

## Disturbances drive changes in coral community assemblages and coral calcification capacity

TRAVIS A. COURTNEY<sup>1,†</sup>, BRIAN B. BARNES<sup>2</sup>, ILIANA CHOLLETT<sup>3</sup>, ROBIN ELAHI<sup>4</sup>, KEVIN GROSS<sup>5</sup>,  
 JAMES R. GUEST<sup>6</sup>, ILSA B. KUFFNER<sup>7</sup>, ELIZABETH A. LENZ<sup>8</sup>, HANNAH R. NELSON<sup>9</sup>,  
 CAROLINE S. ROGERS<sup>10</sup>, LAUREN T. TOTH<sup>7</sup>, AND ANDREAS J. ANDERSSON<sup>1</sup>

<sup>1</sup>*Scripps Institution of Oceanography, University of California San Diego, La Jolla, California 92093 USA*

<sup>2</sup>*College of Marine Science, University of South Florida, St. Petersburg, Florida 33701 USA*

<sup>3</sup>*Sea Cottage, Louisburgh, Co Mayo, Ireland*

<sup>4</sup>*Hopkins Marine Station, Stanford University, Pacific Grove, California 93950 USA*

<sup>5</sup>*Department of Statistics, North Carolina State University, Raleigh, North Carolina 27695 USA*

<sup>6</sup>*School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, NE17RU UK*

<sup>7</sup>*U.S. Geological Survey, St. Petersburg Coastal and Marine Science Center, St. Petersburg, Florida 33701 USA*

<sup>8</sup>*Hawai'i Institute of Marine Biology, University of Hawai'i, Kāne'ohe Hawai'i 96744 USA*

<sup>9</sup>*Department of Biology, California State University, Northridge California 91330 USA*

<sup>10</sup>*U.S. Geological Survey, Wetland and Aquatic Research Center, St John, U.S. Virgin Islands, USA*

**Citation:** Courtney, T. A., B. B. Barnes, I. Chollett, R. Elahi, K. Gross, J. R. Guest, I. B. Kuffner, E. A. Lenz, H. R. Nelson, C. S. Rogers, L. T. Toth, and A. J. Andersson. 2020. Disturbances drive changes in coral community assemblages and coral calcification capacity. *Ecosphere* 11(4):e03066. 10.1002/ecs2.3066

**Abstract.** Anthropogenic environmental change has increased coral reef disturbance regimes in recent decades, altering the structure and function of many coral reefs globally. In this study, we used coral community survey data collected from 1996 to 2015 to evaluate reef-scale coral calcification capacity (CCC) dynamics with respect to recorded pulse disturbances for 121 reef sites in the Main Hawaiian Islands and Mo'orea (French Polynesia) in the Pacific and the Florida Keys Reef Tract and St. John (U.S. Virgin Islands) in the western Atlantic. CCC remained relatively high in the Main Hawaiian Islands in the absence of recorded widespread disturbances; declined and subsequently recovered in Mo'orea following a crown-of-thorns sea star outbreak, coral bleaching, and major cyclone; decreased and remained low following coral bleaching in the Florida Keys Reef Tract; and decreased following coral bleaching and disease in St. John. Individual coral taxa have variable calcification rates and susceptibility to disturbances because of their differing life-history strategies. As a result, temporal changes in CCC in this study were driven by shifts in both overall coral cover and coral community composition. Analysis of our results considering coral life-history strategies showed that weedy corals generally increased their contributions to CCC over time while the contribution of competitive corals decreased. Shifts in contributions by stress-tolerant and generalist corals to CCC were more variable across regions. The increasing frequency and intensity of disturbances under 21st century global change therefore has the potential to drive lower and more variable CCC because of the increasing dominance of weedy and some stress-tolerant corals.

**Key words:** carbonate budgets; climate change; coral bleaching; coral disease; ecological traits; environmental monitoring; resilience; scleractinians.

**Received** 13 August 2019; revised 7 January 2020; accepted 10 January 2020. Corresponding Editor: Hunter S. Lenihan.

**Copyright:** © 2020 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** traviscourtney@gmail.com

## INTRODUCTION

The growth of calcium carbonate ( $\text{CaCO}_3$ ) structures is one of the most important functions of coral reefs in providing the ecosystem services that reefs afford to humanity (Kleypas et al. 2001, Edmunds et al. 2016, Courtney et al. 2017, Cyronak et al. 2018, Perry et al. 2018). Scleractinian corals typically account for the majority of  $\text{CaCO}_3$  production on coral reefs (Montaggioni and Braithwaite 2009) and are therefore critical to the provisioning of shoreline protection, fisheries habitat, and tourism revenue services that coral reefs provide (Moberg and Folke 1999). However, the maintenance of these services is threatened by global and local environmental changes that have led to pantropical declines in coral cover (Gardner et al. 2003, Bruno and Selig 2007, Jackson et al. 2014) and shifts in coral community composition (Alvarez-Filip et al. 2013, Perry et al. 2015, Hughes et al. 2018), which will likely prevent some coral reefs around the world from keeping up with 21st century sea-level rise (Perry et al. 2018).

The frequency and intensity of disturbances shape coral community structure (Connell 1978) with enhanced disturbance regimes typically driving a disproportionate loss of fast-growing, architecturally complex corals (e.g., *Acropora* spp.) in favor of slow-growing, massive (e.g., *Porites lobata*, *Siderastrea siderea*) and/or fast-growing, early-successional colonizers (e.g., *Agaricia* spp.; *Porites astreoides*; *Pocillopora damicornis*; e.g., Loya et al. 2001, McClanahan and Maina 2003, McClanahan et al. 2009, Fabricius et al. 2011, van Woesik et al. 2011, Darling et al. 2013, Grottoli et al. 2014, Hughes et al. 2018). These differences in coral traits have been further analyzed in the context of hypothesized coral life-history strategies, which describe consistent traits that characterize an evolutionary survival strategy (Grime 1977, Darling et al. 2012). The pioneering work by Darling et al. (2012) analyzed pantropical coral trait data to define four primary coral life-history strategies: (1) competitive: fast-growing, large-colony, broadcast spawning corals with branching/plating morphologies; (2) stress-tolerant: slow-growing, long-lived, highly fecund, broadcast spawning corals with massive/encrusting morphologies; (3)

weedy: small-colony, brooding corals; and (4) generalists: corals with traits representing a mixture of those found in the previous three groups (e.g., stress tolerance and moderate growth rates). Shifts from reefs dominated by competitive to stress-tolerant and weedy corals can drive declines in reef-scale calcification as evidenced by modeled (Alvarez-Filip et al. 2013) and observed (Perry et al. 2015, Kuffner and Toth 2016, Lange and Perry 2019, Toth et al. 2019) decreases in net coral reef  $\text{CaCO}_3$  production budgets; however, the impacts of shifting coral life-history strategies on reef-scale calcification through time and across broad geographic spatial scales remain to be rigorously characterized.

In this study, we quantified coral calcification capacity (CCC) across a variety of disturbance regimes using a life-history strategies perspective (sensu Darling et al. 2012) for 121 reef sites surveyed from ~1996 to 2015 across four focal regions in the Pacific (Main Hawaiian Islands and Mo'orea) and western Atlantic (Florida Keys Reef Tract and St. John). We tested the hypothesis that disturbances drive decreases in the contribution to CCC by competitive corals and increases in the contribution to CCC by weedy and stress-tolerant corals owing to alterations of coral community composition as coral cover declines. Our results reveal how disturbance-driven shifts in the species composition of coral communities and overall coral cover have altered reef CCC trajectories at our sites in the Pacific and western Atlantic and how these changes may impact the critical reef-building function of coral reefs now and in the future.

## MATERIALS AND METHODS

### *Introduction to focal-region surveys and disturbance histories*

The four focal regions analyzed in this study were selected because of publicly available datasets (Guest et al. 2018b) of coral reef benthic surveys (i.e., total and taxon-specific percent coral cover) that were conducted on a range of reef types (e.g., patch, spur and groove, fringing, barrier, and forereef) across a range of depths from 1 to 22 m. The surveys were conducted using standardized protocols at a total of 121 sites surveyed a minimum of three times over at least ten years

from ~1996 to 2015 (see Guest et al. 2018a supplementary materials for a complete discussion of sites and survey methods). The data from the focal regions overlap from 2005 to 2014, but the total length of the time series varied slightly, with the Main Hawaiian Islands survey data ranging from 1999 to 2014, Mo’orea from 2005 to 2015, Florida Keys Reef Tract from 1996 to 2015, and St. John from 1999 to 2015.

In addition to data availability, the focal regions were chosen to include a broad range of disturbance histories during the survey period (see Guest et al. 2018a; Fig. 1). Although we acknowledge that long-term press disturbances such as land-use change, fishing pressure, eutrophication, and ocean acidification can contribute to ecosystem change, inconsistencies in data availability and the indirect nature of press disturbances (i.e., they do not directly cause coral mortality) led us instead to focus on documented

pulse disturbances in this study. All focal regions experienced recorded coral bleaching events during the study periods including 2002, 2004, and 2014 in the Main Hawaiian Islands (Jokiel and Brown 2004, Bahr et al. 2017, Rodgers et al. 2017); 2007 in Mo’orea (Adjeroud et al. 2018); 1997, 1998, 2005, 2011, 2014, and 2015 in the Florida Keys (Manzello et al. 2007, 2018, Wagner et al. 2010, Ruzicka et al. 2013); and 2005 in St. John (Miller et al. 2006, 2009, Edmunds 2013). While the before and after effects of hurricanes were not directly quantified for each site in this study, we considered hurricanes to potentially impact the focal regions if a Category 1–5 storm passed within 100 nautical miles of the following locations during the respective time series of the focal regions in this study: Hilo Harbor, Kahului Harbor, Honolulu Harbor, or Kalāheo (Main Hawaiian Islands); Pao Pao (Mo’orea); Big Pine Key or Dry Tortugas (Florida Keys Reef Tract);

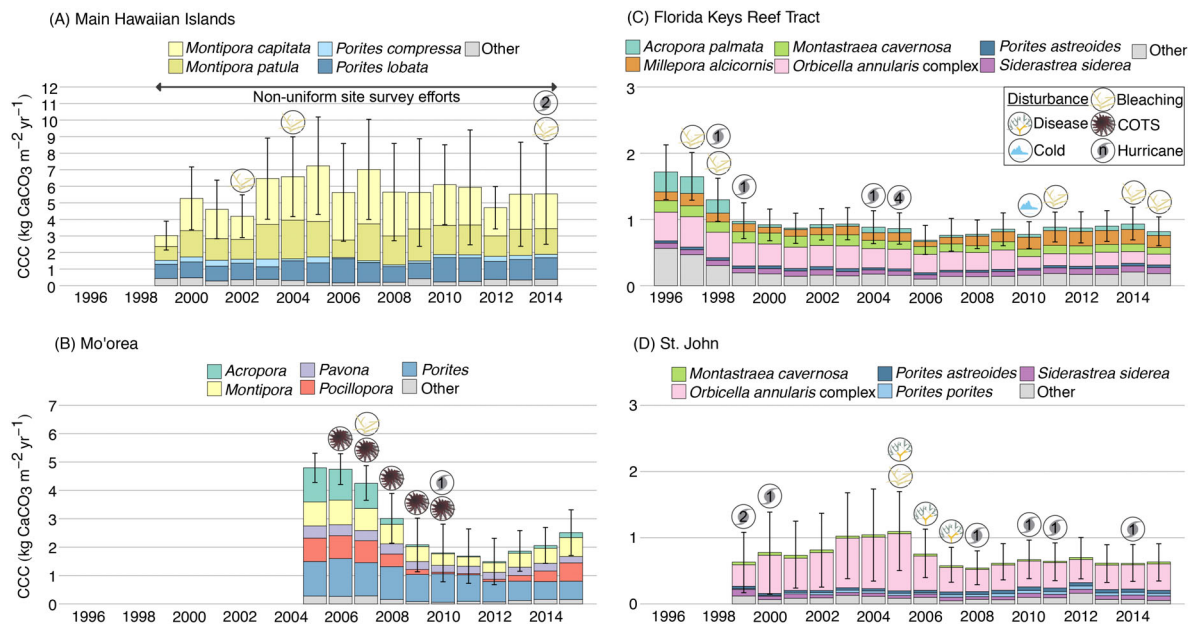


Fig. 1. Mean annual coral calcification capacity (CCC) over time partitioned by the dominant calcifiers relative to recorded disturbance events. Mean ( $\pm 95\%$  confidence interval) annual CCC ( $\text{kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) is reported for scleractinian coral and hydrozoan taxa contributing  $\geq 5\%$  CCC across all reef sites within a focal region for at least one year of the time series with all remaining taxa pooled into the “Other” category. Note the differing scales on the vertical axis for each panel. Disturbances and icons in the legend are Bleaching, severe coral bleaching event; Disease, coral disease event; COTS, crown-of-thorns sea star outbreak; Cold, cold-water mortality event; and Hurricane,  $n$  number of recorded hurricanes/cyclones for the given year. Icons are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

and Virgin Islands National Park (St. John). Based on these search criteria in the NOAA hurricanes database (<https://coast.noaa.gov/hurricanes/>), there were two recorded hurricanes in the Main Hawaiian Islands, no recorded cyclones in the search region for Mo'orea (but waves from Cyclone Oli impacted some reefs in 2010; Han et al. 2016, Adjeroud et al. 2018), seven recorded hurricanes in the Florida Keys Reef Tract, and seven recorded hurricanes in St. John (Fig. 1). Mo'orea additionally experienced a crown-of-thorns sea star (COTS), *Acanthaster planci*, outbreak from 2006 to 2010 (Adam et al. 2011, Pratchett et al. 2011, Han et al. 2016, Adjeroud et al. 2018). The Florida Keys Reef Tract also experienced a cold-water coral mortality event due to anomalously cold winter temperatures in 2010 (Kemp et al. 2011, Lirman et al. 2011, Ruzicka et al. 2013). In St. John, a prolonged period of coral disease occurred from 2005 to 2007 following the 2005 coral bleaching event (Miller et al. 2006, 2009, Edmunds 2013). As a result of these extensive, yet variable disturbance histories and dissimilar initial coral community compositions across sites, there is a large variation in coral cover and community compositions over time across the focal regions, which allowed us to evaluate the community-level drivers of CCC for a range of coral reefs across ocean basins between ~1996 and 2015.

#### *Coral calcification capacity*

We define CCC as an estimate of the annual reef-scale calcification rate ( $\text{kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) by a coral community. This metric is similar to the gross carbonate production terms calculated as part of complete  $\text{CaCO}_3$  budgets, but these budgets also include  $\text{CaCO}_3$  dissolution, bioerosion, and import/export (e.g., Chave et al. 1972, Stearn et al. 1977, Hubbard et al. 1990, Kleypas et al. 2001, Perry et al. 2012). Additionally, CCC does not include calcification by coralline algae, *Halimeda*, and benthic foraminifera, each of which have been measured to produce upwards of  $2 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  (e.g., see Montaggioni and Braithwaite 2009 and references therein) and may contribute greater proportions of reef-scale  $\text{CaCO}_3$  production in lower coral cover and/or bleached reef systems (Courtney et al. 2018). While these other calcifiers can be significant components of reef  $\text{CaCO}_3$  budgets, the usage of

CCC as an ecologically meaningful metric is supported by previous studies documenting that corals are typically the dominant coral reef  $\text{CaCO}_3$  producers (Montaggioni and Braithwaite 2009), by observations of greater net calcification by hard corals relative to calcifying algae on a planar-area basis (Kuffner et al. 2013, Kennedy et al. 2017), and by the high degree of agreement between coral colony and reef-scale calcification (Courtney et al. 2016, 2017). Our measures of CCC utilized the best available calcification rate data from the literature because it was logistically not possible to directly quantify the local variability in calcification rates, which can be considerable (Kuffner et al. 2013), owing to genetic variability and the environmental drivers of coral calcification (e.g., Pratchett et al. 2015) over the broad spatial and temporal scales of this study. The application of literature-based rather than direct measurements of location-specific calcification rates is a common limitation of complete census-based  $\text{CaCO}_3$  budget calculations but is necessary to produce rapid assessments of census-based reef-scale calcification (e.g., see Perry et al. 2012). Nonetheless, the CCC methodologies presented here allow for robust, retrospective analysis of the capacity for annual coral community calcification and provide valuable new insights into how shifting coral communities impact reef-scale calcification from data-limited historical time series.

To calculate temporal trends in CCC for our focal regions, we first estimated annual calcification rates of individual scleractinian coral and hydrozoan *Millepora* taxa (hereafter collectively referred to as "corals") as the product of published taxon-specific linear extension rates ( $\text{cm} \cdot \text{yr}^{-1}$ ), published taxon-specific skeletal densities ( $\text{g CaCO}_3 \cdot \text{cm}^{-3}$ ), and a growth form adjustment factor that estimates the void space between topographic features generated by complex (i.e., branching, plating, corymbose, digitate, columnar, foliose, sub-massive) morphologies following established methods (Morgan and Kench 2012, Perry et al. 2012, Guest et al. 2018a). All extension, density, growth form, and calcification rate data and references are summarized in Guest et al. (2018a: Tables S2 and S3). The contribution of each species to annual, reef-scale calcification was then determined by multiplying taxon-specific calcification rates (kg

$\text{CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) by their respective planar benthic cover (%) after Perry et al. (2012) and Guest et al. (2018a). Reef-wide calcification rates were calculated for each species where species-level benthic cover data were available (i.e., Main Hawaiian Islands, Florida Keys Reef Tract, St. John) and by genus for Mo'orea, where benthic cover was surveyed at the genus level. Annual CCC ( $\text{kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) for each reef site was then determined by summing the calcification ( $\text{kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) by all coral taxa. The average of CCC across all surveyed sites within a focal region for each given year was calculated to determine the changes in mean annual CCC through time. It is important to note, however, that not every reef site in the Main Hawaiian Islands focal region was surveyed each year in this study primarily due to funding limitations and this precludes any robust conclusions about changes in interannual CCC for this focal region.

#### *Dominant calcifying corals and life-history strategies*

Guest et al. (2018a) previously demonstrated that median z-score of coral cover explained 79–87% of the variance in the median CCC within each of our focal regions. Here, we hypothesized that the remaining variance may be due to differences in coral community composition (i.e., CCC is the product of taxa-level coral cover and calcification rates summed for all taxa). We parsed the contribution of each coral taxon to mean annual CCC in each focal region to identify the dominant calcifying taxa, which were defined in this study as taxa that contributed at least an average of 5% to the total CCC across all sites in each focal region for the duration of the time series. To further visualize how the differing calcification rates by the dominant corals have the capacity to impact the variance in CCC within each focal region, hypothetical scaling of calcification rates for each of the dominant calcifying corals from 0% to 100% cover was superimposed on plots relating percent coral cover and CCC (Fig. 2). In effect, these hypothetical calcification trajectories provide a frame of reference for interpreting CCC of the communities at each reef site and year relative to calcification rates of the dominant calcifying corals for the given focal region. The dominant calcifying corals were then characterized as competitive, stress-tolerant, weedy, or

generalist sensu Darling et al. (2012) to evaluate whether shifts in the relative contributions of corals with different life-history strategies are predictive of changes in CCC over the time series in each of the focal regions of this study.

#### *Statistical analyses*

First, we tested whether differences in coral community composition between the focal regions significantly ( $P < 0.05$ ) affected the relationship between percent coral cover and CCC for our focal regions (i.e., to test for significant differences in mean coral community calcification rates between focal regions). Linear mixed effects models were constructed to test whether slopes of CCC vs. coral cover were significantly different for each focal region. Percent coral cover was used as a fixed effect with random slopes and intercepts for each site to account for the fact that each reef site has varying coral community composition and therefore varying calcification rates for a given percent coral cover throughout the respective time series. Statistical models were fit using the R (R Core Team 2017) package nlme (Pinheiro et al. 2017) with model parameters estimated by maximum likelihood.

Second, we tested whether contributions by the dominant calcifying taxa to CCC shifted during the time series in each of the focal regions and whether these changes match the theoretical expectations for the four coral life-history strategies following disturbances (Darling et al. 2012, 2013). To accomplish this task of evaluating long-term changes in the percent contribution of calcifying taxa to CCC, linear mixed effects models were constructed to test whether year was a significant ( $P < 0.05$ ) predictor of percent contribution to CCC by each of the dominant calcifying taxa. The slopes of these models therefore indicate whether there were statistically significant mean increases (positive slope) or decreases (negative slope) in the contribution of the dominant calcifying corals to CCC for the duration of the time series for each of the focal regions. The models used the percentage of annual site-level CCC by each dominant calcifying genus as the response variable and included fixed effects for year and a random intercept and slope for each site using the R (R Core Team 2017) package nlme (Pinheiro et al. 2017) with model parameters estimated by maximum likelihood. Random

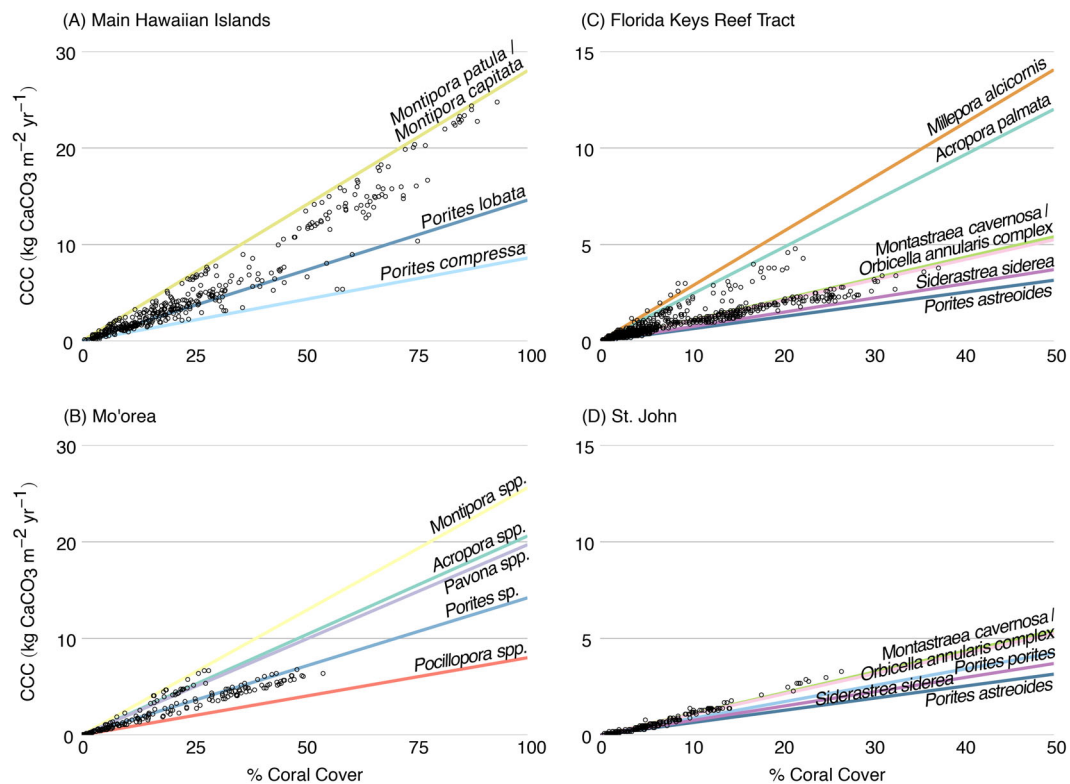


Fig. 2. Coral calcification capacity (CCC) vs. percent coral cover for the Pacific and western Atlantic focal regions. Each point represents the site-level CCC vs. percent coral cover for each year surveyed within each of the four focal regions. Colored lines represent the hypothetical relationship of calcification vs. coral cover for each dominant coral taxa within the focal region to provide additional context for the site-level CCC vs. coral cover data. Note the differing scales on the vertical axes for the Pacific and western Atlantic regions.

intercepts and slopes for each site were included to account for the fact that each site had different initial percent contributions of dominant calcifying coral to CCC (random intercepts) and that each site had different disturbance histories resulting in variable responses in dominant calcifying coral contributions to CCC over time (random slopes). Because sites were repeatedly surveyed through time, a continuous autocorrelation structure (corCAR1 in package nlme; Pinheiro et al. 2017) was included in each model to account for temporal autocorrelation and the variable time interval between surveys in the Main Hawaiian Islands. While temporal fluctuations in CCC may be nonlinear at least for some reef sites and focal regions on interannual timescales (e.g., Fig. 1B), we utilized linear mixed effects models in this study because the purpose of this analysis was to focus on longer term mean

trends in coral contribution to CCC. Notably, this focus on longer timescales prevents the inconsistent interannual sampling effort for the Main Hawaiian Islands from biasing conclusions regarding mean trends in coral contribution to CCC through time.

## RESULTS

Mean of focal-region CCC (mean  $\pm$  95% confidence intervals) through time was generally higher for the Pacific regions than in the western Atlantic (Fig. 1). CCC for the Main Hawaiian Islands was consistently the highest of the four focal regions although the large interannual variability resulting from non-uniform sampling efforts (i.e., not all sites were surveyed in all years) and relatively larger, overlapping confidence intervals (Fig. 1A) preclude any formal

conclusions about interannual changes in mean CCC in this location. In Mo'orea, mean CCC ( $\text{kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1} \pm 95\% \text{ CI}$ ) declined following a combination of a crown-of-thorns outbreak (2006–2010), coral bleaching (2007), and Cyclone Oli (2010) from  $4.8 \pm 0.5$  in 2006 to a minimum of  $1.5 \pm 0.8$  in 2012 and then increased to  $2.5 \pm 0.8$  in 2015 (Fig. 1B). In the Florida Keys, mean CCC ( $\text{kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1} \pm 95\% \text{ CI}$ ) decreased following coral bleaching in 1997/1998 from  $1.7 \pm 0.4$  in 1996 to  $1.0 \pm 0.3$  in 2000 and remained relatively stable through 2015 (Fig. 1C). Mean CCC ( $\text{kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1} \pm 95\% \text{ confidence intervals}$ ) in St. John increased slightly from  $0.6 \pm 0.5$  in 1999 to  $1.1 \pm 0.6$  in 2005, decreased to  $0.5 \pm 0.3$  in concert with the 2005 coral bleaching event and associated 2005–2007 disease outbreak, and remained approximately stable thereafter (Fig. 1D).

Twelve species representing nine genera of corals out of the 84 species and 50 genera surveyed in this study were identified as the dominant calcifying taxa (i.e., calcified mean  $\geq 5\%$  of total CCC across all sites and all years for the respective time series) across the four focal regions with *Acropora*, *Montipora*, *Pavona*, *Pocillopora*, and *Porites* spp. contributing the most to CCC in the Pacific and *Acropora*, *Millepora*, *Montastraea*, *Orbicella*, *Porites*, and *Siderastrea* spp. in the western Atlantic (Fig. 1, Table 1). The dominant calcifying species were further characterized by life-history strategies sensu Darling et al. (2012) to evaluate the respective changes of the dominant calcifying corals with respect to life-history strategies (Table 1).

Although CCC generally increases with increasing coral cover (Guest et al. 2018a), the remaining variability in that relationship is a direct result of the differing calcification rates of the dominant calcifiers for each reef site at each point in time (Fig. 2; Guest et al. 2018a). In the Main Hawaiian Islands, which had sites with the highest coral cover out of any of the focal regions, CCC vs. coral cover data for each site surveyed in each year generally fall along the hypothetical trajectories predicted for *Montipora* spp. or *Porites lobata* corals (Fig. 2A) with a mean ( $\pm 95\% \text{ CI}$ ) CCC vs. coral cover slope of  $0.19 \pm 0.02 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1} \cdot \% \text{ coral cover}^{-1}$  ( $P < 0.001$ , Fig. 3). Coral cover in Mo'orea was

also high relative to most western Atlantic reef sites. However, whereas the annual site-level CCC vs. coral cover data for some sites in Mo'orea appear to follow the hypothetical trajectory predicted for a mixed *Montipora/Acropora* community, most sites appear to follow the *Porites* calcification trajectory (Fig. 2B) with a mean ( $\pm 95\% \text{ CI}$ ) CCC vs. coral cover slope of  $0.14 \pm 0.02 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1} \cdot \% \text{ coral cover}^{-1}$  ( $P < 0.001$ , Fig. 3). In the Florida Keys Reef Tract, where most reef sites have comparatively lower coral cover, the annual site-level CCC vs. coral cover data follow the hypothetical trajectories predicted for the *Orbicella annularis* complex/*Montastraea cavernosa* or *Acropora palmata* (Fig. 2C) with a mean ( $\pm 95\% \text{ CI}$ ) CCC vs. coral cover slope of  $0.17 \pm 0.01 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1} \cdot \% \text{ coral cover}^{-1}$  ( $P < 0.001$ , Fig. 3). Lastly, in St. John the site-level CCC vs. coral cover data suggest that nearly every site follows the hypothetical trajectories predicted for the *Orbicella annularis* complex/*Montastraea cavernosa* (Fig. 2D) with a mean ( $\pm 95\% \text{ CI}$ ) slope of  $0.11 \pm 0.01 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1} \cdot \% \text{ coral cover}^{-1}$  ( $P < 0.001$ , Fig. 3) owing to the dominance of the *Orbicella annularis* complex in this focal region (Fig. 1D).

To assess whether changes in the contribution by each of the dominant calcifying taxa to CCC were consistent with life-history strategy expectations of shifting coral cover following disturbances (Darling et al. 2012, 2013), long-term changes of percent contribution by each of the dominant calcifying corals to total CCC across all sites for the duration of the time series were evaluated. In this analysis, positive slopes indicate mean increases in the percent contribution of the respective coral to CCC within the focal region over the time series whereas the opposite is true for corals with negative slopes and non-significant slopes indicate no detectable change in coral contribution to CCC (Fig. 4, Table 1). In the Main Hawaiian Islands, percent of CCC by *Montipora capitata* (competitive) increased, *Porites compressa* (competitive) decreased, and the other dominant calcifiers exhibited no detectable change (Fig. 4A, Table 1). In Mo'orea, percent calcification by *Montipora* spp. (competitive/intermediate/stress-tolerant) increased, *Acropora* spp. (competitive) decreased, and the other dominant calcifiers exhibited no detectable change (Fig. 4B, Table 1). In the Florida Keys, all dominant

Table 1. Life-history strategies (LHS) classifications from Darling et al. (2012) and linear mixed effects model results (Slope  $\pm$  SE, *P*-value) of the percent contribution by the dominant calcifying corals vs. year are reported for the Main Hawaiian Islands.

Focal region	Coral	Life-history strategy	Slope $\pm$ SE	<i>P</i> -value
Pacific (Mo'orea)	<i>Acropora</i> spp.	<b>Competitive</b> <sup>†</sup>	<b>-1.61 <math>\pm</math> 0.44</b>	<b>&lt;0.001</b>
Pacific (Hawai'i)	<i>Montipora capitata</i>	<b>Competitive</b>	<b>0.27 <math>\pm</math> 0.11</b>	<b>0.014</b>
Pacific (Hawai'i)	<i>Montipora patula</i>	Competitive/generalist/stress-tolerant <sup>‡</sup>	0.08 $\pm$ 0.12	0.511
Pacific (Mo'orea)	<i>Montipora</i> spp.	<b>Competitive/generalist/stress-tolerant</b> <sup>†</sup>	<b>0.63 <math>\pm</math> 0.29</b>	<b>0.029</b>
Pacific (Mo'orea)	<i>Pavona</i> spp.	Stress-tolerant/generalist <sup>†</sup>	-0.07 $\pm$ 0.27	0.808
Pacific (Mo'orea)	<i>Pocillopora</i> spp.	Competitive/weedy <sup>†</sup>	0.41 $\pm$ 0.36	0.258
Pacific (Hawai'i)	<i>Porites compressa</i>	<b>Competitive</b>	<b>-0.15 <math>\pm</math> 0.08</b>	<b>0.046</b>
Pacific (Hawai'i)	<i>Porites lobata</i>	Stress-tolerant	0.04 $\pm$ 0.17	0.798
Pacific (Mo'orea)	<i>Porites</i> spp.	Weedy/stress-tolerant/competitive <sup>†</sup>	0.47 $\pm$ 0.52	0.363
Atlantic (Florida)	<i>Acropora palmata</i>	<b>Competitive</b>	<b>-0.38 <math>\pm</math> 0.11</b>	<b>&lt;0.001</b>
Atlantic (Florida)	<i>Millepora alcicornis</i>	<b>Weedy</b> <sup>§</sup>	<b>0.96 <math>\pm</math> 0.10</b>	<b>&lt;0.001</b>
Atlantic (Florida)	<i>Montastraea cavernosa</i>	<b>Stress-tolerant</b>	<b>-0.15 <math>\pm</math> 0.04</b>	<b>&lt;0.001</b>
Atlantic (St. John)	<i>Montastraea cavernosa</i>	Stress-tolerant	-0.04 $\pm$ 0.11	0.691
Atlantic (Florida)	<i>Orbicella annularis</i> complex	<b>Generalist/stress-tolerant</b> <sup>¶</sup>	<b>-0.55 <math>\pm</math> 0.16</b>	<b>&lt;0.001</b>
Atlantic (St. John)	<i>Orbicella annularis</i> complex	<b>Generalist/stress-tolerant</b> <sup>¶</sup>	<b>-0.56 <math>\pm</math> 0.21</b>	<b>0.008</b>
Atlantic (Florida)	<i>Porites astreoides</i>	<b>Weedy</b>	<b>0.30 <math>\pm</math> 0.08</b>	<b>&lt;0.001</b>
Atlantic (St. John)	<i>Porites astreoides</i>	Weedy	0.29 $\pm$ 0.15	0.054
Atlantic (St. John)	<i>Porites porites</i>	<b>Weedy</b>	<b>0.20 <math>\pm</math> 0.06</b>	<b>0.001</b>
Atlantic (Florida)	<i>Siderastrea siderea</i>	<b>Stress-tolerant</b>	<b>0.46 <math>\pm</math> 0.07</b>	<b>&lt;0.001</b>
Atlantic (St. John)	<i>Siderastrea siderea</i>	Stress-tolerant	-0.18 $\pm$ 0.16	0.269

Notes: Hawai'i df = 358; Mo'orea df = 179; Florida Keys Reef Tract Florida df = 709; and St. John df = 206. Corals with *P*-values < 0.05 are denoted in bold text.

<sup>†</sup> LHS for species from the respective genera described in Darling et al. (2012).

<sup>‡</sup> LHS for all *Montipora* spp. from Darling et al. (2012).

<sup>§</sup> LHS inferred from Brown and Edmunds (2013).

<sup>¶</sup> LHS for all species of *Orbicella annularis* complex described in Darling et al. (2012).

calcifying corals shifted their relative contributions to CCC wherein percent of CCC by *Millepora alcicornis* (weedy), *Porites astreoides* (weedy), and *Siderastrea siderea* (stress-tolerant) increased, and *Acropora palmata* (competitive), *Montastraea cavernosa* (stress-tolerant), and *Orbicella annularis* complex (generalist/stress-tolerant) decreased (Fig. 4C, Table 1). In St. John, percent of CCC by *Porites porites* (weedy) increased, *Orbicella annularis* complex (generalist/stress-tolerant) decreased, and the other dominant calcifiers exhibited no detectable change (Fig. 4D, Table 1).

## DISCUSSION

Here, we have used CCC to retroactively estimate CaCO<sub>3</sub> production by coral communities in historical datasets (Guest et al. 2018a) to explore the ecological drivers of CCC across the Pacific and western Atlantic over an approximately 20-yr period. Our results suggest that coral

bleaching (Mo'orea, Florida Keys, St. John), coral disease (St. John), and a crown-of-thorns sea star outbreak (Mo'orea) were the dominant pulse disturbances that drove reductions in CCC over this period through a combination of reduced coral cover and shifting coral community compositions (Figs. 1, 2, 4). In the Main Hawaiian Islands, the absence of significant, widespread recorded pulse disturbances (e.g., the 2002 and 2004 bleaching events were minor and the reefs recovered; Bahr et al. 2017) and the large interannual CCC variability with overlapping 95% confidence intervals preclude any similar conclusions about the role of disturbance in modulating CCC there. However, widespread bleaching in Hawai'i was recorded in 2014 and 2015 at the conclusion of the time series in this study (Bahr et al. 2017, Rodgers et al. 2017), and it caused reduced reef-scale calcification observed for at least Kāne'ohe Bay in the Main Hawaiian Islands (Courtney et al. 2018). These findings agree with the growing CaCO<sub>3</sub> budget and



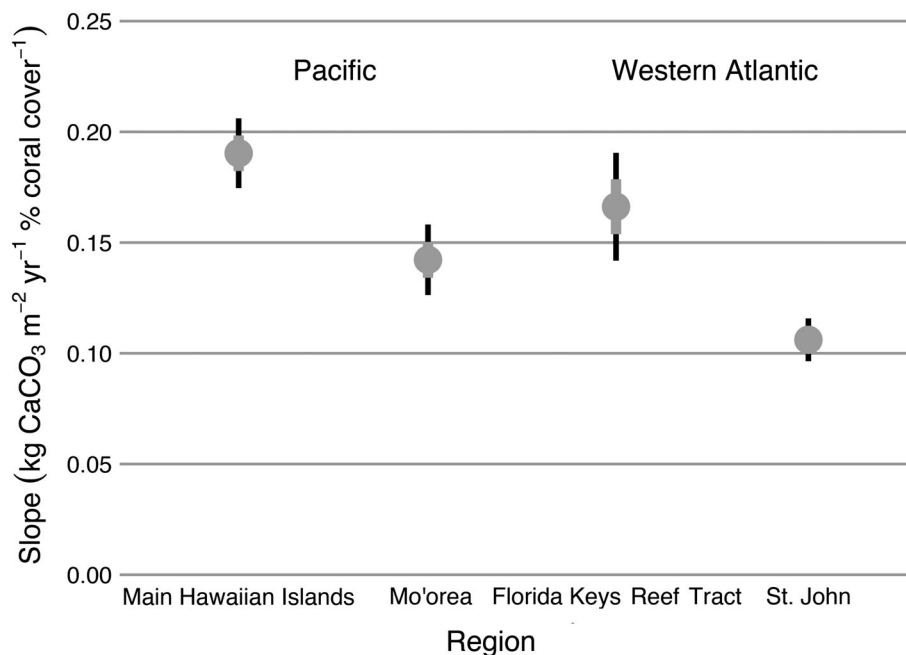


Fig. 3. Mean slopes of the relationship between coral calcification capacity (CCC) and percent coral cover across all sites and years for each focal region. Gray points represent the mean slope, wide gray lines represent standard error, and narrow black lines represent 95% confidence intervals.

chemistry-based net ecosystem calcification literature showing that coral bleaching events and other disturbances can significantly reduce reef-scale calcification rates (e.g., Kayanne et al. 2005, Perry et al. 2008, DeCarlo et al. 2017, Januchowski-Hartley et al. 2017, Perry and Morgan 2017, Courtney et al. 2018, Lange and Perry 2019). Mean CCC in Mo'orea showed signs of recovery following disturbance-induced CCC declines (Fig. 1B). Analogous recoveries in reef-scale calcification have been observed in the Seychelles (Januchowski-Hartley et al. 2017) and Kāne'ohe Bay, Hawai'i (Courtney et al. 2018), suggesting reefs have the capacity to recover CaCO<sub>3</sub> production rates in the absence of continued disturbances. However, it is important to note that reduced CCC rates for many of the lower percent coral cover reefs in this study (Fig. 2) may be exceeded by rates of CaCO<sub>3</sub> bioerosion and dissolution, highlighting the growing need for monitoring of these destructive processes on coral reefs to better predict the future of coral reef CaCO<sub>3</sub> structures under anthropogenic and climatic change (Kleypas et al. 2001; Perry et al. 2008, 2012, 2018,

Andersson and Gledhill 2013, Eyre et al. 2018, van Woesik and Cacciapaglia 2018, Kuffner et al. 2019). Indeed, recent work has already documented net dissolution (Muehllehner et al. 2016) and rapid rates of bioerosion (Kuffner et al. 2019) across the Florida Keys Reef Tract and loss of seafloor elevation occurring for reef ecosystems in the Pacific and western Atlantic (Yates et al. 2017).

Nonetheless, a CCC approach is valuable for estimating changes in coral community calcification because it incorporates variability in both coral cover and coral community composition. For example, there were significant differences in the relationship between mean CCC and percent coral cover across focal regions (i.e., non-overlapping 95% confidence intervals in Fig. 3). St. John had the lowest CCC vs. % coral cover slope of all the focal regions indicating a more slowly calcifying coral community (i.e., dominated by *Orbicella annularis* complex; Fig. 2D) while the Main Hawaiian Islands had the highest slope (Fig. 3) due to an abundance of more rapidly calcifying *Montipora* spp. (Fig. 2A). The slope of the CCC vs. percent coral cover relationship for Mo'orea

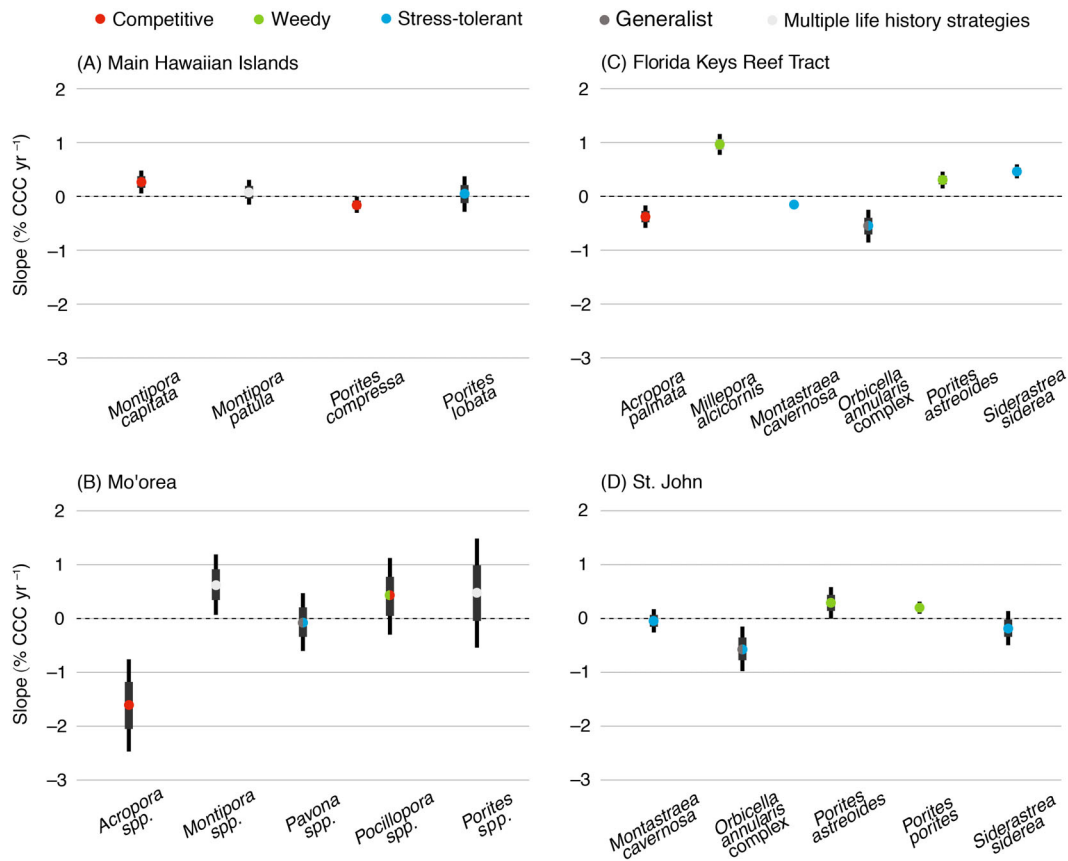


Fig. 4. Mean percent change in coral calcification capacity (CCC) by dominant calcifying corals in each focal region. Each data point describes the coral-specific change in the annual % contribution to CCC over time (i.e., slope represents mean change in contribution to CCC per year) as derived from linear mixed effects models within each focal region, indicating the slope (colored by life-history strategy from Table 1: red, competitive; green, weedy; blue, stress-tolerant; gray, generalist; white, more than two life-history strategies), standard error (wide gray lines), and 95% confidence intervals (narrow black lines). Positive slopes  $\pm$  95% above the dashed zero line indicate annual increases in % of CCC vs. year for the respective genus, slopes  $\pm$  95% overlapping the dashed zero line indicate no detectable change in % of CCC vs. year for the respective genus, and negative slopes  $\pm$  95% below the dashed zero line indicate decreases in annual % of CCC vs. year for the respective coral.

was significantly higher than St. John but lower than the Main Hawaiian Islands (Fig. 3) due to a mixture of reef sites dominated by rapidly calcifying *Montipora*/*Acropora* and more slowly calcifying *Porites* spp. (Fig. 2B). Similarly, the Florida Keys Reef Tract had a slope of the CCC vs. percent coral cover relationship that was not significantly different from the Main Hawaiian Islands or Mo'orea, but greater than St. John (Fig. 3) owing to a mixture of reef sites dominated with calcification by either *Millepora alcicornis* and *Acropora palmata* or *Orbicella annularis* complex

and *Montastraea cavernosa* (Fig. 2C). Thus, while Guest et al. (2018a) found coral cover explained much of the variance in CCC within each focal region, the differing slopes of the CCC vs. percent coral cover relationships between focal regions presented here highlight the importance of incorporating coral community composition into reef-scale calcification studies.

It is important to further note that the CCC approach reveals some sites with relatively high CCC for a given coral cover and high variance in the CCC vs. percent coral cover relationship

across sites and over time within each focal region (Fig. 2), which is consistent with observations from  $\text{CaCO}_3$  budget assessments for reefs across the western Atlantic by Perry et al. (2013). Most importantly, some reef sites within the Main Hawaiian Islands, Mo'orea, and Florida Keys Reef Tract focal regions reflect growth trajectories dominated by faster growing competitive corals (i.e., higher CCC per coral cover points plot along the hypothetical *Acropora* and *Montipora* growth trajectories, Fig. 2 ABC), suggesting those sites may have either experienced fewer disturbances than neighboring sites, locally resisted them, or recovered following disturbances (i.e., are oases sensu Guest et al. 2018a). Although hypotheses regarding why some reefs have escaped, resisted, and/or recovered from disturbances remain to be empirically tested, the use of CCC presented here serves as a potential means of quantifying the reef-growth potential of coral communities to improve our understanding and projections of future coral reef calcification trajectories.

We further explored changes in CCC by investigating the dominant calcifying corals that contributed at least 5% of the total CCC across the time series in this study (Fig. 1). These species represent potentially useful targets for management and restoration as they may be most important in maintaining reef-scale calcification in the future. However, the relative contributions of many of these taxa to CCC shifted over the time series in this study. For example, the dominant calcifying taxa *Montipora capitata*, *Montipora* sp. (Mo'orea), *Millepora alcicornis*, *Porites astreoides*, *Siderastrea siderea*, and *Porites porites* increased in relative contributions to CCC across the focal regions (Fig. 4, Table 1), suggesting they are becoming increasingly important reef builders in the 21st century. Conversely, *Acropora palmata*, *Acropora* spp. (Mo'orea), *Montastraea cavernosa*, *Orbicella annularis* complex, and *Porites compressa* decreased in mean contributions to CCC across the focal regions over the time series in this study (Fig. 4, Table 1) and are, therefore, likely to make diminishing contributions to future reef building.

Dominant calcifying corals were classified by life-history strategies to test whether disturbance events drove decreases in competitive corals' and increases in weedy and stress-tolerant corals' (Darling et al. 2012, 2013) contributions to CCC

in this study (Fig. 2, Table 1). Following the major coral bleaching, crown-of-thorns, and disease-disturbance events, the competitive *Acropora* spp. corals decreased their contributions to CCC across the focal regions in this study, and in the western Atlantic, the weedy *Millepora alcicornis* (Florida), *Porites astreoides* (Florida), and *Porites porites* (Florida and St. John) corals increased their contributions to CCC. These changes are congruent with Darling et al.'s (2012, 2013) expectations for competitive and weedy corals under increased disturbance regimes. Although stress-tolerant corals are predicted to increase in abundance on disturbed reefs (Darling et al. 2012), the generalist/stress-tolerant *Orbicella annularis* complex corals decreased their contributions to CCC throughout the time series across both the Florida Keys and St. John focal regions. It is important to note, however, that *O. annularis* complex was disproportionately affected by white plague disease in St. John (Miller et al. 2009), highlighting the importance of considering disease susceptibility in the framework of shifting coral communities and life-history strategies. Furthermore, *Orbicella* spp. have been disproportionately affected by disturbances in the Florida Keys over the last 20 yr (Ruzicka et al. 2013; Toth et al. 2014, 2019), which suggests that the characterization of these species as stress-tolerant may warrant reconsideration. Lastly, mean contributions to CCC by stress-tolerant *Montastraea cavernosa* decreased and *Siderastrea siderea* increased across the Florida Keys (*Siderastrea siderea* CCC decreased somewhat  $-0.18 \pm 0.16$  albeit not significantly at  $P = 0.269$  in St. John), which, respectively, contradicts and agrees with hypothesized stress-tolerant life-history expectations on disturbed reefs for these corals (Darling et al. 2012, 2013). Thus, while the changing contributions to CCC by competitive and weedy corals in this study appear to agree well with hypothesized life-history expectations for disturbed reefs, the shifting contributions of generalist and stress-tolerant corals to CCC are more variable. Some of these discrepancies could in part be due to the widespread coral disease in St. John and/or other more localized drivers testing the tolerance of coral communities to disturbances and warrants further investigation to improve future projections of coral reef community structures and CCC.

Fast-growing *Acropora cervicornis* and *Acropora palmata* corals were once widespread, dominant calcifiers in the western Atlantic, but declined in the late 1970s and 1980s primarily due to white band disease and hurricanes (Aronson and Precht 2001, Kuffner and Toth 2016, Toth et al. 2019) and are no longer major CaCO<sub>3</sub> producers in this region (Perry et al. 2015). However, Darling et al. (2019) found that competitive corals are still the dominant corals on many reefs across the Indo-Pacific, which suggests they are still major CaCO<sub>3</sub> producers across the region. This may in part be due to greater functional redundancy of competitive coral life-history traits (i.e., faster calcification) in the Pacific relative to the western Atlantic (Kuffner and Toth 2016, McWilliam et al. 2018). Regardless, the declines in contributions of competitive corals to CCC following disturbances in this study imply future projected decreases in overall CCC under predicted increases in coral bleaching and disease-disturbance frequencies and intensities (e.g., Donner et al. 2005, Randall and van Woesik 2015, 2017, van Hooijdonk et al. 2016). The findings of this study agree with previously observed declines in *Acropora* corals owing to coral bleaching and disease in recent decades (e.g., Aronson and Precht 2001, Loya et al. 2001, Perry and Morgan 2017, Hughes et al. 2018).

The relative contribution to CCC by weedy corals may continue to increase as has been observed by the current dominance of non-framework building coral calcification in the western Atlantic (Perry et al. 2015). However, observed fluctuations in weedy coral cover following disturbance events (Brown and Edmunds 2013, Darling et al. 2013) could drive corresponding interannual fluctuations in CCC. This suggests reefs with increased weedy CCC may, therefore, maintain lower and/or less stable CCC through time (Alvarez-Filip et al. 2013). Nevertheless, reefs with a veneer of weedy corals may experience lower rates of physical loss of CaCO<sub>3</sub> by rendering the reef framework less accessible to destructive grazing and bioerosion (Kuffner and Toth 2016, Toth et al. 2018). The observed increase in contributions of some of the stress-tolerant corals in this study to CCC will likely decrease CCC for a given coral cover due to their generally slower calcification rates. Moreover, the greater bleaching resistance hypothesized for

many of these stress-tolerant corals (e.g., Loya et al. 2001, McClanahan and Maina 2003, McClanahan et al. 2009, van Woesik et al. 2011, Darling et al. 2013) and current dominance of stress-tolerant corals across much of the Indo-Pacific (Darling et al. 2019) suggest stress-tolerant corals may act to stabilize CCC under increased thermal stress (e.g., Januchowski-Hartley et al. 2017, Ryan et al. 2019). Further research should therefore be conducted to rigorously quantify coral and reef-scale rates of calcification, bleaching/disease resistance, and recovery to better predict future warming-induced changes in CCC and coral reef CaCO<sub>3</sub> structures (e.g., Swain et al. 2016, Januchowski-Hartley et al. 2017, Courtney et al. 2018, Mizerek et al. 2018, Ortiz et al. 2018, van Woesik et al. 2018, Gouezo et al. 2019).

As many coral reefs around the world continue to decline in coral cover and shift in coral species compositions under increasing frequencies of coral bleaching and other disturbances (Gardner et al. 2003, Donner et al. 2005, Bruno and Selig 2007, Jackson et al. 2014, van Hooijdonk et al. 2016, Hughes et al. 2018), metrics that evaluate historical reef condition from coral community data such as CCC may prove useful for understanding previous changes and projecting future coral reef CaCO<sub>3</sub> structures and functions. Likewise, evaluation of the ecological drivers of CCC in the context of coral life-history strategies and coral reef disturbances could easily expand reef monitoring programs to include estimates and projections of CaCO<sub>3</sub> production. The future of CCC for any given reef site relies on the reduction of the magnitude and frequency of coral reef disturbances through both global (i.e., reduction of greenhouse gas emissions that drive ocean warming and acidification) and local (e.g., reduction of land-based pollution, overfishing, and habitat destruction) efforts.

## ACKNOWLEDGMENTS

The authors of this paper are forever grateful for Ruth D. Gates' extensive contributions to coral research and marine science. With her inspiration came much research included in this paper which, in part, is a product of the U.S. Geological Survey (USGS) John Wesley Powell Center for Analysis and Synthesis working group "Local-scale ecosystem resilience amid

global-scale ocean change: the coral reef example” supported by funding awarded to P. J. Edmunds, R. D. Gates, and I. B. Kuffner with a Powell Fellowship to J. R. Guest. T. A. Courtney and A. J. Andersson additionally received funding from the National Science Foundation. We thank P. J. Edmunds and J. Miller for improving this manuscript with their helpful comments and the Powell Center for their support of the working group. We thank K. Rodgers, E. Brown, R. Ruzicka, M. Colella, J. Miller, A. Atkinson, and M. Feely for providing the raw data used in this study that are now published in a USGS data release <https://doi.org/10.5066/f78w3c7w>. All R code, and associated data files used in this analysis are publicly available on GitHub at <https://github.com/traviscourtney/PowellCCC>. We further thank the reviewers and editor for improving this manuscript with their helpful comments and suggestions. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The authors declare no conflict of interest. TAC and AJA designed the study, TAC analyzed the data, and TAC wrote the first draft of the manuscript with input from AJA and comments from all authors.

## LITERATURE CITED

- Adam, T. C., R. J. Schmitt, S. J. Holbrook, A. J. Brooks, P. J. Edmunds, R. C. Carpenter, and G. Bernardi. 2011. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLOS ONE* 6:e23717.
- Adjeroud, M., M. Kayal, C. Iborra-Cantonnet, J. Vercelloni, P. Bosserelle, V. Liao, Y. Chancerelle, J. Claudet, and L. Penin. 2018. Recovery of coral assemblages despite acute and recurrent disturbances on a South Central Pacific reef. *Scientific Reports* 8:1–8.
- Alvarez-Filip, L., J. P. Carricart-Ganivet, G. Horta-Puga, and R. Iglesias-Prieto. 2013. Shifts in coral assemblage composition do not ensure persistence of reef functionality. *Scientific Reports* 3:3486.
- Andersson, A. J., and D. Gledhill. 2013. Ocean acidification and coral reefs: effects on breakdown, dissolution, and net ecosystem calcification. *Annual Review of Marine Science* 5:321–348.
- Aronson, R. B., and W. F. Precht. 2001. White band diseases and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25–38.
- Bahr, K. D., K. S. Rodgers, and P. L. Jokiel. 2017. Impact of three bleaching events on the reef resiliency of Kāneʻohe Bay, Hawaiʻi. *Frontiers in Marine Science* 4:398.
- Brown, D., and P. J. Edmunds. 2013. Long-term changes in the population dynamics of the Caribbean hydrocoral *Millepora* spp. *Journal of Experimental Marine Biology and Ecology* 441:62–70.
- Bruno, J. F., and E. R. Selig. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLOS ONE* 2:e711.
- Chave, K. E., S. V. Smith, and K. J. Roy. 1972. Carbonate production by coral reefs. *Marine Geology* 12:123–140.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Courtney, T. A., E. H. De Carlo, H. N. Page, K. D. Bahr, A. Barro, N. Howins, R. Tabata, G. Terlouw, K. S. Rodgers, and A. J. Andersson. 2018. Recovery of reef-scale calcification following a bleaching event in Kāneʻohe Bay, Hawaiʻi. *Limnology and Oceanography Letters* 3:1–9.
- Courtney, T. A., et al. 2016. Comparing chemistry and census-based estimates of net ecosystem calcification on a rim reef in Bermuda. *Frontiers in Marine Science* 3:181.
- Courtney, T. A., et al. 2017. Environmental controls on modern scleractinian coral and reef-scale calcification. *Science Advances* 3:e1701356.
- Cyronak, T., et al. 2018. Taking the metabolic pulse of the world’s coral reefs. *PLOS ONE* 13:e0190872.
- Darling, E. S., L. Alvarez-Filip, T. A. Oliver, T. R. McClanahan, and I. M. Côté. 2012. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters* 15:1378–1386.
- Darling, E. S., T. R. McClanahan, and I. M. Côté. 2013. Life histories predict coral community disassembly under multiple stressors. *Global Change Biology* 19:1930–1940.
- Darling, E. S., et al. 2019. Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. *Nature Ecology & Evolution* 3:1341–1350.
- DeCarlo, T. M., A. L. Cohen, G. T. F. Wong, F.-K. 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. *Journal of Geophysical Research: Oceans* 122:745–761.
- Donner, S. D., W. J. Skirving, C. M. Little, M. Oppenheimer, and O. Hoegh-Guldberg. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology* 11:2251–2265.
- Edmunds, P. J. 2013. Decadal-scale changes in the community structure of coral reefs of St. John, US Virgin Islands. *Marine Ecology Progress Series* 489:107–123.
- Edmunds, P. J., et al. 2016. Integrating the effects of ocean acidification across functional scales on tropical coral reefs. *BioScience* 66:350–362.

- Eyre, B. D., T. Cyronak, P. Drupp, E. H. De Carlo, J. P. Sachs, and A. J. Andersson. 2018. Coral reefs will transition to net dissolving before end of century. *Science* 359:908–911.
- Fabricius, K. E., C. Langdon, S. Uthicke, C. Humphrey, S. Noonan, G. De'ath, R. Okazaki, N. Muehllehner, M. S. Glas, and J. M. Lough. 2011. Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change* 1:165–169.
- Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301:958–960.
- Gouezo, M., Y. Golbuu, K. Fabricius, D. Olsudong, G. Mereb, V. Nestor, E. Wolanski, P. Harrison, and C. Doropoulos. 2019. Drivers of recovery and reassembly of coral reef communities. *Proceedings of the Royal Society B* 286:20182908.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Grottoli, A. G., M. E. Warner, S. J. Levas, M. D. Aschaffenburg, V. Schoepf, M. McGinley, J. Baumann, and Y. Matsui. 2014. The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Global Change Biology* 20:3823–3833.
- Guest, J. R., et al. 2018a. A framework for identifying and characterising coral reef “oases” against a backdrop of degradation. *Journal of Applied Ecology* 55:2865–2875.
- Guest, J. R., et al. 2018b. Time-series coral-cover data from Hawai'i, Florida, Mo'orea, and the Virgin Islands: U. S. Geological Survey data release. <https://doi.org/10.5066/78w3c7w>
- Han, X., T. C. Adam, R. J. Schmitt, A. J. Brooks, and S. J. Holbrook. 2016. Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia. *Coral Reefs* 35:999–1009.
- Hubbard, D. K., A. I. Miller, and D. Scaturro. 1990. Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U.S. Virgin Islands): applications to the nature of reef systems in the fossil record. *Journal of Sedimentary Petrology* 60:335–360.
- Hughes, T. P., et al. 2018. Global warming transforms coral reef assemblages. *Nature* 556:492–496.
- Jackson, J. B. C., M. K. Donovan, K. L. Cramer, and V. Lam, editors. 2014. Status and trends of Caribbean coral reefs: 1970–2012. *Global Coral Reef Monitoring Network*, IUCN, Gland, Switzerland.
- Januchowski-Hartley, F. A., N. A. J. Graham, S. K. Wilson, S. Jennings, and C. T. Perry. 2017. Drivers and predictions of coral reef carbonate budget trajectories. *Proceedings of the Royal Society B: Biological Sciences* 284:20162533.
- Jokiel, P. L., and E. K. Brown. 2004. Global warming, regional trends, and inshore environmental conditions influence coral bleaching in Hawai'i. *Global Change Biology* 10:1627–1641.
- Kayanne, H., H. Hata, S. Kudo, H. Yamano, A. Watanabe, Y. Ikeda, K. Nozaki, K. Kato, A. Negishi, and H. Saito. 2005. Seasonal and bleaching-induced changes in coral reef metabolism and CO<sub>2</sub> flux. *Global Biogeochemical Cycles* 19:GB3015.
- Kemp, D. W., C. A. Oakley, D. J. Thornhill, L. A. Newcomb, G. W. Schmidt, and W. K. Fitt. 2011. Catastrophic mortality on inshore coral reefs of the Florida Keys due to severe low-temperature stress. *Global Change Biology* 17:3468–3477.
- Kennedy, E. V., A. Ordoñez, B. Lewis, and G. Diaz-Pulido. 2017. Comparison of recruitment tile materials for monitoring coralline algae responses to a changing climate. *Marine Ecology Progress Series* 569:129–144.
- Kleypas, J. A., R. W. Buddemeier, and J.-P. Gattuso. 2001. The future of coral reefs in an age of global change. *International Journal of Earth Sciences* 90:426–437.
- Kuffner, I. B., T. D. Hickey, and J. M. Morrison. 2013. Calcification rates of the massive coral *Siderastrea siderea* and crustose coralline algae along the Florida Keys (USA) outer-reef tract. *Coral Reefs* 32:987–997.
- Kuffner, I. B., and L. T. Toth. 2016. A geological perspective on the degradation and conservation of western Atlantic coral reefs. *Conservation Biology* 30:706–715.
- Kuffner, I. B., L. T. Toth, J. H. Hudson, W. B. Goodwin, A. Stathakopoulos, L. A. Bartlett, and E. M. Witcher. 2019. Improving estimates of coral reef construction and erosion with in situ measurements. *Limnology and Oceanography* 64:2283–2294.
- Lange, I. D., and C. T. Perry. 2019. Bleaching impacts on carbonate production in the Chagos Archipelago: influence of functional coral groups on carbonate budget trajectories. *Coral Reefs* 38:619–624.
- Lirman, D., et al. 2011. Severe 2010 cold-water event caused unprecedented mortality to corals of the Florida Reef Tract and reversed previous survivorship patterns. *PLOS ONE* 6:e23047.
- Loya, Y., K. Sakai, K. Yamazato, Y. Nakano, H. Sambali, and R. van Woesik. 2001. Coral bleaching: the winners and the losers. *Ecology Letters* 4:122–131.
- Manzello, D. P., R. Berkelmans, and J. C. Hendee. 2007. Coral bleaching indices and thresholds for the Florida Reef Tract, Bahamas, and St. Croix, US Virgin Islands. *Marine Pollution Bulletin* 54:1923–1931.

- Manzello, D. P., I. C. Enochs, G. Kolodziej, R. Carlton, and L. Valentino. 2018. Resilience in carbonate production despite three coral bleaching events in 5 years on an inshore patch reef in the Florida Keys. *Marine Biology* 165:99.
- McClanahan, T. R., and J. Maina. 2003. Response of coral assemblages to the interaction between natural temperature variation and rare warm-water events. *Ecosystems* 6:551–563.
- McClanahan, T. R., E. Weil, J. Cortés, A. H. Baird, and M. Ateweberhan. 2009. Consequences of coral bleaching for sessile reef organisms. Pages 121–138 in *Coral bleaching*. Springer, Berlin, Heidelberg, Germany.
- McWilliam, M., M. O. Hoogenboom, A. H. Baird, C.-Y. Kuo, J. S. Madin, and T. P. Hughes. 2018. Biogeographical disparity in the functional diversity and redundancy of corals. *Proceedings of the National Academy of Sciences of the United States of America* 115:3084–3089.
- Miller, J., E. Muller, C. Rogers, R. Waara, A. Atkinson, K. R. T. Whelan, M. Patterson, and B. Witcher. 2009. Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs* 28:925–937.
- Miller, J., R. Waara, E. Muller, and C. Rogers. 2006. Coral bleaching and disease combine to cause extensive mortality on reefs in US Virgin Islands. *Coral Reefs* 25:418.
- Mizerek, T. L., A. H. Baird, and J. S. Madin. 2018. Species traits as indicators of coral bleaching. *Coral Reefs* 37:791–800.
- Moberg, F., and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. *Ecological Economics* 29:215–233.
- Montaggioni, L. F., and C. J. R. Braithwaite. 2009. Quaternary coral reef systems: history, development processes and controlling factors. Elsevier, Amsterdam.
- Morgan, K. M., and P. S. Kench. 2012. Skeletal extension and calcification of reef-building corals in the central Indian Ocean. *Marine Environmental Research* 81:78–82.
- Muehlllehner, 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 Biogeochemical Cycles* 30:661–688.
- Ortiz, J.-C., N. H. Wolff, K. R. N. Anthony, M. Devlin, S. Lewis, and P. J. Mumby. 2018. Impaired recovery of the Great Barrier Reef under cumulative stress. *Science*. *Advances* 4:ear6127.
- Perry, C. T., E. N. Edinger, P. S. Kench, G. N. Murphy, S. G. Smithers, R. S. Steneck, and P. J. Mumby. 2012. Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral Reefs* 31:853–868.
- Perry, C. T., and K. M. Morgan. 2017. Bleaching drives collapse in reef carbonate budgets and reef growth potential on southern Maldives reefs. *Scientific Reports* 7:40581.
- 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. *Nature Communications* 4:1402.
- Perry, C. T., T. Spencer, and P. S. Kench. 2008. Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. *Coral Reefs* 27:853–866.
- Perry, C. T., R. S. Steneck, G. N. Murphy, P. S. Kench, E. N. Edinger, S. G. Smithers, and P. J. Mumby. 2015. Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. *Global Change Biology* 21:1153–1164.
- Perry, C. T., et al. 2018. Loss of coral reef growth capacity to track future increases in sea level. *Nature* 558:396–400.
- Pinheiro, J., D. Bates, D. S. DebRoy, D. Sarkar, and R Core Team. 2017. nlme: linear and nonlinear mixed effects models. R Package version 3.1-131. <https://CRAN.R-project.org/package=nlme>
- Pratchett, M. S., K. D. Anderson, M. O. Hoogenboom, E. Widman, A. H. Baird, J. M. Pandolfi, P. J. Edmunds, and J. M. Lough. 2015. Spatial, temporal and taxonomic variation in coral growth - implications for the structure and function of coral reef ecosystems. *Oceanography and Marine Biology: An Annual Review* 53:215–295.
- Pratchett, M. S., M. Trapon, M. L. Berumen, and K. Chong-Seng. 2011. Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. *Coral Reefs* 30:183–193.
- R Core Team. (2017). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Randall, C. J., and R. van Woesik. 2015. Contemporary white-band disease in Caribbean corals driven by climate change. *Nature Climate Change* 5:375–379.
- Randall, C. J., and R. van Woesik. 2017. Some coral diseases track climate oscillations in the Caribbean. *Scientific Reports* 7:5719.
- Rodgers, K. S., K. D. Bahr, P. L. Jokiel, and A. R. Donà. 2017. Patterns of bleaching and mortality following widespread warming events in 2014 and 2015 at the Hanauma Bay Nature Preserve, Hawai'i. *PeerJ* 5:e3355.

- Ruzicka, R. R., et al. 2013. Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. *Marine Ecology Progress Series* 489:125–141.
- Ryan, E. J., K. Hanmer, and P. S. Kench. 2019. Massive corals maintain a positive carbonate budget of a Maldivian upper reef platform despite major bleaching event. *Scientific Reports* 9:6515.
- Stearn, W., T. P. Scoffin, and W. Martindale. 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados. *Bulletin of Marine Science* 27:479–510.
- Swain, T. D., J. B. Vega-Perkins, W. K. Oestreich, C. Triebold, E. DuBois, J. Henss, A. Baird, M. Siple, V. Backman, and L. Marcelino. 2016. Coral bleaching response index: a new tool to standardize and compare susceptibility to thermal bleaching. *Global Change Biology* 22:2475–2488.
- Toth, L. T., I. B. Kuffner, A. Stathakopoulos, and E. A. Shinn. 2018. A 3,000-year lag between the geological and ecological shutdown of Florida's coral reefs. *Global Change Biology* 24:5471–5483.
- Toth, L. T., A. Stathakopoulos, I. B. Kuffner, R. R. Ruzicka, M. A. Colella, and E. A. Shinn. 2019. The unprecedented loss of Florida's reef-building corals and the emergence of a novel coral-reef assemblage. *Ecology* 100:e02781.
- Toth, L. T., R. Van Woesik, T. J. T. Murdoch, S. R. Smith, J. C. Ogden, W. F. Precht, and R. B. Aronson. 2014. Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary. *Coral Reefs* 333:565–577.
- van Hooidek, R., J. Maynard, J. Tamelander, J. Gove, G. Ahmadi, L. Raymundo, G. Williams, S. F. Heron, and S. Planes. 2016. Local-scale projections of coral reef futures and implications of the Paris Agreement. *Scientific Reports* 6:39666.
- van Woesik, R., and C. W. Cacciapaglia. 2018. Keeping up with sea-level rise: carbonate production rates in Palau and Yap. *Western Pacific Ocean. PLOS ONE* 13:e0197077.
- van Woesik, R., S. Köksal, A. Ünal, C. W. Cacciapaglia, and C. J. Randall. 2018. Predicting coral dynamics through climate change. *Scientific Reports* 8:17997.
- van Woesik, R., K. Sakai, A. Ganase, and Y. Loya. 2011. Revisiting the winners and the losers a decade after coral bleaching. *Marine Ecology Progress Series* 434:67–76.
- Wagner, D. E., P. Kramer, and R. van Woesik. 2010. Species composition, habitat, and water quality influence coral bleaching in southern Florida. *Marine Ecology Progress Series* 408:65–78.
- Yates, K. K., D. G. Zawada, N. A. Smiley, and G. Tilling-Range. 2017. Divergence of seafloor elevation and sea level rise in coral reef regions. *Biogeosciences* 14:1739–1772.