

Research Article

Small-Scale Spatial Analysis of *In Situ* Sea Temperature throughout a Single Coral Patch Reef

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Thermal stress can cause geographically widespread bleaching events, during which corals become decoupled from their symbiotic algae. Bleaching, however, also can occur on smaller, spatially patchy scales, with corals on the same reef exhibiting varying bleaching responses. Thus, to investigate fine spatial scale sea temperature variation, temperature loggers were deployed on a 4 m grid on a patch reef in Kāne'ohe Bay, Oahu, Hawai'i to monitor *in situ*, benthic temperature every 50 minutes at 85 locations for two years. Temperature variation on the reef was characterized using several summary indices related to coral thermal stress. Results show that stable, biologically significant temperature variation indeed exists at small scales and that depth, relative water flow, and substrate cover and type were not significant drivers of this variation. Instead, finer spatial and temporal scale advection processes at the benthic boundary layer are likely responsible. The implications for coral ecology and conservation are discussed.

1. Introduction

As one of the most biodiverse ecosystems in the world, coral reefs are generally limited to tropical, shallow waters and cover less than 0.1% of the Earth's surface [1]. Their restricted distribution, sessile adult stage, and narrow habitat preferences all point to corals as being vulnerable to global climate change and threatened by projected increases in sea temperature [2–4]. While corals, like many aquatic organisms, have physiological mechanisms for dealing with thermal stress [5, 6], the fact that they already inhabit waters that often are within a few degrees Celsius of their tolerance limits [7, 8] underscores the scientific and conservation urgency to understand how global climate change will affect sea temperatures and how corals will respond.

A major response to thermal stress exhibited by corals is the phenomenon known as bleaching, whereby intracellular symbiotic algae, *Symbiodinium* spp., either leave or are expelled from the coral host. For corals, bleaching has been shown to result in decreased skeletal growth and reproductive output [9], reduced resistance to disease [10–12], as well as local extirpation and shifts in community composition

[13, 14]. While multiple environmental factors acting in concert result in bleaching [15], thermal stress causing protein damage and disrupting photosynthetic reactions in *Symbiodinium* spp., has been implicated as the primary stressor in recent mass bleaching events [16, 17]. It is also the most important parameter in predicting when events will occur [18]. One curiosity with regards to bleaching, however, is that it often appears as spatially patchy phenomena, such that bleached and unbleached corals of the same species can be found adjacent to one another on the same reef (Figure 1). Yet, despite observing variation among corals on the scale of a single reef, very little is known about how sea temperature may vary at the same scale. Thus, while the threat of climate change puts corals at risk on a global scale, their narrow range of environmental tolerance implies that habitat differences that exist on much smaller geographic scales may also prove to be biologically and ecologically significant. Indeed, one of the major challenges in understanding ecological processes is the quantification of physical and biological patterns at appropriate spatial scales [19].

On large geographic scales, mass bleaching episodes have been shown to correlate with anomalously high sea surface

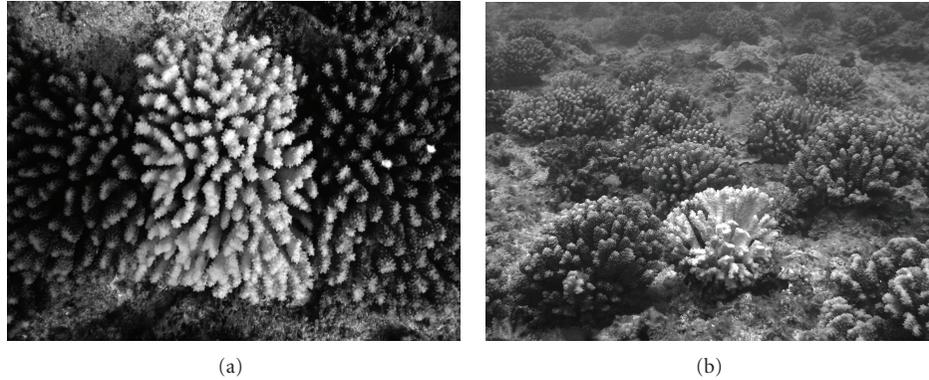


FIGURE 1: Microspatial heterogeneity in degree of coral bleaching seen in *Pocillopora* sp. (photograph by K. Gorospe) (a) and *P. meandrina* (photograph by K. Tice) (b) on a reef at Kure Atoll, Hawai‘i.

temperatures (reviewed in [20]). For example, the largest documented coral bleaching event occurred between mid-1997 and the end of 1998 and affected reefs in the Caribbean, Mediterranean, Persian Gulf, Red Sea, Indian Ocean, and throughout the Pacific Ocean. This event coincided with elevated sea temperatures caused by a strong El Niño–Southern Oscillation [7]. Such macrogeographic scale (e.g., ocean basin wide) bleaching events have captured the interests of conservation scientists because they offer possible clues as to how reefs will be affected by widespread rising sea temperatures caused by global climate change. This interest, combined with technological advances in satellite remote sensing of the marine environment [21], has driven scientific focus towards studying these ecosystems on broad geographic scales. Unfortunately, while a macrogeographic approach may be appropriate for the prediction of mass bleaching events, it may also inadvertently obscure smaller-scale ecological processes affecting individual reef organisms that are equally important.

Some attention has been turned to characterizing environmental variation among reefs and reef systems at a more regional scale [22]. This has provided insight into explaining mesoscale (i.e., 10s–100s km) patterns of coral bleaching in the field. For example, experimental evidence shows that high and intermediate water flow environments can help to increase coral resistance to bleaching, presumably by increasing diffusion rates between the coral and external environment and thus, preventing the build up of toxic free radicals [23]. Some field studies, however, point to the opposite effect, whereby low water flow may expose corals to greater thermal fluctuations, possibly allowing them to acclimatize to temperature extremes [24, 25]. Other studies have shown that the thermal history of a reef (e.g., lagoon versus fringing reefs) may produce colonies better able to cope with high temperature stress [24]. These studies of regional variability highlight some of the myriad of factors contributing to bleaching and point to the need for additional data to tease apart multiple, bleaching-related environmental factors. From a conservation standpoint, investigating bleaching on a variety of spatial scales may help to identify individual reefs that have proven to be

more resistant to bleaching. Prioritizing such reefs as marine reserves could be the best, preemptive strategy for protecting reefs in the face of global climate change [26].

Identifying processes that affect individual reef organisms *within* reefs, however, requires that microspatial (i.e., on the scale of meters or centimeters) environmental variation be measured. For example, despite the observation that corals of the same species separated by just a few centimeters can exhibit variable bleaching responses (Figure 1), sea temperature variation in the context of bleaching potential has largely been ignored at this spatial scale. Furthermore, laboratory methods, from which our current models of bleaching thresholds are derived, have primarily been limited to prolonged, shock-based experiments that mimic the conditions of mass-bleaching episodes [7, 16, 17]. Rarely do these experiments take into account the temperature variability that corals are exposed to *in situ*. In addition, while numerous temperature indices have been described as good predictors of coral bleaching events [27], our understanding of temperature-sensitivity in corals has recently become more nuanced with the recognition that bleaching susceptibility may also be dependent upon the individual coral colony’s past environmental experience and recent thermal history [15, 25, 28]. Thus, characterization of temperature variation as it relates to coral bleaching will require an investigation of not only spatial but temporal variation over a range of scales.

Here, we present a spatiotemporal analysis of a two-year, *in situ*, microspatial scale dataset of benthic sea temperature variation in the context of coral bleaching on a single patch reef in Kāne’ohe Bay, Oahu, Hawai‘i. While some studies suggest the possible existence of microspatial environmental variability on reefs—even as a potential mechanism for explaining spatial patterns of bleaching [29]—here, we describe such variation in detail. Our goal is not to implicate microspatial sea temperature variation as the sole or even primary mechanism by which patchy bleaching may occur, but instead, to investigate whether or not biologically relevant variation in temperature exists on small spatial scales across a reef.

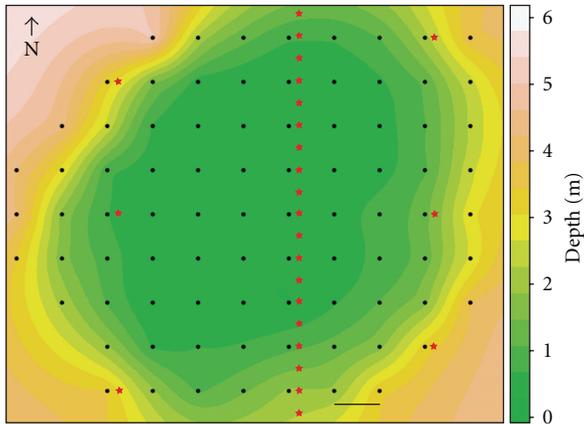


FIGURE 2: Ordinary kriging interpolation of depth across the reef. Small black dots are the locations of 85 temperature data loggers. Red stars are the locations of rebar placed for orientation. Scale bar in the lower right is 4 meters. Green areas are shallow, and peach ones are deep.

2. Materials and Methods

2.1. Study Site. A circular, patch reef in Kāneʻohe Bay, Oahu (21.45767°N, 157.80677°W) was selected for its accessibility (snorkeling depth between one and five meters), size (~40 m in diameter), and appropriateness to the spatial scale of interest. This reef is typical of the type of reefs found in Kāneʻohe Bay as well as at some of the atolls of Northwestern Hawaiian Islands (e.g., Pearl and Hermes). Labeled reinforcing bars were placed at 2 m intervals, running north to south down the center of the reef, as well as at several points on the reef edge to be used as orientation markers during deployment and recovery of temperature data loggers (Figure 2).

2.2. Temperature Data Collection. High-Resolution Thermochron iButton temperature and time data loggers (model DS1921H; Maxim Integrated Products, Inc., Sunnyvale, CA, USA) were used to monitor spatiotemporal temperature at the study site. The iButton has a manufacturer-specified temperature range of 15°C to 46°C, an accuracy of $\pm 1^\circ\text{C}$, a resolution of 0.125°C, and a lifetime of seven to eight years (when used in 20°C–30°C environments and at a sampling rate of 10 minutes).

A total of 85 sites, situated 4 m apart in a grid pattern, were monitored for temperature (Figure 2). The loggers were waterproofed using liquid electrical tape and secured to the benthic substrate—rock, sand, rubble, or dead coral—using either an aluminum wire or nail. Before each deployment, all loggers were time-synchronized and programmed to begin to take temperature readings simultaneously at a user-defined time delay and sampling rate. Each logger is capable of storing 2048 temperature readings after which, data must be downloaded and cleared from memory before redeployment. Thus, loggers were collected every two to eight weeks and replaced with newly programmed loggers to ensure a virtually continuous time series. Due to the need to redeploy loggers on a regular basis throughout the

study period, small gaps in the temperature time series were inevitably created. In order to minimize the duration of these time series gaps, the reef was divided into a western and eastern half, and loggers from each half were set to different redeployment schedules. As a result, time series gaps due to redeployments only lasted between one and four hours (i.e., from 1 to ~5 readings). Two other sources of time series gaps in the data resulted from (1) data saturation of the loggers occurring *in situ* before they could be replaced and (2) when individual loggers were lost or damaged during deployment.

Before their first deployment, all loggers were calibrated at room temperature for at least 24 hours by placing them in a sealed plastic container, free from air circulation. To account for any systematic logger-to-logger differences, we determined a calibration coefficient for each logger by dividing the individual logger's average calibration temperature by the global average temperature over all loggers. Field-recorded temperatures then, were adjusted by multiplying the raw temperature by the logger-specific calibration coefficient. As loggers were lost in the field, new loggers were calibrated in batches as described above on an as-needed basis. Midstudy and poststudy calibration tests also were conducted on loggers that had previously been deployed. Furthermore, each logger has an internal counter that tallies the total number of sampled points it has recorded over its lifetime. This data was used to determine if there was any significant drift in the loggers' measurements over the course of the study period.

Temperature recordings began in June 2007 for the western-half and October 2007 for the eastern-half of the reef and continued until October 2009. Initially, the sampling rate was set to 25 minutes (June 2007 to July 2008 for the western-half and October 2007 to May 2008 for the eastern-half). Subsequently, and for the remainder of the study period, the sampling interval was increased to 50 minutes to allow for longer deployments and greater flexibility in the logger redeployment schedule.

2.3. Other Environmental Variables. Depth, relative water flow, and substrate type and cover were measured for each of the 85 monitoring sites as potential explanatory variables to be used in modeling spatial variation in temperature. For the shallow portions of the reef, a metric-labeled PVC pipe and a bubble level were used to measure depth. A standard dive computer depth gauge (IQ700, Tabata Co., Ltd., Tokyo, Japan) was calibrated using a pressurized instrument test chamber with 0.25% accuracy to 90 m of sea water (no. 48310, Global Manufacturing Company, West Allis, WI, USA) and used to measure the deeper portions of the reef.

To obtain estimates of relative water flow, half-sphere casts of plaster of Paris (100 mL of water per 250 mg of calcium sulfate hemihydrate) were deployed at each temperature-monitoring site and allowed to dissolve. This "clod card" approach [30], although limited, is an elegant field method that provides time-averaged measurements of multidirectional, water flow. Clod cards were deployed on the reef for several days on each of two occasions (October 2009 and May 2010). The mass of each clod card was weighed

TABLE 1: Categories and abbreviations used in benthic characterization.

Category	Abbreviation
Coral	
<i>Porites compressa</i>	PCO
<i>Montipora</i> sp.	MSP
<i>Pocillopora damicornis</i>	PDA
other corals	OCOR
Macroalgae	
<i>Dictyosphaeria</i> sp.	DSP
<i>Eucheuma</i> sp. or <i>Kappaphycus</i> sp.	EKSP
other macroalgae	OMAC
Other substrates	
dead coral with algae	DCA
recently dead coral	RDC
rubble	RUB
sand	SAN
Miscellaneous	
other invertebrates	OINV
unknown	UNK

before and after deployment in the field, and the percent loss in mass due to dissolution, averaged between the two deployments, was used as a measure of relative water flow between sites.

Finally, characterizing benthic coverage was accomplished by taking digital photographs of 30 cm × 30 cm quadrats centered at each temperature-monitoring site. The program CPCe [31] was used to generate 90 spatially stratified random points on each photograph and to calculate percent coverage statistics at each location. There were four major benthic cover categories: coral, macroalgae, other substrates (e.g., dead coral, rubble, or sand), and miscellaneous (Table 1). Each category was subdivided into subcategories along taxonomic lines or substrate composition (Table 1). The two miscellaneous subcategories were other invertebrates (OINV), which primarily consisted of sponges and feather duster worms (*Sabellastarte sanctijosephi*), and “unknown” (UNK) for substrates that could not be identified. A Shannon diversity index was calculated for each temperature-monitoring site.

2.4. Data Analysis. All spatiotemporal analyses of temperature variation were accomplished using the open source computer programming languages, Python (Python Software Foundation, <http://www.python.org/>) and R (R Development Core Team, <http://www.R-project.org/>). After logger calibration, the time series data for each monitoring site was smoothed by calculating the average hourly temperature. This created a more consistent dataset since the data consisted of both the initial 25- and subsequent 50-minute sampling intervals. In addition, this allowed for a simpler comparison of eastern versus western reef data loggers, which were not time-synchronized to each other due to different deployment schedules. Since temperature generally

remained stable over the course of several hours (within the 0.125°C resolution of the iButton data loggers), it is unlikely that small-scale temporal variation is being lost as a result of smoothing.

Fourier transforms were used to decompose time series data into a linear combination of sinusoids each representing different frequencies present in the original signal [32]. There were a total of 15 monitoring sites that had complete time series datasets (see Results for details), thus making it possible to investigate the various periodicities of temperature variation and compare across sites. Before spectral analysis, each dataset was detrended (i.e., linear trend and mean removed) and smoothed by twice applying a modified Daniell kernel (bandwidth $[L/n] = 0.000689$; [32]). The resulting time series was then used to perform a Fourier Transform and create a scaled periodogram. The periodogram can be regarded as a measure of the squared correlation between the original time series data and sinusoids oscillating at all possible frequencies between 0.0 and 0.5 (for our data, frequency represents cycles per hour). The powers of the dominant frequencies as well as the 95% confidence intervals associated with each frequency were calculated. Furthermore, the same calculations described above were performed on a time series of standard deviation across all monitoring sites. Finally, to increase our resolution at low frequencies (i.e., between seasonal and diurnal periods), spectral analysis was repeated after daily averaging both the mean temperature and standard deviation across all monitoring sites.

Since the goal is to look for biologically relevant temperature variation, a series of temperature indices were developed to encompass one or more of the following temperature characteristics that have previously been implicated as potential thermal stress indicators in corals: (1) absolute temperature stress (e.g., temperature above some threshold), (2) duration at a particular temperature or cumulative stress, and (3) temperature variability or rate of change in temperature. In addition, some of the analyses performed here were modeled after techniques developed by the National Oceanic and Atmospheric Administration as part of Coral Reef Watch’s satellite observation and coral bleaching monitoring program. Two products developed by them—Hotspots and Degree Heating Weeks [33]—were modified slightly in our analysis. We define relative Hot- and Coldspots as any monitoring site whose temperature is more than one standard deviation above or below, respectively, the average temperature for the entire reef at a given hour. We define relative Hot- and Coldhours for each site as any hour the temperature is one standard deviation above or below, respectively, the average temperature experienced at that particular location in the past twelve hours. Twelve hours were chosen because this was the smallest cyclical period of temperature variation indicated in the spectral analysis. Thus, relative Hot- and Coldspots are based on spatially averaged temperatures, while relative Hot- and Coldhours are based on site-specific temporally averaged temperatures. The number of times that each site was a Hot- or Coldspot or a Hot- or Coldhour was tallied and normalized by the total number of logged hours for that site. Furthermore,

the dataset was truncated to exactly two years (31 October 2007 to 31 October 2009) to minimize any seasonal bias by avoiding the pre-October 2007 (i.e., summer) data.

The approach described above of summarizing temperature variation over two years effectively obscures our ability to look for temporal variation. Thus, to assess temporal variation, the Hot- and Coldspot and Hot- and Coldhour analyses were repeated for the following seasonal subsets: Winter 2007 (22 November 2007 to 13 January 2008), Summer 2008 (13 June 2008 to 13 August 2008), Winter 2008 (22 November 2008 to 13 January 2009), and Summer 2009 (13 June 2009 to 13 August 2009). Sites whose loggers were lost or broken during these seasonal data subsets were excluded from subsequent analysis and small, redeployment gaps linearly interpolated. In addition, the seasonal subsets were used in calculating average daily maximum and minimum temperatures, average daily temperature ranges, as well as overall average temperature.

Finally, the Degree Heating Hours (DHHs in units of °C-hour) were used to simultaneously characterize both the duration and intensity of heating. DHHs are calculated by tallying the number of hour equivalents the temperature at a site exceeds the maximum monthly mean (MMM) sea surface temperature of 27°C (as defined for Hawaii by Coral Reef Watch's Degree Heating Weeks Index; http://www.osdpd.noaa.gov/ml/ocean/cb/virtual_stations.html). Thus, for example, 2°C-hours are equivalent to two hours at 28°C or one hour at 29°C. The number of DHHs was summed per monitoring site for Summer 2008 and Summer 2009.

Overall, there were a total of 9 temperature indices: Hotspot, Coldspot, Hothour, and Coldhour (two-year and four seasonal subdatasets); overall, daily minimum, daily maximum, and daily range temperature averages (four seasonal subdatasets); DHHs (Summer 2008 and Summer 2009).

Ordinary kriging using *gstat* [34], an extension package of R, was used to create spatially interpolated maps of the various temperature summary indices and environmental predictors. Kriging is a geostatistical spatial interpolation method that models the relationship between distance and variance of sampled points to predict values at unsampled locations. Depth, water flow, and benthic coverage data were tested for correlation with each temperature summary index using Dutilleul's modified *t*-test. The modification corrects for spatial autocorrelation in the data by adjusting the variance of the test statistic as well as the degrees of freedom. This correction is necessary because tests of significance using an unmodified *t*-test are subject to inflated rates of type I error when both the response and explanatory variables are spatially autocorrelated [35].

Furthermore, in order to explain spatial variation in each temperature summary index, spatial filters were generated by performing principal coordinates of neighbor matrices analysis (PCNM, also known as spatial eigenvector mapping or SEVM) on the distance matrix of the temperature monitoring sites. The resulting eigenvectors serve as spatial descriptors of the temperature monitoring sites [36]. Finally, the eigenvector-based spatial filters that were statistically significant at a $P < .1$ level were used, along with the

potential explanatory environmental variables as part of a partial regression model in determining the relative contributions of pure environmental, pure spatial, and shared (i.e., environmental and spatial) variation in explaining temperature variation on the reef. Incorporating location as an explanatory variable in the partial regression model also reduces or eliminates spatial autocorrelation among the residuals, thus minimizing type I error rates. For each of the temperature summary indices, five models were tested: (1) a regression of the temperature summary index on depth, (2) temperature on location, (3) temperature on depth and location, (4) temperature on depth and substrate, and (5) temperature on depth, location, and substrate. Models were chosen based on minimizing Akaike's Information Criterion. Both the principal coordinates and the partial regression analyses were performed in the computer program, Spatial Analysis in Macroecology (SAM, ver. 3.1; [37]).

3. Results

3.1. Calibration Data. Over the course of the study period, a total of 201 loggers, or approximately 16.5% of the data, were lost in the field. For any given location on the reef, the percent of missing data (not including saturation or redeployment gaps) ranged from 0.3% to 49.1%. Fifteen of the sites, however, had only 0.3% missing data entirely due to the unavoidable gaps during redeployment and are considered to be complete data sets.

Calibration tests revealed that among logger variation in recorded temperatures ranged from 0.79 to 1.35°C ($\bar{x} = 0.80^\circ\text{C}$) and calibration coefficients ranged from 0.97868 to 1.01991 ($\bar{x} = 1.00004$). Comparing pre-, mid-, and poststudy calibration tests showed that the mean change in calibration coefficients across 171 possible comparisons was 0.00021, indicating that loggers did not show significant drift in their calibration coefficients. A linear regression, however, indicated a small but significant relationship between the magnitude of the change in calibration coefficient (i.e., with no regard to the direction of change) and the number of sampled points between calibration tests ($r^2 = 0.03$; $P < .05$). The amount of change, however, is negligible with a regression slope of 2.666×10^{-8} . Thus, the maximum possible calibration drift a logger could have experienced (i.e., 10 data-saturated deployments with 2048 sampled points per deployment) would be 0.00287. To put this into perspective, using the maximum observed calibration coefficient of 1.01991, the difference in pre- and postdrift calibration of a 25°C raw data point would only be 0.07°C. Therefore, we think that drift can be safely ignored.

3.2. Spectral Analysis. Figure 3 shows the temperature time series, averaged daily and across all monitoring sites, with shaded bars indicating the various data subsets used in creating the temperature summary indices described above. Figure 4 shows a representative scaled periodogram for the hourly averaged temperature time series at a single monitoring site. The periodograms point to five dominant frequencies corresponding to both solar- and lunar-driven

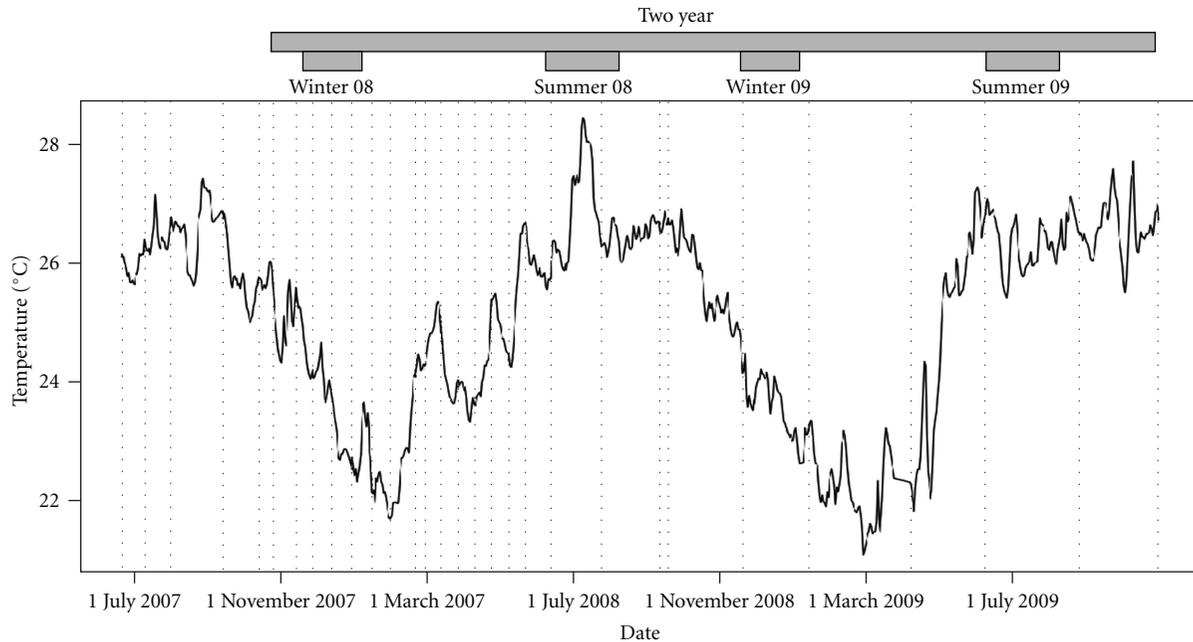


FIGURE 3: Temperature graph for the entire temperature data set (June 2007 to October 2008). Dashed vertical lines indicate deployment days when temperature data loggers in the field were collected and replaced. Bars above graph indicate the two-year and seasonal subsets that were used in the analyses.

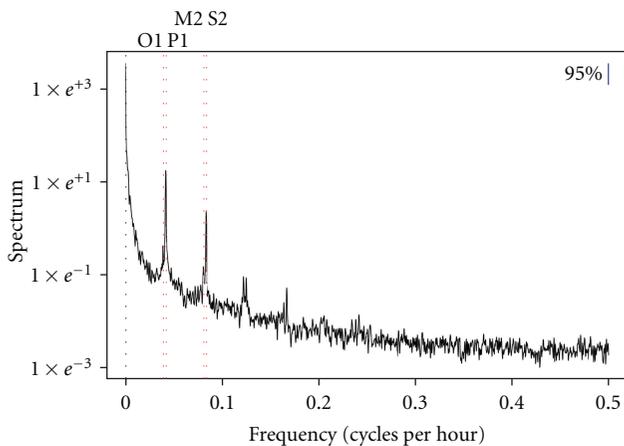


FIGURE 4: Fourier transform scaled periodogram of two years of temperature data at one monitoring site. Principal frequencies are marked with vertical, dashed lines and correspond to (from left to right) seasonal (365 days), lunar (O1, 25.82 hours), solar (P1, 24 hours), lunar semidiurnal (M2, 12.42 hours), and solar semidiurnal (S2, 12 hours). Other peaks between 0.1 and 0.2 cycles per hour are likely echoes of O1 and P1. Scale bar in the upper right corner is the 95% confidence limit.

periodicities: seasonal (365 days), principal lunar diurnal or O1 (24.83 hours), principal solar diurnal or P1 (24 hours), principal lunar semidiurnal or M2 (12.42 hours), and principal solar semidiurnal or S2 (12 hours). Peaks at eight- and six-hour periods (between 0.1 and 0.2 cycles per hour) most likely are harmonics of the principal lunar (O1) and solar diurnal (P1) components. Most notable,

an expected ~ 28 day lunar monthly periodicity (between the seasonal and O1 peaks) is not present. Repeating the spectral analysis for the daily averaged temperature across all monitoring sites revealed no additional periodicities. Furthermore, comparing the periodograms for each of the 15 monitoring sites with complete time series datasets revealed that the relative distribution of power over the major driving periodicities was the same across the reef (seasonal signal \gg P1 \gg S2 $>$ O1 $>$ M2). Finally, the scaled periodogram for the hourly standard deviation time series revealed the same five periodicities as well as an additional periodicity at 2.5 hours (frequency = 0.4 cycles per hour; see Figure 1S in Supplementary Material available on line at doi:10.1155/2011/719580.) Smoothing by calculating daily averages, as above, failed to reveal additional periodicities.

3.3. Modeling Spatial Variation. Ordinary kriging interpolation of depth (Figure 2) shows a smooth transition from the center, shallow areas of the reef to the outer, deeper areas and, as such, can be regarded as a representation of the reef's bathymetry. The map of water flow shows broad similarities with depth such that high and low relative flows correspond to shallow and deep sites, respectively (Figure 5(a)). In fact, depth also correlated with many of the substrate variables (discussed below). On the other hand, maps for the various temperature summary indices ranged from being visually consistent with depth, such as the proportion of time spent as a Coldhour and Winter 2008 range in daily temperature (Figures 2AS and 2BS, resp.), to being strikingly patchy as is seen for the proportion of time spent as a relative Hotspot and Summer 2008 DHHs (Figures 5(b) and 5(c), resp.).

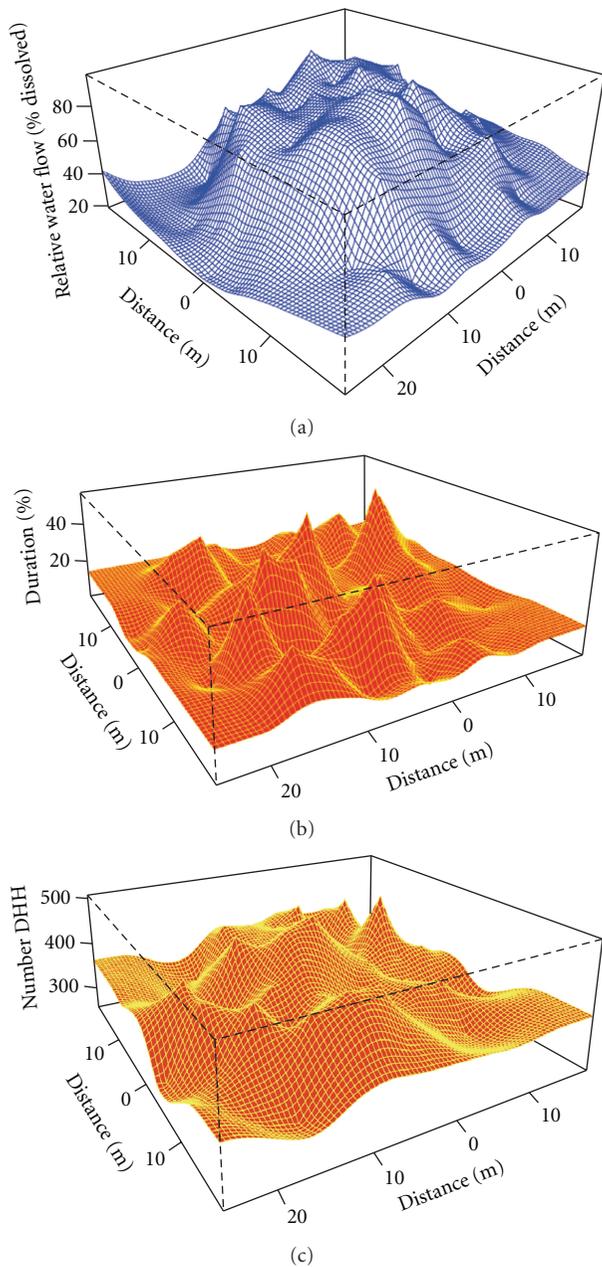


FIGURE 5: Ordinary kriging interpolation of water flow (a), percent of time spent as a relative Hotspot over two years (b), and number of Degree Heating Hours for Summer 2008 (c).

Tukey boxplots of the temperature summary indices reveal considerable microspatial temperature variation on the patch reef. For example, sites ranged from spending 0% to nearly 60% of the two years of temperature monitoring as a relative Hotspot (Figure 6(a)). In addition to the expected temporal variation seen in average daily minimum and maximum temperatures (Figure 3S), the boxplots also indicate seasonal and annual variation with regards to Hothours and Coldhours (Figure 4S), with a greater proportion of time being spent as a Hothour or Coldhour in the summer as opposed to the winter months (Figures 4S). Finally, Summer

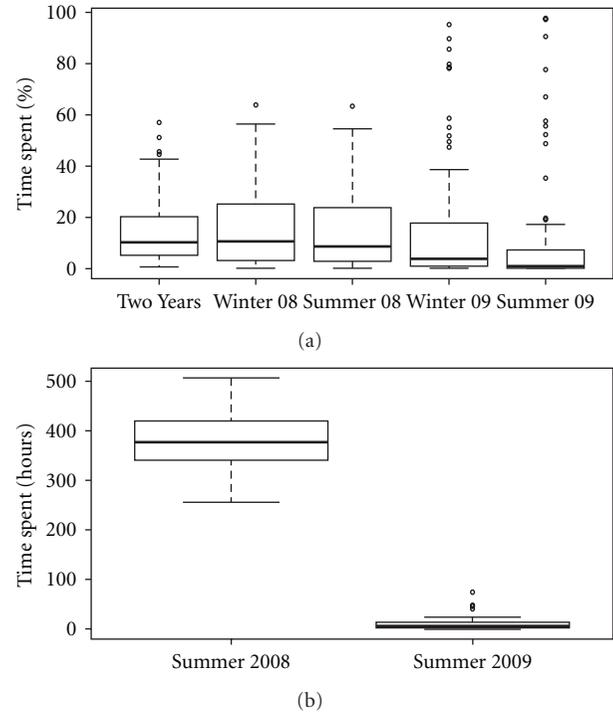


FIGURE 6: Tukey boxplots of the seasonal and annual variation in the proportion of time spent as a relative Hotspot (a) and total Degree Heating Hours for Summer 2008 and 2009 (b). The rectangle represents the interquartile range (i.e., the 25th percentile, median, and 75th percentile), the “whiskers” represent all values that are within 1.5 times the interquartile range, and the open circles represent outliers, defined as data points that lie outside the whiskers. Paired Welch’s *t*-tests were used to test for statistically significant temperature differences between seasonal subdatasets. One-tailed tests were used for comparing winter versus summer or two-year versus summer or winter datasets. Two-tailed tests were used for comparing winter versus winter or summer versus summer datasets.

2008 resulted in a considerably larger number of DHHs as compared to Summer 2009 (Figure 6(b)).

Spatial correlation analyses of substrate type using Dutilleul’s modified *t*-test revealed that depth was significantly correlated ($P < .1$) with PCO, EKSP, RUB, SAN, and OINV (Table 1S). In addition, depth correlated with all coral (all subcategories combined) and all macroalgae (all subcategories combined). Variables that correlated significantly with depth were excluded from the PCNM and partial regression analyses to avoid collinearity among variables. The results of the partial regression analyses—reported as the percent of variation explained by location, environment (i.e., depth and/or substrate), and shared environment and location—can be found in Table 2S. For each temperature summary index, only the best model (i.e., the one with the lowest AIC value) is reported. Thus, if a standard linear regression model (i.e., models with no shared component) fits better than a partial regression model (i.e., models that include a shared environmental and location component), then only the standard linear

regression model is reported. Among the competing models, location, as described by the PCNM-generated eigenvector filters, was a component of the best model in 35 out of the 38 temperature index regressions and was the dominant (i.e., greatest explanatory power) component in 25 (Table 2S). The percent of temperature variation explained by purely spatial factors ranged from 4.6% to 48.9% (Table 2S). On the other hand, environmental variables (i.e., depth, substrate, etc.) were included in the model for 22 regressions (Table 2S). Compared with location, environmental variables had a much greater range in explanatory power (from 2.3% to 75.5%) when comparing across temperature datasets, but was a dominant component only five times (Table 2S). Finally, while depth was always included among the 22 regressions with environmental variables, AIC-based model comparisons only included substrate as part of the best model for two temperature summaries: DHHs and average daily temperature range for Summer 2009.

4. Discussion

4.1. Temperature Variation in Time and Space. It is often stated that the environment is neither perfectly regular nor entirely random and that spatial patterns are, therefore, a common characteristic of the natural world [38]. Visual inspection of our spatially interpolated maps of water flow, depth, and by extension, most substrate variables, which correlated significantly with depth, reveal that our choice of environmental variables cannot by themselves account for our observed variation in temperature across the reef. Furthermore, results from the regression analyses indicate that location was the most ubiquitous statistically significant explanatory variable and, when compared to the environmental variables, was more commonly found to be the dominant component. Thus, location was the most important explanatory variable in accounting for temperature variation at the spatial scale of this study. To many, our finding that location was a significant predictor of observed temperature will not be surprising. What is unexpected, however, is how the explanatory power of location compared with that of the other environmental variables were tested. Depth, water flow, and substrate were chosen specifically because they incorporate one or several processes and characteristics that should affect benthic sea temperature (i.e., advection, insolation, light absorption and reflection of the substrate, etc.). Yet, most of the temperature summary indices were not significantly predicted by these environmental explanatory variables or, when they were included in the model, were only a small fraction. In other words, these results indicate that at microspatial scales, two locations as little as 4 m apart on a reef may have similar depth, water flow, and substrate coverage and yet still exhibit different temperature profiles. Conversely, two locations that differ with respect to depth, water flow, and substrate coverage may in fact have very similar temperature profiles. Thus, while temperature variation at large spatial scales might be explained by certain intuitive environmental variables, the importance of these variables at much smaller spatial scales is diminished and in fact eclipsed by microspatial considerations.

It is important to note, however, that even though the calibrations applied were small (i.e., no more than 0.07°C), calibration can only correct any systematic bias present. The reported accuracy of the loggers is $\pm 1.0^\circ\text{C}$, and it is possible that some of the among site temperature differences that were found were due to poor logger accuracy. We doubt, however, that this is a major factor because all sites had at least two different loggers due to alternating deployments and logger loss. It is also difficult to imagine a stochastic process favoring specific sites and asymmetrically erring either too high or too low for long periods of time (e.g., up to 60% of the two-year recording period for the relative Hotspot analysis). The absolute temperature also is unimportant to many of our temperature indices because they are relative measures. If spatially patchy temperature variation were being caused by stochastic, among logger inaccuracies, we would expect all of our temperature indices to be affected equally by this. Each temperature index, however, exhibited distinct overall spatial patterns, with some indices (e.g., Coldhour and Winter 2008 range in daily temperature; Figures 2AS and 2BS, resp.) even exhibited nonpatchy patterns.

Although we present data from only a single reef, we have no reason to suspect that our findings are particular to this reef. Overall diversity and coral cover vary from reef to reef in Kāneʻohe Bay (as elsewhere), but the monitored reef is typical of what is found in the bay and at some of the atolls in the Northwestern Hawaiian Islands. It is located in the center of the bay and does not appear to be uniquely influenced by external inputs (e.g., river outflow, oceanic currents, etc.). Even so, further testing on other reefs is necessary to indicate how universal our results are.

Interpreting location as an explanatory variable can be abstract. Environmental variables themselves have an inherent spatial structure, which is why in a partial regression analysis, there is a distinction made between pure environment, pure location, and shared environment and location components. In other words, the pure location component is separate from the common spatial structure that is shared by the environment and response variable (i.e., the shared environment and location component). This does not exclude the possibility, however, that the pure location component in our analysis is comprised of other environmental features that were not captured by our choice of explanatory variables [36]. It is also possible that our choice of environmental variables is sound, but that the spatiotemporal scale at which they were measured was too large, and thus, limited their explanatory power. This is most likely to be true for our measurement of water flow, since relative depth and substrate cover measurements are less likely to significantly change at finer spatiotemporal scales. That location helps to explain sea temperature variation at a microspatial scale simply means that locations that are close together in space have more similar temperature characteristics than points farther apart. Thus, the most parsimonious explanation here is that location, in this study, likely refers to microscale water flow processes that were not captured by the clod card measurements.

Relative water flow was negatively correlated with depth (high flow in the shallow portions of the reef and low flow in the deeper portions)—a pattern that is consistent with the decay of oscillatory wave-driven flow with increasing depth. Water flow in the benthic boundary layer, or the layer of water at which flow is influenced by reef structure [39], can be very different from wave- or tide-driven flow seen in the water column in terms of direction and magnitude as well as net transport, and these microscale differences can be lost as a result of time-averaging [40, 41]. Thus, finer-scale processes (spatial or temporal) not captured by our clod card measurements should not be excluded as a driver of temperature variation at this scale. For example, water flow velocity influences the thickness of the coral thermal boundary layer, which in turn influences the rate of heat transfer between the substrate and the surrounding water [42]. Coral pigmentation can also affect temperature such that darker-pigmented corals experience greater temperatures, but the effect is mediated by differences in water flow [43]. Furthermore, temporally stable temperature variation, such as that observed in this study, points to the possible influence of reef bathymetry in channeling warm or cold water across a reef (e.g., from internal waves) [44]. Finally, small-scale temperature heterogeneity may be influenced by the movement of water into and through the interstitial structure of whole reefs, as evidenced by dye transport experiments (Koehl, Cooper, and Hadfield, unpublished data). All of these studies suggest that fine-scale water flow heterogeneity could be a potential driver of fine-scale temperature heterogeneity. That our observed temperature differences could not be explained by wave-driven water flow as measured by clod cards highlights the need for future research to focus on even finer spatial and temporal scale flow patterns across reefs in explaining microspatial temperature variation at the benthos.

The results of spectral analysis also lend insight into the temporal scale of the processes that are driving temperature variation. Scaled periodograms of the 15 monitoring sites with complete time series datasets reveal the same power distribution pattern across the same lunar- and solar-associated periodicities. This suggests that large temporal scale processes such as tides are not causing the observed temperature difference among sites. Interestingly, in addition to the lunar- and solar-associated signals, the periodogram for the time series of standard deviation of temperature data revealed a high frequency peak at 0.4 cycles per hour corresponding to 2.5-hour periodicity. Unfortunately, it is beyond the scope of this study to identify the specific processes involved, but other studies have pointed to high-frequency internal waves and internal tides as being potential drivers of high-frequency, subsurface temperature variation [44, 45].

If depth, relative water flow, and substrate composition are not significant predictors of temperature variation within a single coral reef, then what is? Our results suggest that benthic temperature differences on microspatial scales are likely due to finer spatial and temporal scale advection processes. Specifically, these advection processes are on a spatial scale finer than oscillatory wave-driven flow and a temporal

scale finer than tide-associated frequencies. Furthermore, our finding that biologically significant, benthic temperature variation exists on a microspatial scale demonstrates the need for future research to further explore the physical drivers of this variation as well as its ecological significance for benthic organisms.

4.2. Implications for Corals. Since the 1970s, research on coral reef ecosystems has been shifting from small-scale research focused on ecological processes (e.g., competition and herbivory) to large-scale conservation and management driven research. This expansion in spatial scale was also accompanied by a paradigm shift, from one that viewed coral reefs as stable ecosystems to one that began to emphasize the vulnerability and decline of coral reefs due to a host of environmental stressors [46]. As our understanding of coral reefs progresses, it is important to acknowledge the rapid pace of these shifts and consider the possibility that coral reef scientists may have been pushed to scale up prematurely, obscuring the importance of ecological processes that may be occurring more locally and creating a knowledge gap in our understanding of these threatened ecosystems. It should be acknowledged, however, that high-density studies at much smaller geographical scales may involve a considerable amount of effort and expense and in some cases prohibitively so. It also is important to note that reliable, accurate data loggers for other important and interesting parameters (salinity, current, irradiance, etc.), which are necessary for this type of study, often do not exist. Even so, it is clear from this study that even reasonable outputs of money and effort can result in interesting and unexpected findings and deepen our understanding of coral reefs.

Our study demonstrated the existence of microscale temperature heterogeneity on a single patch reef based on temperature summary indices that were developed specifically to investigate different aspects (e.g., absolute temperature, duration of temperature, and temperature variability) of coral thermal stress. But what relevance do microscale studies have in helping conservationists to better understand coral biology? For example, remotely sensed sea surface temperature (SST) data have been crucial to providing the first evidence of thermal stress as a primary environmental driver of bleaching. Even so, satellite-derived SST data are spatially and temporally averaged and are based on the reflective properties of just the top few mm of the water column. They therefore do not reflect thermal stress levels experienced by individual coral colonies [47]. We suspect that the finer scale processes occurring at the boundary layer are important.

As mentioned above, our current understanding of coral bleaching thresholds are based on either correlations between macrogeographic bleaching episodes and SST data or on laboratory-based experiments that ignore the actual temperature variability experienced by corals *in situ*. The former hides finer-scale variability that may be important for refining our bleaching models, while the latter suffers from temporal isolation that may obscure the importance of long-term acclimatization of corals to environmental conditions.

In both cases, *in situ* temperature data at the scale of the individual colony can provide the environmental context for interpreting results and gaining a more comprehensive understanding of the spatial heterogeneity seen in bleaching patterns and thresholds of thermal stress for coral.

A full understanding of the spatial patterns of bleaching is further obscured by the biological complexity of the coral holobiont (a term used to describe the coral animal host, intracellular *Symbiodinium* spp., as well as associated bacterial and viral communities). For example, it is now well known that the genus *Symbiodinium* spp. is composed of several evolutionarily distinct clades and that these different clades have distinctive physiological tolerances and ecological roles [48, 49]. The patchy distribution and zonation of *Symbiodinium* spp. have been implicated as a possible explanation for patchy bleaching [50, 51]. Some evidence also points to the possibility that symbiont communities can be reshuffled after recovering from bleaching events to include more heat-tolerant clades [52, 53]. Other studies, however, report stable algal symbiont communities before and after bleaching episodes [54] or after transplant experiments [55]. Some evidence has pointed to *Symbiodinium* spp. clade D to be heat tolerant (reviewed in [48]), but as with our understanding of coral bleaching patterns, this conclusion is based on data following severe bleaching episodes. Uncovering finer-scale differences in the physiological roles and tolerances of the remaining *Symbiodinium* spp. clades may require a consideration of more finer temporal and spatial scale environmental differences. Nevertheless, what is clear is that there are other sources of small spatial scale or even individual-level variation on a reef. This study allows us to conclude that temperature variation can exist on the scale of meters and that this environmental heterogeneity is yet another source of individual-level variation that could explain why bleaching is patchy. Our finding that a significant amount of temperature variation was not explained by depth also is consistent with the fact that patchy bleaching is not generally described as a depth-associated phenomenon.

It is possible that temperature is acting as an organizing force at small spatial scales, influencing the distribution of individuals and species within a single reef. Thus, while climate change is a global-scale phenomenon, the appropriate spatial scale at which coral reefs should be managed to cope with this threat remains an open question and underscores the need for coral studies to proceed at multiple scales. As genetic or species diversity is thought to lend stability and resilience to communities [56], habitat heterogeneity may likewise structure reefs in ways that increase their ability to respond to climate change. In such a scenario, reefs that offer more intrareef microhabitat heterogeneity may also harbor heterogeneous communities acclimated to a range of environmental conditions and might therefore be prioritized as marine reserves. Microspatial scale environmental heterogeneity is information that probably should be incorporated into evolving coral reef management strategies. Our study demonstrates that while corals continue to be threatened on a global scale, integrating across multiple spatial scales is essential to understanding the ecological processes relevant to their survival.

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