Rapid assessments of Pacific Ocean net coral reef carbonate budgets and net calcification following the 2014-2017 global coral bleaching event

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Key words: coral reefs, net carbonate budgets, net ecosystem calcification, coral bleaching, biogeochemistry, ecosystem assessment, ecological monitoring

Running head: Net reef calcification and carbonate production

Abstract

The 2014–2017 global coral bleaching event caused widespread coral mortality; however, its impact on the capacity for coral reefs to maintain calcium carbonate structures remained to be determined. Here, we quantified remotely sensed maximum heat stress during the 2014-2017 bleaching event, census-based net carbonate budgets from benthic imagery and fish survey data, and net calcification from salinity normalized seawater total alkalinity anomalies collected from 2017-2019 for 56 Pacific coral reef sites (Mariana Islands, Northwestern Hawaiian Islands, Pacific Remote Island Areas, and American Samoa). We incorporated the census-based and chemistry-based metrics to determine a calcification vulnerability index for each site to maintain calcium carbonate balance to provide accessible information to managers and policy makers. Most coral reef sites likely experienced ecologically severe (79%,n=44) or significant (9%,n=7) heat stress during the 2014-2017 coral bleaching event. Census-based net carbonate budgets (mean±95%=2.1±0.6 kg $CaCO_3$ m^{-2} yr^{-1}) were positive for 77% of sites (n=43), neutral for 16% of sites (n=9), and negative for 7% of sites (n=4). Chemistry-based net calcification (mean±95%=22±10 µmol kg^{-1}) was positive for 84% of sites (n=47), neutral for 11% of sites (n=6), and negative for 5% of sites (n=3). The calcification vulnerability index suggested the Pacific Ocean reef sites surveyed were of minimal (68%,n=38) to moderate (32%,n=18) concern for maintaining calcium carbonate balance following the bleaching event. This suggests that many reefs maintained positive calcium carbonate balance, but that a large number of reefs may be approaching a potential threshold for maintaining their calcium carbonate balance under the climate crisis.

Introduction

Scleractinian corals are the primary reef-builders of the coral reef structures that sustain ecosystem services ranging from shoreline protection, fisheries provisioning, cultural significance, and tourism revenue for billions of people worldwide (Kleypas et al. 2001; Perry and Alvarez-Filip 2019; Woodhead et al. 2019). However, global coral cover has declined precipitously in recent decades under local and global environmental change (Gardner et al. 2003; Bruno and Selig 2007; De'ath et al. 2012) with the third global coral bleaching event from 2014-2017 further jeopardizing coral dominated reef states and associated maintenance of coral reef structures (Eakin et al. 2019). Quantifying these changes in coral reef structures and their associated geo-ecological functions represents a challenging task, but is essential to be able to predict future changes to the ecosystem services coral reefs provide to the people that depend on them (Perry and Alvarez-Filip 2019).

Quantifying changes in coral reef geo-ecological functions can be accomplished through measuring the net accumulation of calcium carbonate ($CaCO_3$), but direct measurements of changes in coral reef bathymetry or accretion rates from sediment cores typically require multiple years to detect changes (Aronson and Precht 2001; Yates et al. 2017; Lange et al. 2020a). Census-based net carbonate budgets and chemistry-based net coral reef calcification have been widely used to provide insights into the maintenance of coral reef structures under environmental change (e.g., see discussion in (Courtney and Andersson 2019; Lange et al. 2020a; Browne et al. 2021) and references therein). Census-based methods sum annual $CaCO_3$ production and erosion rates of different functional groups to estimate net carbonate budgets from ecological surveys, but are limited by survey biases (i.e., what the observer can see) and typically rely on literature derived annualized rates (Chave et al. 1972; Perry et al. 2018b; Lange et al. 2020a). Chemistry-based methods utilize changes in seawater total alkalinity (TA) to provide temporal snapshots of net coral reef calcification (i.e., TA changes by a factor of two for every mole of $CaCO_3$ precipitated or dissolved (Broecker and Takahashi 1966; Smith and Key 1975; Chisholm and Gattuso 1991)), but difficulties in constraining seawater hydrodynamics can generate significant uncertainties (Venti et al. 2012; Lowe and Falter 2015; Courtney and Andersson 2019). As a result, census-based net carbonate budgets (i.e., carbonate production – bioerosion) and chemistry-based net calcification (i.e., calcification – $CaCO_3$ dissolution) are inherently quantifying slightly different processes to provide independent snapshots of the capacity for coral reefs to produce and maintain $CaCO_3$ structures. These methods quantify processes on different spatial scales with census-based budgets typically quantifying net carbonate production at the spatial scale of transects (i.e., tens of meters squared) and ecosystem-scale chemistry-based metrics typically integrating net calcification of the hydrochemical footprint modified by the benthos (i.e., hundreds to thousands of meters squared) (Courtney et al. 2016) (but see also tens of meters squared footprints for chemistry-based eddy covariance methods (Berg et al. 2007)). Furthermore, depending on the frequency of observations, the two methods reflect the net sum of processes on different timescales, i.e., census-based observations typically reflect processes on annual timescales whereas individual chemistry-based observations reflect the sum of processes occurring over hours to days depending on reef seawater residence time (Figure 1). Both methods are generally time intensive, require a great deal of careful consideration, and are typically associated with a range of uncertainties (Courtney et al. 2016; Courtney and Andersson 2019; Lange et al. 2020a). These characteristics effectively limit each method's power and capacity to quantify global-scale changes in coral reef geo-ecological functions to ongoing ocean warming, acidification, and deoxygenation over a broad spectrum of spatial and temporal scales.

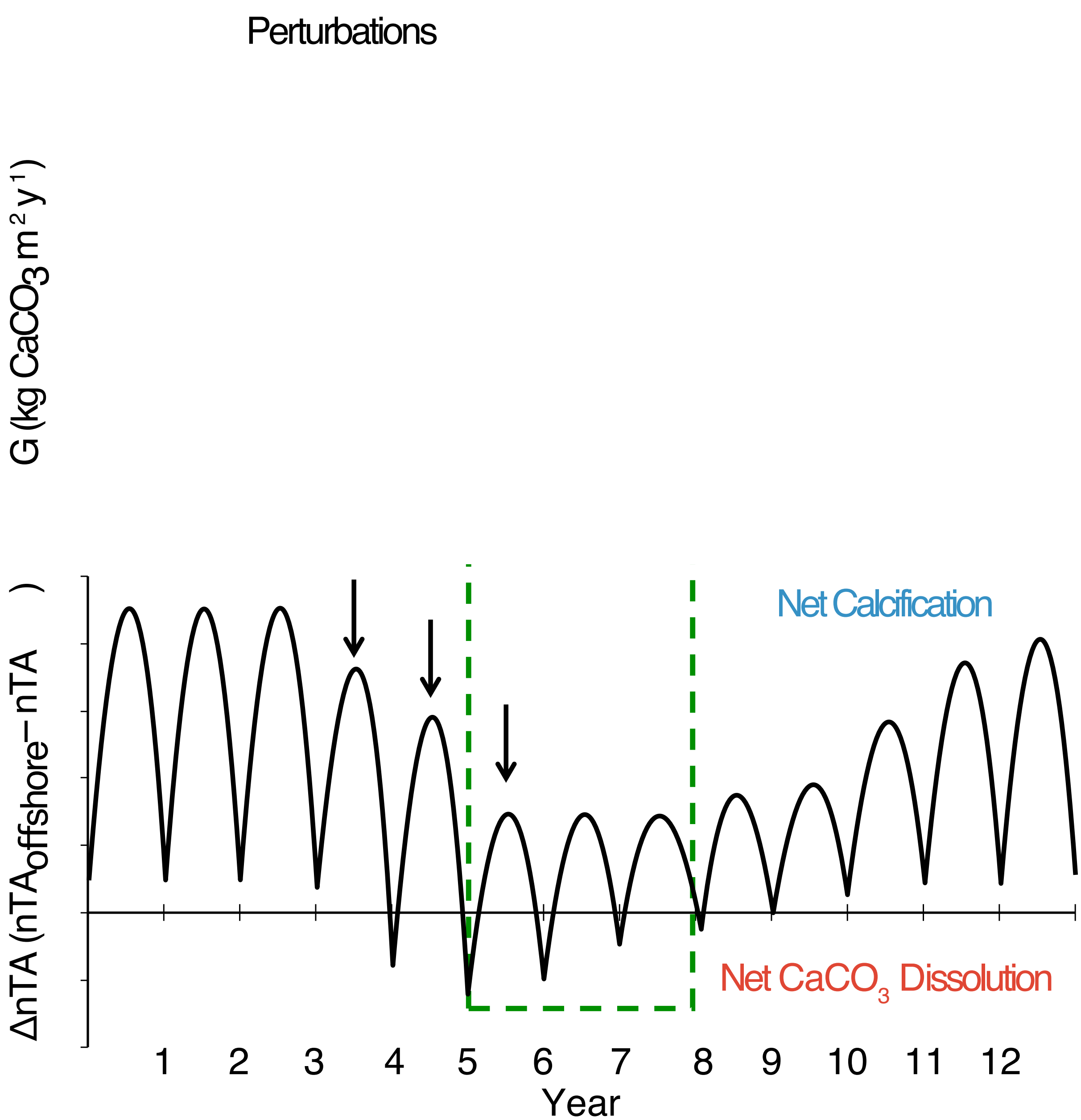

Figure 1. Conceptual figure showing hypothesized trends in census-based carbonate budget (G; top panel) and chemistry-based net community calcification based on salinity normalized alkalinity anomalies (ΔnTA; bottom panel) for a coral reef exposed to multiannual perturbations (black arrows) over a 12-year period. The census-based and chemistry-based data are based on annual and monthly observations, respectively. Note that individual measurements over a limited observation period represent the net sum of processes occurring annually (census-based) to over hours or days (chemistry-based), and thus, may not track each other and could even appear contradicting without a complete temporal perspective. Regardless, these observations serve as important metrics in

the context of future global environmental change and observations, and especially if the measurements encompass multiple reefs over a large spatial area. The hypothesized trends in the figure were adopted from observations presented in (Yeakel et al. 2015; Courtney et al. 2018, 2020).

To address this limitation, we combined simplified assessments of census-based carbonate budgets from benthic imagery and fish survey data and chemistry-based net calcification from the difference between coral reef seawater TA and offshore seawater TA. While each of these simplified metrics is associated with uncertainty, leveraging two independent approaches increases confidence in assessing the maintenance of coral reef $CaCO_3$ structures, and also offers insight to chronic vs. acute concerns of the $CaCO_3$ balance across varying spatial scales (Courtney et al. 2016; Courtney and Andersson 2019; Lange et al. 2020a). We therefore applied these methods to pre-existing monitoring data from 56 coral reef sites across the Mariana Islands, Northwestern Hawaiian Islands, Pacific Remote Island Areas, and American Samoa to assess the following questions: (1) What is the capacity for coral reefs to maintain their $CaCO_3$ structures following the 2014-2017 coral bleaching event based on the census-based and chemistry-based approaches? (2) Does maximum heat stress experienced during the 2014-2017 coral bleaching event or the commonly used metric of coral cover predict our simplified carbonate budget and net calcification estimates? In addition to addressing these questions, this synthesis provides critical baseline data and simplified, categorical assessments of coral reef capacity to maintain $CaCO_3$ structures for managers and policymakers as part of ongoing monitoring and conservation efforts.

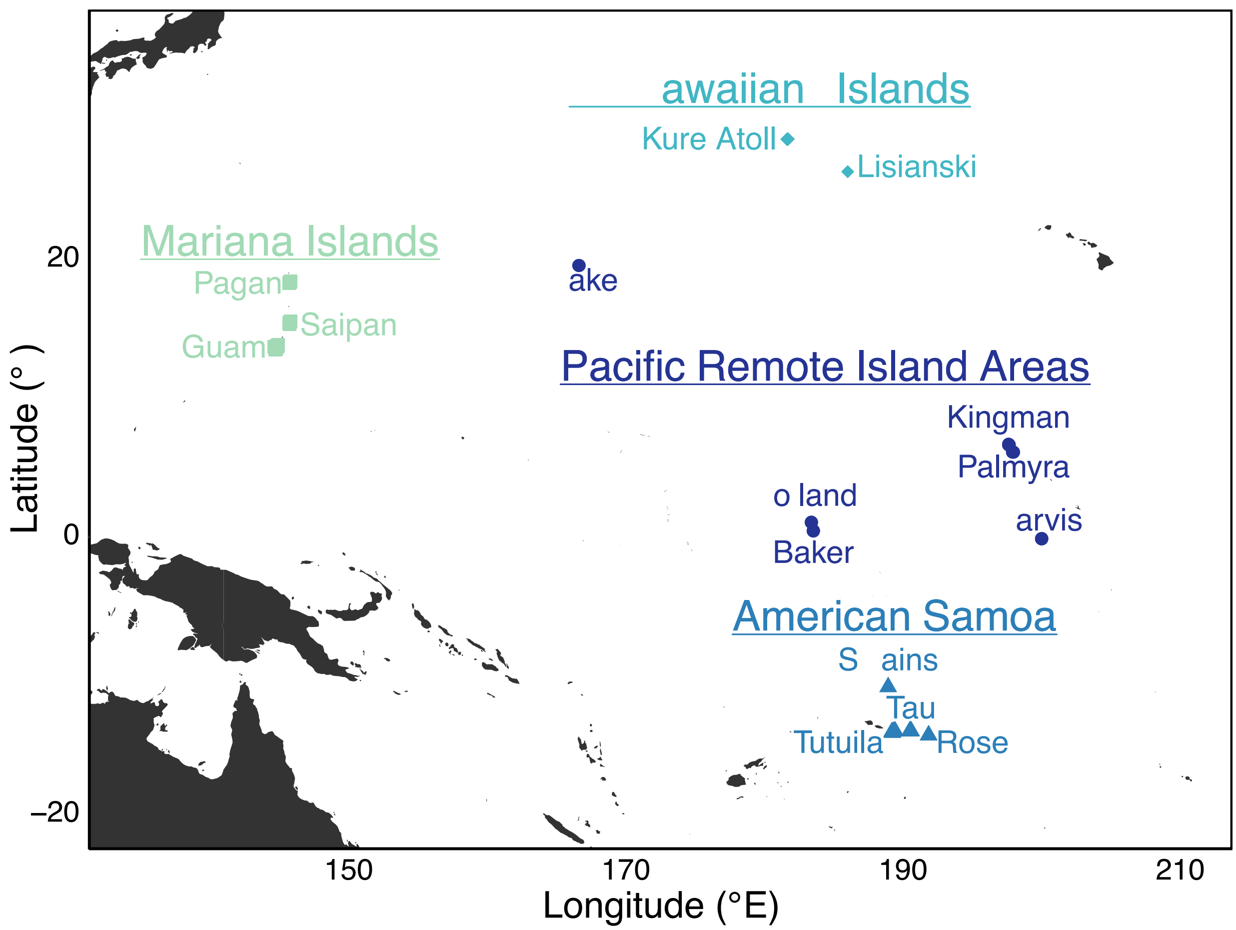

Figure 2. Map of coral reef sites across the Mariana Islands, Northwestern Hawaiian Islands, Pacific Remote Island Areas, and American Samoa that were surveyed as part of the NOAA National Coral Reef Monitoring Program.

Methods

Survey locations

We leveraged coral reef benthic community composition, fish community composition, and carbonate chemistry data collected from designated coral reef climate monitoring sites (n=56) across the Pacific Ocean between 2017 and 2019 as part of the National Oceanic and Atmospheric Administration's (NOAA) Pacific National Coral Reef Monitoring Program. Surveyed reef locations included forereef sites at ~15 m depth in the Mariana Islands (16 sites around Guam, Pagan, and Saipan in 2017), Northwestern Hawaiian Islands (6 sites around Kure and Lisianski in 2019), Pacific Remote Island Areas (2 sites around Wake in 2017 and 18 sites around Baker, Howland, Jarvis, Kingman, and Palmyra in 2018), and American Samoa (14 sites around Rose, Swains, Tau, and Tutuila in 2018) (Figure 2).

Census-based net carbonate budgets

We used a simplified version of the census-based *ReefBudget* methodology (Perry et al. 2018b) to retroactively estimate carbonate production from benthic imagery data. At each site, images were taken with a Canon G9x one meter off the substrate, every meter along each side of a 15 m "L" shaped transect for a total of 30 images per site (see (Pacific Islands Fisheries Science Center 2021) for further details on data collection). Ten random points in each image were then annotated using the *CoralNet* image annotation software for a total of 300 annotations per site (Beijbom et al. 2015). Corals were identified to genus or a combination of genus and growth form for select genera (*Acropora, Montipora, Pavona* and *Porites*), macroalgae to genus, and other benthic features to functional group or higher-level taxonomic grouping (e.g., 'crustose coralline algae', 'sand', 'sponge', 'turf algae') using the NOAA CRED label set (n=95 labels) in *CoralNet* (Lozada-Misa et al. 2017). Points were pooled across the transect tape to determine the percent composition of each benthic feature at each site (Pacific Islands Fisheries Science Center 2021). The percent cover of each label was then multiplied by the area normalized Indo-Pacific calcification rates with endolithic bioerosion for each benthic feature by (Courtney et al. 2021a) and summed to calculate gross carbonate production and endolithic bioerosion for each site (Perry et al. 2018b). These rates adapt the *ReefBudget* Indo-Pacific Carbonate Production v1.2 datasheet (Perry et al. 2018b) for use with *CoralNet* imagery by accounting for median colony size, rugosity, colony morphology, linear extension, and skeletal density for all of the "NOAA

CRED" *CoralNet* identification labels *ReefBudget* methodologies (see (Courtney et al. 2021a) for further details). While the uncertainty ranges in the rates from (Courtney et al. 2021a) used in this study account for some degree of variability in rates across the Pacific Ocean, the use of constant rates (±uncertainties) between sites does not account for any potential systematic differences in rates between sites, which is a common limitation of census-based carbonate budgets.

In the absence of co-located benthic survey and fisheries data, we used coral reef fish survey data collected from stratified random sites around each of the islands (Pacific Islands Fisheries Science Center 2017a; b; c, 2019a; b) to quantify gross parrotfish bioerosion (Perry et al. 2018b). In each survey, two divers quantify the fish communities in paired 15 m diameter cylinders using the stationary point count (SPC) method, identifying, counting, and estimating the total length of fishes (see (Ayotte et al. 2011) for further details on data collection). We used the data collected at mid-depth sites (>6-19 m) around islands in survey years that correspond with the climate monitoring sites. However, matching fish community data was missing for the 2019 Northwestern Hawaiian Islands surveys so we used fish community data from 2017 and therefore must make the assumption that parrotfish bioerosion rates determined from the 2017 data were similar to 2019 when the other benthic community composition and carbonate chemistry data were collected.

Parrotfish bioerosion was estimated from the survey data as per the following allometric relationship between body size and bioerosion rate from (Lange et al. 2020b): Bioerosion (kg $CaCO_3$ ind^{-1} y^{-1}) = $a \times TL^b$. Constants *a* and *b* were empirically derived from linear regressions between the log of the mid-point of total length (TL) in cm for each size bin and the log of the corresponding bioerosion rate (kg $CaCO_3$ ind^{-1} y^{-1}) for initial and terminal phase fish for each species from the *ReefBudget* Indo-Pacific Parrotfish erosion rates v1.3 data sheet (Perry et al. 2018b). We used the fixed bioerosion rate for *Bolbometopon muricatum* following (Perry et al. 2018b) and substituted mean genus-level bioerosion rates for taxon lacking species-level data. While previous studies have documented differences between initial and terminal phase bioerosion rates (Lange et al. 2020a), this information was lacking in the fish surveys so *a* and *b* were therefore estimated for all parrotfish regardless of phase in this study. The resulting species-specific bioerosion rates for each size bin and the resulting *a* and *b* constants used to quantify parrotfish bioerosion rates from observed total length in this study are summarized in Table S1. Individual parrotfish bioerosion per m^2 (survey area = πr^2, where r = 7.5 m radius of a cylinder) was summed in each replicate and then averaged between paired cylinders at each survey site. Estimates were averaged across sites within a given stratum (island, reef zone, and depth bin [all mid-depth]) and then pooled up to the scale of individual islands by weighting strata by their proportional area within each island in accordance with the stratified survey design (Heenan et al. 2017) to quantify mean (±SE) parrotfish bioerosion rates for each island.

Sea urchins were not directly quantified in the survey data, but the reef-fish surveys qualitatively assessed relative abundance of sea urchins at each site and listed them as rare in 74.8% to 99.8% across the respective regions in this study (Pacific Islands Fisheries Science Center 2017a; b; c, 2019a; b). Given the lack of robust sea urchin test size and density data necessary to estimate sea urchin bioerosion following established methods (Perry et al. 2018b) and their rare abundance at the majority of sites, we have omitted sea urchin bioerosion from this study and therefore implicitly assume that they are not major sources of bioerosion across our study sites.

Net carbonate budgets (kg $CaCO_3$ m^{-2} y^{-1}) were thus calculated as carbonate production minus endolithic bioerosion and parrotfish bioerosion × 50% reincorporation rate for each site following (Perry et al. 2018a). While mechanical bioerosion by parrotfish is represented as a net loss of $CaCO_3$ following *ReefBudget* methods (Perry et al. 2018b), there is limited data quantifying the proportion of mechanically bioeroded $CaCO_3$ that is ultimately exported from the reef environment (Browne et al. 2021). Here we have assumed that 50% of mechanical parrotfish bioerosion was reincorporated back into the reef matrix with the remaining 50% exported from the reef following (Hubbard et al. 1990; Perry et al. 2018a). We conservatively calculated the lower bound of the net carbonate budgets as the lower bound of carbonate production minus the upper bound of bioerosion (i.e., parrotfish bioerosion × 50% reincorporation) and, conversely, the upper bound of the net carbonate budgets as the upper bound of carbonate production minus the lower bound of bioerosion (i.e., parrotfish bioerosion × 50% reincorporation). We therefore determined net carbonate budgets as a categorical variable that was positive if the net carbonate budgets (±uncertainties) were greater than zero (i.e., net $CaCO_3$ production), neutral if the net carbonate budgets (±uncertainties) overlapped zero, and negative if the net carbonate budgets (±uncertainties) were less than zero (i.e., net $CaCO_3$ loss).

Chemistry-based net calcification

Differences in coral reef and offshore seawater total alkalinity were used to assess chemistry-based net calcification for each reef site (Langdon et al. 2010; Cyronak et al. 2018). Seawater carbonate chemistry samples were collected via a 5 L Niskin bottle at 0-20 m depth, stored in 500 mL borosilicate glass bottles with a 200 μL saturated mercuric chloride solution, and analyzed for TA (±0.1% uncertainty) following best practices on an open cell potentiometric acid titration system developed by the laboratory of Professor A. Dickson (see (Barkley et al.

2021) for further details on data collection). Salinity (±0.0005 S m^{-1} uncertainty) was measured in situ via a Seabird Electronics 19+ CTD (2017–2018) or RBR Concerto[3] (2019) at the time of sampling (Barkley et al. 2021). Salinity normalized total alkalinity anomalies (ΔnTA) for each coral reef location were calculated from NOAA Pacific NCRMP offshore and coral reef total alkalinity (TA) data: $\Delta nTA = nTA_{offshore} - nTA_{reef}$ (Langdon et al. 2010; Cyronak et al. 2018) so that positive values reflected net calcification and negative values net $CaCO_3$ dissolution. TA was normalized according to the protocols outlined in (Courtney et al. 2021b). To assess the uncertainties introduced by the salinity normalization calculation and the potential influence of zero salinity end members with a TA > 0, multiple calculations were conducted for a range of potential freshwater TA end members ($TA_{S=0}$=15–1298 µmol kg^{-1}) and for salinity normalization with respect to both the mean offshore or mean reef salinity (Courtney et al. 2021b). The mean, maximum, and minimum of all $\Delta nTA_{offshore}$ and ΔnTA_{reef} values for each cruise and location were then used to determine ΔnTA and the associated uncertainties (ΔnTA±uncertainties).

While the magnitude of ΔnTA can be used to calculate net coral reef calcification rates if seawater depth and residence time are known, these factors were not quantified as part of the monitoring efforts in this study so the magnitude of ΔnTA for each reef only reflects the total change in alkalinity, but not the rate of change. The sign of ΔnTA nonetheless elucidates whether the reef system was net calcifying (i.e., positive ΔnTA) or net $CaCO_3$ dissolving (i.e., negative ΔnTA) at the time of measurement. We therefore determined chemistry-based net calcification from the ΔnTA for each reef as a categorical variable that was positive if the ΔnTA (±uncertainties) was greater than zero (i.e., net calcifying), neutral if the ΔnTA (±uncertainties) overlapped zero, and negative if the ΔnTA (±uncertainties) was less than zero (i.e., net $CaCO_3$ dissolving).

Degree Heating Weeks

Owing to the proximity of the 2014-2017 global coral bleaching event (Eakin et al. 2019) to the 2017-2019 survey dates in this study, we extracted the maximum accumulated degree heating weeks (DHW) at each reef site for each year between 2014 and 2017 to quantify the number of reef sites experiencing ecologically significant (DHW≥4) or ecologically severe (DHW≥8) heat stress (Eakin et al. 2010; Heron et al. 2016; Skirving et al. 2019, 2020) from the NOAA Coral Reef Watch DHW v3.1 dataset (NOAA Coral Reef Watch 2018).

Correlations between coral reef metrics

Linear mixed effects models were used to quantify the relationships between net carbonate budgets, salinity normalized total alkalinity anomalies, percent coral cover, and maximum degree heating weeks experienced during the 2014–2017 global coral bleaching event. Random effects were incorporated to allow the estimated slopes and intercepts for each response variable to vary by island. All models were constructed and evaluated using the *R* package *nlme* (Pinheiro et al. 2019).

Calcification Vulnerability Index

In response to the need for simple, but comprehensive and meaningful metrics of coral reef function and status under global environmental change that offer insight for researchers, managers, and policymakers (NOAA Ocean Acidification Program 2018), we combined the census-based and chemistry-based assessments in a term referred to as the calcification vulnerability index. This index was determined as a categorical variable from the census-based net carbonate budgets and chemistry-based net calcification assessments for each reef. Calcification vulnerability index was therefore positive for reefs with positive net carbonate budgets and net calcification assessments, negative for reefs with negative net carbonate budgets and net calcification assessments, and neutral for any other combination of positive, neutral, or negative net carbonate budgets and net calcification assessments. While there is nonetheless uncertainty in quantifying the maintenance of coral reef $CaCO_3$ structures from snapshot data, we interpret positive calcification vulnerability index as reefs that are of minimal concern for maintaining their $CaCO_3$ balance, neutral calcification vulnerability index as reefs that are of moderate concern for maintaining this balance, and negative calcification vulnerability index as reefs that are of imminent concern for maintaining their $CaCO_3$ balance. We then used Kruskal-Wallis tests to evaluate how well the categorical census-based net carbonate budgets (i.e., positive, neutral, or negative), categorical chemistry-based net calcification assessments (i.e., positive, neutral, or negative), and calcification vulnerability index corresponded to the maximum heat stress experienced during the 2014–2017 global coral bleaching event and the commonly used reef condition metric of percent coral cover (Gardner et al. 2003; Bruno and Selig 2007; De'ath et al. 2012). Pairwise comparisons of maximum heat stress and coral cover between positive, neutral, and negative classifications for each metric were then conducted using post hoc Dunn's Tests with Bonferroni corrections using the statistical package *FSA* (Ogle et al. 2021).

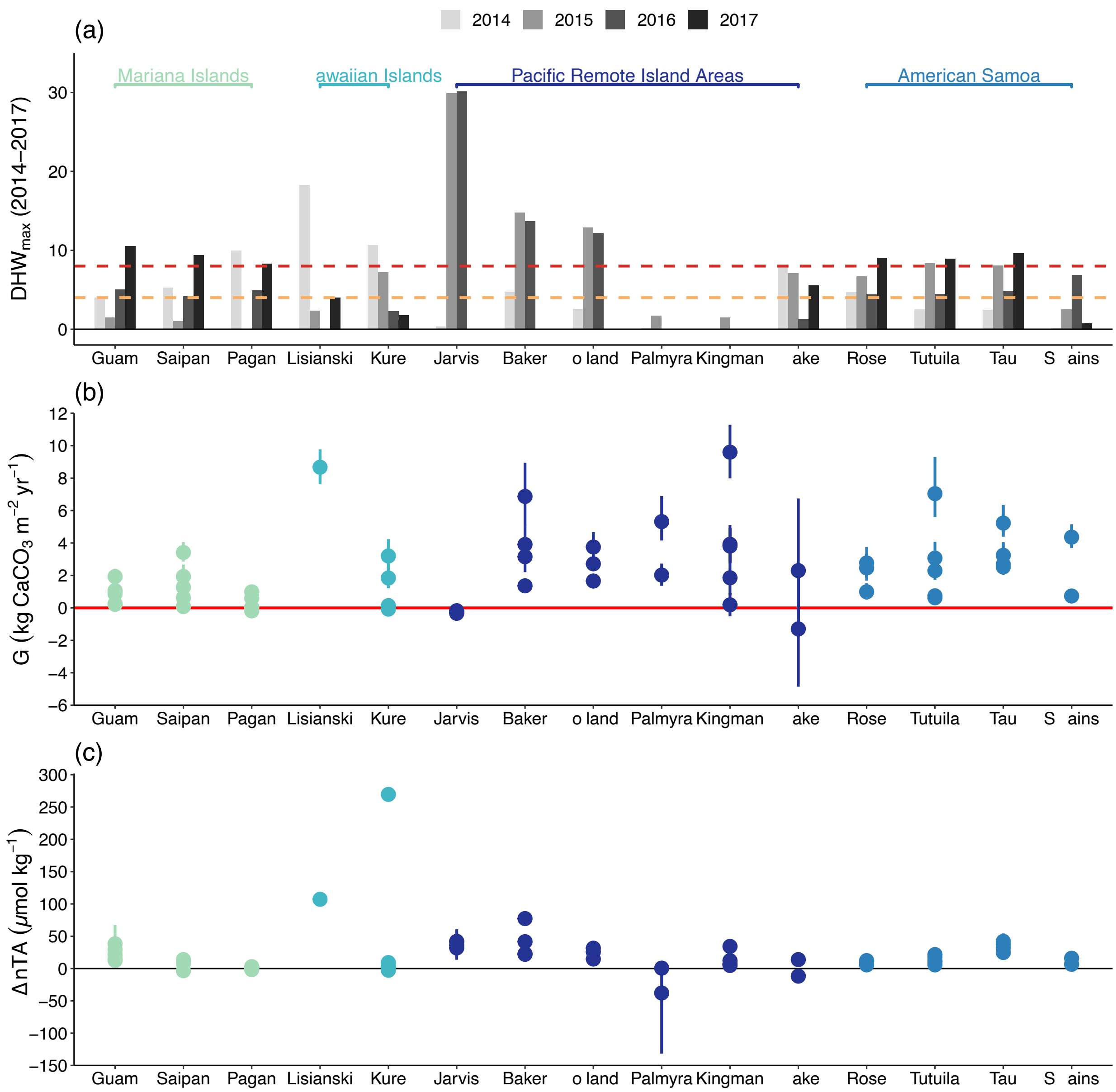

Figure 3. (a) Maximum Degree Heating Weeks (DHW) experienced at each island in each year of the 2014–2017 global coral bleaching event. Dashed orange line indicates ecologically significant coral heat stress (4 DHW) and dashed red line indicates ecologically severe coral heat stress (8 DHW). (b) Net carbonate budget (G) ± uncertainties are reported for each site around each island. (c) Salinity normalized total alkalinity anomaly (ΔnTA) ± uncertainties are reported for each site around each island. All sites are denoted by the name of the respective island or atoll.

Results

Accumulated Bleaching-relevant Heat Stress 2014-2017

The majority of coral reef sites likely experienced ecologically severe (i.e., DHW ≥ 8) heat stress (i.e., 79% of reef sites; n=44; DHW ≥ 8) at some point during the 2014–2017 coral bleaching event with multiple years of bleaching-level stress recorded in the remotely sensed data (Figure 3a). While we refer to the accumulated heat stress from 2014–2017 as the global coral bleaching event following (Eakin et al. 2019), we acknowledge that many reefs in this study experienced multiple years with projected bleaching level heat stress suggesting this was a series of bleaching events for many locations (Figure 3a). Additional reef sites around the islands of Wake, Swains, and Tutuila likely experienced ecologically significant (i.e., DHW ≥ 4) heat stress (i.e., 9% of reef sites; n=5; $4 \leq$ DHW ≤ 8; Figure 3a). The islands of Kingman and Palmyra in the Pacific Remote Island Areas harbored the only sites (i.e., 13% of reef sites; n=7) that likely did not experience ecologically significant heat stress (i.e., DHW < 4) during the 2014–2017 coral bleaching event (Figure 3a).

Figure 4. The number of reef sites classified as having either positive, neutral, or negative (a) census-based net carbonate budget, (b) chemistry-based net calcification, and (c) calcification vulnerability index are reported for each island within the Mariana Islands, Northwestern Hawaiian Islands, Pacific Remote Island Areas, and American Samoa. All sites are denoted by the name of the respective island or atoll.

Coral Reef Calcification Metrics

The mean (±95%) of site-level census-based net carbonate budgets was 2.1±0.6 kg $CaCO_3$ m^{-2} yr^{-1} (range = -1.3 to 9.6 kg $CaCO_3$ m^{-2} yr^{-1}) (Figure 3b) with 43 reef sites exhibiting net positive carbonate budgets, 9 sites exhibiting neutral net carbonate budgets, and 4 sites exhibiting net negative carbonate budgets (Figure 4a). The mean (±95%) of site-level chemistry-based salinity normalized alkalinity anomalies was 22±10 µmol kg^{-1} (range = -38 to 270 µmol kg^{-1}) (Figure 3c) with 47 sites exhibiting positive net calcification, 6 sites exhibiting neutral net calcification, and 3 sites exhibiting negative net calcification (Figure 4b). Calcification vulnerability index was positive for 38 reef sites, neutral for 18 reef sites, and negative for 0 reef sites (Figure 4c).

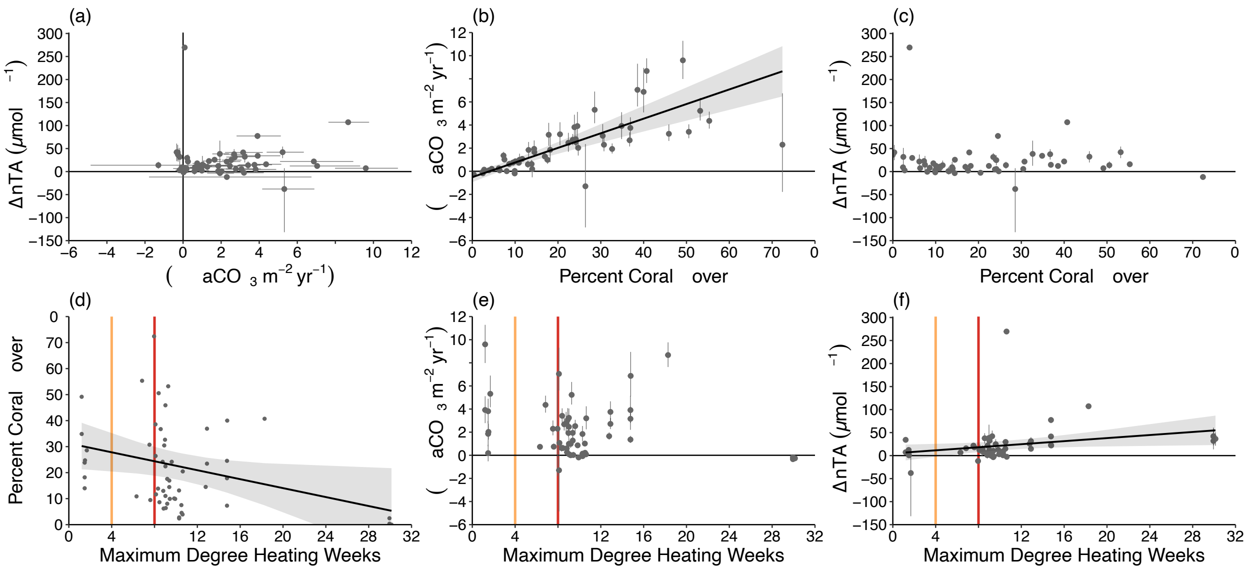

Figure 5. Site-level correlations between census-based net carbonate budgets (G), chemistry-based salinity normalized total alkalinity anomalies (ΔnTA), percent coral cover, and maximum degree heating weeks. (a) ΔnTA is evaluated as a function of G, (b) G is evaluated as a function of percent coral cover, and (c) ΔnTA is evaluated as a function of percent coral cover. (d, e, f) Maximum degree heating weeks refers to the maximum accumulated degree heating weeks experienced during the 2014-2017 global coral bleaching event. (d) Percent coral cover, (e) G, and (f) ΔnTA were each evaluated as a function of maximum degree heating weeks. Linear regressions (±95%) are plotted for linear mixed effects models for all slopes with $p<0.05$. The vertical orange line indicates ecologically significant coral heat stress (4 DHW) and vertical red line indicates ecologically severe coral heat stress (8 DHW).

Correlations Between Coral Reef Metrics

There were no detectable correlations between site-level ΔnTA and G ($p=0.929$), ΔnTA and percent coral cover ($p=0.551$), and G and maximum DHW ($p=0.430$) (Figure 5). In contrast, positive correlations were observed between G and percent coral cover (slope = 0.13 G per % coral cover; $p<0.001$) and ΔnTA and maximum DHW (slope = 1.66 µmol/kg per DHW; $p=0.044$) (Table S2). A negative correlation was observed between coral cover and maximum DHW (slope = -0.86 % coral cover per DHW; $p=0.042$). The threshold for maintaining positive net carbonate budgets was 8.6±6.0% from the linear mixed effects models (Figure 4b, Table S2).

Degree Heating Weeks and Coral Cover as Predictors of Coral Reef Calcification Metrics

There were detectable differences in maximum DHW experienced during the 2014–2017 coral bleaching event between positive, neutral, and negative net carbonate budgets (Kruskal-Wallis Test, $p<0.004$) with higher maximum DHW for negative net carbonate budgets than positive (Dunn's Test, $p=0.003$, Figure 6a) and neutral (Dunn's Test, $p=0.014$, Figure 6a) net carbonate budgets. Conversely, there were no detectable differences in maximum DHW experienced during the 2014–2017 coral bleaching event between classifications of chemistry-based net calcification estimates (Kruskal-Wallis Test, $p=0.780$, Figure 6b) or calcification vulnerability index (Kruskal-Wallis Test, $p=0.243$, Figure 6c).

There were detectable differences in coral cover between positive, neutral, and negative net carbonate budgets (Kruskal-Wallis Test, $p<0.001$) with lower coral cover for reefs with negative net carbonate budgets compared to positive net carbonate budgets (Dunn's Test, $p=0.001$), with no detectable differences in coral cover between reefs with negative net carbonate budgets compared to neutral net carbonate budgets (Dunn's Test, $p=0.193$) or neutral net carbonate budgets compared to positive net carbonate budgets (Dunn's Test, $p=0.157$) (Figure

6d). Conversely, there were no detectable differences in coral cover between net calcification classifications (Kruskal-Wallis Test, p=0.381) (Figure 6e). Lastly, we observed detectable differences in coral cover between classifications of calcification vulnerability index (Kruskal-Wallis Test, p=0.003) with greater coral cover at positive calcification vulnerability index sites compared to sites with a neutral (Dunn's Test, p=0.003) calcification vulnerability index. There were no sites with a negative calcification vulnerability index (Figure 6f).

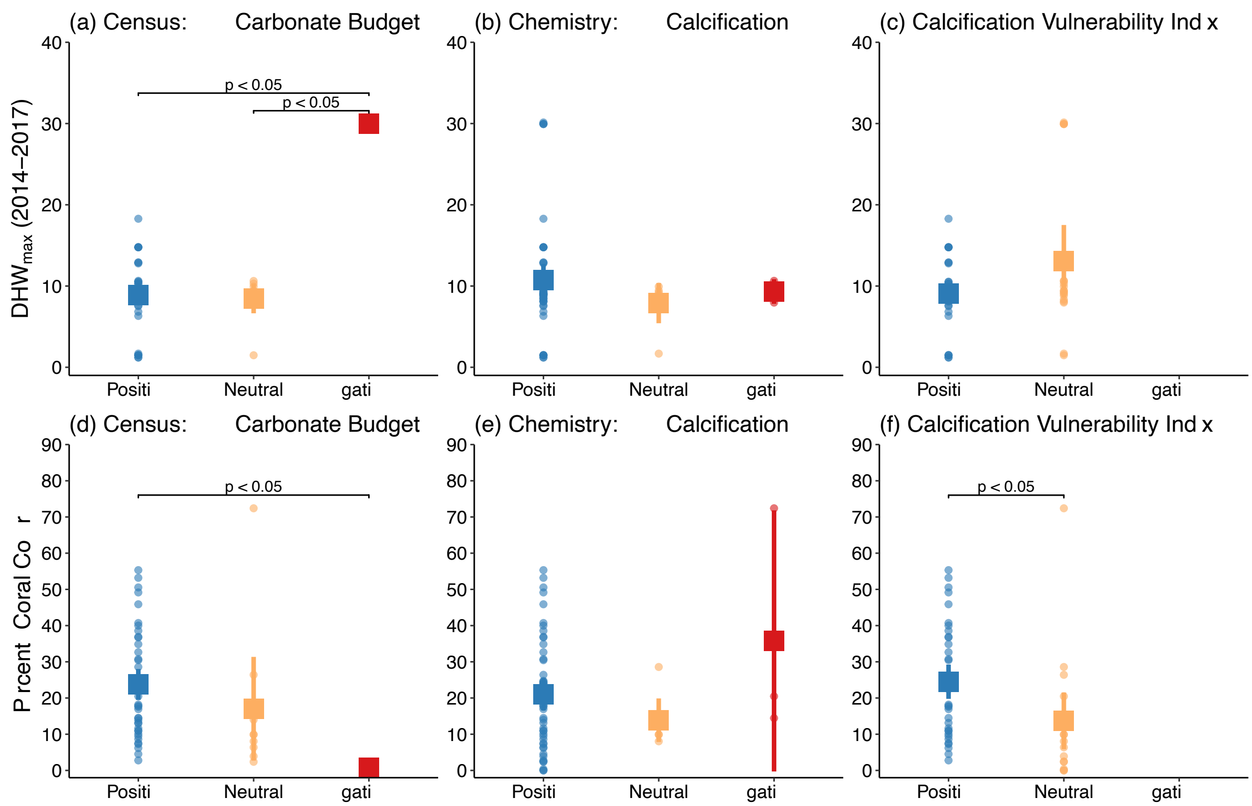

Figure 6. Maximum degree heating weeks (DHW) experienced during the 2014-2017 global coral bleaching event are reported for positive, neutral, and negative classifications of the (a) census-based net carbonate budget, (b) chemistry-based net calcification, and (c) calcification vulnerability index as circles for each coral reef. Percent coral cover is reported for positive, neutral, and negative classifications of the (d) census-based net carbonate budget, (e) chemistry-based net calcification, and (f) calcification vulnerability index as circles for each coral reef. Mean ± 95% maximum DHW and percent coral cover are plotted as squares with line range on top of the site level circles for each category. Horizontal pairwise comparisons above the categorical variables represent statistical significance at

the alpha=0.05 level from post hoc Dunn's Tests with Bonferroni Corrections conducted on Kruskal-Wallis Tests of maximum DHW and percent coral cover, respectively, vs. the coral reef calcification metric in each panel.

Site-level coral reef summary data

In addition to the primary analyses presented here, site-level benthic community composition, seawater carbonate chemistry data, census-based net carbonate budgets, chemistry-based net calcification estimates (i.e., salinity normalized total alkalinity anomalies), calcification vulnerability index, and maximum DHW experienced for each of the 56 coral reefs in this study are available in the supplementary material (Table S3).

Discussion

While the majority of the Pacific Ocean reef sites investigated here most likely experienced ecologically severe (n=44, 79% of total) or significant (n=5, 9% of total) heat stress, mean (±95%) census-based net carbonate production (G=2.1±0.6 kg $CaCO_3$ m^{-2} yr^{-1}) and chemistry-based net calcification (ΔnTA=22±10 µmol kg^{-1}) were positive in this study (Figure 3). Moreover, 77% (n=43 sites) of coral reef locations exhibited positive net carbonate budgets while positive net calcification states were observed for 84% (n=47 reefs) of coral reef locations (Figure 4). The combined census-based and chemistry-based calcification vulnerability index suggests that all reef sites were therefore classified as minimal (68%, n=38 sites) to moderate (32%, n=18 sites) concern for maintaining their $CaCO_3$ balance (Figure 4) at the time of observation in the years following the global bleaching event. However, some caution is advised in interpreting these results, as we do not know how these properties changed in response to the bleaching event. Regardless, at the time of the observations it can be concluded that more than half of the reefs surveyed showed a positive $CaCO_3$ balance from both a census-based and chemistry based perspective, but that many coral reefs may be approaching a potential tipping point for maintaining calcium carbonate structures and accretion under ongoing and future climate change. The metrics presented here assess concern for maintaining $CaCO_3$ balance based on census and chemistry-based approaches; however, the question remains whether thresholds other than zero may be more relevant to the sustained geo-ecological function of coral reefs? The mean net carbonate budgets in this study were low (mean±95%=2.1±0.6 kg $CaCO_3$ m^{-2} yr^{-1}) supporting the notion that reefs may be unable to keep up with accelerating sea level rise under higher CO_2 emissions scenarios (Perry et al. 2018a), especially when taking into account the additional role of chemical $CaCO_3$ dissolution and physical transport processes that were omitted from the census-based methods (Browne et al. 2021). Additionally, these assessments of concern for maintaining reef's $CaCO_3$ balances are based on the present assessment and do not take into account the future stressors on net carbonate budgets caused by increases in coral bleaching events, coral disease outbreaks, and $CaCO_3$ dissolution rates (Van Hooidonk et al. 2016; Randall and van Woesik 2017; Eyre et al. 2018).

The present observations of calcification metrics were made after the 2014-2017 global coral bleaching event with no direct estimations of coral reef calcification metrics before the heat stress event so the underlying mechanism for any associations between DHW experienced and the calcification metrics in this study remain equivocal. Nonetheless, coral cover was negatively correlated with maximum DHW during the 2014–2017 global coral bleaching event (Figure 5d), which is consistent with observations of widespread coral mortality observed in these regions during this anomalous warm period (Reynolds et al. 2014; Couch et al. 2017; Vargas-Ángel et al. 2019). At the island scale, Jarvis experienced repeated years with DHW>30 (Figure 3a), high coral mortality during the 2014-2017 coral bleaching event (Vargas-Ángel et al. 2019), and was the only island in this study with negative net carbonate budgets (Figure 3b, 4a). While there was no detectable trend between census-based net carbonate budgets and maximum DHW (Figure 5e), reefs with negative net carbonate budgets did experience greater maximum DHW than reefs with positive or neutral net carbonate budgets (Figure 6a). Collectively, this evidence suggests heat stress may have decreased net carbonate budgets owing to bleaching induced coral mortality from elevated heat stress (Figure 3,5). Notably, there was a positive correlation between ΔnTA and maximum DHW (Figure 5f), with Jarvis maintaining positive chemistry-based net calcification despite experiencing extensive coral mortality (Figure 3). While we lack the data to rigorously explain this seemingly paradoxical correlation between ΔnTA and DHW, there was no difference in maximum DHW between positive, neutral, and negative ΔnTA classifications (Figure 6b). Thus, the sign of net calcification states did not correlate with maximum DHW and, instead, only the magnitude of ΔnTA was correlated with maximum DHW. We posit that longer seawater residence times could account for a greater accumulation of DHW during the coral bleaching event owing to local amplification of warming (sensu (DeCarlo et al. 2017)) and greater ΔnTA owing to longer times for calcifiers to modify the overlying seawater (Courtney and Andersson 2019); however, this remains speculative as we lack the information to rigorously investigate this finding with the currently available data.

There was no detectable relationship between census-based net carbonate budgets and chemistry-based salinity normalized total alkalinity anomalies (Figure 5a), which resulted in a slight mismatch between the sign of net carbonate budgets and net calcification within each focal region (Figure 4). This is not entirely unexpected since census-based net carbonate budgets (i.e., carbonate production – bioerosion) and chemistry-based net calcification (i.e., calcification – $CaCO_3$ dissolution) quantify different processes integrating over different spatial and temporal scales (Figure 1). For example, physical aspects of bioerosion may not necessarily lead to chemical $CaCO_3$ dissolution that would be detected by chemical measurements, and, conversely, sources of $CaCO_3$ dissolution are not directly accounted for in the census-based carbonate budgets. In particular, the omittance of chemical $CaCO_3$ dissolution in microenvironments within the reef framework and sediments is a common limitation of census-based carbonate production estimates and can be a significant driver capable of shifting reefs with otherwise calcifying communities to net $CaCO_3$ dissolution (Tribble et al. 1990; Andersson et al. 2009; Cyronak et al. 2013). Additionally, mismatches in temporal scales between the annualized estimates of carbonate production estimates and nearly instantaneous measurements of net calcification by chemistry-based methods could further decouple estimates of net carbonate budgets and net calcification (Figure 1). For example, coral reef TA samples in this study were primarily collected during daylight hours (Figure S1), which would tend to bias measurements towards net calcification (Cyronak et al. 2018). Moreover, differences in hydrodynamics between sites have significant capacity to decouple rates of benthic calcification from the magnitude of salinity normalized total alkalinity anomalies primarily owing to differences in seawater residence times and depth between locations (Cyronak et al. 2018; Courtney and Andersson 2019). The process of salinity normalization itself may also impart some additional uncertainties (Courtney et al. 2021b), especially in the case of Palmyra Atoll in this study, which experienced the largest salinity difference between the reef and offshore and negative net calcification (e.g., see larger ΔnTA uncertainties for Palmyra in Figure 3c). (Koweek et al. 2015) observed variable net calcification rates with high rates of calcification observed during the daytime with periods of nighttime dissolution at Palmyra Atoll, suggesting a combination of nighttime dissolution and/or entrainment of lagoon water likely led to the negative ΔnTA observed for Palmyra in this study.

This apparent contradiction highlights the value of collecting seawater TA samples over a full diel cycle and/or for extended periods of time while also avoiding sampling over large salinity ranges to reduce uncertainties in chemistry-based net calcification measurements. In contrast, the net carbonate budgets in this study are also somewhat limited by the use of top-down imagery, which does not account for additional sources of calcification or $CaCO_3$ dissolution hidden beneath the overlying canopy (Goatley and Bellwood 2011; Courtney et al. 2016), and mean (±uncertainty) annualized calcification and bioerosion rates from the literature, which does not account for systematic spatiotemporal variability in these sources of carbonate production and loss (Lange et al. 2020a). The categorical metrics were not always in direct agreement in this study, but the calcification vulnerability index more closely followed the census-based net carbonate budgets than the chemistry-based net calcification assessment (Figure 4). While this might suggest that the chemistry-based metric provides little additional information, we conclude that assessing vulnerability of coral reefs to maintain their $CaCO_3$ balance through multiple lines of evidence increases confidence in our assessment while providing different time perspectives of a chronic vs. acute condition (Figure 1) that integrate over varying spatial scales. Tracking changes in simplified net carbonate budgets and salinity normalized total alkalinity anomalies through time within each reef system using directly comparable methods may also provide more quantitative evidence of changes in calcification states through time (Figure 1).

Traditionally, studies have monitored long-term changes in coral cover as a metric for coral reef condition (Gardner et al. 2003; Bruno and Selig 2007; De'ath et al. 2012). While field-based evidence for the correlation between coral cover and net calcification in chemistry-based studies is lacking (Courtney and Andersson 2019), overall coral cover is generally correlated with net carbonate production in census-based studies (Perry et al. 2013, 2015; Januchowski-

Hartley et al. 2017). However, net carbonate production rates can nonetheless vary between reef systems of similar coral cover owing to differences in the relative abundances of coral taxa with varying calcification rates (Perry et al. 2015; Januchowski-Hartley et al. 2017; Courtney et al. 2020) and differences in the relative abundance of scraping, excavating, and browsing parrotfishes (Januchowski-Hartley et al. 2017; Lange et al. 2020a). Nonetheless, previous net carbonate budget studies have suggested that ≥10% coral cover may be a suitable threshold for the maintenance of positive carbonate production states in the Caribbean (Perry et al. 2013), ~2% for *Acropora* dominated reefs and ~12.5% for *Porites/Pocillopora* dominated reefs in the Chagos Archipelago (Perry et al. 2015), and 11-18% coral cover in the Seychelles depending on the relative abundances of excavating parrotfishes (Januchowski-Hartley et al. 2017). In this study, we observed a positive correlation between net carbonate budgets and coral cover (Figure 5b) with a threshold coral cover of 8.6±6.0% for maintaining positive net carbonate budgets (Figure 5b, Table S2). We posit that this slightly lower threshold for maintaining positive net carbonate budgets was likely due to the high abundance of framework building corals across the Pacific Ocean (Darling et al. 2019), potential differences in parrotfish functional groups (Januchowski-Hartley et al. 2017; Lange et al. 2020a), and the 50% reincorporation rate of parrotfish bioerosion applied here that was not used in the former studies (Perry et al. 2013, 2015; Januchowski-Hartley et al. 2017). For example, the large uncertainties in net carbonate budgets for Wake Atoll were owing to a few observations of *Bolbometopon muricatum*, which are responsible for anomalously high estimates of bioerosion (Perry et al. 2018b). Consequently, we found that coral reefs with positive net carbonate budgets had significantly higher coral cover than reefs with negative net carbonate budgets (Figure 6d). No relationship was observed between coral cover and ΔnTA in this study (Figure 5c, 6e; but see the above discussion of coral reef carbonate production estimates and alkalinity anomalies). Coral cover was greater for coral reefs with a positive combined census-based and chemistry-based calcification vulnerability index compared to neutral classifications (Figure 6f). Reefs with a neutral calcification vulnerability index had a mean (±95%) coral cover of 13.7±7.9%, which is in remarkable agreement with the 2-18% previously established thresholds for net carbonate budget tipping points (Perry et al. 2013, 2015; Januchowski-Hartley et al. 2017) despite being based on both census-based and chemistry-based methods.

However, there was considerable variability in coral cover among sites with a neutral calcification vulnerability index and we also observed a wide range of coral cover for sites with a positive calcification vulnerability index with coral cover less than 10% for many of those sites (Figure 6). These findings highlight the nuance and uncertainties associated with using a simplified coral cover threshold as a proxy for assessing the capacity for reefs to maintain $CaCO_3$ structures. Crustose coralline algae and other calcifying organisms are likely to become increasingly important contributors for maintaining $CaCO_3$ structures in low coral cover (<10%) or recently bleached coral reef systems (Kayanne et al. 2005; Courtney et al. 2018). For example, the 12-28% cover of crustose coralline algae at Jarvis in this study may have maintained positive alkalinity anomalies indicative of a net calcifying reef state despite 0 to 2.5% coral cover at the time of the surveys (Figure 3, Table S1). Coupled with the evidence that CCA may be increasing following mass bleaching events on certain reefs in the equatorial Pacific (Pacific Islands Fisheries Science Center 2021), these findings support the need to further assess the role of crustose coralline algae and other non-scleractinian coral calcifiers in maintaining positive net carbonate budgets and net calcification for low coral cover reefs (<10%) (Courtney et al. 2018).

As the climate crisis continues, robust time series measurements of coral reef status and capacity to maintain carbonate structures will become increasingly important to evaluate the current and projected maintenance of coral reef structures and the associated ecosystem services they provide to humanity. The automated annotation of benthic community composition from imagery via *CoralNet* substantially reduces the efforts to generate sustained time series data and is already producing accurate and traceable classification of benthic communities (Williams et al. 2019) with the additional capacity to quantify benthic carbonate production (Chan et al. 2021). We project that these estimates will only continue to improve with the development of location-specific calcification and bioerosion rates from in situ measurements and application of deep learning algorithms to directly assess substrate-specific and entire reef volume changes from repeated three-dimensional coral reef models derived from structure from motion (SfM) (see also (Lange et al. 2020a)). Moreover, snapshots such as the data presented in the current study provide nearly instantaneous evidence to evaluate net calcification states, but alone are unable to capture any changes in coral reef calcification state through time (i.e., increasing, constant, or decreasing) that are essential information for developing any potential intervention strategies. Sustained long-term ecological and biogeochemical monitoring of coral reef state variables such as the calcification metrics presented in this study will therefore prove useful for monitoring the vulnerability of coral reefs to sustain carbonate structures through time to inform evidence-based management of coral reefs and their associated ecosystem services in the Anthropocene.

Acknowledgments

We are grateful for the constructive comments and feedback that Dr. Ines Lange and an anonymous reviewer provided to clarify terminology and improve the synthesis work presented here. TAC, SC, DJK, and AJA were funded by the National Oceanographic and Atmospheric Administration Ocean Acidification Program (NA15OAR4320071). Benthic community, fish community, and carbonate chemistry data collection were funded by the NOAA Coral Reef Conservation Program and NOAA Ocean Acidification Program, as part of the Pacific-National Coral Reef Monitoring Program. All computer code required to generate the analyses herein is currently privately accessible on Figshare (https://figshare.com/s/01af29a8c92f0a51535b) and will be made publicly accessible via Zenodo. All data are currently publicly available in the cited data repositories. On behalf of all authors, the corresponding author declares that there are no conflicts of interest.

Supplementary Materials

Figure S1. Site-level salinity normalized total alkalinity anomalies (ΔnTA) are plotted relative to the local time of sampling the coral reef seawater total alkalinity water.

Table S1. Species-level bioerosion rates and length-scaling coefficients for parrotfishes observed across the Pacific Ocean in this study. Species represents the respective species name, data represents the source of the originating data source, substitution describes any required substitutions for species lacking in the *ReefBudget* methodology, each size bin represents the bioerosion rate (kg $CaCO_3$ ind^{-1} y^{-1}) for the respective fish length (cm) of initial and terminal phase fishes, and a and b represent allometric scaling coefficients of bioerosion for parrotfish length data: Bioerosion (kg $CaCO_3$ ind^{-1} y^{-1}) = $a \times TL^b$.

Table S2. Summary statistics are provided for the linear mixed effects model output. For each model (denoted in bold text in the first row), the table reports the estimates ± 95% and p-values for the respective coefficients, a summary of the random effects, the number of observations, and the resulting R^2 of the model.

Table S3. Site-level summary data are provided for each of the 56 coral reef sites presented in this study including: sample meta-data, summary of benthic community composition, benthic carbonate production, parrotfish bioerosion, net carbonate budgets, salinity normalized total alkalinity anomalies, categorical reef condition metrics, and degree heating weeks associated with the 2014-2017 global coral bleaching event.

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