LETTER

Recovery of reef-scale calcification following a bleaching event in Kāneʻohe Bay, Hawaiʻi

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Scientific 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.

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 Kāneʻohe Bay, Hawaiʻi 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 Kāneʻohe Bay had fully recovered following the 2015 bleaching event.

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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., $CaCO_3$ 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
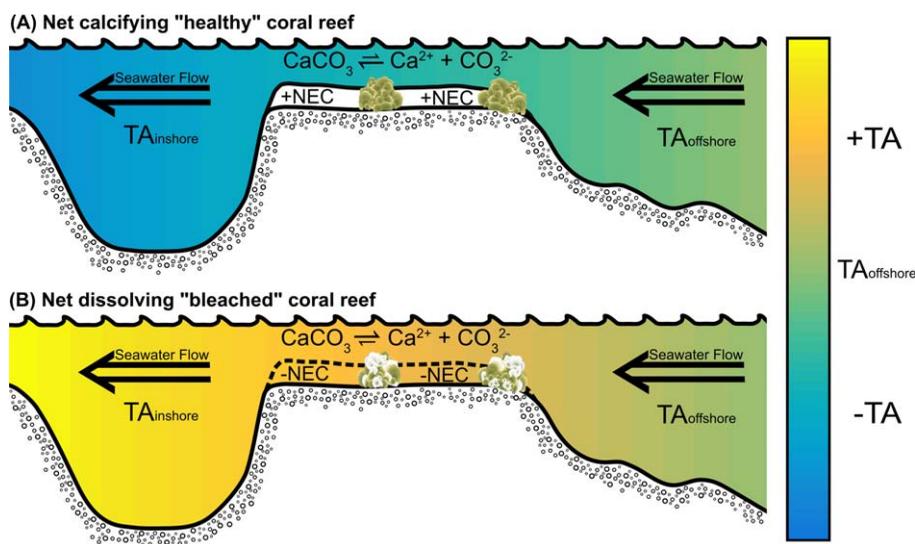
Fig. 1. Conceptual diagram of net coral reef calcification and seawater alkalinity anomalies. (**A**) In a net calcifying "healthy" coral reef system, total alkalinity is depleted ($-$TA) as seawater flows over the coral reef flat owing to the decrease in seawater Ca^{2+} and CO_3^{2-} ions. (**B**) 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 Ca^{2+} and CO_3^{2-} 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).

(Perry et al. 2013). Meanwhile, rates of destructive $CaCO_3$ 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 $CaCO_3$ 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 $\sim 1°C$ 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 $-$ $CaCO_3$ dissolution). In addition, NEC may also decrease owing to increased $CaCO_3$ 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 ΔNEC 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 $CaCO_3$ 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 and Gattuso 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 $CaCO_3$ 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
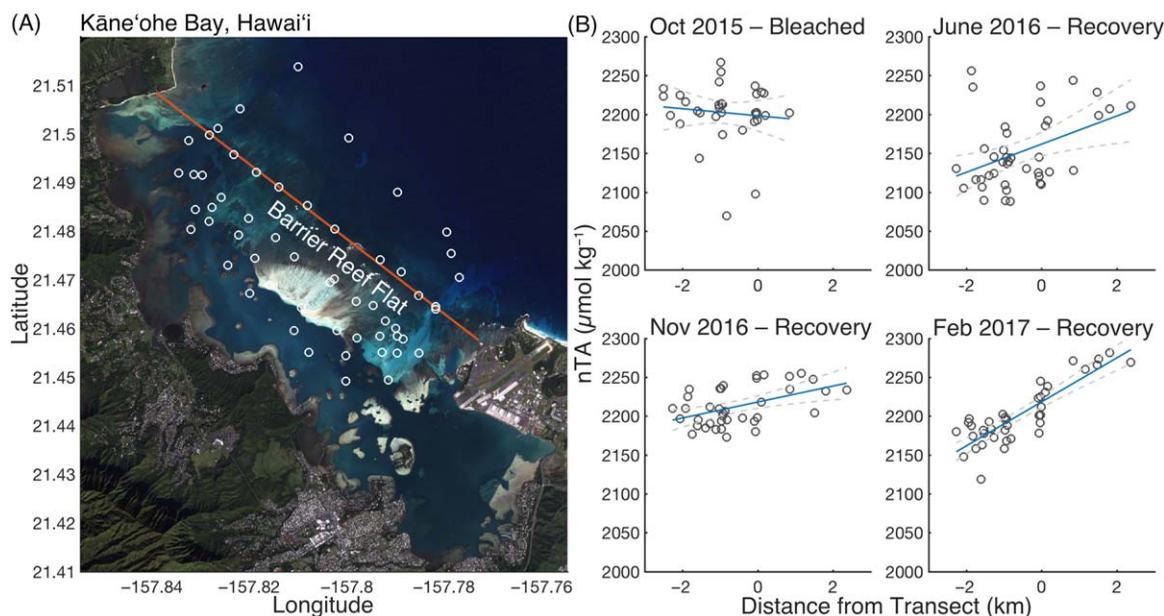
Fig. 2. Spatial map of sample locations and salinity normalized TA across the Kāneʻohe Bay barrier reef. (**A**) Sample locations (white circles) in Kāneʻohe Bay are plotted relative to the Kapapa Island reef flat transect (red line). (**B**) Salinity normalized total alkalinity (nTA) is plotted relative to the inshore-offshore distance (km) of each sample location relative to the Kapapa Island transect such that positive distances are offshore and negative distances are inshore from the red transect line. Regression lines of ΔnTA drawdown are plotted in blue with gray dashed confidence intervals (±SE) for each sample date.

inorganic carbon (DIC) across the entire Kāneʻohe 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 km^2 study area) at multiple time points during the bleaching event and a ~ 1.5 yr recovery period.

Methods

Site description

The Kāneʻohe Bay ecosystem on the northeast shore of Oʻahu, Hawaiʻi 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 Kāneʻohe 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 Kāneʻohe 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).

Kāneʻohe Bay 2015 bleaching event

In this study, we examined the effects of the fall 2015 Kāneʻohe Bay bleaching event and subsequent recovery on NEC of the barrier reef flat. Notably, $46\% \pm 4\%$ (mean ± SE) of corals in Kāneʻohe Bay were observed as pale or bleached in October 2015 with a resulting cumulative mortality of $22\% \pm 5\%$ (mean ± SE) (Bahr et al. 2017). By November 2016, $99.96\% \pm 0.02\%$ (mean ± SE) of corals showed no signs of paling or bleaching with a $5\% \pm 5\%$ (mean ± SE) decline in overall coral cover relative to the October 2015 survey, highlighting the relatively rapid recovery of the Kāneʻohe 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 Kāneʻohe 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 HgCl$_2$ as per standard protocols (Dickson et al. 2007). Handheld *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 (ρ_{sw}), 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 H_s (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
ρ_{sw} (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 CaCO$_3$ m^{-2} d^{-1})	−5 ± 6	15 ± 9	15 ± 9	26 ± 15
NEC (kg CaCO$_3$ 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 (H_s), 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 CaCO$_3$ 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 km^2 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 CaCO$_3$ dissolution are the dominant processes affecting
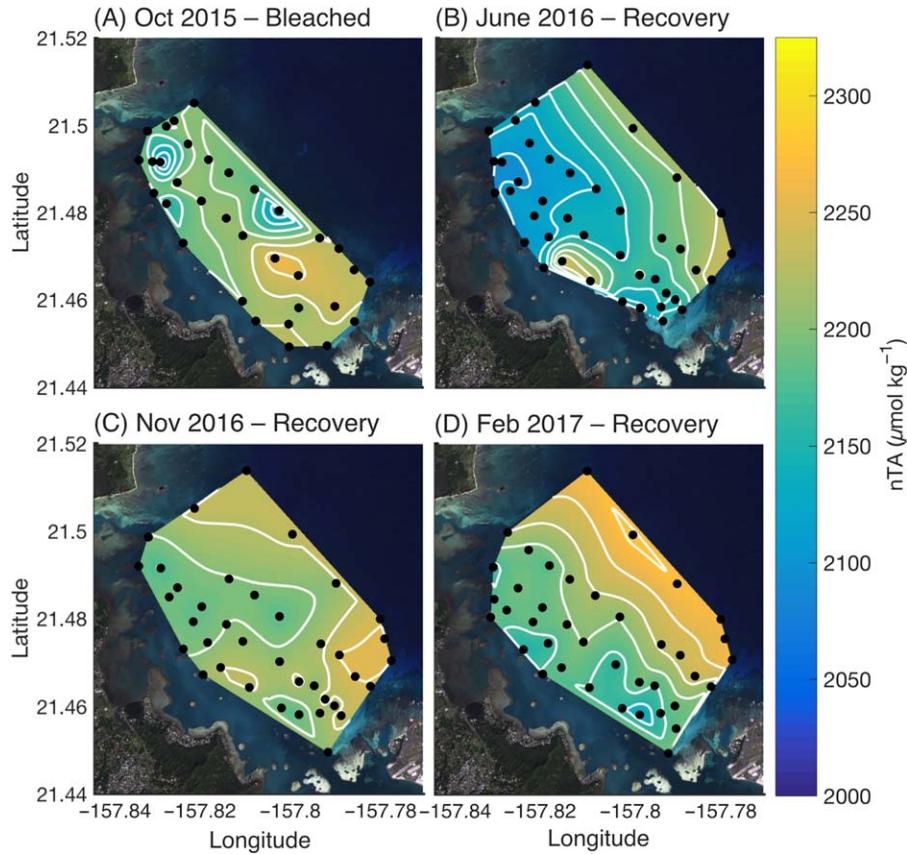
Fig. 3. Seasonal contour plots of salinity normalized total alkalinity. Discrete salinity normalized total alkalinity (nTA) samples from survey stations (black dots) were spatially interpolated to visualize spatial nTA gradients of ΔnTA drawdown occurring during the October 2015 coral bleaching event (A) and during a year of recovery (June 2016 (B), November 2016 (C), February 2016 (D)) following the bleaching event.

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):

$$\text{NEC} = \frac{\rho z (\Delta\text{nTA})}{2\tau} \qquad (1)$$

$$\text{NEP} = \frac{\rho z \left(\Delta\text{nDIC} - \frac{\Delta\text{nTA}}{2}\right)}{\tau} \qquad (2)$$

wherein ρ 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 Kāneʻohe Bay (www.soest.hawaii.edu/pibhmc). ΔnTA and ΔnDIC are the nTA and nDIC drawdowns (μmol kg^{-1} km^{-1}) × 2 km width of the barrier reef flat. τ 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 Kāneʻohe Bay reef flat during the October 2015 bleaching event suggesting NEC $\sim$ 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 μmol kg^{-1} km^{-1}, $R^2 = 0.011$, $n = 33$, $F = 0.333$, $p = 0.568$) or nDIC (slope ± SE = -6 ± 8 μmol 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
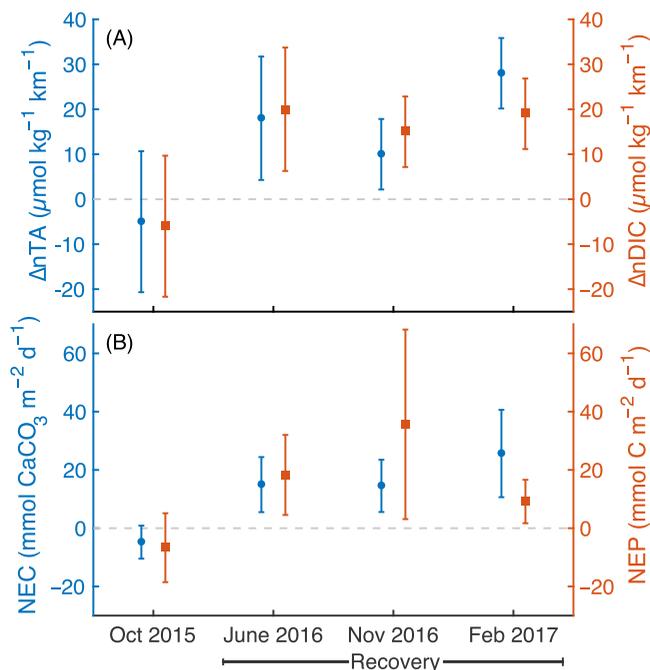
Fig. 4. NEC and NEP in Kāneʻohe Bay. (**A**) Slopes ($\pm$ 95% confidence intervals) of salinity normalized total alkalinity (ΔnTA km^{-1}, in blue) and DIC (ΔnDIC km^{-1}, in red) drawdown of seawater flowing over the reef flat. Positive values signify a net drawdown of nTA or nDIC whereas negative values signify production of nTA or nDIC. If the confidence intervals overlap the dashed zero line, ΔnTA or ΔnDIC drawdown is not significantly different from zero. (**B**) Calculated mean ($\pm$ uncertainty) NEC (in blue) and NEP (in red). Values with estimated uncertainty above zero indicate positive reef NEC or NEP whereas values with estimated uncertainty overlapping zero indicate zero NEC or NEP.

observed in February of 2017 (slope $\pm$ SE = 28 $\pm$ 3 μmol kg^{-1} km^{-1}, $R^2 = 0.737$, $n = 39$, $F = 103.9$, $p < 0.001$) followed by June 2016 (slope $\pm$ SE = 18 $\pm$ 6 μmol kg^{-1} km^{-1}, $R^2 = 0.174$, $n = 41$, $F = 8.222$, $p = 0.007$) and November 2016 (slope $\pm$ SE = 10 $\pm$ 3 μmol kg^{-1} km^{-1}, $R^2 = 0.227$, $n = 38$, $F = 10.598$, $p = 0.002$). The strongest nDIC drawdown was observed in June 2016 (slope $\pm$ SE = 20 $\pm$ 7 μmol kg^{-1} km^{-1}, $R^2 = 0.166$, $n = 41$, $F = 7.78$, $p = 0.008$) followed by February 2017 (slope $\pm$ SE = 19 $\pm$ 4 μmol kg^{-1} km^{-1}, $R^2 = 0.383$, $n = 39$, $F = 23$, $p < 0.001$) and November 2016 (slope $\pm$ SE = 15 $\pm$ 4 μmol kg^{-1} km^{-1}, $R^2 = 0.274$, $n = 38$, $F = 13.6$, $p < 0.001$). Calculations of NEC and NEP showed values close to zero (-5 ± 6 mmol CaCO$_3$ m^{-2} d^{-1} and -7 ± 12 mmol C m^{-2} d^{-1}, respectively) during the October 2015 bleaching event while positive NEC (15–26 mmol CaCO$_3$ m^{-2} d^{-1}) and NEP (9–36 mmol C m^{-2} d^{-1}) rates were calculated for June 2016, November 2016, and February 2017 with overlapping uncertainties implying that NEC and NEP rates were not statistically different between post-bleaching surveys (Fig. 4B; Table 1).

Discussion

Our results show that ecosystem-scale NEC and NEP were essentially zero during the October 2015 coral bleaching

event in Kāneʻohe 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 Kāneʻohe 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 Kāneʻohe 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% $\pm$ 4% (mean $\pm$ SE) corals recorded as either pale or bleached with just 9% $\pm$ 2% of corals observed as pale or bleached and 8% $\pm$ 2% recorded as dead at $\sim$ 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% $\pm$ 0.02% (mean $\pm$ 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 Kāneʻohe 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 $\pm$ 15 mmol CaCO$_3$ m^{-2} d^{-1}) agrees with Kāneʻohe Bay mesocosm NEC rates linearly scaled to 10% coral cover (27 $\pm$ 11 mmol CaCO$_3$ m^{-2} d^{-1} *sensu* Page et al. 2017) suggests NEC has recovered for this $\sim$ 5–10% coral cover ecosystem (Jokiel 1991). While previous estimates of Kāneʻohe 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 residence 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 ($\tau = 4.5$–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 Kāne'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_s 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 Kāne'ohe Bay NEC (Shamberger et al. 2011).

The observation of zero NEC during the fall 2015 coral bleaching event in Kāne'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 NEP 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 Kāne'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 Kāne'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?

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