PERSPECTIVE



The 2014–2017 global-scale coral bleaching event: insights and impacts

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Received: 30 June 2019/Accepted: 15 July 2019/Published online: 22 July 2019 © The Author(s) 2019

Abstract 2014–2017 was an unprecedented period of successive record-breaking hot years, which coincided with the most severe, widespread, and longest-lasting globalscale coral bleaching event ever recorded. The 2014–2017 global-scale coral bleaching event (GCBE) resulted in very high coral mortality on many reefs, rapid deterioration of reef structures, and far-reaching environmental impacts. Through the papers in this special issue of Coral Reefs entitled The 2014–2017 Global Coral Bleaching Event: Drivers, Impacts, and Lessons Learned, as well as papers published elsewhere, we have a good analysis of the 2014-2017 GCBE and its impacts. These studies have provided key insights into how climate change-driven marine heatwaves are destroying coral reef ecosystems: (a) The 2014–2017 GCBE is unique in the satellite record in its spatial scale, duration, intensity, and repetition of bleaching. (b) The impacts have been the most severe ever seen at many reefs. (c) Timing of observations matters and needs to be considered during the analysis of impacts.

Topic Editor: Morgan S. Pratchett

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(d) On both global and local scales, the intensity of heat stress and impacts varied. (e) We continue to see important differences among and within coral taxa, with key roles played by algal symbionts and the microbiome. (f) Heat stress and bleaching both play a role in subsequent disease, which plays a key role in mortality. (g) Impacts ripple far beyond corals, with significant changes to the fish and invertebrate community that may last decades. (h) The structure of both individual coral's skeletons and entire reefs has been eroded much more quickly than previously realized. (i) The 2014–2017 GCBE provided little support for the proposed "lifeboat" hypothesis, whereby deep or mesophotic reefs serve as a means of coral reef salvation. (j) While marine protected areas (MPAs) provide protection from local stressors, they not only do not protect reefs from global-scale stressors, but also here is also little evidence they provide significant resilience.

Keywords Coral bleaching · Heat stress · Coral Reef Watch · CoralTemp · Marine heatwave · Symbionts · Microbiome · Coral disease · El Niño · ENSO

Introduction

Widespread coral bleaching was first witnessed in 1983 as part of the extremely strong 1982–1983 El Niño (Coffroth et al. 1990). The next extremely strong El Niño, arguably stronger than that in 1982–1983 (Wolter and Timlin 1998; McPhaden 1999), resulted in the first global-scale coral bleaching event (GCBE) in 1998, the effects of which were apparent throughout tropical locations (Wilkinson 2000). Just over a decade later, a much milder El Niño gave rise to the second GCBE in 2010, but this was not well documented, in part because integrated assessments such as the



Global Coral Reef Monitoring Network and ReefBase were no longer there to nudge scientists to publish on the bleaching (Heron et al. 2016a, 2016b).

Just 4 yrs later, the incomplete formation of a 2014–2015 El Niño followed by the strong 2015–2016 El Niño initiated the third GCBE that lasted for three full years (Eakin et al. 2014, 2016, 2017). Extreme atmospheric and oceanic temperatures, representing the highest annual globally averaged temperatures recorded since the 1800s, were recorded in 2015, 2016, and 2017 (Blunden and Arndt 2018); notably, 2017 was the warmest non-El Niño year ever recorded. This extended period of record-breaking temperatures brought us the most severe, widespread, and longest-lasting GCBE on record (Eakin et al. 2018a).

What was different in 2014–2017?

As sea surface temperature anomalies at levels capable of causing coral bleaching moved from northern to southern hemispheres repeatedly from 2014 to 2017, a nearly continuous set of bleaching events moved across most of the world's coral reefs. In 2015 and again in 2016, the pattern of bleaching matched that seen during the first global-scale coral bleaching event in 1998 (Hoegh-Guldberg 1999). Thus, the 2014–2017 GCBE represents the first multi-year global-scale coral bleaching event, causing bleaching and mortality two or more times during the 3-yr event (Harrison et al. 2018; Head et al. 2019; Hughes et al. 2019a; Raymundo et al. 2019; Smith et al. 2019; Teixeira et al. 2019). The heat stress on coral reefs has successively increased over the past 3 decades, but the 3-yr event from June 2014 to May 2017 stands out as unique in the multidecadal record (Skirving et al. 2019). The 2014-2017 GCBE lasted 36 months, spanned four calendar years, and included positive (El Niño), negative (La Niña), and neutral phases of the El Niño-Southern Oscillation cycle (Blunden and Arndt 2018; Eakin et al. 2018a).

While the full extent and impacts of the 2014–2017 GCBE are still emerging, this was the longest-lasting, most widespread, and most likely the most damaging on record. Heat stress values in some locations, including the central tropical Pacific, were the highest ever recorded as heat stress lasting for months, with continuous heat stress lasting up to a full year and resulting in almost complete coral loss (Eakin et al. 2017; Brainard et al. 2018; Vargas-Ángel et al. 2019). Even some of the hottest coral reef areas in the world succumbed to heat stress during the 2014–2017 GCBE, showing that heat stress had even exceeded their limits (Burt et al. 2019). In the western Pacific US territories of Guam and the Commonwealth of the Mariana Islands, the 2014–2017 period was only part of a series of repeated heat stress events in a place where we are

beginning to see how the annual return of bleaching levels of heat stress may impact reefs (Raymundo et al. 2019). Successive years of extreme summer temperatures have been predicted to occur a few decades from now (Donner et al. 2018)—so why are we already seeing it before 2020? While it may have resulted from random variations in climate extremes, it is most likely the result of a common problem that climate models underestimate both extreme events and rates of change (Fischer et al. 2018; Schewe et al. 2019).

Heat stress during this event was not distributed evenly across reefs, devastating some areas while leaving some areas relatively unscathed. On the Great Barrier Reef (GBR), heat stress in 2016 was most concentrated in the northern third of the reef (Hughes et al. 2017b), while heat stress in 2017 was farther south (Hughes et al. 2019a). Similarly, 2016 heat stress in Western Australia was strongest above 20°S latitude, diminishing to the south (Le Nohaïc et al. 2017; Gilmour et al. 2019). A surprise was the second area of warming off southern Australia in 2016, resulting in bleaching as high as 34°S in Sydney Harbour (Goyen et al. 2019). At regional scales, these studies found damage largely followed the degree of heat stress recorded.

What have we learned from GCBE-3?

From a practical standpoint, a clear lesson that has emerged during the latest and prolonged bleaching event is the critical importance of the timing of surveys used to document the incidence and severity of coral bleaching (Claar and Baum 2018). While frequent, repeated, and well-timed observations are the best way to monitor bleaching and mortality during heat stress events, this is not always possible, especially at remote locations (e.g., Kiritimati Island). Some remote locations that are typically surveyed every 2-3 yrs have been surveyed annually since the onset of the 2014-2017 GCBE (Brainard et al. 2018; Vargas-Angel et al. 2019). However, even well-resourced, largescale programs to survey much of the GBR or US coral reefs are only conducted at a predetermined time of the year or even every 2 to 3 yrs (Jonker et al. 2008; NOAA 2014). Resulting estimates of bleaching or mortality will depend on whether surveys were conducted before, during, or after the peak of heat stress. While satellite remote sensing of heat stress is readily available and continues to be improved (Liu et al. 2017) and climate-model-based systems can predict heat stress with reasonable skill (Liu et al. 2018), we are currently reliant on direct and timely in-water surveys to establish the incidence and extent of coral bleaching and associated mortality (Hughes et al. 2017b, 2018a). Being able to detect coral bleaching remotely would improve temporal and spatial coverage in



studies of bleaching incidence and greatly advance understanding of the causes and consequences of coral bleaching.

While global-scale tools such as those provided by satellites and climate models provide valuable insights into large-scale patterns, local patterns of heat stress or survival reveal considerable variability within reefs and reef systems (Green et al. 2019; Reid et al. 2019). Past studies have suggested that either the ability of corals to resist heat stress or to recover after heat stress may be related to other environmental factors such as local anthropogenic stress (McClanahan et al. 2012). At one of the hardest-hit locations, local stress and heat stress interacted to influence the survival of the heat-tolerant coral Porites lobata in Kiritimati Island (McDevitt-Irwin et al. 2019). Examination of the microbiome of these corals showed that heat stress in 2016 had a similar impact on microbiome diversity as local stressors (subsistence fishing pressure, minor pollution from sewage runoff, and dredging) during the prior nonbleaching year. However, there was no indication of synergistic interaction between local stress and heat stress in terms of the corals' bleaching response, showing that these patterns may be more complicated than previously thought. Elsewhere, now-familiar patterns of symbiont shuffling were seen in some of the most heat-sensitive coral species but not in those more resistant (Gong et al. 2019; Thinesh et al. 2019).

There are winners, losers, and surprises. Some reefs bleach heavily and suffer significant coral mortality at low levels of heat stress (Hughes et al. 2017b, 2018a). In other cases, high heat stress may cause minimal mortality as corals recover well from bleaching (Fox et al. 2019). Some of this may be the result of inaccuracies in the heat stress products, especially in areas close to the equator with poor seasonal cycles. In some cases, local conditions like upwelling (Riegl et al. 2019) or high turbidity (Morgan et al. 2017; Teixeira et al. 2019) may help corals survive, while local growth of fleshy algae may increase bleaching susceptibility (Smith et al. 2019). In others, reefs may be predominated by a few species that are resilient to bleaching and recover well (Johnston et al. 2019) but may have reduced reproductive output or success (Fisch et al. 2019; Hughes et al. 2019b). Repeated years of heat stress may result in less bleaching during later events (Harrison et al. 2018; Fisch et al. 2019; Hughes et al. 2019a) or may overwhelm reefs to the point that their persistence is in question (Riegl et al. 2018; Raymundo et al. 2019). In a theme repeated from earlier mass bleaching events, heat stress, bleaching, and disease were interrelated, with greater tissue loss from disease in highly bleached corals (Brodnicke et al. 2019). During the 2014-2017 GCBE, scientists in Florida grappled with a multi-species disease that spread through most of their corals (Walton et al. 2018). That disease and tissue loss started during the warmest years on record in Florida, but it is still uncertain what role high temperature may have played.

Not surprisingly, where the broader ecosystem is examined, impacts from severe coral mortality ripple through the associated fauna and impact the entire ecosystem (Richardson et al. 2018; Sikkel et al. 2019; Wilson et al. 2019). Stuart-Smith et al. (2018) surveyed a year after the 2016 marine heatwave hit the GBR, finding widespread impacts throughout coral reef ecosystems, with an expected patchiness as local impacts varied. However, their work showed that heat stress was directly impacting the ecosystem at multiple levels, not just corals. They found greater correlations to the level of local heat stress than to the level of coral loss. A new long-term study of ecosystem impacts shows that severe bleaching persistently changes reef fish communities, lasting for more than 15 yrs (Robinson et al. 2019). Other novel work indicated that fish living within the branches of corals may moderate the impacts of bleaching on their hosts (Chase et al. 2018).

Bioerosion of reef structures is faster than previously understood. At multiple locations, severe bleaching and mortality caused declines in the net carbonate production on reefs by reducing carbonate production and increasing erosion (Couch et al. 2017; Lange and Perry 2019). Such erosion can be much more rapid than previously understood, as endolithic cyanobacteria can rapidly grow, perforating and weakening the outer part a coral's skeleton within days to weeks after mortality. This can rapidly flatten the fine structure of colonies, weaken branches (Leggat et al. 2019), and significantly reduce rugosity/topographic complexity, within less than a year after bleaching (Couch et al. 2017).

What about deep reefs?

Questions still remain unanswered regarding deep and mesophotic reefs. Despite the hypothesis that mesophotic reefs may serve as lifeboats for coral reefs (Baker et al. 2016), subsequent work has yet to bear this out. In fact, work has shown mesophotic reefs generally contain different coral species than shallow reefs and are no less susceptible to anthropogenic and natural impacts (Rocha et al. 2018). In the course of the 2014–2017 GCBE, the answer to this question remains cloudy as two groups working on deep GBR corals found conflicting results. While Baird et al. (2018) found a decline in bleaching with depth in a small part of the northern GBR during April of 2016, Frade et al. (2018) worked across a wider set of northern GBR reefs over a longer time found that upwelling only kept corals cool during the early part of the 2016 marine heatwave, only delaying bleaching until later in the

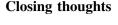


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event. As was discussed for shallow reefs, timing matters for deep reefs—perhaps more so as our observations of these reefs are far more limited. Much more work is needed to document the environmental change and bleaching incidence in deeper habitats, but the "lifeboat" hypothesis still remains an unlikely means of coral reef salvation.

What role does conservation play in bleaching events?

While marine protected areas (MPAs) provide protection from local stressors, they can do nothing to protect reefs from global-scale stressors like the marine heatwaves that caused the 2014–2017 GCBE. The worst heat stress during the 2014-2017 GCBE hit Jarvis Island, one of the most remote coral reefs in the world (Vargas-Ángel et al. 2019), and high heat stress again hit the remote reefs far offshore from Western Australia (Gilmour et al. 2019). Examining the patterns of the 2016 bleaching across a gradient of local stressors in the GBR showed no sign of bleaching protection where water quality was high (Hughes et al. 2017b). Examination of some of the world's best-managed reefs, those falling in World Heritage properties, showed that 72% of these were exposed to severe and/or repeated heat stress during the 2014–2017 GCBE (Heron et al. 2017). Fortunately, studies of reef recovery after severe bleaching and mortality in 1998 showed that some reefs have an ability to bounce back (Golbuu et al. 2007; Gilmour et al. 2013; Graham et al. 2015). However, recovery success was controlled by reef morphology (Graham et al. 2015) and hydrodynamics (Golbuu et al. 2007), not protection from fishing (Graham et al. 2015)—one of the stressors most often controlled in MPAs. Studies of mortality from heat stress over the last 2 decades, along with the multi-year bleaching in 2014–2017, are leading to a new hypothesis: While local protection such as MPAs can protect reefs against local stressors, they neither protect reefs against marine heatwaves caused by climate change nor even provide significant aid in reef recovery (Hughes et al. 2017b; Bates et al. 2019). Past conservation approaches do not address the scale of the greatest threats corals face in the Anthropocene—the growing climate crisis (Hughes et al. 2017a; Bellwood et al. 2019). Clearly, this points to the need for action to avert the growing climate crisis rather than relying on local action. In fact, perceptions of the importance and impact of climate change increased among GBR visitors after the bleaching events of 2016 and 2017, suggesting a strengthening base of support to address the sources of climate change (Curnock et al. 2019).



The papers in this special issue of Coral Reefs, together with the numerous papers on the 2014-2017 GCBE published elsewhere, and the papers still being prepared, provide significant insights into this multi-year bleaching event. However, as we saw with the 1998 global-scale bleaching event, the full impacts will not be known for years to come. Hopefully, papers will emerge on the recovery of coral reefs after the damage from the 2014-2017 GCBE. However, marine heatwaves have increased in frequency and intensity across the oceans, increasing heat stress on coral reefs (Eakin et al. 2018b; Oliver et al. 2018). This has resulted in an increase in the frequency of severe bleaching from once in every 25-30 yrs in the 1980s to once in 5.9 yrs today (Hughes et al. 2018b). Given 10-15 year recovery times for fastgrowing corals on the most ideally located, least-disturbed reefs (Riegl 2002; Baker et al. 2008; Gilmour et al. 2013; Head et al. 2019), it is far more likely we will witness the repeat of severe bleaching on most reefs around the world rather than their recovery.

Acknowledgements The reinvigorated Global Coral Reef Monitoring Network is initiating preparation of the next Status of Coral Reefs of the World for 2020—after a 12-yr hiatus since its 2008 report (Wilkinson 2008). This report will most likely include regional- and national-scale assessments of recent bleaching events. In the meantime, it was clear that action was needed to begin assessing the impacts and identifying key lessons from the 2014-2017 Global Coral Bleaching Event. This special issue, The 2014-2017 Global Coral Bleaching Event: Drivers, Impacts, and Lessons Learned, is the result of that call. The National Oceanic and Atmospheric Administration's (NOAA) Coral Reef Watch was supported by funding through the NOAA Coral Reef Conservation Program and Ocean Remote Sensing Program. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect the views of NOAA or the Department of Commerce. On behalf of all authors, the corresponding author states that there is no conflict of interest.

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