching-sensitive (van Woesik et al. 2011, Darling et al. 2013). Foliose coral could be either bleaching-sensitive taxa (e.g. *Montipora*) or bleaching-resistant taxa (e.g. *Echinopora*), and hence 50% of this form's cover was assigned to resistant cover. Although this is an arbitrary solution, we anticipated that this would not unduly affect the bleaching sensitivity classes, as foliose coral was only seen in 4 RHIS replicates and covered <10% in these areas. The correlation between bleached and resistant coral cover was investigated using Pearson's correlation coefficient.

Additional explanatory variables for bleached coral cover at the scale of Madivaru included fixed effects of 'depth' and 'reef zone', and the model included 'site' as a random factor. The regional comparison of North Ari included the additional variable 'wave exposure' and used 'island' as a random factor. COTS-affected reefs were assumed to have a heavily modified coral community and were excluded from the main North Ari analysis, meaning this model used 48 RHIS replicates from 7 islands. A third LMM was conducted to investigate the level of bleaching on sheltered reefs between COTS-affected and unaffected reefs, using 'COTS' as the explanatory variable and 'island' as the random variable (n = 44, island = 5). In each of the 3 analyses the null model (bleach ~ 1 + [random]) was compared with successive models including fixed effects and their interactions. The performance of models was compared using Akaike's information criterion (AIC), and log-likelihood (LL) outputs, and likelihood ratio tests (LRT) were used to determine if the increased power of the model was statistically significant. Differences in the benthic cover of categories other than bleached coral, but relevant to the bleaching response and general health of the reef (e.g. macroalgae, RKC and resistant cover), were compared between groups of RHIS replicates using unpaired *t*-tests.

Coral mortality from Reef Check photo-quadrats was analysed using a binomial logistic regression (BLR) where the dependent variable was total or partial colony survival (alive) or recently killed. The explanatory variables were bleaching resistance (resistant or sensitive) based on taxonomic identification (Obura & Grimsditch 2009, van Woesik et al. 2011), depth (shallow and mid) and wave exposure (semi-exposed and sheltered). The significance of explanatory variables was evaluated using LRTs and by comparing AIC values of successive models in a similar manner to the LMMs above. All analyses were conducted using R v.3.5.1 software (R Core Team 2018) and LMMs were implemented using the package 'lmerTest' (Kuznetsova et al. 2017). Means ± SE are reported.

3. RESULTS

3.1. Thermal stress

The SST_{ann} in North Ari from 1982–2016 was 28.76 ± 0.048°C (mean ± SE), varying from 27.85 ± 0.044°C during the coolest month (i.e. SST_{min}) to 29.68 ± 0.067°C in the warmest (SST_{max}) (Fig. 2). During normal years, the temperature was ~29°C from February–September and ~28°C from October–January, but with periodic (1–5 wk) fluctuations in temperature which spanned the entire annual range. The 3 hottest periods occurred in 1982, 1998 and 2016, where SSTs exceeded the bleaching threshold over several weeks and enough DHWs (>6) accumulated to cause extensive coral bleaching (Figs. 2 & 3). In these years, severe El Niño-Southern Oscillation (ENSO) events (SOI < −20) caused SSTs to rise a further 1–2°C above normal conditions during March, and remained at >30°C until June.

Most temperature loggers in Madivaru recorded their highest temperatures during the first week in May 2016, with absolute maximum temperatures (i.e. LOG_{abmax}^{16}) of >31°C and average temperatures for May (i.e. LOG_{max}^{16}) of > 30°C being recorded at

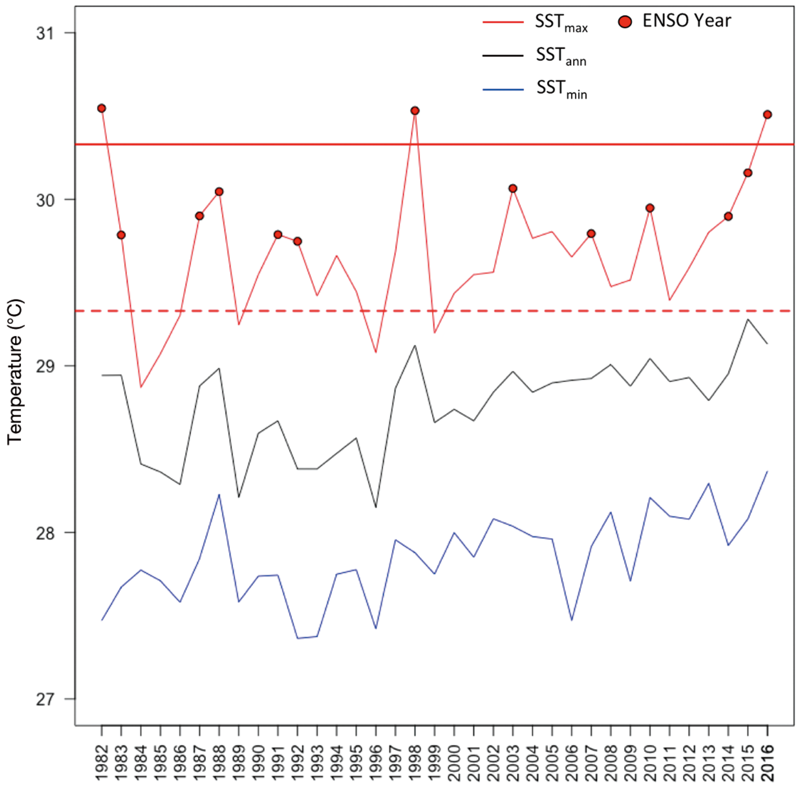

Fig. 2. Annual sea surface temperature (SST) profiles in North Ari from 1982–2016, showing the average of all months (SST_{ann}), the coolest month (SST_{min}) and the hottest month (SST_{max}). Horizontal dashed red line: maximum monthly mean (MMM); horizontal solid red line: bleaching threshold (MMM + 1°C). El Niño-Southern Oscillation (ENSO) years with Southern Oscillation Index values below −10 are displayed

all zones and depths (Fig. 4a). The highest LOG_{abmax}^{16} and LOG_{max}^{16} temperatures were recorded in the shallow lagoon, which, unlike the other areas, occurred in early April. The lowest LOG_{abmax}^{16} temperature was in the deep lagoon and the lowest LOG_{max}^{16} temperature was on the deep fore reef. The temperatures recorded on most loggers were highly correlated with the AVHRR satellite-derived SSTs (R^2 = 0.939–0.947). The logger on the deep fore reef had slightly lower correlation (R^2 = 0.929), and the logger in the shallow lagoon was much less correlated with the AVHRR readings (R^2 = 0.876). The deep fore-reef had the narrowest mean range in 2015 of just 1.8°C between SST_{max}^{15} and SST_{min}^{15}. Interestingly, the fore-reef 20 m logger had the widest absolute range, with temperatures of <26°C on occasions, when sudden drops (>1°C in <6 h) in temperature occurred independently of other depths in this habitat (Fig. 4b). The shallow lagoon logger recorded the largest mean, absolute and daily range, experiencing large (1–2°C) diel fluctuations (Fig. 4c)

3.2. Local variation in reef type and bleaching around Madivaru

Coral communities varied greatly between zones. The fore-reef coral community in May 2016 was dominated by bleaching-resistant growth forms and moderate coral cover (21.3 ± 1.88 %) on deep reefs increasing to high cover (65.5 ± 2.93 %) in the shallows (Fig. 5). In the lagoon, high coral cover (67.0 ± 4.04 %) was observed at all depths and consisted of thermally sensitive branching, tabulate and corymbose growth forms. The channel had low coral cover (15.5 ± 1.53 %) at all depths, with high levels (52.2 ± 3.08 %) of unconsolidated substrate (sand and rubble) (Fig. 5a). In the channel, the deep replicates had the highest proportion of bleaching-sensitive corals, whereas in the lagoon and fore reef, the shallows had the highest proportion of sensitive corals (Fig. 5b). There was a reasonably strong negative correlation (r = −0.679) between resistant coral cover and bleached coral cover in Madivaru, with fore reefs having the most resistant coral and lagoons the least (Figs. 5b & 6). The LMM including the 3 fixed effects (bleach ~ resist + depth + zone + [site]) outperformed the null model (χ^2 = 40.24, df = 5, p < 0.001) (Table 1), indicating all of these variables influenced bleached coral cover. Adding interaction between resistant coral cover and depth (bleach ~ resist × depth + zone + [site]) did not improve the predictive power of the additive model (χ^2 = 3.21, df = 2, p = 0.201), but the interaction between resistant coral and zone (bleach ~ resist × zone + depth + [site]) did significantly improve the predictive power (χ^2 = 11.36, df = 2, p = 0.003), suggesting that bleaching-resistant growth forms covary with reef zone but are consistent across depths within these zones.

3.3. Reef condition and bleaching response in North Ari

Coral community on reefs in North Ari varied with wave exposure and COTS impacts. In exposed replicates, the coral cover was low (12.7 ± 2.07 %), half of the cover consisted of resistant coral growth

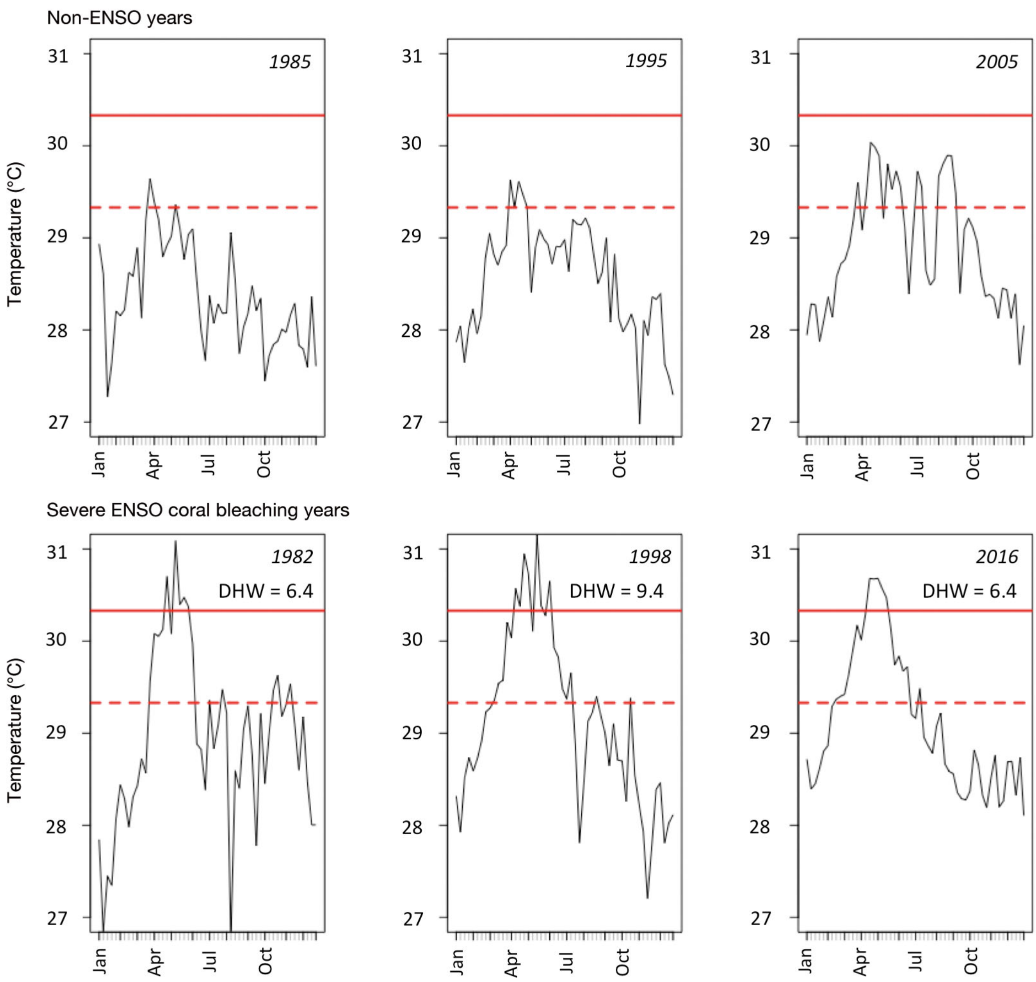

Fig. 3. Sea surface temperature (SST) profiles in North Ari during normal non-El Niño-Southern Oscillation (ENSO) years (1985, 1995, 2005) and the 3 most severe ENSO events during the time series (1982, 1998 and 2016). Black line: weekly average of SSTs derived from the advanced very high resolution radiometer satellite; horizontal dashed red line: maximum monthly mean (MMM); horizontal solid red line: bleaching threshold (MMM + 1°C). Degree heating weeks (DHWs) for severe ENSO years are displayed

forms (55.3 ± 5.31%) (Fig. 7), and had low bleached coral cover (24.9 ± 6.16%). Semi-exposed reefs had high coral cover (42.7 ± 5.35%) and low levels of unconsolidated substrate (23.0 ± 4.83%). These replicates had similar cover of resistant growth forms (45.0 ± 5.26%) as exposed reefs, but had higher bleached cover (36.4 ± 5.95%). Sheltered islands unaffected by COTS had moderately high coral cover (29.8 ± 3.98%), low cover of resistant corals (21.7 ± 2.78%) and similar levels of bleaching (34.1 ± 7.39%) as semi-exposed sites. Replicates at all wave exposure levels had low cover of macroalgae (2.4 ± 0.62%) and RKC (2.4 ± 0.42%). Resistant coral cover was not significantly different between exposed and semi-exposed replicates (t = 1.37, df = 28.0, p = 0.182), but was significantly lower on sheltered reefs compared to exposed and semi-exposed reefs combined (t = −6.05, df = 45.9, p < 0.001). There was a weak negative correlation (r = −0.348) between the cover of bleached and resistant corals (Fig. 8), but with a variable bleaching response in replicates with low resistant coral cover. Of the 24 replicates with <20% resistant corals, 8 had low bleaching (<30%), while the rest had high bleaching (>50%). In the LMMs, adding resistant coral cover as a variable significantly improved the model compared to the null model (χ^2 = 6.44, df = 1, p = 0.011), but adding wave exposure to this model did not result in better explanatory power (χ^2 = 2.01, df = 2, p = 0.366) (Table 2).

Reefs impacted by COTS had moderately low coral cover (16.4 ± 3.58%) and resistant coral cover (31.8 ± 4.87%). Kandholhudhoo and Alikoirah had similar growth forms to other sheltered reefs, where-

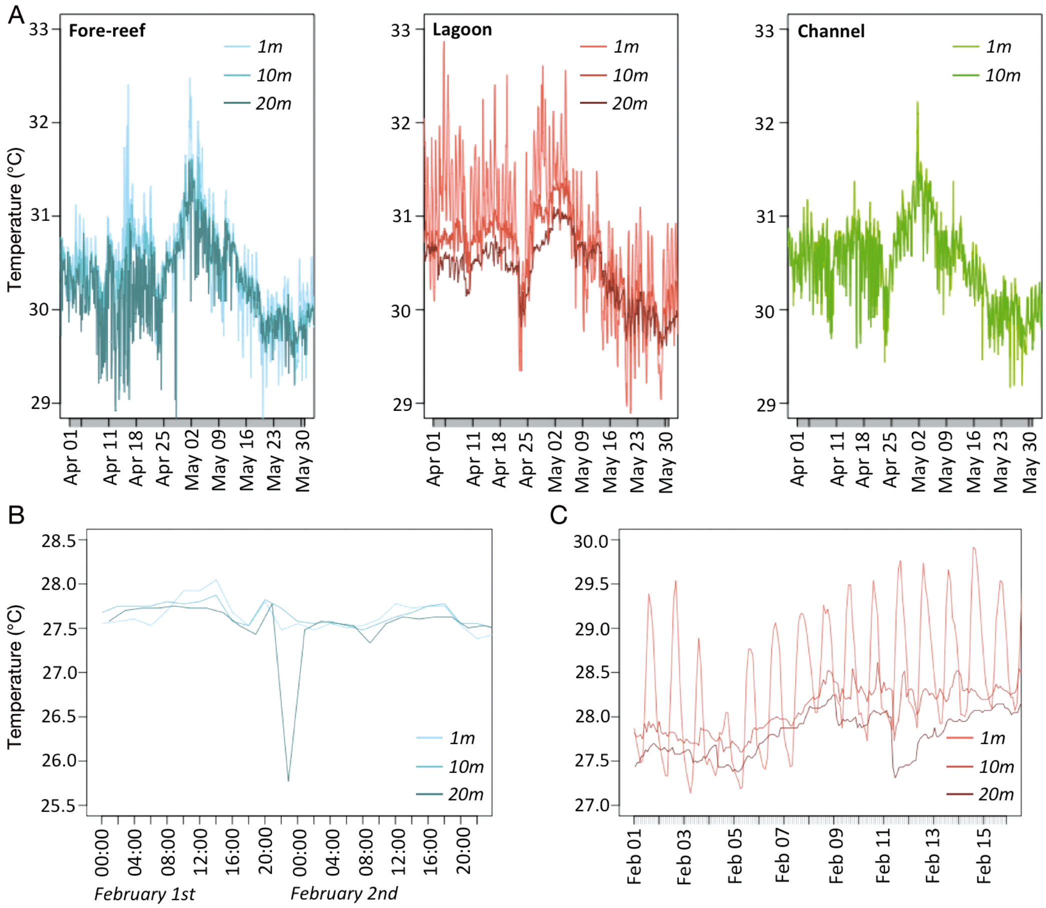

Fig. 4. Temperature logger readings from Madivaru. (A) Fore reef, lagoon and channel temperature profiles during peak thermal stress (1 Apr–30 May 2016); examples of (B) a large (>1°C) temperature drop observed at 20 m on fore reef but not at other depths (1–2 Feb 2015), and (C) daily fluctuations in the lagoon at all depths (1–15 Feb 2015)

as Alikoirah, which had the lowest coral cover (10.6%) of any island, had a community more similar to exposed reefs with more bleaching-resistant encrusting and massive corals. The difference between resistant coral at COTs-affected and unaffected sheltered reefs was not significant (t = −1.80, df = 38.0, p = 0.080). There was significantly more macroalgae in COTS-affected replicates (t = 4.19, df = 26.6, p < 0.001) (COTS: 21.3 ± 4.47%; no COTS: 2.2 ± 0.81%) and significantly more RKC (t = 3.07, df = 39.5, p = 0.004) (COTS: 7.9 ± 1.26%; no COTS: 3.3 ± 0.79%). Bleached cover was higher (50.8 ± 5.85%) in COTS replicates compared to other sheltered reefs (34.1 ± 7.39%), but the null LMM (bleach ~ 1 + [island]) was not significantly improved by adding COTS as an explanatory variable (χ^2 = 1.68, df = 1, p = 0.195) (Table 3), indicating COTS presence did not alter bleaching response at sheltered islands.

3.4. Recent trends for North Ari Atoll and post-bleaching mortality

The earliest Reef Check records in Madivaru showed moderate coral cover at both shallow (39.4%) and medium depths (34.4%), which was maintained (~40%) from 2011 to 2017 (Fig. 9). On Bathalaa, coral cover was low in 2011 (mean: shallow, 10.0%; medium, 17.5%), but rose to 41.9 and 41.3%, respectively, in shallow and medium depths by 2015. Both semi-exposed sites were also characterised by dominance of bare rock and low (<25%) levels of unconsolidated substrate. In 2011, Kudafalhu had high coral cover (shallow, 73.8%; mid, 35.0%) dominated by table and branching acroporids (e.g. *Acropora hyacinthus*) at shallow depths, but also high levels of loose sediment at mid depths (48.1%). Between 2011 and 2015, coral cover decreased by 20% on the reef flat (from 73.8 to 58.8%) and 52%

at medium depths (from 35.0 to 16.9%) as a result of the COTs outbreak and storm damage in 2015. Holiday Thila also had moderately high coral cover in 2011 (shallow, 50.0%; medium, 30.6%), which had decreased to 14.4% (70% decrease) and 11.3% (63% decrease), respectively, in 2015.

In photo-quadrats from 2016, semi-exposed islands had high colony density (23.9 ± 1.91 m^{-2}) and were dominated by bleaching-resistant colonies (77.0%), whereas sheltered islands had lower colony abundance (12.0 ± 1.38 m^{-2}) with fewer bleaching-resistant corals (35.4%) (Table 4). Colony density was higher at shallow sites (23.3 ± 2.41 m^{-2}) than at mid-depths (16.0 ± 1.36 m^{-2}), and resistant corals were more prevalent at mid-depth (78.3%) than at shallow sites (62.1%). Madivaru at 5 m had the highest colony density of any site–depth (38.6 ± 5.79 m^{-2}) and the lowest proportion of bleaching-resistant colonies (56.3%) of semi-exposed site–depths. Just 6% of colonies from semi-exposed reefs were completely dead, with the highest mortality at Madivaru 5 m (14.1%), whereas sheltered reefs had much higher mortality (41.7%) The highest mortality was seen at Kudafalhu, where 68% of colonies at shallow depth and 55% of colonies at mid-depth were dead. High densities of COTS were spotted at Kudafalhu during surveys in July 2016, so not all of the mortality observed may have been due to bleaching. Branching and corymbose corals were completely dead in 56% (n = 36) and 28% (n = 26) of cases, respectively, whereas only 3% (n = 8) of massive and encrusting growth forms were recently killed and 9% (n = 30) partially killed. Survival for both bleaching-resistant and sensitive growth forms was higher on semi-exposed islands,

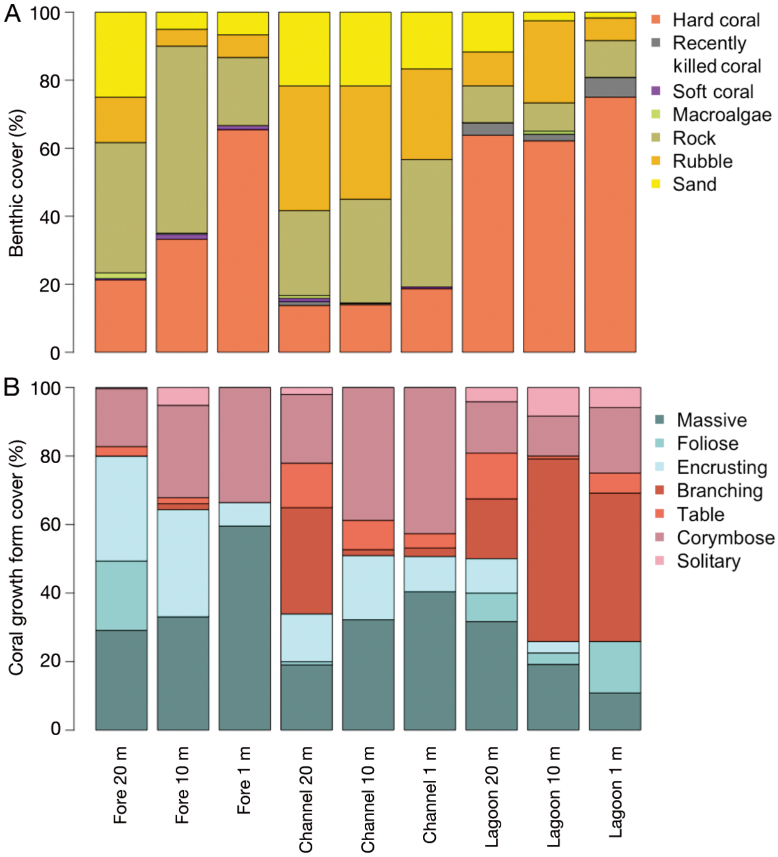

Fig. 5. Benthic composition of different depths and reef zones around Madivaru showing (A) total benthic cover of major categories and (B) growth forms of coral as a percentage of total coral cover

Table 1. Performance of linear mixed models to explain the variation in cover of bleached corals in Rapid Health and Impact Survey (RHIS) replicates from Madivaru, showing Akaike's information criterion (AIC) and log likelihood (LogLik) values for the models

Model	AIC	LogLik
~ 1 + (site)	418.8	−206.4
~ Resistant coral + (site)	404.1	−198.1
~ Resistant coral + depth + (site)	393.1	−190.6
~ Resistant coral + depth + habitat + (site)	388.5	−186.3
~ Resistant coral × depth + habitat + (site)	389.3	−184.7
~ Resistant coral × habitat + depth + (site)	381.2	−180.6

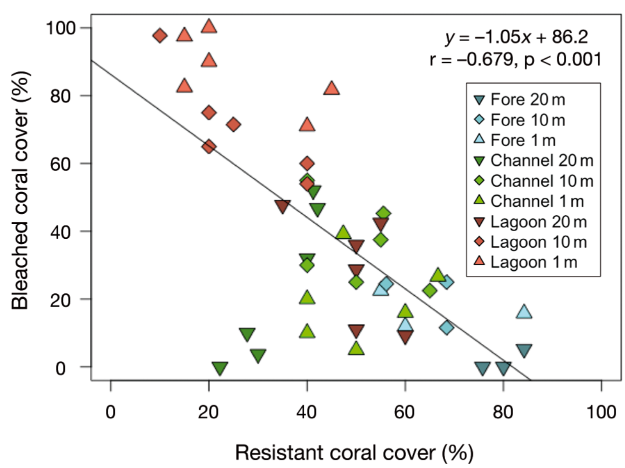

Fig. 6. Resistant versus bleached coral cover at Rapid Health and Impact Survey replicates from Madivaru, with zone and depth indicated. The fitted line from the linear model is indicated by a black line along with its equation and the Pearson's correlation coefficient of the bleached~resistant relationship

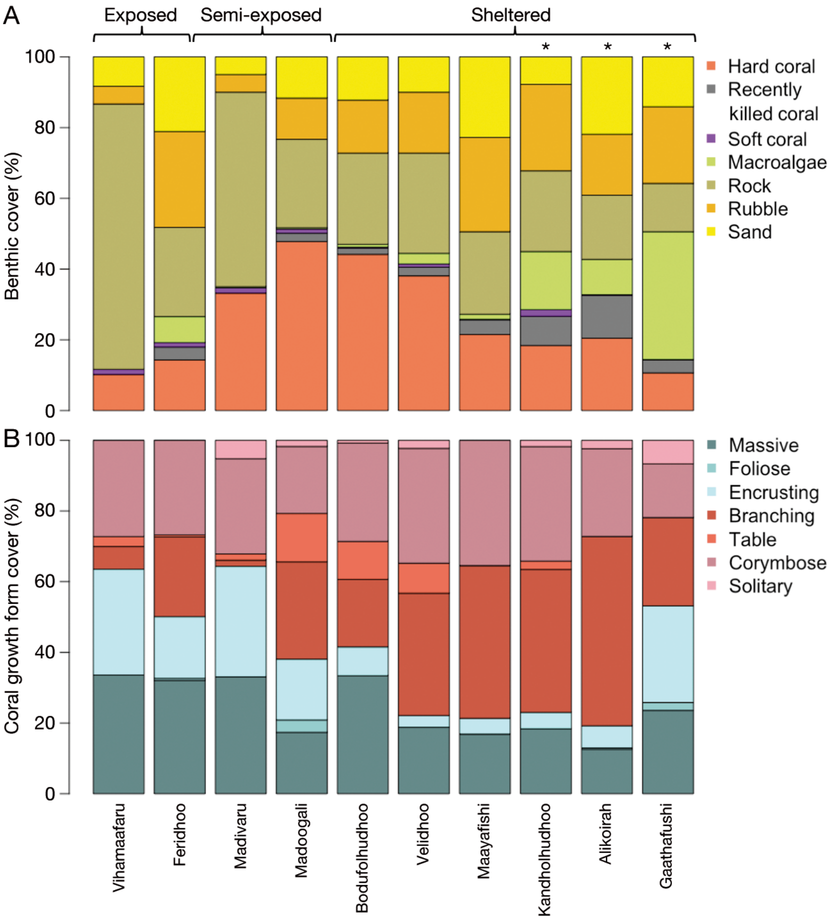

Fig. 7. Benthic composition of islands in North Ari assessed by Rapid Health and Impact Surveys in May 2016, showing (A) total benthic cover of major categories and (B) growth forms of coral as a percentage of total coral cover. (*) Crown-of-thorns starfish-affected islands

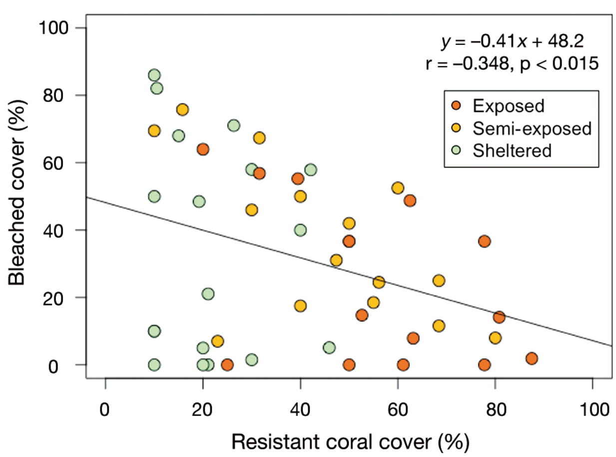

Fig. 8. Resistant versus bleached coral cover at Rapid Health and Impact Survey replicates from North Ari, unaffected by crown-of-thorns starfish, with wave exposure indicated. The fitted line from the linear model is indicated by a black line along with its equation and the Pearson's correlation coefficient of the bleached~resistant relationship

with just 21% mortality of sensitive forms compared to 58% mortality on sheltered reefs. The null BLR model of colony mortality was significantly improved by adding resistant coral (χ^2 = 87.2, p < 0.001) and exposure (χ^2 = 28.7, p < 0.001), whereas adding depth and the interaction between resistant coral and exposure did not improve the explanatory power (Table 5).

In 2017 (15 mo after peak thermal stress), shallow and mid-depth Bathalaa and shallow Madivaru increased in coral cover to ~15% and mid-depth Madivaru remained at >30% (Fig. 9). Sheltered islands showed continued decline in coral cover — which was most severe in Kudafalhu, with a further ~60% decrease in coral from 2016 levels resulting in a coral cover of 3% in the shallows and <1% at mid-depth in 2017.

4. DISCUSSION

4.1. Past bleaching impacts and recovery of Maldivian coral reefs

There were only 2 years (1982 and 1998) in North Ari's 33 yr satellite record from 1982–2015 where >4 DHWs were experienced. The most severe thermal stress was

Table 2. Performance of linear mixed models to explain the cover of bleached corals in Rapid Health and Impact Survey (RHIS) replicates from North Ari, excluding crown-of-thorns starfish-affected replicates, showing Akaike's information criterion (AIC) and log likelihood (LogLik) values for the models

Model	AIC	LogLik
~ 1 + (island)	455.8	−224.9
~ Resistant coral + (island)	451.4	−221.7
~ Resistant coral + exposure + (site)	453.3	−220.7

Table 3. Performance of linear mixed models to explain the cover of bleached corals in Rapid Health and Impact Survey (RHIS) replicates from sheltered sites in North Ari, showing Akaike's information criterion (AIC) and log likelihood (LogLik) values for the models. COTS: crown-of-thorns starfish

Model	AIC	LogLik
~ 1 + (island)	430.2	−212.1
~ COTS + (island)	430.5	−211.2

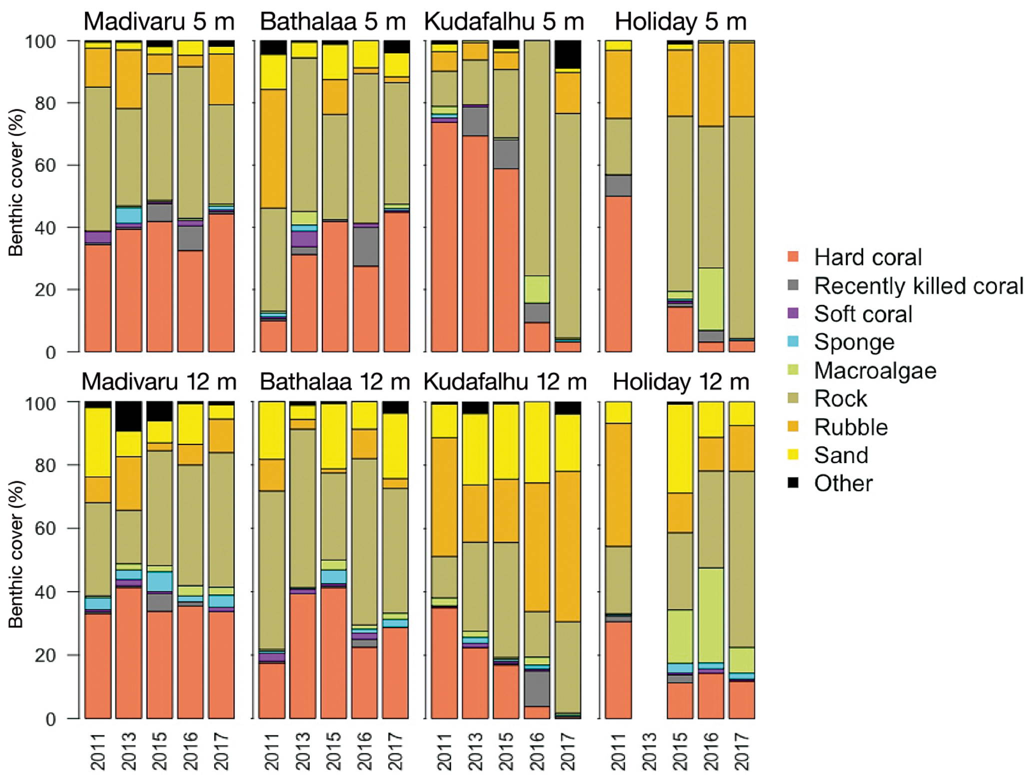

Fig. 9. Benthic cover from Reef Check transects during 2011–2017 in Madivaru, Bathalaa (semi-exposed), Kudafalhu and Holiday Thila (sheltered) at shallow and mid depths. Data are missing from Holiday Thila in 2013 because it was not possible to survey this site during that year

experienced in 1998, associated with extensive mortality (80–90%) on shallow reef flats in the central Maldives (McClanahan 2000, Zahir 2000, Edwards et al. 2001). Elevated temperature occurred on several occasions during El Niño years and caused bleaching (e.g. 2003, 2010 and 2015) with low levels of mortality in most locations (Tkachenko 2015, Pisapia et al. 2016), apart from some reefs in north Maldives where mortality in 2010 was extensive (Tkachenko 2012). In a recent global assessment of SST trends in coral reef regions, the Maldives were highlighted as a potential bleaching refuge because of the low occurrence of

Table 4. Photo-quadrat data from Reef Check sites at different sites, exposure and depth showing the sampling effort, mean colony density quadrat^{-1} (extrapolated to density m^{-2}), proportion of bleaching-resistant colonies and proportion of recently killed corals

Site (depth)	Quadrats	Area (m^2)	No. of colonies	Colony density (m^{-2})	Resistant colonies (%)	Recently killed colonies (%)
Madivaru (5 m)	14	3.50	135	38.6 ± 5.79	56.3	14.1
Madivaru (12 m)	9	2.25	53	23.6 ± 3.89	88.7	1.9
Madivaru (all)	23	5.75	188	32.7 ± 3.98	65.4	10.6
Bathalaa (5 m)	18	4.50	86	19.1 ± 2.25	93.0	0
Bathalaa (12 m)	21	5.25	95	18.1 ± 1.74	85.3	2.1
Bathalaa (all)	39	9.75	181	18.6 ± 1.38	89.0	1.1
Kudafalhu (5 m)	6	1.50	28	18.7 ± 2.25	28.6	67.9
Kudafalhu (12 m)	11	2.75	20	7.3 ± 1.18	25.0	55.0
Kudafalhu (all)	17	4.25	48	11.3 ± 1.72	27.1	62.5
Holiday (5 m)	11	2.75	36	13.1 ± 3.06	36.1	27.8
Holiday (12 m)	4	1.00	12	12.0 ± 1.63	66.7	0
Holiday (all)	15	3.75	48	12.8 ± 2.25	43.8	20.8
Semi-exposed	62	15.50	369	23.8 ± 1.91	77.0	6.0
Sheltered	32	8.00	96	12.0 ± 1.38	35.4	41.7
Shallow	49	12.25	285	23.3 ± 2.41	62.1	16.8
Mid	45	11.25	180	16.0 ± 1.36	78.3	7.7

Table 5. Performance of binomial logistic regression models to explain the mortality of corals in photo-quadrats from Reef Check sites, showing Akaike's information criterion (AIC) values, the deviance of the null model and residual deviance of successive models

Model	Residual deviance	AIC
~ 1	365.2 (null deviance)	367.2
~ Resistant coral	268.0	272.0
~ Resistant coral + exposure	239.2	245.3
~ Resistant coral + exposure + depth	236.2	244.2
~ Resistant coral × exposure	238.8	246.8

acute thermal stress to date and the slow rate of average and summer warming (Heron et al. 2016).

On the COTS-free shallow and sheltered reefs visited in 2016, coral cover was high, with a dominance of thermally sensitive branching, tabular and corymbose growth forms. There were 18 years between bleaching events in 2016 and 1998, during which coral communities recovered (Morri et al. 2015, Pisapia et al. 2016). The community prior to 2016 in these reef zones appeared to be similar to the earliest baseline condition for North Ari (Scheer 1974), with a dominance of Acroporidae including large mature colonies. Several factors may be responsible for this high recovery rate: high recruitment on reefs of the Central Indian Ocean allow many new colonies to settle after disturbance (Sheppard 1999, Edwards et al. 2001, Cardini et al. 2012), while high light levels, good water quality and low water pollution promote rapid growth (McClanahan et al. 2012, Shedrawi et al. 2017). Many corals re-grow from surviving living tissue patches if their skeletons remain intact (Diaz-Pulido et al. 2009), which may have been an important factor in the recovery on sheltered reefs in the Maldives, where low wave action allowed skeletons to remain intact (Pisapia et al. 2016).

The impacts of the recent COTS outbreak in the central part of North Ari Atoll were evident, with very low coral cover and high amounts of rubble and macroalgae. At Kudafalhu in July 2016, there were 1430 COTS ha^{-1} (Solandt & Hammer 2017), which is 3 orders of magnitude higher than various thresholds considered an ecologically important outbreak (Pratchett et al. 2014). Prior to the outbreak and the 2016 bleaching event, these reefs also had high coral cover similar to sheltered reefs found further north in the atoll. The shallow reef at Kudafalhu had a dominance of tabular *Acropora*, *A. hyacinthus*, which are highly palatable corals to COTS compared to more resistant *Porites* (Pratchett et al. 2014) making the inner, more sheltered reefs not only more susceptible to bleaching, but also to COTS predation.

On deeper and wave-exposed reefs, coral cover was lower and was dominated by thermally resistant massive and encrusting forms. Much of the historical reef data from the Maldives come from shallow (<10 m) reef flat and crest habitats, hence the historical condition of deeper and wave-exposed reefs is harder to ascertain. Higher cover of massive and encrusting corals was noted at the outer crest at depth (~8 m) near Madivaru (Scheer 1974). An exposed fore reef in Addu Atoll in the Southern Maldives also had encrusting and massive forms, but this fore reef also had abundant robust branching corals such as *A. palifera*, *A. abrotanoides* and *Pocillopora eydouxi* (Stoddart 1966). In the ecologically similar Chagos Archipelago, these corals were present on exposed reef slopes prior to 1998, but largely disappeared after the bleaching event (Sheppard et al. 2008). These species were present on some exposed reefs (e.g. Madivaru) but were not dominant, and were absent on others, suggesting there may have been a shift to a more stress-tolerant coral assemblage dominated by massive and encrusting forms (Darling et al. 2012, McClanahan & Muthiga 2014). Sheppard et al. (2008) also noted slower coral regrowth on exposed fore reefs post-1998 bleaching in Chagos compared to reef flats and lagoon habitats. One reason for this could be high wave energy creating mobile rubble from dead coral skeletons, impeding regrowth of tissue and recruitment through abrasion (Chong-Seng et al. 2014). As observed in this study, Stoddart (1966) noted that channels between the lagoon and the open ocean were poor in coral growth, citing sediment abrasion as the likely cause.

4.2. Bleaching impacts in 2016 and evidence of resilience

Based on SST records, thermal stress in 2016 was similar to 1982 and lower than in 1998. In the Great Barrier Reef (GBR) in 2016, mortality increased steeply—between 6 and 10 DHW (Hughes et al. 2018)—suggesting that 6 DHW in 2016 in North Ari was at the lower threshold of extensive mortality, whereas 9 DHW in 1998 was above this. Bleaching was low to moderate at depth and on exposed reefs and high in shallow and sheltered areas, with similar patterns for mortality. In the Southern Maldives (Gaafu Dhaalu) on sheltered shallow reefs, 75% mortality of mostly branching growth forms was reported in 2016 (Perry & Morgan 2017). A nation-wide study of the Maldives showed similar patterns to our results with overall higher bleaching and mortality in shallow waters and sheltered coral reefs dominated by *Acropora* and with less impact on more exposed reefs (Ibrahim et al. 2016).

Temperature logger data around Madivaru showed that shallow reefs had the highest variation in temperatures on a daily and annual basis. Corals growing in shallow and changeable environments exposed to chronic stress can possess various adaptations to their environment that can help protect them from acute thermal stress (Brown et al. 2002, Welle et al. 2017). However, loggers also showed that shallow reefs also experienced the greatest amount of acute thermal stress in 2016 and presumably the highest light intensity (Welle et al. 2017), leading to higher bleaching levels than at deeper reefs (see also Muir et al. 2017). Features of deeper and more wave-exposed fore reefs, including proximity to deep water, pitch (that leads to shading), current flow and wave exposure, have been suggested to reduce thermal stress, UV penetration and hence bleaching severity (Lesser et al. 1990, West & Salm 2003, Obura & Grimsditch 2009). Throughout the time series, loggers recorded short (~6 h), large (>1°C) drops in temperatures on the deep fore reef that in other locations have been attributed to internal waves, which periodically bathe the reef in cooler, deeper water (Tkachenko & Soong 2017). One such temperature drop occurred during peak thermal stress in 2016, which may have provided some reduction in thermal stress during the bleaching event and reduced impacts on the fore reef coral community (DeCarlo et al. 2017). Loggers in the deep lagoon showed less chronic and acute thermal variation than the deep fore reef, suggesting that low water circulation in these habitats maintains more consistent conditions below a layer of warm surface waters.

Comparing the bleaching severity between exposed and sheltered reefs was hampered by the fact that the bleaching resistance of the coral community co-varied with exposure, with much more bleaching-resistant coral on exposed reefs. We postulate that the physical disturbance of waves—especially on the most ocean-exposed western fringes of the atoll—combined with thermal stress in the past 3 decades, could have been enough to shift this community to a more stress-tolerant and bleaching-resistant state. Bleaching-resistant coral cover was the most important factor determining bleaching and mortality in this study, showing similar patterns of high Acroporid and Pocilloporid mortality as seen in the GBR (Hughes et al. 2018), with no signs of acclimatisation or reduced bleaching sensitivity of these corals (e.g. Langlais et al. 2017). Wave exposure did not significantly explain the variation in bleached coral cover, but was a significant explanatory variable for mortality, with lower mortality of both resistant and sensitive forms on more exposed reefs. Hence, the results of this study concur with other studies that wave exposure reduced bleaching severity (e.g. Shedrawi et al. 2017, Welle et al. 2017). It is not clear the degree to which this was due to thermal protection or because more resistant coral communities dominate exposed Maldivian reefs.

Recovery from the 2016 event is probable, as the Maldives has relatively low anthropogenic stress as a result of its low human population density per reef area, limited land-based pollutants/nutrients and low fishing pressure on herbivores (Burke et al. 2011, Moritz et al. 2017). By 2017, the semi-exposed fore reefs at Madivaru and Bathalaa appeared to have recovered from the small amount of coral loss they experienced in 2016. Nevertheless, since 1998 the number of tourists visiting the Maldives has doubled, from 500000 to ~1 million annually, with approximately 30 new resorts being built (Domroes 2001, Cowburn et al. 2018). Nutrient input around inhabited islands (community and resort) in North Ari is noticeable in the foraminifera community (Pisapia et al. 2017) and it is possible that this was a contributing factor to the COTS outbreak in the central part of the atoll (Wolfe et al. 2017). Recovery on these reefs with low coral cover and high amounts of rubble will require a high level of recruitment from elsewhere and consolidation of dead skeletons by other organisms (e.g. calcifying algae). It is important to recognise that the last major bleaching was 18 yr prior to 2016, allowing for fast-growing, competitive bleaching-sensitive corals to return (Darling et al. 2012). Yet despite low historical thermal stress, the Maldives are predicted to receive annual severe bleaching (ASB) as soon as 2026 (van Hooidonk et al. 2016). Combined with rising human pressures in the archipelago, which may reduce recovery potential, the apparent resilience of Maldivian reefs to date should not be considered permanent.

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LITERATURE CITED

Allison WR (1995) Changes in the Maldivian reef system. Coast Manage Tropical Asia 4:6–8

Allison WR (1996) Snorkeler damage to reef corals in the Maldive Islands. Coral Reefs 15:215–218

Anthony KRN, Marshall PA, Abdulla A, Beeden R and others (2015) Operationalizing resilience for adaptive coral reef management under global environmental change. Glob Change Biol 21:48–61

Ateweberhan M, Feary DA, Keshavmurthy S, Chen A, Schleyer MH, Sheppard CRC (2013) Climate change impacts on coral reefs: synergies with local effects, possibilities for acclimation, and management implications. Mar Pollut Bull 74:526–539

Baker AC (2003) Flexibility and specificity in coral-algal symbiosis: diversity, ecology, and biogeography of symbiodinium. Annu Rev Ecol Evol Syst 34:661–689

Beeden RJ, Turner MA, Dryden J, Merida F and others (2014) Rapid survey protocol that provides dynamic information on reef condition to managers of the Great Barrier Reef. Environ Monit Assess 186:8527–8540

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833

Brown B, Dunne RP (1988) The environmental impact of coral mining on coral reefs in the Maldives. Environ Conserv 15:159–165

Brown B, Dunne R, Goodson M, Douglas A (2002) Experience shapes the susceptibility of a reef coral to bleaching. Coral Reefs 21:119–126

Burke L, Reytar K, Spalding MD, Perry A (2011) Reefs at risk revisited. World Resources Institute, Washington, DC

Cardini U, Chiantore M, Lasagna R, Morri C, Bianchi CN (2012) Size-structure patterns of juvenile hard corals in the Maldives. J Mar Biol Assoc UK 92:1335–1339

Chong-Seng KM, Graham NAJ, Pratchett MS (2014) Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33: 449–461

Cowburn B, Moritz C, Birrell C, Grimsditch G, Abdulla A (2018) Can luxury and environmental sustainability coexist? Assessing the environmental impact of resort tourism on coral reefs in the Maldives. Ocean Coast Manage 158:120–127

Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM, Bellwood D (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15:1378–1386

Darling ES, McClanahan TR, Côté IM (2013) Life histories predict coral community disassembly under multiple stressors. Glob Change Biol 19:1930–1940

DeCarlo TM, Cohen AL, Wong GTF, Davis KA, Lohmann P, Soong K (2017) Mass coral mortality under local amplification of 2°C ocean warming. Sci Rep 7:44586

Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R and others (2009) Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. PLOS ONE 4:e5239

Domroes M (2001) Conceptualising state-controlled resort islands for an environment-friendly development of tourism: the Maldivian experience. Singap J Trop Geogr 22:122–137

Edwards AJ, Clark S, Zahir H, Rajasuriya A, Naseer A, Rubens J (2001) Coral bleaching and mortality on artificial and natural reefs in Maldives in 1998, sea surface temperature anomalies and initial recovery. Mar Pollut Bull 42:7–15

Fabricius KE, Cséke S, Humphrey C, De'ath G (2013) Does trophic status enhance or reduce the thermal tolerance of scleractinian corals? A review, experiment and conceptual framework. PLOS ONE 8:e54399

Grimsditch G, Mwaura JM, Kilonzo J, Amiyo N (2010) The effects of habitat on coral bleaching responses in Kenya. Ambio 39:295–304

Guest JR, Baird AH, Maynard JA, Muttaqin E and others (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLOS ONE 7:e33353

Heron SF, Maynard JA, van Hooidonk R, Eakin CM (2016) Warming trends and bleaching stress of the world's coral reefs 1985-2012. Sci Rep 6:38402

Hodgson G, Hill J, Kiene W, Maun L and others (2006) Reef Check instruction manual: a guide to reef check coral reef monitoring. Reef Check Foundation, Pacific Palisades, CA

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG and others (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373–377

Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2018) Global warming transforms coral reef assemblages. Nature 556:492–496

Ibrahim N, Mohamed M, Basheer A, Haleem NF and others (2016) Status of coral bleaching in the Maldives in 2016. Marine Research Centre, Malé

Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on coral reefs. PLOS Biol 6:e54

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) 'lmerTest' package: tests in linear mixed effects models. J Stat Softw 82:1–26

Langlais CE, Lenton A, Heron SF, Evenhuis C, Gupta A, Brown JN, Kuchinke M (2017) Coral bleaching pathways under the control of regional temperature variability. Nat Clim Chang 7:839–844

Lesser MP, Stochaj WR, Tapley DW, Schick JM (1990) Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. Coral Reefs 8: 225–232

Liu G, Strong AE, Skirving WJ (2003) Remote sensing of sea surface temperatures during 2002 barrier reef coral bleaching. EOS 84(15): 2002–2003

Loya Y, Sakai K, Yamazato K, Nakano H, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. Ecol Lett 4:122–131

McClanahan TR (2000) Bleaching damage and recovery potential of Maldivian coral reefs. Mar Pollut Bull 40: 587–597

McClanahan TR, Muthiga NA (2014) Community change and evidence for variable warm-water temperature adaptation of corals in Northern Male Atoll, Maldives. Mar Pollut Bull 80:107–113

McClanahan TR, Ateweberhan M, Sebastián CR, Graham NAJ, Wilson SK, Bruggemann JH, Guillaume MMM (2007) Predictability of coral bleaching from synoptic satellite and in situ temperature observations. Coral Reefs 26:695–701

McClanahan TR, Donner SD, Maynard JA, MacNeil MA and others (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. PLOS ONE 7:e42884

Moritz C, Ducarme F, Sweet MJ, Fox MD and others (2017) The 'resort effect': Can tourist islands act as refuges for coral reef species? Divers Distrib 23:1301–1312

Morri C, Montefalcone M, Lasagna R, Gatti G and others (2015) Through bleaching and tsunami: coral reef recovery in the Maldives. Mar Pollut Bull 98:188–200
Muir PR, Marshall PA, Abdulla A, Aguirre JD (2017) Species identity and depth predict bleaching severity in reef-building corals: Shall the deep inherit the reef? Proc R Soc B 284:20171551
Obura DO (2005) Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. Estuar Coast Shelf Sci 63:353–372
Obura DO, Grimsditch G (2009) Resilience assessment of coral reefs: assessment protocol for coral reefs, focusing on coral bleaching and thermal stress. IUCN Working Group on Climate Change and Coral Reefs, Gland
Obura DO, Mangubhai S (2011) Coral mortality associated with thermal fluctuations in the Phoenix Islands, 2002–2005. Coral Reefs 30:607–619
Penin L, Vidal-Dupiol J, Adjeroud M (2013) Response of coral assemblages to thermal stress: Are bleaching intensity and spatial patterns consistent between events? Environ Monit Assess 185:5031–5042
Perry CT, Morgan KM (2017) Post-bleaching coral community change on southern Maldivian reefs: Is there potential for rapid recovery? Coral Reefs 36:1189–1194
Pisapia C, Burn D, Yoosuf R, Najeeb A, Anderson KD, Pratchett MS (2016) Coral recovery in the central Maldives archipelago since the last major mass-bleaching, in 1998. Sci Rep 6:34720
Pisapia C, Kateb A, Hallock P, Spezzaferri S (2017) Assessing coral reef health in the North Ari Atoll (Maldives) using the FoRAM Index. Mar Micropaleontol 133:50–57
Pratchett M, Caballes C, Rivera Posada J, Sweatman H (2014) Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). Oceanogr Mar Biol Annu Rev 52:133–200
R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Scheer G (1974) Investigation of coral reefs at Rasdu Atoll in the Maldives with the quadrat method according to phytosociology. Proc 2nd Int Coral Reef Symp, Brisbane 2: 655–670
Shedrawi G, Falter JL, Friedman KJ, Lowe RJ and others (2017) Localised hydrodynamics influence vulnerability of coral communities to environmental disturbances. Coral Reefs 36:861–872
Sheppard CRC (1999) Coral decline and weather patterns over 20 years in the Chagos Archipelago, Central Indian Ocean. Ambio 28:472–478
Sheppard CRC, Harris A, Sheppard ALS (2008) Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. Mar Ecol Prog Ser 362:109–117
Solandt JL, Hammer M (2017) Little and large: surveying and safeguarding coral reefs & whale sharks in the Maldives. Biosphere Expeditions technical report, Ross-on-Wye
Stoddart DR (1966) Reef studies at Addu Atoll, Maldive Islands: preliminary results of an expedition to Addu Atoll in 1964. Atoll Res Bull 116:1–107
Tkachenko KS (2012) The northernmost coral frontier of the Maldives: the coral reefs of Ihavandippolu Atoll under long-term environmental change. Mar Environ Res 82: 40–48
Tkachenko KS (2015) Impact of repetitive thermal anomalies on survival and development of mass reef-building corals in the Maldives. Mar Ecol 36:292–304
Tkachenko KS, Soong K (2017) Dongsha Atoll: a potential thermal refuge for reef-building corals in the South China Sea. Mar Environ Res 127:112–125
van Hooidonk R, Maynard J, Tamelander J, Gove J and others (2016) Local-scale projections of coral reef futures and implications of the Paris Agreement. Sci Rep 6:39666
van Oppen MJH, Gates RD, Blackall LL, Cantin N and others (2017) Shifting paradigms in restoration of the world's coral reefs. Glob Change Biol 23:3437–3448
van Woesik R, Sakai K, Ganase A (2011) Revisiting the winners and the losers a decade after coral bleaching. Mar Ecol Prog Ser 434:67–76
Welle PD, Small MJ, Doney SC, Azevedo IL (2017) Estimating the effect of multiple environmental stressors on coral bleaching and mortality. PLOS ONE 12:e0175018
West JM, Salm RV (2003) Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conserv Biol 17:956–967
Wilson SK, Graham NAJ, Fisher R, Robinson J and others (2012) Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance. Conserv Biol 26:995–1004
Wolfe K, Graba-Landry A, Dworjanyn SA, Byrne M (2017) Superstars: assessing nutrient thresholds for enhanced larval success of *Acanthaster planci*, a review of the evidence. Mar Pollut Bull 116:307–314
Zahir H (2000) Status of the coral reefs of Maldives after the bleaching event in 1998. In: Coral Reef Degradation in the Indian Ocean (CORDIO): status report 2000. SAREC Marine Science Program, Stockholm, p 64–68

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