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LETTER

Diel temperature and pH variability scale with depth across diverse coral reef habitats

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Scientific Significance Statement

Climate change is altering the environmental conditions of marine ecosystems across the globe. Coral reefs already experience intense variability in seawater temperature and pH over short time scales, which could influence how reef organisms respond to changes in average oceanic conditions. Our study provides evidence that the average daily range of seawater temperature and pH within coral reefs can be reasonably predicted from water column depth. This suggests that local environmental variability regimes within shallow coral reef ecosystems, and potentially the vulnerability of reef organisms, can be predicted from widely available bathymetry data.

Abstract

Coral reefs are facing intensifying stressors, largely due to global increases in seawater temperature and decreases in pH. However, there is extensive environmental variability within coral reef ecosystems, which can impact how organisms respond to global trends. We deployed spatial arrays of autonomous sensors across distinct shallow coral reef habitats to determine patterns of spatiotemporal variability in seawater physicochemical parameters. Temperature and pH were positively correlated over the course of a day due to solar heating and light-driven metabolism. The mean temporal and spatial ranges of temperature and pH were positively correlated across all sites, with different regimes of variability observed in different reef types. Ultimately, depth was a reliable predictor of the average diel ranges in both seawater temperature and pH. These results demonstrate that there is widespread environmental variability on diel timescales within coral reefs related to water column depth, which needs to be included in assessments of how global change will locally affect reef ecosystems.

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Coral reefs are critical marine ecosystems that provide numerous goods and services including the creation of habitat both above and below sea level. Global changes in sea surface temperature and seawater pH due to anthropogenic CO_2 emissions represent two of the biggest threats to the future persistence of coral reefs (Hoegh-Guldberg et al. 2007). Elevated seawater temperatures cause mass coral bleaching events, which can lead to significant coral death and the restructuring of reef ecosystems (Hughes et al. 2017). Ocean acidification, and the resulting changes to seawater carbonate chemistry, threaten the accretionary status of coral reefs by reducing biological calcification and increasing calcium carbonate dissolution (e.g., Chan and Connolly 2013; Eyre et al. 2018). Despite the widespread acknowledgment of these global threats to coral reefs, it is still unclear how local environmental variability will interact with global changes to impact their future.

High-frequency fluctuations (minutes to hours) in seawater temperature and pH have been documented across coral reef ecosystems (e.g., Leichter et al. 2005; Price et al. 2012; Shaw et al. 2012; Guadayol et al. 2014; Reid et al. 2019). These local, short-term dynamics can be likened to the variability of weather within terrestrial systems. "Ocean weather" can be thought of as the state of seawater (e.g., temperature, currents, chemistry, etc.) at a given place and time, and is determined by interconnected biogeochemical and physical processes (Bates et al. 2018). Exposure to variability in ocean weather, or the local seawater conditions, can determine how organisms respond to global stressors (Rivest et al. 2017; Kapsenberg and Cyronak 2018). For example, exposure to intense diel fluctuations in temperature can enhance bleaching resistance in some corals (Oliver and Palumbi 2011; Safaie et al. 2018), while fluctuations in pH can modulate the effects of ocean acidification on coral calcification rates (Dufault et al. 2012; Chan and Eggins 2017; Enochs et al. 2018). The complex geomorphic structure of coral reefs creates unique habitats and zonation that can span spatial scales of meters to hundreds of kilometers (Blanchon 2011). These coral reef habitats and zones have defining characteristics including depth, seawater residence times, exposure to the open ocean and terrestrial runoff, current speeds, biological diversity and biomass, among others. Therefore, it is likely that spatiotemporal variability in environmental conditions across coral reef ecosystems is related to a range of biological, physical, chemical, and geological properties within each habitat (Falter et al. 2013). Critically, contemporary variability in temperature and carbonate chemistry will determine how local seawater conditions change as the mean global ocean temperature rises and pH falls (Shaw et al. 2013; Lowe et al. 2016; Bates et al. 2018).

Despite the importance of site-specific temperature and pH variability in determining the future response of coral reefs to environmental change, it is not well known how temperature and pH covary across space and time in different types of shallow reef habitats. Understanding the prevailing fluctuations of seawater properties within coral reefs is critical to gaining a better picture of how reef seawater chemistry will change in the future, and how corals and other reef organisms will respond to anthropogenically induced global warming and ocean acidification. To assess local, short-term seawater temperature and pH dynamics within coral reefs, we deployed spatial arrays of autonomous sensors in diverse shallow reef habitats spanning the Atlantic and Pacific Oceans. This approach allowed us to gain insights into the large, natural spatiotemporal variability within reefs and will help guide future studies aimed at understanding local coral reef responses to global change.

Methods

Study sites

Sensor arrays consisting of 3–4 pH and temperature sensors were deployed at five locations representing six distinct coral reef habitats (Fig. 1; Table 1). Most deployments were made during summer months, and the length of each array deployment ranged between 5.6 and 17.5 d, highlighting that this study was designed to assess short-term (e.g., diel) spatiotemporal variability in seawater temperature and pH. Sensors were placed on the bottom at each site, with average depths ranging from 0.7 to 17.1 m (Table 1). Detailed descriptions of each location and sensor array deployment can be found in the Supporting Information.

Autonomous sensors and data analysis

Sensors were affixed directly to the benthos at all study sites in order to record the seawater conditions experienced by benthic communities at 15- or 30-min intervals (Cyronak et al. 2019). In most cases, SeapHOx sensors were deployed, although in some cases SeaFETs were used (Table 1). The SeapHOx is an autonomous sensing package outfitted with a Honeywell Durafet III combination pH electrode and Seabird MicroCAT (SBE37) to measure temperature and salinity (Bresnahan et al. 2014). The SeaFET uses the same pH sensing technology as the SeapHOx; however, there is no integrated salinity sensor and seawater temperature is measured by the Durafet thermistor. Factory calibrations were used for both the Seabird and Durafet temperature sensors, both with reported precisions of ±0.002°C. However, the Durafet temperature sensors have been reported to have an offset of up to ~ 0.3°C, but have been demonstrated to measure changes in temperature very accurately (Fox et al. 2019). Conductivity measurements from the MicroCAT were factory calibrated by Seabird, with a reported accuracy of $\pm$ 0.003 mS cm^{-1}. Seawater pH was calibrated to the total scale by taking bottle samples next to the sensors either predeployment in a holding tank or during the deployment, following best practices (Bresnahan et al. 2014). Bottle sample pH was calculated using CO2SYS with inputs of dissolved inorganic carbon (DIC) and total alkalinity (TA) measurements made in the laboratory and salinity and temperature measurements from the SeapHOx (Pierrot et al.

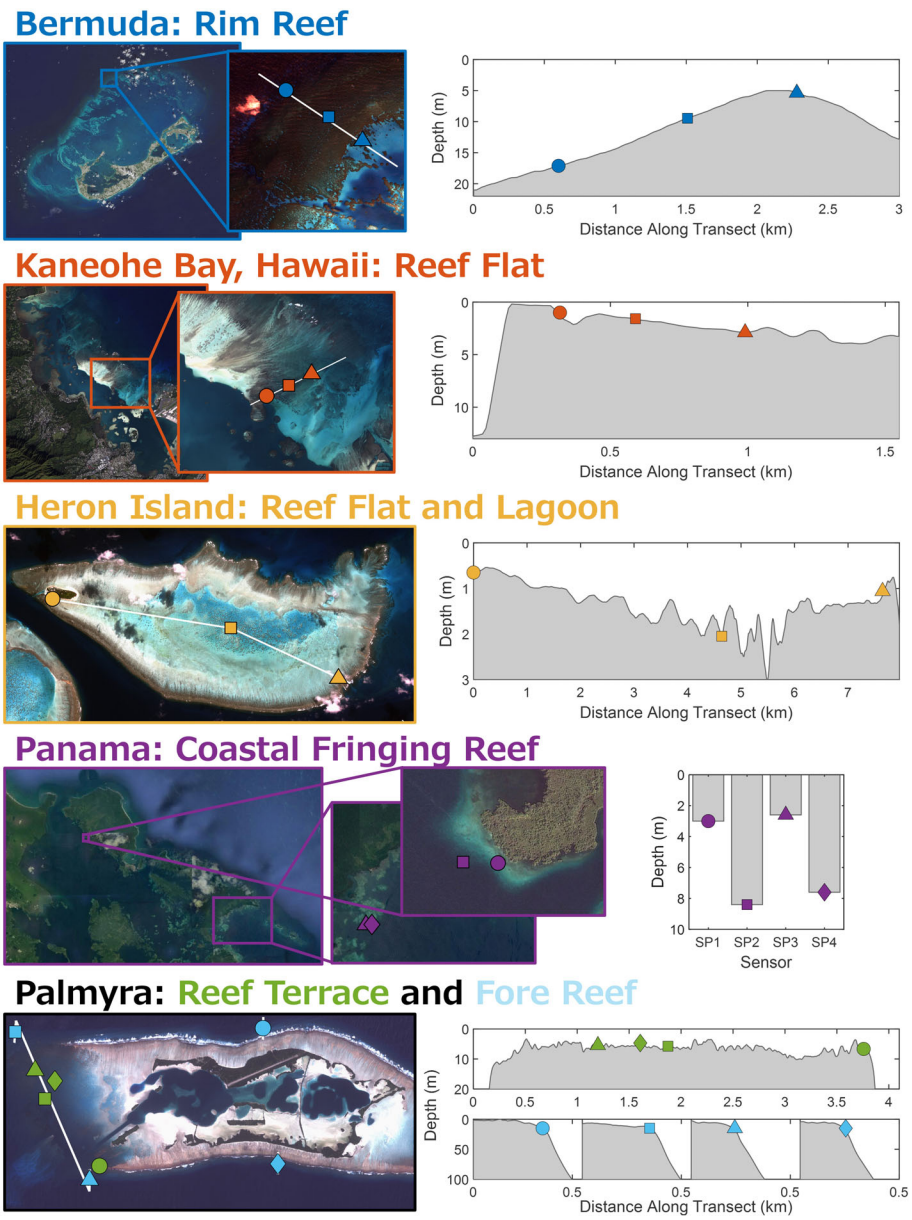

Fig. 1. Satellite images and cross sections of bathymetry showing the locations and depths where spatial sensor arrays were deployed. The bathymetry was derived from a transect through the sensor array designated as white lines in the satellite images. For each cross section the x-axis is the distance along the transect from the start, except for Panama and the Palmyra fore reef. For Panama, bar graphs show the sensor depth at each location. For the Palmyra fore reef, each cross section is a 0.5 km transect inshore to offshore centered around the sensor in order to demonstrate the steeply sloping bathymetry. A combination of 3–4 SeapHOxes or SeaFETs were deployed on the bottom at each location to measure seawater temperature and pH at 15- or 30-min intervals. Satellite images courtesy of the DigitalGlobe Foundation.

2006; Takeshita et al. 2018). At most locations, bottle samples were also taken throughout the deployments to assess any instrumental pH drift, and none was detected. All pH values are reported on the total hydrogen ion concentration scale, and the accuracy of individual pH sensors is estimated to be $\pm$ 0.015 (Bresnahan et al. 2014). The effect of changing temperature on pH was calculated in CO2SYS at a constant salinity (35), TA (2300 μmol kg^{-1}), and DIC (1900 μmol kg^{-1}), and determined to be –0.015 pH units per +1°C over a temperature range of 15–35°C. Changes in salinity can also impact pH, with a linear decrease of 0.01 pH units per increase in salinity unit between the range of 30–36 (calculated at 25°C, TA = 2300 μmol kg^{-1}, DIC = 1900 μmol kg^{-1}). However, changes in salinity are usually associated with changes in TA

Table 1. Characteristics of the different reefs where sensor arrays were deployed. Under the instrument heading SP refers to SeapHOx and SF refers to SeaFET. Depth is the mean depth at each sensor location derived as described in the Supporting Information. Salinity is the mean and range over the entire time series at each location. The mean diel ΔTemp and ΔpH are the average diel ranges in temperature and pH at each sensor location (± 1σ). The mean spatial ΔTemp and ΔpH are the average ranges across each sensor array (±1σ).

Location	Reef type	Year	Season	Duration (days)	Mean tidal range (m)	Instrument	Depth (m)	Lat	Lon	Mean salinity (range)	Mean diel ΔTemp (°C)	Mean diel ΔpH	Mean spatial ΔTemp (°C)	Mean spatial ΔpH
Hog reef, Bermuda	Rim reef	2015	Summer	16.9	0.8	SP1	5.4	32.4527	−64.8286	36.5 (0.7)	0.4 ± 0.1	0.06 ± 0.01	0.2 ± 0.2	0.02 ± 0.01
						SP2	17.1	32.4620	−64.8427	—	0.3 ± 0.3	0.04 ± 0.02		
						SF1	7.3	32.4573	−64.8348	36.5 (0.5)	0.4 ± 0.1	0.06 ± 0.02		
Kaneohe Bay, Hawaii	Reef flat	2016	Summer	12.6	0.5	SP1	2.1	21.4616	−157.7920	34.9 (0.2)	1.7 ± 0.3	0.22 ± 0.04	0.4 ± 0.2	0.06 ± 0.03
						SP2	2.9	21.4586	−157.7980	34.9 (0.2)	1.4 ± 0.3	0.14 ± 0.03		
						SF1	1.6	21.4600	−157.7960	—	1.7 ± 0.2	0.19 ± 0.01		
Heron Island, Australia	Reef flat and lagoon	2015	Spring	5.6	1.9	SP1	2.1	−23.4512	151.9578	35.8 (0.4)	1.9 ± 0.4	0.13 ± 0.05	1.2 ± 0.7	0.10 ± 0.06
						SP2	1.2	−23.4637	151.9848	35.8 (0.4)	3.1 ± 0.5	0.24 ± 0.04		
						SP3	0.7	−23.4440	151.9130	35.8 (0.4)	5.3 ± 1.4	0.46 ± 0.03		
Bocas del Toro, Panama	Coastal fringing reef	2015	Fall	9.8	0.3	SP1	3.0	9.3779	−82.3030	34.0 (1.3)	0.7 ± 0.2	0.06 ± 0.02	0.4 ± 0.2	0.04 ± 0.02
						SP2	8.4	9.3777	−82.3034	34.3 (1.5)	0.4 ± 0.2	0.07 ± 0.01		
						SP3	2.6	9.2552	−82.1255	34.2 (1.9)	0.5 ± 0.2	0.05 ± 0.01		
						SP4	7.6	9.2552	−82.1255	35.1 (1.5)	0.4 ± 0.1	0.07 ± 0.01		
Palmyra	Reef terrace	2012	Summer	17.5	0.7	SP1	5.0	5.8693	−162.1110	35.1 (0.4)	1.0 ± 0.4	0.18 ± 0.04	0.6 ± 0.3	0.11 ± 0.04
						SF1	5.1	5.8828	−162.1220	—	1.3 ± 0.4	0.15 ± 0.04		
						SP2	6.2	5.8886	−162.1240	35.1 (0.5)	0.9 ± 0.2	0.14 ± 0.02		
						SF2	3.5	5.8864	−162.1200	—	1.5 ± 0.4	0.22 ± 0.04		
Palmyra	Fore reef	2012	Summer	10.2	0.7	SF1	15	5.8665	−162.1130	—	0.1 ± 0.1	0.03 ± 0.02	0.2 ± 0.1	0.09 ± 0.03
						SP1	15	5.8697	−162.0750	35.0 (0.2)	0.2 ± 0.0	0.06 ± 0.01		
						SP2	15	5.8971	−162.0780	35.1 (0.2)	0.3 ± 0.1	0.11 ± 0.03		
						SF2	15	5.8964	−162.1280	—	0.3 ± 0.1	0.09 ± 0.03		

and DIC concentrations due to mixing of water masses, which could have more of an impact on carbonate chemistry than the direct effects of changing salinity at constant TA and DIC concentrations.

To assess both temporal and spatial variability across the sensor arrays, the mean and range of temperature and pH between all the sensors within each array at each sampling time were calculated. This resulted in a "mean" time series for each sensor array, with spatial variability calculated as the range across the array at each sampling time. The diel range of temperature and pH was calculated at each instrumented site by finding the minimum and maximum values during a full 24-h cycle from local midnight, and the mean temporal range of each sensor location was calculated as the average of these values (i.e., average diel peak-to-peak amplitude). The mean spatial range across each sensor array was calculated by averaging the range of temperature or pH across the entire array at each sampling time. Throughout this article, diel ranges are referred to as temporal while spatial ranges are referred to as spatial. Power spectral density estimations were performed on the temperature and pH time series in order to determine the dominant frequencies of variability. Lomb-Scargle periodograms were calculated in MATLAB using the *plomb* function across a frequency range of 0.25–5 d^{-1} in 0.001 d^{-1} steps. Regression coefficients and 95% confidence bounds were determined using the MATLAB function *fit*, with fit types of *poly1* for linear regressions and *power1* for power regressions (Supporting Information Table S1).

Results

Across all the individual sensors, the mean diel range in temperature and pH varied from 0.1°C to 5.3°C and 0.03 to 0.46, respectively (Fig. 2; Table 1). The mean spatial range across each sensor array was generally lower than the diel range of any given sensor, with the mean spatial range in temperature varying from 0.2°C to 1.2°C and pH from 0.02 to 0.11. Seawater temperature and pH variability across all study

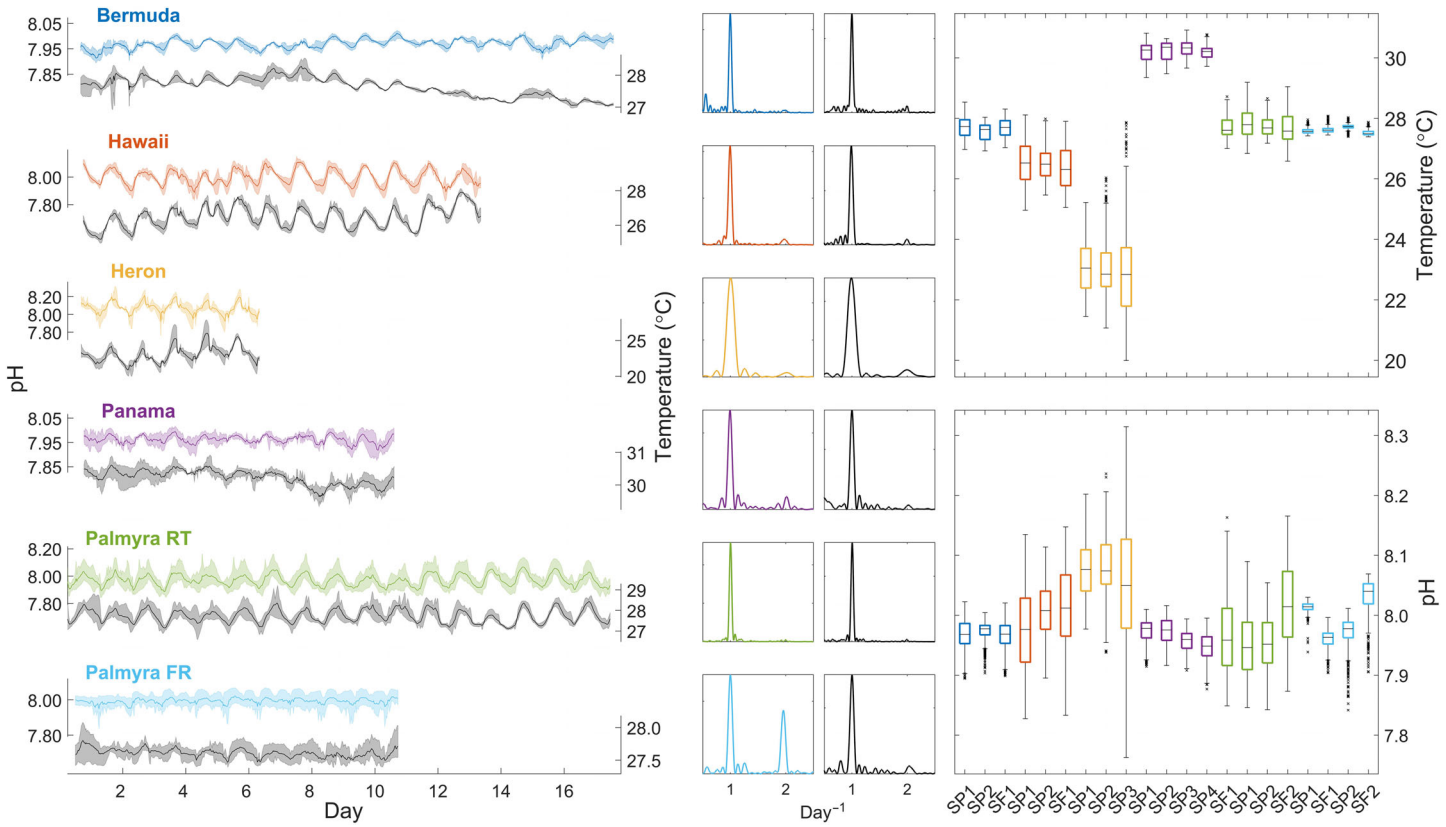

Fig. 2. (Column 1) Spatiotemporal variability of pH (colored) and temperature (black) from each autonomous sensor array. The bold line is the mean and the shaded area represents the range (minimum and maximum) at each time point across the spatial sensor array (*see* "Methods" section for details). The x-axis is normalized to days since midnight on the first day of each array deployment, note the different y-axis scales. (Column 2) Periodograms of the corresponding pH (colored) and temperature (black) mean time series in the first column. (Column 3) Box plots of the entire temperature and pH time series from each instrumental location, the colors correspond to the same reef locations as in Column 1. The individual instruments are labeled as a SeapHOx (SP) or SeaFET (SF) and correspond to the same sensor numbers in Table 1 at each location. The solid black line is the median, the box represents the 25th and 75th percentiles, whiskers represent $\pm$ 2.7σ, and black crosses are outliers beyond the range of the whiskers. See Supporting Information Figs. S1–S3 for the individual time series and spectral density analyses.

sites oscillated predominantly on a 1 d^{-1} frequency (Fig. 2, Supporting Information Figs. S1, S2). This supports using diel range as a robust estimate for the predominant measure of temporal variability at each site for the duration of the deployments. There was also a weaker tidal (2 d^{-1}) signal in some of the sensor time series, with the Palmyra fore reef showing the strongest peak at this frequency. The mean temperature and pH of the individual sensor time series varied between 23.0°C and 30.3°C and 7.95 and 8.08, respectively (Fig. 2). The mean salinity of the individual sensor sites varied from 34.0 to 36.5, with a maximum range of 1.9 at any given site over the full deployment, with the biggest range observed at the coastal fringing reefs in Panama (Table 1). Excluding the Panama sites, the average range in salinity was 0.37, which corresponds to a ~ 0.005 change in pH. However, most variations in salinity occurred on longer timescales than once per day, most likely related to mixing of water masses and freshwater inputs (Supporting Information Fig. S3). Therefore, it was assumed that changes in salinity on a daily time scale had minimal impact on diel pH variability at the sites in this study.

In general, there was a wider range in mean temperatures between the different locations as compared to pH (Fig. 2). Daily composites of the time series show that reef habitats with the greatest diel temperature variability also experienced greater diel pH variability across the spatial extent of each sensor array (Fig. 3A,B). This is supported by a positive relationship between the mean range in temperature and pH across both space and time within all systems (Fig. 3C,D). Overall, the shallowest reef systems tended to have the greatest spatio-temporal variability in temperature and pH, indicating that shallow reef habitats such as reef flats, back reefs, and lagoons can exhibit extensive changes in environmental conditions. The mean diel range of both temperature and pH at each sensor site followed a power function relationship with water column depth, and were linearly correlated to each other (Fig. 4). To test the robustness of the variability-depth relationship, mean diel ranges of temperature and pH were calculated from

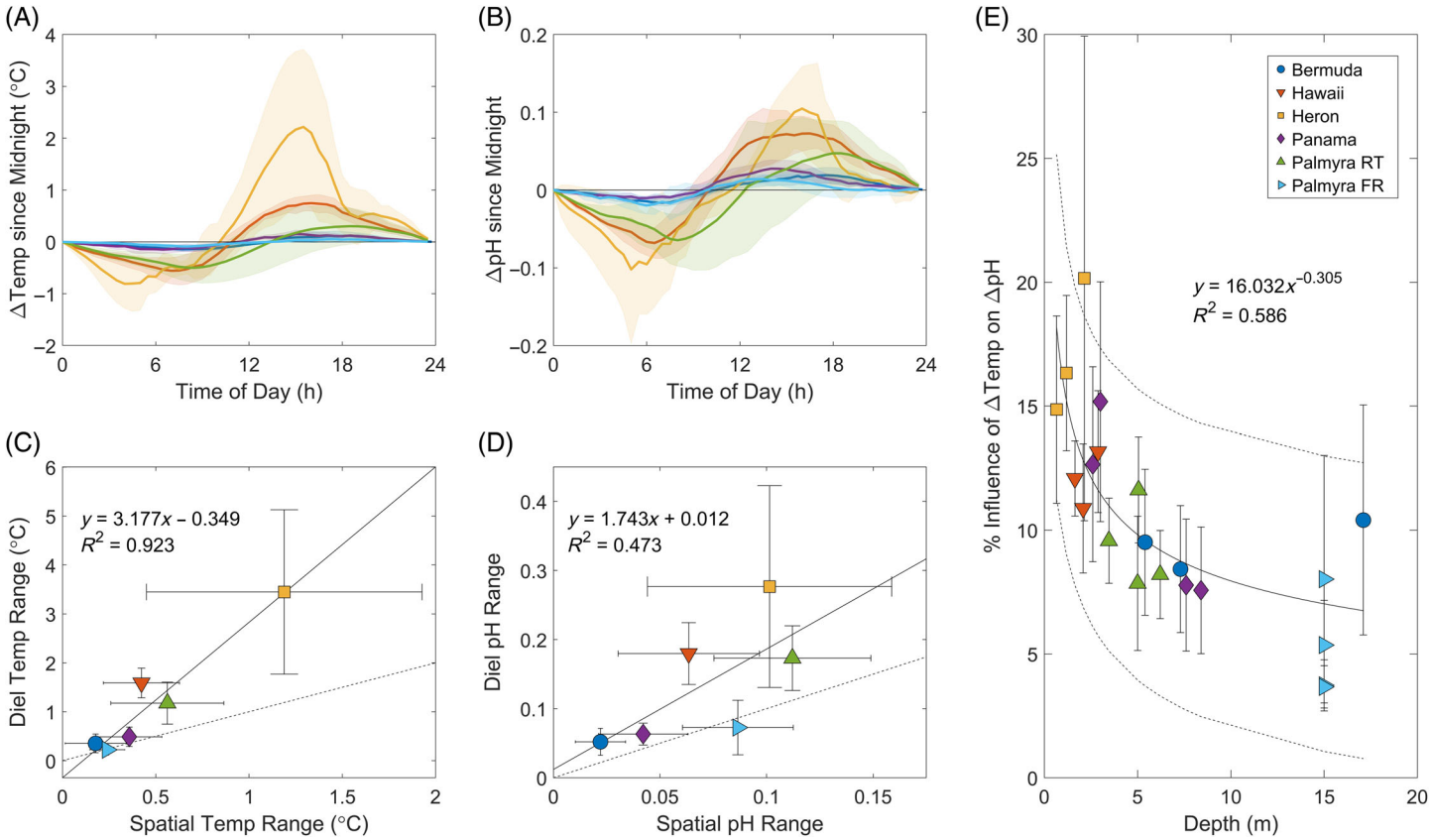

Fig. 3. Diel composite time series of (**A**) temperature and (**B**) pH constructed from each sensor array. In order to normalize the data between the different sites, it is plotted as the change since midnight and time of day is hours since midnight. The line is the mean and the shaded area is ± 1σ between all sensors within each array. The mean diel range in (**C**) temperature and (**D**) pH plotted against the mean spatial range within each sensor array over the duration of each time series. The solid lines are linear regressions and dashed lines represent the 1:1 line. (**E**) The maximum % influence of the mean range in temperature on the mean range in pH from each sensor. Percent influence was calculated assuming a decrease of 0.015 pH units per 1°C increase. The solid line is the fit to a power function and dashed lines are the 95% prediction intervals. In all panels, the error bars are ± 1σ.

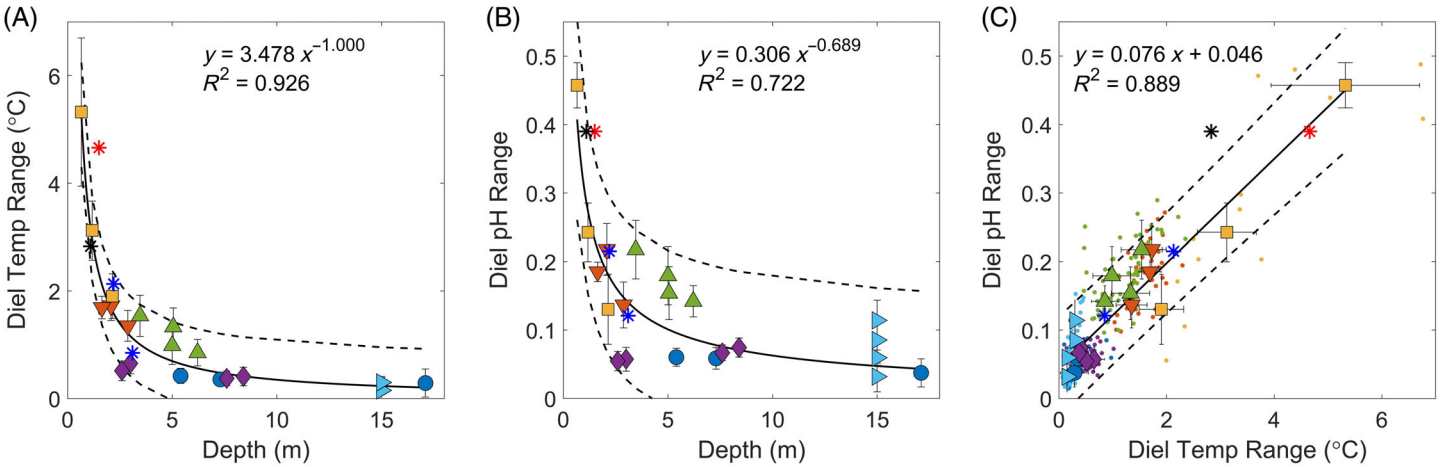

Fig. 4. The relationship of diel temperature and pH variability with depth. The mean diel range in (**A**) temperature and (**B**) pH at each sensor location plotted against depth. The solid lines represent fits to a power function and dashed lines are the 95% prediction intervals. (**C**) The mean diel ranges in temperature and pH plotted against each other. The large colored symbols are averages of individual sensor time series and small colored dots are the discrete days. The solid line represents a linear regression of the mean data and dashed lines are the 95% prediction intervals. In all panels, the error bars are $\pm 1\sigma$ and the color and symbol scheme is the same as in Fig. 3. Colored stars in each panel represent data taken from the literature, which were not included in the fits. The black star is from Lady Elliot Island, Australia (Shaw et al. 2012), the blue stars are from two sites on Oahu, Hawaii (Lantz et al. 2013), and the red star is from Ofu, American Samoa (Koweek et al. 2015).

previously published time series (Shaw et al. 2012; Lantz et al. 2013; Koweek et al. 2015), which fit well within our observed relationship (mean ΔTemp residual = 0.6 ± 1.2, mean ΔpH residual = 0.07 ± 0.08; $\pm 1\sigma$). A comparison of the temperature data was also made to a larger data set (n = 118 reefs; Safaie et al. 2018) with further discussion below. Coefficients and statistics for the regression fits in Figs. 3, 4 can be found in Supporting Information Table S1.

Discussion

Diel variability of seawater temperature and pH in coral reef ecosystems

Within all the reef systems, the highest temperatures occurred between midday and dusk, and the lowest temperatures occurred between 04:00 h and midmorning local time. This indicates that average diel fluctuations in temperature are mainly driven by solar irradiance, and not advection at these sites (Zhang et al. 2013). However, advection, mixing of water masses, and tidal processes most likely drive the higher frequency (> 1 d^{-1}) variability that was apparent at some sites (Fig. 2, Supporting Information Figs. S1, S2). Fluctuations in pH exhibited minima and maxima at similar times of the day as those for temperature. Elevated pH during the day and lower pH during the night indicate that reef metabolism is the predominant driver of these short-term fluctuations, with net ecosystem production (i.e., the net balance between photosynthesis and respiration) playing the dominant role (Cyronak et al. 2018). While it is well known that reef metabolism drives short-term changes in seawater pH (Gattuso et al. 1999), the large changes in temperature also have a thermodynamic effect on pH. The positive correlation between seawater temperature and pH creates a circumstance where fluctuations in temperature act to temper the diel range in pH. This is because times with lower pH from net respiration (night) are cooler, acting to thermodynamically raise pH, while times with higher pH from net photosynthesis (day) are warmer, acting to thermodynamically lower pH. Based on a –0.015 change in pH per +1°C (i.e., a negative correlation which is opposite to the observed positive relationship in situ), the observed diel fluctuations in temperature could attenuate diel ranges in pH by up to 20%, with a more pronounced effect in shallower habitats where water temperatures fluctuate more (Fig. 3E). These coupled changes in temperature and pH, ultimately driven by solar irradiance, have been hypothesized to result in divergent short-term stressors during different times of the day, with highest temperatures (and highest pH) occurring during the day and the lowest pH (and lowest temperatures) during the night (Kline et al. 2015).

The mean diel range in both temperature and pH at each site fit a power function relationship with water column depth (Fig. 4), similar to previous observations made across a reef ecosystem in Hawaii (Guadayol et al. 2014). This nonlinear relationship between diel physicochemical variability and depth is not surprising based on the power relationship between the ratio of benthic planar surface area to volume and depth. Since areal solute fluxes due to benthic metabolism occur across the bottom planar surface, the influence of a given benthic flux on the seawater solute concentration should decrease according to a power function with increasing depth. This is probably more complex for heat

fluxes as there are multiple physical processes involved, including fluxes from the benthos, latent heat fluxes, and absorption by the water column (MacKellar et al. 2013). Overall, diel variability of temperature and pH was drastically reduced at depths greater than ~ 6 m, indicating reef habitats deeper than this experience muted short-term variability. However, deeper habitats exposed to deep ocean water from upwelling and internal tides can experience intense high-frequency variability (Leichter et al. 2005; Reid et al. 2019). It is important to note that the relationship between depth and diel temperature and pH variability is based on the mean diel ranges during the time period of observations, and there are most likely interday variations based on day-to-day changes in physical and biogeochemical drivers. Based on these data, it is not clear how long a time series needs to be in order to robustly calculate a mean diel range, but this will probably be site-specific and tidal cycles should be considered.

To better assess the general applicability of our observed trends, temperature data from 118 reef sites (Safaie et al. 2018) were compared to our data set. The two data sets show a similar power function relationship between depth and diel temperature variability (Supporting Information Fig. S4). However, different coefficients between the two studies demonstrate that more measurements may be needed to develop a more generally applicable relationship across coral reefs. One important difference between the two studies is that some sites from Safaie et al. (2018) included temperature measurements from sensors deployed on buoy lines at different depths within the water column. Because of this, some of the depths reported by Safaie et al. (2018) reflect the sensor depth within the water column and not water column depth itself, which could skew the depth and temperature variability relationship. This reflects the need to design studies where instruments are deployed on the benthos so measurements reflect the conditions experienced by corals and other sessile benthic organisms. Unfortunately, a similar data set was not available to compare our observed trends in pH variability to a broader range of coral reef sites.

It is somewhat unexpected that short-term variability in temperature and pH had such a strong relationship with depth across coral reef sites with such distinct physical and biogeochemical properties. For example, one might expect seawater residence time, or the amount of time a parcel of water spends within a reef system, to influence mean diel ranges in environmental conditions, as systems with longer residence time allow seawater to become more highly modified (Zhang et al. 2013; Lowe et al. 2016). Although estimates of seawater residence times are not available at all sites, the sites with previously published residence times range from 0.3 to 1.5 d at Heron Island (Mongin and Baird 2014), 1.4 to 4.5 d at Bermuda (Venti et al. 2012), and 2.8 to 7.0 d at Kaneohe Bay (Lowe et al. 2009), which do not scale with observed variability in temperature and pH at these locations (Table 1). A large part of this inconsistency may be explained by the fact that these short-term diel changes oscillate around a mean, with rapid and intense forcing of seawater temperature and pH over a diel cycle (Fig. 3). Since residence time is an integrated measurement, it may have less of an effect on short-term variability as the tracer signal (e.g., temperature and pH) is changing quickly, and much more of an impact on mean conditions (Falter et al. 2013; Zhang et al. 2013; Takeshita et al. 2018). Despite the fact that average diel variability is largely predicted by depth, mean seawater conditions can change drastically across different reef systems (Cyronak et al. 2018). This suggests that even if shallow areas of reefs experience intense variations over short frequencies, the mean conditions could be representative of the open ocean or highly influenced by residence times (Price et al. 2012; Falter et al. 2013; Guadayol et al. 2014; Takeshita et al. 2018). It is unclear if the relationship between temperature and pH variability observed here is a persistent feature over seasonal to interannual time scales. For example, changes in both diel temperature and pH variability would be expected due to seasonal variability in solar irradiance (Falter et al. 2012) and reef metabolism (Courtney et al. 2017). Our results suggest that this pattern persists over seasonal cycles, as deployments were made between spring and fall. However, wintertime observations were lacking in higher latitude reefs where the biggest changes in temperature and pH regimes would be expected (Bates 2002).

While depth appears to be a strong predictor of environmental variability in these shallow coral reef systems, there are most likely situations where the observed relationship breaks down. For instance, if currents are fast and seawater is rushing over a shallow part of the reef, it is unlikely that the seawater will be significantly modified unless it traverses a lengthy reef section. Also, reefs can be exposed to colder, highly modified deep water due to physical processes acting on high frequencies (> 1 d^{-1}) such as upwelling and internal waves (Leichter et al. 2005; Reid et al. 2019). Exposure to deep ocean water is more likely to occur in habitats exposed to the open ocean such as fore reefs, and will be dependent on physical characteristic such as slope angle and steepness (Schramek et al. 2018). Even though Palmyra is located in a region with strong vertical stratification (Hamann et al. 2004), temperature and pH variability at the fore reef sites still fit within the broader depth-variability relationships (Fig. 4). This could just be a function of the time period and/or length of our observations and demonstrates the need for more high-resolution and extended time series observations across different types of coral reef ecosystems (e.g., Reid et al. 2019). While the depth and temperature relationship is likely controlled by physical mechanisms, biological mechanisms could change the relationship between pH variability and depth. For example, a bleaching event reduced the diel range in pH by ~ 0.15 units on a reef in the South China Sea, most likely due to a reduction in net ecosystem production (DeCarlo et al. 2017). Nutrient additions have been shown to impact the net ecosystem production of coral communities, subsequently impacting pH variability in a mesocosm experiment (Silbiger et al. 2018).

More in situ studies assessing rates of ecosystem production and calcification alongside measurements of pH variability are needed to better assess the biological control on diel pH cycles.

Impacts of variability on organisms

Even if reefs experience distinct spatiotemporal variability of temperature and pH compared to the open ocean, does it matter to corals and other reef organisms? There is evidence that exposure to short-term oscillations in temperature and pH can mitigate the impact of these environmental stressors on corals (Warner et al. 1996; Oliver and Palumbi 2011; Dufault et al. 2012; Safaie et al. 2018). Corals exposed to large diel temperature oscillations living in naturally variable environments demonstrated increased thermal tolerance when compared to corals from less variable environments (Warner et al. 1996; Oliver and Palumbi 2011). In support of these experimental studies, recent findings demonstrated that high-frequency temperature variability was the primary predictor of bleaching prevalence across 81 coral bleaching events (Safaie et al. 2018). Likewise, corals exposed to oscillating pH conditions had higher calcification rates compared to corals in stable conditions with the same mean pH (Chan and Eggins 2017; Enochs et al. 2018). Coral recruits have also been shown to grow larger and have greater survivorship under oscillating compared to stable pH conditions (Dufault et al. 2012). The increased bleaching tolerance of corals exposed to oscillating temperature is most likely due to acclimatization (Palumbi et al. 2014), whereas the mechanisms governing the tempered response of calcification and recruitment to pH under oscillating conditions are not fully elucidated (Rivest et al. 2017). Irrespective of the underlying physiological mechanisms, the widespread variability observed across coral reef ecosystems in this study indicates that there are extensive shallow sections of coral reefs inhabited by organisms that are potentially better able to cope with global changes in temperature and pH.

On the other hand, habitats and ecosystems that undergo dramatic variability in seawater temperature and pH could create more harmful exposures for organisms in the future (Shaw et al. 2013; Kline et al. 2015). Local variability regimes of temperature and pH will respond differently to global climate change, potentially altering the spatiotemporal relationships of seawater properties across coral reefs. A global reduction in seawater buffering capacity is expected to cause more short-term extremes in seawater pH (Shaw et al. 2013), which could mean that future diel pH variability will increase even more at sites with the greatest variability today. Negative feedbacks to ocean warming, such as latent heat fluxes and cloud cover, could modulate temperature variability in the future, although those are not expected to keep temperatures below the critical thresholds for coral bleaching (Kleypas et al. 2008). Depending on how the feedback systems driving temperature and pH interact, there could be fundamental changes in the temperature and pH relationship across shallow coral reef habitats in the future (Fig. 4C). It is also important to consider that rising sea levels could reduce both fluctuations in temperature and pH as the water column becomes deeper over reefs (Lowe et al. 2016). This demonstrates the need to holistically examine "ocean weather" patterns across coral reefs in order to better elucidate the future local changes we can expect due to global anthropogenic changes to the Earth system.

Conclusions

This study adds to a diverse body of work demonstrating how the different habitats and geomorphic structure of coral reef ecosystems can create complex variability in seawater temperature and pH. Diel oscillations in temperature and pH were both ultimately driven by solar irradiance, and as a result, the diel range of both parameters were positively correlated across all sites. This coupling of temperature and pH creates a natural thermodynamic tempering of diel pH fluctuations due to the occurrence of elevated temperatures during the day and lower temperatures at night. In general, temporal variability in both temperature and pH was correlated with spatial variability across the sensor arrays. However, for both parameters, the mean diel range was greater than or equal to the mean spatial range, indicating that variability is most intense at one location over a 24-h cycle. Average water column depth seems to be a good first order indicator of the average short-term variability of seawater temperature and pH across coral reef habitats, and future studies should be designed to test the robustness of this relationship and whether it can be used to predict local variability regimes. Combined with current research investigating the impacts of environmental variability on the vulnerability of reef organisms to global change, these results suggest that depth surveys of coral reef ecosystems could provide critical insights into where populations of corals and other reef organisms harboring increased resilience may exist. Other methods for assessing small-scale variability and associated biological responses should also be explored, including remote sensing technologies, modeling, and genetic techniques. It is likely that the dynamic seawater conditions within coral reefs will interact with global changes to the Earth system, creating both hotspots and refugia for marine organisms (Kapsenberg and Cyronak 2018). Therefore, it is important to gain a more comprehensive understanding of the contemporary variability within coral reefs to better predict how global change will impact these locally dynamic ecosystems.

References

Bates, A., and others. 2018. Biologists ignore ocean weather at their peril. Nature **560**: 299–301. doi:10.1038/d41586-018-05869-5

Bates, N. R. 2002. Seasonal variability of the effect of coral reefs on seawater CO_2 and air-sea CO_2 exchange. Limnol. Oceanogr. **47**: 43–52. doi:10.4319/lo.2002.47.1.0043

Blanchon, P. 2011. Geomorphic zonation, p. 469–486. *In* D. Hopley [ed.], *Encyclopedia of modern coral reefs*. Springer.

Bresnahan, P. J., T. R. Martz, Y. Takeshita, K. S. Johnson, and M. LaShomb. 2014. Best practices for autonomous measurement of seawater pH with the Honeywell Durafet. Methods Oceanogr. **9**: 44–60. doi:10.1016/j.mio.2014.08.003

Chan, N. C. S., and S. R. Connolly. 2013. Sensitivity of coral calcification to ocean acidification: A meta-analysis. Glob. Chang. Biol. **19**: 282–290. doi:10.1111/gcb.12011

Chan, W. Y., and S. M. Eggins. 2017. Calcification responses to diurnal variation in seawater carbonate chemistry by the coral *Acropora formosa*. Coral Reefs. **36**: 763–772. doi:10.1007/s00338-017-1567-8

Courtney, T. A., and others. 2017. Environmental controls on modern scleractinian coral and reef-scale calcification. Sci. Adv. **3**: e1701356. doi:10.1126/sciadv.1701356

Cyronak, T., and others. 2018. Taking the metabolic pulse of the world's coral reefs. PLoS One **13**: e0190872. doi:10.1371/journal.pone.0190872

Cyronak, T., and others. 2019. Data from: Diel temperature and pH variability scale with depth across diverse coral reef habitats. Dryad, [accessed 2019 Aug 23]. Available from https://doi.org/10.5061/dryad.tj1nf5f

DeCarlo, T. M., and others. 2017. Community production modulates coral reef pH and the sensitivity of ecosystem calcification to ocean acidification. J. Geophys. Res. Oceans **122**: 745–761. doi:10.1002/2016JC012326

Dufault, A. M., V. R. Cumbo, T.-Y. Fan, and P. J. Edmunds. 2012. Effects of diurnally oscillating pCO_2 on the calcification and survival of coral recruits. Proc. R. Soc. Lond. B Biol. Sci. **279**: 2951–2958. doi:10.1098/rspb.2011.2545

Enochs, I. C., and others. 2018. The influence of diel carbonate chemistry fluctuations on the calcification rate of *Acropora cervicornis* under present day and future acidification conditions. J. Exp. Mar. Biol. Ecol. **506**: 135–143. doi:10.1016/j.jembe.2018.06.007

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. doi:10.1126/science.aao1118

Falter, J. L., R. J. Lowe, M. J. Atkinson, and P. Cuet. 2012. Seasonal coupling and de-coupling of net calcification rates from coral reef metabolism and carbonate chemistry at Ningaloo Reef, Western Australia. J. Geophys. Res. **117**: C05003. doi:10.1029/2011JC007268

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

Fox, M. D., and others. 2019. Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, Central Pacific. Coral Reefs **38**: 701–712. doi:10.1007/s00338-019-01796-7

Gattuso, J.-P., D. Allemand, and M. Frankignoulle. 1999. Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. Am. Zool. **39**: 160–183. doi:10.1093/icb/39.1.160

Guadayol, Ò., N. J. Silbiger, M. J. Donahue, and F. I. M. Thomas. 2014. Patterns in temporal variability of temperature, oxygen and pH along an environmental gradient in a coral reef. PLoS One **9**: e85213. doi:10.1371/journal.pone.0085213

Hamann, I. M., G. W. Boehlert, and C. D. Wilson. 2004. Effects of steep topography on the flow and stratification near Palmyra Atoll. Ocean Dyn. **54**: 460–473. doi:10.1007/s10236-004-0091-x

Hoegh-Guldberg, O., and others. 2007. Coral reefs under rapid climate change and ocean acidification. Science **318**: 1737–1742. doi:10.1126/science.1152509

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

Kapsenberg, L., and T. Cyronak. 2018. Ocean acidification refugia in variable environments. Glob. Chang. Biol. **25**: 3201–3214. doi:10.1111/gcb.14730

Kleypas, J. A., G. Danabasoglu, and J. M. Lough. 2008. Potential role of the ocean thermostat in determining regional differences in coral reef bleaching events. Geophys. Res. Lett. **35**: L03613. doi:10.1029/2007GL032257

Kline, D. I., and others. 2015. Six month *in situ* high-resolution carbonate chemistry and temperature study on a coral reef flat reveals asynchronous pH and temperature anomalies. PLoS One **10**: e0127648. doi:10.1371/journal.pone.0127648

Koweek, D., R. Dunbar, S. Monismith, D. Mucciarone, C. B. Woodson, and L. Samuel. 2015. High-resolution physical and biogeochemical variability from a shallow back reef on Ofu, American Samoa: An end-member perspective. Coral Reefs **34**: 979–991. doi:10.1007/s00338-015-1308-9

Lantz, C. A., M. J. Atkinson, C. W. Winn, and S. E. Kahng. 2013. Dissolved inorganic carbon and total alkalinity of a Hawaiian fringing reef: Chemical techniques for monitoring the effects of ocean acidification on coral reefs. Coral Reefs **33**: 105–115. doi:10.1007/s00338-013-1082-5

Leichter, J. J., G. B. Deane, and M. D. Stokes. 2005. Spatial and temporal variability of internal wave forcing on a coral reef. J. Phys. Oceanogr. **35**: 1945–1962. doi:10.1175/JPO2808.1

Lowe, R. J., J. L. Falter, S. G. Monismith, and M. J. Atkinson. 2009. A numerical study of circulation in a coastal reef-lagoon system. J. Geophys. Res. Oceans **114**: C06022. doi:10.1029/2008JC005081

Lowe, R. J., X. Pivan, J. Falter, G. Symonds, and R. Gruber. 2016. Rising sea levels will reduce extreme temperature variations in tide-dominated reef habitats. Sci. Adv. **2**: e1600825. doi:10.1126/sciadv.1600825

MacKellar, M. C., H. A. McGowan, and S. R. Phinn. 2013. An observational heat budget analysis of a coral reef, Heron Reef, Great Barrier Reef, Australia. J. Geophys. Res. Atmos. **118**: 2547–2559. doi:10.1002/jgrd.50270

Mongin, M., and M. Baird. 2014. The interacting effects of photosynthesis, calcification and water circulation on carbon chemistry variability on a coral reef flat: A modelling study. Ecol. Model. **284**: 19–34. doi:10.1016/j.ecolmodel.2014.04.004

Oliver, T. A., and S. R. Palumbi. 2011. Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs **30**: 429–440. doi:10.1007/s00338-011-0721-y

Palumbi, S. R., D. J. Barshis, N. Traylor-Knowles, and R. A. Bay. 2014. Mechanisms of reef coral resistance to future climate change. Science **344**: 895–898. doi:10.1126/science.1251336

Pierrot, D., E. Lewis, and D. W. R. Wallace. 2006. MS Excel program developed for CO_2 system calculations. *In* ORNL/CDIAC-105a. Carbon dioxide information analysis center, oak ridge national laboratory, US Department of Energy, Oak Ridge, Tennessee, V. **3**. doi:10.3334/CDIAC/otg.CO2SYS_XLS_CDIAC105a

Price, N. N., T. R. Martz, R. E. Brainard, and J. E. Smith. 2012. Diel variability in seawater pH relates to calcification and benthic community structure on coral reefs. PLoS One **7**: e43843. doi:10.1371/journal.pone.0043843

Reid, E. C., T. M. DeCarlo, A. L. Cohen, G. T. Wong, S. J. Lentz, A. Safaie, A. Hall, and K. A. Davis. 2019. Internal waves influence the thermal and nutrient environment on a shallow coral reef. Limnol. Oceanogr. **64**: 1949–1965. doi:10.1002/lno.11162

Rivest, E. B., S. Comeau, and C. E. Cornwall. 2017. The role of natural variability in shaping the response of coral reef organisms to climate change. Curr. Clim. Change Rep. **3**: 271–281. doi:10.1007/s40641-017-0082-x

Safaie, A., and others. 2018. High frequency temperature variability reduces the risk of coral bleaching. Nat. Commun. **9**: 1671. doi:10.1038/s41467-018-04074-2

Schramek, T. A., P. L. Colin, M. A. Merrifield, and E. J. Terrill. 2018. Depth-dependent thermal stress around corals in the tropical Pacific Ocean. Geophys. Res. Lett. **45**: 9739–9747. doi:10.1029/2018GL078782

Shaw, E. C., B. I. McNeil, and B. Tilbrook. 2012. Impacts of ocean acidification in naturally variable coral reef flat ecosystems. J. Geophys. Res. **117**: C03038. doi:10.1029/2011JC007655

Shaw, E. C., B. I. McNeil, B. Tilbrook, R. Matear, and M. L. Bates. 2013. Anthropogenic changes to seawater buffer capacity combined with natural reef metabolism induce extreme future coral reef CO_2 conditions. Glob. Chang. Biol. **19**: 1632–1641. doi:10.1111/gcb.12154

Silbiger, N. J., and others. 2018. Nutrient pollution disrupts key ecosystem functions on coral reefs. Proc. R. Soc. B Biol. Sci. **285**: 20172718. doi:10.1098/rspb.2017.2718

Takeshita, Y., T. Cyronak, T. R. Martz, T. Kindeberg, and A. J. Andersson. 2018. Coral reef carbonate chemistry variability at different functional scales. Front. Mar. Sci. **5**: 175. doi:10.3389/fmars.2018.00175

Venti, A., D. Kadko, A. Andersson, C. Langdon, and N. Bates. 2012. A multi-tracer model approach to estimate reef water residence times. Limnol. Oceanogr.: Methods **10**: 1078–1095. doi:10.4319/lom.2012.10.1078

Warner, M. E., W. K. Fitt, and G. W. Schmidt. 1996. The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral: A novel approach. Plant Cell Environ. **19**: 291–299. doi:10.1111/j.1365-3040.1996.tb00251.x

Zhang, Z., J. Falter, R. Lowe, G. Ivey, and M. McCulloch. 2013. Atmospheric forcing intensifies the effects of regional ocean warming on reef-scale temperature anomalies during a coral bleaching event. J. Geophys. Res. Oceans **118**: 4600–4616. doi:10.1002/jgrc.20338

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