Coral Reefs
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REPORT

When depth is no refuge: cumulative thermal stress increases with depth in Bocas del Toro, Panama

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Abstract Coral reefs are increasingly affected by high-temperature stress events and associated bleaching. Monitoring and predicting these events have largely utilized sea surface temperature data, due to the convenience of using large-scale remotely sensed satellite measurements. However, coral bleaching has been observed to vary in severity throughout the water column, and variations in coral thermal stress across depths have not yet been well investigated. In this study, in situ water temperature data from 1999 to 2011 from three depths were used to calculate thermal stress on a coral reef in Bahia Almirante, Bocas del Toro, Panama, which was compared to satellite surface temperature data and thermal stress calculations for the same area and time period from the National Oceanic and Atmospheric Administration Coral Reef Watch Satellite Bleaching Alert system. The results show similar total cumulative annual thermal stress for both the surface and depth-stratified data, but with a striking difference in the distribution of that stress among the depth strata during different high-temperature events, with the greatest thermal stress unusually recorded at the deepest measured depth during the most severe bleaching event in 2005. Temperature records indicate that a strong density-driven temperature inversion may have formed in this location in that year, contributing to the persistence and intensity of bleaching disturbance at depth. These results indicate that depth may not provide a stress refuge from high water temperature events in some situations, and in this case, the water properties at depth appear to have contributed to greater coral bleaching at depth compared to near-surface locations. This case study demonstrates the importance of incorporating depth-stratified temperature monitoring and small-scale oceanographic and hydrologic data for understanding and predicting local reef responses to elevated water temperature events.

Keywords Temperature stress · Bleaching · Depth stratification · Caribbean

Introduction

Globally, coral reefs have been subject to increasing episodes of coral bleaching, caused largely by periods of elevated ocean water temperatures over the past two decades (Glynn and D'Croz 1990; Knowlton 2001; Hughes et al. 2003). In 2005, much of the coral reef habitat in the Caribbean basin was affected by a record-breaking warm water-mediated mass-bleaching event (Eakin et al. 2010), causing significant mortality and an attendant loss of ecologically important structural complexity (Alvarez-Filip et al. 2009). Such acute bleaching events are predicted to increase in both frequency and geographic scale in future years (McWilliams et al. 2005). Therefore, an improved understanding of the causes, effects, and variations of

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thermal stress on corals is essential for management and conservation of reefs (Marshall and Schuttenberg 2006).

Spatial and temporal patterns of sea surface temperature (SST) conditions and the consequent thermal stress on coral reefs have been well described (Pandolfi et al. 2005; Maina et al. 2011), and monitoring efforts have primarily focused on these surface temperature trends. For example, the decision support system (DSS) operated by the United States' National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch (CRW) is the most extensive program providing near-real-time coral bleaching thermal stress monitoring information (Liu et al. 2005, 2008), but is based on satellite SST, and thus reflects only near-surface temperature conditions with a spatial resolution of 0.5° by 0.5° (approximately 50 km by 50 km cells) and a twice-weekly temporal resolution.

In normally stratified conditions, most physical stressors that originate at the sea surface, such as thermal stress caused by high SST, photic stress from visible or ultraviolet radiation, and physical stress from surface waves, can be expected to attenuate with depth (Brown 1997; Glynn 1996). Colonies at greater depths, if protected from disturbance, may serve as potential recruitment sources (Hughes and Tanner 2000; Mumby et al. 2011), and this recruitment has been proposed as a resilience mechanism supporting future recovery and resettlement of disturbed corals in shallower waters that have suffered major stress (Hoegh-Guldberg et al. 2007). However, depth may not always provide this function, as corals in different depth strata in reef environments can be subject to thermal conditions different from those at the surface due to local circulation patterns (Leichter et al. 2006). Further, colonies living at deeper depths may also be differently acclimated and potentially more sensitive to temperature changes of smaller magnitude (Oliver and Palumbi 2011; Carilli et al. 2012). Our study area provides a case study for investigating the structure and impacts of depth-dependent thermal dynamics on reef environments, as it is an area of extensive coral development that experiences large variation in both temperature and salinity (Kaufmann and Thompson 2005).

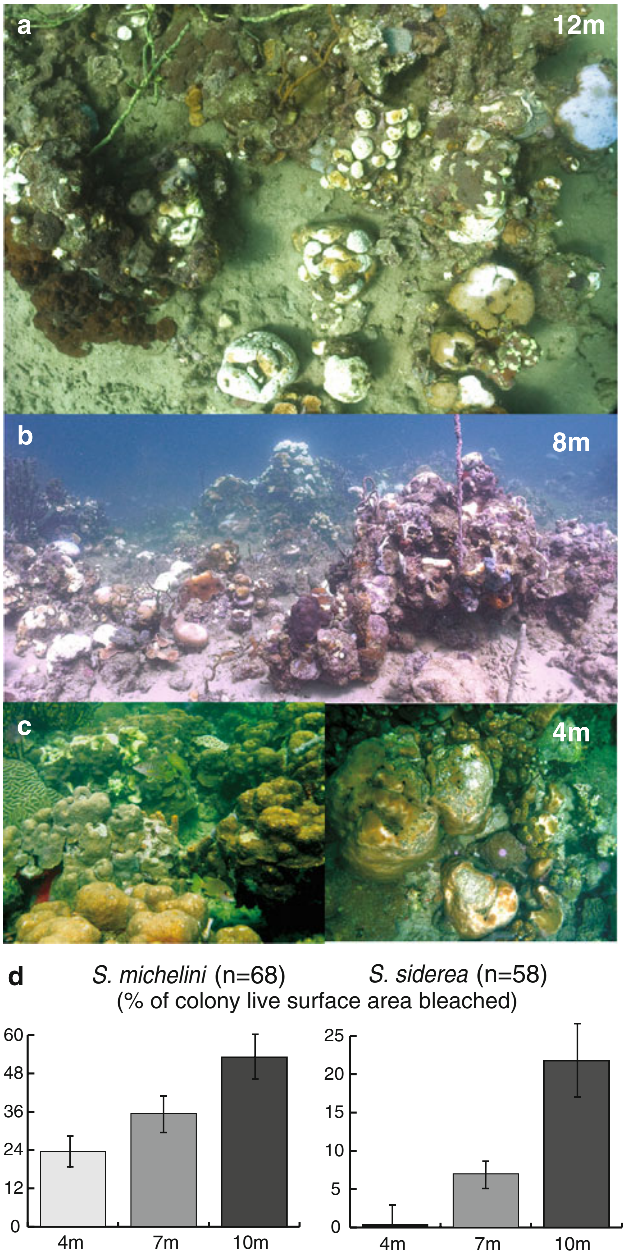


Fig. 1 *Photos* from the inshore location in September 2005 showing bleaching across a number of coral taxa at three depths; **a** 12 m, **b** 8 m, and **c** 4 m. **d** Shows bleaching extent (% of live area) for two species, *S. siderea* and *S. michelini*, at three depths (D. Kline, personal observation)

During the widespread 2005 Caribbean mass-bleaching event, one of the authors (D. Kline) noted strikingly increased coral bleaching extent at 10 m depth compared to bleaching observed at 1–3 m (Fig. 1), contravening expectations that the impacts of thermal stress would be greater near the surface. This observation was supported by measurements of bleaching extent through planar area analysis of photographs of individual colonies, showing bleaching extent per colony increasing with depth for some species (*Siderastrea siderea* and *Stephanocoenia michelini*; D. Kline, personal observation). To investigate the etiology of this unusual vertical distribution of bleaching severity, depth-stratified temperature data were used to calculate thermal stress indices through time and across depth. Specifically, the potential impact of localized, depth-specific temperature forcing was investigated by comparing the NOAA CRW satellite SST-based coral bleaching thermal stress index for this area to similar indices calculated from in situ temperature loggers from three depths. Given projected increases in severity and frequency of bleaching events (Maynard et al. 2009), understanding the impacts of patterns in thermal stress throughout the water column will be critical for making spatially accurate predictions about the extent and severity of bleaching.

Materials and methods

Two separate sea temperature time series were used to calculate coral thermal stress indices near Bocas del Toro, Panama: (1) NOAA CRW satellite SST from the closest cell to the area; and (2) stratified in situ seawater temperature measurements from the Smithsonian Tropical Research Institute (STRI) Physical Monitoring Program. The former is a single record, while the latter consists of three independent records from different depths at one location. All four datasets were analyzed identically to produce directly comparable calculated stress metrics. The NOAA CRW 50-km satellite cell and record will hereafter be referred to as the offshore site and record, and the three STRI datasets will collectively be referred to as the inshore site and record.

The NOAA CRW SST record is from a single satellite data cell of 0.5° × 0.5° spatial resolution (approximately 2,500 km^2) centered at 10°00′ north/82°00′ west (Fig. 2). This is the cell closest to Colon Island, Bocas del Toro. In the absence of other data, this would be the most applicable cell for predicting local coral bleaching thermal stress. However, the large size of the cells and the necessary exclusion of cells containing terrestrial surface due to potential contamination of the satellite's temperature measurement have the consequence of precluding direct coverage of actual coral habitat, most of which lies within the embayment; rather, this nearest reference cell contains only open ocean water. This dataset is a twice-weekly whole-cell mean SST time series, derived from nighttime measurements by advanced very high resolution radiometers (AVHRRs) on NOAA's Polar Operational Environmental Satellites (POES). Only nighttime SSTs were used to reduce the influence of daily warming from surface solar heating and to avoid potential contamination from solar glare (Liu et al. 2008). Nighttime SST compares favorably with in situ temperature at 1 m depth (Gleeson and Strong 1995).

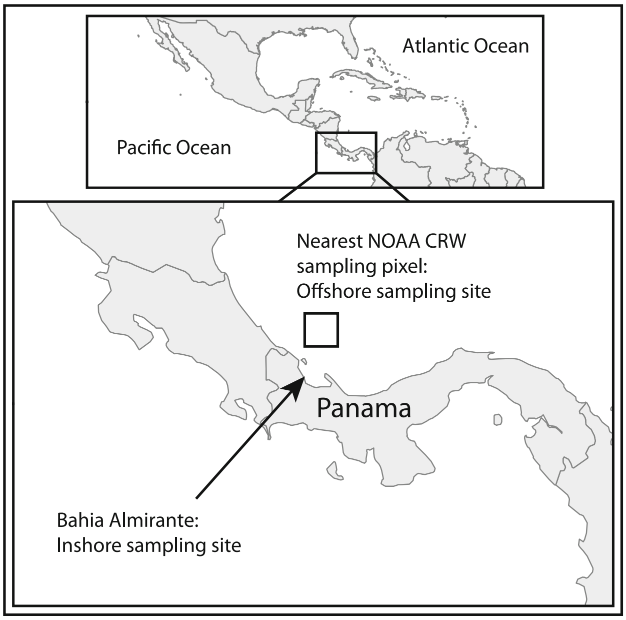


Fig. 2 *Map* of region and sampling locations. Bocas del Toro, Panama, is located in the southwest Caribbean Sea, with the *inset* showing the area of the Bahia Almirante embayment. The *square* in the *inset* indicates the closest NOAA CRW-SBA sampling pixel, and the *arrow* indicates the inshore sampling location, located on the reef inside Bahia Almirante

Unlike the offshore surface record from NOAA CRW, which does not include any coral area and thus may not accurately represent actual ecosystem conditions, the inshore depth-stratified site was located on a patchy coral reef (Guzman and Guevara 2001). Three HOBO Stow-Away TidbiT and HOBO Water Temperature Pro V2 instruments (Onset Computer Corporation, Bourne, MA, USA) were placed near the bottom along the reef slope at 4, 10, and 20 m deep. The site is located to the northwest of the STRI station on the western shore of Colon Island, in the embayment of Bahia Almirante, Panama, at 9°20.8′N/82°15.75′W, known locally as Sunset Point. This location is a long-term coral and sea grass physical and biological monitoring site for STRI (Kaufmann and Thompson 2005) and was also a Caribbean Coastal Marine Productivity Program (CARICOMP) monitoring site (Guzman et al. 2005). Temperature data were collected hourly from 1999 to present, and sensors were changed and calibrated biannually immediately prior to deployment in a water bath at 21 °C against a traceable thermometer, with data adjusted post-deployment. Accuracy of the data is ±0.25 °C (Kaufmann and Thompson 2005). The hourly record used for this analysis is continuous from March 28, 1999 to September 28, 2011. Nighttime-only data (between 2400 and 0800 hours local time) were extracted to match the nighttime constraint of the offshore satellite record.

The four temperature time series were processed with the same algorithm used to calculate NOAA CRW's operational thermal stress monitoring products (Liu et al. 2008). Thus, direct evaluation of differences could be made across depths and between the two sites. First, a long-term temperature reference baseline (historical climatology) was calculated for each of the three in situ temperature records. This baseline is comprised of 12 monthly values, each the mean of all monthly nighttime temperature means for that month across the reference period. The single largest value in this set was then selected as the climatological maximum monthly mean sea temperature (MMM-ST), which was used as the base value for calculating temperature anomalies specific to the location or depth of each of the datasets. MMM-ST is thus the highest mean monthly condition to which the corals in that location have been subjected (Liu et al. 2004). The historical MMM-ST value thus varies for each site and depth, but remains static for that site or depth for all subsequent analysis. For the offshore site, the MMM-ST was provided by NOAA CRW, as originally derived from reprocessed satellite SST data from the multi-channel SST dataset (MCSST) at the Rosenstiel School of Marine and Atmospheric Science (RSMAS), University of Miami, for the period 1985–1993, with 1991–1992 excluded to avoid aerosol contamination of the satellite measurements from the eruption of Mt. Pinitubo (Gleeson and Strong 1995). The MMM-ST for the inshore temperature records was derived from a reference period consisting of the first six calendar years of these records (March 28, 1999 through December 31, 2004).

The climatology time period for the three inshore records thus does not correspond to the climatology time period for the surface site due to time limitations in the former time series. To assess any possible difference in climatologies introduced by using two different baseline time periods, differences in regional temperature anomalies specific to these two periods were compared to a mean of the monthly NOAA Caribbean Temperature Index (CAR) (Penland and Matrosova 1998) for both reference time periods (i.e., the 108 months from 1985 to 1993 and the 57 months from April 1999 through January 2004). The later period had a positive anomaly difference of 0.14 °C when compared to the former time period. This difference indicates that the earlier period was slightly cooler across the basin, suggesting that using the later time period as reference climatology for the inshore sites may have resulted in a slightly more conservative calculation of thermal stress for the inshore site compared to offshore. However, this potential difference was deemed to be small enough to not affect the analysis, and no correction was made for the difference in climatology time periods.

Two primary coral bleaching thermal stress indices were calculated, following NOAA CRW's nomenclature: (1) the twice-weekly Coral Bleaching HotSpot and (2) the 3-month cumulative coral bleaching Degree Heating Weeks (DHW). The HotSpot product is an anomaly metric reflecting the instantaneous occurrence and intensity of thermal stress conducive to coral bleaching, defined as the positive difference between the measured nighttime daily temperature record and the long-term maximum monthly mean sea temperature climatology (MMM-ST) (Liu et al. 2004). In our analysis, the HotSpot record is a continuous daily product for the three inshore study site records and is a twice-weekly product for the offshore NOAA CRW satellite cell, corresponding to the dates of the twice-weekly satellite SST record. HotSpot values of 1.0 °C or greater are considered sufficient to cause thermal stress to corals.

DHW are a running sum, calculated for each date by adding HotSpot values equal to or greater than 1.0 °C for the previous 12 weeks, including the reference date, consistent with NOAA CRW methodology. This cumulative parameter is designed to account for the impact of chronic thermal stress, which has been shown to have significant correlation with observed intensity of coral bleaching (Liu et al. 2005; McClanahan et al. 2007), as compared to the HotSpot metric, which reflects only instantaneous conditions. DHW are expressed in units of °C-weeks, with values of 4 °C-weeks or above indicating the onset of potentially damaging coral bleaching, and values of 8 °C-weeks or above indicating risk of widespread bleaching and coral mortality.

A second high-resolution satellite SST record was used to investigate basin-scale hydrologic conditions that could have contributed to bleaching events in Bahia Almirante during the period 1998–2011. AVHRR Pathfinder version 5.2 (PFV5.2) SST data were obtained for the Caribbean Basin at 4-km resolution from the Group for High Resolution Sea Surface Temperature (GHRSST) and the NOAA National Oceanographic Data Center (NODC) (Casey et al. 2010). Aggregated monthly SST values were generated from these data for January 1, 1998–December 31, 2011 for two rectangular polygons, the first is a coastal area close to the mouth of Bahia Almirante representing nearshore water that could be carried into the bay, and the second is an area in the open southern Caribbean Sea, representing offshore water for comparison. The first box is from 80.8°W to 82.3°W, and from 8.7°N to 9.4°N, and the second is from 75°W to 78°W, and from 14°N to 15°N. These two areas are hereafter referred to as the Bocas del Toro nearshore SST reference area and the Caribbean Sea SST mid-basin reference area.

Vertical temperature differences reflecting water column stratification through time at the inshore site were calculated by taking the difference between 4 and 10 m nighttime temperatures, and between 4 and 20 m, with positive values indicating inverted temperature conditions (i.e., warmer water at depth). Local rainfall over the period 2000–2012 was investigated to determine whether unusual rainfall contributed to stratification within Bahia Almirante. A monthly record of rainfall was compiled from two records collected at the STRI laboratory. The first was a daily record from a 15-min electronic automated sensor, and the second was a backup daily record from a manually collected tipping rain gauge. The electronic record was used for the majority of the compilation, with the exception of three short

(<10 days each) missing periods, which were augmented by the backup record. Rainfall was compiled into mean daily rainfall for all months, which was tested for correlation with the monthly inversion magnitude using Pearson's product-moment correlation coefficient test. Correlations were also investigated with the temperature record projected forward and backward 6 months at monthly intervals to reveal possible time-lagged correlations.

Results

Comparison of the four temperature records is limited to the continuous period from June 1, 2001 to October 15, 2011 (Fig. 3a–d). Nearly all of the annual temperature profiles across the 11-year time frame show two mid-year peaks, characteristic of the tropics, from the passage of the sun directly overhead twice a year (Rich et al. 1993) in

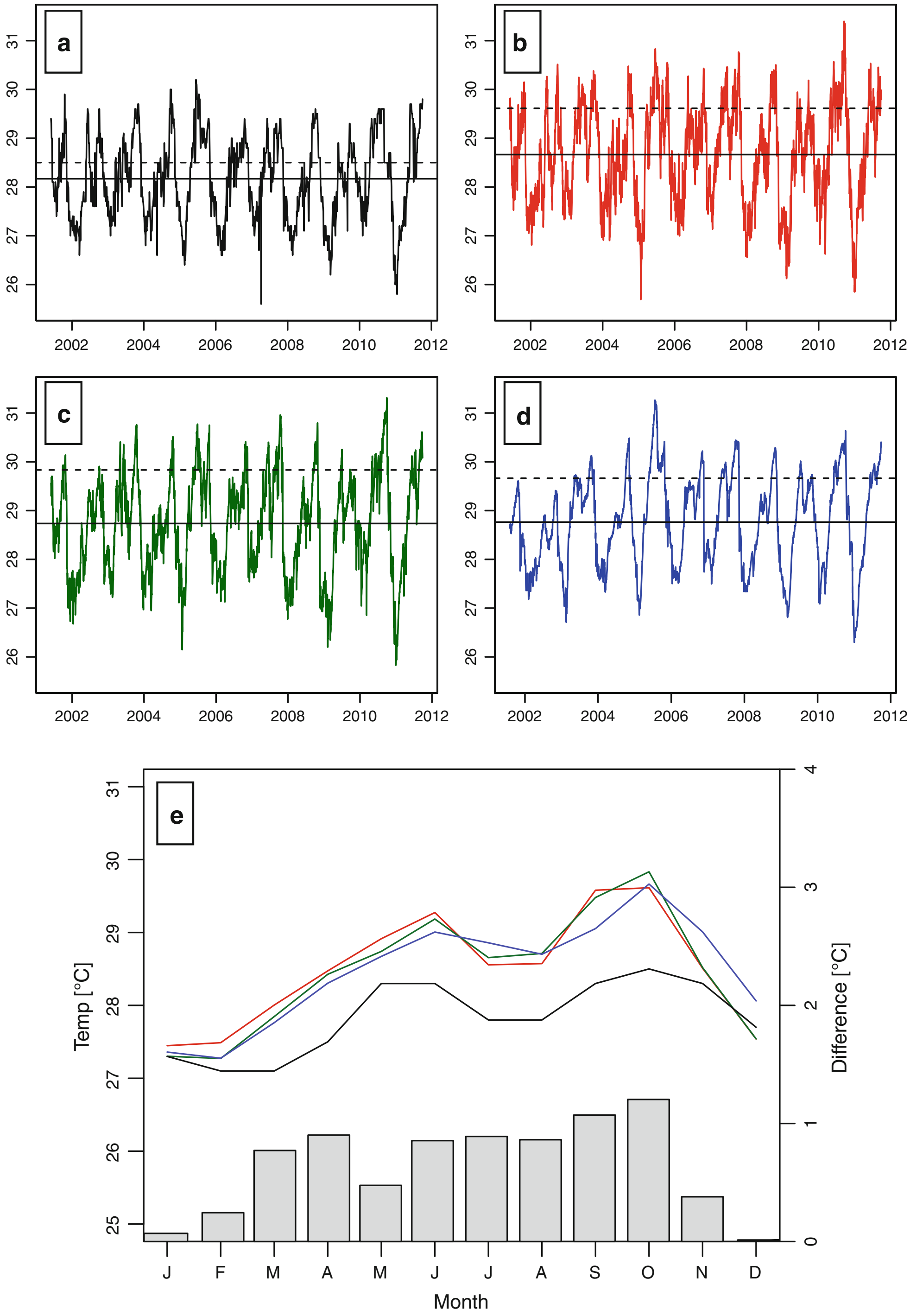


Fig. 3 Daily nighttime mean sea temperature for the four sites near Bocas del Toro, Panama, from June 1, 2001 to October 15, 2011. **a** NOAA CRW surface satellite record; **b** inshore 4 m (*red*); **c** inshore 10 m (*green*); **d** inshore 20 m (*blue*), with *dashed horizontal lines* indicating respective MMM-ST values, and *solid black line* indicating respective mean temperature; **e** monthly climatology for each of the sites, with *barplot* of difference between offshore climatology and the mean inshore climatology from all depths

April and September. Daily nighttime mean temperatures for all sites and years ranged from a high of 31.26 °C on July 22, 2005 at 20 m at the inshore site to a low of 25.6 °C on March 30, 2007 at the offshore surface site. Collectively, mean monthly conditions from January to March were very similar across both sites and at all depths (Fig. 3e), ranging in January from a low of 27.3 °C at the offshore site to a high of 27.44 °C at 4 m at the inshore site, differing by only 0.14 °C. Maxima, minima, and seasonal temperature trends were generally in agreement with earlier reports for this embayment (Kaufmann and Thompson 2005).

During the peak insolation season from April to October, in contrast to the thermal similarity seen across all sites and depths for January to March, both daily and monthly mean nighttime temperatures were consistently higher for the inshore sites than for the offshore site and generally remained elevated over the offshore signal through November. Differences in the annual mean temperature for the entire 11-year period for all sites reflect these higher inshore temperature levels during this warmer time, ranging from 28.11 °C for the offshore site to 28.64, 28.66, and 28.71 °C for the 4, 10, and 20 m sites, respectively (Table 1). Maximum daily mean values reveal that the inshore sites reached 1.06–1.19 °C warmer than the maximum daily mean recorded offshore, with the highest maxima in the shallowest strata, as expected from solar heating (Table 1).

Maximum monthly means were also higher inshore than offshore, ranging from 0.87 to 1.16 °C warmer (Table 1). However, the inshore monthly means reveal an important difference in structure from the daily means, with the deepest depth reaching the warmest levels, as opposed to the surface. The maximum monthly mean at the 20 m depth is 0.05 °C warmer than the 10 m depth and is warmer than the 4 m depth by 0.24 °C. This difference between maximum daily and monthly means indicates that a persistent reverse thermal gradient occurs during some points of the year, despite the occasionally greater thermal input at the surface demonstrated by the higher maximum daily mean. Quarterly means were compiled from the monthly means, and both sites and all depths have the highest quarterly peak in the September–November period and are lowest in the December–February period. The deepest depth inshore exhibits the warmest quarterly mean temperatures in every quarter except March–May, when the profile is reversed, with the water column getting cooler with depth, likely due to surface heating from increased direct solar radiation. This depth also reaches the highest quarterly mean of any site or depth, at 29.44 °C during the September–November period.

Table 1 Temperature ranges and means for all sites and depths; nighttime only (for inshore sites 0000–0800 hrs), °C

Location	Offshore	Inshore 4 m	Inshore 10 m	Inshore 20 m
Maximum daily mean	30.20	31.39	31.31	31.26
Minimum daily mean	25.60	25.69	25.83	26.30
Maximum monthly mean	29.80	30.67	30.91	30.96
Minimum monthly mean	26.18	26.62	26.37	26.52
Mean 2000–2010	28.11	28.64	28.66	28.71
Dec–Feb mean 2000–2010	27.23	27.46	27.48	27.66
Mar–May mean 2000–2010	27.76	28.59	28.49	28.35
June–Aug mean 2000–2010	28.61	29.14	29.19	29.30
Sept–Nov mean 2000–2010	28.88	29.30	29.40	29.44

The historical climatologies differed among sites primarily in that the inshore sites collectively experienced greater seasonal differences compared to the offshore site (Table 2). The largest difference between inshore and offshore was in October when the difference between the coolest and warmest means of monthly sea temperature values increased to a difference of 1.33 °C, with the offshore site the least warm of the four at 28.5 °C (note that this nevertheless was still the single warmest value in the offshore climatology) as compared to the 10 m depth with the warmest October climatology of 29.83 °C. Differences between inshore and offshore decreased rapidly in November and December as the inshore sites cooled, however, and remained small through February, with the inshore sites showing historical temperatures similar to offshore, differing in January by only 0.15 °C, with the warmest value for this month at 4 m at the inshore site (27.45 °C), and the offshore surface site the coldest of the four sites (27.3 °C). Climatologies for all four time series demonstrated the characteristic mid-year dip in sea temperatures, with July and August lower than the 2 months preceding and the 3 months following. The three inshore climatologies were similar in this seasonal pattern, but displayed temporal and magnitude differences over the summer that illustrate differences between them in rate of thermal increase and retention of that energy. The 20-m site reached the first annual peak in June, as did the other 2 months, but was 0.27 °C lower. However, in the following month, during the mid-summer reduction in solar angle, the climatology for the two shallower depths both fell below that of the 20 m depth. This pattern was repeated in the second peak event, in October, with the deepest depth retaining more heat for the following 2 months. These climatological values indicate that temperature at depth is higher than that at the surface on a regular basis during warm periods of the year and that this inversion difference can peak weeks after maximum temperatures are recorded at shallower depths. The MMM-ST values from which anomalies are calculated were also considerably

Table 2 Long-term historical climatologies for all sites and depths. Offshore climatology from 1985 to 1993, excluding 1991–1992, and inshore climatologies from 28 March 1999 through 31 January 2004

Month	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Offshore	27.30	27.10	27.10	27.50	28.30	28.30	27.80	27.80	28.30	**28.50**	28.30	27.70
Inshore 4 m	27.45	27.49	28.00	28.47	28.91	29.27	28.56	28.57	29.58	**29.61**	28.51	27.54
Inshore 10 m	27.30	27.27	27.85	28.43	28.74	29.18	28.66	28.71	29.48	**29.83**	28.52	27.54
Inshore 20 m	27.36	27.27	27.76	28.31	28.67	29.01	28.86	28.70	29.05	**29.66**	29.01	28.06

Bold values are MMM-ST for each record, used as baseline for anomaly calculations

higher for the inshore sites, reflecting these higher monthly means, varying from 28.50 °C in the offshore site to a mean of 29.70 °C for the three inshore locations.

In the offshore site, the HotSpots rose above the 1 °C threshold most notably in 2005 and 2010 (Fig. 4a). In the inshore site, the HotSpot intensity at the 4 and 10 m depths was greatest in 2010, whereas at the 20 m depth, the HotSpots rose above the 1 °C threshold only in 2005 (Fig. 4b–d). There was a general decrease in most years from 4 to 20 m in both HotSpot magnitude and persistence, with the exception of 2005. Across both sites and at all depths, many of the years showed a two-peaked pattern in HotSpot occurrence. This was similar to the distribution of temperature maxima, with peaks in June and October. The June peak was commonly lower than the October peak, with 2005 notable as the only year where the earlier mid-year peak in HotSpot intensity was much greater than the later peak, indicating an unusually large temperature anomaly earlier that year. Initial onset of HotSpot > 1.0 °C for the inshore records was similar for both 2005 and 2010 (June 13 and June 2, respectively) and differed primarily in the pattern of maximal level.

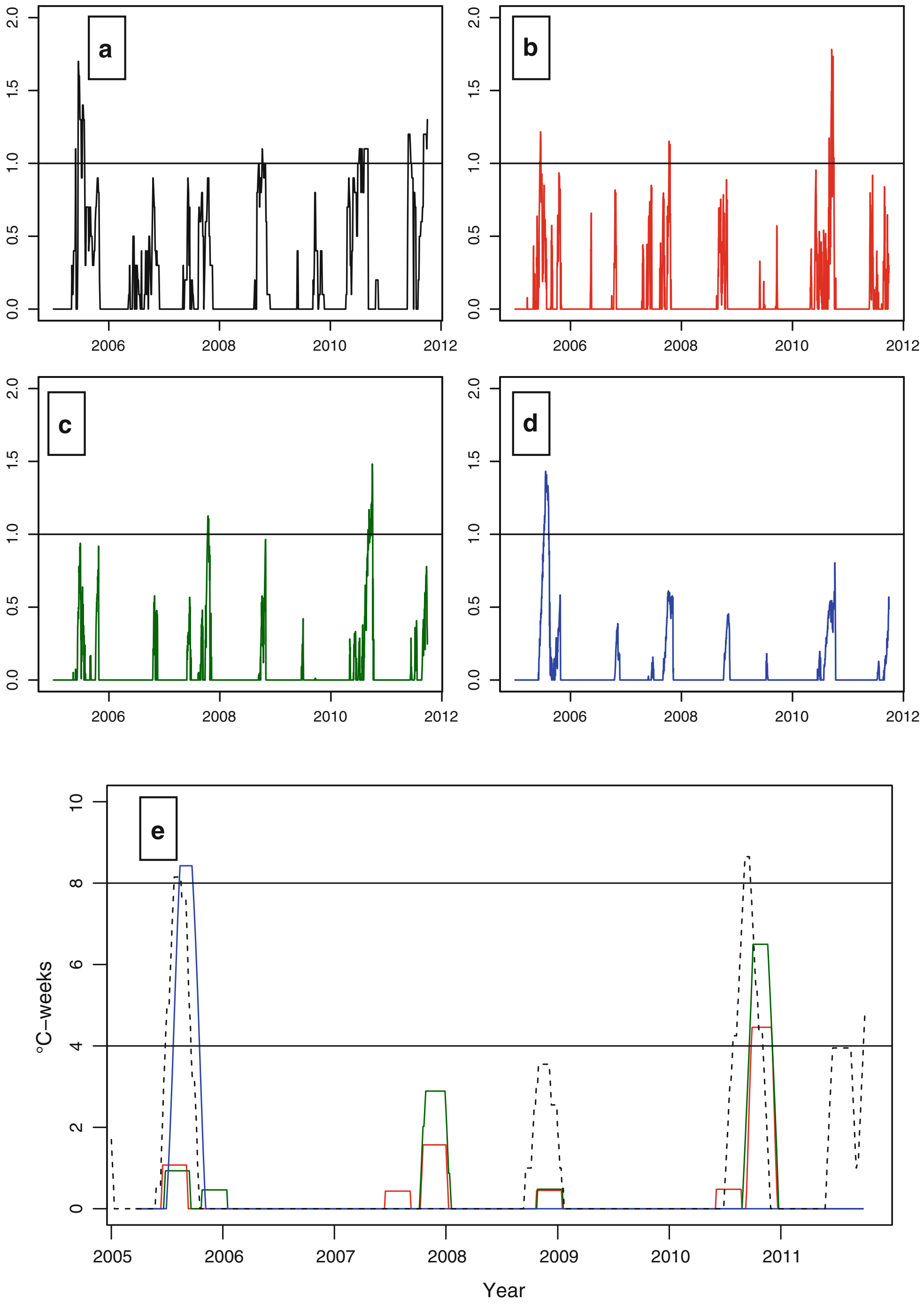
The calculated DHW stress parameter for the surface offshore site was highest in 2005 and 2010, in both years rising above the NOAA CRW defined threshold of 8 °C-weeks associated with widespread bleaching and coral mortality risk (Fig. 4e). NOAA CRW issued bleaching alerts for this area in both of those years. In 2009, the DHW for this site also approached near the 4 °C-week threshold identified by NOAA for onset of significant bleaching conditions, but did not rise to the 8 °C-week threshold. DHW for the depth-stratified sites collectively matched this pattern, being highest in 2005 and 2010, but showed sharply different distribution of stress levels across depth strata between these 2 years. In 2005, the stress was predominantly limited to the deepest 20-m stratum, while in 2010, elevated stress levels were seen only at the upper two strata. Temporally, DHW at the two shallower sites (10 and 4 m) were in all years very similar to each other in temporal pattern, with the 10-m site slightly higher in magnitude in two of the three highest heating events of 2005, 2007, and 2010. There was a consistent temporal lag between occurrence of peak stress at the offshore surface site and occurrence at any of the inshore sites in both 2005 and 2010. Onset of maximum stress in 2005 at the offshore site was on July 23, compared to August 14 at the inshore site (at 20 m depth), and in 2010, maximum stress occurred September 6 at the offshore site and October 3 at the inshore site (at 4 m depth).

Average annual rainfall for the period March 2000 to September 2012 (Fig. 5a) was 3,435.4 mm yr^{-1} ($n = 12$, $\text{SD} = 576$), similar to an earlier report of mean rainfall of 3,277 mm yr^{-1} ($n = 28$, $\text{SD} = 461$ mm) for this area for 1972–2000 (Kaufmann and Thompson 2005). Monthly rainfall means were very stochastic (Fig. 5b); the lowest individual month was 29.46 cm month^{-1} in February 2007, and the highest was 1,045.72 cm month^{-1} in November 2008, during a record rainfall event on the Panamanian isthmus. Mean monthly rainfall (Fig. 5c) varied from a high of 467.27 cm month^{-1} for November ($n = 10$, $\text{SD} = 251.11$) to a low of 152.92 cm month^{-1} for September ($n = 10$, $\text{SD} = 51.68$).

Temperature differences among the inshore strata showed regular periods of both classical thermal structure development (temperature declining with depth) as well as temperature inversions (temperature increasing with depth). Occurrence of these thermal structures was irregular, but generally the first 6 months of the calendar year exhibited classical thermal structure development and the later 6 months exhibited periods of thermal inversion (Fig. 6). Monthly inversion strength was significantly but weakly correlated with monthly rainfall anomaly ($r = 0.48$, $n = 139$, $p = 0.05$). Time-lagging the rainfall by monthly intervals over 6 months both past and future did not reveal any significant correlations with inversion strength.

Analysis of the two sea surface reference areas from the AVHRR PFV5.2 satellite temperature record showed that the Caribbean Sea offshore SST reference area was nearly always cooler than the Bocas del Toro inshore SST reference area (Fig. 7). Over the period 1982–2011, the means for these two areas were and 27.286 and 28.089 °C, respectively, for a difference of 0.803 °C. In order to assess

Fig. 4 HotSpots at the four study sites from January 1, 2005 to October 15, 2011. **a** NOAA CRW surface satellite record; **b** inshore 4 m (*red*); **c** inshore 10 m (*green*); **d** inshore 20 m (*blue*), with *solid horizontal line* indicating the NOAA threshold of 1 °C for HotSpot inclusion in DHW calculations; **e** DHW cumulative stress parameter for each of the sites, with *dashed line* indicating the NOAA CRW surface satellite record, and other colors following the schema in **b**–**d**, and *horizontal black lines* at 4 °C-weeks indicating NOAA threshold for bleaching onset and at 8 °C-weeks indicating widespread coral mortality risk



long-term change, the time series was split into two time periods, one from 1982 to 1997 (inclusive) and the other 1998–2011. For the inshore reference area, there was no significant difference between the early and late periods, with means for the early and late time periods of 28.036 and 28.149 °C, respectively ($p = 0.2628$, $F_{1,357} = 1.1216$), but for the open Caribbean Sea offshore reference area, the later time period was significantly warmer than the earlier period, with means for the early and late time periods of 28.04 and 28.15 °C, respectively ($p < 0.0001$, $F_{1,356} = 5.2553$).

Discussion

Calculations of thermal stress from both the offshore satellite data (NOAA CRW) and the inshore depth-stratified in situ data resulted in very similar overall levels of thermal stress (Fig. 4e). The years with highest stress corresponded with the authors' observations of coral bleaching in this location, specifically 2005 and 2010. However, there were important differences in the stratification of this stress within the water column in the inshore site, with 2005

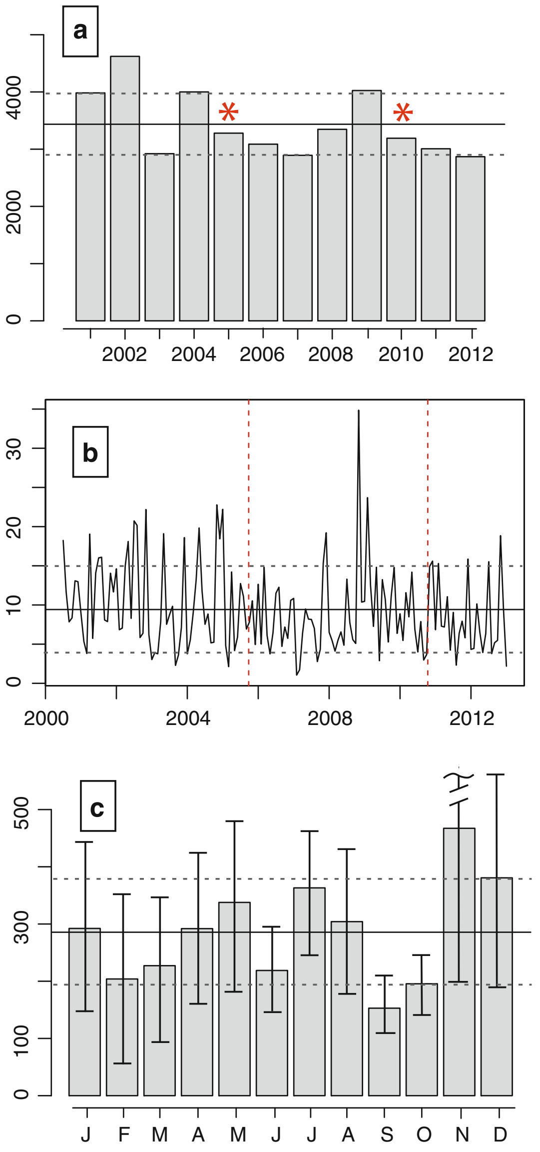


Fig. 5 Rainfall summaries for 2001–2012 at the Smithsonian Tropical Research Station at Bocas del Toro, ~4 km from the study site. **a** Total annual rainfall (mm), with annual mean shown as *solid black horizontal line*, *horizontal dashed lines* indicating ±1 SD, and *red asterisks* indicating bleaching years; **b** daily mean rainfall (mm) by month for the time period, with mean shown as *solid black horizontal line*, *horizontal dashed lines* indicating ±1 SD, and *vertical red dotted lines* indicating bleaching events; **c** monthly rainfall means (mm), with mean for the period shown as a *solid black horizontal line*, *horizontal dashed lines* indicating ±1 SD, and *error bars* indicating ±1 SD for individual months (November *error bar* truncated for plotting)

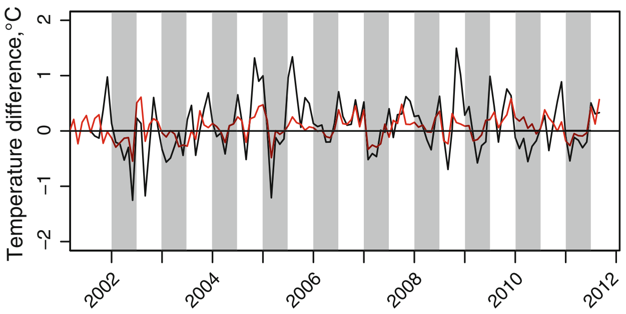


Fig. 6 Seasonal temperature inversions at the inshore sampling site. *Black line* indicates temperature difference between 20 and 4 m, and *red line* is difference between 10 and 4 m. *Positive values* indicate warmer water at depth. *Gray shading* indicates January–June, inclusive, and *non-shaded areas* indicate July–December, inclusive

experiencing maximum stress in the deepest stratum and 2010 exhibiting greater stress in the shallower strata. Furthermore, differences were also found in the timing of onset of thermal stress conditions between the two locations (defined as the date when DHW ≥ 4) with the inshore sites lagging behind the offshore site by roughly 3 weeks. These differences in distribution of stress by depth as well as timing of onset and disturbance duration are important for understanding the bleaching patterns observed in 2005 within this embayment, and also for predicting how other enclosed shallow reef environments experiencing stratified conditions could react to future elevated water temperature conditions. Augmenting the NOAA CRW satellite bleaching alert system with local depth-stratified monitoring could help reveal these disturbance dynamics.

This investigation started with the observation during the 2005 Caribbean warm water event that coral bleaching and mortality intensified with depth at our study site. This contradicted expectations, given that deeper strata were expected to experience dampened temperature fluctuation and reduced radiation stress due to the thermal mass and light attenuation properties of water. This dampening of environmental variation with depth is seen in the pattern of daily HotSpot results across most of the time period from 2005 to 2011, which generally showed a reduction in both intensity and duration of temperature excursions from the surface to the deepest record (Fig. 4a–d). However, this was strikingly not the case in the summer of 2005, when temperature, temperature anomaly, HotSpot, and thermal stress (DHW) reached their highest levels at the deepest strata in the temperature records (20 m). The peak temperatures and stress levels at 20 m were considerably higher than those experienced at 10 and 4 m. The offshore surface site also showed elevated thermal stress levels in this year, prompting a bleaching alert from NOAA, but both shallower inshore depths (4 and 10 m) had only moderate stress levels. This concentration of high thermal stress in the deepest strata in 2005 was in contrast to 2010, the second major event with elevated water temperatures in the study period. In 2010, offshore waters again showed similar levels of significant thermal stress, exceeding the 8 °C-week threshold, but inshore stress levels did not manifest in the same pattern as 2005. Only the two upper

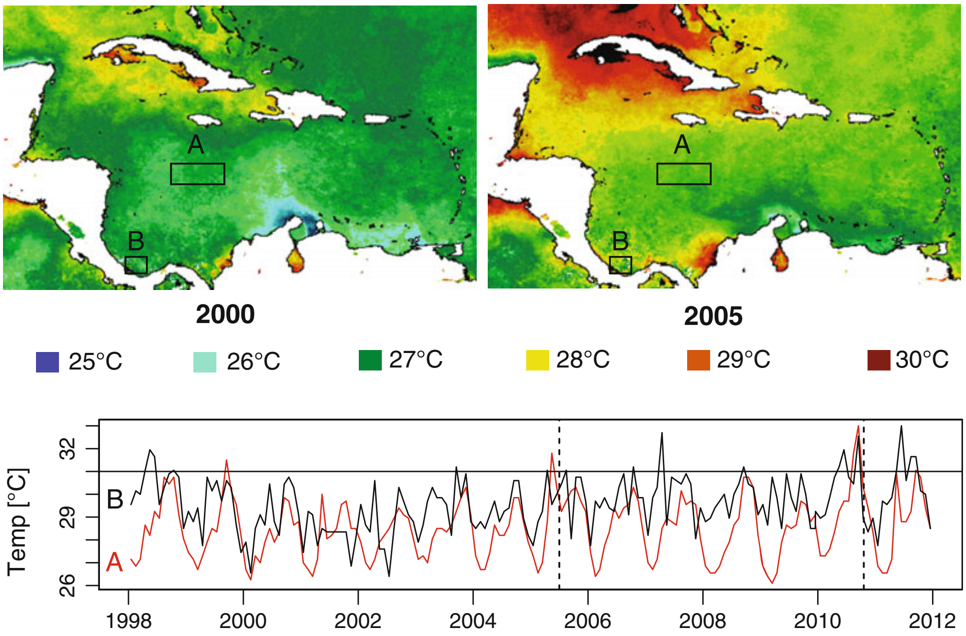


Fig. 7 Sea surface temperatures from the southwestern Caribbean. *Maps* are aggregated monthly means of 4 km AVHRR (PFV5.2) SST data for July 2000 and July 2005. The year 2005 was a major bleaching year, and 2000 is presented for comparison. Maximum temperatures for each month for 1998–2012 were selected from two polygons: *a* the Caribbean Sea SST mid-basin reference area and *b* the Bocas del Toro near-shore SST reference area, and plotted *a* in *red* and *b* in *black*. *Vertical dashed lines* indicate the 2005 and 2010 bleaching events

strata exhibited damaging levels of thermal stress, exceeding the 4 °C-week threshold for onset of bleaching, while at 20 m, there was no stress condition in 2010.

We hypothesize that these differences in thermal stress at different depth strata result from density-driven water column stratification within the bay, which creates a temperature inversion and holds significantly warmer water at deeper levels. Temperature inversions are a previously described irregular feature in Bahia Almirante, occurring from April to December, persisting for durations of weeks (Kaufmann and Thompson 2005). In this study, temperature inversions between 20 and 4 m at the inshore location were present at some time in the second half of every calendar year for the decadal record 2002–2012 (Fig. 5). However, the extreme difference in temperature and stress between the three strata in 2005 indicates that an unusual synergy of forces may have increased the impact of the stratification event this year. We hypothesize that these conditions led to much higher and longer exposure to stressful temperatures for the deeper corals in 2005, contributing to increased bleaching response.

Rainfall was initially investigated as the primary driver of these inversions. Complex local dynamics affect water temperature and vertical mixing within Bahia Almirante, with solar radiation identified in one study as the dominant factor, followed by wind stress and rainfall (Kaufmann and Thompson 2005), with only a weak correlation between the variation in water temperatures and rainfall due to most of the rainfall coming at night, when surface water temperatures are already at their lowest diurnal levels, although rainfall was shown to strongly affect the formation of density-driven stratification layers. Our rainfall record closely agreed in both magnitude and seasonal pattern with this earlier report, with high rainfall across the year and high variability (Fig. 5c). The significant but weak association of monthly rainfall magnitude with monthly temperature inversion strength indicates that higher rainfall does contribute to inversion formation, but does not fully explain differences in the magnitude of inversion strength (temperature difference between 4 and 20 m). The existence of the inversion in every year of the decade demonstrates that higher than normal rainfall is not needed for inversion formation, and the lack of direct correlation between the years with most coral bleaching (2005 and 2010) and highest inversion strength further indicate that neither rainfall amount nor inversion strength fully explain the onset of bleaching conditions. Rather, bleaching at depth appears also to be a function of the temperature of selected water body layers, specifically the temperature in the deeper layers within the embayment and the maximum surface temperatures of the offshore waters, which appear to provide the source waters for advection to these layers.

The fact that the maximum temperature in the early part of the summer in 2005 at 20 m was higher than that reached at 4 or 10 m at any point during the year indicates that this peak could not have been caused by vertical heat transfer from the surface at that location (i.e., from direct solar radiation at that site combined with wind or density-driven mixing), and therefore it appears that this water was horizontally advected to the 20 m location with thermal properties conserved from some other relatively near-by location, likely sea surface water just outside the bay close to the entrance. High-temperature, high-salinity water could enter the embayment through normal current and tidal water movement and be subducted by a fresher and cooler surface layer creating the described temperature inversion. Due to normal temporal gaps in the satellite record from cloud cover and satellite sampling frequency, it is not possible to follow individual packets of surface water entering the embayment on a daily or weekly basis. However, the monthly means do show increased temperature in localized areas of the near-shore waters along the Panama and Costa Rican Caribbean coastline in July 2005 and exhibit a thermal patchiness not evident in earlier years (Fig. 6).

Maximum SSTs for the two chosen reference areas from the AVHRR PFV5.2 satellite temperature record are also correlated with the years of most extensive bleaching for the decade 2000–2010 (2005 and 2010). Only in these years does the maximum summer SST in the Caribbean Sea offshore reference area exceed that in the Bocas del Toro inshore reference area at the same time (Fig. 6). Furthermore, these are the only points after 2000 in this time period where the offshore surface temperature exceeds 31 °C. The correlation of these unusual conditions with the main periods of bleaching, along with the ubiquitous nature of temperature inversions in the summer months, indicates that the severity of the inversion and consequent bleaching event is driven mainly by incursions of warm offshore waters, which enter the embayment and subduct to form the deeper strata during these inversion events.

The difference in the magnitude of bleaching between the three inshore depth strata during the two primary warm water stress events may also reveal a depth-specific susceptibility to thermal disturbance. The 2010 DHW levels for the offshore site actually slightly exceeded the levels in 2005, even though the intensity of bleaching witnessed at the deepest stratum in 2005 greatly exceeded any bleaching seen in 2010 at any depth. If these two events are seen as parallel disturbances of comparable magnitudes but affecting different depth strata, this difference in intensity could be explained by an acclimatization hypothesis. The raw temperature record from 1999 shows only one brief period of temperatures >30 °C prior to 2005, whereas the records from the 4 and 10 m depths show repeated excursions >30 °C from 2005 to 2010. This difference in historical exposure of individual colonies and depth-specific communities may have amplified the reactions seen in 2005. Physiologically, corals experiencing smaller ranges of temperature variation have reduced tolerance to temperature stress (Guzman et al. 2005; Oliver and Palumbi 2011; Barshis et al. 2013). Therefore, if the community at 20 m had experienced many years of reduced temperature variations compared to the surface community, then small variations in the thermal pattern at this depth would represent an unusual pattern and could elicit an elevated physiological response. The bleaching observed in this location at depth is thus potentially a synergistic result of the early and persistent increase in temperature demonstrated in the stress calculations combined with reduced resistance to this type of disturbance for this depth. If this location continues in future years to exhibit the thermal conditions described here, an increasing mortality gradient could develop, with the reef dying from the bottom up, even if the temperature changes in the deeper strata are of a lesser magnitude compared to those at the surface. This likelihood of increased occurrence of thermal stress, given predictions of increasing water temperatures across the Caribbean, along with the amplified impact these conditions have on the deeper coral communities, warrants further investigation into the specific set of environmental variables that contribute to these inversions.

Temporal differences in the development of thermal stress conditions within each year were also seen between 2005 and 2010, with onset and peak of thermal stress at the inshore location occurring later than at the offshore location. In 2005, this delay in onset of peak stress conditions was 22 days, and in 2010 was 27 days. This time lag in onset was similar in both years, even though the regional-scale onset of stress conditions was very different in 2005 and 2010; in 2005, warm water anomalies appeared offshore earlier in the year, reaching 4 °C-weeks on the 25th of June, whereas in 2010, this was first recorded July 22. For the inshore site in 2005, the DHW rose above the 4 °C-week threshold for onset of bleaching conditions on 7 July, and in 2010, this level was exceeded over 2 months later, on September 16. These two dates fall on either side of the usual August reduction in sea temperatures caused by the decreased angle of the sun moving farther to the north, prior to the second peak in temperatures in September when the rays of the sun again strike more directly at this latitude. The year 2005 was one of only 2 years in the 1999–2011 period with the highest temperature for that year occurring in the first of these two warming periods and had the earliest peak of temperature of any year in the decade. Also, 2005 did have a normal mid-year temperature reduction (in fact a larger than normal mid-year decrease) but because the temperature peaked so much higher before this decrease, even this significant decline did not bring the temperature below the MMM-ST and thus did not pause the accumulation of thermal stress. This early onset of stressed conditions on the reef in 2005 along with the lack of mid-summer temperature reprieve at 20 m effectively extended the duration of thermal stress in this year across many weeks. This unusually early and atypically chronic condition may have contributed to the eventual severity of bleaching seen later that year.

The temporal delay in the onset of thermal stress inshore, compared to offshore, is further circumstantial indication that inshore conditions are primarily driven by warm water inputs from offshore. The consistency of occurrence and length of this delay in maximum temperature onset supports the use of the NOAA CRW as a predictive indicator for onset of bleaching conditions in shallow reef areas. Furthermore, the correlation between maximum offshore summer surface temperatures and the years of greatest bleaching validates the use of this indicator for inshore bleaching. However, NOAA CRW products, providing a large-scale view of the background coral bleaching thermal stress condition, do not predict how this stress could stratify in response to local bathymetric, climatological, or hydrologic conditions, and are thus not able to predict local vertical distribution of this stress.

Here, we have demonstrated that thermal stress can manifest on the reef in a surprising fashion, increasing rather than reducing with depth under some stratified conditions. The historical lack of temperature variability at deeper locations also means that small increases in temperature at these depths can significantly increase calculated thermal stress, resulting in an increased risk of bleaching even when absolute temperature variation may not reach that experienced at the surface. Climate change could result in the deeper parts of a reef being increasingly subject to these smaller but potentially disproportionately damaging anomalies in water temperature. Our single observation of differential distribution of bleaching stress with depth in one location tentatively supports this idea, but more extensive investigation is warranted, as this effect will be limited to areas with physical and hydrologic conditions that support water column stratification. The relatively shallow depths involved in this work (up to 20 m) do not allow for direct comparison to the deep reef refugia hypothesis (DRRH) (Glynn 1996), which explicitly applies to mesophotic reef depths greater than 30 m, but this observation does provide a point for considering how offshore surface thermal changes could manifest as ecological impacts on deeper areas of an inshore reef, potentially with a complex and nonlinear increase in disturbance impact with depth. We conclude that monitoring and analysis of local depth-stratified temperature records would complement NOAA CRW's large-scale coral bleaching thermal stress monitoring, particularly in years when bleaching is predicted. This additional monitoring could reveal bleaching risk not fully expressed at larger scales, and incorporating depth-stratified temperature monitoring and small-scale oceanographic and hydrologic factors will be important for accurately understanding observed patterns of bleaching response across the coral community and predicting response to future water temperature changes.

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References

Alvarez-Filip L, Dulvy NK, Gill JA, Cote IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proc R Soc Lond B 276:3019–3025

Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, Palumbi SR (2013) Genomic basis for coral resilience to climate change. Proc Natl Acad Sci USA 110:1387–1392

Brown BE (1997) Adaptations of reef corals to physical environmental stress. Adv Mar Biol 31:221–299

Carilli J, Donner SD, Hartmann AC (2012) Historical temperature variability affects coral response to heat stress. PLoS One 7:e34418

Casey KS, Brandon TB, Cornillon P, Evans RD (2010) The past, present and future of the AVHRR pathfinder SST Program. In: Barale V, Gower JFR, Alberotanza L (eds) Oceanography from space: revisited. Springer, Berlin

Eakin CM, Morgan JA, Heron SF, Smith TB, Liu G, Alvarez-Filip L, Baca B, Bartels E, Bastidas C, Bouchon C, Brandt M, Bruckner AW, Bunkley-Williams L, Cameron A, Causey BD, Chiappone M, Christensen TRL, Crabbe MJC, Day O, de la Guardia E, Diaz-Pulido G, DiResta D, Gil-Agudelo DL, Gilliam DS, Ginsburg RN, Gore S, Guzman HM, Hendee JC, Hernandez-Delgado EA, Husain E, Jeffrey CFG, Jones RJ, Jordan-Dahlgren E, Kaufman LS, Kline DI, Kramer PA, Lang JC, Lirman D, Mallela J, Manfrino C, Marchal J-P, Marks K, Mihaly J, Miller WJ, Mueller EM, Muller EM, Orozco Toro CA, Oxenford HA, Ponce-Taylor D, Quinn N, Ritchie KB, Rodriguez S, Ramirez AR, Romano S, Samhouri JF, Sanchez JA, Schmahl GP, Shank BV, Skirving WJ, Steiner SCC, Villamizar E, Walsh SM, Walter C, Weil E, Williams EH, Roberson KW, Yusuf Y (2010) Caribbean corals in crisis: record thermal stress, bleaching, mortality in 2005. PLoS One 5:e13969

Gleeson MW, Strong AE (1995) Applying MCSST to coral reef bleaching. Adv Space Res 16:151–154

Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. Global Change Biol 2:495–509

Glynn PW, D'Croz L (1990) Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. Coral Reefs 8:181–191

Guzman HM, Guevara CA (2001) Coral reefs of Bocas del Toro, Panama: IV. Distribution, structure and conservation state of continental reefs of Peninsula Valiente. Rev Biol Trop 49:53–66

Guzman HM, Barnes PAG, Lovelock CE, Feller IC (2005) A site description of the CARICOMP mangrove, seagrass and coral reef sites in Bocas del Toro, Panama. Caribb J Sci 41:430–440

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933

Kaufmann KW, Thompson RC (2005) Water temperature variation and the meteorological and hydrographic environment of Bocas del Toro, Panama. Caribb J Sci 41:392–413

Knowlton N (2001) The future of coral reefs. Proc Natl Acad Sci USA 98:5419–5425

Leichter JJ, Helmuth B, Fischer AM (2006) Variation beneath the surface: quantifying complex thermal environments on coral reefs in the Caribbean, Bahamas and Florida. J Mar Res 64:563–588

Liu G, Strong AE, Skirving W, Arzayus LF (2004) Overview of NOAA Coral Reef Watch Program's near-real time global satellite coral bleaching monitoring activities. In: Proceedings of the 10th international coral reef symposium, pp 1783–1793

Liu G, Strong AE, Skirving W, Arzayus LF (2005) Overview of NOAA Coral Reef Watch Program's near-real time satellite global coral bleaching monitoring activities. Proc 10th Int Coral Reef Symp 1:1783–1793

Liu G, Matrosova LE, Penland C, Gledhill DK, Eakin CM, Webb RS, Christensen TRL, Heron SF, Morgan JA, Skirving WJ, Strong AE (2008) NOAA Coral Reef Watch coral bleaching outlook system. In: Proceedings of the 11th international coral reef symposium, pp 956–960

Maina J, McClanahan TR, Venus V, Ateweberhan M, Madin J (2011) Global gradients of coral exposure to environmental stresses and implications for local management. PLoS One 6:e23064

Marshall P, Schuttenberg H (2006) Adapting coral reef management in the face of climate change. Coast Estuar Sci 61:223–241

Maynard J, Johnson J, Marshall P, Eakin C, Goby G, Schuttenberg H, Spillman C (2009) A strategic framework for responding to coral bleaching events in a changing climate. Environ Manage 44:1–11

McClanahan TR, Ateweberhan M, Muhando CA, Maina J, Mohammed MS (2007) Effects of climate and seawater temperature variation on coral bleaching and mortality. Ecol Monogr 77:503–525

McWilliams JP, Cote IM, Gill JA, Sutherland WJ, Watkinson AR (2005) Accelerating impacts of temperature-induced coral bleaching in the Caribbean. Ecology 86:2055–2060

Mumby PJ, Elliott IA, Eakin CM, Skirving W, Paris CB, Edwards HJ, Enriquez S, Iglesias-Prieto R, Cherubin LM, Stevens JR (2011) Reserve design for uncertain responses of coral reefs to climate change. Ecol Lett 14:132–140

Oliver TA, Palumbi SR (2011) Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs 30:429–440

Pandolfi JM, Jackson JB, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP, Sala E (2005) Are U.S. coral reefs on the slippery slope to slime? Science 307:1725–1726

Penland C, Matrosova L (1998) Prediction of tropical Atlantic sea surface temperatures using linear inverse modeling. J Clim 11:483–496

Rich PM, Clark DB, Clark DA, Oberbauer SF (1993) Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photography. Agric For Meteorol 65:107–127