

VARIATION IN *ACROPORA PALMATA* BLEACHING ACROSS BENTHIC ZONES AT BUCK ISLAND REEF NATIONAL MONUMENT (ST. CROIX, USVI) DURING THE 2005 THERMAL STRESS EVENT

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ABSTRACT

At Buck Island Reef National Monument (BIRNM) in St. Croix, U.S. Virgin Islands, *Acropora palmata* (Lamarck, 1816) experienced extensive bleaching in 2005. Water temperatures at BIRNM in 2005 were higher than at any time since at least 1991, and exceeded the bleaching threshold by over 2 °C, causing extensive coral bleaching. Forty-four *A. palmata* colonies at three sites in BIRNM were sampled before, during, and after the thermal stress event. Additionally, colonies at randomly located sites on the reef shelf were surveyed to extend results over a larger portion of BIRNM; these colonies were surveyed during and after the thermal stress event. *Acropora palmata* colonies located in the backreef benthic zone exhibited a different response to the thermal stress event than those located elsewhere in BIRNM: backreef colonies bleached earlier and suffered greater tissue loss than those located elsewhere. We hypothesized that increased water temperature coupled with reduced water flow and increased light penetration caused higher mortality in backreef locations. Since *A. palmata* in the backreef benthic zone is least resistant and resilient to thermal stress events, backreef areas are a poor focal area for *A. palmata* marine protected areas.

Coral bleaching refers to the loss of photosynthetic dinoflagellate algal symbionts (zooxanthellae), the reduction of photosynthetic pigments, or both (Glynn, 1993; Brown, 1997). Many reef-building coral species live very close to their natural thermal tolerance limits (Jokiel and Coles, 1990; Lesser, 1997). When sea surface temperatures (SSTs) exceed the “bleaching threshold”, 1 °C above the mean monthly maximum SST (Goreau and Hayes, 1994), corals are likely to experience bleaching. If zooxanthellae are not reassimilated into coral tissues, the coral animal will die.

Although bleaching is a generalized coral response to stress associated with a wide variety of factors such as thermal stress, irradiance, pollution, sedimentation, aerial exposure, and disease (Glynn, 1993; Brown, 1997; Hoegh-Guldberg, 1999), mass coral bleaching appears to be triggered by sustained elevated water temperature (thermal stress event) (Brown, 1997; Hoegh-Guldberg, 1999; Lesser, 2004). Predictive models correlate the magnitude and duration of water temperatures above bleaching thresholds to forecast thermal stress events (Gleeson and Strong, 1995; Strong et al., 2004; Liu et al., 2003). Average water temperatures have risen 0.4–0.8 °C since the late eighteenth century (Barton and Casey, 2005) and it is predicted that water temperatures will continue to rise approximately 1–2 °C per century (Hoegh-Guldberg, 1999; Barton and Casey, 2005), which suggests more frequent thermal stress events in the future.

During thermal stress events, bleaching can be patchy, locally exacerbated, or inhibited by multiple factors. For example, high solar irradiance coupled with thermal stress appears to be particularly effective at promoting mass coral bleaching (Brown, 1997; Lesser, 2004). Conversely, shading and cloud cover have been shown to decrease

coral bleaching (Mumby et al., 2001; West and Salm, 2003). Particular benthic zones can be subject to different hydrodynamic conditions. Corals which live in sheltered benthic zones, such as the backreef, are protected by a reef crest; they experience decreased sea surface disturbance and water flow, and are exposed to elevated water temperature and increased light penetration (Warner et al., 1996; Jokiel and Brown, 2004). Increased water flow has been shown to protect corals from bleaching (Jokiel and Brown, 2004) and/or to enhance recovery from bleaching (Nakamura and van Woessik, 2001; Nakamura et al., 2003). Corals that are regularly subjected to backreef conditions are thought to be more physiologically acclimated to higher irradiance and temperature, or may host algal symbiont communities that are more tolerant of higher irradiance and temperature (Rowan et al., 1997; Kinzie et al., 2001).

Ghiold and Smith (1990) reported *Acropora palmata* (Lamarck, 1816) to be generally tolerant of bleaching. Nonetheless, in 2005 *A. palmata* in the U.S. Virgin Islands bleached on a regional scale for the first time on record (Muller, 2008). *Acropora palmata* historically has been a dominant Caribbean coral in shallow high-energy habitats < 6 m deep, and a major reef-building coral in the Caribbean. However, in 2006, *A. palmata* was listed as “threatened” under the Endangered Species Act (NMFS, 2006). Major natural threats continue to contribute to the decline of this species throughout its historic range including thermal stress, disease, and hurricanes; while anthropogenic impacts such as pollution, sedimentation, and anchoring damage have further stressed this species.

Buck Island Reef National Monument (BIRNM), a unit of the U.S. National Park Service in the U.S. Virgin Islands, was originally created to preserve and protect one of the finest *A. palmata* barrier reef systems in the Caribbean. In 2001, BIRNM was expanded to include substantial reef shelf habitat suitable for *A. palmata*, and in 2004, a comprehensive assessment of *A. palmata* was undertaken at BIRNM. This survey documented the spatial distribution of *A. palmata*, and estimated that 97,232–134,371 *A. palmata* colonies with at least 1 m of connected live tissue were present at BIRNM at densities varying between 0.004 colonies m⁻² and 0.160 colonies m⁻² (Mayor et al., 2006).

In 2005, SSTs elevated above the bleaching threshold persisted for more than 2 mo in the U.S. Virgin Islands. Temperatures were not only higher than had been previously recorded (1991–present) at BIRNM, but also remained above the bleaching threshold for longer. The objective of this study was to evaluate how *A. palmata* colonies were affected in different benthic zones by documenting *A. palmata* bleaching and mortality at BIRNM.

METHODS

BIRNM is located adjacent to the northeast coast of St. Croix, U.S. Virgin Islands, and consists of a 176 acre island surrounded by approximately 18,135 acres of marine habitat (Fig. 1). The island is ringed by an incomplete emergent barrier reef with extensive backreef extending to the west; north of the island is a reef shelf approximately 10 m deep. At BIRNM, *A. palmata* is found in shallow backreef and forereef zones, as well as in the deeper reef shelf zone.

The impact of the 2005 thermal stress event on *A. palmata* colonies at BIRNM was measured by monitoring 44 colonies at three study sites. The three study sites were located in each of the benthic zones (Fig. 1). Located in the backreef zone, the Underwater Trail site included 17 colonies (~3–5 m depth); in the forereef zone, the South Forereef site included 16 colonies (~2 m depth); and on the reef shelf, the North Bar site included 12 colonies (~10 m).

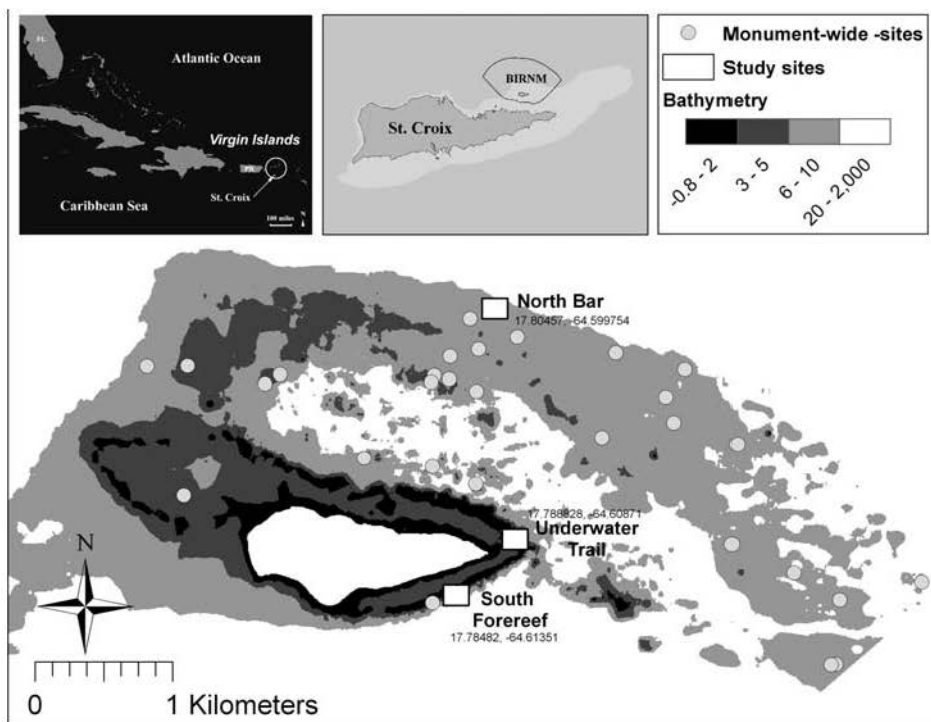


Figure 1. Survey sites where *Acropora palmata* bleaching and mortality were evaluated at Buck Island Reef National Monument. Study sites are represented by squares and monument-wide sites by circles. Forty-four colonies were assessed at the three study sites from August 2005–January 2006 and 65 colonies were assessed at monument-wide sites from November 2005–February 2006.

Because the sample size at each study site was small and spatially limited (sites ranged from 890 m²–2792 m²), results could not be inferred to *A. palmata* throughout BIRNM. Thus, a monument-wide survey was initiated to provide a broad-scale assessment of the extent and pattern of bleaching. This survey involved the sampling of 65 colonies located in 29 random sites (Fig. 1).

The study sites were sampled in August and November 2005, and again in January 2006, while Monument-wide coral colonies were sampled in November 2005 and February 2006. All sampled colonies were required to have a minimum of 1 m continuous live tissue. These colonies were digitally photographed from the planar perspective, although in some cases planar photography was not practical (i.e., some colonies were too shallow) and photographs were taken from an oblique angle to the colony. Each photograph was evaluated for the percent of bleached and partially bleached (mottled) coral tissue, unbleached coral tissue, and algae-covered skeleton. Bleached and mottled tissue present in photographs was averaged for all colonies at each study site and for colonies included in the monument-wide survey for each sampling event. A photographic series of the same colony over time was compiled and mortality was estimated by comparing the change in percent of algae-covered skeleton (no live tissue) from the first photograph in a series to the next (Fig. 2); percent change (tissue mortality) was averaged for colonies at each study site and for the monument-wide survey.

To test whether results observed at different sites were significantly different, a non-parametric Kruskal-Wallis test was performed. Comparison of bleaching between study sites was performed for each sample event (August 2005, November 2005, and January 2006). Comparison of mortality between study sites was performed for intervals between sampling events and from the beginning of sampling to the end of sampling (August 2005–January 2006).

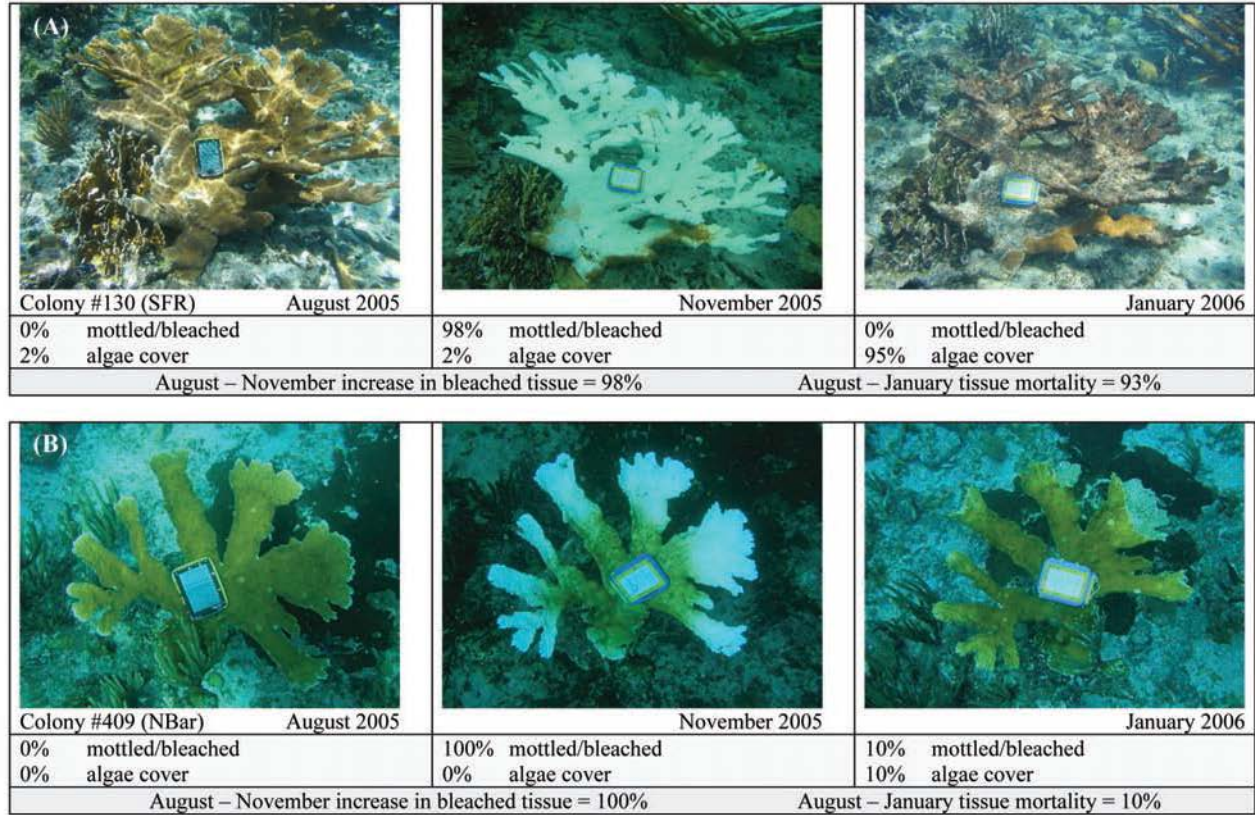


Figure 2. Three photographs were taken of colonies at study sites (August 2005, November 2005, and January 2006). Bleaching estimates were made by averaging the percent of live tissue with a white or mottled appearance among colonies at each site. Similarly, mortality estimates were made by averaging change in live tissue cover for colonies over time. (A) Digital photographs from the South Forereef site (oblique perspective) with associated bleaching and mortality assessments. (B) Digital photographs from the North Bar site (planar perspective) with associated bleaching and mortality assessments. Monument-wide colonies (not shown) were only photographed twice: in November 2005 and February 2006.

Throughout the thermal stress event in 2005 water temperature was measured with temperature loggers (Hobo Water Temp Pro) deployed at 2 m in the backreef and 10 m at the interface of the forereef and the reef shelf, capturing the entire sample period except for 11 November–15 December 2005. Water temperatures collected at the forereef / reef shelf in 2005 were compared to the 16-yr average (1991–2006) water temperature from the same location collected by Ryan RTM2000 (1991–2002) and Hobo Water Temp Pro (2003–2006) data loggers.

RESULTS

WATER TEMPERATURE.—Water temperature loggers at BIRNM showed three periods of heating during the 2005 thermal stress event (Fig. 3A). Initially there was a “pre-bleaching” period when average daily temperatures fluctuated around the bleaching threshold of 29.3 °C (Edmunds, 2004). The backreef water temperature exceeded the bleaching threshold for all but 5 d from 14 June 2005 to 16 July 2005. This pre-bleaching period lasted longer on the forereef by almost 2 wks, but average daily temperatures were below the bleaching threshold for 20 d. Average daily temperatures exceeded the bleaching threshold constantly for 85 d on the backreef and for 73 d on the forereef during the bleaching period from July–October 2005. The “post-bleaching” period began one day apart at the forereef and backreef in the second week of October 2005 and lasted until the end of the month. Post-bleaching temperatures fluctuated similarly around the bleaching threshold for both the forereef and the backreef (12 and 11 d > 29.3 °C, respectively). NOAA’s Coral Reef Watch reported temperatures exceeding 29.5 °C for approximately 12 wks (NOAA Coral Reef Watch, <http://coralreefwatch.noaa.gov/caribbean2005/>, Accessed 6/10/2008), which is consistent with data collected by our loggers. Water temperatures during the 2005 thermal stress event were higher than in any of the previous 14 yrs (Fig. 3B). Furthermore, water temperatures peaked at over 2 °C above the long-term average maximum (31.6 °C recorded on September 29, 2005).

EXTENT OF BLEACHING.—Bleaching peaked at study sites in November 2005. The highest average percent bleaching was recorded at the South Forereef site in November 2005; an average of 79.8%, followed by 64.1% at North Bar, and 45.8% at Underwater Trail (Table 1). Backreef colonies of *A. palmata* (Underwater Trail site) were impacted before colonies at both South Forereef and at North Bar. By August 2005, colonies at Underwater Trail experienced average tissue bleaching of 24.1%, whereas on South Forereef there was 11.2% average tissue bleaching, and no bleaching was observed at the North Bar. A Kruskal-Wallis test confirmed that during the August 2005 sampling event, bleaching at Underwater Trail was significantly higher than the other sites ($H = 6.37$, $P = 0.04$). No significant differences were found in percent bleaching among the sites during the November 2005 and January 2006 sampling events.

Among the 65 monument-wide colonies examined for bleaching in November 2005, 40 colonies (61.5%) showed some bleaching of live tissue. Average tissue bleaching at the monument-wide sites in November 2005 was 40.5% (SE = 4.7%).

MORTALITY.—Although early in the thermal stress event (August 2005–January 2006) mortality at Underwater Trail, the backreef site, was significantly higher than at the other two sites (Kruskal-Wallis: $H = 16.88$, $P < 0.0001$), later in the thermal stress event mortality did not differ significantly among the three sites, ranging from 66.4% at Underwater Trail to 36.4% at North Bar (Table 2). Additionally, the site that

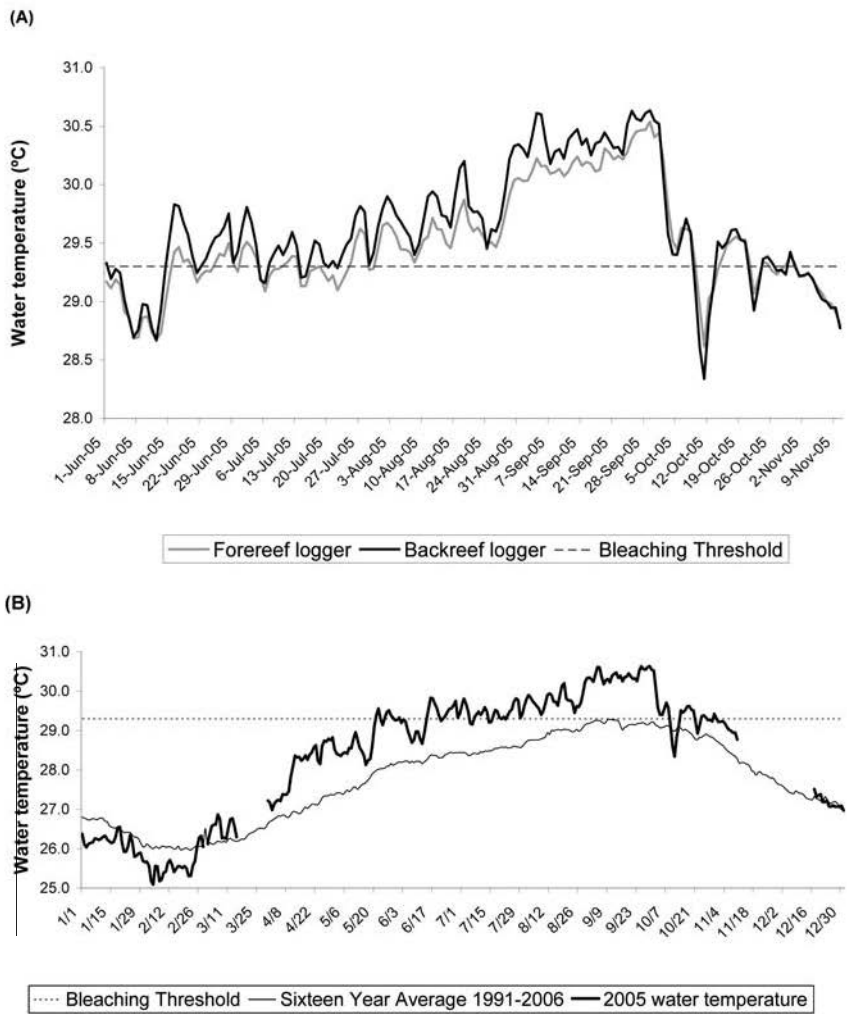


Figure 3. Water temperature measurements made at Buck Island Reef National Monument (some data gaps exist) by temperature loggers installed on (A) the backreef (2 m) and forereef (10 m) during the 2005 thermal stress event; the backreef experienced the higher temperatures longer, and the “bleaching threshold” (29.3 °C) was exceeded for approximately 12 wks; and (B) the forereef (30 m) averaged over 16 yrs (1991–2006); data are plotted for a single calendar year; values for 2005 are contrasted to the average to show the extent that temperatures exceeded normal during the thermal stress event.

experienced the most complete colony mortality was Underwater Trail (64.7%) compared to North Bar (36.4%) and South forereef (18.8%).

Twenty-six of 65 (40%) monument-wide colonies surveyed for mortality experienced some measure of tissue loss during the thermal stress event. Monument-wide colonies surveyed for mortality experienced 20.7% average tissue mortality (SE = 3.7%); but this result only measured mortality that occurred from November 2005–February 2006.

Table 1. Average percent *Acropora palmata* tissue bleaching at the three study sites at Buck Island Reef National Monument, St. Croix, during the 2005 thermal stress event. A Kruskal-Wallis one-way analysis of variance was performed to test differences among sites; * denotes significant results (critical $\chi^2 = 5.991$).

Site	Percent tissue bleached	August 28, 2005	November 1, 2005	January 26, 2006
North Bar	Mean	0.0	64.1	2.0
	Median	0.0	63.0	0.0
	SD	—	36.7	3.6
	SE	—	11.1	1.1
	95% confidence interval	—	22.7	2.2
South Forereef	Mean	11.2	79.8	3.2
	Median	0.0	92.0	0.0
	SD	25.0	34.2	6.6
	SE	6.2	9.1	1.8
	95% confidence interval	12.6	18.6	3.7
Underwater Trail	Mean	24.1	45.8	0.0
	Median	0.0	40.0	0.0
	SD	33.7	32.0	—
	SE	8.2	10.7	—
	95% confidence interval	17.1	22.2	—
Kruskal-Wallis		H = 6.37*	H = 3.67	H = 2.68
		P = 0.04	P = 0.16	P = 0.26

DISCUSSION

Water temperature associated with the 2005 thermal stress event was higher than in the previous 14 yrs and caused mass bleaching of *A. palmata* colonies at BIRNM, an unprecedented event in recorded history. Since extensive monitoring of coral reefs in the Virgin Islands has only occurred for roughly five decades, *A. palmata* may have bleached previously without detection. The 2005 thermal stress event potentially caused more mortality at a faster rate than any previous disease or hurricane at BIRNM, including the white-band disease outbreak (Rogers et al., 1982; Gladfelter, 1982) and Hurricane Hugo (Hubbard et al., 1991). Bleaching in 2005 affected coral colonies in all benthic zones rapidly; whereas white-band disease progressed gradually and hurricanes left deeper colonies intact throughout BIRNM.

Acropora palmata colonies exhibited significant inter-zone variability (bleaching and mortality) during the 2005 thermal stress event, which may be explained by physical and hydrodynamic characteristics specific to distinct benthic zones. In the backreef zone, water temperature was slightly higher for longer than in the other benthic zones. *Acropora palmata* colonies in this zone (Underwater Trail) bleached more quickly and experienced more coral tissue mortality than in other benthic zones. It is likely that decreased water flow and sea surface disturbance in the backreef zone exacerbated thermal stress and caused the pronounced response observed. High water flow over coral surfaces has been positively correlated with resistance and resilience to thermal stress (Nakamura and van Woesik, 2001). Additionally, colonies at sites with more water flow would have a better chance to supplement photosynthesis-derived energy with heterotrophic feeding strategies in the absence of zooxanthellae (Heidelberg et al., 1997). Calmer sea surface water conditions in backreef zones allow light to penetrate deeper in the water column, which can produce more marked

Table 2. Average percent *Acropora palmata* tissue mortality at the three study sites at Buck Island Reef National Monument, St. Croix, during the 2005 thermal stress event. A Kruskal-Wallis one-way analysis of variance was performed to test differences among sites; * denotes significant results (critical $\chi^2 = 5.991$).

Site	Percent tissue mortality	August 2005– November 2005	August 2005– January 2006
North Bar	Mean	9.1	36.4
	Median	0.0	10.0
	SD	19.3	41.4
	SE	5.8	12.5
	95% confidence interval	12.0	25.7
South Forereef	Mean	14.3	58.1
	Median	0.0	77.0
	SD	30.9	39.0
	SE	7.7	9.8
	95% confidence interval	15.6	19.8
Underwater Trail	Mean	57.2	66.4
	Median	60.0	85.0
	SD	39.4	36.0
	SE	9.6	8.7
	95% confidence interval	19.9	17.7
Kruskal-Wallis		H = 16.88*	H = 5.17
		P < 0.0001	P = 0.08

bleaching response in corals (Brown, 1997). Because the *A. palmata* population in the backreef appears to be less resistant to thermal stress than colonies elsewhere in BIRNM; these colonies could serve as indicators of species-specific mass bleaching. Understanding how benthic zones can influence coral response to thermal stress events would allow managers to trigger specific monitoring protocols to collect the most complete and robust data regarding *A. palmata* mass bleaching.

The monument-wide survey was intended to validate the results at the three study sites and allow inferences to be made across the whole monument, but aspects of the study design were flawed. Because colonies included in the monument-wide survey were mostly representative of the reef shelf (other benthic zones were undersampled), comparisons should include the North Bar site, but exclude the South Forereef and Underwater Trail sites. The monument-wide survey only sampled corals after the water temperatures returned below the bleaching threshold, capturing coral response to only part of the thermal stress event. Despite variability and problems with comparisons associated with the study design, results indicated that the reef shelf study site, North Bar, was a representative subsample of this benthic zone throughout the monument. If more sites were included in the other two benthic zones a more complete inference could be pursued.

Aspects of the sampling design (e.g., planar photography and coral disease) may have overestimated bleaching and mortality. Planar photography only captures upward-facing coral surfaces which are exposed to direct sunlight. Recent evidence (Brown et al., 2000; West and Salm, 2003) has shown that shaded portions of *A. palmata* colonies are less likely to bleach. Differentiating between mortality attributable to disease vs that attributable to thermal stress can be problematic because both cause zooxanthellae to be expelled from coral tissue, and bleached tissue may

be simultaneously stressed by both thermal stress and disease. Richie (2006) showed that *A. palmata* loses its ability to fight pathogens during and immediately following a thermal stress event, and Muller et al. (2008) documented a positive relationship between the 2005 thermal stress event and disease in *A. palmata*. Even though these limitations may have skewed the data, the sampling protocol was consistent which preserved the differences observed within study areas.

Acropora palmata was listed as a Threatened species in 2006 because a variety of natural and anthropogenic impacts have severely depleted populations across the Caribbean region. Climate change has made thermal stress events more frequent and intense, ending preconceptions about resistance of *A. palmata* to thermal stress. Our assessment of *A. palmata* has revealed how benthic zones can shape coral bleaching and mortality patterns in response to a thermal stress event. Such information is valuable for resource managers who wish to use *A. palmata* colonies in the backreef zone as indicators of thermal stress events that can cause mass *A. palmata* bleaching. Perhaps more importantly, this information informs conservation decisions relevant to marine protected area (MPAs) design and management. West and Salm (2003) recommend that MPA design should be based on resistance and resilience attributes of coral reefs. Backreef *A. palmata* coral colonies do not appear to be resistant to thermal stress, making that benthic zone a poor choice for inclusion in MPAs that focus on protecting *A. palmata*.

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LITERATURE CITED

- Barton, A. D. and K. S. Casey. 2005. Climatological context for large-scale coral bleaching. *Coral Reefs* 24: 536–554.
- Brown, B. E. 1997. Coral bleaching: causes and consequences. *Coral Reefs* 16: 129–138.
- _____, R. P. Dunne, M. S. Goodson, and A. E. Douglas. 2000. Bleaching patterns in reef corals. *Nature* 404: 142–143.
- Edmunds, P. J. 2004. Coral recruitment tracks rising seawater temperature on a Caribbean reef. *Mar. Ecol. Prog. Ser.* 269: 111–119.
- Ghiold, J. and S. H. Smith. 1990. Bleaching and recovery of deep-water, reef-dwelling invertebrates in the Cayman Islands, BWI. *Caribb. J. Sci.* 26: 52–61.
- Gladfelter, W. B. 1982. White-band disease in *Acropora palmata*: Implications for the structure and growth of shallow reefs. *Bull. Mar. Sci.* 32: 639–643.
- Gleeson, M. W. and A. E. Strong. 1995. Applying MCSST to coral reef bleaching. *Adv. Space Res.* 16: 151–154.
- Glynn, P. W. 1993. Coral reef bleaching: ecological perspectives. *Coral Reefs* 12: 1–17.
- Goreau, T. J. and R. M. Hayes. 1994. Coral bleaching and ocean 'hot spots'. *Ambio* 23: 176–180.

- Heidelberg, K. B., K. P. Sebens, and J. E. Purcell. 1997. Effects of prey escape behavior and water flow on prey capture by the Scleractinian Coral, *Meandrina meandrites*. Proc. 8th Int. Coral Reef Symp. 2: 1081–1086.
- Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar. Freshwat. Res. 50: 839–866.
- Hubbard, D. K., K. M. Parsons, J. C. Bythell, and N. D. Walker. 1991. The effects of Hurricane Hugo on the reefs and associated environments of St. Croix, U.S. Virgin Islands—a preliminary assessment. J. Coast. Res. 8: 33–48.
- Jokiel, P. L. and E. K. Brown. 2004. Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii. Global Change Biol. 10: 1627–1641.
- _____ and S. L. Coles. 1990. Response of Hawaiian and other Indo Pacific reef corals to elevated temperatures. Coral Reefs 8: 155–162.
- Kinzie III, R. A., M. Takayama, S. R. Santos, and M. A. Coffroth. 2001. The adaptive bleaching hypothesis: Experimental tests of critical assumptions. Biol. Bull. 200: 51–58.
- Lesser, M. P. 1997. Oxidative stress causes coral bleaching during exposure to elevated temperatures. Coral Reefs 16: 187–192.
- _____. 2004. Experimental biology of coral reef ecosystems. J. Exp. Biol. 300: 217–252.
- Liu, G., A. E. Strong, and W. Skirving. 2003. Remote sensing of sea surface temperatures during 2002 Barrier Reef coral bleaching. EOS 84: 137–144.
- Mayor, P. A., C. S. Rogers, and Z. M. Hillis-Starr. 2006. Distribution and abundance of elkhorn coral, *Acropora palmata*, and prevalence of white-band disease at Buck Island Reef National Monument, St. Croix, US Virgin Islands. Coral Reefs 25: 239–242.
- Muller, E. M., C. S. Rogers, A. S. Spitzack, and R. van Woesik. 2008. Bleaching increases likelihood of disease on *Acropora palmata* (Lamarck) in Hawksnest Bay, St John, US Virgin Islands. Coral Reefs 27: 191.
- Mumby, P. J., J. R. M. Chisholm, A. J. Edwards, S. Andréfouët, and J. Jaubert. 2001. Cloudy weather may have saved Society Islands coral reefs during the 1998 ENSO event. Mar. Ecol. Prog. Ser. 222: 209–216.
- Nakamura, T. and R. van Woesik. 2001. Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998-bleaching event. Mar. Ecol. Prog. Ser. 212: 301–304.
- _____, H. Yamasaki, and R. van Woesik. 2003. Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata*. Mar. Ecol. Prog. Ser. 256: 287–292.
- National Marine Fisheries Service. 2006. Endangered and threatened species: final listing determinations for elkhorn and staghorn Coral. Federal Register 71: 26852–26861.
- Ritchie, K. B. 2006. Regulation of microbial populations by coral surface mucus and mucus-associated bacteria. Mar. Ecol. Prog. Ser. 322: 1–14.
- Rogers, C. S., T. H. Suchanek, and F. A. Pecora. 1982. Effects of Hurricanes Davis and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, USVI. Bull. Mar. Sci. 32: 532–548.
- 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.
- Strong, A. E., G. Liu, J. Meyer, J. C. Hendee, and D. Sasko. 2004. Coral Reef Watch 2002. Bull. Mar. Sci. 75: 259–268.
- Warner, M. E., W. K. Fitt, and G. W. Schmidt. 1996. The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospice from four different species of reef corals: a novel approach. Plant Cell Environ. 19: 291–299.
- West, J. M. and R. V. Salm. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conserv. Biol. 17: 956–967.

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