SPATIAL AND TEMPORAL PATTERNS OF CORAL BLEACHING AROUND BUCK ISLAND REEF NATIONAL MONUMENT, ST. CROIX, U.S. VIRGIN ISLANDS

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ABSTRACT

Since 2001, biannual fish and habitat monitoring has been conducted for the shallow (> 30 m), colonized pavement and gorgonian dominated Buck Island Reef National Monument (BIRNM) St. Croix, USVI and adjacent waters. During October, 2005, widespread coral bleaching was observed within the ~50 km^2 study area that was preceded by 10 wks of higher than average water temperatures (28.9–30.1 °C). Random transects (100 m^2) were conducted on linear reefs, patch reefs, bedrock, pavement, and scattered coral/rock habitats during October 2005, and April and October 2006, and species specific bleaching patterns were documented. During October 2005 approximately 51% of live coral cover was bleached. Nineteen of 23 coral species within 16 genera and two hydrocoral species exhibited signs of bleaching. Coral cover for *Montastraea annularis* and species of the genus *Agaricia* were the most affected, while other species exhibited variability in their susceptibility to bleaching. Bleaching was evident at all depths (1.5–28 m), was negatively correlated with depth, and positively correlated with habitat complexity. Bleaching was less prevalent at all depths and habitat types upon subsequent monitoring during April (15%) and October (3%) 2006. Four species and one genus did not exhibit signs of bleaching throughout the study period (*Dendrogyra cylindrus*, *Eusmilia fastigata*, *Mussa angulosa*, *Mycetophyllia aliciae*, *Scolymia* spp.).

Over the past two decades coral reef ecosystems in the Caribbean (Rogers and Beets, 2001; Gardner et al., 2003) and world-wide have experienced tremendous degradation attributed primarily to anthropogenic and environmental factors (Pandolfi et al., 2003; Wilkinson, 2004; Bruno and Selig, 2007). Temperature is a crucial factor that affects the coral-zooxanthellae symbiosis, and increases in temperatures of 0.5–2 °C above average summer maxima can stress coral colonies and result in bleaching, i.e., the loss of photosynthetic pigments or expulsion of zooxanthellae from coral tissue (Glynn and D'Crox, 1990; Fitt et al., 2001; Podesta and Glynn, 2001). Prolonged bleaching adversely affects the productivity of coral colonies, which can result in death and permanent loss of living coral, and ultimately may have dire consequences for coral reef ecosystems and economies they support (Glynn, 1991, 1996; Hoegh-Guldeberg, 1999; Marshall and Shuttenberg, 2006).

The frequency and intensity of bleaching episodes in coral reef ecosystems has increased dramatically worldwide (Glynn, 1991; Buddemeier and Fautin, 1993; Wilkinson, 2004). In the Caribbean, mass bleaching events were documented in 1987, 1990, 1995, and 1998, each with increasing severity. In 1998, coral bleaching occurred globally, and extensive bleaching-induced mortality (20%–99%) was reported in the Indian and Pacific Oceans (Goreau et al., 2000; Goldberg and Wilkinson, 2004). In the Caribbean Sea, approximiately 60%–80% of coral colonies were bleached during 1998 (Goreau et al., 2000), but estimates of bleaching-induced mortality were low (< 5% of colonies, Goldberg and Wilkinson, 2004).

During June to October 2005, a significant coral bleaching event took place ranging throughout the Caribbean and the southeastern U.S. (Wilkinson and Souter, 2008). The bleaching event was linked to anomalously warm water that was centered on the northern Antilles near the Virgin Islands and Puerto Rico. Satellite sea surface temperature data indicated that the thermal stress associated with this warm water was the highest experienced during the previous 20 yrs (NOAA Coral Reef Watch, http://coralreefwatch.noaa.gov/caribbean2005/, Accessed 6/27/2007). Data on species specific occurrence and extent of coral bleaching were recorded during the biannual monitoring of Buck Island Reef National Monument (BIRNM) in St. Croix, U.S. Virgin Islands, conducted by scientists from NOAA's National Center for Coastal Ocean Science's Biogeography Branch (BB) and the National Park Service's BIRNM. Greater intensity of sea surface temperature and other environmental factors are likely to impact marine biodiversity (Goreau et al., 2000; Wilkinson, 2004), and resource managers with the responsibility for managing the health of coral reef ecosystems require spatially explicit information on the impacts of coral bleaching to inform the public and assess ramifications throughout the ecosystem.

This study quantifies spatial patterns of coral bleaching observed along the northeastern shore of St. Croix (henceforth termed the study region) comprised of habitats within and adjacent to BIRNM and the northern portion of the East End Marine Park (EEMP) in the U.S. Virgin Islands during October 2005 through October 2006 (Fig. 1). Relatively little information exists regarding species-specific bleaching with-

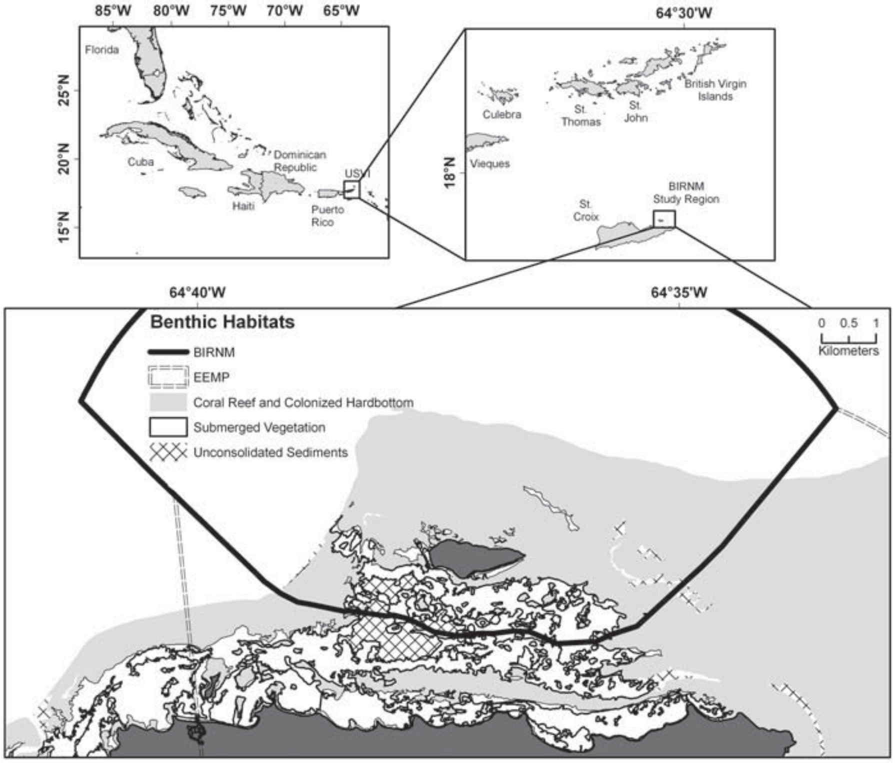

Figure 1. Map of study area around Buck Island Reef National Monument, St. Croix, USVI. BIRNM = Buck Island Reef National Monument, EEMP = East End Marine Park.

in a broad region, spanning different depths and habitat types. Specific objectives were to (1) describe the extent and spatial patterns of coral bleaching before, during, and after the 2005 bleaching event; and (2) describe differences in the occurrence of bleaching experienced by different coral species and possible correlations with depth and/or habitat complexity.

Methods

In situ water temperature data provided by BIRNM were used to document local conditions before, during, and after the 2005 bleaching event. Daily mean water temperature (°C) was obtained for the period January 1999 through December 2006 from a single data logger that was located at a depth of 10 m on the fore-reef at BIRNM. Mean monthly temperatures for summer and fall months (June–October) were compared using Student's *t*-test (Sokal and Rohlf, 1995). Temporal patterns of bleaching were examined from satellite imagery in relation to water temperatures exceeding the bleaching threshold (29 °C), defined by Goreau et al. (1993) as the annual summer temperature maxima plus 1 °C during 1985–1993.

Underwater visual surveys were conducted biannually by a team of trained divers within the 49.8 km^2 study region (Fig. 1). The area is comprised of a complex mosaic of habitat types, including linear reefs and other hard substrate (colonized pavement, reef rubble, patch reefs, scattered coral in sand), seagrasses, and soft sediments with varying depth (3–30 m) and rugosity. Data on live unbleached and bleached coral were collected only on hard substrates within the study area.

Data on benthic composition were recorded along randomly selected 25 × 4 m belt transects (100 m^2). These transect surveys were part of a larger project, in which 2790 surveys were conducted between 2001 and 2006 to characterize and monitor fishes and benthic composition in coral reef ecosystems in southwestern Puerto Rico and the Virgin Islands (http://ccma.nos.noaa.gov/ecosystems/coralreef/reef_fish.html). Survey sites were selected using a stratified random sampling design incorporating two strata (hard and soft benthic habitat types) derived from NOAA's nearshore benthic habitat maps (Kendall et al., 2001). These maps define the offshore extent of the study area, which corresponds approximately to the 33-m isobath. Hard strata were situated within five zones: intertidal, lagoon, backreef, forereef, and bank shelf (Table 1) and encompassed several hard strata habitat types including, linear reef, colonized pavement, colonized bedrock, patch reef, scattered coral in sand, and reef rubble. The sample design was based on fish populations and not coral communities, thus coral bleaching data were pooled and analyzed according to hard substrate and not compared by zone or habitat type.

Data on live coral cover, bleached coral cover, water depth (m), and other benthic biota were collected from 276 benthic surveys completed between October 2005 and October 2006. Coral species were identified to the lowest possible taxon. Species identified as *Montastraea*

Table 1. Area (km^2) of hard bottom habitat types and number of sites surveyed at Buck Island Reef National Monument during October 2005–October 2006.

	Area (km^2)	October 2005	April 2006	October 2006	Total samples
Colonized bedrock	0.62	0	1	6	7
Colonized pavement	22.46	68	59	60	187
Linear reef	1.19	4	2	3	9
Patch reef	4.11	1	1	2	4
Reef rubble	0.12	6	5	3	14
Scattered coral in sand	3.24	14	18	19	51
Uncolonized bedrock	0.01	0	0	0	0
Uncolonized pavement	0.02	1	3	0	4
Total	31.77	94	89	93	276

annularis refer to the *M. annularis* complex. During each survey, the percent areal cover occupied by bleached and unbleached coral colonies was estimated to the nearest 1 cm^2 or 0.1% in a two-dimensional plane perpendicular to the observer's line of vision within a 1 m^2 quadrat divided into 100 smaller (10 × 10 cm) squares. The quadrat was placed at five random locations resulting in a sample within every 5 m interval along each transect. Colonies were considered entirely bleached if they contained white, blotchy/mottled, or pale tissue. Normal coral colonies were those that were not bleached, diseased, or dead. Means and standard errors of percent cover of live (bleached and unbleached combined), unbleached coral, and bleached coral were calculated for each site. Sites were used as independent sample units and were considered replicates within survey missions. Multiple quadrat measurements (percent cover and depth) within each transect were averaged using the equation: $\Sigma(Q_{i-n})/n$, where Q_i = quadrat i, and n = total number of quadrats. Average site values were then used to calculate means and standard errors of measured variables per 100 m^2 by survey mission. Standard errors of the mean represent variability among sites rather than variability among quadrats within a site. Spearman's correlation coefficients were used to examine the relationship between the proportion of total and species-specific bleached coral cover with depth and habitat complexity. Only species with sighting frequency greater than 10 were included. Statistically significant ($\alpha < 0.05$) correlations > 0.60 (positive and negative) were considered strong, 0.40–0.59 were considered moderate, and 0.10–0.39 were considered weak. Correlation coefficients < 0.10 indicated no correlation observed. The proportion of coral cover that was bleached was determined with the equation % bleached = bleached cover ⁄ bleached + unbleached cover. Using ArcMap 9.3 spatial analyst, habitat complexity was calculated by interpolating (inverse distance weighting) mean complexity values using the 6 m chain method from 1400 surveys conducted since 2001.

Spatial patterns of bleached corals within and among sampling missions were mapped using a GIS. The proportion of live coral that was normal or bleached was mapped for each survey to examine spatial patterns.

Results

Water Temperature.—Maximum water temperatures were consistently higher during the study period when compared with the 8 yr mean (Fig. 2). During 2005, mean water temperature was significantly greater (*t*-test: $P < 0.0001$) for each summer/fall month (June–October) than all other years. Water temperatures during 2005 were above average for 249 d and were consistently above average from March-November (226 d). Water temperature surpassed the bleaching threshold (29.5 °C) on 91 d during 2005 and was consistently high from early August through mid-October (70 d).

Water temperatures during June–October 2006 were significantly lower (*t*-test: $P < 0.0001$) than observed in 2005, but were significantly greater (*t*-test: $P < 0.0001$) than observations during 1999–2004. Water temperatures were well above the mean from June through August and exceeded the bleaching threshold during 29 d between the end of August and the beginning of October.

Study Area/General Patterns.—Approximately 64% of the study area (31.77 km^2) was classified as hard substrate, with the majority being colonized pavement (Table 1). Benthic samples were not evenly distributed at all zone/habitat type combinations. As such, 67% of the samples were conducted on colonized pavement (Table 1) while limited surveys were conducted on linear reef (3%) and patch reefs (1.4%). Throughout the study period (October 2005–October 2006), 28 scleractinian coral species within 20 genera and two species of the hydrocoral (*Millepora*) were observed within 276 transects (Table 2). Total percent coral cover was low during all sampling

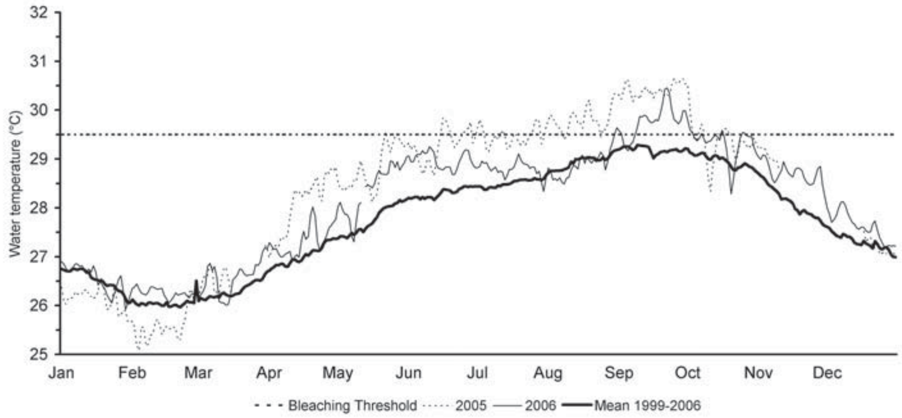

Figure 2. In-situ water temperature observations from the forereef (10 m) of Buck Island, St. Croix, USVI, 2005–2006. Dark line is mean water temperature from 1999–2006; horizontal dashed line is bleaching threshold (29.5 °C). Bleaching threshold was calculated using data from 1985–1993.

months: 3.7% per 100 m^2 in October 2005, 4.1% per 100 m^2 in April 2006, and 2.81% per 100 m^2 in October 2006.

Bleaching Event.—Bleaching was observed at 86 of 94 (91%) survey sites during October 2005 (Table 2). Colonies that were bleached were completely white, with a few being mottled or pale. Overall, 51% of the total coral cover within surveys was bleached and species-specific bleaching proportions ranged from 0–100% (Table 2). Coral species frequency of occurrence was variable throughout the study area (Table 2). The most frequently observed species (65%–75%) were *Porites asteroides*, *Diploria strigosa*, *Agaricia* spp., *Siderastrea radians*, while *Porites porites*, *Montastraea cavernosa*, *M. annularis*, and *Siderastrea siderea* were common (35%–50%). The remaining species were observed in less than a third of the surveys. Site bleaching frequency (the number of surveys where bleaching was observed/total surveys) ranged from 0–100% where 19 of 33 taxa (including *Millepora*) exhibited frequencies > 50%. Five taxa showed no signs of bleaching: *Acropora cervicornis*, *Eusmilia fastigata*, *Dendrogyra cylindrus*, *Madracis decactis*, and *Scolymia* spp., although their overall frequency of occurrence was low. Species that exhibited 100% bleaching in surveys in which they occurred were also low in frequency of occurrence. Among the species that exhibited bleaching, proportional site bleaching frequency was highly variable. For example, both *Agaricia* spp. and *S. radians* exhibited bleaching at 60 of the 94 surveys (64%) and exhibited 96% and 35% bleaching, respectively, at those stations.

Similarly, the proportion of mean bleached coral cover per total mean cover for each species was highly variable (Table 2). Nearly all *Agaricia* spp. cover was bleached while only 42% of *P. asteroides* was bleached. Species that exhibited > 75% bleached cover included *Diploria labyrinthiformis*, *Mycetophellia ferox*, *Isophyllia rigida*, *Mycetophyllia* spp., *M. annularis*, *Agaricia* spp., *P. porites*, *Millepora complanata*, and *Isophyllia sinuosa*.

The distribution of survey sites and the percentage of total bleached coral cover (Fig. 3) were extensive throughout the study area with little obvious spatial pattern. Overall, the proportion of bleached coral cover was not correlated with depth (P = 0.99) while a weak positive correlation (P = 0.0008) with habitat complexity was observed (Table 3). The proportion of species bleached/not bleached was positive but

Table 2. Frequency of occurrence, total percent coral cover, and percent bleached coral cover at randomly selected sites at Buck Island Reef National Monument during October 2005–October 2006.

	October 05	April 06	October 06
	Total site frequency (bleach frequency)		
Acropora palmata (Lamarck, 1816)	9 (7)	3 (0)	4 (0)
Millepora complanata Lamarck, 1816	9 (6)	1 (1)	1 (0)
Porites asteroides Lamarck, 1816	70 (51)	65 (5)	64 (5)
Isophyllia sinuosa (Ellis and Solander, 1786)	7 (6)	4 (1)	
Madracis spp.	7 (3)		5 (0)
Diploria strigosa (Dana, 1848)	64 (46)	53 (26)	61 (1)
Agaricia spp.	60 (58)	20 (6)	22 (2)
Siderastrea radians (Pallas, 1766)	60 (21)	18 (4)	51 (2)
Diploria labyrinthiformis (Linnaeus, 1758)	6 (6)	3 (2)	1 (0)
Favia fragum (Esper, 1797)	6 (4)	10 (0)	4 (0)
Solenastrea spp.	5 (2)	4 (2)	
Manicina areolata (Linnaeus, 1758)	5 (2)	6 (0)	1 (0)
Porites porites (Pallas, 1766)	45 (39)	31 (1)	29 (0)
Millepora alcicornis (Linnaeus, 1758)	45 (32)	14 (0)	41 (1)
Montastraea cavernosa (Linnaeus, 1766)	42 (12)	30 (2)	41 (4)
Siderastrea siderea (Ellis and Solander, 1786)	41 (14)	48 (12)	32 (3)
Montastraea annularis (Ellis and Solander, 1786)	34 (28)	32 (15)	24 (4)
Stephanocoenia intersepta (Lamarck, 1816)	32 (6)	18 (1)	37 (0)
Diploria clivosa (Ellis and Solander, 1786)	28 (13)	12 (0)	4 (0)
Meandrina meandrites (Linnaeus, 1767)	26 (1)	19 (2)	24 (0)
Dichocoenia stokesii Milne-Edwards and Haime, 1848	21 (4)	13 (3)	25 (0)
Siderastrea spp.	2 (1)		
Acropora cervicornis (Lamarck, 1816)	2 (0)	3 (1)	1 (0)
Eusmilia fastigata (Pallas, 1766)	2 (0)	3 (0)	
Millepora spp.	18 (10)	38 (0)	21 (0)
Mycetophyllia spp.	15 (13)		3 (0)
Colpophyllia natans (Houttyn, 1772)	10 (5)	7 (0)	8 (0)
Mycetophyllia ferox Wells, 1973	1 (1)		
Isophyllastrea rigida (Dana, 1848)	1 (1)		
Dendrogyra cylindrus Ehrenberg, 1834	1 (0)	1 (0)	
Porites spp.	1 (0)	2 (0)	
Madracis decactis (Lyman, 1859)	1 (0)	3 (0)	5 (1)
Scolymia spp.	1 (0)	3 (0)	5 (0)
Diploria spp.		2 (0)	
Madracis mirabilis (Lyman, 1859)			1 (0)
Mussa angulosa (Pallas, 1766)		1 (0)	2 (0)
Mycetophyllia aliciae Wells, 1973		2 (0)	
Total	94 (86)	89 (48)	93 (13)

Table 2. Continued.

	October 05		April 06		October 06	
	% total coral cover/100 m^2 (SE)					
Acropora palmata (Lamarck, 1816)	0.499	(0.212)	0.064	(0.063)	0.016	(0.105)
Millepora complanata Lamarck, 1816	0.040	(0.024)	0.001	(0.001)	0.002	(0.021)
Porites asteroides Lamarck, 1816	0.574	(0.094)	0.559	(0.082)	0.391	(0.525)
Isophyllia sinuosa (Ellis and Solander, 1786)	0.008	(0.003)	0.008	(0.004)		
Madracis spp.	0.009	(0.005)			0.003	(0.015)
Diploria strigosa (Dana, 1848)	0.594	(0.117)	0.614	(0.141)	0.813	(2.956)
Agaricia spp.	0.215	(0.040)	0.033	(0.009)	0.017	(0.059)
Siderastrea radians (Pallas, 1766)	0.195	(0.034)	0.035	(0.014)	0.132	(0.248)
Diploria labyrinthiformis (Linnaeus, 1758)	0.026	(0.016)	0.029	(0.019)	0.004	(0.034)
Favia fragum (Esper, 1797)	0.005	(0.003)	0.009	(0.003)	0.002	(0.009)
Solenastrea spp.	0.007	(0.004)	0.004	(0.003)		
Manicina areolata (Linnaeus, 1758)	0.002	(0.001)	0.006	(0.003)	0.002	(0.016)
Porites porites (Pallas, 1766)	0.123	(0.030)	0.063	(0.014)	0.067	(0.170)
Millepora alcicornis (Linnaeus, 1758)	0.149	(0.033)	0.046	(0.014)	0.144	(0.368)
Montastraea cavernosa (Linnaeus, 1766)	0.213	(0.042)	0.361	(0.110)	0.321	(0.649)
Siderastrea siderea (Ellis and Solander, 1786)	0.172	(0.067)	0.385	(0.084)	0.129	(0.406)
Montastraea annularis (Ellis and Solander, 1786)	0.422	(0.137)	0.811	(0.243)	0.356	(1.063)
Stephanocoenia intersepta (Lamarck, 1816)	0.041	(0.009)	0.050	(0.019)	0.047	(0.102)
Diploria clivosa (Ellis and Solander, 1786)	0.154	(0.034)	0.250	(0.119)	0.026	(0.208)
Meandrina meandrites (Linnaeus, 1767)	0.065	(0.020)	0.033	(0.013)	0.055	(0.170)
Dichocoenia stokesii Milne-Edwards and Haime, 1848	0.025	(0.008)	0.032	(0.001)	0.042	(0.117)
Siderastrea spp.	0.061	(0.055)				
Acropora cervicornis (Lamarck, 1816)	0.007	(0.006)	0.230	(0.227)	0.000	(0.004)
Eusmilia fastigata (Pallas, 1766)	< 0.001	(< 0.001)	0.006	(0.005)		
Millepora spp.	0.038	(0.001)	0.117	(0.037)	0.049	(0.207)
Mycetophyllia spp.	0.014	(0.006)			0.004	(0.026)
Colpophyllia natans (Houttyn, 1772)	0.031	(0.015)	0.062	(0.034)	0.176	(1.149)
Mycetophyllia ferox Wells, 1973	0.005	(0.005)				
Isophyllastrea rigida (Dana, 1848)	0.001	(0.001)				
Dendrogyra cylindrus Ehrenberg, 1834	0.004	(0.004)	0.003	(0.003)		
Porites spp.	0.004	(0.004)	0.027	(0.023)		
Madracis decactis (Lyman, 1859)	0.001	(0.001)	0.006	(0.005)	0.006	(0.032)
Scolymia spp.	0.001	(0.001)	0.002	(0.001)	0.002	(0.011)
Diploria spp.			0.234	(0.223)		
Madracis mirabilis (Lyman, 1859)					< 0.001	(0.002)
Mussa angulosa (Pallas, 1766)			0.000	(0.000)	0.001	(0.011)
Mycetophyllia aliciae Wells, 1973			0.003	(0.003)		
Total	3.705	(0.437)	4.085	(0.637)	2.808	(0.471)

Table 2. Continued.

	October 05		April 06		October 06	
	% bleached coral cover/100 m² (SE)					
Acropora palmata (Lamarck, 1816)	0.084	(0.046)	0	(0)	0	(0)
Millepora complanata Lamarck, 1816	0.031	(0.023)	0.001	(0.001)	0	(0)
Porites asteroides Lamarck, 1816	0.244	(0.056)	0.008	(0.004)	0.007	(0.035)
Isophyllia sinuosa (Ellis and Solander, 1786)	0.006	(0.002)	0.001	(0.001)		
Madracis spp.	0.001	(0.001)			0	(0)
Diploria strigosa (Dana, 1848)	0.343	(0.090)	0.151	(0.038)	0.001	(0.011)
Agaricia spp.	0.198	(0.040)	0.008	(0.005)	0.002	(0.015)
Siderastrea radians (Pallas, 1766)	0.052	(0.017)	0.007	(0.005)	0.010	(0.085)
Diploria labyrinthiformis (Linnaeus, 1758)	0.026	(0.016)	0.016	(0.014)	0	(0)
Favia fragum (Esper, 1797)	0.002	(0.001)	0	(0)	0	(0)
Solenastrea spp.	0.004	(0.004)	0.002	(0.001)		
Manicina areolata (Linnaeus, 1758)	< 0.001	(< 0.001)	0	(0)	0	(0)
Porites porites (Pallas, 1766)	0.097	(0.025)	< 0.001	(< 0.001)	0	(0)
Millepora alcicornis (Linnaeus, 1758)	0.085	(0.022)	0	(0)	< 0.001	(0.00212)
Montastraea cavernosa (Linnaeus, 1766)	0.062	(0.022)	0.002	(0.002)	0.051	(0.311)
Siderastrea siderea (Ellis and Solander, 1786)	0.089	(0.062)	0.067	(0.034)	0.004	(0.023)
Montastraea annularis (Ellis and Solander, 1786)	0.396	(0.137)	0.370	(0.176)	0.012	(0.086)
Stephanocoenia intersepta (Lamarck, 1816)	0.006	(0.003)	0.002	(0.002)	0	(0)
Diploria clivosa (Ellis and Solander, 1786)	0.046	(0.017)	0	(0)	0	(0)
Meandrina meandrites (Linnaeus, 1767)	0.001	(0.001)	0.001	(0.001)	0	(0)
Dichocoenia stokesii Milne-Edwards and Haime, 1848	0.001	(0.001)	0.005	(0.005)	0	(0)
Siderastrea spp.	0.053	(0.053)				
Acropora cervicornis (Lamarck, 1816)	0	(0)	< 0.001	(< 0.001)	0	(0)
Eusmilia fastigata (Pallas, 1766)	0	(0)	0	(0)		
Millepora spp.	0.001	(0.003)	0	(0)	0	(0)
Mycetophyllia spp.	0.013	(0.006)			0	(0)
Colpophyllia natans (Houttyn, 1772)	0.016	(0.012)	0	(0)	0	(0)
Mycetophyllia ferox Wells, 1973	0.005	(0.005)				
Isophyllastrea rigida (Dana, 1848)	0.001	(0.001)				
Dendrogyra cylindrus Ehrenberg, 1834	0	(0)	0	(0)		
Porites spp.	0	(0)	0	(0)		
Madracis decactis (Lyman, 1859)	0	(0)	0	(0)	< 0.001	(0.00424)
Scolymia spp.	0	(0)	0	(0)	0	(0)
Diploria spp.			0	(0)		
Madracis mirabilis (Lyman, 1859)					0	(0)
Mussa angulosa (Pallas, 1766)			0	(0)	0	(0)
Mycetophyllia aliciae Wells, 1973			0	(0)		
Total	1.873	(0.265)	0.641	(0.214)	0.086	(0.036)

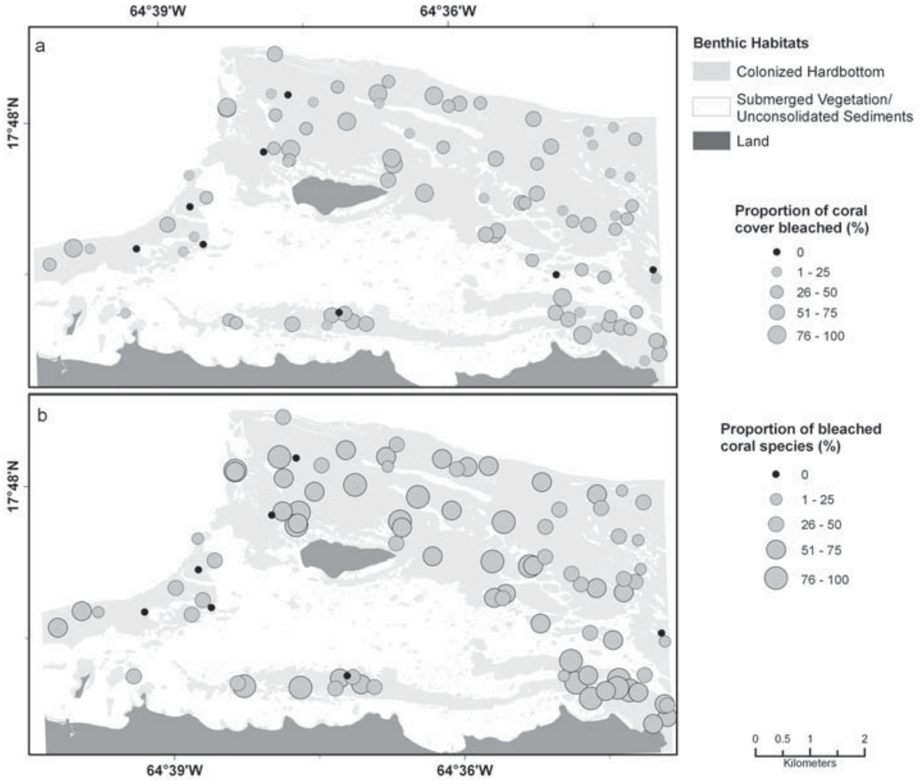

Figure 3. Spatial distribution and proportion of (A) bleached coral cover and (B) bleached species at individual monitoring stations at Buck Island Reef National Monument, October 2005.

weakly correlated with habitat complexity (P = 0.0046), while correlation with depth was weak and negative (P = 0.0003). Only one species, *P. asteroides*, exhibited a statistically significant (P = 0.018) correlation (negative and weak) with depth and none was significantly correlated with habitat complexity (Table 3).

Post Bleaching Periods.—Bleaching was observed less frequently (48 of 89 [53%] of surveys) throughout the study area during April 2006 (Fig. 4). Sixteen species (including *Millepora* spp.) exhibited bleaching characteristics (Table 2) where colonies were mottled or pale with the exception of *Agaricia* spp., which were completely bleached. Fifteen species exhibited no bleaching effects (Table 2). *Acropora cervicornis* was the only species exhibiting bleaching during April that was not bleached during October 2005. Observed mean coral cover was 4.08% per 100 m^2 and 15% of cover exhibited signs of bleaching.

Bleaching was rare in the southern and western portion of the study area (Fig. 4) and the greatest proportions of bleached cover and species were located north and east of Buck Island.

Montastraea annularis and *D. strigosa* were the most commonly observed species exhibiting bleaching and accounted for 81% of the total observed bleached cover. Only two species exhibited bleaching proportions > 50% (*M. complanata* and *D. labyrinthiformis*) during April 2006, but these were infrequently observed and percent cover was limited (Table 2).

Table 3. Spearman's correlation coefficients r for the percentage of bleached coral cover, by taxa and total, with depth and habitat complexity. Taxa were limited to sighting frequency > 10. Bleaching in October 2006 was insufficient to perform correlations. * indicates statistical significance at $\alpha = 0.05$.

	October 2005		April 2006	
	Depth r	Complexity r	Depth r	Complexity r
Agaricia spp.	–0.19	–0.13	0.19	0.39
Dichocoenia stokesii	–0.07	0.10		
Diploria clivosa	0.14	0.31		
Diploria strigosa	0.20	0.11	0.23	0.11
Meandrina meandrites	0.12	0.01		
Millepora alcicornis	–0.23	0.17		
Millepora spp.	0.29	0.14		
Montastraea annularis	–0.21	0.33	0.01	0.30
Montastraea cavernosa	–0.14	0.07		
Mycetophyllia spp.	–0.41	–0.27		
Porites asteroides	–0.28*	0.18	–0.12	0.08
Porites porites	–0.07	–0.05		
Siderastrea radians	–0.07	0.13	–0.03	–0.31
Siderastrea siderea	0.20	0.18	0.37*	0.17
Stephanocoenia intersepts	–0.31	0.25		
all coral	–0.01	0.34*	0.22*	0.25*
bleached spp %	–0.36*	0.29*	0.14	0.24*

During April, bleaching was observed at depths between 0.5–30 m with the majority of bleached cover occurring at depths between 6–17 m. The proportion of total bleached cover was positive and weakly correlated with depth (P = 0.04) and habitat complexity (P = 0.02; Table 3). The ratio of bleached/nonbleached coral species per survey site was significantly correlated with habitat complexity (P = 0.025) but not depth (Table 3). On a species level, only bleaching in *S. siderea* was significantly correlated with depth (P = 0.009). No other species were significantly correlated with depth or complexity (Table 3).

During October 2006, bleaching was evident within 13 of 93 transects (14%). Coral cover was estimated at 2.8% per 100 m^2 and bleached coral percent cover comprised 3% of total cover. Bleaching frequency of occurrence was highest for *P. asteroides*, *M. annularis*, *M. cavernosa,* and *S. siderea* and accounted for 85% of the total bleached cover (Table 2). Eighteen species did not exhibit any signs of bleaching. Two species, *M. alcicornis* and *M. decactis*, were bleached during October 2006, but not in April 2006. All species that were bleached during October 2006 were also bleached during October 2005. Bleaching was observed at depths from 3–21 m, with the majority of bleached cover occurring between 6–14 m.

Bleaching was predominantly observed to the east of Buck Island with a few observations scattered to the northwest and southeast (Fig. 5). Sites that contained bleaching exhibited low proportions of bleached cover and low ratios of bleaching/nonbleaching species. Bleaching frequency was not sufficient to examine correlations with depth and or habitat complexity.

Four species and one genus did not exhibit signs of bleaching throughout the study period: *D. cylindrus*, *E. fastigata*, *Mycetophyllia angulosa*, *Mycetophyllia aliciae*,

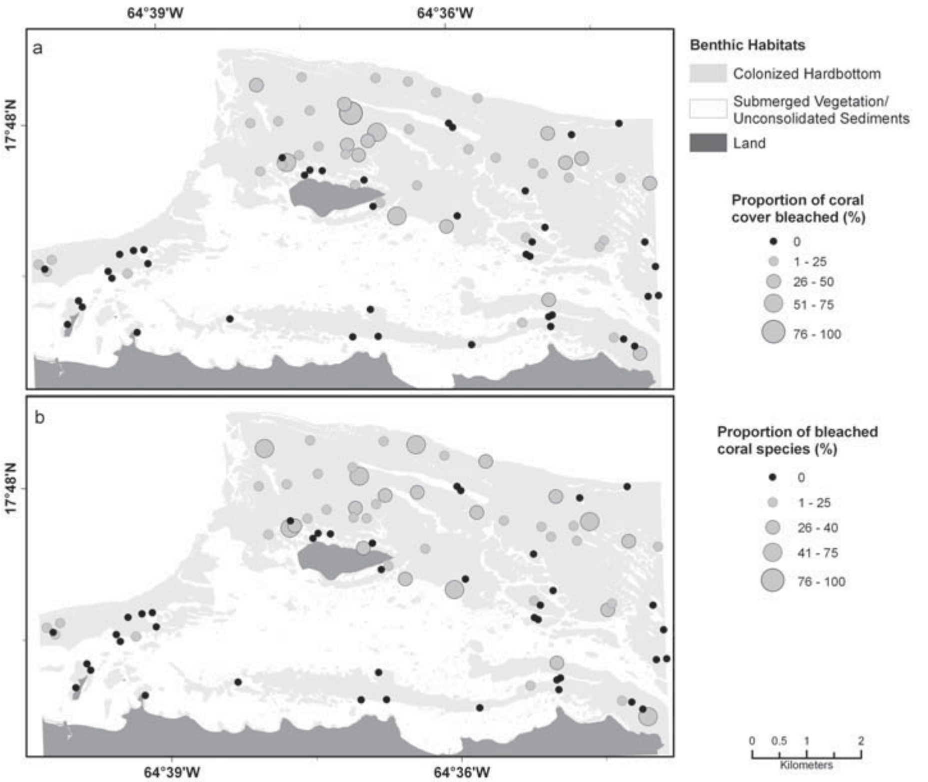

Figure 4. Spatial distribution and proportion of (A) bleached coral cover and (B) bleached species at individual monitoring stations at Buck Island Reef National Monument, April 2006.

Scolymia spp., however both *Mycetophyllia* species may have bleached but were not identified to species in the field.

Discussion

Water temperatures were consistently higher than average throughout the Caribbean basin for an unprecedented amount of time during the summer of 2005 (Wilkinson and Souter, 2008). As a result, the majority of coral within the study region experienced acute bleaching. It is uncertain when the bleaching started at this location, but was reported as early as June in Puerto Rico. At the time of monitoring in 2005, the majority of coral species observed exhibited signs of bleaching and 50% of the total coral cover was bleached. Bleaching prevalence was less in April 2006, corresponding with decreased water temperature, and by October 2006 bleaching was infrequently observed.

Considerable variability was observed within and among coral species, over a range of substrate complexity and depth. There were large differences observed in species-specific bleaching and few significant correlations with depth and habitat complexity. Considering all coral taxa together, bleaching was not correlated with depth during October 2005 but was weakly positively correlated with depth in April 2006. This trend reflects the broad spatial extent of the 2005 event with subsequent reduced

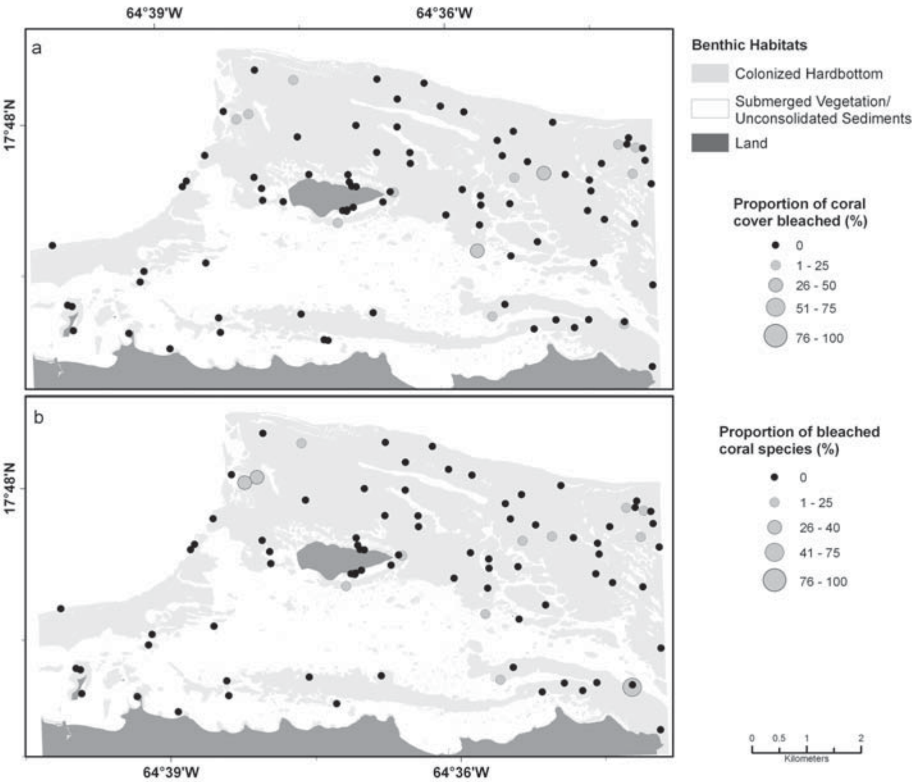

Figure 5. Spatial distribution and proportion of (A) bleached coral cover and (B) bleached species at individual monitoring stations at Buck Island Reef National Monument, October 2006.

localized bleaching during April 2006. Bleaching was significantly correlated with habitat complexity during October 2005 and April 2006, suggesting that extrinsic factors, such as natural water flow, may be impeded on more complex habitats. This may impose greater environmental variability on highly structured habitats (McClanahan et al., 2005) where corals are less tolerant. In contrast, continued exposure to high variability may also promote resiliency (McClanahan and Maina, 2003).

Species such as *M. annularis*, *D. strigosa*, *Agaricia* spp., *S. siderea*, *Millepora* spp., and *P. asteroides* have been documented as being the most susceptible to bleaching (Jaap, 1985; Williams and Bunkley-Williams, 1988; Manzello et al., 2007). These species were among the most affected at BIRNM during each monitoring period; however, high variability among sites and habitat types precluded any strong correlations with depth or habitat complexity. Bleaching was observed within all habitat types sampled, and no specific spatial patterns were apparent.

Jaap (1985) observed increased bleaching variability, typically at deeper reefs, associated with locally driven underflows of warm, low dissolved oxygen waters in the Florida Keys. The hypothesis was that shallow water corals were constantly satiated with above average water temperatures and were thus more susceptible to bleaching while deeper corals were not as influenced, except for colonies in the paths of these underflows which were more susceptible to bleaching.

The spatial variability in the level of coral bleaching observed among sites and habitat types at BIRNM indicates that elevated temperatures do not affect coral reefs equally across the seascape, and suggests that other factors may be synergistically modifying the effects of elevated temperature. Goenaga et al. (1989) and Hoegh-Guldberg (1999) suggest that complementing factors such as light intensity, currents, or physiological differences among zooxanthellae may intensify or weaken bleaching in conjunction with elevated water temperature. Micro-scale variation in wind speed and tidal flows may result in localized differences in solar radiation and heating that may affect coral colonies differently (Lang et al., 1992; Glynn, 1993). Additionally, coral species can vary substantially in their susceptibility to bleaching because of differences among species in structural shading mechanisms (Salih et al., 1997; Hoegh-Guldberg and Jones, 1999) and variation in genetic resistance of zooxanthellae to thermal stress (Trench and Blank, 1987; Rowan et al., 1997). Although most coral colonies observed during October 2005 were almost completely white, some appeared mottled or pale, and some others (e.g., *D. strigosa* and *M. annularis*) that exhibited complete loss of zooxanthellae were only 20-30 cm away from unaffected conspecifc colonies. This pattern has been commonly observed in the Caribbean (Glynn, 1990; Lang et al., 1992), and more research is needed to understand within species variability in susceptibility to bleaching. The spatial patterns in coral bleaching observed at BIRNM may have correlated with spatial variability in oceanographic variables at small scales (10–100 m); however, relevant data on oceanic conditions were not available to test this hypothesis.

The results presented here reflect species-specific responses to the bleaching event across the study area. *Montastraea annularis* and *Agaricia* spp. appeared to be the most affected species during October 2005, where cover was abundant and over 90% was bleached. These species have been observed to be the first to react to elevated water temperatures (Williams and Bunkley-Williams, 1988). Other species have displayed variable responses at certain locations and/or depths, suggesting that differential bleaching may reflect the inherent tolerance of species-specific zooxanthellae (Fitt and Warner, 1995). Over a broad area or within a single reef, zooxanthellae in corals can acclimate to stressful conditions, become more resistant, and significantly affect spatial patterns in coral bleaching (Rowan et al., 1997).

Our study did not monitor specific coral colonies at permanent stations through time but used a randomized stratified sampling design to generate unbiased synoptic estimates of the variance in mean coral cover for the study area. Therefore, it is unknown whether bleached corals observed in April and October 2006 were still bleached from the 2005 event or if a new mild bleaching event was in progress. The observed decline in the prevalence of bleaching may be indicative of initial recovery of BIRNM coral reef ecosystem from the October 2005 bleaching episode. Even though seawater temperatures were elevated in October 2006, the proportion of bleached coral was markedly less than it was 1 yr earlier.

It is likely, however, that some of the colonies that bleached in 2005 died and did not recover from the October 2005 bleaching event. Lundgren and Hillis-Starr (2008) observed 36.4%–66.4% bleaching-associated mortality of tissue on colonies of *Acropora palmata* at three sites within different benthic zones in the study region between August 2005 and January 2006. Miller et al. (2006) reported significant disease-related mortality of *M. annularis* and *P. porites* in St. John, USVI, which resulted in 26%–48% loss of coral cover 4 mo after the October 2005 bleaching event. Muller et al. (2008) also observed that bleached colonies of *A. palmata* in St. John had higher prevalence of diseases and disease-associated mortality than unbleached colonies following the October 2005 bleaching event.

Although there are many factors responsible for coral mortality, bleaching has been regarded as the major factor responsible for both the widespread mortality of corals as well as changes in coral reef community structure (Bruno et al., 2001; Diaz-Pulido and McCook, 2002). The current pattern of reef degradation and coral loss in the Caribbean comes with great ecological and economical consequences. Scientists and managers can sometimes identify more apparent causes of reef degradation (e.g., over-fishing, anchor damage, predators), but there is a parallel lack of understanding relating to reef resilience and ecological function that must be addressed (Done, 1992). Further research is needed to identify areas within reef systems that have reduced temperature stress, enhanced water movement, and decreased ultraviolet radiation, which may correlate with enhanced coral resistance and resilience to bleaching (West and Salm, 2003). Identification of such areas can help managers design and manage protected areas to promote ecosystem conservation. Our description of the spatial and taxonomic patterns of bleaching provides a foundation for identifying species of corals and specific areas within BIRNM that may be resistant and resilient to future mass bleaching events.

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