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Cover: Reef at American Samoa prior to and during bleaching event.
Photo credit: XL Catlin Seaview Survey

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Introduction

Coral reefs are the most diverse ecosystems on the planet despite evolving in nutrient depleted water and within a narrow range in temperature, salinity, and water quality. Corals are predominantly limited to tropical, shallow waters in the euphotic zone due to their light-dependent symbiotic relationship with photosynthetic algae called zooxanthellae. Primarily of the dinoflagellate genus *Symbodinium*, zooxanthellae translocate fixed carbon needed for productivity, respiration, and growth (Schmitz and Kremer 1977; Muscatine et al. 1989; Lesser 2013). Environmental changes catalyze the breakdown of coral-symbionts by triggering corals to expel their zooxanthellae, causing coral tissue to pale and, in extreme cases, reveal their underlying skeleton and appear white. This phenomenon is called coral bleaching. Coral bleaching and the expulsion of zooxanthellae may have evolved as an adaptive mechanism to rapid environmental or physiological changes (Buddemeier and Fautin 1993; Stat et al. 2006). However, repercussions of mass coral bleaching are generally detrimental and include nutritional deprivation (Porter et al. 1989), reduced growth (Cantin et al. 2010), impaired reproduction (Szmant and Gassman 1990), coral mortality (Lesser and Farrell 2004), reef degradation (Eakin et al. 2019), shifts in coral assemblages (Hughes et al. 2018b), and habitat regime shifts from a hard coral framework to a macroalgae dominated reef (Ostrander et al. 2000). Coral recovery capacity is variable spatially and is in part dependent on species-specific responses and the severity of bleaching experienced(Baker et al. 2008), but is also determined by the underlying drivers that initially caused the bleaching event.

Environmental stressors, site-level factors, depth, and thermal variability strongly influence bleaching onset and severity. Mass coral bleaching is primarily linked to elevated seawater temperatures but is also associated with increased solar irradiance (both PAR and UV portions of the spectrum)(Lesser and Farrell 2004) and oxidative stress (Lesser 1997; Downs et al. 2002). Furthermore, enriched nutrients (Wooldridge 2009) and ocean acidification(Anthony et al. 2008) can also influence the degree to which corals bleach during heat stress events. Bleaching severity also depends on coral taxa susceptibly to thermal stress, with faster growing and branching taxa (e.g., *Acropora* and *Pocillopora*) more likely to experience rapid bleaching and high mortality than slower growing, mounding taxa (e.g., *Porites*) (Baird and Marshall 2002). Variability in bleaching level and coral taxa susceptibility to bleaching highlight the need for more nuanced research linking multiple drivers to response variables.

Mass bleaching events have been occurring at unprecedented rates in recent decades and are associated with anthropogenic global warming and elevated temperature stages of the El Niño-Southern Oscillation (ENSO) (Glynn 2000; Hughes et al. 2017). Global warming has caused the trajectory of water temperatures to gradually and continuously increase at a rate of 0.005 °C yr^{-1} in the upper ocean with mean temperatures 1–2 °C warmer compared to 50 years ago (Roemmich et al. 2015; Hughes et al. 2018a). Asymmetric differences between hemispheres indicate that net heat gain has been confined to the southern hemisphere during the last two decades, making coral reefs in the southern hemisphere especially vulnerable to anthropogenic warming (Rathore et al. 2020). Inter-decadal variability in seawater temperature and carbon storage capacity are associated with ENSO and are correlated with atmospheric patterns in the tropical Pacific, with decreased sea surface temperatures associated with la Niña and increased temperatures associated with El Niño (Winguth et al. 1994; Enfield and Mayer 1997). Prior to the 1980s, mass bleaching events were rare. After the 1980s, global warming increased the thermal stress during El Niño-Southern Oscillation phases, and global bleaching events coincided with cyclic El Niño events (Barkley et al. 2018; Claar et al. 2018) and rapid shifts from El Niño to La Niña (Dalton et al. 2020). In the last decade, however, global warming has exceeded even the cooler la Niña events from 30 years ago, and mass bleaching events are occurring at greater frequencies even outside of El Niño (Hughes et al. 2018a) resulting in less time for reefs to recover between events.

In an effort to predict future bleaching events, various temperature predictor variables have been calculated primarily from sea surface temperatures (SST) derived from satellite data. The most extensively used thermal stress metric is degree heating weeks (DHW), which calculates accumulated heat stress in an area by adding temperature values exceeding the bleaching threshold (maximum monthly mean temperature + 1 °C) over a three month period(Liu et al. 2003, 2014). Satellite-derived products like DHW have proven reliable as a mass bleaching index and have the advantage that the data are publicly available through the U.S. National Oceanic and Atmospheric Administration's (NOAA) Coral Reef Watch Program. However, limitations of satellite-derived products include calculations extended over large spatial areas (typically 5 km or 50 km). Satellite-derived SST also ignores daily temperature variability as well as temperature variability that may occur between reefs in an area that large. Furthermore, surface temperatures are generally a few degrees different than the water temperature at depth where corals actually exist. Recently, a depth-biased method to calculate DHW was developed to account for the temperature differences between corals at depths versus satellite-derived at sea surface, but this method requires in situ temperature at reef depth (Venegas et al. 2019). In situ temperature logger deployment and maintenance are generally cost prohibitive and loggers cover less area compared to satellite data its major advantages are (a) depth specific temperature data co-located at a given reef, and (b) high sampling frequencies (e.g., data could be collected every 5 minutes). High frequency temperature data can provide informative measures to predict bleaching prevalence that may be overlooked if only satellite-derived metrics are evaluated. For example, additional heating metrics like acute heat stress (high heat stress on the order of hours or days), heating rates, and temperature variability over different time scales (e.g., diurnal, tidal, seasonal) can be calculated from in situ temperature logger data and used as bleaching metrics (Safaie et al. 2018).

To better understand vertical thermal structure of reefs at depth and identify predictors of mass bleaching events using high frequency time series data, we used long-term (2012–2018) in situ temperature data collected at multiple reefs and depths around the island of Tutuila in American Samoa. Located in the central South Pacific, Tutuila is 1 of 5 volcanic islands and 2 atolls that comprise American Samoa. Lying just a few kilometers from shore, Tutuila contains shallow fringing reefs and a deep offshore bank (Birkeland et al. 2008). American Samoa experienced severe bleaching in 1994, 2003, 2015 and 2017 (Coward et al. 2020). The objectives of our study are to (1) conduct a time series analysis on in situ temperature data (2012–2018) and calculate heating metrics and (2) determine whether heating metrics predicted coral bleaching prevalence during the 2015 bleaching event.

Methods

Subsurface temperature recorders (STR) were deployed at 6 sites and at 3 depths through NOAA's Pacific Reef Assessment and Monitoring Program from 2012 to 2018. We performed a time series analysis on the in situ temperature data using the following steps:

1. Applied the time series analysis to determine trends and associated periodicities that may be drivers of mass bleaching events.
2. Compared the temperature time series between sites and depth strata to observe any potential differences in temporal patterns.
3. Calculated multiple metrics for five heat stress types: cumulative heat stress, acute heat stress, heating rates, trends, and temperature variability.

During the deployment of the STR time series (2012–2018), two massive bleaching events occurred during the austral summer months of 2015 and 2017. Unfortunately, the extent of bleaching during peak thermal stress was not quantitatively measured for either year. However, the beginning of bleaching in 2015 happened to occur during the regularly scheduled monitoring surveys. Thus, we assessed the relationship between thermal stress metrics and bleaching prevalence at the beginning of the 2015 bleaching event through the following steps:

4. Determined the spatial variation in heating metrics between sites and depths calculated just for the 2015 period when the mass bleaching event occurred.
5. Determined if bleaching prevalence of hard corals varied between depth (shallow: 0–6 m, middle: 6–18 m, and deep: 18–25 m) and island sector (northeast, northwest, southeast, southwest)).
6. Determined if bleaching prevalence of hard corals and dominant coral genera varied with heating metrics from the 2014–2015 heating period.

In situ temperature recorder deployment

Sea-Bird SBE56 temperature sensors were deployed in 4 sectors (Northwest, Northeast, Southwest, Southeast) circumnavigating Tutuila, American Samoa, at multiple sites at three different depths (5 m, 15 m, and 25 m) from 2012 through 2018. Two additional sites were added in 2015 for a total of 6 sites (Figure 1). Measurements were taken every 5 minutes and averaged per hour, resulting in hourly temperature data over 6 years.

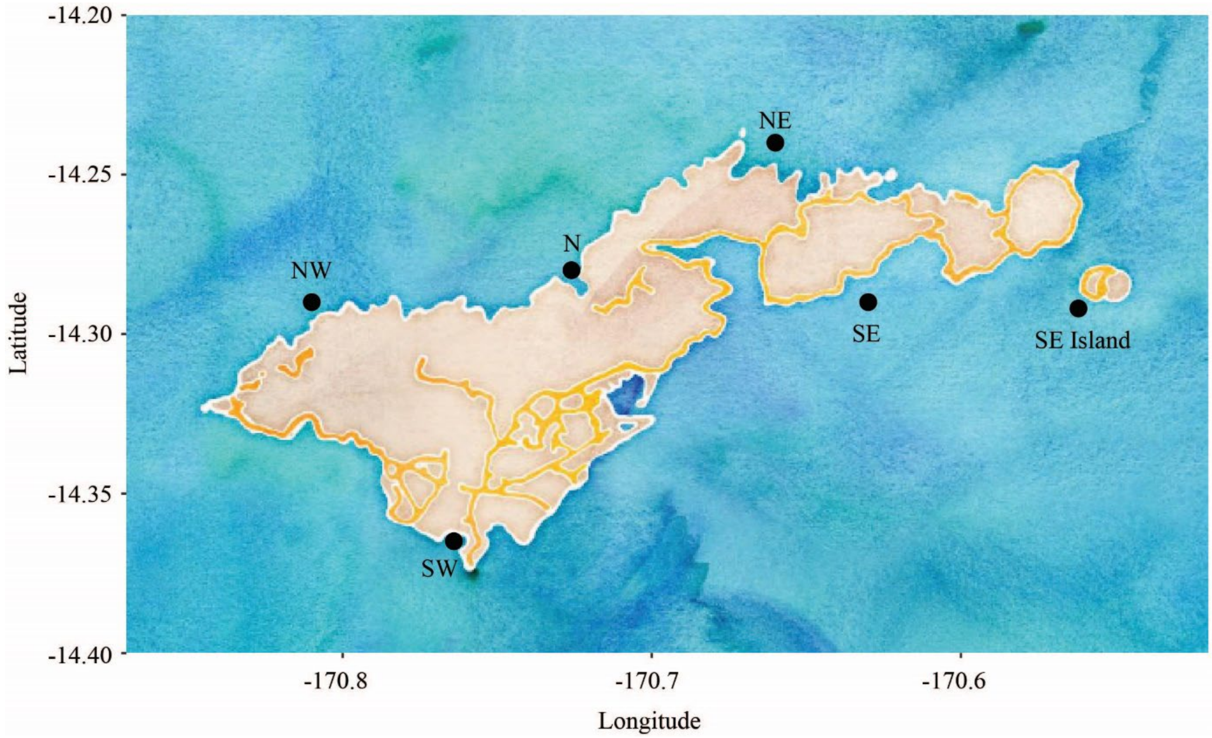

Figure 1. Map of Tutuila, American Samoa. Black points represent the location of the temperature loggers. Sectors included are the Northwest (NW), North (N), Northeast (NE), Southwest (SW), Southeast (SE), and Southeast Island (SE Island). At each point, a temperature logger was deployed at depths of 5 m, 15 m, and 25 m.

Determining trend through time series analysis

Hourly seawater temperature records were analyzed using a detrended fluctuation analysis (DFA) to reveal long-range correlations in temperature time series. Most time series statistical analyses require the data to be stationary; however, DFA allows for the detection of intrinsic self-similarity embedded in nonstationary time series (Király and Jánosi 2005). Stationary time series require that (a) the mean value of the time-series stays constant through time, i.e., the trend component is nullified, (b) the variance does not increase over time, and (c) seasonal effect is minimal. With global warming causing an increasing temperature trend and the temperature time series being seasonally dependent, the first and third constraints are automatically violated. Whether or not a time series data set is stationary or non-stationary can be statistically tested with an Augmented Dickey-Fuller (ADF) test in which results of $p < 0.05$ indicate a stationary time series data set, while p-values > 0.05 indicate a non-stationary time series data set. An ADF was applied to all temperature time series at 6 sites across the three depths and results indicated that all temperature time series were nonstationary (p-value > 0.05 for all sites and depths). Consequently, applying a statistical method designed for nonstationary time series data is relevant for this study and is within the scope of the DFA.

Before the DFAs were applied to each temperature time series, they were tested to determine if they were additive or multiplicative time series. An additive time series adds the trend, seasonality, and residual add together to make the time series, whereas a multiplicative time series multiplies the three components to make the time series. Distinguishing between an additive and multiplicative time series is completed by first plotting the detrended time series of the additive model. If the noise from the additive model were to steadily increase, then the best fit model would be multiplicative. However, in the case of our time series data, the noise variable after detrending does not steadily increase making additive time series model was the best fit for our time series data. DFAs were then applied to all additive time series models, and temperature time series were decomposed for trends, seasonality (daily, weekly, annual), and remainder (i.e., error).

Temperature time series are highly autocorrelated, thus, we avoid linear regression modelling and utilize other time series statistical analysis instead (e.g., DFA analysis). Temperature time series were cross-correlated to look at the relationship between two different time series. Cross-correlations were calculated between sites for each depth, and similarly between depths for each site. The results are presented using a correlation matrix with a scatterplot of two time series plotted against each other, fitted with a Lowess regression, and shown with the correlation value.

Heat stress metrics

Cumulative thermal stress

Cumulative heat stress was determined by first calculating the maximum monthly mean (MMM) which was then used to calculate degree heating week (DHW). DHW is the integral of time spent above the bleaching threshold of MMM+1 °C. If MMM is calculated from a short time series that includes temperatures from a bleaching event, then the MMM will be skewed high. Therefore, to determine a more accurate MMM that has not been influenced by rare bleaching events, we used a longer climatological data set acquired from satellite. To then account for temperature differences between satellite data and reefs at depth, we applied the methods developed by Venegas et al. (2019) to all in situ temperature time series data(Venegas et al. 2019). Historical sea surface temperatures (SST) from satellite data were downloaded through the NOAA's Coral Reef Watch (CRW) for years 1985–2020 (the longest available time series). Specifically, the 'CRW Daily Global 5 km Satellite Coral Bleaching Heat Stress Monitoring' (version 3.1) data sets were downloaded through ERRDAP using the closest 5 km grid (i.e., nearest neighbor) to each in situ subsurface temperature recorder (STR) location. The daily mean SST were used to calculate the maximum monthly mean temperature from the satellite data ($MMM_{satellite}$). Next, the MMM was calculated from the in situ temperature data for each site and depth ($MMM_{in\ situ}$). Then, the mean offset for in situ temperature data to account for warming temperatures and depth was calculated. This was completed by determining the $MMM_{satellite}$ from the years 2012–2018, then determining the $MMM_{in\ situ}$ for each year, calculating the difference in MMM between the satellite data and STR, and averaging them.

$$\text{Offset} = \text{mean}((MMM_{\text{satellite }2012} - MMM_{\textit{in situ}\ 2012}) + (MMM_{\text{satellite }2013} - MMM_{\textit{in situ}\ 2013}) , \ldots , (MMM_{\text{satellite }2018} - MMM_{\textit{in situ}\ 2018}) \div 8)$$

The offset was then applied to each in situ temperature time series:

$$MMM_{\textit{in situ}\ \text{corrected}} = MMM_{\text{satellite}} - \text{offset}$$

And finally, a depth-biased DHW was calculated for each STR site at all depths:

$$DHW_{\text{depth-biased}} = \int (MMM_{\textit{in situ}\ \text{corrected}} + 1\ °C)\ dt$$

The trapezoid integration for DHW at depth was calculated using the 'AUC' function in the R package 'DescTools.' DHW at depth values were calculated each year the temperature climbed above the bleaching threshold. Additionally, the DHW at depth was also calculated only for the 30 days prior to the ecological surveys. For this study, only $DHW_{depth\text{-}biased}$ was calculated (henceforth just called DHW), not the DHW traditionally calculated via satellite data.

Acute heating

Acute heating stress, for this study, is defined as any short-term spike in the temperature time series away from the normal seasonal cycle that occurred in the austral summer months. Specifically, any time the temperature rose above the bleaching threshold (MMM +1) for an intense, but relatively short period (lasting a few hours to a few days), it was considered to be an acute stress event. Acute heat stress was initially treated as binary to indicate the presence or absence of an acute thermal stress event per annum. Acute heat stress was also quantified by the number of events per year and also by the duration of the acute stress event (hours above the bleaching threshold during this short-term temperature spike).

Heating rates

The heating rate (°C hr^{-1}) for each warming period was calculated for each year for all sites and depths. The warming period is the period in which the temperature increased throughout the year, meanwhile the cooling period was the time in which temperature decreased. The exact dates in which the cooling period ended and the warming period started varied slightly from year to year, but generally the warming period occurred from September to March, and the cooling period occurred between April and August.

Measures of temperature variability

Temperature time series show complex periodic behavior, and one technique that can be applied to identify underlying periodicities is called a power spectral density (PSD) analysis. Essentially, the covariance of the time series can be represented by a function known as the spectral density. PSD analyses were applied to the time series temperature data to observe any possible underlying periodicities. The temperature data were first transformed to the frequency domain via the non-parametric Daniell-Kernal method, which calculates the smooth spectral density by using centered moving averages(Shumway and Stoffer 2017). The spectral density represents the covariance of the time series. Periodograms are used to present the squared correlation between temperature time series data and sine and cosine waves (Venables and Ripley 2002). Periodograms were calculated using a fast Fourier transform for all temperature time series from all sites and depth strata(Bloomfield 2013). The frequency axis for the periodograms were converted to cycles per unit time by extracting the frequency data from the PSD and dividing by the length of the sample interval. The spectral density was then multiplied by 2 so that the area under the curve of the periodogram equals the variance of the time series. Periodograms were applied to the entire time series of a site (all data that were collected between 2012 and 2018), and PSD was calculated for the warming and cooling cycles for each time series. Furthermore, a few additional metrics were calculated from the PSD output just for the 2014–2015 time period. Specifically, the peaks for the power spectral density plots for variability in the temperature time series due to tides (12 hr), daily (24 hr), and interval waves (48 hr) were quantified and compared between sites and depths.

Daily temperature ranges were calculated for the warming and cooling seasons of each year for the entire time series. In 2015, daily temperature ranges and daily mean temperatures were calculated for the 30 days prior to the ecological surveys. The intent was to determine if the daily temperature means and ranges may have been extra warm at the beginning of the bleaching event when bleaching prevalence in corals was being recorded.

The coefficient of variation (CV) was calculated for all sites and depths each year. It is a measure of relative variability and is the ratio of standard deviation to the mean; a high CV value suggests more variation relative to its mean compared to a low CV value. CV is a useful calculation to determine the variance of the historical mean temperature and the current mean temperature, and thus a method to evaluate inter-annual variability in seawater temperatures.

Ecological surveys

As a regular part of NOAA's National Coral Reef Monitoring Program (NCRMP), bleaching surveys were collected at sites using a stratified random sampling design. These surveys were conducted during February and March of 2015, which coincided with the beginning of the thermal stress event. American Samoan coral reefs were exposed to hot water anomalies from January to June of 2015; peak heat occurred from mid-March to late April. Thus, the full extent of coral bleaching was not captured in these ecological surveys, but they may provide a glimpse into how corals react to the early stages of heat stress. Only the NCRMP benthic survey sites that were within 3 nautical miles of the STR were used in this study. The total number of NCRMP benthic survey sites that fit within the 3 nautical miles of the STR are included in Table 1.

Bleaching surveys were conducted using the Rapid Ecological Assessment methods (Winston et al. 2019). Random sites are selected across three depth categories (shallow, 0–6 m; mid > 6–18 m and deep > 18–25 m) on the forereef. Surveys at each site were conducted within four segments (1 m × 2.5 m) along an 18-m belt transect. Adult coral colonies (≥ 5 cm) abundance by genus and bleaching extent and severity were recorded. The four segments were pooled together, and site-level bleaching prevalence was calculated by dividing the number of corals displaying any loss of pigmentation (paled to fully bleached) by the total number of colonies multiplied by 100. Bleaching prevalence was calculated for all hard corals combined, along with the dominant coral genera.

In addition to the recorded bleaching in 2015, jurisdictional partners in American Samoa also observed bleaching during the austral summers of 2015 and 2017. Unfortunately, the full extent of bleaching around the whole of Tutuila was not surveyed by any institute or agency, so quantitative information is not available. However, qualitative information from locals observing mass bleaching and occasionally photographing devastated reefs suggests that mass bleaching events occurred in both 2015 and 2017.

Table 1. The number of benthic surveys within 3 nautical miles of each site where a temperature logger was deployed.

Site	Depth	Number of benthic surveys within 3 nautical miles to the STR
Northwest (NW)	deep	3
	mid	3
	shallow	2
Northeast (NE)	deep	5
	mid	7
	shallow	5
Southwest (SW)	deep	6
	mid	6
	shallow	6
Southeast (SE)	deep	5
	mid	6
	shallow	5

Statistical analysis

Time series analysis and temperature trend

As previously described, temperature time series analysis was conducted via detrended fluctuation analysis (DFA). DFAs were applied to all additive time series models, and temperature time series were decomposed for trends, seasonality (daily, weekly, annual), and remainder (i.e., error). All DFAs were conducted in R version 4.0.3 using the 'mstl' function in the R package 'forecast'. Since temperature data were recorded hourly, the seasonality variables set in each model were defined as 24, 168, and 8,766 for daily, weekly, and yearly periodicity. The time series analysis identified years that were warmer than the previous years, and they were identified as having a warming trend.

Heat stress metrics from full temperature time series (2012–2018)

A series of generalized linear models (GLMs) were applied to the heating metrics to determine if they varied by site, depth, or years. Specifically, GLMs with a binomial distribution and logit link were applied to test for differences in presence/absence of acute and cumulative heat stress events between site, depth, and year. GLMs with a Gaussian distribution and identity function tested for differences in heating rates between sites, depth, and years. Additionally, GLMs with a gamma distribution and log link function were used to determine if daily temperature ranges were significantly different between sites, depths, years, months, and heating versus cooling seasons. GLMs with a Gaussian distribution and identity link function were applied to test for differences in CV values between site, depth, year, and warming versus cooling seasons

For all GLMs, model assumptions of independence, homogeneity of variance, and normality of error were evaluated through diagnostic leverage, Cook's distance, dfbetas (Cohen and Cohen

2008). Checks for all GLMs indicated that no influential data points or outliers were present in the data and model assumptions were met.

Heat stress metrics from bleaching year (2015)

In addition to the GLMs applied to the heating metrics across the full time series (2012–2018), additional GLMs were applied to the heating metrics calculated during the 2015 bleaching events to test for spatial differences between sites. Specifically, GLMs with a Gaussian distribution and identity function were applied to acute stress and cumulative (DHW) heat stress, and the number of acute heat stress events experienced, between site and depth for the 2015 bleaching season only. Additionally, GLMs with a Gaussian distribution and identity function tested for differences in heating rates between sites and depth. GLMs with a gamma distribution and log link function were used to determine if daily temperature ranges were significantly different between sites and depths. Furthermore, the peaks from the periodograms produced by the spectral analysis that were associated with 24-hr (daily), 12-hr (tidal), and 48-hr (internal wave) cycling were quantified, and GLMs were applied to the quantified peaks to determine which of these parameters varied with depth and site.

Heat stress metrics associated with bleaching from ecological surveys

Ecological data (i.e., bleaching prevalence data) were only used from NRCMP survey sites within 3 nautical miles of the temperature logger at the same depth. A series of univariate distributional regression models was used to assess the association between bleaching prevalence and heating metrics. While exploring the ecological survey data, generalized additive models for location, scale, and shape (GAMLSS) were used to test for differences in bleaching prevalence for all hard coral genera combined and separately for the dominant coral genera.

The primary advantage of applying GAMSLSS (as opposed to Generalized Linear Models (GLMs) or Generalized Additive Models (GAMs)) is that these univariate distributional regression models allow for flexibility in the distributions and have over 100 continuous, discrete, and mixed models for the response data. Bleaching prevalence data are notoriously skewed to data values of either 0 (0% bleaching prevalence) or 1 (100% bleaching prevalence). GAMLSS allow for data that are bounded by 0 and 1, but also have values in between. Additionally, GAMLSS allow for the distribution parameters (mu, sigma, tau, and nu), not just the mean values, to be modelled in terms of both fixed and random effects. The optimal GAMLSS were chosen following steps in Stasinopoulos et al. (2017) by testing for the best model family to fit the data (zero-inflated, one-inflated, inflated at zero and one), determining the significant variables, determining the best fit distribution parameters (mu, sigma, tau, and nu), and applying AIC (Stasinopoulos et al. 2017).

While determining the best-fit model, the variance of inflation factor (VIF) was calculated between the heating metrics to determine the amount of multi-collinearity between multiple regression variables. Cumulative heating stress (DHW) and acute heat stress (short-term spike in temperature) were highly correlated (r^2=93%, VIP > 10), but when either DHW or acute heat stress were removed from the VIF calculation with the rest of the heating metrics (trend, heating rates, etc.), there was no collinearity (low VIP value of 1.6). Despite the strong relationship between cumulative and acute heat stress, neither metric was removed from the optimal due to the ecological relevance that both metrics have on the physiology of a coral. Corals physiologically react to both short-term heat stress and long-term heat stress; thus, both predictors were retained in the models. This was justified by comparing the AIC values among the three models: (1) bleaching prevalence ~ cumulative + acute + other metrics, (2) bleaching prevalence ~ cumulative + other metrics, and (3) bleaching prevalence ~ acute + other metrics), in which both parameters are kept or one or the other is removed. The AIC values were within 2 units of each other and thus the models were not significantly different from each other. Due to their ecological relevance, both cumulative and acute heat stress metrics were kept in the models, despite being highly correlated. All the other heating metrics did not exhibit multi-collinearity.

GAMLSS were initially applied to bleaching prevalence data to test for differences between depth, site, and the interactions between the two for all hard corals and the dominant coral genera. GAMLSS were also applied to determine whether bleaching prevalence varied according to heat stress metrics. Heating metrics were only applied to ecological sites that fell within a 3 nautical mile radius of the temperature logger and at the same depth. Five types of heat stress were identified: cumulative heat stress, acute heat stress, warming trend, heating rates, and variability. Several heating metrics were calculated for each type of heat stress. For example, acute heat stress is one type of heat stress, measured by multiple metrics such as its presence or absence, the number of acute heat stress events, and we also quantified how long the acute heat stress events lasted. Initially, we chose one heating metric from each type of heat stress and used GAMLSS to determine if each heating stress type impacted the bleached prevalence of all hard corals combined, as well as the dominant coral genera. This particular analysis cumulative heat stress: DHW; acute heat stress: hours above the bleaching threshold; increasing trend, heating rate, variability: mean daily temperature range for the 2014–2015 warming season. Trend was removed in the GAMLSS analysis because all reefs and sites experienced a warming trend in 2015 so there were no differences in trend. Bleaching prevalence was the response variable in the models. Furthermore, GAMLSS were also applied to bleaching prevalence data with only temperature variability metrics included in the model. Specifically, we tested to see if bleaching prevalence varied according to the diurnal, tidal, or internal wave period, as well as the daily temperature ranges for the entire warming period linked to the 2015 bleaching event, and also the temperature range for the 30 days prior to the ecological survey.

Results

Time series analysis

Trends and detrended seasonality

Temperature time series were detrended to decompose the trend from the data and also observe seasonality periodicities. In the case that less than two years of data were available, then the trend could not be determined. However, daily and weekly periodicities could still be evaluated. Daily, weekly, and yearly time factors were the strongest variables controlling the temperature time series (Figure 2).

The time series analysis revealed a few key patterns. Firstly, overall patterns in each temperature logger were similar between site and depth, with acute heat stress (spikes in temperature above the bleaching threshold, MMM+1°C, lasting for a few hours to a few days with high peaks) occurring in austral summers of 2015, 2016, and 2017 for most sites at all depths (Figure 2c). The acute heat stress also occurred in 2018 for the middle and deep reefs, but not for the shallow reefs. Secondly, all sites and depths showed an overall increasing temperature trend through time, with the exception of 2016 when the mean annual temperature decreased in between the two massive bleaching events, and in 2018 when temperature decrease following the second massive bleaching event (Figure 2b). Thirdly, daily temperature variability is only high while waters are warm; however, during cooling seasons the daily temperature has less range (Figure 2c). The highest daily ranges only occur for a few days and coincide with the acute heat stress period. Fourthly, measurements from week to week indicate that the biggest variability in temperature occurred in the few weeks prior to the highest seasonal temperatures reached each year (Figure 2d). In other words, daily variability is greater during warming periods, but in the beginning of the warming season, the first few weeks have lower variability. However, at the end of the heating season, the week-to-week variability is highest right before the peak seasonal temperature is met. This is true for 2013–2016, but not for 2017 or 2018. And finally, when looking at the periodicity due to yearly cycles, every single annual pattern had a double high peak in which there was an initial heating rate increase, followed by a slight decrease, and then another increase in temperatures during the warming period (Figure 2e).

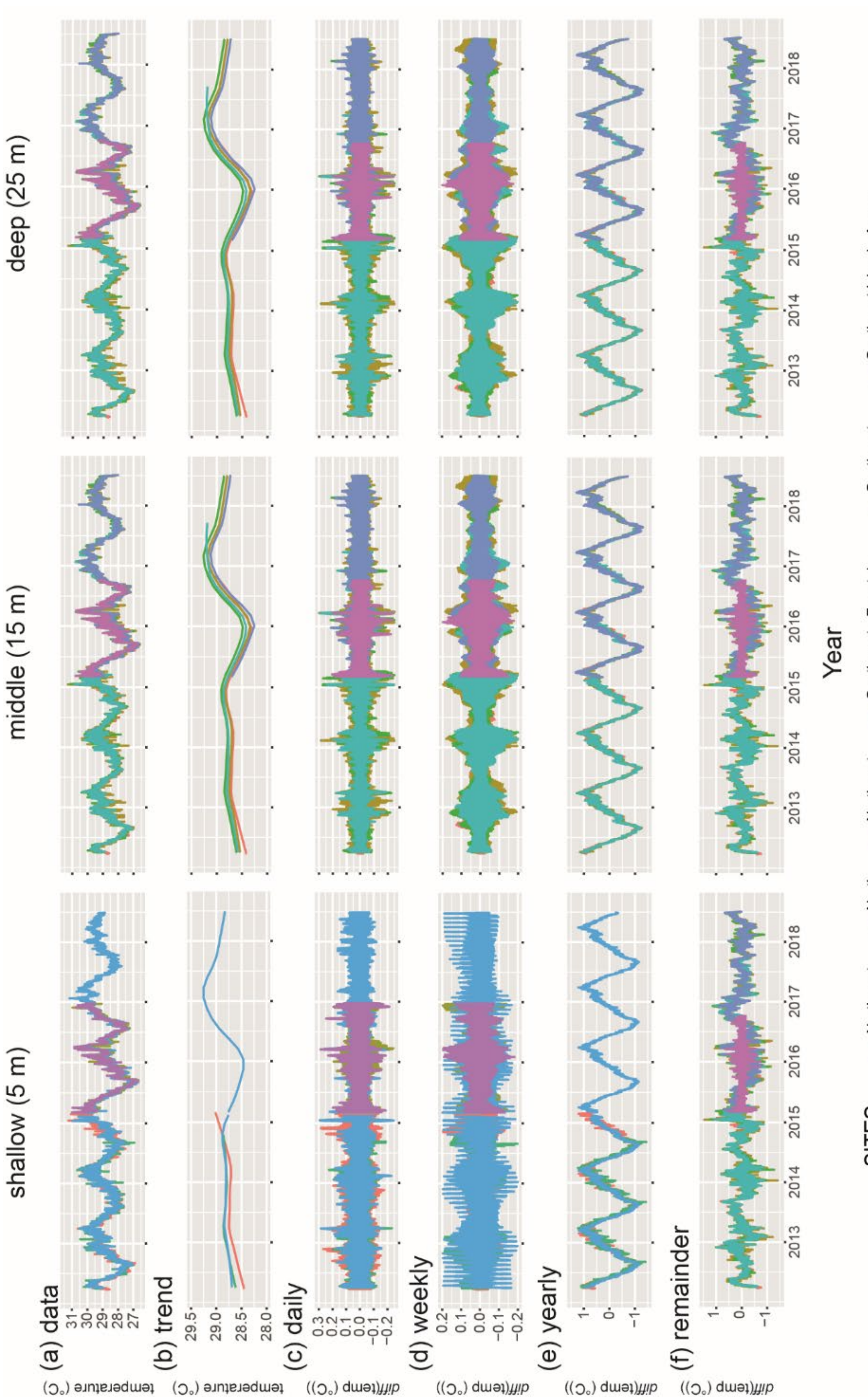

Figure 2. Temperature time series from shallow (5 m), middle (15 m), and deep (25 m) reefs at six sites located around Tutuila, America Samoa. Plots show (a) hourly temperature data (°C) from 2012–2018, (b) trend, and the difference in temperature from trend due to (c) daily, (d) weekly, and (e) yearly periodicities. The leftover noise in the data unexplained by the trend or defined periodicities is show as (f) the remainder.

Cross-correlation analysis

Temperature time series were highly correlated when compared between sites and depths (Figure 3). In fact, temperature patterns were nearly identical between shallow, middle, and deep reefs for the same site, especially at the Northwest, Northeast, Southeast, and Southeast Island sites where cross correlation values were all above 0.90 (i.e., at least 90% similar temperature time series between depths). No distinct geographic patterns were observed, except that the Northeast and Southeast sites were highly correlated for shallow, middle, and deep reefs (correlation coefficient = 0.80, 0.89, 0.89, respectively). Upon investigation for cross-correlations between sites that had correlation coefficients of ~0.50, the lower values were due to differences in time period (i.e., one logger may have only collected half the data), and when equal time periods were applied, then the time series were highly cross-correlated. Although temperature time series are shown to have similar patterns between sites and depth strata at the reefs around Tutuila, further analyses explored potential differences in variability and other metrics between sites and depths. Together, these results suggest that there is very little temperature structure across depth, and temperature patterns are fairly consistent even across a variety of oceanographic conditions at the island level.

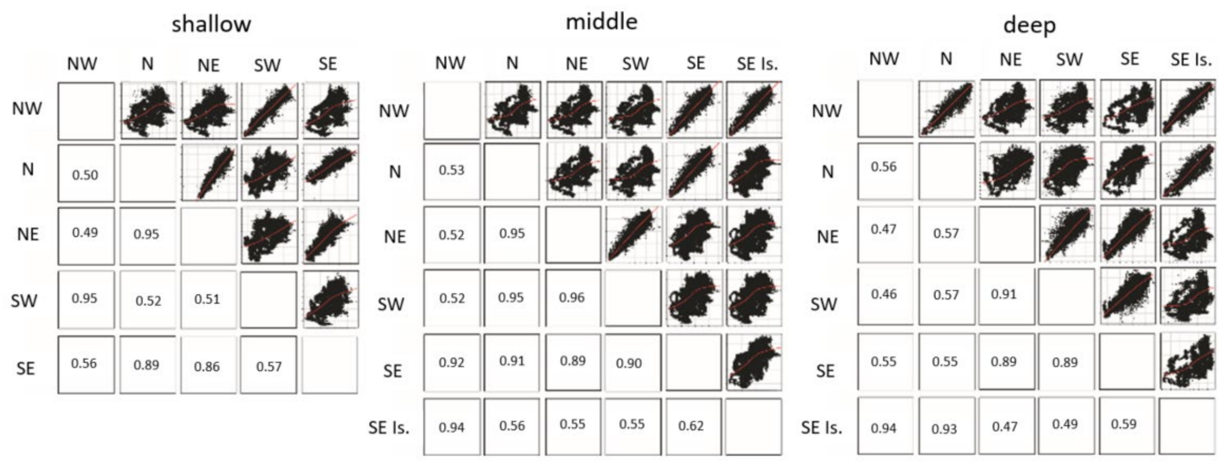

Figure 3. Cross-correlation matrix comparing temperature time series between sites for different depths. Scatterplots of two pairs of time series temperature values are plotted against each other and the estimated correlation is displayed in the counterpart matrix box. Red lines indicate the Lowess fit between two time series. Cross-correlations were made between sites (NW, N, NE, SW, SE, SE Island) for (a) shallow, (b) middle, and (c) deep reefs. No data were collected at the SE Island site for the shallow reefs.

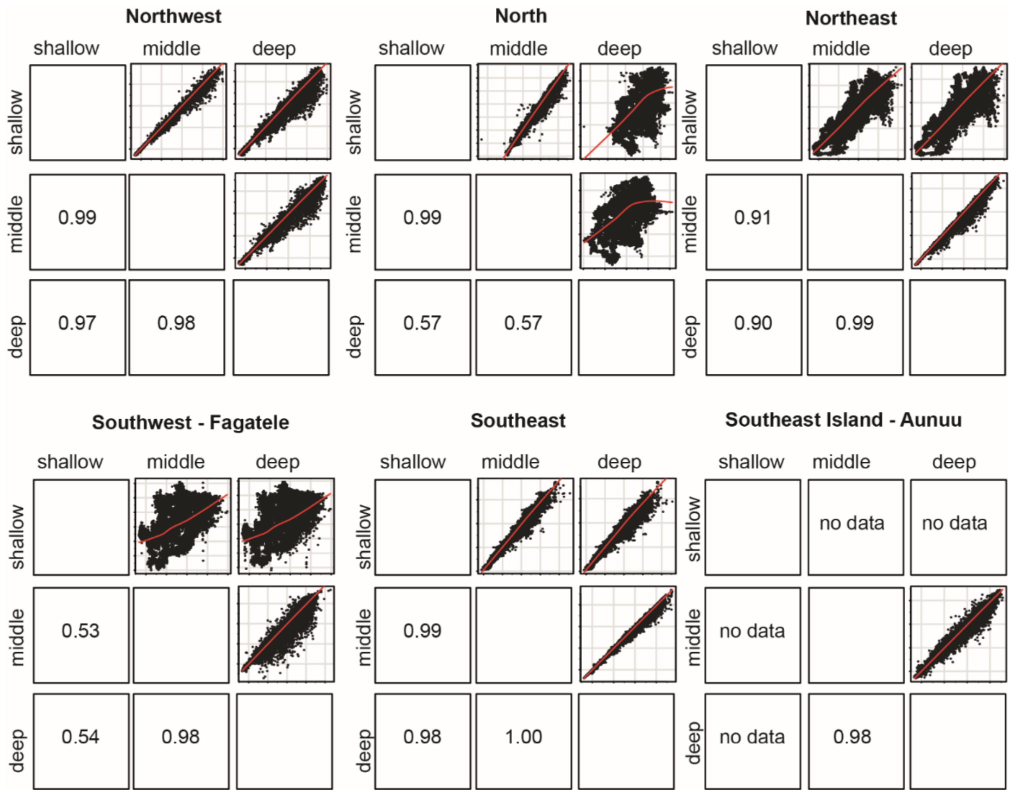

Figure 4. Cross-correlation matrix comparing temperature time series between depth strata for all sites. Scatterplots of two pairs of time series temperature values are plotted against each other and the estimated correlation is displayed in the counterpart matrix box. Red lines indicate the Lowess fit between two time series. Cross-correlations were made between depth strata (shallow 5 m, middle 15 m, and deep 25 m) for six sites (NW, N, NE, SW, SE, SE Island) around Tutuila, American Samoa. No data were collected at the SE Island site for the shallow reefs.

Heat stress metrics

A summary of how the heating metrics varied by year, site, and depth for the full time series (years 2012–2018) can be found in Table 2. Furthermore, a summary of how the heating metrics varied by site and depth for the bleaching event of 2015 are found in Table 3.

Table 2. Generalized linear model results (F and p-values) examining the temporal (year) and spatial (site and depth) differences in heating metrics across year, site, depth, and their interactions (year*site*depth) for the entire temperature time series (2012–2018). Heating metrics include cumulative heat stress (long-term accumulated time above the temperature bleaching threshold), acute heat stress (short-term spike in temperature above the bleaching threshold), warming trend, heating rates, and measures of temperature variability.

Type of Heat Stress	Heating Metric	Year		Site		Depth		Year*Site*Depth	
		F	p-value	F	p-value	F	p-value	F	p-value
Cumulative stress	presence/absence	7.67	0.007 *	0.02	0.885	1.25	0.292	0.52	0.598
	DHW	40.25	< 0.001 *	161.6	< 0.001 *	68.4	< 0.001 *	35.8	<0.001 *
Acute stress	presence/absence	6.1	0.02	1.5	0.21	0.17	0.84	0.11	0.89
	number of acute stress events during summer	13.7	0.0005 *	0.06	0.809	0.33	0.717	0.16	0.849
	hours above bleaching threshold	1.07	0.304	5.45	0.023 *	0.83	0.439	3.63	0.033 *
Warming trend	presence/absence	4.62	0.03 *	0.0	1.0	0.0	1.0	0.0	1.0
Heating rates	warming	10.4	< 0.001 *	2.5	0.04 *	4.1	0.02	2.1	0.05
Variability	daily temperature range	12.3	< 0.001 *	10.8	0.001 *	11.3	0.003	0.73	0.484
	CV	6.9	< 0.001 *	11.5	<0.001 *	6.8	0.002 *	2.6	0.002 *

Asterisk (*) indicates a significant result.

Table 3. Generalized linear model results (F and p-values) examining the spatial differences in heating metrics across site, depth, and the interaction between site and depth just for the 2014-2015 period when the massive bleaching event occurred in American Samoa. Heating metrics include cumulative heat stress (long-term accumulated time above the temperature bleaching threshold), acute heat stress (short-term spike in temperature above the bleaching threshold), warming trend, heating rates, and measures of temperature variability

Type of Heat Stress	Heating Metric	Site	Depth	Site*Depth
Cumulative stress	presence/absence	No significant difference detected because cumulative stress occurred at all sites and all depths in 2015		
	DHW	p = 0.004 *	p = 0.003 *	p = 0.019 *
Acute stress	presence/absence	No significant difference detected because acute stress occurred at all sites and all depths in 2015		
	number of acute stress events during summer	p < 0.001 *	p < 0.001 *	p < 0.001 *
	days above bleaching threshold	p = 0.031 *	p = 0.032 *	p = 0.065
Warming Trend	presence/absence	No significant difference detected because trend was warming for all sites and reefs		
Heating rates	warming	p = 0.087	p = 0.106	p > 0.05
Variability	Tides: Peak of PSD at 12 hr	p = 0.111	p = 0.327	p = 0.113
	Daily: Peak of PSD at 24 hr	p = 0.006 *	p = 0.0009 *	p = 0.005 *
	Internal Waves: Peak of PSD at 48 hr	p = 0.009 *	p = 0.005 *	p = 0.0173
	Daily Temperature Range (2014-2015)	p = 0.008 *	p = 0.016 *	p = 0.62
	Daily Temperature Range (30 days prior to ecological survey)	p < 0.001 *	p < 0.001 *	p <0.001 *
	Daily Temperature Mean (30 days prior to ecological survey)	p < 0.001 *	p < 0.001 *	p < 0.001 *

Asterisk (*) indicates a significant result.

Cumulative heating

(a) Full time series (2012–2018)

Cumulative stress (i.e., depth-corrected DHW) varied significantly by year ($p < 0.001$) and was only detected in 2015 and 2017 (Figure 5; shows only the NE site which has the longest temperature time series data available). For the years DHW was present, it also varied to a lesser extent by depth ($p < 0.001$) with shallow reefs having slightly higher cumulated heat stress, and site, with the Southwest sector experiencing slightly higher levels of cumulated stress.

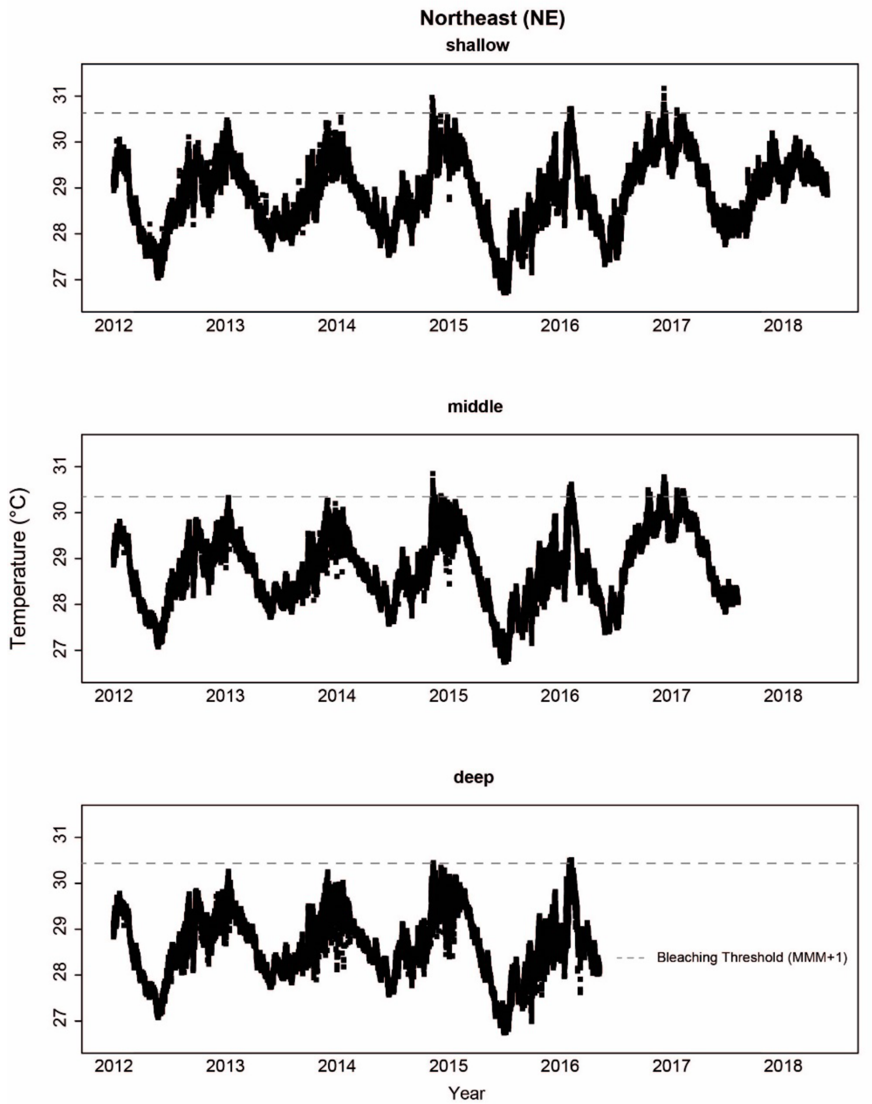

Figure 5. Bleaching thresholds (MMM+1) applied to temperature time series for shallow, mid, and deep reefs at the Northeast site. Bleaching was observed in the austral summers of 2015 and 2017.

(b) Bleaching year (2015)

All reefs at all sites and depths experienced cumulative heat stress events (measured as depth-corrected DHW). When the values of depth-corrected degree heating weeks (DHW) were compared between sites, the Southwest site in Fagatele Bay had slightly more cumulative stress than the other sites. All of the other sites had similar cumulative heat stress exposure to each other. When the values of DHW were compared between depths, then the shallow reefs experienced higher values while the mid and shallow reefs were exposed to similar levels of DHW.

Acute heat stress

(a) *Full time series (2012–2018)*

The presence or absence of acute heat stress was significantly different between years ($p_{(1,6)} = 0.02$), but not between sites ($p_{(1,2)} = 0.21$) or depth ($p_{(2,0.17)} = 0.84$); acute stress events occurred primarily in the austral summer months of 2015, 2016, and 2017. However, when the number of hours above the threshold were evaluated, acute stress did vary spatially with shallow reefs experiencing slightly longer acute stress events (up to 52 hours of an acute heat stress in the shallow reefs compared to only a few hours (< 10 hr) in the deeper middle and deep reefs). Furthermore, the Southeast sector of Tutuila experienced slightly longer acute heat stress events than the other sectors (average acute heat stress event lasted 27 hours in the SE Sector, while the SW, NW, and NE Sectors experienced acute heat events that lasted an average of 19, 13, and 10 hours, respectively). Also, the number of acute stress events that occurred varied; one event occurred in 2015 and 2016, and three events occurred in the summer months of 2017.

(b) *Bleaching year (2015)*

All reefs at all sites and depths experienced acute stress events in 2015. The Southeast site had more hours above the threshold, while all the other sites experienced relatively equal hours above the bleaching threshold. The Southeast site in Fagatele Bay, experienced more hours of intense short-term heat because there were two acute heat stress events while only one event occurred at. The two acute heat stress events occurred in the shallow reefs and not the mid or deep reefs.

Heating rates

(a) *Full time series (2012–2018)*

Heating rates were significantly different between depths ($p_{(2,4)} = 0.02$) with shallow reefs generally warming more rapidly than mid and deep reefs. Heating rates were also significantly different between years ($p_{(5,10)} < 0.001$), with the heating rate increasing each year except in 2018. In 2017, seawater temperature rose rapidly in the first few weeks of the warming season, and then continued to warm but at a slightly slower rate (Figure 2a).

(b) *Bleaching year (2015)*

Heating rates did not vary by site nor by depth for this one year. Heating rates in 2015 were greater than heating rates in 2014.

Temperature variability

(a) *Full time series (2012–2018)*

The power spectral density analysis showed that high temperature variation (i.e., peaks in the dendrograms) occurred at multiple frequencies (Figure 6). The PSD also revealed that reefs at different depths exhibit different drivers for temperature variation. Expectedly, 24 diurnal light cycles was a significant peak for all three depths, especially in the shallow waters where the strongest frequency for both warming and cooling seasons was at 24 hours. The PSD also allowed us to observe the influence of tides on the reefs at each depth, with semidiurnal tides occurring every 12 hours and influencing the water temperature at all reefs and at all depths but becoming increasingly important with depth. Furthermore, in the shallow reefs, the diurnal cycle had a stronger influence on temperature variation than semidiurnal tides. However, for some mid water reefs, the diurnal daylight cycles and semidiurnal tides had almost a similar influence on the temperature variation, i.e., 24 hr and 12 hr frequency peaks were nearly the same height, at least for reefs at the North, Northeast, and Southeast Island sites during the warming season. Interestingly, the deep reefs at all sites except the North site were also influenced by internal waves occurring at a frequency of every 48 hours, which was not observed at shallow or middle reefs. Furthermore, these internal waves only appear during the warming season and are not detectable during the cooling months. In general, the PSD analysis confirmed the cross-correlation analysis showing similar large-scale temporal patterns, and yet the PSD analysis also provided additional information on fine-scale temporal patterns, revealing that they differ slightly by depth.

Daily temperature ranges were significantly different ($p_{(df,F)}$ = values) between depth ($p_{(2,11)} = 0.003$), year ($p_{(5,12)} < 0.001$), periods of heating versus cooling ($p_{(1,7)}$ <0.001), and site ($p_{(5,10)} < 0.001$). Temperature ranges were more variable during the heating part of year compared to the cooling periods (Figure 7a). The greatest temperature ranges were observed in the austral summer months of January, February, and March. Unexpectedly, however, the deeper reefs experienced the greatest temperature ranges (Figure 7b), not the shallow reefs. There were also significant differences between sites; the reefs at Southwest Fagatele had higher daily temperature ranges than the other sites, but there was no apparent spatial pattern. Furthermore, daily temperature ranges were also statistically different between years, but there was no relationship between daily temperature ranges and the massive bleaching events; the 2014–2015 year had high variability in daily temperature, but the 2016–2017 year did not.

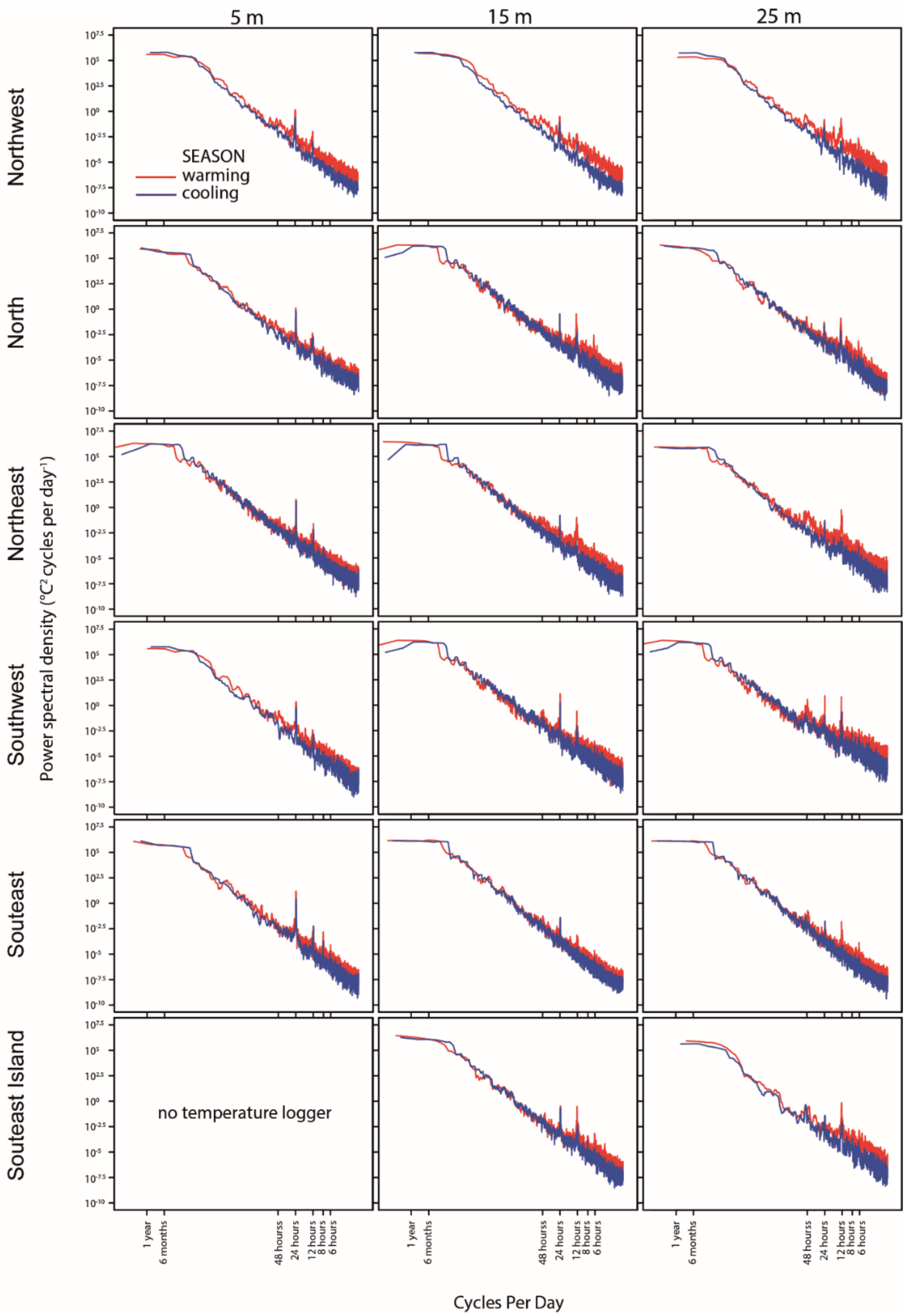

Figure 6. Periodograms of power spectral density analysis applied to all sites at each depth show the frequencies at which high variation in the temperature time series occurred. The frequency y-axis for the periodograms were converted to cycles per unit time by extracting the frequency data from the PSD and dividing by the length of the sample interval. The spectral density was then multiplied by 2 so that the area under the curve of the periodogram equals the variance of the time series.

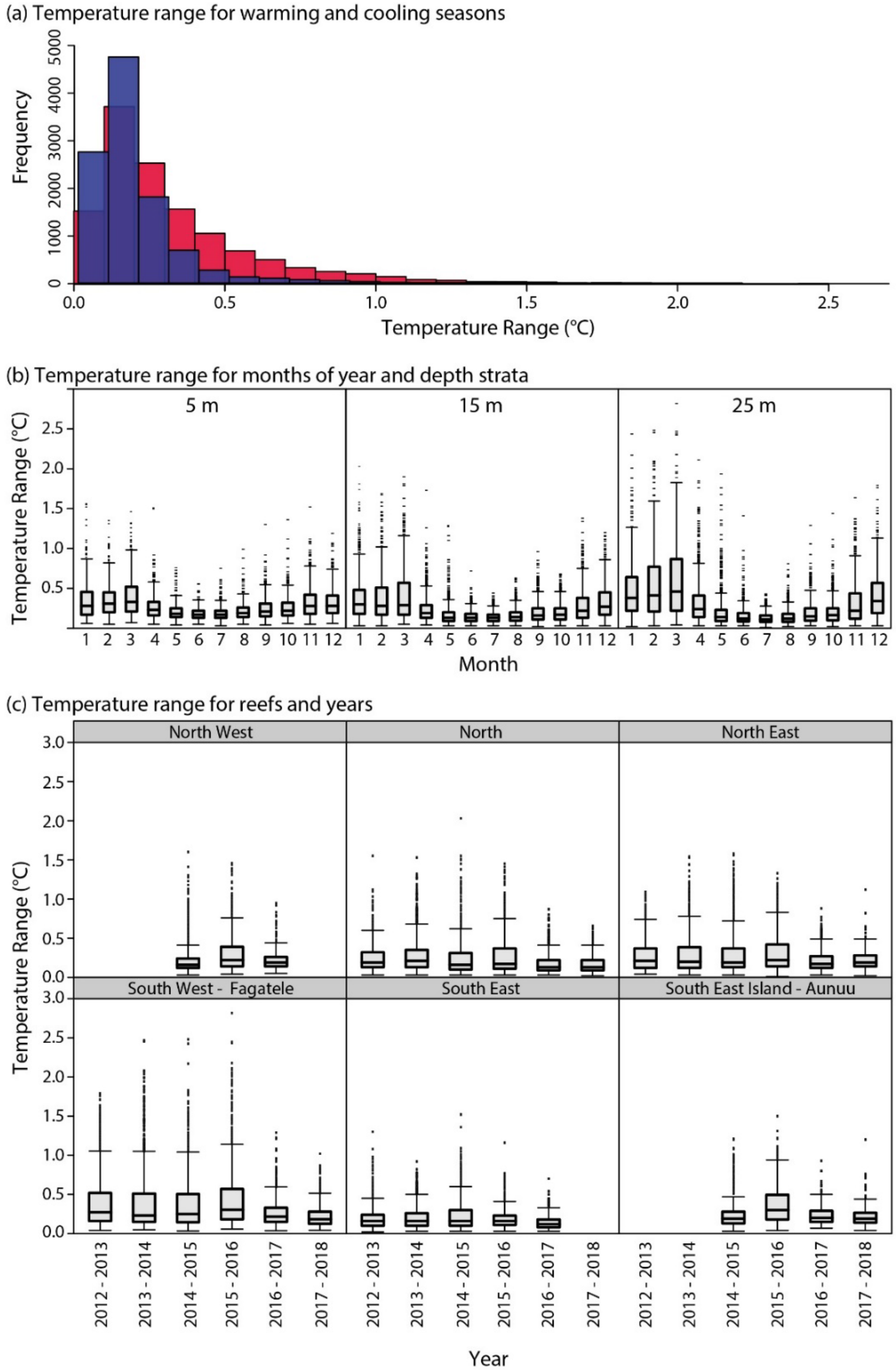

Figure 7. Daily temperature ranges: (a) histogram of daily temperature range for warming and cooling seasons, (b) temperature range for months of year and depth strata, and (c) temperature range for reefs and years.

Coefficient of variation (CV) values differed significantly between sites ($p_{(5,12)} < 0.001$), depth ($p_{(2,7)}$–0.002), and year ($p_{(5,7)} < 0.001$), but not between warming and cooling seasons ($p_{(1,0.009)} = 0.93$). The interactive effect between sites, depth, and year was also significant ($p_{(20,2)} < 0.01$). Due to the interaction effect, no consistent pattern was evident between sites and years. However, post-hoc Tukey tests reveal that deep reefs varied more from their long-term mean compared to the middle and shallow reefs (Figure 8). On average, deep reefs vary ± 72.3% from their long term mean temperature, whereas mid and shallow reefs vary ± 63.8% and ± 62.0%, respectively, from their long term temperature.

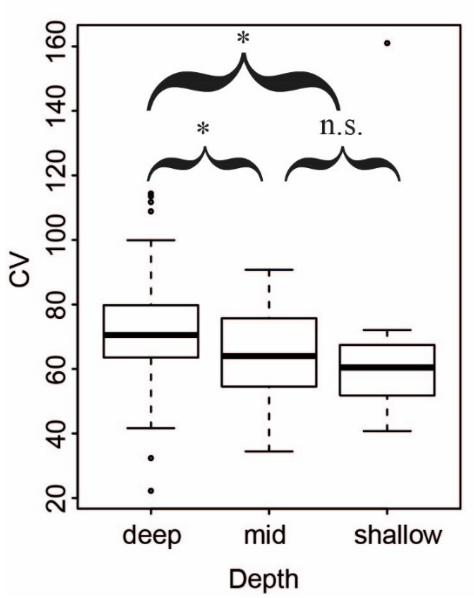

Figure 8. Boxplots of coefficient of variation (CV) values for shallow (5 m), mid (15 m), and deep (25 m) reefs. Deep reef CV values are significantly different from middle and shallow reefs (*), but the CV of middle and shallow reefs are not significantly different from each other (n.s.).

(b) Bleaching year (2015)

Tides (measured by peak in PSD at 12 hr) had similar influences on reefs at all sites and depths (Table 3). Daily fluctuations (measured by peak in PSD at 24 hr) were greater at shallow depths compared to the mid and deep reefs, and Southwest site in Fagatele showed greater daily fluctuations compared to the other sites. Internal tides (measured by peak in PSD at 48 hr) occurred more at the deep reefs compared to the mid and shallow reefs. The Southwest site in Fagatele was exposed to more internal waves compared to the other sites. For the warming period prior to the mass bleaching event, daily temperature ranges varied between site and depth. Unexpectedly, the deeper reefs experienced greater daily temperature ranges than the shallow reefs. Also, Southeast Island Aunuu experienced high daily temperature ranges, while the Southeast experienced lower daily temperature ranges. Daily temperature means and ranges 30 days prior to the ecological survey date varied between site and depth, as well as day, since the ecological surveys were conducted on different days over a month long period.

Linking heating metrics from 2015 bleaching event to NCRMP benthic surveys

Dominant coral taxa at the ecological sites around Tutuila, American Samoa

Table 4 provides a list of all the coral genera (with acronym) recorded in the survey sites in 2015. The topmost abundant coral taxa present are in bold.

Table 4. Hard coral genera observed at survey sites and their acronym. Dominant genera are in bold.

Genera	Acronym	Genera	Acronym
Acanthastrea	ACA	*Hydnophora*	HYD
Acropora	**ACR**	***Isopora***	**ISO**
Alveopora	ALV	*Leptoria*	LEA
Astreopora	AST	***Leptastrea***	**LEP**
Coeloseris	COE	*Leptoseris*	LET
Coscinaraea	COS	*Lobophyllia*	LOB
Ctenactis	CTE	*Merulina*	MER
Cyphastrea	CYP	***Montastrea***	**MON**
Cycloseris	CYC	*Montipora*	MOT
Diploastrea	DIP	*Pachyseris*	PAC
Echinophyllia	ECL	***Pavona***	**PAV**
Echinopora	ECP	*Platygyra*	PLA
Favia	FAA	***Pocillopora***	**POC**
Favites	FAV	***Porites***	**POR**
Fungia	FUN	*Psammorcora*	PSA
Gardineroseris	GAR	*Sandalolitha*	SAN
Galaxea	**GAL**	*Stylocoeniellla*	STC
Goniastrea	GON	*Stylophora*	STY
Goniopora	GOP	*Symphyllia*	SYM
Herpolitha	HER	*Turbinaria*	TUR

Regardless of bleaching, coral assemblage varied with depth, and the pattern was not necessarily the same between sectors. At the NE and SE sectors around Tutuila, most of the coral genera present were the same in the shallow and middle reefs; they were also present in the deep reefs, along with additional genera. In the SW Sector (of Fagatele), the coral genera in the deep reefs varied from the middle and shallow reefs, with some overlap in genera between the shallow and middle reefs. At this location, the shallow reefs also had quite a few genera not found in either the middle or deep reefs. Coral assemblage varied with sector for all depths, although there was more overlap in coral genera in the middle reefs.

Spatial patterns of bleaching prevalence dominant hard coral taxa

In general, the percentage of coral colonies that bleached was fairly low for all dominant coral genera (Figure 9). This is likely due to the ecological surveys being conducted early on in the bleaching event. These plots do not necessarily portray the full extent to which bleaching occurred in American Samoa the months after the surveys were conducted.

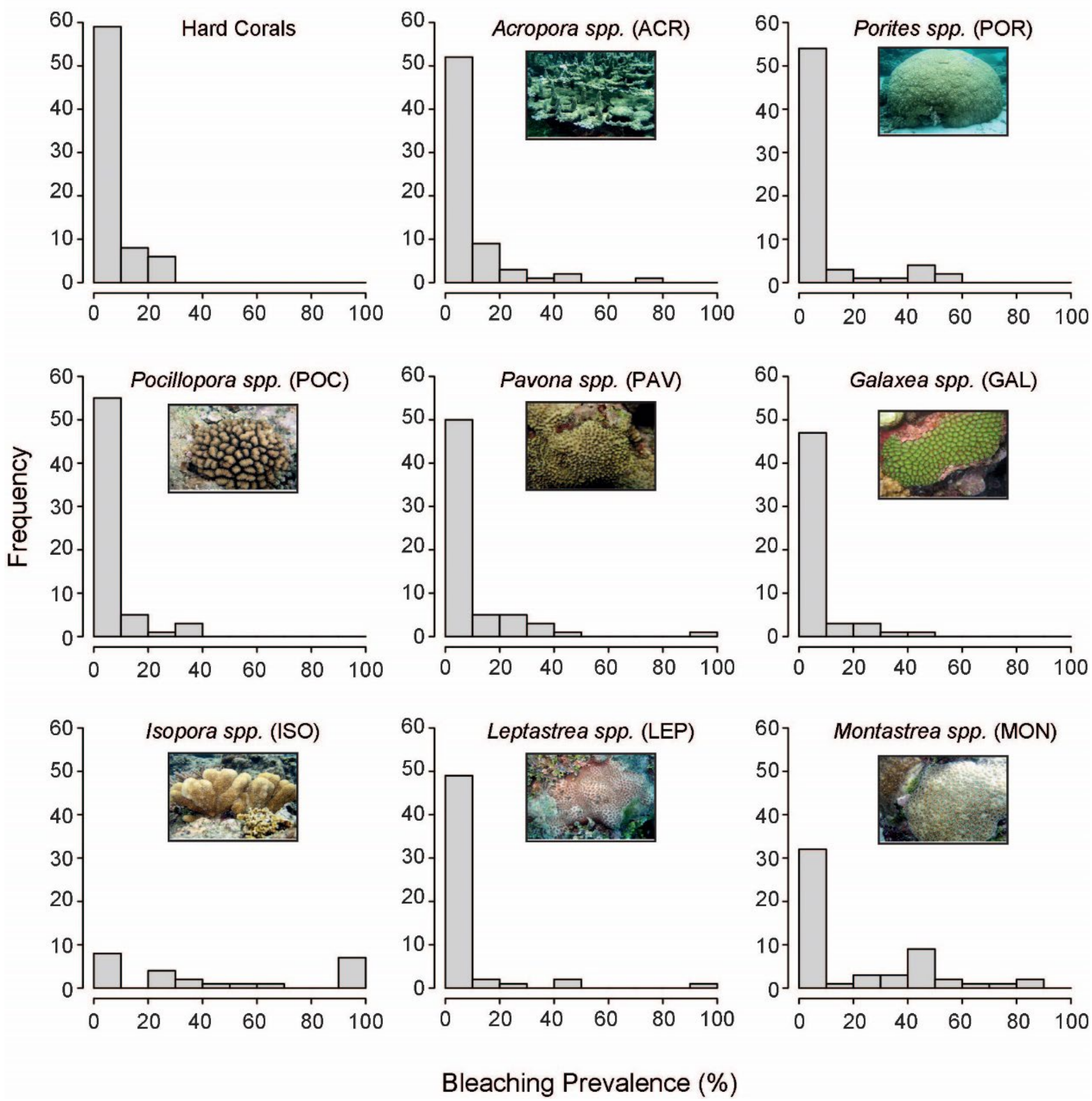

Figure 9. Histogram of bleaching prevalence for the dominant coral taxa.

The spatial variations between depth and sector in bleaching prevalence of all hard coral and dominant coral genera were explored through GAMLSS. Bleaching prevalence varied by depth for all hard corals (Table 5; Figure 10). It appears that the bleaching prevalence of most dominant coral genera did not vary by depth; the overall trend of hard corals was driven by a few genera (*Leptastrea* and *Montastrea*). Since the ecological surveys were conducted at the beginning of the bleaching event, this may suggest that *Leptastrea* and *Montastrea* were the first two coral genera to respond to heat stress. Bleaching prevalence did not differ across sectors in any taxa, except for *Pocillopora* which experienced the most bleaching in the Southwest Sector in Fagatele Bay. Bleaching prevalence was significantly impacted by the interaction of both depth and sector for *Galaxea.*

Table 5. GAMLSS model output (Likelihood Ratio Test (LRT) and p-value) testing the significance of depth, sector, and the interaction between the two for all hard corals combined and the dominant genera.

Coral	**Depth**		**Sector**		**Depth*Sector**	
	LRT	p-value	LRT	p-value	LRT	p-value
hard corals	4.15	0.045 *	3.94	0.247	0.70	0.863
Acropora	0.01	0.917	0.05	0.924	0.31	0.957
Porites	0.59	0.466	0.06	0.997	4.21	0.247
Pocillopora	3.79	0.051	9.44	0.024 *	1.87	0.600
Pavona	3.34	0.067	2.72	0.437	2.32	0.509
Galaxea	1.44	0.231	3.97	0.264	8.77	0.033 *
Isopora	0.15	0.703	0.99	0.369	5.77	0.056
Leptastrea	3.21	0.036 *	0.86	0.564	2.55	0.467
Montastrea	9.72	0.002 *	2.3	0.513	0.74	0.864

Asterisk (*) indicates a significant result.

Bleaching prevalence was greater in shallow reefs for all hard corals. It remained fairly low at the deeper depths and reached values of up to 18%. Shallow reefs reached bleaching prevalence levels of up to 27%.

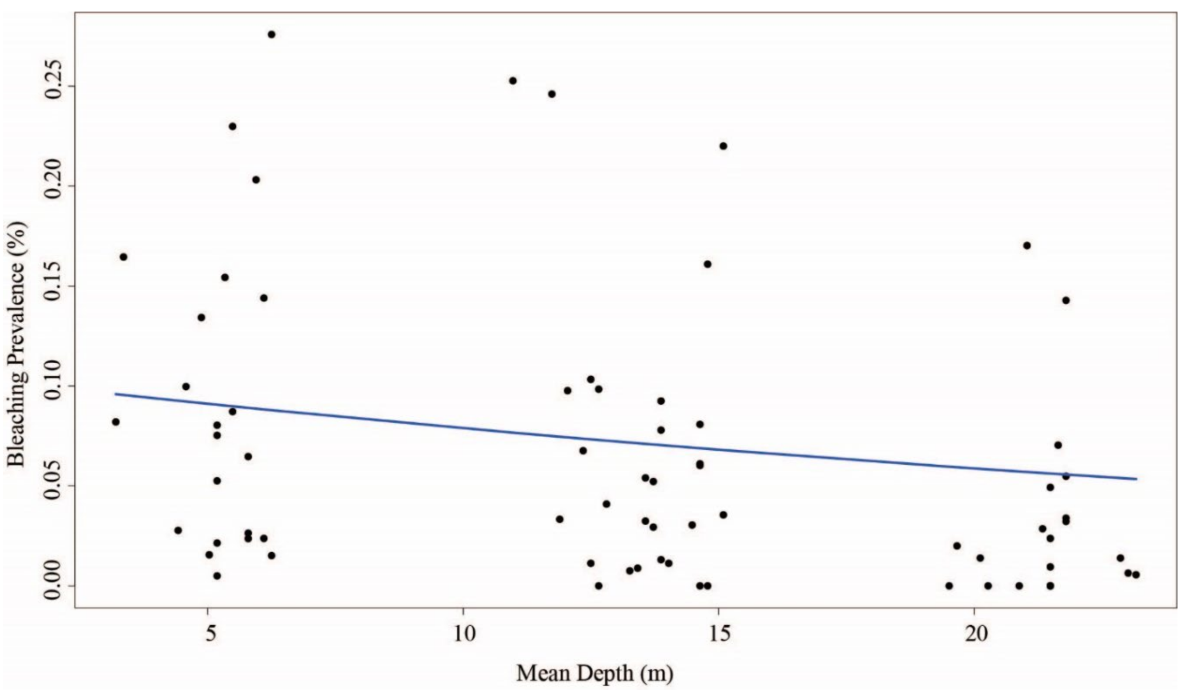

Figure 10. Bleaching prevalence (%) for all hard corals at shallow, mid, and deep reefs for all sites and sectors combined. The blue line represents the fitted smoothing penalized spline (p-spline).

Associations between heating metrics of 2015 and bleaching prevalence

Only one metric for each heat stress type was used in the GAMLSS models to examine impacts of heat stress on bleaching prevalence. The GAMLSS results for heat stress impacts on coral bleaching prevalence are found in Table 6.

Temperature variability (daily temperature range for the warming season of 2014–2015) was the only heat stress type that influenced the bleaching prevalence of all hard corals. All heating rates were high in 2014–2015, but heating rate did not vary between site and depth, and thus heating rate had no detectable impact on bleaching prevalence for corals when examining data just for one year. In other words, heating rates vary with time, but our bleaching data are spatial not temporal, and thus heating rates appeared to have no influence on the bleaching prevalence. Cumulative heat stress, acute heat stress, and temperature variability impacted the bleaching prevalence of a few coral genera.

All reefs at all sites and depths were exposed to high heat stress in the austral summer of 2014–2015. Thus, all reefs experienced cumulative heat stress, acute stress, increased warming trend, and high heating rates most of which varied by year (Figure 2, Figure 5, Figure 7), although there are some spatial differences observed even just for the austral summer of 2015. Most of the spatial differences in heat stress occurred through the variability parameters. Temperature variability was the only parameter to influence the bleaching prevalence of all the hard corals combined. Thus, we ran additional GAMLSS tests to examine the variability metrics on bleaching prevalence.

The mean daily temperature range was the primary variability parameter linked to changes in bleaching prevalence of corals (Table 7). Despite many of the variability metrics differing between site and depth (Table 3), these metrics did not seem to best predict bleaching prevalence for most coral general (Table 7).

Table 6. GAMLSS results (likelihood ratio test (LRT) and p-values) examining the impact of heat stress types on bleaching prevalence of all hard corals and the dominant coral genera.

Coral	Cumulative heat stress: DHW		Acute heat stress: days above threshold		Increasing trend		Variability: daily temperature range		Heating rate	
	LRT	p-value	LRT	p-value	LRT	p-value	LRT	p-value	LRT	p-value
All hard corals	0.24	0.626	0.04	0.850	Not applicable due to no variation in trend - all sites and depths experience a warming trend in the year of 2014-2015		4.95	0.026 *	1.80	0.180
Acropora	2.31	0.129	0.49	0.480			0.97	0.324	0.02	0.890
Porites	2.99	0.084	1.31	0.252			1.83	0.176	0.18	0.669
Pocillopora	4.04	0.044 *	0.50	0.478			3.10	0.078	3.03	0.081
Pavona	0.54	0.4632	2.34	0.126			0.19	0.663	0.38	0.541
Galaxea	4.09	0.043 *	4.94	0.026 *			1.09	0.297	2.04	0.154
Isopora	0.63	0.426	0.65	0.420			0.48	0.490	0.24	0.622
Leptastrea	16.36	< 0.001 *	16.86	< 0.001 *			14.982	< 0.001 *	0.32	0.573
Montastrea	7.97	0.005 *	8.10	0.004 *			6.04	0.014 *	0.05	0.829

Asterisk (*) indicates a significant result.

Table 7. GAMLSS results (likelihood ratio test (LRT) and p-values) examining the impact of temperature variability metrics on bleaching prevalence of all hard corals and the dominant coral genera.

Coral	**Tide: PSD peak at 12 hr**		**Daily: PSD peak at 24 hr**		**Internal Wave: PSD peak at 48 hr**		**CV for 2015**		**Mean daily temperature range for 2015**		**Mean daily temperature range for 30 days prior to survey**		**Mean temperature for 30 days prior to survey**	
	LRT	p-value	LRT	p-value	LRT	p-value	LRT	p-value	LRT	p-value	LRT	p-value	LRT	p-value
All hard corals	0.84	0.369	0.05	0.824	2.87	0.090	0.23	0.630	5.50	0.019 *	0.54	0.464	0.16	0.691
Acropora	0.11	0.741	0.26	0.613	0.18	0.668	0.24	0.627	0.25	0.614	3.71	0.053	3.57	0.059
Porites	5.34	0.021 *	1.32	0.249	2.59	0.107	0.13	0.715	1.53	0.215	0.49	0.485	0.17	0.681
Pocillopora	0.62	0.431	1.98	0.16	2.38	0.122	0.90	0.343	5.68	0.017 *	0.0003	0.986	1.33	0.249
Pavona	1.16	0.281	0.80	0.37	0.43	0.512	0.71	0.400	0.06	0.807	0.26	0.610	0.44	0.507
Galaxea	5.05	0.025 *	4.56	0.032 *	3.67	0.055	14.02	0.002 *	0.95	0.329	0.67	0.673	0.40	0.396
Isopora	0.51	0.475	0.56	0.454	0.79	0.373	0.82	0.365	0.0008	0.978	0.008	0.930	0.04	0.851
Leptastrea	0.20	0.655	2.66	0.103	0.19	0.660	9.64	0.001 *	24.61	< 0.001 *	0.57	0.448	0.46	0.496
Montastrea	0.24	0.624	0.24	0.627	1.66	0.200	0.01	0.914	7.65	0.005 *	0.22	0.636	0.48	0.488

Asterisk (*) indicates a significant result.

Discussion

Concurrent heat stress metrics led to bleaching events

A 'perfect storm' of increased warming trend, increased heating rates, and the impact of cumulative and acute heat stress events caused the massive bleaching events of 2015 and 2017 in Tutuila. This conclusion comes from time series analyses linking heating metrics to observed, though not quantified, bleaching events that occurred during those years. A conglomerate of heating stressors cumulatively led to mass bleaching events, one metric independently did not predict mass bleaching (Table 8). This suggests that only using one heating metric will inaccurately predict bleaching events. For example, if cumulative heat stress (i.e., DHW) was the only metric used to predict mass bleaching, then the reefs in American Samoa should have had another massive bleaching event in 2016.

Table 8. Presence/absence of each heat stressor for each year. Green represents a presence, and grey an absence, of each heat stress for each year. Asterisks (*) mark the years that incurred a massive bleaching event. Bold outline around bleaching year indicates that multiple heat stressors collectively led to the mass bleaching events. A green box in the cumulative heat stress row indicates the presence of a long-term heat stress event (measured as DHW). A green box in the acute heat stress row indicates the presence of a short-term heat stress event (last on a few hours and measured as DHH).

Stressor	2013	2014	2015*	2016	2017*	2018
Increased warming trend						
Cumulative heat stress						
Acute heat stress						
Increased heating rate						
Decreased daily temperature range						

Temporal patterns were the main drivers in patterns for heat stress

Heat stress varied greatly over time, primarily from year to year, for warming trend, heat rates, acute stress, and cumulative stress. For temperature variability metrics, temperature ranges were greater during warming months compared to the cooling months, but in general there was no distinct pattern in temperature variability that changed from year to year. Overall, the patterns in temperature time series were similar across reefs and sites (Figure 3 and Figure 4); thus, if a hot anomaly occurred in a given year, then generally the entire island and all depths experienced that hot anomaly, though to slightly varying degrees of severity.

Temporal patterns were the main drivers in patterns for heat stress; however, small spatial differences were observed for some metrics between depth and site. For example, during the beaching event of 2015, all sites and all depths experienced an increased warming trend, cumulative heat stress, acute heat stress, and increased heating rates. The degree to which each site and depth experienced each heat stressor varied slightly, though shallow reefs generally experienced warmer waters for longer periods of time. Fagatele, in the Southwest sector of Tutuila, experienced slightly warmer conditions compared to other sites around the island. Spatial variations were more prominent in the metrics for temperature variability, with depth being the largest gradient.

Warming trends are expected to increase globally due to climate change, with uneven ocean warming affecting regional changes in global climate sensitivity (Xie 2020). The southern hemisphere has absorbed 90% of the net ocean heat gain in recent years compared to the northern hemisphere (Rathore et al. 2020), making corals in the southern hemisphere, like those at Tutuila in American Samoa, more vulnerable to future conditions. Not only are waters warming faster, but the intensity of the heatwave is increasing with new all-time high temperature records observed regularly(Cheng et al. 2021). Ocean warming is exacerbated by increasingly stronger and more frequent el Nino events (Claar et al. 2018), which compounds stress on corals. Ocean warming has resulted in the longest global coral bleaching event lasting from 2014–2017 (Eakin et al. 2019). Global reefs are currently experiencing annual trends that exceed summertime trends at most locations, and winter periods are shortening allowing less time for corals to recover from high temperatures(Heron et al. 2016; Lough et al. 2018).

Reefs in Tutuila, American Samoa, were experiencing an increased warming trend for the years when massive bleaching events occurred. Detrended fluctuation analysis of the temperature time series revealed that the warming trend was not linear, but instead had a few peaks. For example, the temperature increased compared to the previous year in 2013, 2015, and 2017. The trend in the water temperature for 2014 remained similar to the previous year and did not increase. Meanwhile, in 2016, the trend decreased between the two peaks of 2015 and 2017. Thus, warming trend alone did not predict mass bleaching events or bleaching would have occurred in 2013.

Even though the trend did not increase in 2016, the heating rate did increase from the prior year. In fact, the heating rates progressively increased from year to year. Thus, the combined effects of increased warming trend and heating rates exacerbated any other heat stress on the reefs and amplified any acute or cumulative stress that the corals were experiencing in Tutuila.

Not only is the temperature trend expected to increase under future climate change conditions, but cumulative and acute heat stress events are expected to increase in frequency, intensity, and duration (Skirving et al. 2019). Reefs in Tutuila experienced both short-term (lasting for a few hours) and long-term (lasting for multiple weeks) heat stress events in 2015 and 2017, which were associated with observed massive bleaching events. Temperature data from the 2015 bleaching event indicated that cumulative and acute stress were present at all sites and depths, but the degree of heat stress slightly varied between site and depth, with shallow reefs having longer and more frequent periods of heat stress. Fagatele, in the southwest of Tutuila, experienced more cumulative and acute heat stress compared to the other sites (i.e., shallow reefs in Fagatele experienced two acute heat stress events instead of one like the deeper reefs there). All other sites and depths only experienced one acute and one cumulative heat stress event. Oceanographic differences and low residence times in the shallow bay may explain why Fagatele was exposed to more heat stress than the other sites.

Measuring multiple heating metrics during peak bleaching is key to accurately linking heat stress to coral bleaching

Cumulative heat stress is often measured through the metric degree heating week (DHW), which can have different definitions based on the time over which cumulative heat stress is calculated and whether or not hot anomalies are included in the calculation for the bleaching threshold. Currently, the most widely used definition of DHW is based on the NOAA Coral Reef Watch

(CRW) calculation that uses satellite sensor data to monitor global sea surface temperatures. In this satellite-derived definition, DHW is calculated over a 12-week period and is the sum of the temperature anomalies exceeding the bleaching threshold, i.e., the maximum monthly plus 1 °C (MMM + 1°C) for either 5 km or 50 km gridded regions (Liu et al. 2014). DHW is a highly effective metric used for predicting mass coral bleaching and has been validated for historical mass bleaching events (Kayanne 2017). This study calculated DHW corrected at depth, as opposed to DHW calculated at the sea surface just using satellite data and has identified a few issues with any definition of DHW. For example, using only one heating metric can lead to an erroneous prediction for bleaching, e.g., reefs in Tutuila experienced cumulative heat stress in 2016, but did not bleach.

The bleaching threshold is usually defined as MMM + 1 °C, but this term gets applied in a general sense to all corals globally. However, bleaching susceptibility in corals is highly variable. When observed in the field, it can appear as patchy even within a single coral colony experiencing different levels of bleaching. Bleaching thresholds for corals measured in situ varies by site, between coral taxa, and also by the age of the coral(Edmunds 2004; Shuail et al. 2016). In the case of Tutuila reefs, depth-corrected DHW varied slightly between depth (shallow reefs experiencing greater DHW values) and site (Fagatele in the southwest of Tutuila experienced higher DHW values compared to the other sites), but DHW did not impact the overall bleaching prevalence of all hard corals. DHW, however, did impact the bleaching prevalence of just a few select taxa (*Leptastrea, Montastrea, Galaxea, Pocillopora*). The bleaching threshold of these taxa may be lower compared to other coral species in the community, highlighting the need to further examine the underlying mechanisms that drive such patchiness in bleaching during heat waves.

Bleaching thresholds may also shift through time. Corals may shift their thermal tolerance due to adaptation or through natural selection of heat-tolerant symbionts(Rowan 2004; Berkelmans and Van Oppen 2006). Additionally, successive heatwave exposure may also change the coral community response through selective mortality(Fox et al. 2021). The ability of the past to influence the present trajectory of an ecosystem has been termed ‘ecological memory’, and evidence from the successive bleaching events in 2016 and 2017 on the Great Barrier Reef suggests that the extent of bleaching during the second heat wave was contingent on the physiological and ecological responses of the corals from the previous year’s heatwave (Hughes et al. 2019). Understanding how bleaching thresholds may or may not shift through time and how coral communities respond will be imperative to best predict future bleaching events.

Historical temperature exposure impacts coral tolerance through yet another mechanism. Not only does repetitive exposure to acute and cumulative heat stress alter bleaching thresholds and heat tolerance for some coral species, but exposure to large ranges in temperature variability can mean that some corals are subject to less bleaching(Carilli et al. 2012). Daily or tidal fluctuations in temperature can sufficiently increase the tolerance of some corals and reduce their likelihood to bleach (Safaie et al. 2018). Safaie et al. (2018) observed that high temperature variability 30 days prior to a bleaching event was the main metric out of 20 variables with the highest predictive power to best explain when bleaching events may occur (Safaie et al. 2018). This was not observed for reefs in Tutuila, however. Temperature variability 30 days prior to the ecological survey was not correlated with bleaching prevalence on hard corals. Nonetheless, the temperature range throughout the entire warming period was a main predictor for bleaching prevalence for hard corals. This pattern was primarily driven by the taxa *Leptastrea*, *Montastrea*, and *Pocillopora*.

One advantage of using in situ temperature loggers for this study is the capacity to collect information on finely-scaled temporal patterns. For example, temperatures at the shallow reefs in Tutuila were driven by diurnal periods, while reefs at depth experienced variable temperatures due to internal waves. The statistical results, however, revealed that internal waves did not significantly explain any differences observed in bleaching prevalence. Specifically, in Tutuila, temperature variability was driven by daily cycles in the shallow reefs, and internal waves influenced the temperature variability for deeper reefs. Reefs in the shallow, middle, and deep reefs were all influenced by tides. Despite differences observed in the influence of diurnal cycles and internal waves on temperature variability, these two parameters were not significant at predicting bleaching prevalence for hard corals when all genera were combined. *Galaxea* was an exception and bleaching prevalence was significantly impacted by tidal and daily temperature fluctuations. Bleaching prevalence in *Porites* was also impacted by tidal influences on temperature variability. Temperature variability due to internal waves had no impact on bleaching prevalence in any coral genera. This observation is contrary to some studies that suggest internal waves will help mitigate heat stress by pulsating cool temperatures onto deeper reefs exposed to internal waves(Wall et al. 2015; Wyatt et al. 2020).We suggest that some of the observations linking heating metrics to bleaching prevalence in this study might portray a different assumption if bleaching data from the peak event were used here. This result may suggest that internal waves are not important at the beginning of a heat wave, but the next step would be to determine if internal waves become more important to Tutuila reefs after long-term heat stress exposure.

Deeper reefs (~20–25 m), in general, have been hypothesized to be a refugia for corals from heat stress. One of the conditions of the deep reef refugia hypothesis is that they must be at or below the first thermocline during the annual thermal maximum (Riegl and Piller 2003). The deep reefs in Tutuila were not below the thermocline and experienced high temperature values and ranges in temperature. However, the deep reefs in Tutuila did experience slightly less bleaching prevalence than the shallow reefs. Thus, depth did mitigate bleaching to some capacity, but was not a complete refugia because severe heat stress was still recorded on deep reefs.

Although not quantified, multiple observations recorded mass bleaching events in 2015 and 2017(Coward et al. 2020); thus, the temporal analysis linking heating metrics calculated through time to observed bleaching events revealed that many heat stressors simultaneously are associated with accurately predicting bleaching events. However, the spatial analysis using 2015 ecological survey data did not reveal compelling evidence that multiple heat stressors caused bleaching for all the hard corals combined, potentially due the timing of the surveys during the early stages of heat stress. Given the low bleaching prevalence, statistical analyses linking heating metrics to bleaching prevalence are limited under this framework and should be repeated with bleaching prevalence data collected during the peak bleaching event. Only then can the full extent to which all the heating metrics impacted coral communities and specific coral genera be understood. Nonetheless, a few coral genera, *Leptastrea* and *Montastrea*, seemed to have bleached more than the rest of the hard corals and were sensitive to cumulative heat stress (DHW corrected at depth), acute heat stress (short term spikes in the temperature that would last for a few days), and temperature variability (mean daily temperature range). *Galaxea* and *Pocillopora* also had increased bleaching prevalence due to cumulative and acute heat stress. Since these corals were some of the first genera to bleach, perhaps they can serve as forecasters of mass bleaching.

The time series for in situ temperature data (2012–2018) will allow further studies to associate this with time series of ecological data instead of just a single time point for benthic data as was completed here. Matched temperature and ecological time series data would help illuminate the full extent to which the benthos is impacted by vertical thermal structure through time and changing temperature.

The long-term in situ temperature data collected at these reefs provide detailed information on multiple types of heat stress to which reefs throughout Tutuila have been exposed throughout time. These heating metrics could be combined with other anthropogenic stressors to the reefs, like carbonate chemistry variables indexing ocean acidification, and measured variables of water quality to determine how multi-stressors may impact reef communities over time. Urgent effort at the global scale is needed to combat climate change, but local efforts of monitoring can be used to prevent or lessen coral reef loss.

Key Findings

The time series analysis revealed a few key patterns:

- Overall patterns in each time series data were similar between site and depth.
- Acute heat stress (spikes in temperature for a few days) occurred in austral summers of 2015, 2016, and 2017 for most sites at all depths. The acute heat stress also occurred in 2018 for the middle and deep reefs, but not for the shallow reefs.
- For all sites and depths, the overall trend is that temperature is increasing through time, with the exception of 2016 and 2018.
- Daily temperature variability is only high while waters are warm. The highest daily ranges only occur for a few days and coincide with the acute heat stress period.
- Weekly measurements indicate that the biggest variability in temperature occurs in the few weeks prior to the highest seasonal temperatures reached each year. In other words, daily variability is already greater during warming, but the first few weeks of the warming season start with low variability. However, at the end of the heating season, the week-to-week variability is highest right before the peak seasonal temperature is met. This was true for 2013–2016, but not for 2017 or 2018.
- When looking at the periodicity due to yearly cycles, every singly annual pattern has a double high peak in which there is an initial heating rate increase, followed by a slight decrease, and then another increase in temperatures during the warming period.
- Temperature time series were highly correlated when compared between sites.
- No distinct geographic patterns were observed, except that the Northeast and Southeast sites were highly correlated for shallow, middle, and deep reefs (correlation coefficient = 0.80, 0.89, 0.89, respectively).
- Temperature patterns were nearly identical between shallow, middle, and deep reefs for the same site, especially at the Northwest, Northeast, Southeast, and Southeast Island sites where cross correlation values were all above 0.90 (i.e., at least 90% similar temperature time series between depths).

Summary of results for heating parameters calculated for the entire temperature time series (2012–2018):

Cumulative heat stress

- Cumulative heat stress (DHW) varied primarily through time (years) and less so spatially (little difference between sites).
- Cumulative heat stress impacted reefs at all sites and at all depths. Shallow and middle reefs had more cumulative heat than the deeper reefs, but the deeper reefs still experienced cumulative heat stress.

Acute heat stress

- The presence or absence of acute heat stress was significantly different between years ($p_{(1,6)} < 0.05$), but not between sites ($p_{(1,2)} = 0.17$) or depth ($p_{(2,0.4)} = 0.81$).

- Acute stress events primarily occurred in the austral summer months of 2015, 2016, and 2017.
- One acute stress event occurred both in 2015 and 2016, while three acute stress events occurred in the summer months of 2017.

Heating rates

- Heating rates were significantly different between depths ($p_{(2,4)} < 0.05$).
- Shallow reefs generally warm at a faster rate than mid and deep reefs.
- Heating rates were also significantly different between years ($p_{(5,10)} < 0.001$).
- Heating rate progressively increased each year except in 2018.
- Seawater temperature steadily increased throughout each warming season, except in 2017 when seawater warmed rapidly in the first few weeks, and then continued to warm but at a slightly slower rate.

Temperature variability

(1) Power spectral density (PSD)

- The power spectral density analysis showed that high temperature variation, i.e., peaks in the dendrograms, occurs at multiple frequencies,
- The PSD also revealed that reefs at different depths exhibit different drivers for temperature variation.
- Expectedly, diurnal temperature cycles drive most of the temperature variability in the shallow reefs for both warming and cooling seasons.
- The PSD also allowed us to observe the influence of tides on the reefs at each depth; semidiurnal tides occur every 12 hours and influence the water temperature at all reefs and at all depths but become increasingly important with depth.
- In the shallow reefs the diurnal cycle has a stronger influence on temperature variation than semidiurnal tides.
- At some mid water reefs (at North, Northeast, and Southeast Island sites), the diurnal daylight cycles and semidiurnal tides have almost a similar influence on the temperature variation, i.e., 24 hr and 12 hr frequency peaks are nearly the same height during the warming season.
- Interestingly, the deep reef sites are influenced by a third driver of temperature variation, internal waves occur every 48 hours. Shallow and middle reefs are not exposed to these waves.
- Deep reefs at all sites except the North site were exposed to internal waves that influenced the variability in temperature.
- The internal waves only appear during the warming season and are not detectable during the cooling months.

(2) Daily temperature ranges

- Daily temperature ranges were significantly different ($p_{(df,F)}$ = values) between depth ($p_{(2,127)} < 0.001$), year ($p_{(5,238)} < 0.001$), periods of heating versus cooling ($p_{(1,2982)} <0.001$), and site($p_{(5,393)} < 0.001$).
- Temperature ranges were more variable during the heating part than the cooling periods, with the greatest temperature ranges observed in the austral summer months of January, February, and March.
- Unexpectedly, the deeper reefs experienced the greatest temperature ranges, not the shallow reefs.
- There were significant differences between sites; the reefs at Southwest Fagatele had higher daily temperature ranges than the other sites, but there was no apparent spatial pattern.
- Daily temperature ranges were also statistically different between years, but there was no relationship between daily temperature ranges and the massive bleaching events since the 2014–2015 year had high temperature variability in daily temperature, but the 2016–2017 year did not.

(3) The coefficient of variation (CV)

- Coefficient of variation (CV) values differed significantly between sites ($p_{(5,8)} < 0.001$), depth ($p_{(2,6)} < 0.01$), and year ($p_{(5,4)} < 0.01$), but not between warming and cooling seasons ($p_{(1,0.009)} = 0.93$).
- The interactive effect between sites, depth, and year was also significant ($p_{(20,2)} < 0.01$). Due to the interaction effect, no consistent pattern was evident between sites and years.
- Deep reefs varied more from their long-term mean compared to the middle and shallow reefs.
- On average, deep reefs vary ±72.3% from their long term mean temperature, whereas mid and shallow reefs vary ±63.8% and ±62.0%, respectively, from their long term temperature.

Summary of heating metrics just for the bleaching event of 2015:

Cumulative heat stress

- All reefs at all sites and depths experienced cumulative heat stress events.
- When the values of degree heating week (DHW) were compared between sites, the Southeast site had slightly more cumulative stress than the other sites, which all had similar cumulative heat stress exposure to each other.
- When the values of degree heating week (DHW) were compared between depths, the shallow reefs experienced higher values of DHW while the mid and shallow reefs were exposed to similar levels of DHW.

Acute heat stress

- All reefs at all sites and depths experienced acute stress events in 2015.

- When acute stress was measured in hours above the bleaching threshold (sometimes lasting over a few days), then the Southeast site had more hours above the threshold, while all the other sites experienced relatively equal hours above the bleaching threshold.
- The Southeast site experienced more hours above the threshold because it experienced two acute heat stress events; meanwhile, all other sites each experienced only one acute stress event.
- The two acute heat stress events occurred in the shallow reefs and not the mid or deep reefs.

Heating rates

- Heating rates did not vary by site or by depth

Variability

- Tides (measured by peak is PSD at 12 hr) have similar influence on reefs at all sites and depths.
- Daily fluctuations (measured by peak in PSD at 24 hr) are greater at shallow depths compared to the mid and deep reefs, and Southwest Fagatele has greater daily fluctuations than the other sites.
- Internal tides (measured by peak at the PSD at 48 hr) occur more at the deep reefs compared to the mid and shallow reefs, and the site at Southwest in Fagatele Bay are exposed to more internal waves.
- For the warming period prior to the massive bleaching event, daily temperature ranges varied between site and depth. Unexpectedly, the deeper reefs experienced greater daily temperature ranges than the shallow reefs. Also, Southeast Island Aunuu experienced high daily temperature ranges, while the Southeast experience lower daily temperature ranges.
- Daily temperature means and ranges 30 days prior to the ecological survey date varied between site and depth as well as day, since the ecological surveys were conducted on different days over a month-long period.

Summary of results for coral bleaching:

- In general, bleaching prevalence was fairly low for all dominant coral genera. This is likely due to the ecological surveys being conducted in the early days of the bleaching event.
- Bleaching prevalence varied by depth for all hard corals.
- It appears that the bleaching prevalence of most of the dominant coral genera did not vary by depth, so the overall trend of hard corals was driven by a few genera (*Leptastrea* and *Monastrea*).
- Since the ecological surveys were conducted at the beginning of the bleaching event, this may suggest that *Leptastrea* and *Monastrea* were the first two coral genera to react to heat stress.
- Bleaching prevalence did not differ across sectors, except for *Pocillopora.*

- Bleaching prevalence was significantly impacted by the interaction of both depth and sector for *Galaxea.*

Summary of results linking heating parameters of 2015 to coral bleaching:

- Temperature variability (daily temperature range for the warming season of 2014–2015) was the only heat stress type that influenced the bleaching prevalence of all hard corals.
- All heating rates were high in the 2014–2015 year, but heating rate did not vary between site or depth. Thus, heating rate has no detectable impact on bleaching prevalence for coral when examining data for just one year. In other words, heating rates vary with time, but we have spatial, not temporal, data for bleaching prevalence; thus, heating rates appear to have no influence on the bleaching prevalence.
- Cumulative heat stress, acute heat stress, and temperature variability impacted the bleaching prevalence of a few coral genera.
- Since the ecological surveys were conducted at the beginning of the bleaching event, this may indicate that *Leptastrea* and *Monastrea* were the first coral genera to react to heat stress.
- The mean daily temperature range was the primary variability parameter that was best linked to changes in bleaching prevalence of corals.
- Despite many of the variability metrics varying between site and depth, this does not seem to the best predictor for bleaching prevalence

Concluding Remarks

A 'perfect storm' of heat stress events caused observed bleaching events of 2015 and 2017

Massive bleaching events were observed in American Samoa during 2015 and 2017 (Coward et al. 2020). A conglomerate of heating stressors cumulatively led to bleaching events in 2015 and 2017 at coral reefs in Tutuila, American Samoa. One metric independently did not predict mass bleaching. Instead, multiple stressors including cumulative and acute heat stress, a warming trend, and increased heating rates, collectively led to the mass bleaching events of 2015 and 2017. Temperature variability between years was not the strongest predictor for bleaching. Only using one heating metric can inaccurately predict bleaching events. For example, if cumulative heat stress (i.e., DHW) was the only metric used to predict mass bleaching, then the reefs in American Samoa should have had another massive bleaching event in 2016. Fortunately, 2016 did not have a massive bleaching event, likely due to the trend not increasing that year.

Certain coral genera may be the beacon of bleaching events

Since the ecological surveys were conducted at the very beginning of the bleaching event before it was widespread, the coral genera that had the most bleaching prevalence (*Leptastrea* and *Monastrea*) may be the genera that first react to heat stress, and therefore may be the warning that a mass bleaching event is imminent.

The way forward

This study has highlighted that most heating metrics vary through time and not necessarily though space and depth. This limits the scope of scientific questions unless you have co-located temporal and spatial data. For example, in the case of the 2015 bleaching event in American Samoa, even though there was some variation in heat stress spatially, most of the variation in heat stress occurred from year to year. Meaning that during a hot year where reefs experience a bleaching event, all the reefs are exposed to cumulative heat stress, acute heat stress, increasing trend, and increased heat rates. That makes it difficult to answer questions like, "how do corals react to cumulative heat stress?" if you only have ecological data from one point in time when everything is hot. To answer this question, you need ecological data from when it was not hot for comparison. The next step is to link time series temperature data with time series ecological data.

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