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Bleaching impacts on carbonate production in the Chagos Archipelago: influence of functional coral groups on carbonate budget trajectories

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Abstract Reefs in the remote Chagos Archipelago (central Indian Ocean) were severely affected by sea surface temperature warming and coral bleaching in 2015–2016. Here we assess the impacts of this event on community composition and reef carbonate production at twelve fore reefs sites across three atolls. Bleaching caused a 69% decline in coral cover, mostly driven by mortality of tabular *Acropora* spp. and a 77% decline in mean coral carbonate production (2015: 13.1 ± 4.8; 2018: 3.0 ± 1.2 kg $CaCO_3$ m^2 yr^{-1}). Changes were accompanied by a major shift from competitive to stress-tolerant coral taxa, with magnitudes of decline comparable to those reported elsewhere in the Indian Ocean, despite inter-site differences in dominant coral species. These trends differ from those on reefs already dominated by stress-tolerant taxa, which experienced minor declines in production post-warming. The study highlights the potential for different suites of functional coral groups to drive divergent post-bleaching budget responses.

Keywords Coral bleaching · Carbonate production · *ReefBudget* · Chagos Archipelago · British Indian Ocean Territory

Introduction

Climate change poses a major threat to coral reef ecosystems worldwide through warming sea waters and ocean acidification (Hoegh-Guldberg et al. 2007). Of greatest concern is the increasing frequency and severity of global warming events and associated coral bleaching. The most recent event in 2015–2016 impacted reefs at magnitudes and across spatial scales comparable to the (then-unprecedented) 1997–1998 mass bleaching (Hughes et al. 2018). The severity of bleaching-induced coral mortality and subsequent recovery trajectories varied temporally and spatially and was often influenced by additional local anthropogenic stressors. For example, bleaching-impacted reefs exposed to additional local stressors in the Seychelles recovered only slowly from the 1997–1998 event or even phase-shifted to macroalgal-dominated states (Graham et al. 2015). In contrast, coral communities on more remote reefs in the Maldives and the Chagos Archipelago recovered within 7–10 yrs (Morri et al. 2015; Sheppard et al. 2017).

Bleaching impacts many facets of reef ecology, but where rates of carbonate production and reef budget states (a measure of the net balance between carbonate production and erosion) are negatively impacted, the capacity of reefs to maintain their physical three-dimensional structures and vertical growth potential can be severely impaired (Perry et al. 2008). Reef carbonate production rates can be reduced by decreasing coral cover, changing species composition, and depressed coral calcification during sub-lethal thermal stress (Perry and Morgan 2017; Manzello et al. 2018). Few studies have quantified magnitudes of carbonate production decline following bleaching, although there is a pressing need to understand the reasons for spatial differences in trajectories to assess

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which reefs may be better able to cope with future challenges such as sea-level rise (Perry et al. 2018).

Here we report on the impacts of the 2015–2016 warming event on reef carbonate production rates in the remote Chagos Archipelago, part of the British Indian Ocean Territory, in the central Indian Ocean. Pre-bleaching (April 2015) most fore reefs had high coral cover (averaging 40–50%; Sheppard et al. 2017) and high net positive carbonate budgets (up to 9.8 kg $CaCO_3$ m^{-2} yr^{-1}; Perry et al. 2015). Coral bleaching in 2015 and 2016 reduced hard coral cover to $< 10\%$ (Sheppard et al. 2017), with so far unknown implications for reef carbonate budgets. We analysed data from twelve sites across three atolls (April 2015 and May 2018) to address three main questions: (1) What impact did the 2015–2016 warming event have on carbonate production rates across the Chagos Archipelago? (2) How does the magnitude and trajectory of carbonate production decline observed compare to that reported at other bleaching-impacted sites?; and (3) How do different trajectories of decline influence carbonate budget recovery potential?

Study area and methods

To quantify changes in reef carbonate production rates, we compared data collected from fore reefs across the Chagos Archipelago during March–April 2015 and May 2018. In 2015, 28 sites across five atolls were surveyed (Perry et al. 2015). In 2018, we resurveyed a subset of 12 of these sites along the north-west coasts of islands in the atolls of Salomon, Peros Banhos and Great Chagos Bank (GCB) ($n = 4$ sites/atoll; Fig. 1a), with sites repositioned as close as possible to those surveyed in 2015. However, due to wind and wave conditions, the Île Diamante (Peros Banhos) 2018 site was located 1.2 km from the 2015 site, but along the same island front. All sites were defined as sheltered from predominant wind direction and wave exposure, except at Middle and South Brother (GCB) where sites were located along the more exposed south-west coasts of these islands. At each site, we collected data along four replicate transects (10 m long) running parallel to the reef crest at depths of 8–10 m, with the exception of Île de la Passe (Salomon) ($n = 3$). Each transect was surveyed for substrate composition and reef rugosity using a modified version of the *ReefBudget* method (Perry et al. 2015; Perry and Morgan 2017). For substrate composition, we measured the distance (in cm) covered by each benthic group within each linear metre beneath a 10-m guide line using a separate flexible tape. Recorded groups included scleractinian corals to the genera and morphological level, e.g. *Acropora* branching, *Porites* massive, etc.; crustose coralline algae (CCA); turf algae; fleshy macroalgae; non-encrusting coralline algae (e.g. *Halimeda* spp.); sediment; rubble; and other benthic organisms. Distances of benthic categories were collected as a function of the true three-dimensional surface of the reefs, thus including cover on overhangs and vertical surfaces. The cumulative total reef surface was divided by linear distance (10 m) to yield reef rugosity (a completely flat surface would therefore have a rugosity of (1). We then used the morphology and size of individual coral colonies in combination with published genera-specific skeletal density (g cm^{-3}) and linear growth rates (cm yr^{-1}) to estimate carbonate production rates (G = kg $CaCO_3$ m^{-2} yr^{-1}). Density and growth rate data used have been expanded in 2018, and survey data from 2015 were rerun with updated rates (see Supplementary Table 1). Due to the paucity of local data, we currently assume that growth rates are consistent across biogeographic regions and throughout the bleaching event. Efforts are currently underway to address both of these data gaps. To test for statistical differences in variables pre- and post-bleaching, paired t-tests were run in R 3.3.0 (R Core Team 2016). Relationships between carbonate production and specific substrate groups were explored using Pearson's product–moment correlations. Differences in production rates among regions were tested by fitting an analysis of variance model. All values are given as mean ± standard deviation (SD).

Results and discussion

Impact of the 2015–2016 bleaching event on Chagos reefs

Strong sea surface temperature warming across the Indian Ocean (https://coralreefwatch.noaa.gov) caused extensive coral mortality across the Chagos Archipelago in 2015 and 2016 (Sheppard et al. 2017). Live coral cover (as a function of 3-D reef surface area) across the study sites declined by 69% between April 2015 ($27.1 \pm 10.5\%$) and May 2018 ($8.5 \pm 3.9\%$; $t(11) = 7.483$, $p < 0.001$; Fig. 1b). Coral mortality in turn significantly reduced coral carbonate production rates (Coral G), which declined by 77% between 2015 (13.1 ± 4.8 G) and 2018 (3.0 ± 1.2 G; $t(11) = 7.919$, $p < 0.001$; Fig. 1c). Carbonate production by crustose coralline algae (CCA G) decreased by 15% (2015: 0.5 ± 0.1 G; 2018: 0.4 ± 0.2 G; $t(11) = 2.233$, $p = 0.047$; Fig. 1d), and the cumulative decrease in total carbonate production (Gross G) was 75% (2015: 13.6 ± 4.7 G; 2018: 3.4 ± 1.2 G, $t(11) = 8.025$, $p < 0.001$). We caution that the actual magnitude of production decline could be even more severe, as local growth and calcification rates can decline significantly after bleaching (Manzello et al. 2018), but which could not be

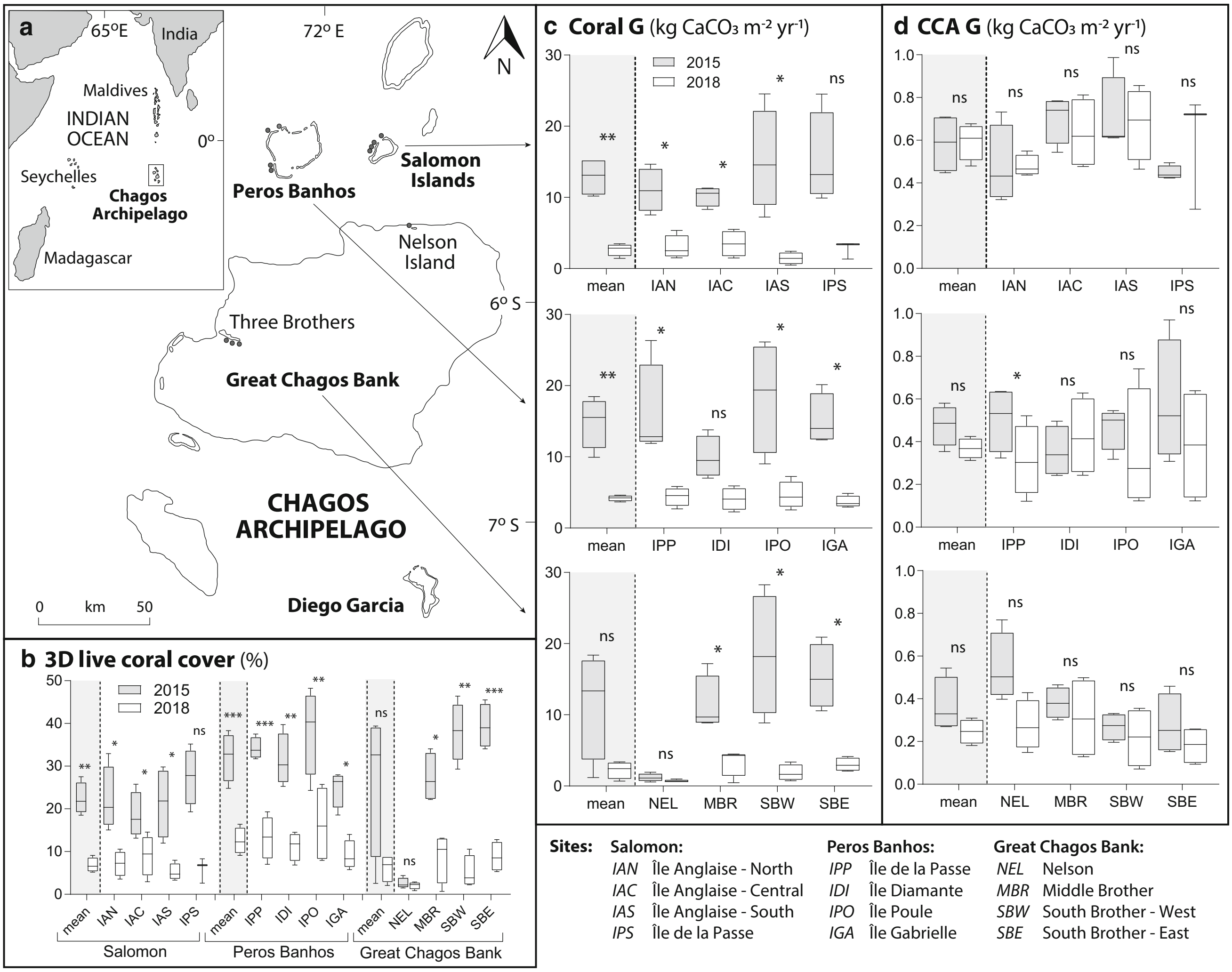


Fig. 1 **a** Location of the Chagos Archipelago and study sites (dots) across the atolls of Salomon, Peros Banhos and Great Chagos Bank; **b** three-dimensional live coral cover; carbonate production by **c** corals and **d** crustose coralline algae (CCA) comparing pre- and post-bleaching values at each site and averages across each atoll (shaded) in the atolls of Salomon (first row), Peros Banhos (middle row) and Great Chagos Bank (third row). The difference between pre- and post-bleaching values was tested for significance using two-sided paired *t*-tests (*ns* not significant, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$)

taken into account in this study. The one outlier in our data set was Nelson Island on the northern margin of GCB, which in 2015 had very low coral cover (2.6%) and carbonate production rates (1.2 G) due to a localised crown-of-thorns outbreak (Perry et al. 2015); in 2018, this site was still characterised by the lowest coral cover (2.1%) and carbonate production (0.7 G) measured across our sites.

Coral cover and carbonate production decline were driven mainly by mortality of *Acropora* spp., the relative abundance of which declined by 96% between 2015 (13.3 ± 7.0%) and 2018 (0.5 ± 0.4%; $t(11) = 6.410$, $p < 0.001$). The contribution of competitive taxa (*Acropora* spp. and other branching species, after Darling et al. 2012) to Coral G decreased by 76% from an average relative contribution of 66.2% (2015) to 15.9% (2018) (Fig. 2a). Cover of *Porites* spp. only decreased by 7% (2015: 5.0 ± 2.6%; 2018: 4.7 ± 3.1%; not significant), and stress-tolerant taxa (mainly massive and encrusting species) increased their relative contribution to Coral G by 164% from 31.4% (2015) to 82.8% (2018) (Fig. 2a). The importance of competitive taxa for sustaining high carbonate production rates has been discussed previously (Perry and Morgan 2017), and data from this study demonstrate clearly that *Acropora* spp. abundance pre-bleaching is a strong predictor of the magnitude of bleaching-driven Gross G decline across the Indian Ocean (Chagos Archipelago: $t(10) = 11.456$, $p < 0.001$, $r = 0.964$; Maldives: $t(3) = 4.203$, $p = 0.024$, $r = 0.925$; Seychelles: $t(8) = 5.224$, $p < 0.001$, $r = 0.879$; Fig. 2b). This observation is particularly concerning, given that loss of *Acropora* spp. is likely to impact reef capacity to track projected rates of sea-level rise (Perry et al. 2015) and that

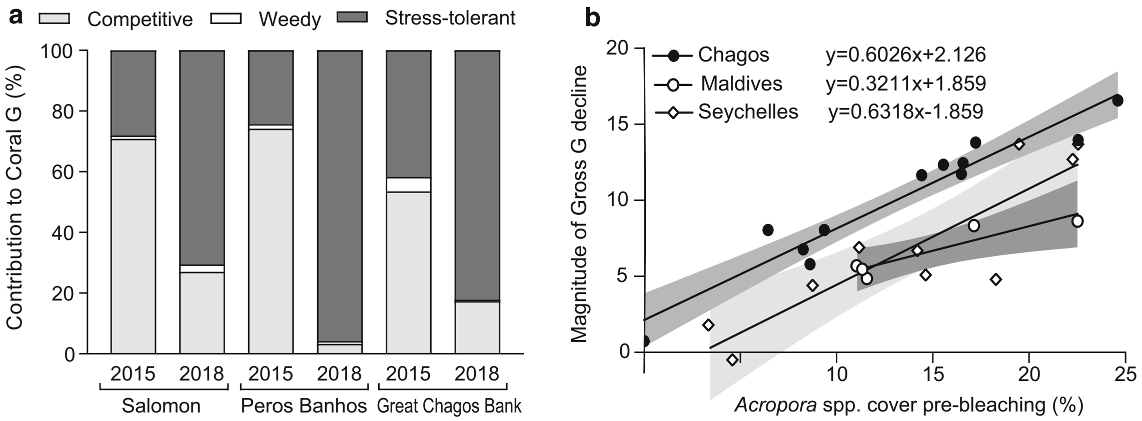


Fig. 2 **a** Contribution of functional coral groups (classified after Darling et al. 2012) to coral carbonate production (Coral G); **b** linear correlation (line) and 95% confidence intervals (shaded area) between cover of *Acropora* spp. prior to bleaching and the magnitude of total carbonate production (Gross G) decline. Additional data from Perry and Morgan (2017) and Perry et al. (2018)

recovery of *Acropora* spp. may be limited if subject to further disturbance events (Burt et al. 2011; Pratchett et al. 2017). To this point, there are no data on the effects of bleaching on carbonate budgets along the most exposed eastern sides of the atolls. As coral communities at those sites were dominated by *Porites* spp. and *Pocillopora* spp. prior to bleaching (Perry et al. 2015), the decline in carbonate budgets may be less severe that at the formerly *Acropora* spp.-dominated sites on the western atoll margins.

A further key impact of the widespread coral mortality has been an initial loss of reef rugosity (2015: 2.3 ± 0.2; 2018: 1.9 ± 0.3; 16% decrease; $t(11) = 8.025$, $p < 0.001$; Fig. 3a). At the same time, we observed a 103% increase in coral rubble (2015: 5.3 ± 2.7%; 2018: 10.8 ± 2.9%; $t(11) = 9.905$, $p < 0.001$; Fig. 3b), indicating ongoing structural changes in the reefs following bleaching. Given observed high levels of endolithic sponge infestation, this process of collapse is projected to continue, although high abundances of coral recruits (including *Acropora* spp.) suggest a positive prognosis for coral community recovery.

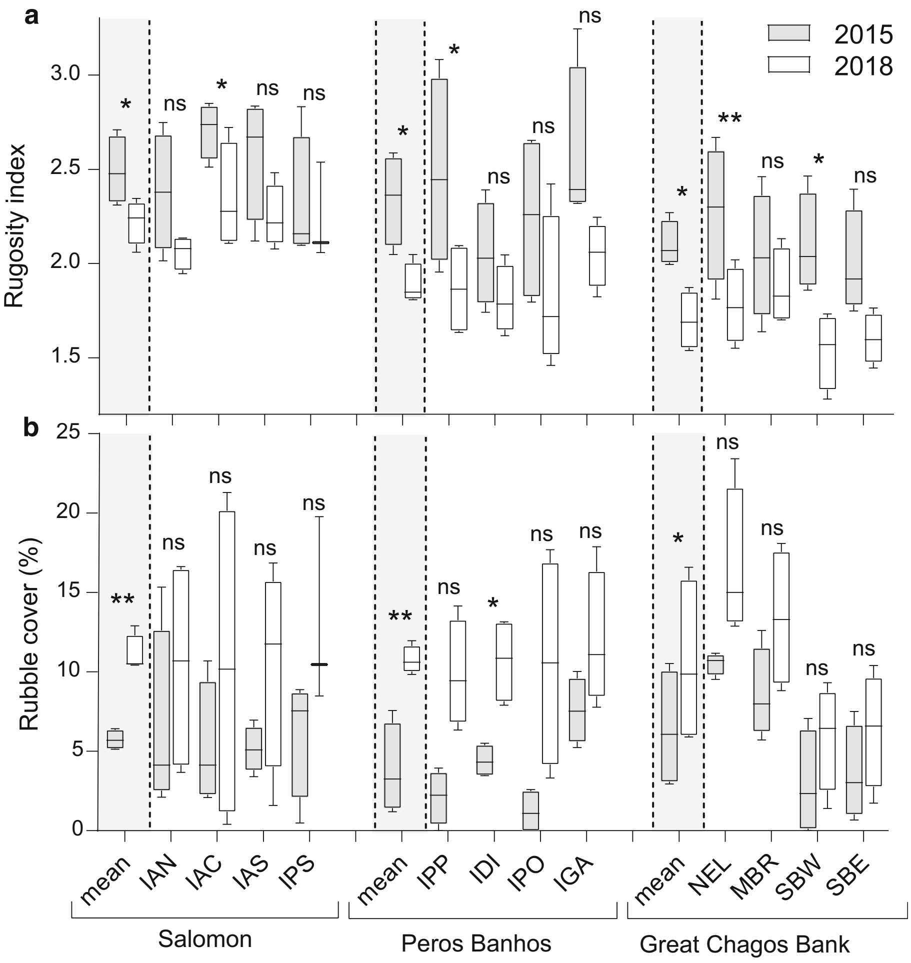
Trajectories of different reef community types

While the importance of carbonate budgets as an indicator for reef health has recently gained attention, studies quantifying bleaching impacts on carbonate budgets are rare (but see Eakin 1996). Comparing our results with data sets from the Maldives (Perry and Morgan 2017), Seychelles (raw data from Perry et al. 2018), and Florida Keys (Manzello et al. 2018) (all based on the *ReefBudget* methodology), we make two observations. First, that while coral cover was similar across all Indian Ocean sites before the 2016 bleaching, mean carbonate production rates were significantly higher in the Chagos Archipelago due to the dominance of large tabular, as opposed to branching Acroporids ($F_{2,24} = 3.635$, $p = 0.042$; Fig. 4a). Second, that despite pre-bleaching differences in the relative abundance of competitive taxa (Fig. 4b), declines in coral cover (69–79%) and Gross G (74–75%) were comparable, and post-bleaching cover and Gross G rates were similar (Fig. 4b). In contrast, recent work in the Florida Keys, at a site dominated by encrusting/massive *Orbicella annularis*, and devoid of competitive coral taxa, exhibited a very different response to warming events. The generally high coral cover only decreased by 4% after a warming event in 2014 and then actually increased slightly despite a stronger event in 2015 (Fig. 4a). Production rates only decreased by 28%, mostly due to depressed coral calcification rates, and quickly recovered towards pre-bleaching production state. During both warming events, production stayed well above local erosion rates, which in the Caribbean generally are lower than in the Indo-Pacific due to lower parrotfish biomass (Perry et al. 2018). These observations are in keeping with conceptual ideas about the higher resilience of stress-tolerant coral-dominated reefs to climate-induced disturbances (Côté and Darling 2010), but are here extended in the context of carbonate budget changes. It is pertinent to note, however, that despite higher pre-event coral cover in Florida compared to the Indian Ocean reefs, carbonate production rates were substantially lower, emphasising the trade-off that exists between more resilient assemblages with low production potential, compared to high carbonate production rates that define more vulnerable competitive taxa-dominated reefs.

Implications for recovery

Despite the large post-bleaching decline in carbonate production observed across Indian Ocean sites, calculated production rates are only slightly lower than measured pre-bleaching erosion rates (Fig. 4), suggesting a high

Fig. 3 Measured **a** reef rugosity and **b** rubble cover comparing pre- and post-bleaching values at each site and averages across each atoll (shaded). The difference between pre- and post-bleaching values was tested for significance using two-sided paired *t*-tests (*ns* not significant, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$)



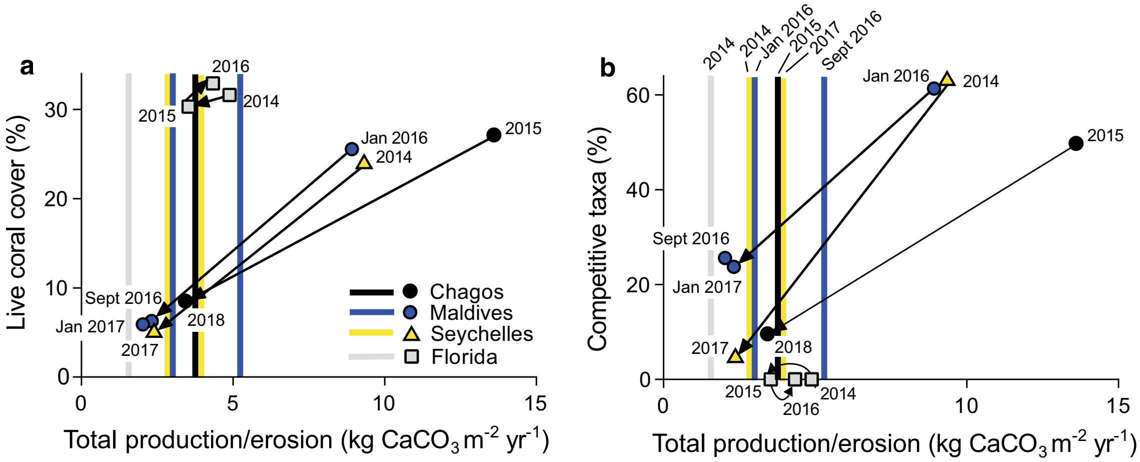


Fig. 4 Shifts in average total carbonate production rates relative to **a** live coral cover and **b** the relative abundance of competitive taxa. Warming events occurred in 2016 in the Chagos Archipelago (black), Maldives (blue) and Seychelles (yellow), and in 2014 and 2015 in Florida (grey). Arrows indicate transitions in carbonate production rates and community composition in response to bleaching. Vertical lines indicate measured erosion rates pre-bleaching (Chagos: 2015, Maldives: January 2016, Seychelles: 2014, Florida: 2014) and post-bleaching (Maldives: September 2016, Seychelles: 2017) which have to be offset by sufficiently high production rates to maintain reefs in positive carbonate budget states. Additional data from Perry and Morgan (2017), Perry et al. (2018) and Manzello et al. (2018)

likelihood of rapid post-bleaching budget recovery. However, erosion rates by parrotfish increased substantially immediately after bleaching in the Maldives and Seychelles (Fig. 4), suggesting that a return to positive carbonate budget states might be more delayed than indicated by pre-bleaching erosion values. Additionally, while most Chagos and Maldives reefs demonstrated an impressive capacity for relatively rapid recovery after the 1997–1998 bleaching event (Morri et al. 2015; Sheppard et al. 2017), some Seychelles reefs phase-shifted to macroalgal-dominated states, specifically at sites with low initial structural complexity, low juvenile coral densities, low herbivore biomass and high nutrient concentrations (Graham et al. 2015). It is thus reasonable to hypothesise that these divergent recovery trajectories may be exacerbated after the 2015–2016 event. Sites with low abundance of fast-growing and structurally complex coral taxa, and with local anthropogenic pressures, may also become locked into macroalgal-dominated states with negative carbonate budgets, while reefs in more remote areas may retain the capacity to recover to high positive carbonate budgets in the absence of more frequent bleaching events. Ongoing observations of reef carbonate budget trajectories should shed light on the interacting influences of ecological assemblages and disturbance pressures on carbonate budget responses.

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Compliance with ethical standards

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

References

Burt J, Al-Harthi S, Al-Cibahy A (2011) Long-term impacts of coral bleaching events on the world's warmest reefs. Mar Environ Res 72:225–229

Côté IM, Darling ES (2010) Rethinking ecosystem resilience in the face of climate change. Plos Biol 8:e1000438

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

Eakin CM (1996) Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Niño at Uva Island in the eastern Pacific. Coral Reefs 15(2):109–119

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JPA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

Manzello DP, Enochs IC, Kolodziej G, Carlton R, Valentino L (2018) Resilience in carbonate production despite three coral bleaching events in 5 years on an inshore patch reef in the Florida Keys. Mar Biol 165:99

Morri C, Montefalcone M, Lasagna R, Gatti G, Rovere A, Parravicini V, Baldelli G, Colantoni P, Bianchi CN (2015) Through bleaching and tsunami: coral reef recovery in the Maldives. Mar Pollut Bull 98:188–200

Perry CT, Morgan KM (2017) Bleaching drives collapse in reef carbonate budgets and reef growth potential on southern Maldives reefs. Sci Rep 7:40581

Perry CT, Spencer T, Kench PS (2008) Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. Coral Reefs 27(4):853–866

Perry CT, Murphy GN, Graham NAJ, Wilson SK, Januchowski-Hartley FA, East HK (2015) Remote coral reefs can sustain high growth potential and may match future sea-level trends. Sci Rep 5:18289

Perry CT, Alvarez-Filip L, Graham NAJ, Mumby PJ, Wilson SK, Kench PS, Manzello DP, Morgan KM, Slangen ABA, Thomson DP, Januchowski-Hartley F, Smithers SG, Steneck RS, Carlton R, Edinger EN, Enochs IC, Estrada-Saldívar N, Haywood MDE, Kolodziej G, Murphy GN, Pérez-Cervantes E, Suchley A, Valentino L, Boenish R, Wilson M, Macdonald C (2018) Loss of coral reef growth capacity to track future increases in sea level. Nature 558:396–400

Pratchett MS, Baird AH, Bauman AG, Burt JA (2017) Abundance and composition of juvenile corals reveals divergent trajectories for coral assemblages across the United Arab Emirates. Mar Pollut Bull 114:1031–1035

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 15 June 2018

Sheppard CRC, Sheppard A, Mogg A, Bayley D, Dempsey AC, Roche R, Turner J, Purkins S (2017) Coral bleaching and mortality in the Chagos Archipelago. Atoll Res Bull 613:1–26