Variation beneath the surface: Quantifying complex thermal environments on coral reefs in the Caribbean, Bahamas and Florida

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ABSTRACT

Analysis of in situ temperature records collected on six coral reefs in the Caribbean, Bahamas, and Florida Keys reveal significant variability across a range of temporal and spatial scales from minutes to seasons, across depths, and among sites. Subsurface variability occurring at daily and faster frequencies is prevalent across the region, likely driven by combinations of diurnal heating and cooling, wind driven advection, and internal waves at tidal and faster frequencies. This high frequency variability is not detected in records of remotely-sensed sea surface temperature alone. Diurnal variability likely caused by diurnal solar heating and cooling and possibly by advection associated with diurnal winds (daily sea breeze) was significant at all sites and showed greatest magnitude of variation at shallowest depths. Temperature fluctuations at tidal and faster frequencies were common at 5 out of the 6 sites. The magnitude of this variability is not well explained by measured vertical temperature stratification combined with oscillations of the water column associated with barotropic surface tides. Rather, the magnitude and nature of the temperature changes point to the presence of internal waves generated at tidal and faster frequencies. Power spectra calculated seasonally show greatest variability within both diurnal and semi-diurnal frequency bands in Spring and Summer at Florida, Bahamas, Jamaica, and St. Croix. Variability within the semi-diurnal frequency band at Belize and Bonaire was greatest in Winter. Warming in Summer estimated as degree-hours per day above 29.0°C increased with increasing latitude and varied significantly among sites and depths in a manner not predictable from remotely sensed SST data alone. Site latitude was directly related to the amplitude of the seasonal thermal variability, but was not tightly related to variability at daily and faster frequencies which was greatest at the highest and lowest latitude sites. The interactions of depth, site, and season across the study region are associated with distinct signals of thermal variability, and have significant implications for the physiology and ecology of corals and other reef organisms.

1. Introduction

Ambient temperature strongly influences a broad range of physiological functions in all ectothermic invertebrates including corals (Hochachka and Somero, 2002). Reef-building
corals normally live within only a relatively narrow range of water temperatures, and rates of calcification, respiration of coral host tissue, and photosynthesis and photosynthesis by zooxanthellae are all strongly temperature dependent (Lesser, 2004; Warner et al., 2002; Warner et al., 1996). Exposure to either high or low temperatures outside the range to which corals are locally acclimatized can elicit rapid physiological responses leading to severe impairment or death of the coral host and/or zooxanthellae symbionts (Hoegh-Guldberg and Smith, 1989; Jokiel and Coles, 1990; Yonge, 1940). During the last few decades, large-scale coral bleaching and mortality events have been observed on regional to global scales, and while many environmental factors have been implicated as potential causes (Brown, 1997; Mumby et al., 2004; West and Salm, 2003), high water temperature has consistently emerged as a major determinant of coral mortality (Coles and Brown, 2003; Glynn and D’Croz, 1990; Winter et al., 1998). Understanding patterns of water temperature in the field is therefore of prime importance in forecasting patterns of physiological stress due to changing environmental conditions (Clark et al., 2001). Additionally, in order to understand the mechanisms by which temperature may act in concert with other environmental stressors such as light (Lesser, 1997) or restricted water motion (Nakamura and van Woesik, 2001; Nakamura et al., 2003; West and Salm, 2003) it is important first to determine accurate temperature patterns in the field.

Thermal variability on coral reefs occurs across a broad range of temporal and spatial scales. Variability in daily mean temperatures on the order of several degrees can be conspicuous across seasons and large spatial scales such as latitudinal gradients, and is largely driven by predictable seasonal variation in solar radiation. Fluctuations of comparable magnitude can also occur at much smaller temporal and spatial scales both as the result of warming and cooling of the ambient water column, and from advection of water masses with distinct thermal signatures onto or off of reefs. For example, multi-day cooling events can result from the passage of atmospheric cold fronts, especially when combined with strong wind events (Coles and Fadlallah, 1991). Daily heating and deepening of surface warm layers can result both from diurnal insolation and from onshore wind-driven transport associated with the diurnal sea breeze (Monismith et al., In Press; Sonu et al., 1973). A variety of mechanisms such as tidal exchange and tidal jets (Wolanski et al., 1988), alongshore currents and eddies (Lee et al., 1994), wind-driven upwelling, and internal waves (Leichter et al., 1996; Wolanski and Pickard, 1983) can be associated with the movement of distinct thermal fronts onto and off of reefs. Thermal fronts are often associated with gradients in other properties such as salinity, density, concentrations of dissolved gases and inorganic nutrients, sediment loads, or density of suspended particles including plankton such as the larvae of invertebrates and fish. Thus, in addition to their potential physiological importance, rapid temperature fluctuations can be important indicators of changing water masses in reef environments and may be associated with the transport of nutrients, suspended particles, or larvae to and from reefs.

Temperature is one the easiest environmental variables to measure, and analysis of records collected at high frequencies over long periods of time can provide valuable insight
into underlying oceanographic forcing mechanisms. Sea surface temperature (SST) data can also be readily acquired locally from buoys and moorings and over regional to global spatial scales via remote sensing platforms such as satellite borne Advanced Very High Resolution Radiometers (AVHRR) which are sensitive to ocean ‘skin’ temperature in the top few mm of the water column (Kilpatrick et al., 2001). In situ data, however, can reveal temperature patterns at depth that differ significantly from those at the surface (Quinn and Kojis, 1999; Quinn and Kojis, 2003). For example, extensive high frequency variability is a persistent feature of the thermal environment at depths greater than 10 m on coral reefs at the outer margin of the Great Barrier Reef (Wolanski and Pickard, 1983), and the Florida Keys, USA (Leichter et al., 1996). In Florida, at depths of 20–30 m, within-day temperature fluctuations on the order of 2–5°C are common from May through Sep with peak ranges of 8–10°C occurring at times (Leichter et al., 1996). These fluctuations are associated with vertical and horizontal transport of subthermocline water masses by non-linear internal waves at tidal and faster frequencies, with temperature changes often occurring on time scales of minutes and events lasting tens of minutes to several hours. This transient upwelling of subthermocline water represents an important source of dissolved inorganic nutrients (Leichter et al., 2003), zooplankton and suspended particles (Leichter et al., 1998) as well as temporal and spatial variation in temperature per se (Leichter et al., 2005). Few published studies have investigated the high-frequency, subsurface thermal regimes of coral reefs at multiple reef sites particularly in the Caribbean (but see Quinn and Kojis, 1999; Wellington et al., 2001). Specifically, while considerable information is available regarding low frequency (seasonal) patterns in sea surface temperature, comparatively little is known about the variation of subsurface thermal environments within and among reefs and at short time scales.

In this study we investigate patterns of high frequency temperature variability across a range of depths on multiple coral reefs in the Caribbean, Florida Keys, and the Bahamas. Our goals are to examine the relative importance of fine-scale temporal and spatial variability across a range of sites, and to describe a method for quantifying differences among depths, sites, and seasons. Specifically, we ask: (1) What temperature fluctuations are corals exposed to across a range of depths, seasons, and sites? (2) How prevalent is high frequency diurnal and semi-diurnal variability across the study region? (3) Can we define quantitative differences among sites, depths, and seasons within the diurnal and semi-diurnal frequency bands, and how do patterns of both high and low frequency variability change with latitude? (4) How do thermal signals sampled in situ at depth differ from sea surface temperature (SST) records?

2. Methods

a. Study sites and data collection

Study sites were established at multiple locations in the Caribbean, Florida Keys, and Bahamas between 1997 and 2003. These sites were (1) Conch Reef, Florida, U.S.A., (2)
Lee Stocking Island, Bahamas, (3) Discovery Bay, Jamaica, (4) Salt River Canyon, St. Croix, (5) Carrie Bow Cay, Belize, and (6) Nikki Boko, Bonaire. Figure 1 and Table 1 show site locations. At each site (except Carrie Bow) stations were established at depths of 10, 20, and 30 m across the seaward reef slope and temperature recorders were fixed 1 m above the bottom. At Carrie Bow the reef is characterized by a double slope, where an inner slope extending from 3–25 m is separated by a sand trench at 30 m depth from an outer reef which comes up to 18 m depth before dropping into significantly deeper water (Rützler and Macintyre, 1982). At this site stations were established at 9, 18, and 27 m on the inner slope and at 18, 27, and 36 m on the outer slope. Data from 9 m on the inner slope and 18 and 27 m on the outer slope were used in the analysis presented here.

Sites were established sequentially starting at Florida (Dec 1997), Bahamas (Jun 1998), Jamaica (Jan 1999), Belize (Mar 2000), St. Croix (Apr 2000) and Bonaire (Jun 2003). A combination of Onset Computer Stowaway, Tidbit, and Watertemp Pro loggers (0.2°C resolution, 1–5 min response time) were used to record temperature at all study sites. These instruments sampled every 0.5 s and recorded 10 min averages (except Watertemp Pro loggers which recorded 10 min interval points). For deployments in Jamaica, and Belize, sampling was at 10 min in most cases and 16 min in some. In 2000 higher resolution Seabird Electronics SBE 39 loggers (0.001°C resolution, 20 s response time) were added to the study site in FL. These instruments sampled at 1 min intervals.

AVHRR Pathfinder SST data for the period Jan 1998–Jun 2004 were obtained from the
Table 1. Latitude and longitude of the study sites, and site-specific statistics for AVHRR sea surface temperature (°C) for 6 × 5 pixel boxes (area = 480 km²), 01 Jan 1998 to 30 Jun 2004. Percent good represents the number of days for which SST data were available after quality control processing divided by the total number of days (2373) in the study period.

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude (N)</th>
<th>Longitude (W)</th>
<th>Mean</th>
<th>Min</th>
<th>Max</th>
<th>Range</th>
<th>Stdev</th>
<th>% Good</th>
</tr>
</thead>
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<td>76°05.40'</td>
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<td>22.46</td>
<td>30.90</td>
<td>8.44</td>
<td>2.08</td>
<td>27.90</td>
</tr>
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<td>77°24.50'</td>
<td>27.84</td>
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<td>5.13</td>
<td>1.07</td>
<td>22.26</td>
</tr>
<tr>
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<td>64°45.80'</td>
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<td>24.75</td>
<td>30.33</td>
<td>5.58</td>
<td>1.14</td>
<td>25.84</td>
</tr>
<tr>
<td>Carrie Bow Cay, Belize</td>
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<td>88°04.60'</td>
<td>27.44</td>
<td>24.53</td>
<td>30.64</td>
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<tr>
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<td>6.23</td>
<td>1.16</td>
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</tbody>
</table>

U.S. National Aeronautics and Space Administration (NASA) Jet Propulsion Laboratory Physical Oceanography Distributive Active Archive Center (JPL PODAAC). The data are gridded at 4 km × 4 km and collected twice daily, once during the ascending satellite pass (daytime) and once during the descending pass (nighttime). The Pathfinder SST algorithm is based on the National Oceanic and Atmospheric Administration (NOAA)/National Environmental Satellite Data and Information Service nonlinear SST operational algorithm (NLSST) (Kilpatrick et al., 2001; Walton et al., 1998). We applied the highest quality flags to retrieve only data collected during the nighttime passes which represent the most accurate SST values. The global data were averaged across adjacent pixels to obtain daily SST values for a 6 × 5 pixel box corresponding to an area of 24 × 20 km (480 km²) seaward of each site. Because cloud cover and other technical issues result in large numbers of blank points for any individual pixel it is helpful to average over contiguous pixels to reduce the number of missing points. A multi-pixel box size was chosen to be as small as possible while yielding an acceptable number of data points. Test processing with varying box sizes for one site (FL) yielded data for 7, 13, and 24 % out of the 2,373 total days in the study period for box sizes of 1, 3 × 3, and 6 × 5 pixels respectively. Therefore, 6 × 5 pixels was chosen as an acceptable box size and used for all sites. At one site, Conch Reef, Florida, in situ SST data were also available from the nearby meteorological buoy at Molasses Reef approximately 15 km to the north. Hourly SST from station MLRF1 were obtained from NOAA National Data Buoy Center.

b. Data analyses

Site-specific values of the SST mean, minimum, maximum, range, and standard deviation were calculated for each year and across the entire study period. For the in situ
data from the Florida site, which is the longest continuous in situ record (6.5 yr), power spectra across the entire dataset were calculated for each depth using Welch’s averaged periodogram method following Emery and Thompson (2001). Low and high frequency components of the signal at each depth were separated by processing with a 40-h low-pass running mean filter and then subtracting the low-pass signal from the raw record. The length of the spectrum window for the high frequency components was set at 60 d to help resolve potentially overlapping peaks associated with the various astronomical tidal components and diurnal solar heating/cooling following Pidgeon and Winant (2005).

Patterns of high frequency variability among sites were examined in several ways. To assess the prevalence of high frequency variability at depth the high frequency component of the temperature signal and corresponding spectrograms (variance plotted as a function of frequency and time) were calculated and plotted for the first full year of available data at 30 m depth (27 m at Belize) for each site. Spectrograms for the 365 d data segments were calculated with a 7 d moving window with 50% overlap. To examine site-, depth-, and season-specific patterns within the high frequency data in greater detail the high frequency signals from each site and depth were divided into 4 equal-length seasonal segments per year. Each year was considered to consist of 365.25 days (52596 points at 10 min sampling interval) with each quarterly season being 91.3125 days long (13149 points at 10 min interval). Seasonal breaks were defined as day-of-year 81, 173, 264, 355 (calendar days 22 Mar, 21 Jun, 21 Sep, 21 Dec for the non leap years). For the site at Bonaire a full year of data was not available so the data were divided into only two sections termed Winter, and Spring. Power spectra with 95% confidence intervals were then calculated for each site, depth, and season across all years using Welch’s averaged periodogram method with the length of the fast Fourier transform (FFT) chosen as an even factor of the length the quarterly data segments (13149/9 = 1461 points) with zero overlap. The integral of the estimated power spectral density function calculated in this manner was approximately equal to the total variance of the corresponding de-trended (zero-mean) data records (satisfying Parseval’s Theorem).

To quantify patterns among sites, depths, and seasons, the variance within a defined diurnal and semi-diurnal band was calculated by integrating the power spectral density functions for periods of 33–18 h (frequencies 24/33 ≤ f ≥ 24/18) and 14–11 h (frequencies 24/14 ≤ f ≥ 24/11). These integrals were estimated as the sum from \(f_i\) to \(f_j\) of \(\Gamma(f) \times \Delta f\), where \(f_i\) and \(f_j\) define the lower and upper frequency range of the defined band, \(\Gamma(f)\) is the power spectral density function, and \(\Delta f\) is width of the frequencies bins at which \(\Gamma(f)\) is evaluated. The square root of the variance within each band represents the root mean square temperature deviation, with units of °C.

The average vertical thermal stratification of the water column as a function of time at each site was estimated by calculating the 28 d running mean temperature at each depth, finding the difference between SST and temperature at depth, and dividing by the vertical separation (in meters) among sensors. The maximum vertical stratification was then multiplied by an estimate of the maximum amplitude of the barotropic surface tide to
obtain an estimate of the amount of observed thermal variability that could be attributed to the simple effect of surface tides moving the stratified water column up and down past the fixed depth, bottom-mounted sensors.

The variance of both the low frequency and the high frequency portions of the signal from each site and depth were plotted as a function of latitude. Site- and depth-specific patterns of warming at the surface and at depth during Summer were estimated by calculating the degree-hours above 29.0°C per day at each site. 29.0°C was chosen as a generic threshold temperature above which corals are potentially subject to thermal stress (e.g., Gleeson and Strong 1995) but not intended as a specific measure of thermal stress to corals (see Discussion). Rates of warming were normalized by the total number of Summer days (defined as 21-Jun to 21-Sep) with available data at each depth.

3. Results

Overall patterns of the SST data for each site are shown in Figure 2, and summary statistics are presented in Table 1. Seasonal patterns of winter cooling and summer warming were relatively consistent across years. Peak summer temperatures were also generally consistent across years, with 1998 the warmest year in this study period, possibly related to ENSO conditions in the Eastern Pacific. Sites differed significantly with respect to means, standard deviation, minima, maxima and ranges of SST. Both the coolest mean surface temperature, 26.57°C, and minimum, 21.38°C, as well as the warmest maximum, 31.65°C, were detected at Florida. The corresponding overall temperature range and standard deviation for the Florida site were 10.28 and 2.53°C respectively. The Bahamas site had the next largest overall range, 8.44°C, and standard deviation, 2.08°C. The 4 Caribbean sites had very similar means, maxima, ranges, and standard deviations, with overall variability markedly smaller than in Florida or the Bahamas. The sites can, therefore be described as falling into two general categories with respect to SST patterns: (1) Florida and the Bahamas with mean temperatures of ~26.5°C, winter minima ~21 to 22°C, and summer maxima ~30–31.5°C, and (2) the Caribbean sites with winter minima ~24 to 25°C, means ~27 to 28°C, and summer maxima similar to Florida and the Bahamas but slightly lower. This broad categorization of sites based on the full 6.5 year dataset also holds for individual years. Warming quantified as degree hours per day above 29.0°C was also highly variable among sites and depths (Table 2). Rates of warming detected in the SST data were not, in general, a good indicator of warming at depth. Rather, patterns of heating among depths appears to vary strongly among sites. For example, in Florida mean heating at the surface was 18.04 degree-hours per day while heating at 20 and 30 m depth were 11.14 and 6.01 degree-hours per day, while in the Bahamas heating at the surface estimated from the SST data was 12.61 degree-hours per day, while heating at 20 and 30 m depth were 14.48 and 10.75 degree-hours per day. These site-specific patterns reflect the greater frequency and magnitude of cooling events at depth in Florida compared with Bahamas. Similarly, while mean heating rates estimated for St. Croix and Belize were nearly equal (4.07 and 3.68 degree-hours per day respectively) the heating at 20 and 30 m
was markedly less at St. Croix (1.11 and 1.05 vs 4.48 and 3.06 degree-hours per day).
While the estimates in Table 2 are normalized for number of Summer days, the among site comparisons should be viewed with the caveat that data collection days were not equal or entirely concurrent among all sites.

Subsurface thermal variability was present at all sites and was extensive at some sites and seasons. Figure 3 shows the surface and subsurface temperature for all of 1998 at the Florida site. The available satellite SST data are shown as individual points, and the solid line shows the time series with the linear interpolation across missing points. SST data from the nearby NDBC buoy are also shown. There was close overall agreement between the two SST datasets, although the hourly buoy data clearly contained a level of high frequency variability that was not captured in the daily satellite data. In general the SST data from both the AVHRR and the buoy were quite consistent from day to day and the primary variability occurred at seasonal time scales. By contrast, there was extensive
variability at high frequencies in the data from 10, 20, and 30 m depths, particularly in the Spring and Summer, and the magnitude of this variability increased with depth.

Figure 4 shows power spectra for the buoy SST and the subsurface data calculated for the entire 6.5 yr record from Florida. At low frequencies the spectra are dominated by a single peak corresponding to the annual periodicity. At frequencies greater than 0.5 cycles per day, the spectra contain distinct peaks corresponding closely to diurnal (24 h period) and the M2 (12.42 h period) semi-diurnal frequencies. Within the diurnal band a peak corresponding to the O1 tidal frequency (0.929 cpd) can be resolved from the peak corresponding to diurnal frequency (1.0 cpd). While the height of the peak at the diurnal frequency decreases with increasing depth, the height of O1 and M2 peaks increase from 10 to 30 m. The diurnal peak label S1 in Figure 4 may also contain variability associated with the P1 (0.997 cpd) and K1 (1.003 cpd) astronomical tidal components. At frequencies greater than semi-diurnal the thermal variability decreased smoothly with increasing frequency. The proportion of the overall variance contained in the portions of the spectra at frequencies greater than 0.5 cycles per day are approximately 1, 2, and 5% at 10, 20, and 30 m depth respectively. Close examination of the semi-diurnal peak for the buoy SST data suggest the presence of 2 partially overlapping peaks, a small M2 peak and a larger peak at exactly 12 h period, which may be a harmonic of the diurnal peak.

Examples of the high frequency temperature variability at all sites are shown in Figure 5. Each plot shows 1 month of data from each of three depths with the SST data. Time periods were chosen to illustrate the high frequency variability at each site. At all 6 sites there were clear differences between the variability in the SST data and patterns measured at depth. The satellite SST data capture general trends but were quite sparse on a daily time scale. By contrast, the subsurface data showed periods of rapid temperature oscillations, at all sites except Jamaica. The magnitude of the variability was strongly site dependent (note the differences in temperature scale among plots). The prevalence of high frequency thermal variability at depth across sites is shown in more detail in Figures 6 and 7. While the magnitude and extent of high frequency fluctuations at 30 m depth was clearly greatest at FL (note the difference in y-axis scaling for the FL panel in Fig. 6) and smallest at JA,

Table 2. Site- and depth-specific warming expressed as mean degree hours above 29.0°C per day during summer (21-Jun to 21-Sep). Surface data from remotely sensed SST, data at depth from in situ recorders. Depths at BZ are 0, 9, 18, 27 m, depths at all other sites as indicated. Number of days: FL 550, BH 162, SC 209, DB 184 (except DB-10 m n = 92), BZ 331 (except BZ-18 m n = 240, BZ-9m n = 199). Insufficient in situ summer data available from Bonaire to include. Site abbreviations as in Figure 1.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>FL</th>
<th>BH</th>
<th>DB</th>
<th>SC</th>
<th>BZ</th>
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<td>30</td>
<td>6.01</td>
<td>10.75</td>
<td>5.86</td>
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</table>

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bursts of variability occurring at diurnal, semi-diurnal, and faster frequency are evident in the spectrograms for all sites.

Figures 8 and 9 show the power spectra calculated for each site, depth, and season. The spectra show distinct peaks corresponding to diurnal and semi-diurnal variability as well as a generally smooth roll-off of variability at higher frequencies. The overall level of variability and the height of the semi-diurnal peaks were greatest at Florida. With the exception of Jamaica, the other sites also show evidence of semi-diurnal forcing, with the largest peaks occurring in the Spring and Summer in Florida, Bahamas, and St. Croix, and in Winter in Belize and Bonaire. At all sites, the magnitude of the semi-diurnal peaks increased with depth. In contrast, the peaks corresponded to diurnal variability were largest in shallow water at all sites.

Figure 10 shows the root-mean-square (rms) amplitude and 95% confidence intervals for the total spectrum and for the diurnal and semi-diurnal bands for each site, season, and
depth. The confidence intervals, which are calculated a function of the length of the FFT and number of individual spectra in the average, may be underestimates because the variance in the underlying data was not necessarily stationary within seasons. Consistent with the power spectra, both the total and the semi-diurnal rms amplitude were greatest at the Florida site. Strong seasonality with increases in the rms variability in Spring and Summer was also evident. In addition to varying seasonally, the rms amplitudes varied significantly among sites. For the diurnal variability, at all sites except Florida the amplitude was greatest in shallow water. For the semi-diurnal variability the rms amplitude

Figure 4. Power spectral density ($^\circ$C$^2$ per cycle per day) as a function of frequency (cycles per day) calculated for the hourly sea surface temperature data from station MLRF1 (top set of panels) and ten minute data from 10, 20, and 30 m depth (lower 3 sets of panels) from Conch Reef, Florida, for the period 01 Jan 1998–30 Jun 2004. Panels on left show spectra for the low frequency components of the data after processing with a low pass 40-h running mean filter. Panels on right show spectra for the high frequency components after subtraction of the 40 h running mean from the raw data calculated on 60 d data segments ($N_{fft} = 8640$ for the 10 min internal sampling). Vertical dashed lines indicate frequencies corresponding to annual (1y), near diurnal ($O1 = 0.929$ cpd and $S1 = 1.00$ cpd), and lunar semi-diurnal ($M2 = 1.94$ cpd) cycles.
at the Florida 30 m site in the Spring and Summer were 0.41 and 0.32°C respectively. By contrast, the rms amplitude for the same depth and seasons at Bahamas were only 0.07, 0.05, and 0.08, 0.06 at St. Croix. The corresponding mean temperature range within the frequency bands was twice the mean amplitude. In Bonaire (where the data record was less than a full year) and in Belize the seasonality of the semi-diurnal variability was different than at the other sites, with maximum amplitude in the Winter. In Belize the amplitude of the semi-diurnal band in Winter was nearly constant across depths.

Figure 11 shows the temperature range and variance as a function of site latitude. The upper two panels show the temperature standard deviations calculated for the overall
records and for the high frequency components (frequencies $\geq 1/40$ cycles per hour) of the records. The lower two panels show mean and maximum within-day temperature ranges as a function of site latitude. The low frequency variability was dominated by the seasonal fluctuations and appears closely related to latitude. The magnitude of variability

Figure 6. The high frequency component of temperature signals at 30 m depth for a representative year of continuous data at each site (data from 27 m depth at BZ). A 40 h low-pass running mean filter was used to separate the low and high frequency variability at each site. Site abbreviations as in Fig 1. Specific data years as follows: FL 1-Jan-1998 to 1-Jan-1999; BH 16-Jun-1998 to 16-Jun-1999; JA 18-Jan-1998 to 18-Jan-1999; SC 3-Apr-2000 to 3-Apr-2001; BZ 21-Mar-2001 to 21-Mar-2002; BN 10-Nov-2003 to 18-Jun-2004. Note difference in scale of temperature variation at FL relative to other sites.
shows little change with depth, and agrees well with variability calculated for the SST data (shown in Table 1). For the Bonaire data, the in situ data set covered less than a full year, and thus the overall variability was less than that calculated for the SST data. In contrast to the patterns of overall variability, the standard deviation of the high frequency component of the records and the daily temperature ranges were not simple functions of latitude. High frequency variability and within day ranges were greatest in Florida, and relatively similar at the other sites. The two lowest latitude sites, Belize and Bonaire, had more high frequency variability and greater within-day temperature ranges than the three sites at Jamaica, St. Croix, and the Bahamas. At both the northern-most and southern-most sites,
Florida and Bonaire, there were relatively large differences in variability and range across depths, while these were relatively similar across depths at the other four sites.

4. Discussion

a. Patterns across space and time

Two clear messages emerge from this study: (1) the thermal environments on coral reefs across the study region are variable on a range of frequencies with consistent peaks of variability occurring at seasonal, diurnal, and semi-diurnal frequencies; (2) the magnitude

Figure 8. Power spectral density for quarterly seasons at 10, 20, and 30 m depth for sites FL, BH, and JA. Spectra calculated by Welch’s average periodogram method after subtraction of 40-h running mean from the raw records. Vertical bar in upper right corner of each plot shows 95% confidence interval for the spectra. Vertical gray bars represent the width of the diurnal and semi-diurnal frequency bands.
of the high frequency fluctuations vary significantly with depth, site, and season, and this variability is not well captured in sea surface temperature data alone. While seasonal variability was relatively limited, especially at the lower latitude sites, the high frequency in situ data reveal significant variability at daily and shorter time scales across the study region. The combined approach of deploying in situ instrumentation at depth and analyzing available SST data allows consideration of site-specific, high frequency variability within the context of broader geographic patterns.

At low frequencies associated with the seasonal variability the temperature records appear strongly coherent among sites. However, the seasonal range of temperatures was significantly greater at the two highest latitude sites, FL and BH, than at the four sites in the Caribbean. This was driven primarily by the cooler Winter temperatures (21–22°C) at FL.
and BH compared with Winter temperatures of 24–26°C at the other four sites. Winter cooling is likely to be a function of latitude, ocean basin, and proximity to the land mass of North America and associated atmospheric cold fronts. In contrast to the patterns of seasonal variability, the extent of variability at daily and faster time scales does not appear to follow a simple relationship with latitude. For example, while the Florida site had by far the greatest thermal variability, the Bahamas site at nearly the same latitude had considerably less variability, equivalent to that at the sites in the central latitudes of the Caribbean. The lowest latitude site, Bonaire, had greater high frequency variability than the other Caribbean sites further to the North. Neither SST patterns nor the amplitude of local surface tides appear to explain the differences in high frequency variability among sites.
Figure 11. Standard deviations and within-day ranges of the subsurface temperature data as a function of latitude for all study sites. Top two panels show standard deviation for the overall records and for the high frequency components (frequencies $\geq 1/40$ cycles per hour). Lower two panels show mean and maximum within-day temperature ranges. Solid circles represent data from 10 m (9 m at BZ), open circles represent data from 20 m (18 m at BZ), and open squares represent data from 30 m (27 m at BZ).
For example, the tidal amplitude near the Florida and the Bahamas sites are roughly equivalent, yet these sites differed significantly with respect to the extent of temperature variability at semi-diurnal and faster frequencies. Rather than being a simple function of latitude or local surface tides, high frequency temperature variability at each site is likely a complex function of water column stratification, alongshore currents and their interaction with the shelf break, and local topography.

Seasonal patterns associated with Summer warming are also evident at low frequencies and, as with the Winter cooling, the higher latitude sites show somewhat more extreme (warmer) values than the sites in the Caribbean. Patterns of cumulative heating across depths and among sites are not, however, well captured by the SST data alone. The calculation of heating degree hours above 29°C per day (Table 2) suggest that the SST data can underestimate heating in shallow water, for example at 10 m depth. This is likely due to transient heating during the daylight hours that is not detected in the once-per-day remotely sensed SST records. More importantly, the in situ data show significant variation among sites in the patterns detected across depths. For example, while Florida appears to be the hottest site at the surface, rates of cumulative heating at 20 and 30 m depth were less than those measured at the Bahamas site. This is due to the prevalence of short term cooling events at depth in Florida that may act to buffer deeper portions of the reef from surface warming especially in Summer. Similarly, while the rates of heating at St. Croix and Belize appear to have been similar at the surface, the 20 and 30 m depths in St. Croix appear to have experienced less heating than any of the other sites at comparable depths. The data clearly show that site-specific patterns can play a significant role in the relationships between heating at the surface and at depth for a given site. Clearly it is essential to collect continuous data at depth and concurrently among sites in order to make accurate site comparisons of heating rates. These data also suggest that the any depth-specific responses of corals to thermal stresses may vary among sites. While analyses such as calculating cumulative heating above threshold temperatures (e.g. 29°C) can be a useful means of comparing environmental data among sites, the range of temperatures and cumulative heating that induce stress responses such as bleaching are likely to be both depth- and site-dependent. Consequently, threshold temperatures based on temperatures recorded at the surface or at a single depth are unlikely to provide accurate estimates bleaching across depths or locations.

b. Mechanisms of high frequency thermal variability

The patterns revealed by the time series analyses clearly point to the importance of forcing at both diurnal and semi-diurnal frequencies. At the scale of within-day variability, strong diurnal temperature fluctuations are evident, particularly in shallow water. The data from 10 m at Bonaire (Fig. 5) are a good example of this regular variability within the diurnal cycle. The amplitude of these diurnal fluctuations was approximately 0.5°C at 10 m depth and decreased markedly with increasing depth. These diurnal fluctuations most likely reflect daily solar warming and nightly cooling of the water column. Additionally,
diurnal sea breezes can be associated with onshore transport of warm surface layers in coastal systems. For example, Kaplan et al (2003) attributed strong diurnal variability in temperature at coastal sites in Chile to a combination of solar warming and a daily onshore sea breeze. Strong daily offshore winds have also been observed for example in the Gulf of Oman where they are associated with diurnal intrusions of cool bottom water onto coral reefs (Quinn and Johnson, 1996). Daily sea breezes may play an important role in onshore transport of warm surface layers on the reefs studied here. The effects of diurnal solar heating/cooling and of diurnal sea breezes would both be expected to decrease with increasing depth and these mechanisms cannot be distinguished on the basis of spectral analysis alone as they both occur at frequencies close to 1.0 cpd (Pidgeon and Winant, 2005). The presence of a spectral peak at the near diurnal O1 tidal frequency (0.929 cpd) for the long time series from Florida is consistent with observations in coastal Southern California, and suggests that some of the variability within the range of frequencies we define as the diurnal band (33/24 to 18/24 cpd) can be associated with tidal forcing mechanisms as well as diurnal heating/cooling and wind driven advection.

The concentration of variance at tidal frequencies, especially at the M2 lunar semi-diurnal frequency, clearly point to mechanisms acting at tidal frequencies. However, neither the magnitude of the observed variation, nor the site-, depth-, and season-specific patterns can be explained as simple effects of surface tides moving a stratified water column past fixed sensors. The maximum value of the mean vertical thermal stratification ($dT/dz$ where $T$ is temperature and $z$ is depth) varied from 0.01 to 0.1°C m$^{-1}$ among sites, and the tidal amplitude is not more than 1.0 m at any of the sites. Therefore, the measured thermal gradients and the effects of a 1 m surface tide can only explain approximately 0.01 to 0.1°C of observed variability of 1.0 to 4.0°C occurring within the tidal cycle. Additionally, the rapid temperature fluctuations observed at depth tended to occur not as smooth cycles but as sharply defined events and/or a series of rapid drops in temperature followed by a subsequent return to pre-event conditions. This suggests the temperature changes are caused by the movement of distinct water masses onto and off of the reef slopes. Examples of such events were present in the data from 30 and 20 m depth at all of the sites except Jamaica (see Fig. 5). Individual events are characterized by cooling first detected at the deepest stations followed by cooling at successively shallower depths, indicating the movement of cool water masses up the reef slopes. The warming at the end of these events starts in shallow water and is subsequently detected at successively deeper stations, suggesting subsidence of the cool water down the slopes.

Strong evidence for the impact of internal waves at the study sites include the clear peaks of thermal variability at tidal (and faster) frequencies, the observations of coherent thermal fluctuations across depths and increases in the magnitude of fluctuations with increasing depth, and the lack of an explanation of the magnitude of cooling by simple effects of surface tides and vertical stratification. The patterns are well explained by effects of internal waves at tidal frequencies (‘internal tides’) as well as higher frequency, non-linear internal waves. These observations are consistent with prior observations of the vertical
and horizontal movement of cool, subsurface water masses at the Florida site (Leichter et al., 2003; Leichter et al., 1996), but represent, to our knowledge, the first report of similar forcing at the regional scale of the Caribbean and Bahamas. Similar processes have been described for the outer margin of the Great Barrier Reef (Wolanski and Pickard, 1983), Tahiti (Wolanski and Delesalle, 1995), and the Seychelles Islands (Novozhilov et al., 1992). In temperate coastal systems in Southern California and Oregon internal waves have also been linked to onshore transport of surface warm fronts (Pineda, 1999; Shanks and McCulloch, 2003), and this may be a consequence of internal wave impacts on reefs as well. Large amplitude internal waves have been observed in the Caribbean on the coast of Puerto Rico (Giese et al., 1990) and may be one of the sources of variability reaching near-by St. Croix as well. The present data do not allow us to determine the ultimate sources of internal waves impacting the study reefs. However, high frequency, subsurface thermal variability associated with internal waves may be a general phenomenon on the deep slopes of fringing, barrier, and atoll reefs that are open to forcing associated with the vertical structure of the offshore water column.

At a given site and season the nature of the high frequency temperature variability at depth should be influenced by the vertical stratification of the offshore water column, the nature of local mechanisms producing vertical oscillations of the thermocline, the proximity to the shelf break or other zones of internal wave generation, and the shelf bathymetry. The spectrograms and seasonal power spectra (Figs. 7–9) and the rms amplitude calculations (Fig. 10) clearly show that the magnitudes of the diurnal and semi-diurnal variability are functions of site, depth, and season. In Florida, Bahamas, and St. Croix the peak semi-diurnal variability was measured in Spring and Summer, while in Belize and Bonaire the peak semi-diurnal variability occurred in Winter. This seasonality likely reflects variation in the strength and mean depth of the offshore thermocline. At longer time scales, variation in water column thermal and density structure at inter-annual and longer times scales may have significant impacts on the ‘thermal climatology’ of reefs and nature of high frequency variability.

c. Potential importance to corals and coral reefs

A growing body of evidence suggests that corals are physiologically sensitive to rapid temperature changes on time scales of minutes to hours. For example, Coles and Jokiel (1977) exposed four species of Pacific corals to elevated temperatures (18–31°C) for periods of 10–40 min and found a positive relationship between temperature and productivity for 3 of the 4 species, and noted an increase in respiration for all 4 species. Hoegh-Guldberg and Smith (1989) reported increased expulsion of zooxanthellae by Pacific corals Stylophora pistillata and Seriatopora hystrix within 30 min to 2 h exposure to 32°C water. Jones et al. (1998) showed significant changes in photosynthetic parameters measured by fluorescence in S. pistillata in 1 and 4 h exposures at 32–34°C. Hill et al., (2004) found early signs of bleaching after exposures of 5 h at 33°C, and Castillo and Helmuth (2005) showed changes in rates of photosynthesis and respiration in the
Caribbean coral *Montastrea annularis* after exposures of 1–3 hr at 31–32°C. The incidence of mass coral bleaching at regional scales has been strongly correlated with warm SST anomalies at weekly to seasonal time scales (Aronson *et al.*, 2002; Gleeson and Strong, 1995; Sheppard and Rayner, 2002). However, it also appears likely that aspects of the temperature environment at frequencies higher than those measured in the daily SST records can play important roles in coral bleaching (Winter *et al.*, 1998). Winter *et al.* (1998) examined correlations between bleaching and a series of seven temperature metrics and found that three of the seven metrics predicted bleaching events equally well. In some cases, cumulative temperature stress measured as degree hours above a defined threshold (Gleeson and Strong, 1995) predicted bleaching, but only when acting in concert with a sharp change in temperature (Hoegh-Guldberg and Smith, 1989). Previous studies have also shown that thermal stress and bleaching can be highly heterogeneous across vertical (depth) and horizontal temperature gradients (Brown, 1997; Hill *et al.*, 2004; West and Salm, 2003) as well as at the small scales of individual coral colonies (Edmunds, 1994).

The general pattern of increasing thermal variability with increasing depth between 10 and 30 m suggests reef zones at still greater depths may be exposed to even more thermal variability than exists in shallow water. On many reefs the distribution of reef building corals extends as deep as 50–80 m or more. Even at sites such as Jamaica, where the subsurface temperature variability is relatively small compared with other sites, it is entirely possible that temperature variability in deeper reef environments could be quite large. Data from 45–55 m depth at Jamaica do show evidence of internal wave forcing not evident at 30 m (Leichter and Genovese, 2006). Thus, while deeper reef environments may be more stable than shallower regions with respect to physical variables such as light availability and surface wave-induced water motion, deep reefs are likely to be areas of extensive thermal variability. The high frequency thermal variability arises from the movement of distinct, subsurface water masses onto and off of reefs. Factors such as salinity, and the concentration of dissolved nutrients that also vary with distinct water masses are, therefore, also likely to be highly variable in deep reef environments, and forcing associated with internal waves may have significant ecological implications for deep reef environments. Marked increases in the concentrations of dissolved nutrients and suspended particles can accompany the movement of cool, subsurface water masses onto a reef slope under the influence of internal waves at semi-diurnal and higher frequencies (Leichter *et al.*, 1998; Leichter *et al.*, 2003; Leichter *et al.*, 1996). Cooling events can, therefore, represent transient bouts of food particle and nutrient availability for benthic suspension feeders and primary producers such as corals and macroalgae. Benthic suspension feeders and primary producers are well equipped for rapid particle capture and nutrient uptake under favorable conditions such as short term pulses.

Attempting to predict the impacts of the physical environment on coral reefs requires understanding not only physiological responses of organisms to parameters such as temperature, water flow, and salinity, but knowing how these factors vary in space and in time. The data presented here clearly show that temperatures experienced by corals at
depth can fluctuate considerably on diurnal, semi-diurnal, and faster time scales and cannot be completely characterized from daily SST records. These high frequency patterns can be quantified using in situ data, and vary considerably between seasons, sites and over depths. An obvious set of questions is what consequences do these high frequency fluctuations have for the physiology and ecology for corals and other reef organisms? Unfortunately, current knowledge of the thermal physiology of benthic organisms especially over short time scales does not provide sufficient answers.

Previous studies have emphasized spatial patchiness in bleaching on reefs (Mumby et al., 2001), particularly in areas of restricted water flow (West and Salm, 2003). Others have noted considerable variability between sites in the depths to which bleaching extends. While environmental factors such as light (Mumby et al., 2001; Warner et al., 2002) and water flow (Finelli et al., 2005; Nakamura and van Woesik, 2001) undoubtedly play a role, variability in thermal regimes likely contribute in important ways to these patterns. Several studies have shown that the oxygen demand of coral host tissue increases with temperature (Coles and Jokiel, 1977; Lesser, 2004). Similarly, temperature has direct effects on the photosynthetic performance of zooxanthellae, and these effects can vary between species (Warner et al., 1996). By reducing overall mean temperatures, bouts of subsurface cooling may protect deeper reef environments from thermal bleaching particularly in summer when surface temperatures are warmest. The roles of thermal history and rates of temperature change in driving coral physiological stress are also likely to be significant but are presently unknown. Clearly, we are far from completely understanding the physiological effects of high frequency temperature variability for corals. It appears likely, however, that these fluctuations may have important, species-specific impacts on coral physiological performance and survival. Recognizing and quantifying the extent of in situ thermal variability is an important step to understanding their biological and ecological importance and in providing the environmental context for physiological studies (Helmuth et al., 2005). Moreover, it is an important step in linking large-scale pattern detectable via remote sensing and modeling techniques with mechanistic, physiological processes at the scale of individual reef organisms.

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