Recovery of reef-scale calcification following a bleaching event in Kāne‘ohe Bay, Hawai‘i

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Abstract

Increasing anthropogenic disturbances have driven declines of many coral-dominated reef states, threatening critical ecosystem functions such as reef-scale calcification and accretion. Few studies have investigated the effect of coral bleaching on reef-scale calcification. In this study, we monitored bay-wide alkalinity anomalies in Kāne‘ohe Bay, Hawai‘i along an inshore-offshore transect as a proxy for net calcification during the 2015 coral bleaching event and following recovery over a full seasonal cycle. We observed no net calcification in October 2015 during the bleaching event followed by a recovery to significant, positive net calcification rates in June 2016, November 2016, and February 2017 across a range of seawater temperatures and hydrodynamic conditions. Post-bleaching net calcification rates were not significantly different between survey dates and agreed with the range of pre-bleaching net calcification rates from a previous study suggesting that net calcification in Kāne‘ohe Bay had fully recovered following the 2015 bleaching event.

Science signiﬁcance statement

Although bleached coral reef states have been extensively studied, reef-scale net calcification during and after bleaching events has received less attention. As a result, it is unclear what the impacts of coral bleaching are on the ability for coral reefs to calcify and maintain reef structure following bleaching. Our study of reef-scale net calcification provides evidence for rapid recovery to positive reef-scale calcification if there is limited coral mortality and fast return of the coral’s symbiotic algae. Our results raise questions on the limit of coral reef resilience to maintain positive calcification under future climate change.

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Data Availability Statement: Data are available in the figshare repository at https://doi.org/10.6084/m9.figshare.5425906.

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Particular attention has been given to understanding how resilient coral reef systems are able to maintain the roles and functions that coral-dominated reef states provide during the current period of coral reef declines (Done 1992; Hughes et al. 2003). Of specific concern for the decline of less-resilient coral-dominated systems is the balance between the constructive (i.e., calcification and accretion) and destructive (i.e., CaCO₃ dissolution and erosion) processes and the resulting net impact on reef growth (Kleypas et al. 2001; Hughes et al. 2003; Perry et al. 2013; Muehllehner et al. 2016; Yates et al. 2017). Rates of constructive reef-scale calcification have decreased across the Caribbean in recent decades owing to declining coral cover and coral community shifts toward more slowly growing species.
Perry et al. 2013). Meanwhile, rates of destructive CaCO3 dissolution and bioerosion processes are anticipated to increase under anthropogenic ocean warming and acidification (Andersson and Gledhill 2013). These trends toward decreasing reef-scale calcification and increasing CaCO3 erosion have already produced net erosional reefs in the Caribbean and Pacific thereby threatening the persistence of coral reef structure and the ecosystem services (e.g., food production, shoreline protection, and tourism; Moberg and Folke 1999) coral reefs provide to humanity (Perry et al. 2013; Muehllehner et al. 2016; Perry and Morgan 2017; Yates et al. 2017).

Coral bleaching events have increased in both frequency and intensity, further reducing the accretion capacity of many coral-dominated systems (Hughes et al. 2003). Global coral bleaching events occurred in 1997–1998, 2010, and 2015–2016 (Hughes et al. 2017). Thermal stress induced coral bleaching, the breakdown of symbiosis between host coral and symbiont zooxanthellae, can occur if sea surface temperatures exceed ~1°C above mean ambient summer temperatures with coral mortality correlated to the magnitude and duration of thermal stress (Jokiel and Coles 1977; Glynn 1993). Because corals are the dominant reef-calcifiers (Hart and Kench 2007) and bleached corals exhibit reduced calcification rates (Jokiel and Coles 1977; Glynn 1993; Hughes et al. 2003), coral bleaching events are expected to reduce coral reef net ecosystem calcification (NEC = calcification − CaCO3 dissolution). In addition, NEC may also decrease owing to increased CaCO3 dissolution fueled by increased heterotrophy resulting from decomposition of coral derived organic matter and decreased primary production. While coral bleaching events have been well documented (e.g., Glynn 1993; Hughes et al. 2003, 2017; Bahr et al. 2017), only a few studies known to the authors have explored coral bleaching impacts on NEC finding reduced NEC rates associated with bleaching for coral reefs in Palau and Taiwan (Kayanne et al. 2005; Watanabe et al. 2006; DeCarlo et al. 2017) and no change in NEC for a bleached coral reef in Japan (Kayanne et al. 2005). An additional study utilizing census-based carbonate production budgets observed a bleaching-induced shift from positive to negative carbonate production budgets in the Maldives (Perry and Morgan 2017). This previously observed variability in coral reef NEC and net carbonate production budgets reflects differential responses to coral bleaching events and highlights the need to better understand these responses in light of projected increases in frequency and severity of coral bleaching events.

Because calcification reduces total alkalinity (TA) by two moles for each mole of CaCO3 formed, reef-scale calcification can be measured by changes in salinity-normalized seawater TA, with the magnitude of TA depletion a function of benthic NEC rates and volumetric seawater flow rates over the benthos (Smith 1973; Chisholm andGattuso 1991; Falter et al. 2013; Muehllehner et al. 2016). Here, we utilized alkalinity anomalies to test the hypothesis that NEC of the Kāne‘ohe Bay, Hawai‘i barrier reef flat would decrease in fall 2015 owing to the predicted reduction of coral calcification and or enhanced CaCO3 dissolution during the coral bleaching event (Fig. 1). We then hypothesized that the barrier reef flat would return to positive NEC following the recovery of corals in Kāne‘ohe Bay. These hypotheses were tested by surveying seawater TA and dissolved

Fig. 1. Conceptual diagram of net coral reef calcification and seawater alkalinity anomalies. (A) In a net calcifying “healthy” coral reef system, total alkalinity is depleted (−TA) as seawater flows over the coral reef flat owing to the decrease in seawater Ca2+ and CO32− ions. (B) For a net dissolving “bleached” coral reef system, TA increases (+TA) as seawater flows over the coral reef flat owing to the increase in seawater Ca2+ and CO32− ions. Bleached and non-bleached *Porites* lobata coral animations are attributed to Joanna Woerner, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary).
inorganic carbon (DIC) across the entire Kāne‘ohe Bay barrier reef flat during the bleaching event (fall 2015) and over a full seasonal cycle (summer 2016, fall 2016, winter 2017) of coral reef recovery. This study addresses bleaching impacts on truly ecosystem-scale calcification (~ 12.4 km² study area) at multiple time points during the bleaching event and a ~ 1.5 yr recovery period.

**Methods**

**Site description**

The Kāne‘ohe Bay ecosystem on the northeast shore of O‘ahu, Hawai‘i represents a coral reef exhibiting elevated resilience to centuries of human perturbations (Bahr et al. 2015) with thermal stress driven coral bleaching events in 1996, 2014, and 2015 (Bahr et al. 2017). The system consists of an estuarine bay separated from the open ocean by a highly productive barrier reef flat consisting of ~5–10% coral cover interspersed by coral rubble, algae, coarse sand, and volcanic rock (Smith et al. 1981; Jokiel 1991). Water circulation in Kāne‘ohe Bay is predominately wave-driven with the additional effects of wind and tides driving a landward flow over the barrier reef flat and seaward flow out of the bay through channels in the north and south (Smith et al. 1981; Jokiel 1991; Lowe et al. 2009). Previous work using TA anomalies in Kāne‘ohe Bay found that positive NEC is maintained year-round (Fagan and Mackenzie 2007; Shamberger et al. 2011) with no significant seasonal variability in rates (Shamberger et al. 2011).

**Kāne‘ohe Bay 2015 bleaching event**

In this study, we examined the effects of the fall 2015 Kāne‘ohe Bay bleaching event and subsequent recovery on NEC of the barrier reef flat. Notably, 46% ± 4% (mean ± SE) of corals in Kāne‘ohe Bay were observed as pale or bleached in October 2015 with a resulting cumulative mortality of 22% ± 5% (mean ± SE) (Bahr et al. 2017). By November 2016, 99.96% ± 0.02% (mean ± SE) of corals showed no signs of paling or bleaching with a 5% ± 5% (mean ± SE) decline in overall coral cover relative to the October 2015 survey, highlighting the relatively rapid recovery of the Kāne‘ohe Bay coral reef ecosystem to the 2015 coral bleaching event (Bahr et al. 2017).

**Seawater TA and DIC spatial surveys**

TA and DIC spatial surveys were conducted across the entire Kāne‘ohe Bay barrier reef flat including samples offshore from the reef flat boundary (Fig. 2A) on 31 October 2015, 29 June 2016, 12 November 2016, and 26 February 2017. Surface seawater samples were collected by hand at ~ 0.25 m depth using 250 mL Pyrex glass bottles and immediately fixed with 100 µL HgCl₂ as per standard protocols (Dickson et al. 2007). Hand-held YSI multiprobes (October 2015: YSI 6600 V2; June 2016, November 2016: YSI Professional Plus; February 2017: YSI 556) were calibrated and used to measure temperature (~ 0.2°C) and salinity (~ 0.3 g kg⁻¹) at the time of sampling. All seawater samples were transported to the Scripps Coastal and Open Ocean Biogeochemistry lab and analyzed for TA via an open-cell potentiometric acid titration system developed at Scripps.
Table 1. Summary of measured and calculated environmental data. Measured and calculated environmental data during each survey are reported as the mean ± SD for the portion of each sampling day that samples were collected. Seawater height is measured with respect to Mean Lower Low Water. ΔnTA and ΔnDIC are the mean ± SE TA and DIC drawdowns (μmol kg⁻¹ km⁻¹) multiplied by the 2-km width of the Kāne‘ohe Bay barrier reef flat. ΔnTA and ΔnDIC were combined with seawater density (ρsw), depth (z), and residence time (τ) in Eqs. 1, 2, respectively, to calculate NEC and NEP with uncertainty estimated from Monte Carlo simulations.

| Environmental parameters | 31 Oct 15 Bleached | 29 Jun 16 Recovery | 12 Nov 16 Recovery | 26 Feb 17 Recovery |
|--------------------------|--------------------|--------------------|--------------------|--------------------|
| Temperature (°C)         | 27.6 ± 0.3         | 27.6 ± 1.0         | 26.6 ± 0.3         | 23.2 ± 0.4         |
| Wind (m s⁻¹)             | 1.0 ± 0.4          | 3.3 ± 0.5          | 0.9 ± 0.3          | 0.6 ± 0.3          |
| Wave H₆ (m)              | 1.38 ± 0.08        | 1.18 ± 0.03        | 2.03 ± 0.10        | 1.22 ± 0.06        |
| Measured tidal range (m) | 0.8                | 0.5                | 0.6                | 0.9                |
| Tidal cycle              | Flood             | Ebb                | Flood-slack-ebb    | Flood-slack-ebb    |
| ρsw (kg m⁻³)             | 1021.5 ± 0.5       | 1022.5 ± 0.5       | 1022.7 ± 0.1       | 1023.4 ± 0.2       |
| Depth (m)                | 5 ± 4              | 4 ± 4              | 4 ± 4              | 5 ± 4              |
| τ (d)                    | 6.0 ± 2.8          | 6.0 ± 2.8          | 3.4 ± 1.5          | 6.0 ± 2.8          |
| NEC                      |                    |                    |                    |                    |
| ΔnTA/km (μmol kg⁻¹ km⁻¹) | −5 ± 8             | 18 ± 6             | 10 ± 3             | 28 ± 3             |
| ΔnTA (μmol kg⁻¹)         | −10 ± 16           | 36 ± 12            | 20 ± 6             | 56 ± 6             |
| NEC (mmol CaCO₃ m⁻² d⁻¹) | −5 ± 6             | 15 ± 9             | 15 ± 9             | 26 ± 15            |
| NEC (kg CaCO₃ m⁻² yr⁻¹) | −0.2 ± 0.2         | 0.5 ± 0.3          | 0.5 ± 0.3          | 0.9 ± 0.5          |
| NEP                      |                    |                    |                    |                    |
| ΔnDIC/km (μmol kg⁻¹ km⁻¹) | −6 ± 8             | 20 ± 7             | 15 ± 4             | 19 ± 4             |
| ΔnDIC (μmol kg⁻¹)        | −12 ± 16           | 40 ± 14            | 30 ± 8             | 38 ± 8             |
| NEP (mmol C m⁻² d⁻¹)     | −7 ± 12            | 18 ± 14            | 36 ± 33            | 9 ± 7              |

Institution of Oceanography (SIO) by A. G. Dickson (Dickson et al. 2007) and DIC via an automated infrared inorganic carbon analyzer (AIRICA, Marianda). The mean accuracy (TA ± 1.3 μmol kg⁻¹, DIC ± 1.6 μmol kg⁻¹) and precision (TA ± 1.3 μmol kg⁻¹, DIC ± 1.4 μmol kg⁻¹) of TA and DIC measurements were evaluated using certified reference materials provided by the laboratory of A. G. Dickson at SIO. Seawater TA and DIC were normalized to a mean salinity across all bottle samples of 34.6 g kg⁻¹ to directly compare nTA and nDIC between samples of variable salinity (e.g., as discussed in Shamberger et al. 2011).

Environmental data

Environmental data were aggregated for each spatial survey. Temperature and salinity were measured at each sample location as previously described. Mean significant wave height (H₆), the mean of the 1/3 highest waves measured over the 30 min averaging interval, was determined by the Coastal Data Information Program (CDIP) Kāne‘ohe Buoy 198 (http://cdip.ucsd.edu). Wind speed and tidal range from recorded water levels were measured every 6 min at the Moku o Lo‘e monitoring station in Kāne‘ohe Bay (https://tidesandcurrents.noaa.gov). Each parameter was averaged over the respective sampling duration to determine the mean environmental conditions for each sample date (Table 1).

Statistical analysis

Salinity-normalized seawater TA was interpolated across the survey regions using the MATLAB “natural” three-dimensional triangulation-based nearest neighbor interpolation to visualize spatial heterogeneity in nTA (Fig. 3). The distance between each sampling location and a transect drawn parallel to the barrier reef along Kapapa Island (Fig. 2A) was calculated to analyze inshore-offshore changes in nTA and nDIC of seawater flowing across the barrier reef flat. The fitlm() and anova() functions of the MATLAB Statistics and Machine Learning Toolbox were used to generate and assess linear least-squares fits of nTA and nDIC as functions of distance from the Kapapa Island transect for each spatial survey. These responses are hereafter referred to as the ΔnTA and ΔnDIC drawdowns wherein positive ΔnTA slopes represent net coral reef calcification (i.e., reduction in seawater nTA flowing over the reef flat) and organic carbon negative ΔnTA slopes represent net CaCO₃ dissolution. ΔnDIC slopes represent the sum of net calcification and net organic carbon production.

NEC and NEP

NEC and net ecosystem production (NEP) for the entire ~12.4 km² barrier reef flat (i.e., Kapapa Island transect to 2 km inshore of transect) were calculated using the following modified equations based on the assumptions that (1) calcification and CaCO₃ dissolution are the dominant processes affecting
the TA balance and (2) that changes in DIC owing to CO$_2$ air–sea exchange are negligible relative to the influence of NEC and NEP (Langdon et al. 2010; Page et al. 2017):

\[
\text{NEC} = \frac{\rho z (\Delta nTA)}{2 \tau} \\
\text{NEP} = \frac{\rho z (\Delta nDIC - \Delta nTA)}{\tau}
\]

wherein \(\rho\) is mean ± SD seawater density calculated from measured temperature, salinity, and pressure using the Gibbs Seawater (GSW) Oceanographic Toolbox (McDougall and Barker 2011), and \(z\) is the mean ± SD seawater depth for the sample sites calculated from a 4-m bathymetric grid of Kāne‘ohe Bay (www.soest.hawaii.edu/pibhmc). \(\Delta nTA\) and \(\Delta nDIC\) are the nTA and nDIC drawdowns (\(\mu\)mol kg$^{-1}$ km$^{-1}\) × 2 km width of the barrier reef flat. \(\tau\) is the mean ± SE seawater residence time derived for the barrier reef flat by Lowe et al. (2009) for the following forcing conditions: tidal range of 0.7 m; mean wind velocity of 5 m s$^{-1}$; and mean significant wave height (\(H_s\)) of 1.0 m (October 2015, June 2016, February 2017) or 2.0 m (November 2016) (for details, see zones 1–3 as described in Lowe et al. 2009). A Monte Carlo approach was used to estimate uncertainty in NEC and NEP using random numbers \((n = 10^7)\) generated within the range of SD or SE for each NEC and NEP equation parameter (Table 1) using the MATLAB `rand()` function. The mean ± SD of the Monte Carlo output for each NEC and NEP survey was used to estimate mean NEC and NEP rates ± uncertainty.

**Results**

No net reduction in seawater nTA in the dominating shoreward seawater flow direction was observed in the nTA gradients across the Kāne‘ohe Bay reef flat during the October 2015 bleaching event suggesting NEC = 0 at this time (Fig. 3). This finding was quantified with linear models for the October 2015 data, which showed no statistically significant drawdown in nTA (slope ± SE = −5 ± 8 \(\mu\)mol kg$^{-1}$ km$^{-1}$, \(R^2 = 0.011, n = 33, F = 0.333, p = 0.568\)) or nDIC (slope ± SE = −6 ± 8 \(\mu\)mol kg$^{-1}$ km$^{-1}$, \(R^2 = 0.019, n = 33, F = 0.612, p = 0.44\)) across the reef (Figs. 2B, 4A). In contrast, significant reductions in seawater nTA and nDIC were observed across the reef and along the predominant flow direction in June 2016, November 2016, and February 2017 (Figs. 2B, 4A). The strongest nTA drawdown was
Our results show that ecosystem-scale NEC and NEP were essentially zero during the October 2015 coral bleaching event in Kāne’ohe Bay, but exhibited rapid recovery as evidenced by positive NEC and NEP in the year following the bleaching event (June 2016, November 2016, February 2017). These observations support the hypotheses of reduced NEC during the coral bleaching event with a subsequent return to positive NEC as the corals recovered (Figs. 2B, 4B; Table 1). While no measurements of NEC were conducted before the bleaching event as part of this study, previous work (2003–2004; 2008–2010) has quantified year-round positive NEC occurring on the Kāne’ohe Bay barrier reef (Fagan and Mackenzie 2007; Shamberger et al. 2011) suggesting the cessation of NEC observed in this study was a direct consequence of the bleaching event.

Our findings of positive NEC with overlapping uncertainties (Fig. 4B; Table 1) for each of the spatial surveys conducted following the bleaching event (June 2016, November 2016, February 2017) suggest that Kāne’ohe Bay NEC recovered at a rate faster than the temporal resolution of the first spatial sampling events (i.e., October 2015 to June 2016). This is partially supported by visual observations of the recovery of coral coloration. For example, peak bleaching was observed in October 2015 with 46% ± 4% (mean ± SE) corals recorded as either pale or bleached with just 9% ± 2% of corals observed as pale or bleached and 8% ± 2% recorded as dead at ~ 2 months post-bleaching in December 2015 (Bahr et al. 2017). However, gradual and sequential increases in NEC during the post-bleaching period that are less than the uncertainty measured in this study may also be possible, but are not quantifiable given the limits of our uncertainty (Fig. 4B; Table 1).

Additionally, the findings that 99.96% ± 0.02% (mean ± SE) of corals observed in November 2016 were neither bleached nor pale and total coral cover did not decrease relative to October 2015 suggest a post-bleaching recovery of corals in Kāne’ohe Bay (Bahr et al. 2017) and that a similar recovery in NEC is probable. The finding that post-recovery NEC in this study (February 2017 NEC = 26 ± 15 mmol CaCO_3 m^{-2} d^{-1}) agrees with Kāne’ohe Bay mesocosm NEC rates linearly scaled to 10% coral cover (27 ± 11 mmol CaCO_3 m^{-2} d^{-1} sensu Page et al. 2017) suggests NEC has recovered for this ~ 5–10% coral cover ecosystem (Jokiel 1991). While previous estimates of Kāne’ohe Bay barrier reef flat NEC before the bleaching event are much higher (range = 174–331 mmol CaCO_3 m^{-2} d^{-1}, Shamberger et al. 2011), this discrepancy is primarily due to differences in estimating seawater residence times (i.e., numerical time models in this study compared to current flow velocities across the reef flat in Shamberger et al. 2011) and differing spatial scales between the two studies. Nonetheless, if the post-recovery NEC rates from this study are recalculated utilizing the average depth (z = 2 m) and range of residence times (t = 4.5–13.6 h) from Shamberger et al. (2011), the much higher recalculated February 2017 post-recovery NEC rates (range = 101–306 mmol CaCO_3 m^{-2} d^{-1}) from this
study agree with the range of rates (174–331 mmol CaCO$_3$ m$^{-2}$ d$^{-1}$) from Shamberger et al. (2011). This lends strong support that NEC indeed has recovered for Kane‘ohe Bay and reconciles the divergent rates presented here and in Shamberger et al. (2011).

Differences in environmental parameters between survey dates may also explain variations in measured ΔnTA and calculated NEC in this study via changes in coral reef metabolism and/or seawater residence time (Falter et al. 2013). Mean residence times of ~3–6 d (Table 1) show that NEC rates represent integrations over multiple days and are therefore less influenced by anomalous daily phenomena. Environmental conditions were similar across sample dates with the exception that $H_w$ was ~1 m higher in November 2016 relative to the other surveys and the February 2017 survey was ~3–4°C cooler than previous surveys (Table 1). Lowe et al. (2009) have shown that the barrier reef flat seawater residence time is directly related to the wave height. Consequently, significantly lower ΔnTA drawdown was observed in November 2016 compared to February 2017 (nonoverlapping 95% confidence intervals in Fig. 4A, Table 1), but NEC was not significantly different between those dates (overlapping uncertainties in Fig. 4B, Table 1) due to the reduced seawater residence time in November 2016. Neither ΔnTA drawdown nor NEC was significantly different between February 2017 and June 2016, suggesting reductions in temperature did not affect net reef-scale calcification. This finding agrees with previous work showing no significant seasonal variability in Kane‘ohe Bay NEC (Shamberger et al. 2011).

The observation of zero NEC during the fall 2015 coral bleaching event in Kane‘ohe Bay agrees with decreased calcification rates observed in bleached coral colonies (Jokiel and Coles 1977; Glynn 1993; Hughes et al. 2003) and with reductions in total coral cover (Page et al. 2017; Perry and Morgan 2017). For example, a 75% reduction in coral cover (i.e., from 25.6% to 6.3%) following the 2016 coral bleaching event in the Maldives was the primary driver of a shift from net positive (mean 5.92 kg m$^{-2}$ yr$^{-1}$) to net negative (mean $-2.96$ kg m$^{-2}$ yr$^{-1}$) carbonate production budgets (Perry and Morgan 2017). However, observed reductions in NEC may also be due to enhanced metabolically driven CaCO$_3$ dissolution associated with coral bleaching events. For example, the zero NEC observed during the bleaching event (Table 1; Fig. 4B) suggests a shift toward net heterotrophy that could have fueled an increase in CaCO$_3$ dissolution rates (Andersson and Gledhill 2013). Irrespective of this, the cessation of NEC in this study is unique among results from previous hydrochemical field observations wherein positive NEC was maintained during bleaching events at similar or reduced rates compared to non-bleaching conditions (Kayanne et al. 2005; Watanabe et al. 2006; DeCarlo et al. 2017). In Palau, reef flat NEC was found to decrease ~43% between surveys conducted before (July 1994) and after (September 2000) the 1998 coral bleaching event, coinciding with a reduction in pre-bleaching coral cover of 8.1 to 1.4% after bleaching (Kayanne et al. 2005), while lagoon NEC decreased 60–70% over that same interval (Watanabe et al. 2006). During a widespread bleaching event in June 2014 at Dongsha Atoll, Taiwan, a 40% reduction in NEC rates was observed for a reef flat with 25% total coral cover (DeCarlo et al. 2017). In contrast, measurements of NEC at Shiraho Reef, Japan did not change during the September 1998 bleaching event, where 51% of the total 7.1% total coral cover was bleached compared to a recovery survey conducted in September 1999 with 6.7% total coral cover and no bleaching observed (Kayanne et al. 2005). Kayanne et al. (2005) hypothesized that calcification by living bleached corals, calcifying algae, and benthic foraminifera may have compensated for bleaching-induced losses in NEC at Shiraho Reef. Indeed, the dominant calcifiers of coral reefs include corals, red coralline algae, molluscs, green calcifying algae, and benthic foraminifera (Montaggioni and Braithwaite 2009), but their relative contributions to coral reef CaCO$_3$ budgets and how these change under different reef states are uncertain. This raises the question and need to further quantify the relative importance of contributions by other calcifiers to coral reef NEC especially for low coral cover (<10%) and bleached coral reefs.

In summation, the results of this study suggest that a temporary reduction in coral reef NEC can be expected during a coral bleaching event while rapid post-bleaching recovery of positive NEC is possible given limited coral mortality and rapid regain of symbiotic algae. As coral bleaching events are expected to increase in both frequency and magnitude (Hughes et al. 2003), the resilience capacity of coral reef systems such as Kane‘ohe Bay will continue to be tested (Done 1992; Hughes et al. 2003; Bahr et al. 2017), with bleached coral reefs that recover quickly likely experiencing ephemeral reductions in reef NEC while systems shifting to alternative non-coral-dominated states are likely to face lasting decreases in NEC. Although the Kane‘ohe Bay coral reef system appears to have recovered to a net calcifying system following the recent global mass bleaching event, other reefs around the world including parts of the Great Barrier Reef in Australia that experienced >80% bleaching (Hughes et al. 2017) may be faced with a different outcome. It is prudent that future investigations of reef-scale NEC target these sites to evaluate the impact and time to recover to guide future management. In either case, the increasing frequency of time during which an intermittently bleached coral reef is predicted to calcify at reduced rates during the 21st century threatens the ability for contemporary coral reef structures to maintain ecological form and function. The question thus remains, for how long can we depend on coral reef resiliency to maintain calcifying reef states and the ecosystem services they provide?
References

Andersson, A. J., and D. Gledhill. 2013. Ocean acidification and coral reefs: Effects on breakdown, dissolution, and net ecosystem calcification. Ann. Rev. Mar. Sci. 5: 321–348. doi:10.1146/annurev-marine-121211-172241

Bahr, K. D., K. S. Rodgers, and P. L. Jokiel. 2017. Impact of Three Bleaching Events on the Reef Resiliency of Kane‘ohe Bay, Hawai‘i. Front. Mar. Sci. 4: 398. doi:10.3389/fmars.2017.00398

Bahr, K. D., P. L. Jokiel, and R. J. Toonen. 2015. The unnaturally high history of Kane‘ohe Bay: Coral reef resilience in the face of centuries of anthropogenic impacts. PeerJ 3: e950. doi:10.7717/peerj.950

Chisholm, J. R. M., and J.-P. Gattuso. 1991. Validation of the alkalinity anomaly technique for investigating calcification and photosynthesis in coral reef communities. Limnol. Oceanogr. 36: 1232–1239. doi:10.4319/lo.1991.36.6.1232

DeCarlo, T. M., A. L. Cohen, G. T. F. Wong, F. Shiah, S. J. Lentz, K. A. Davis, K. E. F. Shamberger, and P. Lohmann. 2017. Community production modulates coral reef pH and the sensitivity of ecosystem calcification to ocean acidification. J. Geophys. Res. Oceans 122: 745–761. doi:10.1002/2016JC012326

Dickson, A. G., C. L. Sabine, and J. R. Christian [eds.]. 2007. Guide to best practices for ocean CO₂ measurements, p. 191. PICES special publication 3. North Pacific Marine Science Organization.

Done, T. J. 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247: 121–132. doi:10.1007/BF00008211

Fagan, K. E., and F. T. Mackenzie. 2007. Air-sea CO₂ exchange in a subtropical estuarine-coral reef system, Kaneohe Bay, Oahu, Hawaii. Mar. Chem. 106: 174–191. doi:10.1016/j.marchem.2007.01.016

Falter, J. L., R. J. Lowe, Z. Zhang, and M. McCulloch. 2013. Physical and biological controls on the carbonate chemistry of coral reef waters: Effects of metabolism, wave forcing, sea level, and geomorphology. PLoS One 8: e53303. doi:10.1371/journal.pone.0053303

Glynn, P. W. 1993. Coral reef bleaching: Ecological perspectives. Coral Reefs 12: 1–17. doi:10.1007/BF00303779

Hart, D. E., and P. S. Kench. 2007. Carbonate production of an emergent reef platform, Warraber Island, Torres Strait, Australia. Coral Reefs 26: 53–68. doi:10.1007/s00338-006-0168-8

Hughes, T. P., and others. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301: 929–933. doi:10.1126/science.1085046

Hughes, T. P., and others. 2017. Global warming and recurrent mass bleaching of corals. Nature 543: 373–377. doi:10.1038/nature21707

Jokiel, P. L. 1991. Jokiel’s illustrated scientific guide to Kane‘ohe Bay, O‘ahu, p. 1–65. Hawai‘ian Coral Reef Assessment and Monitoring Program.

Jokiel, P. L., and S. L. Coles. 1977. Effects of temperature on the mortality and growth of Hawaiian reef corals. Mar. Biol. 43: 201–208. doi:10.1007/BF00402312

Kayanne, H., and others. 2005. Seasonal and bleaching-induced changes in coral reef metabolism and CO₂ flux. Global Biogeochem. Cycles 19: 1–11. doi:10.1029/2004GB002400

Kleypas, J. A., R. W. Buddemeier, and J. P. Gattuso. 2001. The future of coral reefs in an age of global change. Int. J. Earth Sci. 90: 426–437. doi:10.1007/s005310000125

Langdon, C., J.-P. Gattuso, and A. Andersson. 2010. Measurements of calcification and dissolution of benthic organisms and communities, p. 213–232. In U. Riebesell, V. Fabry, L. Hansson, and J. Gattuso [eds.], Guide to best practices for ocean acidification research and data reporting. Office for Official Publications of the European Communities.

Lowe, R. J., J. L. Falter, S. G. Monismith, and M. J. Atkinson. 2009. A numerical study of circulation in a coastal reef-lagoon system. J. Geophys. Res. Oceans 114: 1–18. doi:10.1029/2008JC005081

McDougall, T. J., and P. M. Barker. 2011. Getting started with TEOS-10 and the Gibbs Seawater (GSW) oceanographic toolbox, p. 1–28. SCOR/IAPSO WG 127.

Moberg, F., and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29: 215–233. doi:10.1016/S0921-8009(99)00009-9

Montaggioni, L., and C. Braithwaite. 2009. Quaternary coral reef systems: History, development processes and controlling factors. Elsevier B.V.

Muehllehner, N., C. Langdon, A. Venti, and D. Kadko. 2016. Dynamics of carbonate chemistry, production, and calcification of the Florida Reef Tract (2009–2010): Evidence for seasonal dissolution. Global Biogeochem. Cycles 30: 661–688. doi:10.1002/2015GB005327

Page, H. N., T. A. Courtneay, A. Collins, E. H. De Carlo, and A. J. Andreas. 2017. Net community metabolism and seawater carbonate chemistry scale non-intuitively with coral cover. Front. Mar. Sci. 4:161. doi:10.3389/fmars.2017.00161

Perry, C. T., G. N. Murphy, P. S. Kench, S. G. Smithers, E. N. Edinger, R. S. Steneck, and P. J. Mumby. 2013. Caribbean-wide decline in carbonate production threatens coral reef growth. Nat. Commun. 4: 1402. doi:10.1038/ncomms2409

Perry, C. T., and K. M. Morgan. 2017. Bleaching drives collapse in reef carbonate budgets and reef growth potential on southern Maldives Reefs. Nat. Sci. Rep. 7: 40581. doi:10.1038/srep40581

Shamberger, K. E. F., R. A. Feely, C. L. Sabine, M. J. Atkinson, E. H. DeCarlo, F. T. Mackenzie, P. S. Drupp, and D. A. Butterfield. 2011. Calcification and organic production on a Hawaiian coral reef. Mar. Chem. 127: 64–75. doi:10.1016/j.marchem.2011.08.003

Smith, S. V. 1973. Carbon dioxide dynamics: A record of organic carbon production, respiration, and calcification
in the Eniwetok reef flat community. Limnol. Oceanogr. 18: 106–120. doi:10.4319/lo.1973.18.1.0106

Smith, S. V., W. J. Kimmerer, E. A. Laws, R. E. Brock, and T. W. Walsh. 1981. Kaneohe Bay sewage diversion experiment: Perspectives on ecosystem responses to nutritional perturbation. Pac. Sci. 35: 279–395. doi: hdl.handle.net/10125/616

Watanabe, A., and others. 2006. Analysis of the seawater CO₂ system in the barrier reef-lagoon system of Palau using total alkalinity-dissolved inorganic carbon diagrams. Limnol. Oceanogr. 51: 1614–1628. doi:10.4319/lo.2006.51.4.1614

Yates, K. K., D. G. Zawada, N. A. Smiley, and G. Tiling-Range. 2017. Divergence of seafloor elevation and sea level rise in coral reef regions. Biogeosciences 14: 1739–1772. doi:10.5194/bg-14-1739-2017

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