

Caribbean mesophotic coral ecosystems are unlikely climate change refugia

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Abstract

Deeper coral reefs experience reduced temperatures and light and are often shielded from localized anthropogenic stressors such as pollution and fishing. The deep reef refugia hypothesis posits that light-dependent stony coral species at deeper depths are buffered from thermal stress and will avoid bleaching-related mass mortalities caused by increasing sea surface temperatures under climate change. This hypothesis has not been tested because data collection on deeper coral reefs is difficult. Here we show that deeper (mesophotic) reefs, 30–75 m depth, in the Caribbean are not refugia because they have lower bleaching threshold temperatures than shallow reefs. Over two thermal stress events, mesophotic reef bleaching was driven by a bleaching threshold that declines 0.26 °C every +10 m depth. Thus, the main premise of the deep reef refugia hypothesis that cooler environments are protective is incorrect; any increase in temperatures above the local mean warmest conditions can lead to thermal stress and bleaching. Thus, relatively cooler temperatures can no longer be considered a *de facto* refugium for corals and it is likely that many deeper coral reefs are as vulnerable to climate change as shallow water reefs.

Keywords: climate change, coral bleaching, mesophotic coral reef ecosystems, *Orbicella* spp., refugia, thermocline

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Introduction

Refugia in times of environmental crises may protect species from extinction and habitats from the loss of ecological function (Keppel *et al.*, 2012). Shallow water coral reefs are undergoing historically unprecedented degradation tied to warm-water coral bleaching events of increasing severity and frequency, with some forecasting the end of reef building within the twenty-first century (Hoegh-Guldberg *et al.*, 2007). In contrast, mesophotic coral ecosystems (MCEs) that form in vast areas of the tropical ocean between 30–150 m depth have, in some cases, been spared from the deterioration occurring in shallow reefs (Bak *et al.*, 2005). They are often at or below the first thermocline during the annual thermal maximum; therefore, most MCEs experience lower maximum temperatures than reefs near the surface (Leichter *et al.*, 2006; Lesser *et al.*, 2009), an explicit condition of the deep reef refugia hypothesis (Riegl & Piller, 2003). This hypothesis suggests that cooler conditions in deeper coral reefs, including MCEs, can buffer the impacts of thermally induced mass bleaching events in shallow water. Studies so far suggest that MCE areal coverage may equal or surpass that of shallow reefs in

many of the world's most spectacular coral reef systems, including the Great Barrier Reef (Harris *et al.*, 2013) and the Caribbean (Locker *et al.*, 2010). If MCEs are indeed climate change refugia, then their global extent would make them potent shelters for coral reef biodiversity (Bridge *et al.*, 2013). Furthermore, as the upper mesophotic zone supports many of the species found in shallow reefs, their potential inter-connectivity via larval exchange may contribute to the recovery of shallow ecosystems after catastrophic bleaching events (Bongaerts *et al.*, 2010; Holstein *et al.*, 2015).

The deep reef refugia hypothesis in MCEs rests on whether or not these habitats (1) have been refuges from thermal stress in the past (demonstrated avoidance), (2) that, if impacted, they are able to recover from damage between disturbance events so as to maintain high cover and functionality (demonstrated recovery), and (3) that they will continue to be refuges from thermal stress in the future (i.e., the past portends the future). Presently, too little is known about how MCEs and other deeper coral reef environments experience and cope with thermal stress to predict whether or not they will be refugia. Limited empirical evidence to support the deep reef refugia hypothesis came from observations of greater survival of corals in deeper habitats during shallow water bleaching events (Glynn, 1996; Riegl & Piller, 2003; Smith *et al.*, 2014). These studies lacked temperature data at the depths of the purported

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refugium, which are necessary to estimate the thermal susceptibility of corals and their potential to survive in a warming ocean. We used a biophysical data set of 19 shallow reefs (6–24 m), five upper mesophotic reefs (30–40 m), and one lower mesophotic reef (65 m) to examine the thermal susceptibility of corals in the US Virgin Islands. We sampled coral reefs annually from 2005 to 2013 and observed their response to anomalously high temperatures in 2005, 2010, and 2012. We used multi-year coral bleaching estimates and benthic temperature records to calculate the bleaching thresholds for each reef along the depth gradient. This data was then used to directly test the depth refugia hypothesis by assessing each of the three potential ways that corals might persist in a warming ocean.

Materials and methods

Ecological and taxonomic setting

The responses of Caribbean shallow and mesophotic coral reefs to thermal stress were studied across reef types in the United States Virgin Islands (USVI) (18.0°N, 65.0°W). The USVI is located in the northeastern Antilles island arc at the intersection of the Greater and Lesser Antilles islands and is bounded by the tropical western Atlantic to the north and the Caribbean Sea to the south. The focal study sites represent Caribbean *Orbicella* spp. reefs, which we defined as reefs with >4% absolute cover of *Orbicella* spp. prior to the 2005 coral bleaching event (Table S1). In addition, a larger range of sites with *Orbicella* spp. present, but not dominant, were used for temperature measurements, coral health assessments, and the creation of bleaching thresholds (Table S1). These sites between 6 and 40 m depth experience an annual thermal maximum of temperature between August 16 and November 15 as seen from multi-year benthic temperature records from 2005 to 2013. The deeper reefs in this data set are considered in the upper mesophotic zone (30–60 m) as opposed to the lower mesophotic, which extends from 60 to 100 m in the Caribbean (Slattery *et al.*, 2011). We were able to study one lower mesophotic coral reef at 60–75 m depth between the years 2011–2014 (Text S1).

The USVI Territorial Coral Reef Monitoring Program (TCRMP) collected data from 24 of 25 locations. An additional site monitored by the National Park Service Inventory and Monitoring Program, Tektite, was included for temperature and bleaching threshold development. Tektite had a consistent record of monitoring through the 2005 bleaching event and was a good comparative data set for an MCE location, Tiger, which also was followed for temperature over the 2005 bleaching event. The NPS program followed different methodologies for benthic and health assessment than the TCRMP and, therefore, Tektite was excluded in longitudinal coral cover, bleaching, and disease comparisons.

The star coral group (*Orbicella* spp.) was chosen as the focal genus for this study because it is the dominant reef building genus in shallow reef systems of the Caribbean (Goreau,

1959). This is also the dominant coral genus forming extensive MCE bank systems in the USVI from depths of 30–45 m, with >90% relative cover (Smith *et al.*, 2010). This MCE is largely composed of the species *O. faveolata* and *O. franksi*. In addition, because Caribbean coral bleaching responses are highly species-specific, restricting the biological data set to one genus that has a moderate bleaching response (Smith *et al.*, 2013) had the advantage of reducing variation in the bleaching and disease response signal in reef locations that vary greatly in coral species composition. As *Orbicella* is a genus that is sensitive to thermal stress, it also should show a clear response gradient in different physical environments. There are differences in the peak densities of the three orbicellid species with depth (*O. annularis* < *O. faveolata* < *O. franksi*) but this did not bias the shallow vs. MCE data interpretation as these three species responded very similarly to the 2005 and 2010 thermal events in shallow water (Smith *et al.*, 2013). Although we focused on *Orbicella* spp., we compared the bleaching prevalence of *Orbicella* spp. to the remainder of the coral community at each site and time point to test the generality of our findings. We found that when orbicellids showed elevated bleaching prevalence, the remainder of the stony coral community showed elevated coral bleaching prevalence, indicated by a significant correlations between the two at each site in each time point ($\rho = 0.276$, $P < 0.0001$, $r = 0.309$). For the extension of our data, we also report data from one lower mesophotic coral reef (60–75 m) dominated by lettuce corals *Agaricia* spp., predominantly *Agaricia undata* (Text S1).

Coral reef benthic and health assessments

Longitudinal trends in benthic cover and coral health were assessed at 16 *Orbicella* spp. reef locations with consistent monitoring before and during the 2005 bleaching event, and at least annually thereafter. Benthic cover of corals was estimated at each site with video along six 10-m-long transects following standardized methods (Smith *et al.*, 2013). Transects were laid along permanent paths marked at the start and terminus with steel rods; however, at 10 sites, transects were laid in random directions in the same reef area until they were permanently marked in 2007 (Black Point, Buck Island-St. Thomas, College Shoal, Flat Cay, Hind Bank, Meri Shoal, Savana, Seahorse, South Capella, Tiger). A shift from random to permanent transects did not greatly affect the estimates of the coral cover response variable, as estimates of cover between 2006, when some sites had random transect placement, and 2007, when transects were permanent, was not significant for shallow or MCE reefs (see main text Fig. 3c). *Orbicella* spp. and total coral cover were compared across time and between shallow and MCE strata using a repeated measure ANOVA followed by *post hoc* Wilcoxon pairwise comparisons to determine differences between means.

The assessment of the health of coral colonies followed TCRMP protocols (Smith *et al.*, 2013). Every coral colony intercepted by the benthic transect line was assessed for bleaching and the presence of white disease by an experienced research diver ($n = 4504$ *Orbicella* spp. colony records). Bleaching was scored on *Orbicella* spp. as stark white appearance of tissue

indicating the loss of *Symbiodinium* and the percent of the colony affected (extent) was estimated. The proportion of colonies (prevalence) on a transect experiencing stark white bleaching on some colony portion was calculated. All health variables deviated significantly from assumption of parametric testing in repeated measures ANOVA and, therefore, were compared with nonparametric analyses. Bleaching prevalence was compared over time periods and between the shallow and the MCE strata with a Friedman's rank test, followed by *post hoc* Wilcoxon pairwise comparisons. In addition, bleaching prevalence at a site in a given year was compared to the depth of the site in the 3 years identified with bleaching in shallow or mesophotic reefs (2005, 2010, 2012) using linear regression. The mean extent of colony affected by stark white bleaching was also tested between time and depth strata with the same procedure as bleaching prevalence. White disease was identified as active white lesions that formed a smooth undulating line intersecting polyps, was without the appearance of colonizing algae, and appeared to be progressing across the colony as a band (Bythell *et al.*, 2004). The prevalence of white disease per transect was tested statistically in the same procedure as bleaching prevalence.

The overall MCE bleaching response in 2005 and 2012 was likely stronger than we recorded. More than 50% of the bleaching surveys of MCE in this study were conducted about 1 month prior to the peak of MCE temperatures (November) because prior to this study it was not known that MCE heating is delayed. For example, bleaching at the Tiger site was assessed on October 4, 2005, when there was 4 DHW (Fig. S4), although *in situ* temperature showed that this site eventually peaked at 7.4 DHW on November 12, 2005.

Oceanographic measurements

Benthic temperature within each coral monitoring site was estimated with a logging temperature probe (Hobo Water Temperature Pro V2, Onset Computer Corp., Bourne, MA, USA) and used to create daily mean temperatures. Probes were set to measure with a frequency of 15–60 min and were swapped with different probes during annual maintenance. After 2011, temperature probes were calibration-checked pre- and postdeployment in a freshwater ice bath and ambient temperature bath, and probes were not deployed if their temperature deviated more than 0.3 °C from that recorded with a bulb thermometer. Prior to 2011, probes may have deviated more than 0.3 °C from actual; however, the manufacturer lists accuracy of ± 0.21 °C. At the site Tiger, the temperature record in 2005 was taken from the head sensor of an Aquadopp current profiler (Nortek AS, Oslo, Norway) set to record every 60 min and placed within 5 m of the coral monitoring site and at the same depth. The manufacturer lists a sensor accuracy of ± 0.1 °C.

Conductivity-temperature-depth-chlorophyll (CTD) profiles were taken with a shallow water Seabird SBE 25 recording at 8 Hz (Sea-Bird Electronics, Bellevue, WA, USA). A Wetlabs EcoFLNT fluorometer affixed to the CTD estimated water column chlorophyll concentrations. CTD casts were made at the seaward shelf edge slope within 5 km of the Tiger monitoring

site (Table S1) approximately monthly from 2012 to 2013 to a maximum depth of 100 m and in depths of water from 40 to 200 m.

Derivation of site-based empirical monthly maximum mean temperatures, bleaching thresholds, and degree heating weeks

Since the new millennium, shallow coral reefs (<30 m depth) of the northeastern Caribbean have experienced two mass bleaching events in 2005 and 2010, precipitated by the accumulation of thermal stress from high water temperatures. There are multiple metrics of thermal stress accumulation in scleractinian corals, but one of the most widely applied is the degree heating week (DHW), where a bleaching threshold is established 1 °C above the mean of the month of the year that climatologically has the highest temperature, the monthly maximum mean temperature (MMM) (NOAA, 2006). In the DHW concept, thermal stress accumulation occurs when temperatures surpass the bleaching threshold, with weight given to the time above the threshold (e.g., 1 week at 1 °C above the MMM equals 1 DHW) and the magnitude of the deviation above the threshold (e.g., 1 week at 2 °C above the MMM equals 2 DHW or the same as 2 weeks at 1 °C above the MMM). As a rough guide, 4 DHW is associated with the onset of widespread bleaching and limited mortality, and 8 DHW is associated with more extensive bleaching of most corals and increasing levels of partial and whole colony mortality. As DHW values surpass 8, there will be increasingly catastrophic bleaching-related mortality. The year 2005 showed warm shallow water temperatures in the Caribbean, with extensive and severe shallow water coral bleaching, disease, and mortality at a thermal stress accumulation >10 DHW (Miller *et al.*, 2009; Eakin *et al.*, 2010). The year 2010 showed moderate shallow water bleaching but only localized mortality at about 5 DHW (Brandt *et al.*, 2013; Smith *et al.*, 2013).

At each site, degree heating weeks (DHW) were determined from benthic temperature records following the methods of NOAA Coral Reef Watch (NOAA, 2006). The monthly maximum mean temperature (MMM) for each site was calculated from benthic temperature records from 2007 to 2013, for each site excluding the bleaching years 2005, 2006, 2010 (shallow only), and 2012 (MCE only). The monthly maximum mean temperature (Table S1) was calculated from the mean warmest calendar month determined for each site. The MMM for each site was determined by inspection of the data and excluding years with >10% of the missing data within a month.

The potential DHW accumulation across years at a site was compared with unbiased bleaching records to determine the bleaching threshold at each site. For each year with a complete temperature record in the thermal maximum of sea surface temperatures, a figure of the possible degree heating weeks was created in 0.25 °C increments for a range of bleaching thresholds above the empirically determined MMM for each site (Manzello *et al.*, 2007). A determination of bleaching or no bleaching at a site in a given year was determined blindly. Annual observations of bleaching were presented without

dates and in random order to one of us (T.B.S.). A site was considered bleached for *Orbicella* spp. if the bleaching prevalence or extent (average percent of colony affected) was greater than double normal magnitude in no thermal stress years or when assessed outside the annual thermal maximum period, which was determined *a priori*. The bleaching/no bleaching observations were examined in the context of potential 0.25 °C increment DHW figures. The coolest year that had a value greater than about 4 DHW and bleaching at the time of observation, considered the point of thermal stress accumulation that causes bleaching above the normal background levels (NOAA, 2006), set the upper bound of the bleaching threshold. The warmest year that had a value less than about 4 DHW and no bleaching set the lower bound of the bleaching threshold.

In some cases, the bleaching threshold could be refined closer to an increment <0.25 °C by generating a new DHW figure with an increment of 0.125 °C and comparing to the bleaching/no bleaching estimates. For example, after initial inspection, the mesophotic Tiger site had a bleaching threshold between 28.75 and 29.00 °C. However, 28.75 °C over-predicted bleaching in 2007 (i.e., 4 DHW was generated at the time of coral health observation, but this was a nonbleaching year), and 29.00 °C under-predicted bleaching (i.e., 2012 showed only 1.4 DHW at the time of coral health observation, but this was a bleaching year). A figure created at a bleaching threshold of 28.88 °C more accurately predicted about 3–4 DHW accumulation at the time of coral health observations in 2005 and 2012 and this was chosen as the empirical bleaching threshold.

Empirically derived monthly maximum mean temperatures and bleaching thresholds for each site were compared against site depths with linear regressions. In addition, monthly maximum mean and bleaching threshold were compared against each other with a linear regression after meeting statistical assumptions.

Results

Benthic temperatures in our *Orbicella* spp. mesophotic study sites were cooler than shallow reefs, including over two shallow water thermal stress and bleaching events in 2005 and 2010. We observed a progressive shoaling of the thermocline throughout summer and autumn to depths of 30 m, corresponding to the upper MCE (Fig. S1). During September–November 2005 at the height of the worst recorded shallow water mass bleaching event to affect the northeastern Caribbean (Eakin *et al.*, 2010) stratification resulted in mesophotic temperatures at one mesophotic study site (Tiger) that were 1.0 °C cooler than an inshore shallow reef (Tekite; Fig. 1a). The cause of this cooling was associated with the thermocline at these depths and the apparent activity of internal waves, indicated by the much higher diel variability at the Tiger MCE site (Fig. 1a), which was mirrored in all other MCE sites over the total period of monitoring between 2005 and 2013 (data not

shown). Thus, the effect of internal waves on MCE temperature dynamics was apparent in both thermal stress and nonthermal stress years. In 2010, another shallow water mass bleaching event was recorded in the northeast Caribbean (Brandt *et al.*, 2013; Smith *et al.*, 2013) and stratification also resulted in mesophotic temperatures at the Tiger MCE site that were 1.3 °C cooler than shallow temperatures (Fig. 1a, Fig. S2). This pattern of cooler temperatures at depth was repeated throughout the time series during the annual shallow water thermal maximum at all MCE sites (Fig. 1b, c, Fig. S2).

Cooler conditions in the study MCE corresponded to lower empirically-derived bleaching threshold temperatures with increasing depth because the bleaching threshold temperature is roughly equivalent to the monthly maximum mean temperature +1 °C (NOAA, 2006) (Fig. 2a, b). This relationship also extended to a lettuce coral (*Agaricia* spp.) dominated community type to a depth of 75 m (Text S1). For all MCE and shallow sites, we only observed bleaching in years when temperatures exceeded maximum monthly mean temperatures (Fig. S2), including during the well-established eastern Caribbean bleaching events of 2005 and 2010 and a previously undocumented MCE-only bleaching event in 2012. This confirmed that coral bleaching was related to anomalously warm thermal conditions and supported the thermal bleaching thresholds that we derived for each reef.

Given the interplay between the site-specific bleaching thresholds and recent thermal history, mesophotic reefs of the Virgin Islands have experienced thermal refuge and nonthermal refuge years in the recent past. Upper mesophotic reefs were protected from thermal stress in 2010. In shallow reefs, bleaching prevalence and extent were significantly higher in 2010 than in nonbleaching years, but not in mesophotic reefs (Fig. 3a, Table 1). In contrast, during the 2005 shallow water bleaching event, upper mesophotic reefs were not a thermal refuge. Bleaching extent in mesophotic reefs was higher than in all other years surveyed (Fig. 3a). Bleaching in 2005 was an underestimate for mesophotic reefs because deeper study sites were sampled prior to the peak of thermal stress (see next paragraph). Furthermore, in 2012, mesophotic reefs bleached, while shallow reefs did not (Fig. 3a). In 2012, the ocean surface upper mixed layer was deep during the annual thermal maximum (Fig. S1), exposing the upper MCE corals to shallow water thermal conditions (Fig. S2). The mixed layer depth deepened to about 40 m and brought the near-surface water mass, with a mean temperature below shallow water bleaching thresholds but above MCE bleaching thresholds, in contact with mesophotic corals. This deepening of the

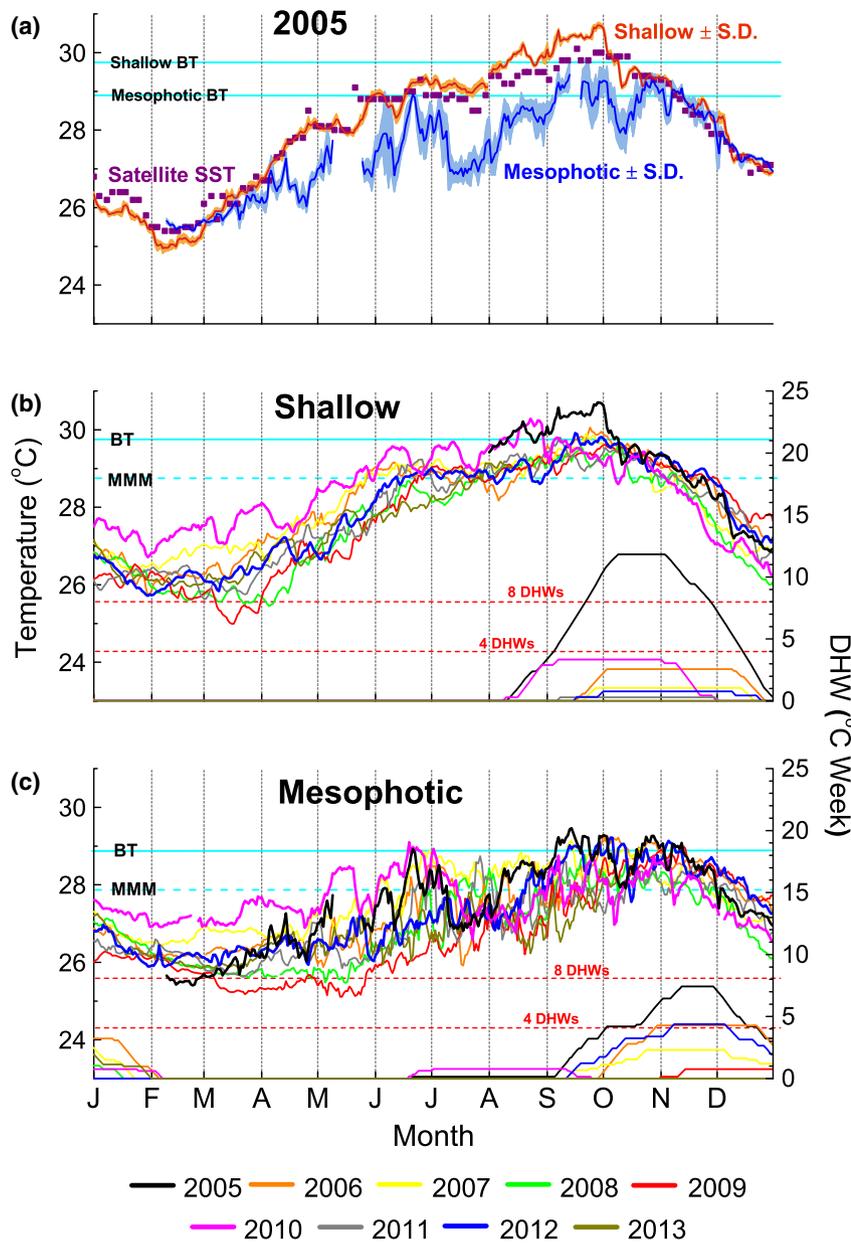


Fig. 1 Benthic temperatures and thermal stress contrasted between shallow and mesophotic coral reef environments. (a) During the 2005 bleaching event a mesophotic reef ('Tiger', 38 m depth) had mean temperatures 1.0 °C cooler than a shallow water reef ('Tektite', 18 m) and 0.75 °C cooler than satellite temperatures (<http://coralreefwatch.noaa.gov/satellite/ge/>). (b and c) Annual temperature and degree heating week (DHW) accumulation from 2005 to 2013 for a shallow (Tektite) and a mesophotic (Tiger) coral reef as shown in (a). DHW = degree heating weeks. DHW > 4 indicate bleaching conditions, DHW > 8 indicate bleaching leading to large-scale coral mortality. BT, bleaching threshold temperature; MMM, monthly maximum mean temperature.

upper mixed layer also increased temperatures in a lower mesophotic study site (60–75 m depth), resulting in partial bleaching of a lettuce coral reef (Text S1), the deepest depth of high thermal stress bleaching yet recorded. As a result, mesophotic reefs accumulated 4 Degree Heating Weeks (DHW), but shallow reefs did not exceed 1 DHW (Fig. 1b, c, Fig. S2, Text S1). The relationship between bleaching prevalence and depth,

which was negative in 2005 and 2010 (Fig. 2c, d), was positive in 2012 (Fig. 2e).

Thermal stress accumulation in the study MCE is delayed and of longer duration relative to shallow reefs. In the Virgin Islands, approximately 1 month after the shallow water thermal maximum, seasonal increases in wind-driven mixing deepen the thermocline and increase the heat flux to the MCE. This is why

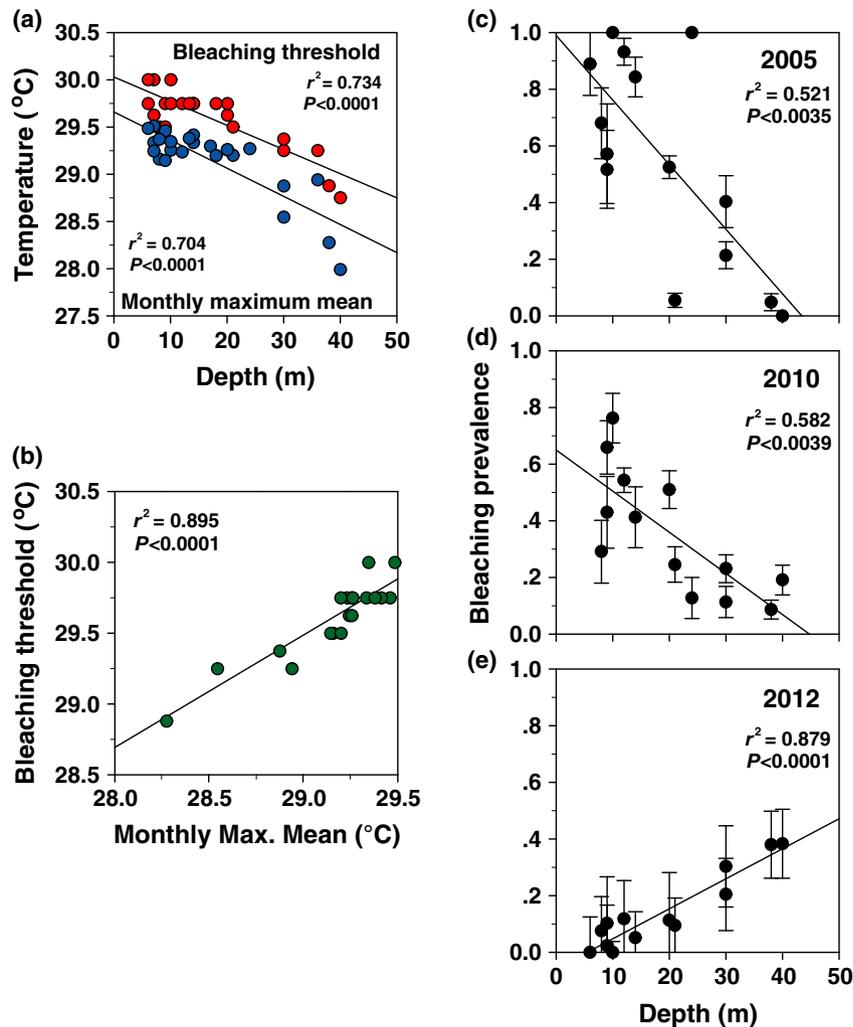


Fig. 2 Depth related *Orbicella* spp. bleaching temperature thresholds, monthly maximum mean temperatures, and bleaching prevalence across coral reefs. Coral reefs of the U.S. Virgin Islands were surveyed for bleaching from 2005 to 2013. (a) Depth vs. the empirically derived bleaching thresholds (red dots, $N = 22$ sites) and empirically derived monthly maximum means (blue dots, $N = 25$). (b) The relationship between the empirically derived bleaching threshold and the empirically derived monthly maximum means for 21 sites. The relationship of depth vs. bleaching prevalence as proportion of colonies with any stark white coloration for 2005 (c) (shallow and mesophotic bleaching; $N = 14$), 2010 (d) (shallow bleaching, $N = 13$), and 2012 (e) (mesophotic bleaching, $N = 12$). Bleaching prevalence estimates at reefs > 30 m depth in 2005 were an underestimate because surveys occurred prior to the peak of thermal stress (see text).

the mean peak of heat stress in the upper MCE is delayed by about 37 days relative to shallow reefs (Fig. 4; $\text{Peak}_{\text{MCE}} = 302.3 \pm 5.0$ Julian Day, $\text{Peak}_{\text{shallow}} = 265.2 \pm 2.3$). However, we also found that the initiation of heat stress in the MCE is delayed by about only 25 days relative to shallow reefs ($\text{Initiation}_{\text{MCE}} = 262.1 \pm 1.4$ SE, $\text{Initiation}_{\text{shallow}} = 237.5 \pm 1.9$), leading to an overall duration of heat stress that is longer by 12 days in the MCE (39.8 as opposed to 28.0 days for shallow reefs).

Bleaching of the focal species (*Orbicella* spp.) in this study mirrored bleaching patterns in other stony corals in the community across sites and years ($\rho = 0.276$,

$P < 0.0001$, $r = 0.309$), confirming that findings apply to the coral community in general. In addition, upper MCE reef bleaching in 2005 was a regional phenomenon. During that event, we also recorded severe coral community bleaching at two 30–40-m-deep coral reefs that were 50 km away from the focal MCE orbicellid reefs near St. Thomas (Table S2, Fig. S3).

Thermal stress increased white disease on *Orbicella* spp. in shallow reefs (Miller *et al.*, 2009; Smith *et al.*, 2013) and the upper MCE (Fig. 3b, Table S1), acting as a multiplier with bleaching-related mortality on coral cover loss. After the 2005 thermal stress event, shallow reefs and the upper MCE had unprecedented and simi-

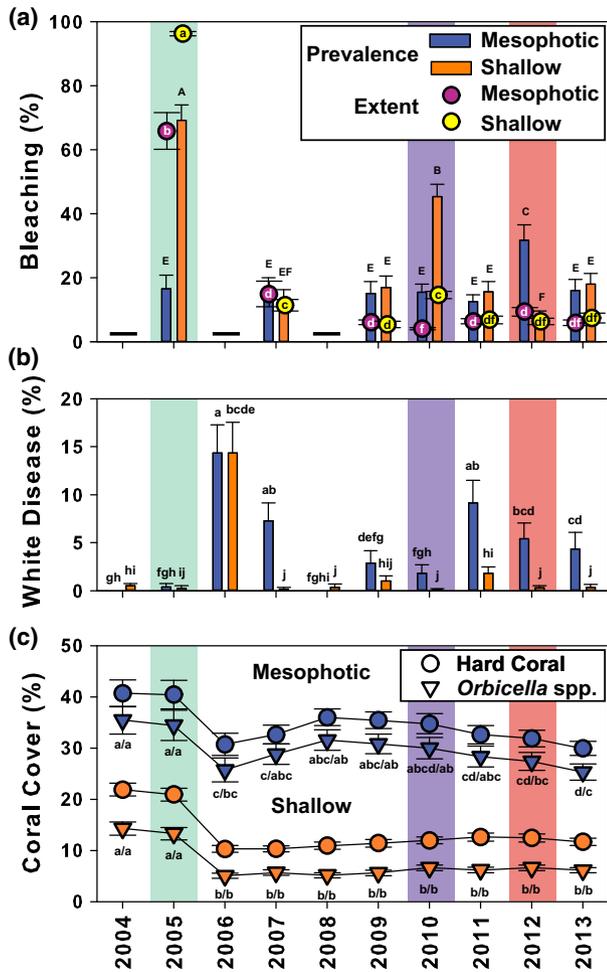


Fig. 3 Bleaching (a), white disease (b), and coral cover (c) of *Orbicella* spp. in shallow and mesophotic coral reefs from 2004 to 2013. Bleaching response was measured for colonies that showed some degree of stark white coloration in the annual thermal maximum response period (September–December) as the prevalence, or proportion of the population affected, and the extent, or the average proportion of colony surfaces affected (\pm SE). Corals were not surveyed during the thermal maximum in mesophotic reefs in 2004, 2006, and 2008 (horizontal black bar). Coral cover (\pm SE) indicated for total hard coral cover and individually for *Orbicella* spp. Results of Wilcoxon pairwise *post-hoc* comparisons indicated by letters. Coral cover *post-hoc* comparisons indicated as total stony coral cover/*Orbicella* cover separately for longitudinal mesophotic and shallow reef data sets. Green bar indicates the shallow and MCE bleaching year (2005), purple bar indicates the shallow-only bleaching year (2010) and the orange bar indicates the mesophotic only bleaching year (2012).

larly high levels of white disease in 2006, whereas elevated white disease continued into 2007 for the MCE. Bleaching and other diseases accounted for an *Orbicella* spp. cover loss of 62.0% in shallow reefs and 24.5% in the upper MCE (Fig. 3c, Table 1). *Orbicella* spp. in the MCE also had a generally higher prevalence of white

Table 1 Statistical comparisons of bleaching, white disease, and coral cover for shallow and upper mesophotic reefs from 2004 to 2013. All comparisons were repeated measures ANOVA or Friedman’s Rank[^] with the strata reef complex (shallow/MCE), year, and year*reef complex interaction. Bleaching was tested for the prevalence in the population (number affected as a proportion of the total) and the extent on living colony surfaces when bleaching was present. *Post hoc* comparisons for significant levels are given in main text Fig. 3

| Source | df | F-value | Probability |
|---|-------|---------|-------------|
| Bleaching prevalence[^] | | | |
| Reef complex | 1/473 | 4.00 | 0.0460 |
| Year | 6/473 | 3.74 | 0.0012 |
| Reef Complex*Year | 6/473 | 9.73 | <0.0001 |
| Bleaching extent[^] | | | |
| Reef complex | 1/973 | 130.33 | <0.0001 |
| Year | 6/973 | 9.17 | 0.0025 |
| Reef Complex*Year | 6/973 | 13.18 | <0.0001 |
| White disease[^] | | | |
| Reef complex | 1/898 | 114.24 | <0.0001 |
| Year | 9/898 | 24.18 | <0.0001 |
| Reef Complex*Year | 9/898 | 9.58 | <0.0001 |
| Coral cover | | | |
| Reef complex | 1/94 | 217.1 | <0.0001 |
| Year | 9/86 | 12.5 | <0.0001 |
| Reef Complex*Year | 9/86 | 3.4 | 0.0012 |
| <i>Orbicella</i> cover | | | |
| Reef complex | 1/94 | 248.8 | <0.0001 |
| Year | 9/86 | 7.4 | <0.0001 |
| Reef Complex*Year | 9/86 | 3.3 | 0.0016 |

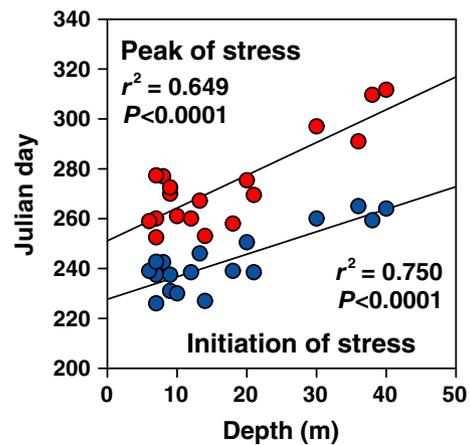


Fig. 4 Depth versus the mean Julian Day of the initiation of heat stress (blue dots) and the peak of heat stress (red dots). When MCE in the Virgin Islands became heat stressed the duration of stress was longer than in shallow reefs and delayed by about one month. Heat stress years were defined as years with >2 DHW at a given site ($N = 18$). The peak of thermal accumulation was considered the Julian Day when stress accumulation reached an asymptote within a given year.

disease than shallow reefs, even in years not associated with immediate or lagged thermal impacts.

Discussion

Our results indicate that the local mean warmest temperatures determine the bleaching threshold for Caribbean MCE and that these findings require a reconsideration of the broader applicability of the deep reef refugia hypothesis. Many studies have shown that, for shallow water corals, the local mean warmest temperatures will determine the bleaching threshold (Coles *et al.*, 1976; McClanahan *et al.*, 2007; Oliver & Palumbi, 2011). Here, we have shown that the same is likely true in Caribbean MCEs that are considered potential bleaching refugia (Bongaerts *et al.*, 2010). Adaptation or acclimatization (Palumbi *et al.*, 2014) to a cooler environment may have decreased the bleaching threshold of deeper corals relative to the same species in shallower water. The decrease in the bleaching threshold temperatures for this MCE and the strong relationship with monthly maximum mean temperatures shows that the response of these corals to high temperatures is specific to the site's thermal history and not based on relative differences in temperature between deeper and shallower habitats. In addition, the strong relationship between mean thermal conditions and the bleaching threshold also suggests that reduced light in MCEs does not temper the bleaching response. Thus, cooler mean temperatures and attenuated light in MCEs relative to nearby shallow reefs are insufficient conditions to predict a depth refugium from thermal stress.

The MCEs we studied have not always been refuges from thermal stress in the past because cooler temperature and reduced light conditions did not prevent thermal bleaching. Recent anomalously warm temperatures in our study MCEs sometimes exceed site-specific bleaching threshold temperatures. If the nominal satellite-derived bleaching threshold for the United States Virgin Islands (29.5 °C) (NOAA, 2006) was applicable to mesophotic reefs, then no damaging heat stress would have accumulated during the years of study, as all MCE sites would have accumulated < 1 DHW (data from DHW algorithm for MCE sites). However, as a direct result of lower bleaching thresholds, heat stress in 2005 accumulated to 7.4 DHW at the Tiger mesophotic reef even when temperatures over the thermal maximum period were 1.0 °C cooler than the shallow Tektite reef, which experienced 11.8 DHW. In addition, avoidance of heat stress was not prevented by higher temperature variability caused by the action of internal waves in the study MCEs. Accumulation of heat stress led directly to bleaching in these upper MCE habitats. Further, the large

increase in white disease prevalence in 2006 over any other period in the record, 57% and 679% for upper MCE and shallow reefs, respectively, strongly implicates an overriding role of the 2005 thermal stress in the disease response (Brandt & McManus, 2009; Randall & Van Woesik, 2015). Thus, warming in 2005 stimulated bleaching and disease that combined to cause a loss of about 25% *Orbicella* spp. cover in this upper MCE. Bleaching in the study MCEs was not restricted to orbicellid reefs, as upper mesophotic wall reefs dominated by *Agaricia* spp. severely bleached in 2005 to at least 40 m depth. Furthermore, thermal stress extended to the lower mesophotic zone, as an *Agaricia undata* reef on a steep slope between 60–75m depth had elevated bleaching when temperatures were anomalously high in 2012. In addition, bleaching in response to temperatures above site-specific bleaching thresholds was not restricted to the major reef building species, as multiple genera in lower relative abundance were affected in the upper MCE orbicellid reefs.

Depth refugia could occur if MCEs are able to recover from damage between disturbance events so as to maintain high cover and functionality, such as might occur if MCEs are more isolated from local stressors (Bridge *et al.*, 2013). However, the upper MCE in the Virgin Islands has not recovered after thermal disturbance, indicating insufficient resilience to those events. A relatively high prevalence of white disease may also be driving the slowly declining coral cover in our mesophotic study sites seen after 2008, following the initial recovery after 2005. Thus, recovery after disturbance in our study MCEs is not sufficiently rapid or in the right direction to allow recovery between disturbances. However, other MCE may have different capacities for recovery depending on unique physical processes, species composition, and resistance to secondary stressors, such as disease. Future studies could focus on regions where MCEs may be more resilient to see if isolation from local stressors could be a basis for depth refugia with a mechanism that is not based on temperature tolerance.

Lastly, the deep reef refugia hypothesis states that deep reefs will be refuges from thermal stress in the future, but this may be very unlikely in warming seas. A recent 0.3 °C decade⁻¹ rate of warming has already been demonstrated for the surface waters of Caribbean (Chollett *et al.*, 2012). Even if temperatures in sub-thermocline waters do not increase substantially, MCEs will still be affected when winds mix surface waters down to deeper depths and increase the size of the upper mixed layer and the depth of the thermocline, as we showed in this study (i.e., the year 2012). Globally, the mixed layer depth in the major reef areas of the Western Atlantic,

Western Pacific, and Western Indian Ocean is typically of similar depths of between 30–60 m during their respective shallow water annual thermal maximum (De Boyer *et al.*, 2004). As a result, many MCEs are associated with a thermal gradient in which temperatures decline with depth (Lesser *et al.*, 2009). Thus, corals in many global MCEs experience mean maximum temperatures that are cooler than shallow reefs and, therefore, our results suggest that they (1) will have a lower bleaching threshold than nearby shallow water corals and (2) are also threatened by predicted increases in heat flux from warming surface waters.

To have the conditions for a thermal refugium, resistance to bleaching in MCEs would need to be reliable over time or with future ocean warming (West & Salm, 2003). Our results suggest that during the annual thermal maximum, it does not matter whether MCEs are in the upper mixed layer, at or below the thermocline, or influenced by internal waves or upwelling if temperatures can be increased above the mean warmest conditions. Only very specific physical conditions would prevent MCE from experiencing thermal stress in all cases and, therefore, supporting a depth refugium based solely on temperature. For example, upwelling to deeper reef areas (>20 m) may be intensified during shallow water high thermal stress years in the outer central Great Barrier Reef (Berkelmans *et al.*, 2010). This is a very specific phenomenon that may involve an unexplained intensification of the East Australia Current. However, it is not known if this refuge is reliable over multiple shallow water thermal stress events, thereby summing to a refugium, nor if deeper reefs here are vulnerable in years without shallow water thermal stress, such as occurred in our study reefs in 2012. In addition, if there were protection of MCEs afforded by boundary currents, this would only influence a fraction of global mesophotic reefs in the western ocean basins. Reliable processes that maintain MCEs, or shallow reefs, below their site-specific bleaching thresholds under most conditions and in the future are still keys to identifying refugia for coral reefs.

Mesophotic reef habitat influenced by certain classes of strong internal waves may be candidates for deep reef refugia. Internal waves occur along fluid density gradients and are common features at mesophotic reef depths (Lesser *et al.*, 2009), and large amplitude solitons (6–9 °C drops) have been shown to reduce the impacts of shallow water (~15 m) thermal stress by delaying the onset and severity of bleaching (Buerger *et al.*, 2015; Wall *et al.*, 2015). Internal waves are ubiquitous in our study MCEs, including during high-temperature events in the annual thermal maximum, but did not prevent bleaching. However, the amplitude of waves that influence our MCE study reefs is relatively small (typically

<2 °C per cycle), and MCEs influenced by larger temperature drops from solitons could be more protected. By breaking up periods of heating, rapid low-temperature drops may decrease the buildup of heat stress predicted by mean conditions, and in one experiment afforded a two-week delay in bleaching onset in mesocosm conditions simulating the western shelf of Thailand (Buerger *et al.*, 2015). Future investigations could determine if and how intermittent cooling processes decrease the intrinsic bleaching threshold temperatures of corals in affected environments, and how this counters the extrinsic process of environmental cooling. It is also important to establish the degree of thermal buffering that is sufficient to support thermal refugia now and under future climate scenarios. This information would help to form a model of the magnitude and dynamics of intermittent cooling that could be used to predict the distribution of deep reef refugia.

Our study indicates that the burden to demonstrate a depth-based refugium is considerably stricter than previously conceived. The deep reef refugia hypothesis should be narrowed to specific conditions where the mean cooler conditions are reliably maintained at the monthly maximum mean temperature and below site-specific bleaching thresholds. Lack of data makes it difficult to demonstrate if and how many global MCEs meet these stricter criteria. We suggest MCEs that meet these conditions will be the exception in a warming ocean and, therefore, many of the world's MCEs are not refugia and are at risk from climate change. The apparent health of many MCEs up until the last decade may have been driven more by geographic isolation from local factors driving reef degradation (e.g., pollution and fishing) than buffering from heat stress. For example, a Jamaican upper MCE exposed to local stressors showed extreme degradation (Hughes, 1994), whereas our upper MCE study reefs were isolated from some local stressors and had high coral cover (Smith *et al.*, 2008), which was reduced by thermal stress in 2005. Alternatively, MCEs may be vulnerable to climate change, but the response of MCEs to a warming ocean may be delayed relative to shallow reefs. This would give a false sense that these systems are refugia, when in fact they have been more limited refuges from only the early stages of ocean warming. In either case, many MCEs that are presently more pristine than nearby shallow coral reefs could be overwhelmed by climate change in this century and our data suggest that in the Caribbean this process is starting to occur.

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Author contributions

T.B.S., J.G., and M.E.B. designed the research, all authors contributed to analysis, and T.B.S. and J.G. wrote the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Study site locations, strata, depths, *Orbicella* spp. cover (prior to 2005 bleaching mortality), and empirical bleaching thresholds for the United States Virgin Islands.

Fig. S1. Oceanographic profiles of temperature, salinity, density, and chlorophyll taken at the southern Puerto Rican shelf edge near the mesophotic Tiger study site (see main text Fig. 1) from 2012 to 2013.

Fig. S2. Annual temperature records and heat stress accumulation for project sites between the years 2005 and 2013.

Text S1. Bleaching of a lower mesophotic coral reef in response to elevated thermal stress in 2012.

Table S2. Mean bleaching prevalence on transects and extent on affected colonies (\pm SE) at non-orbicellid mesophotic coral reefs surveyed during the 2005 coral bleaching event.

Fig. S3. Coral bleaching at 30–45 m depth at the Cane Bay wall, St. Croix on November 23, 2005.