

Bleaching of the giant barrel sponge *Xestospongia muta* in the Florida Keys

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Abstract

The giant barrel sponge *Xestospongia muta* is now the dominant habitat-forming organism on many Caribbean coral reefs and has been observed to undergo cycles of bleaching similar to those seen for reef-building corals. We examined bleaching of *X. muta* at 15-m, 20-m, and 30-m depths over 2000–2005 on Conch Reef, Key Largo, Florida, to determine the spatial and temporal patterns of bleaching, whether bleaching affected sponge mortality, and whether there was a relationship between bleaching and seawater temperatures. Bleaching increased significantly with depth and was greater in autumn than spring, but the response was not uniform across the sponge population. Bleaching of *X. muta* did not result in sponge mortality, corroborating the conclusion that cyanobacterial symbionts of the sponge provide little or no benefit to the host. There was greater sponge bleaching with higher minimum daily seawater temperature anomalies within 30 d of surveys in the spring. For both the spring and autumn, there was greater bleaching with a higher number of positive 0.5°C daily anomalies within 14 d before surveys. Anomalously warm seawater temperatures fail to completely explain the variability of the observed bleaching response, however, and additional work would be required to conclusively determine whether a causal relationship between bleaching and temperature exists. As has been described for corals, bleaching of *X. muta* is likely a complex response that may be affected by multiple factors, including light availability and differences in bleaching susceptibility among *Synechococcus* symbionts.

Associations between benthic invertebrates and photosynthetic endosymbionts are a common feature of coral-reef communities. The coral-zooxanthellae symbiosis has attracted significant attention since reports of large-scale coral-bleaching events first appeared in the 1980s (Williams and Bunkley-Williams 1990). Bleaching is a process in which the host loses coloration due to the loss of symbionts or their photosynthetic pigments. Corals typically undergo seasonal cycles of bleaching that are not visible (Fitt et al. 2000); however, stressful conditions may lead to further reductions of zooxanthellae so that the white calcareous skeleton of the coral becomes apparent (Baker et al. 2008). Because the coral-zooxanthellar symbiosis is mutualistic, coral bleaching can cause a number of sublethal effects and, ultimately, coral mortality (Baker et al. 2008). On a broader scale, coral bleaching can have profound effects on reef community structure and function and the increasing prevalence of coral bleaching has led to long-term coral-reef degradation worldwide (Hoegh-Guldberg 1999; McWilliams et al. 2005).

Bleaching is not limited to reef-building corals, however, and can potentially affect all reef species with photosynthetic endosymbionts (Glynn 1996). In addition to corals, commonly affected hosts include hydrozoans, sea anemones, zoanths, and sponges. Because bleaching effects are observed across many taxa, it has been suggested that the phenomenon be termed ‘coral-reef bleaching’ (Williams and Bunkley-Williams 1990). While intensively studied for reef-building corals, bleaching is poorly understood for other ecologically important reef species.

Sponges are important constituents of coral reefs, where their abundance and diversity in these communities often rivals that of dominant reef-building corals (Diaz and Rützler 2001; Bell 2008). Similar to reef-building corals, many sponges form complex associations with photosynthetic endosymbionts, including zooxanthellae and cyanobacteria (Diaz and Rützler 2001). Although sponge bleaching has been reported in both the Caribbean and Pacific, the majority of sponges harboring photosynthetic endosymbionts do not appear to bleach (Vicente 1990; Williams and Bunkley-Williams 1990; Fromont and Garson 1999). A notable exception, however, is the sponge *Xestospongia muta*, which has commonly been reported to bleach during coral-reef bleaching events (Vicente 1990; Williams and Bunkley-Williams 1990; Dennis and Wicklund 1993).

The giant barrel sponge *Xestospongia muta* is a prominent member of Caribbean coral-reef communities. Individuals can reach > 1 m in height and diameter and live to hundreds or thousands of years old (McMurray et al. 2008). Populations constitute a significant amount of overall reef biomass (McMurray et al. 2010), are an important component of habitat heterogeneity, and filter large volumes of seawater (Southwell et al. 2008). Peripheral tissues harbor cyanobacteria of the genus *Synechococcus* that impart a reddish-brown coloration to unbleached individuals (Gómez et al. 2002; Erwin and Thacker 2007). During bleaching, sponges undergo a lightening of this characteristic coloration to the point that they may appear creamy-white or white in patches or spots (Vicente 1990; Cowart et al. 2006). *Xestospongia muta* has been observed to undergo cycles of bleaching and recovery of pigmentation, but more rarely, catastrophic bleaching

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occurs behind an advancing 'orange band' on the surface of the sponge followed by tissue loss or death (Coward et al. 2006). The more common form of cyclic bleaching is the subject of the present study.

Several stressors can cause reef-building corals to bleach; however, anomalously high water temperatures are the primary causative agent of widespread bleaching events (Glynn 1996; Hoegh-Guldberg 1999). Moreover, the increasing frequency of bleaching events has been attributed to rising ocean temperatures (McWilliams et al. 2005). Indices of seawater temperatures are commonly used by coral-reef managers to forecast and predict coral-reef bleaching and several studies have correlated seawater thermal stress metrics with past bleaching events (Manzello et al. 2007). The occurrence of bleaching of *X. muta* during large coral-bleaching events suggests that the cause of bleaching for this species may be similar. The primary objectives of this study were to examine the spatial and temporal patterns of bleaching of *X. muta*, examine whether bleaching affected rates of sponge mortality, and determine whether there was a correlation between seawater temperatures and bleaching of *X. muta*.

Methods

Surveys of bleaching and mortality of *Xestospongia muta* were conducted from May 2000 to December 2005 on Conch Reef, Florida (24°56.9'N, 80°27.2'W). Three permanent 16-m-diameter circular plots were established at 15-m, 20-m, and 30-m depths. Within each plot, each sponge was mapped and given a unique tag on a masonry nail driven next to the base of the sponge. Surveys were conducted in the spring and autumn of every year (generally May and Oct, respectively), but due to inclement weather, surveys were not conducted in the autumn of 2000 and the spring of 2004 at the 20-m and 30-m sites. Mean (\pm SD) densities of sponges at the 15-m, 20-m, and 30-m sites in the spring of 2000 were 0.148 ± 0.022 , 0.186 ± 0.047 , and 0.065 ± 0.038 sponges m⁻², respectively (McMurray et al. 2010).

The relationship between the visual appearance of cyclic bleaching for *X. muta* and the loss of pigmentation was established previously (López-Legentil et al. 2008), with a 40–60% reduction in chlorophyll *a* associated with bleached sponge tissue. For the present study, pigmentation of each sponge was scored as normal, lightly bleached, spottily bleached, or severely bleached. Sponges with characteristic reddish-brown coloration were defined as normally pigmented, or unbleached; sponges with obvious paling of this pigmentation, so that they appeared light brown, were defined as lightly bleached; sponges with numerous localized patches or spots of white tissue were defined as spottily bleached; and sponges that lost all reddish-brown coloration and appeared creamy white were defined as severely bleached.

Temperature data on Conch Reef were collected near continuously at 10-m, 20-m, and 30-m depths from 01 January 1997 to 31 December 2005. Ryan Tempmentors and Onset Computers Stowaway loggers were fixed 1 m above the substratum and recorded at 20-min intervals.

Additional Onset Computers HOBO Water Temp Pro loggers were deployed at 10-m, 15-m, and 20-m depths from March to December 2005. Using data collected over 2005, a ridge estimator was used to interpolate the temperature series at 15 m with the equation: $T_{15m} = -0.074897 + 0.597144T_{10m} + 0.401723T_{20m}$; where T_{10m} , T_{15m} , and T_{20m} are the mean daily temperatures at 10-m, 15-m, and 20-m depths, respectively. For each depth, the day-of-year mean temperature, across 1997 to 2005, was calculated to produce an annual temperature climatology. Temperature anomalies were calculated as the difference between the daily or monthly mean temperature and the annual temperature climatology at each depth.

Several temperature metrics, analogous to those used in studies of coral bleaching (Manzello et al. 2007), were developed that considered acute thermal stress, cumulative thermal stress, and thermal shock prior to bleaching surveys. A number of temporal scales were examined because the duration of exposure to temperature variables required to potentially elicit a bleaching response was unknown. In addition, because bleaching was observed in both the spring and autumn, both minimum and maximum temperatures were considered. Metrics included the previous monthly and weekly mean temperatures, minimum and maximum monthly mean temperatures over 12 months, previous monthly and weekly temperature anomalies, minimum and maximum monthly temperature anomalies over 12 months, number of months with a positive and negative 0.5°C temperature anomaly over 12 and 18 months, number of months with mean temperatures above and below the 10- and 90-percentile temperatures over 12 months, minimum and maximum daily mean temperatures over 30 d, minimum and maximum daily temperature anomalies over 30 d, number of days with a 0.5°C positive or negative temperature anomaly over 14 and 30 d, and the number of days with mean temperatures above and below the 10- and 90-percentile temperatures over 30 and 365 d.

Binomial regression was used to model the relationship between temperature and sponge bleaching. The analysis was conducted independently in two ways to include both the most liberal and most conservative definition of sponge bleaching by first comparing sponges in all bleached categories (lightly bleached, spottily bleached, and severely bleached) to those that were unbleached (normal pigmentation), then comparing only sponges in the severely bleached category to those that were unbleached. Generalized estimating equations were used to estimate parameters of each model. The deviance statistic and quasi-likelihood under the independence model information criterion (QIC) was used to assess model fit. Analyses were conducted with SAS (version 9.1.3 for Windows; SAS Institute) and SPSS (version 14.0.0 for Windows; SPSS) statistical software.

Results

Annual daily mean seawater temperature variation on Conch Reef was $\sim 10^\circ\text{C}$, with summer highs near 30°C and winter lows near 20°C (Fig. 1). Daily mean temperatures

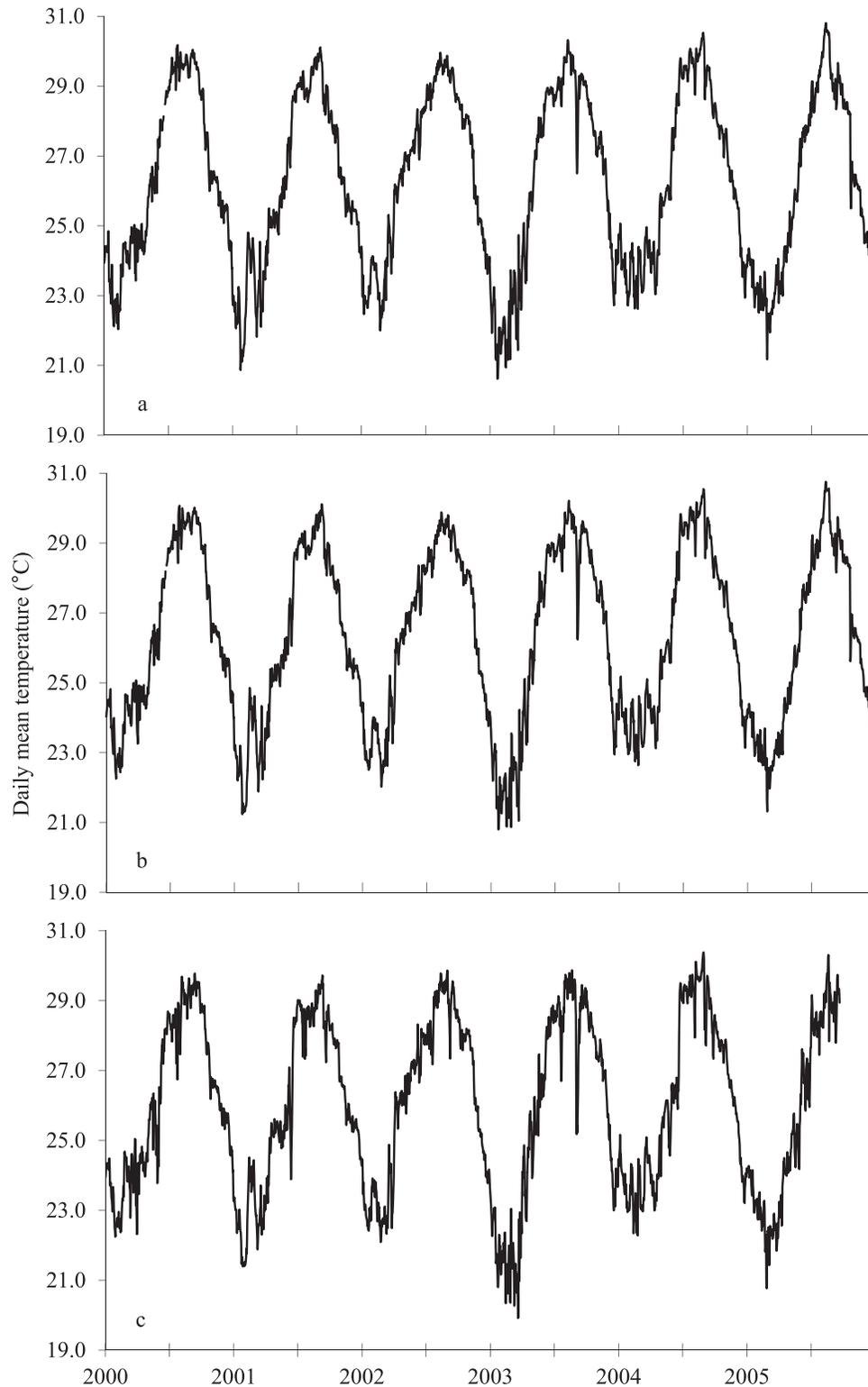


Fig. 1. Daily mean seawater temperatures from 01 January 2000 to 31 December 2005 at (a) 15-m, (b) 20-m, and (c) 30-m depths on Conch Reef.

generally peaked in August and reached minima in January. The warmest daily mean temperatures occurred over the summer of 2005, while the coldest daily mean temperatures occurred over the winter of 2002–2003

(Fig. 1). High-frequency temperatures at 20-m and 30-m depths were more variable during summer months (within-day temperature fluctuations as large as 10°C); therefore, following Leichter and Miller (1999), the temperature series

Table 1. Daily mean seawater temperature summary statistics for 10-m, 15-m, 20-m, and 30-m depths on Conch Reef over summer (S, May–Sep) and winter (W, Oct–Apr) 2000–2005.

Depth (m)	Season	Mean (°C)	SD	Minimum mean	Maximum mean	Range	<i>n</i>
10	S	28.66	1.40	24.55	31.03	6.47	915
15	S	28.43	1.40	24.39	30.81	6.42	915
20	S	28.36	1.42	24.39	30.75	6.36	916
30	S	27.84	1.56	23.78	30.38	6.60	911
10	W	24.91	1.87	20.62	29.15	8.53	1274
15	W	24.76	1.89	20.62	29.14	8.52	1274
20	W	24.81	1.93	20.80	29.40	8.60	1274
30	W	24.57	2.01	19.92	29.36	9.44	1182

at each depth was divided into two seasons: 01 May–30 September ‘summer,’ and 01 October–30 April ‘winter.’ These seasons generally coincided with the intervals between spring (May) and autumn (Oct) sponge surveys. Table 1 shows the daily mean temperature summary statistics for each depth over the summer and winter seasons. Daily mean temperatures were ~ 3.25–3.75 lower in winter than summer at all depths and generally decreased with increasing depth. Differences in mean temperatures between depths were greatest in the summer compared to winter. Minimum daily means generally decreased with depth and maximum daily means generally decreased with depth for both seasons. Daily mean temperature ranges were greatest at the 30-m site (Table 1).

Bleaching of *X. muta* was observed in both the spring and autumn of every year surveyed. Across all years, spotted bleaching of sponge tissue was most prevalent, while severe bleaching was the least common form of bleaching at each depth. Mean (\pm SD) percent of sponges exhibiting spotted, light, and severe bleaching across the study were 19.57 ± 11.41 , 19.16 ± 12.82 , and 17.34 ± 10.03 at 30 m, 21.08 ± 11.78 , 16.79 ± 7.85 , and 10.06 ± 3.08 at 20 m, and 16.29 ± 10.75 , 9.03 ± 10.61 , and 7.40 ± 5.07 at 15 m, respectively. Regardless of the way bleaching was categorized (more

liberally, including all three categories of bleaching, or more conservatively, including only severely bleached sponges), both analyses revealed consistent spatial and temporal patterns of bleaching. For brevity, only the results from the more conservative analysis are shown in the figures.

There was a large range in bleaching across years and between seasons (Fig. 2). For all depths collectively, bleaching was greatest in the autumn of 2003, and lowest in the spring of 2001, with mean (\pm SD) ratios of bleached to unbleached sponges of 0.77 ± 0.68 and 0.05 ± 0.01 , respectively. Bleaching was significantly greater in the autumn compared to the spring for all depths (15 m: $\chi^2 = 7.45$, $df = 1$, $p = 0.0063$; 20 m: $\chi^2 = 6.06$, $df = 1$, $p = 0.0138$; 30 m: $\chi^2 = 7.87$, $df = 1$, $p = 0.0050$; Fig. 2). For all depths combined, the mean (\pm SD) ratio of bleached sponges to unbleached sponges was 0.18 ± 0.21 in the spring and 0.39 ± 0.38 in the autumn.

Bleaching was variable within plots and both bleached and unbleached sponges were observed within each depth in both seasons. Bleaching significantly increased with depth on Conch Reef, but this relationship varied with season (Fig. 2). In the autumn, significantly more bleaching occurred at 30 m compared to 20 m ($\chi^2 = 9.37$, $df = 1$, $p = 0.0022$) and 15 m ($\chi^2 = 18.40$, $df = 1$, $p < 0.0001$), but

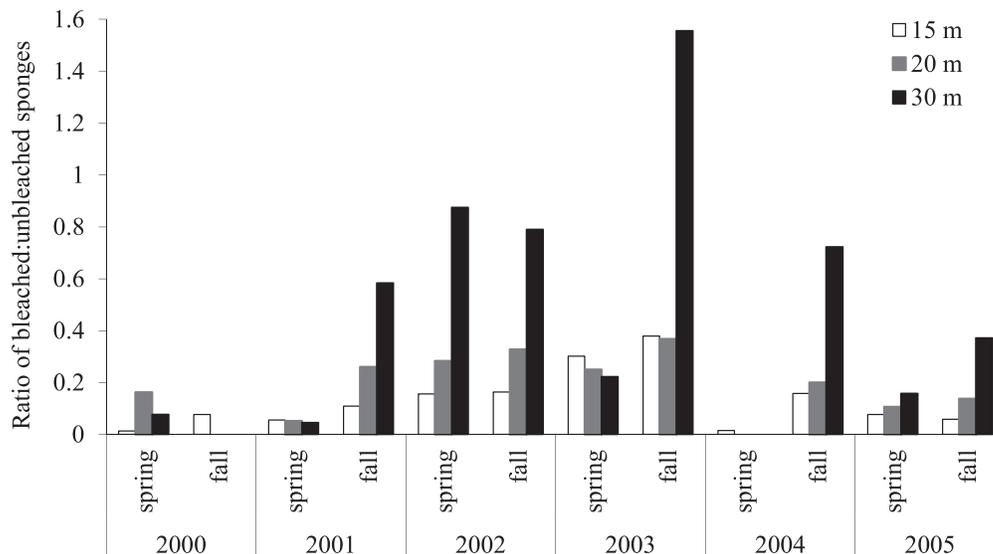


Fig. 2. Ratio of severely bleached to unbleached *Xestospongia muta* from 2000 to 2005 at 15-m, 20-m, and 30-m depths on Conch Reef.

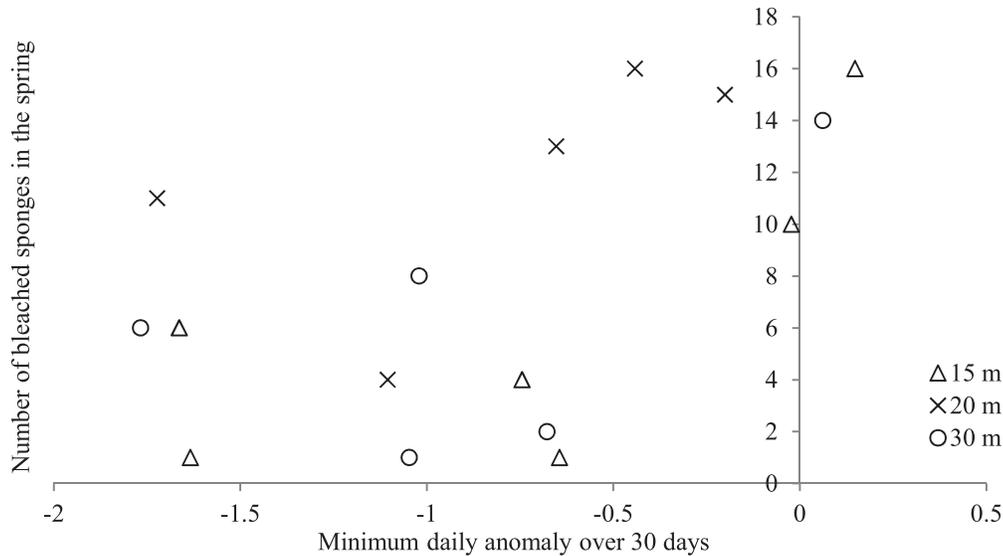


Fig. 3. Scatterplot of the number of severely bleached sponges vs. the minimum daily anomaly within 30 d prior to bleaching surveys in the spring for 15-m, 20-m, and 30-m depths on Conch Reef.

bleaching did not differ between 15-m and 20-m depths. In the spring, bleaching was significantly greater at 30 m compared to 15 m ($\chi^2 = 11.81$, $df = 1$, $p = 0.0006$) and 20 m compared to 15 m ($\chi^2 = 4.92$, $df = 1$, $p = 0.0265$), but bleaching did not differ between 30-m and 20-m depths.

There was no significant effect of bleaching on sponge mortality. Bleached sponges were regularly observed to survive bleaching and regain their normal pigmentation in subsequent field seasons. The mean (\pm SD) percent of bleached sponges that died before a subsequent survey was 3.55 ± 3.75 , compared to 2.81 ± 1.64 percent for unbleached sponges. When sponges with light and spotted bleaching are included, the mean (\pm SD) percent subsequent mortality of bleached sponges becomes 2.18 ± 2.37 .

The minimum daily anomaly within 30 d prior to bleaching surveys was found to best explain the relationship between temperature and bleaching. The ratio of deviance to degrees of freedom was 0.80, indicating a good fit of the model. The incidence of bleaching in the spring, but not the autumn, significantly increased with higher minimum daily anomalies 30 d prior to bleaching ($p < 0.0001$; Fig. 3). The number of positive anomalies over 30-d intervals increased with higher minimum anomalies, indicating a direct relationship between bleaching and warm temperature anomalies. This relationship is supported by the second-best fitting model, in which the incidence of bleaching was found to significantly increase with the number of positive 0.5°C daily anomalies 14 d prior to bleaching ($p < 0.0001$; Fig. 4). The difference in QIC between the models was < 1.0 , indicating comparative fits to the data. Considering all categories of bleaching as the response, the number of days in which there was a 0.5°C temperature anomaly within 14 d prior to bleaching surveys was found to best explain the relationship between temperature and bleaching. The incidence of bleaching was found to significantly increase with the number of days in which there was a positive 0.5°C

anomaly in both the spring ($p < 0.0001$) and autumn ($p = 0.024$) at 30 m ($p < 0.0001$), but not at 15 m or 20 m.

Discussion

Coral bleaching typically occurs during the summer or autumn, when temperatures are the highest or near the end of a prolonged warming period (Hoegh-Guldberg 1999; Baker et al. 2008). Fitt et al. (2000) found that corals from all depths experienced seasonal changes in algal densities, with lowest algal densities experienced in the late summer or autumn and highest densities during the coldest part of the year; however, coral bleaching is not always visually obvious. In contrast, bleaching of *X. muta* was observed in both the spring and autumn of every year, and is commonly observed throughout the year (S McMurray pers. obs.). The bathymetric patterns of bleaching of *X. muta* are also contrary to coral-bleaching patterns, with bleaching of *X. muta* observed to increase with increasing depth. Incidence of bleaching is usually greatest for reef-building corals at shallow depths, but bleaching also affects deep-water corals (Glynn 1996). In some areas, deep-water corals were affected before and to a greater extent than shallow-water species and Fitt et al. (2000) have suggested that deep-water corals appear lighter in color before shallower corals because they normally harbor fewer zooxanthellae. Decreased light intensity has been shown to reduce cyanobacterial abundance in *X. muta* and may partially explain why bleaching is greater at depth (Gómez et al. 2002; López-Legentil et al. 2008).

In contrast to reef-building corals, bleaching did not result in mortality of *X. muta*. This finding supports previous reports of cyclic bleaching of *X. muta* that found mortality did not result following a mass coral-reef bleaching event (Vicente 1990). Few anecdotal reports exist that suggest otherwise (Williams and Bunkley-Williams 1990); however, these reports likely describe mortality of *X.*

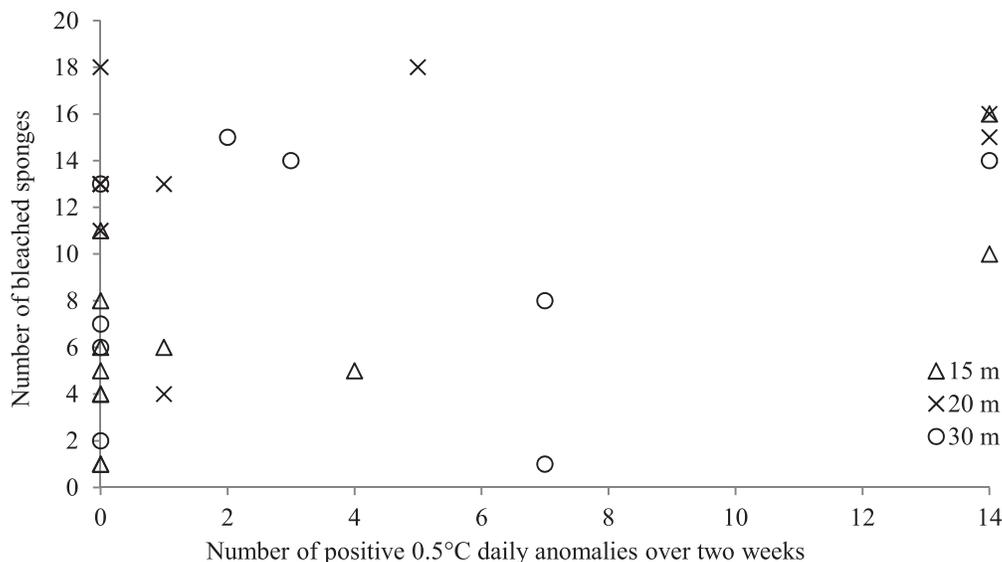


Fig. 4. Scatterplot of the number of severely bleached sponges vs. the number of daily anomalies $> 0.5^{\circ}\text{C}$ within 2 weeks prior to bleaching surveys for 15-m, 20-m, and 30-m depths on Conch Reef.

muta from a less common form of bleaching that results from a pathogenic-like condition (Coward et al. 2006; Angermeier et al. 2011) rather than the cyclic form of bleaching described here. From the limited literature available, the effect of bleaching on sponge survival appears to be variable. Off Australia, individuals of the cyanobacteria-containing sponge *Chondrilla australiensis* were found to die following bleaching (Fromont and Garson 1999); however, Hill and Wilcox (1998) demonstrated that bleached *Anthosigmella varians* survived and acquired a novel, and perhaps more temperature-resistant, strain of zooxanthellae. Unlike the case for *X. muta*, some sponge species appear to gain benefits from cyanobacteria symbionts (Wilkinson 1983; Thacker 2005) and bleaching may be predicted to have deleterious effects on these host sponges (Fromont and Garson 1999).

In the largest survey of sponge bleaching to date, Vicente (1990) found that only 3 of 31 common reef sponge species bleached during a coral-reef bleaching event in Puerto Rico, 1987–1988. To explain why the majority of sponges harboring photosymbionts appear to be unaffected, it was suggested that sponge–cyanobacteria symbioses may be relatively more stable compared to coral–zooxanthellar associations, because the former evolved earlier in geological time (Vicente 1990). Moreover, the association between sponges and cyanobacteria has long been held to be ubiquitously mutualistic (Wilkinson 1983). Our findings, however, add to a growing body of research that suggests *Synechococcus* symbionts of *X. muta* are commensals. Growth rates of the same sponges examined here did not differ between depths on Conch Reef despite a clear bathymetric gradient of bleaching (McMurray et al. 2008). Bleaching also does not affect the population dynamics of *X. muta* (McMurray et al. 2010). Further, López-Legentil et al. (2008) found that bleaching of *X. muta* did not coincide with an increase in the expression of the heat-shock protein hsp70, which is an indication of tissue stress. Bleaching of

X. muta is, therefore, likely to be a response by the cyanobacteria rather than by the host sponge. This corroborates findings for a congeneric species (*X. exigua*) off the Republic of Palau that contains *Synechococcus* symbionts (Thacker 2005), and for which it was concluded that the cyanobacteria are commensal and provide no clear benefits to the host sponge.

There was a significant correlation between anomalously warm seawater temperatures and bleaching of *X. muta*. Temperature metrics of the best-fitting models both suggest that cumulative, rather than acute, anomalously warm thermal stress may affect bleaching. The thermal regime of Conch Reef is characterized by persistent temperature fluctuations due to internal tides, tidal bores generated by breaking internal waves, and cold-water intrusions related to variability of the Florida Current (Leichter et al. 1996; Leichter and Miller 1999). Seawater temperature variation due to these mechanisms corresponds well to the temporal and spatial patterns of bleaching of *X. muta*, because temperature variation increases with depth on Conch Reef and is greater over summer compared to winter (Leichter and Miller 1999). A significant correlation between bleaching and the minimum daily anomaly within 30 d prior to bleaching surveys suggests that bleaching is greatest during periods in which the magnitude and duration of these events is decreased. Therefore, cyanobacteria symbionts of *X. muta* along the bathymetric gradient on Conch Reef may be acclimated to persistent cold-water intrusions, such that bleaching results when these events are minimized or do not occur. These cold-water intrusions are also characterized by episodic variability of thermal patchiness across the reef bathymetry (Leichter et al. 2005), which may partially explain the variable bleaching response observed for *X. muta*.

Laboratory investigations have confirmed that temperature changes are a causative agent of bleaching for reef-building corals (Hoegh-Guldberg 1999). Although the

findings of the present study support a correlation between anomalous water temperature and bleaching of *X. muta*, further experimental work is needed to determine whether this reflects a causal relationship. In laboratory experiments, 15-h exposure of *X. muta* to water temperatures ranging from 10°C to 40°C did not cause bleaching (López-Legentil et al. 2008), but longer exposures may be required to elicit a response. While *X. muta* has been reported as an affected species during coral-reef bleaching events (Vicente 1990; Williams and Bunkley-Williams 1990; Dennis and Wicklund 1993), these reports are relatively small in number compared to the collective number of reports of bleaching in the Caribbean. It is unclear whether this is because coral-reef bleaching surveys typically only include corals, or whether *X. muta* is not regularly affected during these events. Ideally, future bleaching surveys should include all affected and unaffected coral-reef species to gain a better understanding of coral-reef bleaching (Williams and Bunkley Williams 1990). In addition, follow-up surveys of such events are needed to elucidate the effects of bleaching on species other than corals.

Despite a significant correlation between anomalously warm seawater temperatures and bleaching of *X. muta*, this relationship fails to fully explain the observed spatial and temporal patterns of bleaching. For example, bleaching was never observed to affect all individuals at a given site, bleaching manifested in several different forms, and some form of bleaching was always observed, despite the temperature regime. For some sponge species, the proportion of cyanobacteria symbionts is habitat-dependent (Wilkinson and Vacelet 1979) and can be variable among conspecifics (Wilkinson 1978). In addition, the patterns of coral bleaching can be highly variable, with differences between conspecifics in the same area and variation within colonies (Baker et al. 2008). The coral-bleaching response is complex and variability of coral bleaching has been attributed to other environmental factors (e.g., light) that interact with temperature or act alone to influence bleaching and differences in the susceptibilities of corals to bleaching.

Corals host a diverse group of dinoflagellates belonging to the genus *Symbiodinium*, which vary in their response to bleaching (Rowan et al. 1997). Similarly, *Synechococcus* harbored by sponges have been found to be a diverse group of cyanobacteria with a range of host specificities (Erwin and Thacker 2008). Both a generalist and a host-specific clade of *Synechococcus* have been found in *X. muta* (Erwin and Thacker 2008). It remains to be seen whether, as for *Symbiodinium*, these groups of cyanobacteria differ physiologically or can acclimatize to environmental stress (Rowan et al. 1997; Brown et al. 2002); however, these hypotheses may explain variable patterns of bleaching observed for *X. muta* on Conch Reef.

Available evidence also indicates that cyanobacterial abundance in the tissues of *X. muta* is dependent on light intensity. Both shading experiments and transplantation of *X. muta* to deeper depths resulted in decreases in cyanobacterial abundance (Gómez et al. 2002; López-Legentil et al. 2008). Moreover, completely white, aposymbiotic *X. muta* can be found under overhangs and in caves and *X. muta* in deep habitats may be persistently

white (> 60 m; Vicente 1990). Decreased light availability could explain the greater incidence of bleaching of *X. muta* with depth, but fails to fully explain why adjacent individuals can be affected dissimilarly, and this may be explained by cladal differences among cyanobacteria.

In conclusion, bleaching of *X. muta* was greatest in the autumn compared to spring, and increased with depth on Conch Reef. Bleaching also appears to be a cyclic response by the cyanobacteria symbionts of *X. muta* that has no negative effect on the host sponge. Bleaching increased with the minimum daily seawater temperature anomaly within 30 d prior to bleaching surveys in the spring and with the number of positive 0.5°C daily seawater temperature anomalies within 14 d prior to bleaching surveys in both the spring and autumn. These findings suggest that bleaching is correlated with anomalously warm seawater temperatures characterized by decreases in the magnitude and duration of persistent cold-water intrusions on Conch Reef. Additional work is required to deduce a causal relationship between bleaching of *X. muta* and temperature, however, and variability in the bleaching response suggests that other factors, including light availability and differences in the susceptibilities to bleaching among *Synechococcus* symbionts, may be involved.

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References

- ANGERMEIER, H., J. KAMKE, U. R. ABDELMOHSEN, G. KROHNE, J. R. PAWLIK, N. L. LINDQUIST, AND U. HENTSCHEL. 2011. The pathology of sponge orange band disease affecting the Caribbean barrel sponge *Xestospongia muta*. *FEMS Microbiol. Ecol.* **75**: 218–230, doi:10.1111/j.1574-6941.2010.01001.x
- BAKER, A. C., P. W. GLYNN, AND B. RIEGL. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast. Shelf Sci.* **80**: 435–471, doi:10.1016/j.ecss.2008.09.003
- BELL, J. J. 2008. The functional roles of marine sponges. *Estuar. Coast. Shelf Sci.* **79**: 341–353, doi:10.1016/j.ecss.2008.05.002
- BROWN, B. E., R. P. DUNNE, M. S. GOODSON, AND A. E. DOUGLAS. 2002. Experience shapes the susceptibility of a reef coral to bleaching. *Coral Reefs* **21**: 119–126.
- COWART, J. D., T. P. HENKEL, S. E. McMURRAY, AND J. R. PAWLIK. 2006. Sponge orange band (SOB): A pathogenic-like condition of the giant barrel sponge *Xestospongia muta*. *Coral Reefs* **25**: 513, doi:10.1007/s00338-006-0149-y
- DENNIS, G. D., AND R. I. WICKLUND. 1993. The relationship between environmental factors and coral bleaching at Lee Stocking Island, Bahamas in 1990, p. 167–173. *In* R. N.

- Ginsburg [ed.], Proceedings of the colloquium on global aspects of coral reefs: Health, hazards and history, 1993. Rosenstiel School of Marine and Atmospheric Science, Univ. of Miami.
- DIAZ, M. C., AND K. RÜTZLER. 2001. Sponges: An essential component of Caribbean coral reefs. *Bull. Mar. Sci.* **69**: 535–546.
- ERWIN, P. M., AND R. W. THACKER. 2007. Incidence and identity of photosynthetic symbionts in Caribbean coral reef sponge assemblages. *J. Mar. Biol. Assoc. U. K.* **87**: 1683–1692, doi:10.1017/S0025315407058213
- , AND ———. 2008. Cryptic diversity of the symbiotic cyanobacterium *Synechococcus spongiarum* among sponge hosts. *Mol. Ecol.* **17**: 2937–2947, doi:10.1111/j.1365-294X.2008.03808.x
- FITT, W. K., F. K. MCFARLAND, M. E. WARNER, AND G. C. CHILCOAT. 2000. Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnol. Oceanogr.* **45**: 677–685, doi:10.4319/lo.2000.45.3.0677
- FROMONT, J., AND M. GARSON. 1999. Sponge bleaching on the West and East coasts of Australia. *Coral Reefs* **18**: 340, doi:10.1007/s003380050209
- GLYNN, P. W. 1996. Coral reef bleaching: Facts, hypotheses and implications. *Glob. Change Biol.* **2**: 495–509, doi:10.1111/j.1365-2486.1996.tb00063.x
- GÓMEZ, R., AND OTHERS. 2002. Identity of cyanobacterial symbiont of *Xestospongia muta*. *Boll. Mus. Ist Biol. Univ. Genova* **66**–**67**: 82–83.
- HILL, M., AND T. WILCOX. 1998. Unusual mode of symbiont repopulation after bleaching in *Anthosigmella varians*: acquisition of different zooxanthellae strains. *Symbiosis* **25**: 279–289.
- HOEGH-GULDBERG, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw. Res.* **50**: 839–866, doi:10.1071/MF99078
- LEICHTER, J. J., G. B. DEANE, AND M. D. STOKES. 2005. Spatial and temporal variability of internal wave forcing on a coral reef. *J. Phys. Oceanogr.* **35**: 1945–1962, doi:10.1175/JPO2808.1
- , AND S. L. MILLER. 1999. Predicting high-frequency upwelling: Spatial and temporal patterns of temperature anomalies on a Florida coral reef. *Cont. Shelf Res.* **19**: 911–928, doi:10.1016/S0278-4343(99)00004-7
- , S. R. WING, S. L. MILLER, AND M. W. DENNY. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. *Limnol. Oceanogr.* **41**: 1490–1501, doi:10.4319/lo.1996.41.7.1490
- LÓPEZ-LEGENTIL, S., B. SONG, S. E. MCMURRAY, AND J. R. PAWLIK. 2008. Bleaching and stress in coral reef ecosystems: Hsp70 expression by the giant barrel sponge *Xestospongia muta*. *Mol. Ecol.* **17**: 1840–1849, doi:10.1111/j.1365-294X.2008.03667.x
- MANZELLO, D. P., R. BERKELMANS, AND J. C. HENDEE. 2007. Coral bleaching indices and thresholds for the Florida Reef Tract, Bahamas, and St. Croix, US Virgin Islands. *Mar. Pollut. Bull.* **54**: 1923–1931, doi:10.1016/j.marpolbul.2007.08.009
- MCMURRAY, S. E., J. E. BLUM, AND J. R. PAWLIK. 2008. Redwood of the reef: Growth and age of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Mar. Biol.* **155**: 159–171, doi:10.1007/s00227-008-1014-z
- , T. P. HENKEL, AND J. R. PAWLIK. 2010. Demographics of increasing populations of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Ecology* **91**: 560–570, doi:10.1890/08-2060.1
- MCWILLIAMS, J. P., I. M. COTE, J. A. GILL, W. J. SUTHERLAND, AND A. R. WATKINSON. 2005. Accelerating impacts of temperature-induced coral bleaching in the Caribbean. *Ecology* **86**: 2055–2060, doi:10.1890/04-1657
- ROWAN, R., N. KNOWLTON, A. BAKER, AND J. JARA. 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* **388**: 265–269, doi:10.1038/40843
- SOUTHWELL, M. W., J. B. WEISZ, C. S. MARTENS, AND N. LINDQUIST. 2008. In situ fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. *Limnol. Oceanogr.* **53**: 986–996, doi:10.4319/lo.2008.53.3.0986
- THACKER, R. W. 2005. Impacts of shading on sponge–cyanobacteria symbiosis: A comparison between host-specific and generalist associations. *Integr. Comp. Biol.* **45**: 369–376, doi:10.1093/icb/45.2.369
- VICENTE, V. P. 1990. Response of sponges with autotrophic endosymbionts during the coral-bleaching episode in Puerto Rico. *Coral Reefs* **8**: 199–202, doi:10.1007/BF00265011
- WILKINSON, C. R. 1978. Microbial associations in sponges. I. Ecology, physiology and microbial populations of coral reef sponges. *Mar. Biol.* **49**: 161–167, doi:10.1007/BF00387115
- . 1983. Net primary productivity in coral reef sponges. *Science* **219**: 410–412, doi:10.1126/science.219.4583.410
- , AND J. VACELET. 1979. Transplantation of marine sponges to different conditions of light and current. *J. Exp. Mar. Biol. Ecol.* **37**: 91–104, doi:10.1016/0022-0981(79)90028-5
- WILLIAMS, E. H., AND L. BUNKLEY-WILLIAMS. 1990. The worldwide coral bleaching cycle and related sources of coral mortality. *Atoll Res. Bull.* **335**: 1–71.

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