



REPORT

Impacts of the 2014–2017 global bleaching event on a protected remote atoll in the Western Indian Ocean

Julia M. B. Cerutti¹ · April J. Burt^{2,3} · Philip Haupt^{3,4} · Nancy Bunbury^{3,5} · Peter J. Mumby⁶ · Gabriela Schaepman-Strub¹

Received: 30 September 2018 / Accepted: 29 August 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract The third global bleaching event caused prolonged elevated sea surface temperatures from 2014 to 2017 that heavily impacted coral reefs worldwide. This study determines changes in benthic community following this bleaching event at a remote UNESCO World Heritage Site in the Western Indian Ocean. Aldabra Atoll offers a rare opportunity to study global impacts in the absence of local anthropogenic stressors. Analysis of satellite-derived temperature data indicated that Aldabra was exposed to the highest bleaching-risk intensity of the past 20 years during this bleaching event. Bleaching-risk conditions lasted from December 2015 to June 2016 close to the 4 °C-week threshold, when bleaching is expected. Benthic cover was established pre- and post-bleaching from 21 transects

across two reef locations (lagoonal reef, 2 m depth; seaward reef, 5 and 15 m depth). From a pre-bleaching benthic community in which living corals and epilithic algal matrix (EAM) predominated, Aldabra's reefs switched to an EAM-dominated community 8 months after bleaching. Soft corals declined by 93% of their overall pre-bleaching cover to < 1%. Although overall hard-coral cover was also reduced, the decline varied among depths and might indicate local adaptations of the lagoonal reef, due to greater variability in sea surface temperature compared to the seaward reef. With the exception of *Isopora palifera*, all taxomorphic coral groups experienced a decline following bleaching. Overall, *Rhytisma* experienced a near-complete extirpation, Acroporids (excluding *I. palifera*) and branching Poritids declined by more than 80%, Merulinidae lost ca. 60% of their pre-bleaching cover, while massive Poritids cover slightly decreased. Aldabra's benthic community therefore underwent substantial changes following the 2014–2017 bleaching event and showed that live coral cover declines significantly even in protected areas isolated from local anthropogenic pressures.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00338-019-01853-1>) contains supplementary material, which is available to authorized users.

✉ Julia M. B. Cerutti
juliamb.cerutti@gmail.com

- ¹ Department of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland
- ² Department of Plant Science, University of Oxford, South Parks Road, Oxford OX1 3RB, UK
- ³ Seychelles Islands Foundation, PO Box 853, Victoria, Mahé, Seychelles
- ⁴ Rhodes University, PO Box 94, Grahamstown, Eastern Cape 6140, South Africa
- ⁵ Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Penryn TR10 9FE, UK
- ⁶ Marine Spatial Ecology Lab and ARC Centre of Excellence for Coral Reef Studies, School of Biological Sciences, University of Queensland, St Lucia, QLD 4072, Australia

Keywords Coral bleaching · El Niño · Marine protected area · Aldabra Atoll · Seychelles · UNESCO World Heritage Site

Introduction

Climate change is the greatest threat to the long-term persistence of coral reef ecosystems (Hoegh-Guldberg 2011; Hughes et al. 2017). More specifically, ocean warming and associated coral bleaching are one of the foremost causes of coral loss worldwide (Obura et al. 2017; Hughes et al. 2017). Record-breaking high ocean

temperatures that occurred from 2014 to 2017 resulted in prolonged and widespread coral bleaching, which impacted reefs worldwide from the Great Barrier Reef and adjacent Coral Sea (Harrison et al. 2018; Hughes et al. 2018a; Stuart-Smith et al. 2018), Western Australia (Le Nohaïc et al. 2017), the northern (Couch et al. 2017) and central Pacific (Barkley et al. 2018), the Western Indian Ocean (WIO; Obura et al. 2017), the Middle-East (Monroe et al. 2018; Burt et al. 2019), to more isolated reefs worldwide (Heron et al. 2017).

Consequences of extensive coral loss, whether caused by elevated sea surface temperatures (SSTs) and mass coral bleaching, or other large-scale disturbances, may include: (1) changes in the composition of coral assemblages, potentially leading to the dominance of other taxa such as soft corals and macroalgae (Norström et al. 2009; Hughes et al. 2018a); (2) degradation of the structural complexity, with direct effects on associated fish communities (Graham and Nash 2013; Darling et al. 2017); and (3) decline in related ecosystem services such as coastal protection and fisheries production (Mumby and Steneck 2008). The time windows between mass coral loss events allowing for recovery are shortening (Hughes et al. 2018b), hence the urgent need to understand drivers of reef resilience to maximise recovery potential.

Although mass bleaching events generally occur over large spatial scales, local mechanisms may influence the bleaching response within reefs. Depth has been identified as one factor affecting the bleaching response but with diverging findings. While bleaching impacts on some reefs diminished with depth (Mumby et al. 2001b; Furby et al. 2013), other studies have suggested that corals in shallow reefs may be better adapted to thermal stress due to the naturally larger temperature variability they are exposed to (Oliver and Palumbi (2011) and Safaie et al. (2018). Through tides and water flow, reef morphology and location may further result in spatially heterogeneous bleaching patterns (Green et al. 2019). Typically, residence time of water bodies in shallow (semi-)enclosed atolls may be extended, thereby enhancing day-/summer-time warming and night-/winter-time cooling and leading to a large diurnal/seasonal SST variability (Lowe et al. 2016; Green et al. 2019).

This study determines the impacts of the 2014–2017 bleaching event on Aldabra Atoll, a UNESCO World Heritage Site in the Western Indian Ocean (WIO). Being remote and protected contributed to the preservation of Aldabra marine ecosystems. As a Special Reserve under Seychelles' legislation, no industrial fishing pressure occurred at Aldabra since 1981. Beforehand, Aldabra experienced only mild levels of fishing. Stressors like terrestrial sediment, nutrient and pesticide run-offs are negligible. Aldabra thus offers an important baseline to

monitor ongoing ecological processes and long-term impacts of climate change and to disentangle global environmental impacts from local anthropogenic stressors on reef ecosystems (Stoddart 1984; Stobart et al. 2005). As a regional benchmark, Aldabra's reefs may be of substantial ecological and socio-economic importance for the WIO (Teleki et al. 1999), a region within which 16% of the world's reefs are located (Obura et al. 2017). Its potential resilience (or fragility) and recovery (or collapse) may indeed affect ecological dynamics and the genetic variability of a wider reef network (Teleki et al. 1999). Evidence of climate change-driven impacts, based on continued monitoring from remote, protected reefs, isolated from local anthropogenic pressures, is important to inform local marine spatial planning and climate policy (Sandin et al. 2008). Such evidence in the WIO is currently lacking. To fill this gap, the objective of this research is to assess the impacts of the 2014–2017 global bleaching event and drivers of bleaching responses to prolonged elevated SSTs on Aldabra's coral reefs by: (1) establishing the changes in benthic cover pre- and post-bleaching and (2) quantifying variation of responses between reef locations (lagoonal vs. seaward reefs) and depths.

Materials and methods

Study site

Aldabra (9°24'S, 46°20'E) is a large (34 × 14.5 km) semi-enclosed raised coral atoll in the southern Seychelles managed by the Seychelles Islands Foundation (SIF). The four main islands form a discontinuous ring enclosing a 196-km² shallow lagoon (< 5 m depth, channels excluded; Stoddart et al. 1971; Fig. 1). The lagoon flushes with the tidal ebb and flow (2–3 m tidal range; Farrow and Brander 1971) contributing to substantial hydrodynamic exchanges with the open ocean flooding the reefs with nutrients and sediment (Granek 2006). While Aldabra's leeward western reefs are relatively sheltered, the east and south-eastern sides are exposed to high-wave energy caused by strong monsoonal winds (Taylor 1971). The forereef slope is short and steep along the northern and western sides of the atoll and gradual on the more exposed south and east coasts. Climatic conditions are governed by the monsoon, with the wet and warmer north-west monsoon from November/December to March, and dry, cooler south-east trade winds prevailing for the rest of the year.

SSTs and bleaching risk

The US National Oceanographic and Atmospheric Administration's Coral Reef Watch Program (NOAA-

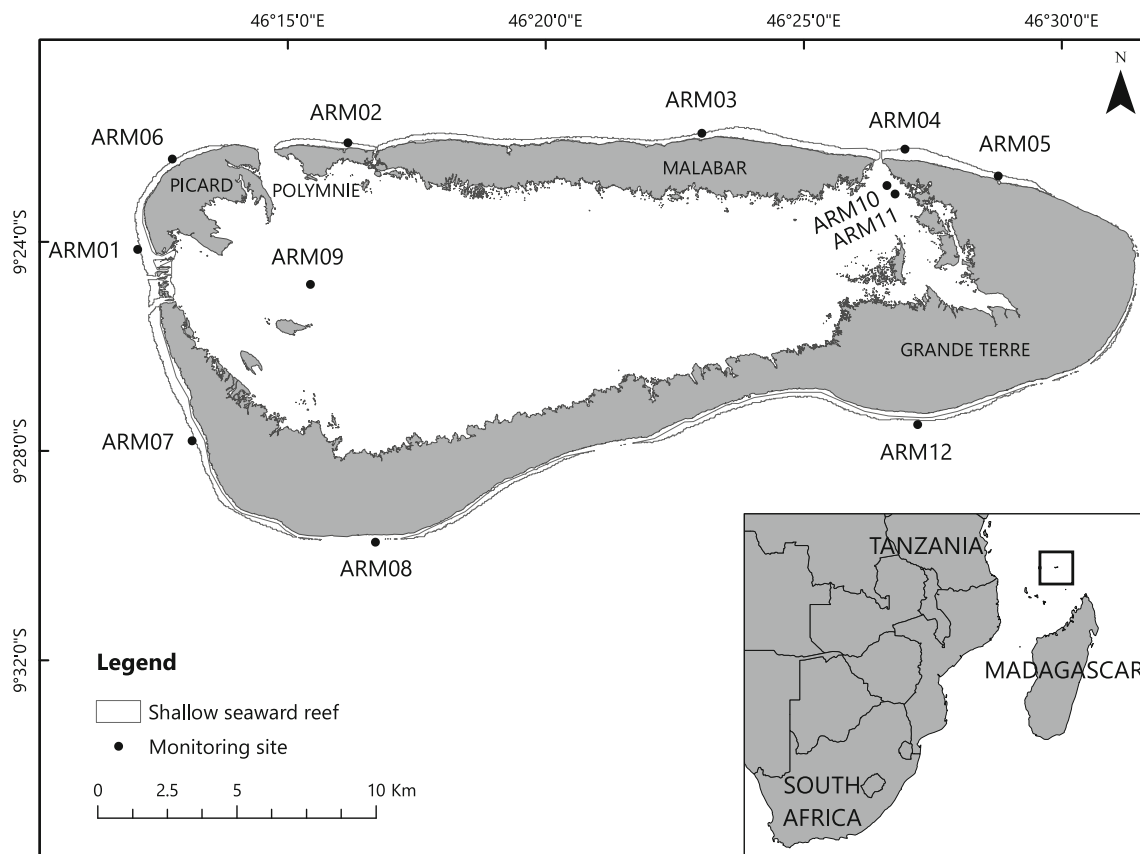


Fig. 1 Aldabra Atoll's location in the Western Indian Ocean (inset) and the atoll's main islands with the 12 permanent Aldabra reef monitoring (ARM) sites (modified from Andréfouët et al. 2009)

CRW) uses satellite observations to provide 50-km resolution data on the bleaching risk for reefs globally. The bleaching risk is expressed as degree heating weeks (DHW) and corresponds to the accumulation of heat stress over the preceding 3-month period (Liu et al. 2013). A Kruskal-Wallis test and associated post hoc tests were performed on north-west monsoon (December to March) NOAA-CRW's DHW values (NOAA-CRW 2000; 2000–2001 to 2018–2019) to evaluate the magnitude of the bleaching risk during the most recent bleaching event compared to other years on Aldabra (virtual station: 9°00'S, 46°50'E; bleaching threshold from February 2016: 30.4 °C, 30.3 °C beforehand). In situ SST was also recorded at 30-min intervals from 9th April 2015 to 7th December 2016 using seven temperature loggers (Onset HOBO U22 Pro V2) deployed at several transects (four, two and one at 15 m, 5 m and 2 m depth, respectively). The lack of loggers at all depths and reef locations prevented the inclusion of in situ data in the benthic analysis. In situ DHW were computed based on (1) diurnal data and (2) the same half-weeks that NOAA-CRW used.

Benthic cover determination

Data collection

In 2013, as part of SIF's Aldabra Reef Monitoring (ARM) programme, 12 permanent sites were established to monitor changes of the benthic substrate in response to environmental conditions (Fig. 1). The 12 sites were selected at the same locations surveyed during the Royal Society's campaign (Drew et al. 1971) and the Aldabra Marine Programme (1999–2008; Stobart et al. 2005), but at shallower depths.

At the nine sites on the seaward foreereef slope, one shallow (5 m) and one deep (15 m) transects were surveyed. A further three sites on the lagoonal reef were surveyed at one depth of ca. 2 m due to the lower depth range in this area (total of 21 transects across 12 sites). On each transect, two sections were demarcated at 0–10 m and 20–30 m. 'Reef location' will hereafter refer to the lagoonal or seaward reef location. Surveys were conducted at high neap tide to ensure standardisation around the indicated depths. Each demarcated transect was 50-m long, parallel to the shore and followed the depth contour. Benthic photoquadrats were collected on all transect

sections using a 70 × 50 cm photoquadrat frame and a GoPro Hero-3 Silver (11 megapixels) at a 70-cm fixed height to provide a permanent and objective record. Photographs were taken along a tape on both sides with a slight overlap between photos. Pre-bleaching surveys were completed in December 2014–January 2015, and post-bleaching surveys in December 2016.

Data processing

The photoquadrat images were analysed using the CPCe software (Coral Point Count with Excel extensions) to estimate the benthic cover of each transect (Kohler and Gill 2006). Following a stratified random sampling approach, the area within the photographed frame was divided into 16 cells, with one point of random coordinates per cell. Points which fell onto the transect tape, photoquadrat frame or in the shadow were excluded. Cover type at the remaining points was identified to the lowest taxonomic level possible (Veron 2000). Hard and soft corals were identified to the species level; when not possible, the genus level, with growth form where relevant (Supplementary Material 1). Except for *Halimeda* species which were identified to species or genus level, other algae were grouped as turf, macroalgae and coralline algae along with their associated substrate (e.g. rubble or dead standing coral). The cover type was identified at 27,082 points for the pre-bleaching survey and at 23,286 points post-bleaching (excluding points on transect tape, photoquadrat frame or in shadow). The differing number of points between the surveys was due to fewer photographs taken post-bleaching.

Statistical analysis

All statistical analyses were performed using the R software (version 3.5.1). To evaluate the benthic cover change, six major categories and seven coral taxomorph groups were assigned for analysis. Hard corals, soft corals, epilithic algal matrix (EAM; combining coralline and turf algae), *Halimeda*, macroalgae and coral rubble were selected as the six major benthic categories. Even though they have different ecological roles, coralline and turf algae often co-occur at Aldabra and the distinction between the two on photoquadrats was difficult under low light exposure, hence their regrouping under EAM. Fire corals and sponges were not included in the analysis due to their very low cover (< 1%). Corals were further explored as seven cohesive taxomorph groups: Acroporids (excluding *I. palifera*), Merulinidae, branching Poritids, massive Poritids, *Isopora palifera* (previously known as *Acropora palifera*), *Rhytisma* species and *Others*. The above first four taxomorph groups correspond to the most encountered hard-coral families and growth forms pre-bleaching. As

key species characterising Aldabra's reefs and their relatively high cover, *I. palifera* (Acroporid family) and *Rhytisma* species (soft coral) were also examined. The *Others* category included 46 least abundant subcategories of hard and soft corals, making up on average < 10% of the overall coral cover both pre- and post-bleaching (Supplementary Material 1).

Restricted maximum-likelihood mixed-effects models were used to test whether cover of each category differed from pre- to post-bleaching, as well as the influence of covariates, i.e. reef location, depth, and their two- and three-way interactions. Restricted maximum likelihood (REML) produces a bias-free estimation for variance components of generalised linear mixed models (Bolker et al. 2009; Rukhin 2011). Moreover, REML was used to handle the unbalanced study design emerging from the varying number of depths per site (Brown and Kempton 1994; Virk et al. 2009). For the analysis, covers of the photoquadrats were averaged to obtain section means. Fixed effects included *Date*, *Reef location*, *Depth*, plus their interactions, while *Site*, *Site:Date*, *Site:Depth*, *Site:Date:Depth*, *Section*, *Site:Section* and *Section:Depth* were treated as random effects. ASReml (version 3.0; Gilmour et al. 2009), allowing unconstrained variance components, was used to estimate variance parameters. Opposed to other linear mixed-effects models, ASReml models allow for negative variance values and for keeping the order of terms as stipulated in the model associating fixed effects with the correct random effects (Schmid et al. 2017). Results and *p* values were computed using the 'test.asreml' function ('pascal' package, version 1.5.2; <https://github.com/pascal-niklaus/pascal>). Model diagnostics, i.e. normality, homoscedasticity and linearity, were visually performed. To meet these assumptions, covers were either arcsine-square-root-transformed (hard coral, EAM, Merulinidae, branching and massive Poritids) or log-transformed (soft coral, Acroporids (excluding *I. palifera*), *I. palifera*), and the *Section:Depth*, *Section:Date* and *Site:Section* random factors were dropped for all (except *Site:Section* for hard coral and massive Poritids; plus *Site:Date:Depth* for Acroporids (excluding *I. palifera*); Supplementary Material 2). Models had a poor fit to *Halimeda*, macroalgae, coral rubble and *Rhytisma*; therefore, no test for significance of change was possible for these categories.

Results

SSTs and bleaching risk

At Aldabra, NOAA-CRW data indicated the half-weekly SST mean exceeded the bleaching threshold (30.4 °C from February 2016, 30.3 °C beforehand) for half a week in late

December 2015 (30.4 °C) and for three consecutive weeks from mid-March to early April 2016, with a maximum of 30.7 °C. This resulted in positive DHW values for about six months from late December 2015 to late June 2016, peaking at 3.4 °C-weeks from March 2016 (Fig. 2). Analysis across years showed DHW was significantly affected by the north-west monsoon period [$H(dF = 18)$, $p < 0.001$], and post hoc tests showed 2015–2016's DHW to be higher than any other north-west monsoon period from 2000–2001 to 2018–2019 (observed differences: 220.8–259.5; critical differences: 160.5–168.5). No other north-west monsoon period was significantly different from any other.

In situ data revealed the half-weekly SST mean and thereby DHW values varied across reef location and depth. At the four 15 m-depth seaward reef sites, the half-weekly SST mean never exceeded the 30.4 °C bleaching threshold throughout the study period, except for ARM06-15 m one half-week in late March 2016, resulting into a 0.5 °C-week DHW value (Supplementary Material 3). At the two 5 m-depth seaward reef sites, the bleaching threshold was exceeded for 3–4 consecutive half-weeks from mid-March 2016, which resulted into DHW peak values of 1.8 °C-weeks and 2.4 °C-weeks depending on the site. At the lagoonal reef site, half-weekly SST means were over the bleaching threshold for a total of nine half-weeks between mid-December 2015 and late March 2016 (including six in March 2016) with a maximum half-weekly SST mean of 31.7 °C. The DHW values were subsequently positive from mid-December 2015 to mid-June 2016 and peaked at 4.8 °C-weeks in late March 2016, prompting the NOAA-CRW 'Alert Level 1' bleaching stress level, indicating

bleaching is likely (Liu et al. 2013), for two non-consecutive half-weeks. In terms of daily SST variability, the standard deviation over the study period was on average higher at ARM09-2 m (0.63) than any other transect (0.16–0.23); and the largest daily SST range of 5.6 °C was recorded at ARM09-2 m.

Benthic cover change

Overall, Aldabra's pre-bleaching reef cover consisted of ca. 40% EAM, 37% living coral (hard and soft corals combined) and 11% *Halimeda*, changing to an algae-dominated community where EAM and *Halimeda* combined represented ca. 75% of the post-bleaching benthos (Fig. 3). Hard-coral cover declined at all depths and reef locations after bleaching; however, the relative loss varied (*Date:Depth* significant interaction, $p < 0.05$). The greatest losses were observed on the seaward reef, where hard corals lost over half their pre-bleaching cover (55% and 54% decline at 5 and 15 m depth, respectively), although declines also occurred at 2 m depth on the lagoonal reef (35% decline; Fig. 3; Supplementary Material 4). Soft-coral cover significantly declined by over an order of magnitude (93% decline; $p < 0.001$) to a post-bleaching cover of < 1%. Concurrent with the decline in live coral cover was the significant increase in EAM ($p < 0.001$), which rose from 36.7 to 54.3% coverage (depending on depths and reef locations) to 59.7–69.0% of the benthos following bleaching. *Halimeda* increased from 0.5% (± 0.1 SE) to 6.2% (± 0.8 SE) on the lagoonal reef but stayed relatively stable on the seaward reef (from 10.6–13.7% to 12.6–13.2% depending on depths).

Fig. 2 Satellite-derived sea surface temperature (SST) and degree heating weeks (DHW) of Aldabra Atoll virtual station from 2015 to 2016; replotted from the NOAA Coral Reef Watch website (https://coralreefwatch.noaa.gov/satellite/vs/westernindianocean.php#Aldabra_Seychelles). From February 2016, the maximum monthly mean and bleaching threshold have been updated to 29.4 °C (previously 29.3 °C) and 30.4 °C (previously 30.3 °C), respectively. For definitions of stress levels, see Liu et al. (2013)

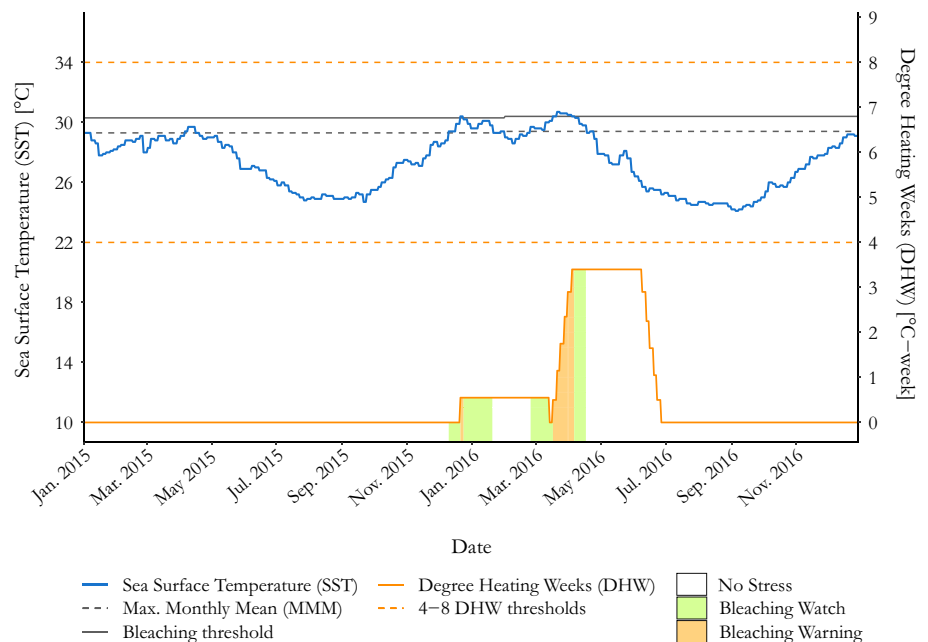
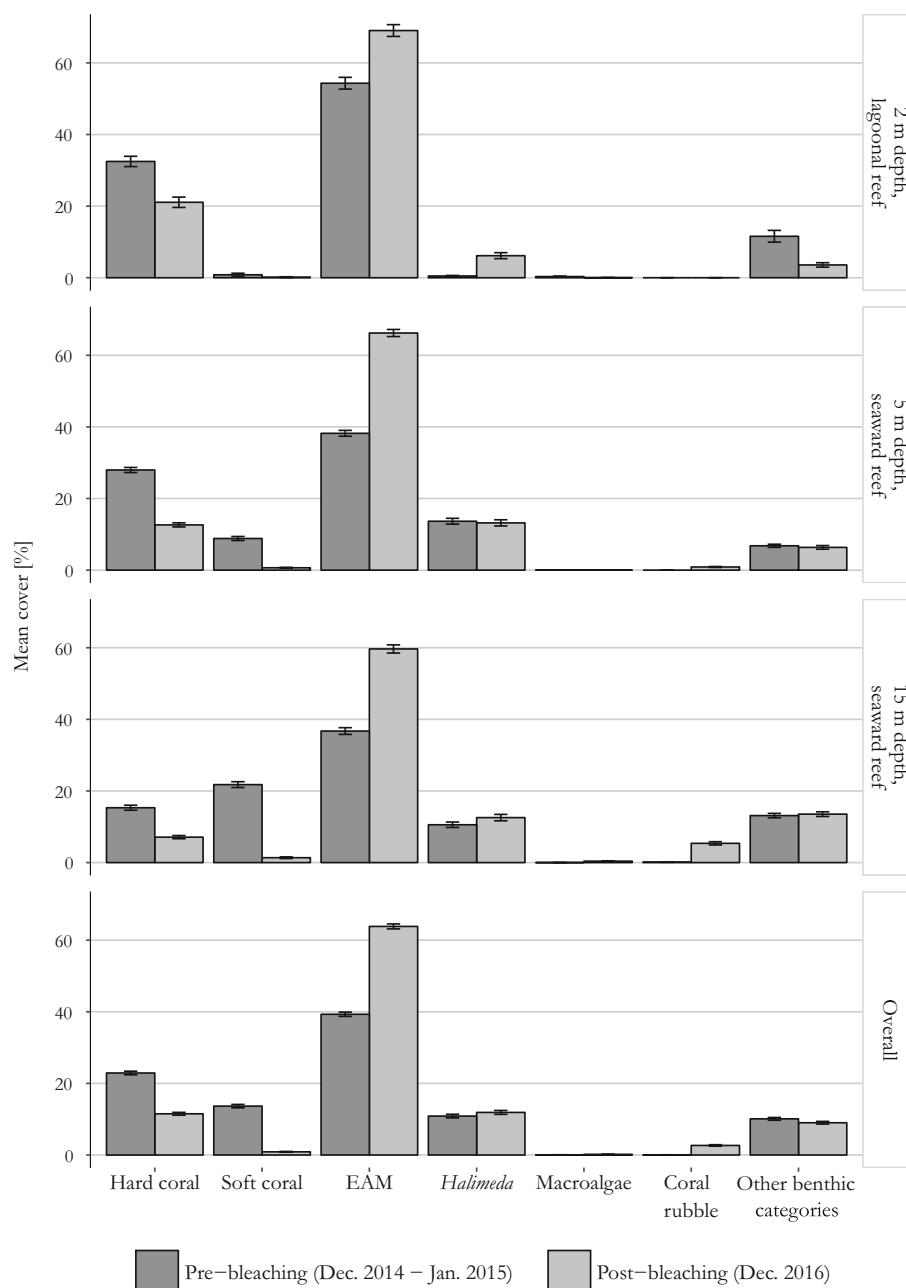


Fig. 3 Change in major benthic categories: pre- and post-bleaching mean cover (in percent, error bars as standard error SE) by depth at the 12 studied reef sites at Aldabra Atoll



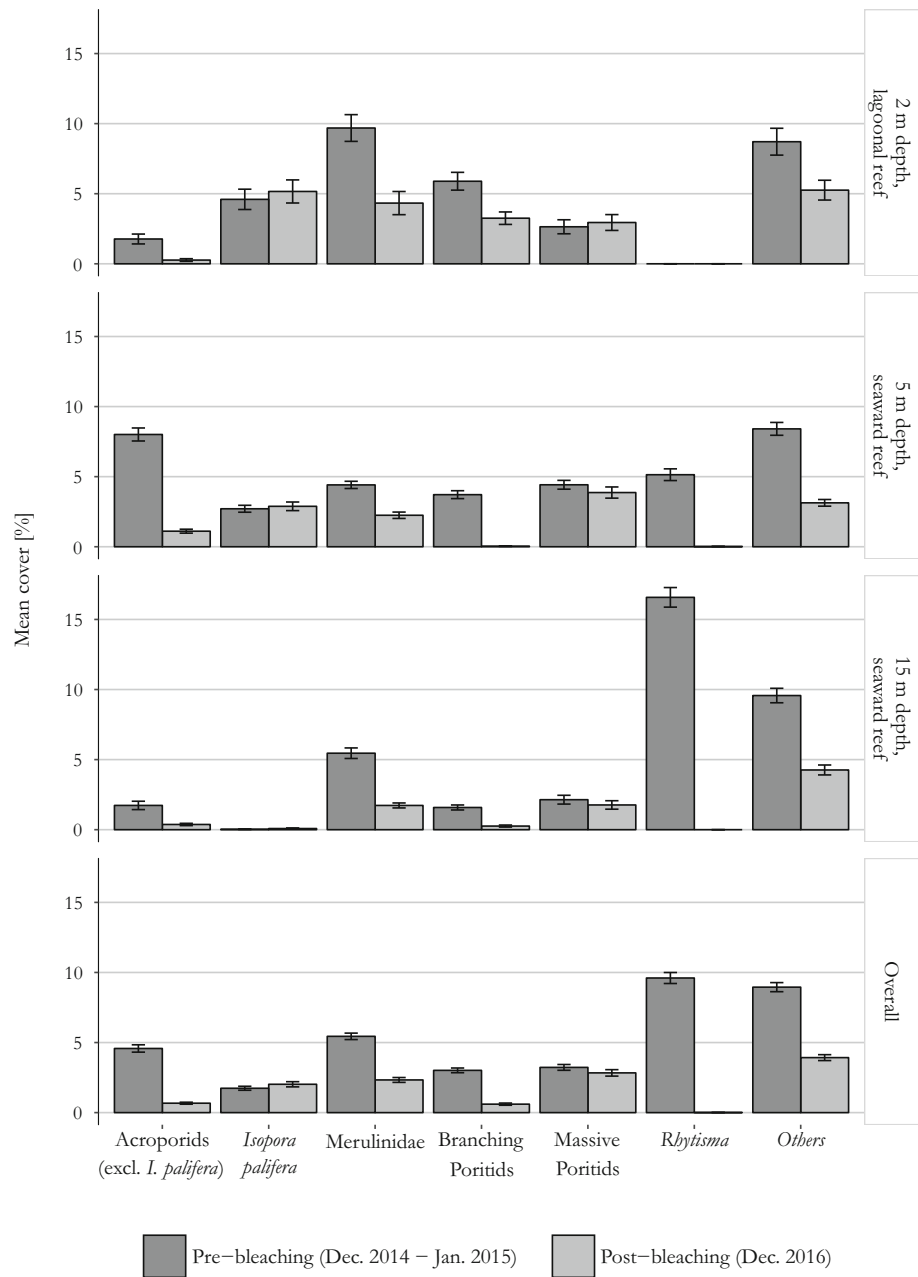
Meanwhile, coral rubble increased from < 0.1% to 2.7% (± 0.2 SE), especially at 15 m depth, and macroalgae remained scarce throughout the study ($\leq 0.2\%$).

Coral composition change

A total of 72 subcategories of hard and soft corals were recorded (66 hard and six soft; Supplementary Material 1). Overall, while the pre-bleaching coral assemblage was dominated by *Rhytisma* ($9.6\% \pm 0.4$ SE), Merulinidae ($5.4\% \pm 0.2$ SE) and Acroporids (excluding *I. palifera*) ($4.6\% \pm 0.3$ SE), most of the taxomorph groups present

post-bleaching were massive Poritids ($2.8\% \pm 0.2$ SE), Merulinidae ($2.3\% \pm 0.2$ SE) and *I. palifera* ($2.0\% \pm 0.2$ SE) (Fig. 4; Supplementary Material 5). With the exception of *I. palifera*, cover of all taxomorph groups experienced decline following bleaching; losses were, however, heterogeneous between groups and among groups across habitats. *Rhytisma*, Acroporids (excluding *I. palifera*) and branching Poritids experienced the greatest declines with an overall cover loss reaching > 99.9%, 85% and 80%, respectively, with post-bleaching covers of < 0.01%, 0.7% and 0.6%, respectively. Acroporids (excluding *I. palifera*) and branching Poritids response varied across depth

Fig. 4 Change in coral taxomorph groups: pre- and post-bleaching mean cover (in percent, error bars as SE) by depth at the 12 studied reef sites at Aldabra Atoll



(Date:Depth significant interaction; $p < 0.01$ and $p < 0.001$, respectively). Acroporids (excluding *I. palifera*) lost a smaller proportion of their pre-bleaching cover at 15 m depth (83%, 86% and 76% decline at 2, 5 and 15 m depth, respectively), while 44% of branching Poritids' pre-bleaching cover was lost at 2 m (lagoonal reef), against 81% at 15 m and > 99% at 5 m depth. Merulinidae and massive Poritids covers also significantly decreased by 57% ($p < 0.001$) and 13% ($p < 0.05$), respectively. Meanwhile and in contrast to the rest of the Acroporids, *I. palifera* cover slightly increased (from $1.7\% \pm 0.1$ SE to $2.0\% \pm 0.2$ SE). Rather than Date ($p > 0.05$), Depth had a significant effect on its cover ($p < 0.001$): almost absent

from 15 m-depth transects, this species mostly occurred at 2 m depth.

Discussion

SSTs and bleaching risk

During the 2014–2017 El Niño, reefs worldwide experienced thermal stress unprecedented over the 1871–2017 period (Lough et al. 2018), exceeding the strong 1998 El Niño's levels both in terms of severity (Lough et al. 2018) and geographical extent (Skirving et al. 2019). During the

2015–2016 north-west monsoon period, Aldabra was exposed to the highest bleaching-risk intensity since the NOAA-CRW data record started. Between December 2015 and April 2016, both NOAA-CRW and in situ data indicated the bleaching threshold (30.4 °C from February 2016, 30.3 °C beforehand) was exceeded on several occasions, particularly in March 2016 when the highest half-weekly SST means of 30.7 °C and 31.7 °C, respectively, were recorded. This resulted in a NOAA-CRW DHW peak value of 3.4 °C-weeks. Compared to the 50-km products of three neighbouring reefs (NOAA-CRW 2000), Aldabra experienced similar thermal stress to Glorieuse (3.45 °C-week peak value) and higher than Comoros and Mayotte (1.92 °C-week and 1.5 °C-week peak value, respectively). Such peak values are lower than those recorded at Montgomery Reef (north-western Australia; 9.3 °C-weeks; Le Nohaïc et al. 2017) and Lisianski Island (northern Pacific; 19.69 °C-weeks; Couch et al. 2017). The mismatch between the 3.4 °C-week NOAA-CRW value reported for Aldabra and the extent of benthic cover change observed here could be due to non-representativeness of the pure-water 50-km resolution virtual station for Aldabra, an atoll surrounded by deep cool oceanic waters (Gudka et al. 2018). However, no substantial bleaching and mortality were expected based on in situ DHW, despite variations across reef location and depth. The bleaching risk was virtually absent from the 15 m-depth seaward reef sites and the 5 m-depth seaward reef sites were exposed to relatively low DHW values (1.8–2.4 °C-weeks), while DHW at the lagoonal reef site peaked at 4.8 °C-weeks, i.e. just above the 4 °C-week threshold. An anecdotal but growing list of cases suggests widespread bleaching, and mortality can occur below the 4 and 8 °C-week thresholds (e.g. Hughes et al. 2018a; Burt et al. 2019). For such reefs, conservative thresholds of 2–3 °C-weeks were suggested (Burt et al. 2019; Skirving et al. 2019). The accuracy of bleaching prediction based on intensity and duration of thermal stress only can typically be lowered by other physical factors such as light (Mumby et al. 2001a; Skirving et al. 2017). Other studies have demonstrated the coral community composition, local adaptation mechanisms, and thermal history may also influence the bleaching response (McClanahan et al. 2007; Heron et al. 2016).

Benthic cover change

The pre-bleaching benthic community dominated by living corals and EAM at Aldabra was degraded to a reef where EAM colonised nearly two-thirds of the benthos. The 66% total live coral loss, however, conceals disparities between hard and soft corals. Soft corals suffered heavily from bleaching, leading to a 93% decline in their overall cover. Collapse of a soft-coral assemblage following bleaching

was also previously recorded in Japan by Loya et al. (2001). With an overall < 1% post-bleaching cover, ecological functions of soft corals on Aldabra's reefs may largely be lost (e.g. Maida et al. 1995). Although hard-coral cover was also reduced, the decline varied among habitats: the seaward reef lost more than half of its hard-coral cover, while it decreased by 35% on the lagoonal reef. This lower loss of hard-coral cover on the lagoonal reef was consistent with a previous study on Aldabra (Stobart et al. 2002) and may reflect local adaptations through SST variability. The large daily temperature range typical of (semi-)enclosed shallow lagoon (Lowe et al. 2016), as reported by Stobart et al. (2002) and confirmed here, likely exposed corals to regular thermal stress. Regular exposure of corals to thermal stress which is high and/or long enough to initiate adaptation mechanisms, but short enough to prevent mortality, may lower their bleaching susceptibility (Oliver and Palumbi 2011; Safaie et al. 2018).

Meanwhile, coral-rubble cover increased on average from > 0% pre-bleaching to < 3% post-bleaching, the overall *Halimeda* cover remained stable, and macroalgae remained rare (< 0.2%). Macroalgae stability and scarcity at Aldabra following the 2014–2017 bleaching event at the time of survey, as well as following the 1998 event (Stobart et al. 2005), indicate a lack of a phase shift after both events. Although sometimes discussed as a primary response to live coral cover loss (Done 1992; Hughes 1994), macroalgal phase shifts are not as common as previously assumed (Bruno et al. 2009). Low macroalgal cover is generally associated with high fish biomass, and severe losses of herbivores can cause macroalgal blooms (Mumby et al. 2006; Steneck et al. 2018). The Aldabra Group (including Aldabra, Assumption, Cosmoledo and Astove) harbours the highest fish biomass density in the Seychelles and among the largest in the Indian Ocean (Friedlander et al. 2015). An abundance of herbivorous fish, which is often associated with remote reefs free from industrial fishing pressure like Aldabra (e.g. Ateweberhan et al. 2013; Friedlander et al. 2015), may confer resilience to coral reefs by suppressing macroalgal cover (Sandin et al. 2008).

Despite disparities between hard and soft corals, the total live cover loss reported here appears lower than the catastrophic decline of 98% at Jarvis Island (South Pacific; Boyle et al. 2017) and of 73% in the southern Persian/Arabian Gulf (Burt et al. 2019), but greater than at the northern Great Barrier Reef which lost about half of its pre-bleaching live cover (Hughes et al. 2018a) and isolated atolls of the Coral Sea where the relative loss reached 15% (Harrison et al. 2018) following the 2014–2017 bleaching event. Compared to the 1998 bleaching event, Aldabra's reefs seemed less impacted. The coral cover, estimated to exceed 50% prior to 1998 (Sheppard and Obura 2005),

dropped to 13.1% at 10 m and 21.6% at 20 m depth in November 1999 (Stobart et al. 2005). Historically, Aldabra's reefs experienced lower coral cover loss than Seychelles' Inner Islands (e.g. coral cover < 5% post-1998 event; Graham et al. 2008). Following the 2014–2017 event, Aldabra's reefs have again suffered lower mortality than Seychelles' Inner Islands (e.g. 81% hard-coral cover loss at North Island; Obura et al. 2017; Gudka et al. 2018), where the bleaching risk was higher (DHW in Mahé peaked at 4.6 °C-weeks in April 2016; NOAA-CRW 2000). This pattern may partly be due to the neighbouring environment: in contrast to Aldabra surrounded by deep cool oceanic waters, shallow banks around the Inner Islands may enhance thermal stress (Gudka et al. 2018). Similarly, free from direct anthropogenic stressors, the Chagos Archipelago was more highly impacted than Aldabra with a hard-coral cover dropping from 50–75% to 12% following 1998 (Sheppard 1999) and from 40–50% to < 10% following the 2014–2017 event (Sheppard et al. 2017), during which DHW peaked at 7.5 °C-weeks in 2015 and 17.6 °C-weeks in 2016 (Head et al. 2019). Gaafu Dhaalu (Maldives), an atoll characterised by minor fishing pressure and direct nutrient inputs (Perry and Morgan 2017) and where the 8 °C-week threshold was crossed (NOAA-CRW 2000), also suffered greater coral mortality than Aldabra following the 2014–2017 bleaching. From a similar pre-bleaching coral cover (25.6% in January 2016), 75% was lost by September 2016. Therefore, the lesser impact on hard-coral cover reported here compared to other reefs in the region may primarily result from lower thermal stress. This points Aldabra as a potential regional climate refugium and therefore an important location for coral persistence in the WIO.

Coral community change, resilience and recovery perspectives

Overall, Aldabra's coral species composition changed in response to bleaching. Prior to the bleaching, coral assemblages were dominated by Acroporids (excluding *I. palifera*) and Merulinidae, as well as the soft coral *Rhytisma* (especially at 15 m depth). Following bleaching, *Rhytisma* was virtually absent from all sites surveyed, and the dominant corals included *I. palifera* and massive Poritids. Between surveys, Acroporids (excluding *I. palifera*), Merulinidae, and branching Poritids abundance experienced marked declines. The negligible decline in the abundance of massive Poritids is consistent with their widely reported relative thermal tolerance (Loya et al. 2001; Pratchett et al. 2013). However, the cover of Merulinidae, which are also considered as stress-tolerant (Hongo and Yamano 2013), more than halved subsequent to bleaching. Branching coral taxa are among the most

sensitive to bleaching (Loya et al. 2001; Pratchett et al. 2013), and their loss has implications on the associated reef fish diversity and abundance through structural complexity degradation (Graham and Nash 2013; Darling et al. 2017). At Gaafu Dhaalu (Maldives), the 75% decline in coral cover following the 2014–2017 event was attributed to the heavy cover loss (91%) of branching and tabular Acroporids (Perry and Morgan 2017). Similarly, the Chagos Archipelago experienced an Acroporids-cover loss of 86% for an overall 60% coral cover decline (Head et al. 2019). At Aldabra, with an overall cover loss of over 80%, Acroporids (excluding *I. palifera*) and branching Poritids contributed substantially to the live coral cover decline. Their response, however, varied across depths. While Acroporids (excluding *I. palifera*) lost a limited proportion of their pre-bleaching cover at 15 m depth compared to 2 m and 5 m depth, branching Poritids-cover loss was almost two times greater at 5 m and 15 m depth (80–81% decline) than 2 m depth (44% decline).

Despite a slight increase from pre- to post-bleaching, *I. palifera* cover was statistically unaffected by bleaching. It, however, varied with depth, i.e. the shallower the reef, the greater the cover. *I. palifera*'s apparent resilience contrasts with the heavy loss of the rest of the Acroporids at 2 m and 5 m depth. At these depths, *I. palifera* made up, respectively, 95% and 73% of the total post-bleaching Acroporids cover, and 24% and 22% of the total post-bleaching live coral cover. Post-1998 bleaching, *I. palifera* was also the most abundant hard-coral species in shallow reef habitats (< 10 m; Teleki et al. 1999) and its surviving colonies on shallow reefs were suggested to not only act as a coral larval source but also as wave-breakers and therefore play a key role in reef recovery at Aldabra (Sheppard and Obura 2005). In the Chagos Archipelago, this species, dominant pre-1998 bleaching, appeared to drive the reef recovery following the 1998 event (Sheppard et al. 2008). This coinciding evidence from two remote reefs in the WIO for the 1998 and 2014–2017 global bleaching events suggests *I. palifera* might have higher resilience capacities to thermal stress and therefore be a key species in reef persistence and recovery in these reefs. Enhanced thermal resistance may emerge from: (1) symbionts through short-term shuffling (Rowan 2004; Berkelmans and van Oppen 2006) or permanent association with thermal-tolerant *Symbiodinium* (Hume et al. 2016); and/or (2) the host (Baird et al. 2009) through, for example, 'front-loaded' genes coding for heat-shock proteins and antioxidant enzymes (Barshis et al. 2013). In southern Taiwan, *I. palifera* was shown capable of acclimatising to SST anomalies through *Symbiodinium* shuffling: when SST anomalies occur, *I. palifera* shuffles to thermal-tolerant *Symbiodinium* D1a, which stay dominant as long as the thermal stress is present; when thermal conditions are back to normal, *I. palifera* promotes

the heat-sensitive *Symbodium* C3 (Hsu et al. 2012). Given its wide distribution in the Indo-Pacific region (Wallace 1999), its relative abundance in sheltered lagoonal reef and slope habitats (Done 1982; Ayre et al. 1991), and its potential importance in reef resilience and recovery, further research on *I. palifera* resilience would be warranted.

Similar to the Chagos Archipelago, where soft corals were almost eradicated by the 2014–2017 event (Sheppard et al. 2017), *Rhytisma* cover at Aldabra dropped to 0.01%, suggesting near-complete extirpation. With their greater plasticity and more widespread geographical distribution than hard corals (Fabricius and Alderslade 2001), fast-growing soft-coral species, although sensitive to elevated SSTs, can rapidly recolonise disturbed reefs (Ateweberhan et al. 2013). Following the 1998 bleaching event on Aldabra, *Rhytisma* species rapidly colonised the reef over the next five years (reaching 10% of the benthic cover at 10 m depth in 2003; Stobart et al. 2005). The increase was such that Norström et al. (2009) argued Aldabra underwent an alternative phase shift from a hard-coral to soft-coral dominance. Hard corals then gradually repopulated the reef (Obura et al. 2017). Monitoring will determine whether Aldabra's reefs follow a similar recovery scenario or via different trajectories.

This research indicates that even remote and relatively pristine reefs were significantly impacted by the 2014–2017 El Niño-induced prolonged elevated SSTs. Although not immune to climate change-induced consequences, reefs free from local anthropogenic stressors exhibited some of the most rapid recovery trajectories following past bleaching events (Sheppard et al. 2008; Ceccarelli et al. 2011; Gilmour et al. 2013). However, the increasing frequency of mass coral bleaching events and subsequent mortality means the interval between major episodes of coral loss is too short to allow for effective recovery of coral assemblages (Hughes et al. 2018b). Based on RCP 8.5 and 4.5 emission pathways, Heron et al. (2017) predicted severe (i.e. 8 °C-weeks) twice-per-decade and annual bleaching events to occur at Aldabra in 2028–2034 and 2039–2042, respectively. This study therefore suggests further loss of hard and soft corals, with some species unlikely to be able to recover over such short time frames, and thereby a compromised future for the marine status of this regional and global benchmark site.

Acknowledgements A special thanks goes to the Seychelles Islands Foundation (SIF) and staff for their invaluable support and help, in particular: Rowana Walton and Anna Koester for the identification of benthic data, as well as the SIF staff who helped with data collection (Daig Romain, Rebecca Filippin, Sheril De Commarmond, Jude Brice, Samuel Basset and Terence Mahoune for pre-bleaching data; Terence Mahoune, Ella Nancy, Joel Bonne, Marvin Roseline for post-bleaching data). Anna Koester is further thanked for cleaning the

temperature dataset. We thank the Global Environment Facility for funding for the diving and research equipment, and the development of the ARM programme. We further thank Anthony Bernard and Nick Riddin from the South African Institute for Aquatic Biodiversity and SIF staff who assisted in the establishment of permanent benthic transects; and Rebecca Klaus for advice on benthic transect set-up and photoquadrat methodology. Prof. Gabriela Schaeppman-Strub was supported by the University of Zürich Research Priority Programme on Global Change and Biodiversity. Prof. Bernhard Schmid and Prof. Pascal A. Niklaus are further thanked for their advice on the statistical analyses. Finally, we would like to thank the editor and reviewers for their constructive feedback.

Compliance with ethical standards

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

References

- Andréfouët S, Chagnaud N, Kranenburg C (2009) Atlas of western and central Indian Ocean coral reefs. Centre IRD de Nouméa, Nouméa, Nouvelle-Calédonie
- Ateweberhan M, Feary DA, Keshavmurthy S, Chen A, Schleyer MH, Sheppard CR (2013) Climate change impacts on coral reefs: synergies with local effects, possibilities for acclimation, and management implications. *Marine Pollution Bulletin* 74:526–539
- Ayre D, Veron JE, Dufty S (1991) The corals *Acropora palifera* and *Acropora cuneata* are genetically and ecologically distinct. *Coral Reefs* 10:13–18
- Baird AH, Bhagooli R, Ralph PJ, Takahashi S (2009) Coral bleaching: the role of the host. *Trends in Ecology & Evolution* 24:16–20
- Barkley HC, Cohen AL, Mollica NR, Brainard RE, Rivera HE, DeCarlo TM, Lohmann GP, Drenkard EJ, Alpert AE, Young CW, Vargas-Ángel B, Lino KC, Oliver TA, Pietro KR, Luu VH (2018) Repeat bleaching of a central Pacific coral reef over the past six decades (1960–2016). *Communications Biology* 1:177
- Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, Palumbi SR (2013) Genomic basis for coral resilience to climate change. *Proceedings of the National Academy of Sciences* 110:1387–1392
- Berkelmans R, van Oppen MJH (2006) The role of zooxanthellae in the thermal tolerance of corals: a ‘nugget of hope’ for coral reefs in an era of climate change. *Proceedings Biological sciences* 273:2305–2312
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135
- Boyle S, De Anda V, Koenig K, O'Reilly E, Schafer M, Acoba T, Dillon A, Heenan A, Oliver TTA, Swanson DW (2017) Coral reef ecosystems of the Pacific Remote Islands Marine National Monument: a 2000–2016 overview
- Brown H, Kempton R (1994) The application of REML in clinical trials. *Statistics in Medicine* 13:1601–1617
- Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VG (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90:1478–1484
- Burt JA, Paparella F, Al-Mansoori N, Al-Mansoori A, Al-Jailani H (2019) Causes and consequences of the 2017 coral bleaching

- event in the southern Persian/Arabian Gulf. *Coral Reefs*. <https://doi.org/10.1007/s00338-019-01767-y>
- Ceccarelli D, Richards Z, Pratchett MS, Cvitanovic C (2011) Rapid increase in coral cover on an isolated coral reef, the Ashmore Reef National Nature Reserve, north-western Australia. *Mar Freshw Res* 62:1214–1220
- Couch CS, Burns JHR, Liu G, Steward K, Gutlay TN, Kenyon J, Eakin CM, Kosaki RK (2017) Mass coral bleaching due to unprecedented marine heatwave in Papahānaumokuākea Marine National Monument (Northwestern Hawaiian Islands). *PLOS One* 12:e0185121
- Darling ES, Graham NA, Januchowski-Hartley FA, Nash KL, Pratchett MS, Wilson SK (2017) Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs* 36:561–575
- Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1:95–107
- Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121–132
- Drew E, Yon L, Lythgoe J (1971) Morphology and ecology of the reef front of Aldabra. Regional Variation in Indian Ocean Coral Reefs: The Proceedings of a Symposium, Organized Jointly by the Royal Society of London and the Zoological Society of London. Held at the Zoological Society of London on 28 and 29 May, 1970:87
- Fabricius KK, Alderslade PP (2001) Soft corals and sea fans: a comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science (AIMS)
- Farrow G, Brander K (1971) Tidal studies on Aldabra. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 260:93–121
- Friedlander A, Ballesteros E, Beets J, Brown EK, Fay JM, Haupt P, Henning B, Rose P, Sala E (2015) Biodiversity and ecosystem health of the Aldabra Group, Southern Seychelles
- Furby KA, Bouwmeester J, Berumen ML (2013) Susceptibility of central Red Sea corals during a major bleaching event. *Coral Reefs* 32:505–513
- Gilmour AR, Gogel B, Cullis B, Thompson R, Butler D (2009) ASReml user guide release 3.0. VSN International Ltd, Hemel Hempstead, UK
- Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated coral reef system following severe disturbance. *Science* 340:69–71
- Graham NA, Nash K (2013) The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32:315–326
- Graham NA, McClanahan TR, MacNeil MA, Wilson SK, Polunin NV, Jennings S, Chabanet P, Clark S, Spalding MD, Letourneur Y (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. *PLOS One* 3:e3039
- Granek EF (2006) Linkages between mangrove forests and coral reefs: quantifying disturbance effects and energy flow between systems. Oregon State University, Department of Zoology, Corvallis, p p171
- Green RH, Lowe RJ, Buckley ML, Foster T, Gilmour JP (2019) Physical mechanisms influencing localized patterns of temperature variability and coral bleaching within a system of reef atolls. *Coral Reefs*. <https://doi.org/10.1007/s00338-019-01771-2>
- Gudka M, Obura D, Mwaura J, Porter S, Yahya S, Mabwa R (2018) Impact of the 3rd Global Coral Bleaching Event on the Western Indian Ocean in 2016. Global Coral Reef Monitoring Network (GCRMN)/Indian Ocean Commission
- Harrison HB, Álvarez-Noriega M, Baird AH, Heron SF, MacDonald C, Hughes TP (2018) Back-to-back coral bleaching events on isolated atolls in the Coral Sea. *Coral Reefs*. <https://doi.org/10.1007/s00338-018-01749-6>
- Head CE, Bayley DT, Rowlands G, Roche RC, Tickler DM, Rogers AD, Koldewey H, Turner JR, Andradi-Brown DA (2019) Coral bleaching impacts from back-to-back 2015–2016 thermal anomalies in the remote central Indian Ocean. *Coral Reefs*:1–14
- Heron S, Johnston L, Liu G, Geiger E, Maynard J, De La Cour J, Johnson S, Okano R, Benavente D, Burgess T (2016) Validation of reef-scale thermal stress satellite products for coral bleaching monitoring. *Remote Sensing* 8:59
- Heron SF, Eakin CM, Douvère F, Anderson KL, Day JC, Geiger E, Hoegh-Guldberg O, Van Hooidonk R, Hughes T, Marshall P, Obura D (2017) Impacts of climate change on World Heritage coral reefs : a first global scientific assessment
- Hoegh-Guldberg O (2011) Coral reef ecosystems and anthropogenic climate change. *Regional Environmental Change* 11:215–227
- Hongo C, Yamano H (2013) Species-Specific Responses of Corals to Bleaching Events on Anthropogenically Turbid Reefs on Okinawa Island, Japan, over a 15-year Period (1995–2009). *PLOS One* 8:e60952
- Hsu C-M, Keshavmurthy S, Denis V, Kuo C-Y, Wang J-T, Meng P-J, Chen CA (2012) Temporal and spatial variations in symbiotic communities of catch bowl coral *Isopora palifera* (Scleractinia: Acroporidae) on reefs in Kenting National Park, Taiwan. *Zoological Studies* 51:1343–1353
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science-AAAS-Weekly Paper Edition* 265:1547–1551
- Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JB, Kleypas J, van de Leemput IA, Lough JM, Morrison TH (2017) Coral reefs in the Anthropocene. *Nature* 546:82–90
- Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359:80–83
- Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G (2018b) Global warming transforms coral reef assemblages. *Nature* 556:492
- Hume BC, Voolstra CR, Arif C, D'Angelo C, Burt JA, Eyal G, Loya Y, Wiedenmann J (2016) Ancestral genetic diversity associated with the rapid spread of stress-tolerant coral symbionts in response to Holocene climate change. *Proceedings of the National Academy of Sciences* 113:4416–4421
- Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences* 32:1259–1269
- Le Nohaïc M, Ross CL, Cornwall CE, Comeau S, Lowe R, McCulloch MT, Schoepf V (2017) Marine heatwave causes unprecedented regional mass bleaching of thermally resistant corals in northwestern Australia. *Scientific Reports* 7:14999
- Liu G, Rauen Zahn JL, Heron SF, Eakin CM, Skirving WJ, Christensen T, Strong AE, Li J (2013) NOAA coral reef watch 50 km satellite sea surface temperature-based decision support system for coral bleaching management
- Lough JM, Anderson KD, Hughes TP (2018) Increasing thermal stress for tropical coral reefs: 1871–2017. *Scientific Reports* 8:6079
- Lowe RJ, Pivan X, Falter J, Symonds G, Gruber R (2016) Rising sea levels will reduce extreme temperature variations in tide-dominated reef habitats. *Science Advances* 2:e1600825
- Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecology Letters* 4:122–131
- Maida M, Sammarco PW, Coll JC (1995) Effects of soft corals on scleractinian coral recruitment. I: Directional allelopathy and

- inhibition of settlement. *Marine Ecology Progress Series* 121:191–202
- McClanahan TR, Ateweberhan M, Sebastian CR, Graham N, Wilson S, Bruggemann JH, Guillaume MM (2007) Predictability of coral bleaching from synoptic satellite and in situ temperature observations. *Coral Reefs* 26:695–701
- Monroe AA, Ziegler M, Roik A, Röthig T, Hardenstine RS, Emms MA, Jensen T, Voolstra CR, Berumen ML (2018) In situ observations of coral bleaching in the central Saudi Arabian Red Sea during the 2015/2016 global coral bleaching event. *PLOS One* 13:e0195814
- Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in ecology & evolution* 23:555–563
- Mumby PJ, Chisholm JR, Edwards AJ, Andrefouet S, Jaubert J (2001a) Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. *Marine Ecology Progress Series* 222:209–216
- Mumby PJ, Chisholm J, Edwards A, Clark C, Roark E, Andrefouet S, Jaubert J (2001b) Unprecedented bleaching-induced mortality in *Porites* spp. at Rangiroa Atoll, French Polynesia. *Marine Biology* 139:183–189
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101
- NOAA-CRW (2000) NOAA Coral Reef Watch 50-km Satellite Virtual Station Time Series Data for Aldabra, Seychelles; Comoros; Glorieuse Island, France; Mahé, Seychelles; Maldives; and Mayotte, France (dataset accessed: 2019-04-04 at https://coralreefwatch.noaa.gov/satellite/vs/docs/list_vs_group_latlon_201103.php; please refer to the according station). Silver Spring, Maryland, USA
- Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Marine ecology progress series* 376:295–306
- Obura D, Gudka M, Abdou Rabi F, Bacha Gian S, Bijoux J, Freed S, Maharavo J, Mwaura J, Porter S, Sola E (2017) Coral reef status report for the western Indian Ocean. global coral reef monitoring network (GCRMN)/international coral reef initiative (ICRI) CORDIO East Africa
- Oliver TA, Palumbi SR (2011) Do fluctuating temperature environments elevate coral thermal tolerance? *Coral Reefs* 30:429–440
- Perry C, Morgan K (2017) Bleaching drives collapse in reef carbonate budgets and reef growth potential on southern Maldives reefs. *Scientific Reports* 7:40581
- Pratchett MS, McCowan D, Maynard JA, Heron SF (2013) Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. *PLOS One* 8:e70443
- Rowan R (2004) Coral bleaching: thermal adaptation in reef coral symbionts. *Nature* 430:742
- Rukhin AL (2011) Maximum Likelihood and Restricted Likelihood Solutions in Multiple-Method Studies. *Journal of research of the National Institute of Standards and Technology* 116:539–556
- Safaie A, Silbiger NJ, McClanahan TR, Pawlak G, Barshis DJ, Hench JL, Rogers JS, Williams GJ, Davis KA (2018) High frequency temperature variability reduces the risk of coral bleaching. *Nature Communications* 9:1671
- Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and Degradation of Coral Reefs in the Northern Line Islands. *PLOS One* 3:e1548
- Schmid B, Baruffol M, Wang Z, Niklaus PA (2017) A guide to analyzing biodiversity experiments. *Journal of Plant Ecology* 10:91–110
- Sheppard CR (1999) Coral decline and weather patterns over 20 years in the Chagos Archipelago, Central Indian Ocean. *Ambio*:472–478
- Sheppard CR, Obura D (2005) Corals and reefs of Cosmoledo and Aldabra atolls: extent of damage, assemblage shifts and recovery following the severe mortality of 1998. *Journal of Natural History* 39:103–121
- Sheppard CR, Harris A, Sheppard A (2008) Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. *Marine Ecology Progress Series* 362:109–117
- Sheppard CR, Sheppard A, Mogg A, Bayley D, Dempsey AC, Roche R, Turner J, Purkis S (2017) Coral bleaching and mortality in the Chagos Archipelago. *Atoll Research Bulletin* 2017
- Skirving W, Enríquez S, Hedley J, Dove S, Eakin CM, Mason R, De La Cour J, Liu G, Hoegh-Guldberg O, Strong A (2017) Remote sensing of coral bleaching using temperature and light: progress towards an operational algorithm. *Remote Sensing* 10(1):18
- Skirving W, Heron SF, Marsh B, Liu G, De La Cour J, Geiger E, Eakin CM (2019) The relentless march of mass coral bleaching: a global perspective of changing heat stress. *Coral Reefs*:1–11
- Steneck RS, Mumby PJ, MacDonald C, Rasher DB, Stoyke G (2018) Attenuating effects of ecosystem management on coral reefs. *Science Advances* 4, eaao5493
- Stobart B, Buckley R, LeClair L, Teleki K, Downing N, Souter D, Callow M (2002) Aldabra: Monitoring the path to recovery. *Coral Reef Degradation in the Indian Ocean* 5:232
- Stobart B, Teleki K, Buckley R, Downing N, Callow M (2005) Coral recovery at Aldabra Atoll, Seychelles: five years after the 1998 bleaching event. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* 363:251–255
- Stoddart D (1984) Coral reefs of the Seychelles and adjacent regions. *Biogeography and Ecology of the Seychelles Islands* W Junk, The Hague, pp 63–81
- Stoddart D, Taylor J, Fosberg F, Farrow G (1971) Geomorphology of Aldabra atoll. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 260:31–66
- Stuart-Smith RD, Brown CJ, Ceccarelli D, Edgar GJ (2018) Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. *Nature* 560:92–96
- Taylor J (1971) Intertidal zonation at Aldabra atoll. *Phil Trans R Soc Lond B* 260:173–213
- Teleki K, Downing N, Stobart B, Buckley R (1999) Aldabra marine programme. Cambridge Coastal Research Unit, Department of Geography, University of Cambridge, p 31
- Veron JE (2000) *Corals of the World*, vol. 1–3. Australian Institute of Marine Science, Townsville 295
- Virk D, Pandit D, Sufian M, Ahmed F, Siddique M, Samad M, Rahman M, Islam M, Ortiz-Ferrara G, Joshi K (2009) REML is an effective analysis for mixed modelling of unbalanced on-farm varietal trials. *Experimental Agriculture* 45:77–91
- Wallace C (1999) *Staghorn corals of the world: a revision of the genus Acropora*. CSIRO publishing, Melbourne

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.