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Assessing coral reef health across onshore to offshore stress gradients in the US Virgin Islands

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ABSTRACT

Managing the effects of anthropogenic disturbance on coral reefs is highly dependant on effective strategies to assess degradation and recovery. We used five years of field data in the US Virgin Islands to investigate coral reef response to a potential gradient of stress. We found that the prevalence of old partial mortality, bleaching, and all forms of coral health impairment (a novel category) increased with nearshore anthropogenic processes, such as a five-fold higher rate of clay and silt sedimentation. Other patterns of coral health, such as recent partial mortality, other diseases, and benthic cover, did not respond to this potential gradient of stress or their response could not be resolved at the frequency or scale of monitoring. We suggest that persistent signs of disturbance are more useful to short-term, non-intensive (annual) coral reef assessments, but more intensive (semi-annual) assessments are necessary to resolve patterns of transient signs of coral health impairment.

1. Introduction

Coral reefs are imperiled by a range of interacting global and local stressors that have contributed to unprecedented degradation over the last half-century (Knowlton, 2001; Hughes et al., 2003). Coral reef degradation is narrowly defined here as the death of living coral tissue and the decline in diversity of scleractinian corals with a concurrent increase in the percent cover of non-living or algal covered substrate. Major stressors driving the degradation of reefs have included fishing and altered trophic structures (Jackson et al., 2001; Pandolfi et al., 2003), pollution from nutrients (Pastorok and Bilyard, 1985), sediments (Rogers, 1990; Fabricius, 2005) and, possibly, toxins (Glynn et al., 1989; Owen et al. 2002), as well as elevated sea surface temperatures (Glynn and D'Croz, 1990; Glynn, 1993, 1996; Hoegh-Guldberg, 1999). These stressors can drive coral reef degradation directly, through increased coral mortality, or indirectly, by increasing susceptibility to coral diseases (Harvell et al., 2002) and decreasing population replenishment via recruitment (Hughes and Tanner, 2000). At longer time scales (decades) stress forces coral reef ecosystem degradation by reducing resiliency after disturbances, such as storms (Hughes, 1994) and bleaching events (Hughes et al., 2007). The combination of these processes has been the "ratcheting down" of coral reef health and the promotion of phase shifts to alternate ecological states (Birkeland, 2004).

Perhaps the most dramatic example of the effects of increasing pressure on coral reef systems has been the high losses of coral cover seen in the Caribbean (Hughes, 1994; Gardner et al., 2003). Coral reefs of the United States Virgin Islands are no exception and may serve as a useful model of the patterns and processes of typical coral reef degradation in the Caribbean. Numerous stressors and disturbances impact reefs surrounding the US Virgin Islands. Hurricanes and tsunamis are potentially catastrophic natural disturbances that recur on decadal to century time scales (Rogers et al., 1991; Bythell et al., 1993; Watlington, 2006). Global factors linked to climate change include increased deposition of African dust carrying pathogens, nutrients, and toxins, that may impact coral reefs systems (Garrison et al., 2003), and increasing sea surface temperatures in Tropical Western Atlantic (Levitus et al., 2000), that has undoubtedly affected coral reef systems. As evidence of the latter, the 2005 mass coral bleaching event in eastern Caribbean was caused by unprecedented high temperatures linked to anthropogenic forcing (Donner et al., 2007), that caused severe bleaching, disease, and mortality in corals of the US Virgin Islands (Manzello et al., 2007; Miller et al., 2006; T.B.S., unpub. data).

Concomitant with globally and regionally increasing stressors, corals reefs of the US Virgin Islands have experienced increasing local stressors, stimulated by population growth and development. Recent and rapid alteration of the landscape through development has been responsible for exponentially increasing rates of terrestrial run-off transporting sediments to marine environments (MacDonald et al., 1997; Brooks et al., 2007) thereby causing high acute rates of sediment deposition on coral reefs (Nemeth and Sladeck Nowlis, 2001). Industrial activities, such as boat maintenance, rum production, and oil refining, have also likely contributed to increased inputs of toxic substances to marine environments. For

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example, Irgarol 1051, a boat anti-fouling paint that causes inhibition of coral photosynthesis (Owen et al., 2002), has been found in high concentrations in some embayments of the US Virgin Islands (Carbery et al., 2006). Fishing has gone largely unregulated in waters of the US Virgin Islands and has increased since the modernization of the commercial fishery, leading to the reduction in the biomass of ecologically important coral reef fishes (Olsen and LaPlace, 1978; Beets, 1997; Beets and Rogers, 2000; Rogers and Beets, 2001). Established no-take areas protecting economically important grouper and snapper spawning aggregations are helping to rebuild some populations (Nemeth, 2005; Nemeth et al., 2006; Kadison et al., 2006) and recently established no-take marine protected areas within US national parks and monuments are likely to maintain and rebuild populations of fish and invertebrate species within their borders. However, only 16.7% of the shelf area (<50 m depth) is under full or partial "no-take" protection (J.B. unpub. data), and in most cases these protected areas were established without robust ecological characterization or consideration (Monaco et al., 2007) and often lack enforcement (Rogers and Beets, 2001; T.B.S., pers. obs.). Currently, there is no comprehensive and effective marine resource management in the US Virgin Islands.

Under the pressure of increasing global and localized stressors, conservation of coral reefs requires a willingness among stakeholders, the public, and decision-makers to protect resources, along with the proper information to guide management. Management will be most responsive when diagnostic characteristics of reefs, such as the nature and magnitude of stresses affecting coral health, are known, and there is a reasonable framework for prognosis of the probable trajectory of reef degradation (Jameson et al., 2001). These assessments can take many forms, and range from high-technology assessments of individual coral colonies (e.g., Downs et al., 2005; Edge et al., 2005), to in situ assessments of visible coral health and population characteristics. Large-scale surveys, typically across a stratified-random seascape, can map disease or predator outbreaks, discern patterns of habitat development, and assess the magnitude and distribution of sessile and mobile reef populations (Ault et al., 2006; Pittman et al., 2007). Spatially repeated surveys, within a particular location or along the same transect, can be used to detect fine scale changes at randomly selected or representative sections of reef habitat and, over time, become the basis for understanding the long-term processes shaping reef communities (Hughes and Connell, 1999). Repeated surveys can provide information about relative indications of stress and degradation of coral reefs across any strata; however, they are typically less spatially comprehensive than stratified-random surveys.

Recently, both large-scale stratified-random surveys and repeated surveys over selected sites have been used to assess spatial and temporal trends in coral reef resources in the US Virgin Islands (Rogers and Miller, 2001; Herzlieb et al., 2005; Rogers and Miller, 2006; Monaco et al., 2007). These combined efforts are providing a new, more complete understanding of US Virgin Islands' reef-scape structure, health, degradation, and resilience. The research presented here analyzed trends and patterns in reef health across potential gradients of stress in the northern US Virgin Islands. We measured rates of sedimentation directly at coral reef locations to understand if increasing run-off of sediments has the potential to impact coral reef environments. We hypothesized that stress should be higher in nearshore environments and that signs of stress and disturbance on coral reefs and their constituent corals should also be highest in nearshore environments. We also examined the efficacy of a commonly used coral reef monitoring method (i.e., repeated surveys at constant locations) to provide information needed for adaptive management and, ultimately, conservation of coral reef resources. Although rapid assessments of coral reef and fish populations have been conducted on a large-scale in the US Virgin Islands (Nemeth et al., 2003a,b), this is the first spatially and temporally comprehensive assessment of the territorial waters of the northern US Virgin Islands and will serve as a baseline for understanding future trajectories of these Caribbean coral reef environments.

2. Methods

2.1. Study region and locations

The northern US Virgin Islands (USVI) consists of two large adjacent islands, St. Thomas (83 km^2) and St. John (52 km^2), and numerous smaller islands surrounded by a diverse, tropical marine environment that includes coral reefs, seagrass beds, and mangrove forests (Fig. 1). St. Thomas and St John are joined by an extensive shallow water platform (the Puerto Rican Shelf) that connects them to Puerto Rico and the British Virgin Islands. St. Croix, approximately 40 km to the south, lies on a separate, relatively narrow platform and is not considered in this manuscript.

Between 2001 and 2005 a total of 18 coral reef monitoring locations, which represented a range of reef types, were established around St. Thomas and St. John (Fig. 1; Table 1). Sites were established based upon a stratified design to test hypotheses involving differences between reef systems distributed across the insular platform along an on-shore to off-shore gradient, as well as to fill gaps in existing knowledge on previously unstudied reef systems. We examined four reef complexes as follows: nearshore, shallow (5–13 m) reefs fringing St. Thomas–St. John shoreline; midshelf-island, shallow (9–15 m) reefs fringing uninhabited cays 2–10 km offshore, midshelf-no island, deep (18–20 m) linear reefs located 2–10 km offshore; and shelf edge, deep (34–42 m) linear reefs located near the edge of the insular platform more than 10 km offshore (Table 1). This stratification among reef complexes allowed for comparisons among sites that were at similar depths but different distances from shore (nearshore vs. midshelf-island and midshelf-no island vs. shelf edge) and comparisons among sites that were at similar distances from shore but at different depths (midshelf-no islands vs. midshelf-island). The three shelf edge reefs were located within no-take or partially no-take marine protected areas: Hind Bank and College Shoal East (St. Thomas Marine Conservation District, est. 1999), Grammanik Bank (trap/net fishing closure and seasonal closure to line fishing, est. 2005). In six locations (Benner Bay, Brewer's Bay, Botany Bay, Fish Bay, Magen's Bay, and Long Bay) transects were haphazardly placed across the fore reef slope and the ends permanently marked with steel rods. At the remaining locations placement of transects in each sampling period was done randomly.

2.2. Benthic cover

At each site 6–10 10 m transects were deployed. Video sampling was conducted following standard methodologies (Aronson et al., 1994; Carleton and Done, 1995; Rogers and Miller, 2001; Rogers and Beets, 2001). A diver swam at a uniform speed (~5 min. per transect), pointing a video camera perpendicular to the substrata and following the vertical contour of the reef at the approximate height of a guide wand, 0.4 m in length. Captured images represented a planar area of reef approximately 0.31 m^2 (0.64 m $\times$ 0.48 m). Ten randomly located points were superimposed on each captured image and the benthic cover under each of the points was then identified to the lowest identifiable taxonomic level or abiotic group and used in calculation of percent cover.

2.3. Coral health assessment

All coral colonies 10 cm or greater in diameter or height that were located directly under the transect lines were assessed

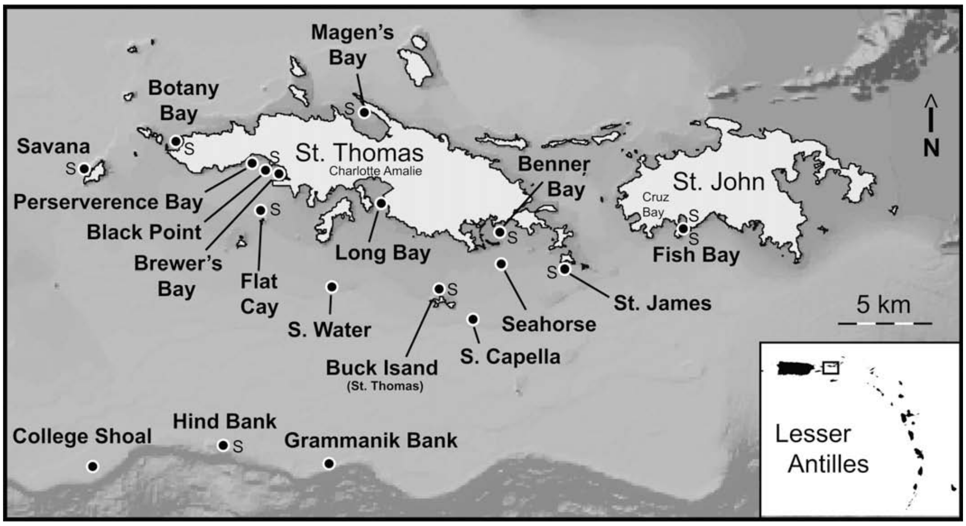

Fig. 1. The northern US Virgin Islands, St. Thomas and St. John, with coral reef study locations denoted by white circles. Sites were arrayed across the shelf from nearshore to offshore locations and corresponded to nearshore, midshelf-island, midshelf-no island, and shelf edge coral reef complexes. Locations marked with "S" were also sites of sedimentation rate monitoring.

Table 1
Coral reefs monitored from 2001 to 2005 around St. Thomas and St. John, US Virgin Islands

Orientation	Site	Depth (m)	Distance to shore (km)	Years sampled	Sampling design	No. of times sampled	No. of transects	Sedimentation rates	
								Sampling period (dd-mm-yy)	No. times sampled
Nearshore	Benner Bay	7	0.3	2001–05	Permanent	5	6[a]	11-01-05 to 03-10-07	23
	Black Point	13	0.05	2003, 2005	Random	2	12	10-02-05 to 23-10-07	23
	Botany Bay	8	0.1	2002–05	Permanent	6	6[a]	16-12-04 to 03-10-07	23
	Brewer's Bay	6	0.1	2002–03	Permanent	2	6[a]		
	Fish Bay	5	0.05	2001-05	Permanent	4	6[a]	10-02-05 to 03-10-07[b]	22
	Magen's Bay	8	0.07	2001–05	Permanent	5	6[a]	16-12-04 to 03-10-07	23
	Perseverance Bay	8	0.15	2003	Random	1	6		
	Long Bay	6	0.1	2001–04	Permanent	3	6[a]		
Midshelf-Island	Buck Island	15	2.8	2005	Random	2	12	15-03-05 to 03-10-07	21
	Flat Cay	15	3.0	2003–05	Random	5(6)	24(30)	10-02-05 to 23-10-07	23
	Savana	9	4.5	2003–05	Random	3	18	13-12-04 to 04-09-07	21
	St. James	18	2.6	2005	Random	2	12(11)	15-03-05 to 03-10-07	21
Midshelf-No Island	Seahorse	18	2.1	2003–05	Random	3	22		
	South Capella	20	4.8	2004–05	Random	3	22		
	South Water	20	2.6	2005	Random	1	6		
Shelf Edge	College Shoal	34	16.9	2003, 2005	Random	2	12		
	Grammanik Bank	39	12.1	2003–05	Random	4(3)	28(22)		
	Hind Bank	42	14.8	2003–05	Random	3	22	01-23-05 to 16-10-07	20

The distance from shore refers to the distance to the shoreline of the closest main island of St. Thomas or St. John. Sampling design refers to method of transect placement (see text). Numbers in brackets are for the number of times sampled and the number of transects used in the health assessment analyzes if different from that used in benthic cover analyzes.
[a] Average of permanent transects.
[b] Includes outer and inner embayment sediment stations with three traps each.

in situ for signs of mortality and disease following a modified atlantic and gulf rapid reef assessment protocol (AGRRA; Kramer et al., 2005). This provided a total coral sample size of 3363 colonies. Partial mortality of coral colonies was broken into two categories. Recent partial mortality, skeleton not eroded (fine corallite structure still intact) and bare or with a thin veneer of sheeting or filamentous algae, is typically visible for up to three months following tissue loss. Old partial mortality, skeleton eroded and covered with turf or macroalgae, is a transition from recent mortality and typically lasts up to 1–4 years (T.B.S. pers. obs.; also see http://www.agrra.org/method/methodcor.html). The three-dimensional surface area (%) of the colony that was dead was also estimated for each partial mortality category.

Diseases were conservatively categorized into recognized Caribbean scleractinian diseases and syndromes that included bleaching, black band disease, dark spots disease, white plague, and yellow blotch (band) disease (following Bruckner, 2007). Bleaching was assessed as abnormal paling of the colony, and, when presents, the severity of the bleaching (paling or total whitening) and the area of the colony affected were assessed. This data was present to ordinate bleaching intensity into one of five categories: (0) unbleached, (1) any degree of paling less than completely white, or 1–10% bleached, (2) 10–50% bleached, and (3) 50–90% bleached, and (4) >90% bleached (after Gleason, 1993). Acroporid corals were very rare at the study sites and their associated white diseases, white band and white pox, were not encountered in our study and are not included. For each transect at each location, the prevalence of colonies with mortality, bleaching, and disease was calculated.

2.4. Sedimentation rates

Sedimentation rates were monitored at a subset of coral reef study locations (11), representing nearshore, midshelf-island, and shelf edge reef complexes (Table 1, and denoted by "S" in Fig. 1). Sedimentation rates were obtained from three sediment traps placed less than 15 m apart at each site and collected at one to two month intervals from December 2004 to October 2007. Traps were cylinders made of PVC with a height of 20.8 cm and a circular aperture of 5.2 cm, suspended 50 cm above the sea floor. Sediment samples from traps were rinsed multiple times with deionized water to remove salts and decanted, then dried to constant weight at 70 °C. The weight of the total fraction and the fraction less than 75 μm (produced by sieving) were measured. The clay and silt fractions have greater negative effects on coral health than larger size particles and are important to monitor apart from total sediment loads (Weber et al., 2006). Due to occasionally missing replicates sedimentation rate estimates (mg cm^{-2} d^{-1}) were averaged between the all traps at a site for each period.

2.5. Analysis

Rates of sedimentation, total and the fraction less than 75 μm, were analyzed between orientation strata with ANOVA. Data were natural log transformed to meet assumptions of normality and homogeneity of variances.

Spatial trends in benthic cover and coral health (here defined as prevalence of corals with partial mortality or disease) were tested for differences across reef complexes. Coral health included impaired health, a novel category that included any colony with at least one sign of mortality or disease. In order to allow comparison with locations containing randomly placed transects, the coverage data for locations with permanent transects were averaged for each transect across years, creating a single estimate for each transect. This loss of power was considered necessary to allow intercomparison among sites. Data were arcsine transformed prior to analysis. After meeting assumptions of normality and homogeneity of variances, data were compared with one-way ANOVA using JMP Statistical Software (v5.0, SAS Institute, Inc.). Where assumptions were not met, data were compared with a Kruskal–Wallis test on rank sums and when significant differences between levels were indicated, group means were compared with a post hoc Tukey–Kramer HSD ranked means test.

3. Results

3.1. Sedimentation rates

Sedimentation rates were dramatically higher on nearshore coral reefs. There were significant differences in sedimentation rates among all reef complexes for total and less than 75 μm sediment fractions (Fig. 2; Total: df = 2, $F = 107.6$, $p < 0.0001$; <75 μm: $df = 2$, $F = 96.1$, $p < 0.0001$). Mean nearshore sedimentation rates for the clay and silt fraction (<75 μm) were over five-fold greater than midshelf-island reefs and over 45-fold greater than the shelf edge reef. In addition, 17 of 136 estimates of the fraction <75 μm taken in nearshore environments surpassed a proposed total daily sedimentation rate threshold (10 mg cm^{-2} day^{-1} for all size fractions) which has been associated with degraded coral reefs, lower coral vital rates, and slower rates of reef accretion (Rogers, 1990). All nearshore reefs experienced at least one period above this threshold for either fraction.

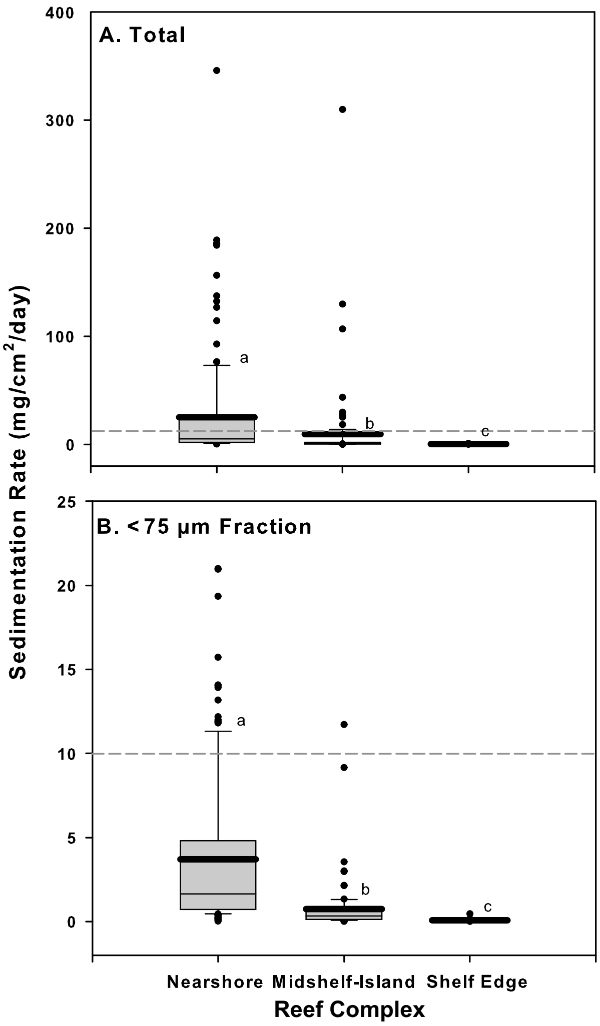

Fig. 2. Box plots of (A) total sedimentation rates and (B) sedimentation of particles less than 75 μm in size among three coral reef complexes. Figure components are mean (thick black line), median (thin black line), 25th and 75th percentiles (bottom and top of box, respectively), 10th and 90th percentiles (bottom and top whiskers, respectively) and values outside 10th and 90th percentile (dots). Homogeneous subsets of means are indicated with lowercase letters (Tukey HSD Post Hoc comparison). Dashed line at 10 mg cm^{-2} day^{-1} is a value above which corals may be greater risk of experiencing increased stress.

3.2. Benthic cover patterns with orientation

Coral cover increased from nearshore to offshore. Coral cover was significantly different between reef complexes (Table 2) and tripled from nearshore to offshore reefs (Fig. 3A). Driving this pattern was the percent cover of *Montastraea annularis* species complex, which represented 50–80% of the total coral cover among reef complexes. Differences in the cover of *M. annularis* species complex was significantly different between reef complexes (Table 2), and four times greater in the shelf edge reefs compared to the nearshore reefs (Fig. 3A). Gorgonian and sponge cover was also significantly different between reef complexes (Table 2). Sponge cover was significantly higher in the midshelf – island reefs, while gorgonian cover was significantly lower, and nearly zero, in the deep shelf edge reefs (Fig. 3A).

Algal cover was lowest on the shelf edge reefs, but for different algal types there were variable patterns of abundance among reef complexes (Fig. 3B), with significant differences for all groups

Table 2
Statistical comparison of benthic cover across the orientation strata

Source	df	F (χ^2)	*p*	Orientation			
				Nearshore	Midshelf-island	Midshelf-no island	Shelf edge
Coral[a]	3	75.7	0.0001	C	BC	B	A
M. annularis complex[a]	3	94.8	0.0001	C	C	B	A
Other Coral	3	7.2	0.0001	A	A	AB	B
Gorgonians[a]	3	111.1	0.0001	A	A	A	B
Sponges[a]	3	23.8	0.0001	B	A	B	B
Algae	3	14.3	0.0001	A	B	AB	C
Macroalgae[a]	3	37.4	0.0001	B	B	A	B
Dictyota spp.	3	51.5	0.0001	A	B	B	C
Lobophora variegata[a]	3	157.9	0.0001	D	C	B	A
Other Macroalgae	3	3.06	0.0287	A	AB	AB	B
Dead coral and turf algae[a]	3	77.2	0.0001	A	B	C	C
Crustose coralline[a]	3	42.5	0.0001	AB	B	B	A
All Algal Substrata[a]	3	42.7	0.0001	A	A	A	B

Statistical tests are given for ANOVA or non-parametric Kruskal–Wallis (χ^2). Letters across orientation strata indicate homogeneous subsets of means (Tukey HSD post hoc comparison). $N = 258$ for all comparisons.
[a] Kruskal–Wallis non-parametric test.

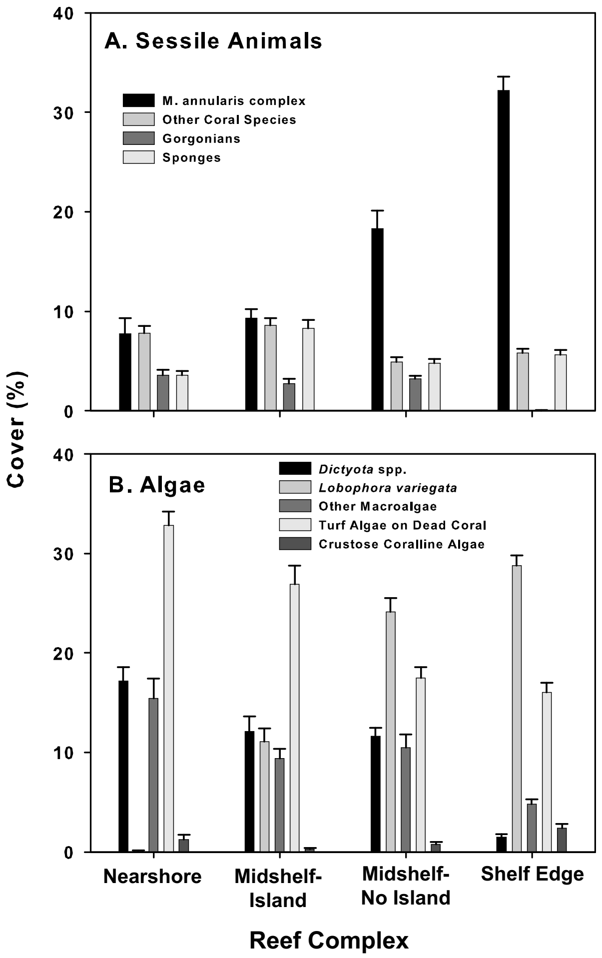

Fig. 3. Mean percent cover (±SE) of (A) sessile epibenthic animals and (B) algae across the coral reef complexes. Categories represented are (A) corals in the *Montastraea annularis* species complex, all other coral species combined, gorgonians, and sponges, and (B) the macroalgae *Dictyota* spp., *Lobophora* variegata, and, other all macroalgae species combined, crustose coralline algae, and dead coral covered with turf algae. All measured categories were significantly different, with differences between strata presented in Table 2.

tested (Table 2). The cover of all combined categories of algae (dead coral covered with turf algae, macroalgae, and crustose coralline algae) was significantly different between reef complexes, with the shelf edge reefs significantly lower than all other reef complexes, which were not significantly different from each other (Table 2). The mean cover of macroalgae was significantly higher only for the midshelf–no island reefs, while all other reef complexes were not significantly different. The mean coverage of two important macroalgae species had opposing trends in cover with depth and distance from shore, with *Dictyota* spp. increasing towards shore, and *Lobophora variegata* decreasing towards shore and nearly absent at nearshore reefs (0.1% mean cover). The cover of turf algae on dead coral significantly decreased from nearshore to offshore reefs, but was not significantly different between the deeper midshelf–no island reefs and shelf edge reefs (Fig. 3B, Table 2). Crustose coralline algae were low in cover in all reef complexes (less than 3%), but tended to be highest in both the nearshore and shelf edge strata.

3.3. Health patterns with orientation

There were apparent and significant trends in some health variables across reef complexes, with a pattern of decreased coral health from offshore to inshore. The prevalence of old mortality was significantly higher (Table 3A), and nearly double, in nearshore coral reefs compared with any of the offshore reef complexes (Fig. 4A). The prevalence of recent mortality was also significantly different between reef complexes (Table 3A), but showed a bi-modal tendency with peaks in nearshore and shelf edge reef complexes (Fig. 4A). The average percent surface area of individual colonies affected by old and recent partial mortality was not significantly different between reef complexes (Table 3A, Fig. 4A) and averaged about 30% for old partial mortality and about 9% for recent partial mortality. Patterns of old partial mortality across reef complexes were not obscured by the effect of increasing partial mortality prevalence with increasing colony size (Hughes and Jackson, 1985; Meesters et al., 1997). Coral colony size (maximum width) was significantly different between orientation strata (Kruskal–Wallis, $\chi^2 = 59.5$, $p < 0.0001$, $N = 219$), however, there was a low correlation between mean colony size per transect and the mean prevalence of old partial mortality ($R = 0.364$) and recent partial mortality ($R = 0.088$) per transect.

Bleaching showed an increasing trend in prevalence from offshore to nearshore, with shelf edge and nearshore reefs significantly different (Table 3B, Fig. 4B). The majority of the bleaching was not related to high temperature stress, as most monitoring occurred outside of the season when seawater temperatures are warmest (i.e., September to November). However, as a precaution

Table 3
Statistical comparisons across orientation strata of (A) prevalence and mean size of colony affected for old and recent partial mortality, (B) prevalence of diseases and bleaching intensity, and (C) prevalence of colony displaying at least one sign of mortality or disease. Statistical tests are given for ANOVA or non-parametric Kruskal–Wallis (χ^2; denoted with asterisks)

Source	df	F (χ^2)	p
A. Mortality			
Prevalence			
Old[a]	3	34.4	0.0001
Recent	3	4.2	0.0068
Percent of colony affected			
Old	3	2.0	0.1202
Recent	3	1.9	0.1304
B. Disease			
Bleaching	3	3.9	0.0089
Bleaching Intensity	3	1.2	0.31
Black Band[a]	3	6.4	0.09
Yellow Blotch[a]	3	19.0	0.001
Dark Spots[a]	3	18.7	0.0003
White Plague[a]	3	5.2	0.159
C. Disease and Mortality			
Total	3	7.3	0.0001

Post hoc comparison of means given in Fig. 4A–D.
[a] Kruskal–Wallis non-parametric test.

we analyzed these data with warm water months excluded and found the differences between orientation strata were the same ($p < 0.002$, identical post hoc comparisons, $N = 201$). Bleaching intensity (BI) was not significantly different between reef complexes (Table 3B), and there was a low combined average intensity (Fig. 4B; BI = 1.3, category one: any degree of paling less than completely white, or 1–10% bleached).

Coral diseases, with the exception of bleaching, showed no clear trends associated specifically with an on-shore to off-shore gradient (Fig. 4C). Dark spots disease and yellow blotch disease were the only diseases significantly different between reef complexes (Table 3B), and the prevalence in nearshore reefs, although relatively high, was not significantly higher than any of the offshore reef complexes. The prevalence of dark spots disease was highest in nearshore and midshelf-island reefs, and trended to lower prevalence in midshelf-no island and shelf edge reefs (Fig. 4C). *Siderastrea siderea* is the most susceptible species to dark spots disease (Gil-Agudelo and Garzón-Ferreira, 2001; Borger 2005a,b; Borger and Steiner, 2005; Calnan et al., 2008), and shows a decreasing abundance (as proportion represented in surveys) in disease surveys from the nearshore to offshore strata ($\text{Mean}_{\text{nearshore}} = 12.1\%$ in, $\text{Mean}_{\text{midshelf-island}} = 9.9\%$, $\text{Mean}_{\text{midshelf-no island}} = 6.1$, $\text{Mean}_{\text{shelf edge}} = 1.3\%$). However, this unequal abundance of a susceptible species was not predominantly driving the spatial pattern of dark spots disease prevalence. There was a low correlation between the abundance of *S. siderea* in coral health surveys and the prevalence of dark spots disease ($R = 0.25$, $N = 219$). The prevalence of yellow blotch disease dropped to zero in the midshelf-no island reefs, but was not different between the remaining reef complexes. Yellow blotch disease is most common in corals of the *M. annularis* species complex (Cervino et al., 2001; Bruckner and Bruckner, 2006). However, as with dark spots disease, differences in species susceptibility were not driving the spatial pattern of yellow blotch disease. There was a low correlation between the proportionate abundance of *M. annularis* complex in coral health surveys and the prevalence of yellow blotch disease ($R = 0.09$, $N = 219$). Furthermore, the abundance of *M. annularis* species complex corals in midshelf-no island sites (0.640) was greater than nearshore (0.301) and midshelf-island reef complexes (0.427), and nearly the same as in shelf edge strata (0.749), a pattern not coincident with the prevalence of yellow blotch disease. Black band disease and white plague were not significantly different between reef complexes and were relatively rare compared to other diseases with a prevalence that never exceeded 1.1% (Fig. 4C).

Assessment of overall health of coral colonies clearly differentiated nearshore reefs from all other reef complexes (Fig. 4D, Table 3C). The total combined prevalence of mortality and disease was significantly greater, by approximately 50%, in nearshore coral reefs than in the offshore coral reef complexes, which were not significantly different from each other.

4. Discussion

Nearshore coral reefs of the northern US Virgin Islands showed greater signs of coral health impairment relative to offshore reefs. This pattern largely upheld our hypothesis that nearshore reefs, closest to terrestrial impacts and human interaction, would show the greatest signs of degradation relative to reefs located in offshore areas. The average surface area of colonies affected by old mortality was not different in nearshore and offshore coral reefs, suggesting that when partial mortality occurred it affected colonies to a similar degree (death of about 30% of the colony surface). Furthermore, bleaching showed an increasing trend from offshore to nearshore coral reefs, and suggests that factors causing bleaching were likely higher in nearshore coral reefs. Bleaching intensity was low (<10% of colony surface) and not associated with seasonal thermal stress, suggesting that between 2002 and 2005, and prior to widespread bleaching in late 2005, local stressors were responsible for the majority of bleaching seen in all reef orientation strata. Overall, the prevalence of all forms of potential colony impairment (mortality and disease) was about 50% higher in nearshore coral reef environments.

Patterns of old mortality across reef complexes and occurrence within reefs suggested that nearshore coral reefs were displaying signs of reduced health that represented the cumulative impacts of a variety of natural and anthropogenic disturbance. Natural processes that cause partial mortality in corals are often tied to direct colony damage from organisms (e.g., fish grazing; Bruggemann et al., 1994), acute disturbance events (e.g., storms; Bythell et al., 1993), or chronic and acute disease (Peters, 1984). The large average extent of old partial mortality (about 30% of colony surface) is not consistent with localized disturbance from fish grazers or corallivorous invertebrates. In addition, the occurrence of old partial mortality on nearly half of all colonies in nearshore reefs seems greater than possible by corallivory alone, without large predator outbreaks; a phenomenon that has not been observed during this coral monitoring program. Furthermore, storms and other large-scale acute disturbances have patchy effects across space, but should, on average, affect nearshore and midshelf island associated reefs similarly, as they are in similar depth ranges. However, the prevalence of old mortality on nearshore coral reefs was nearly 300% greater than on midshelf–island reefs, and the prevalence of all forms of coral health impairment was about 60% greater.

Processes that increased signs of coral health impairment in nearshore coral reefs may be related to the higher concentration of stressors in nearshore waters impacted by run-off and increased human activity. Sedimentation was the only stressor measured in this study, therefore, it was not possible to separate the single or interacting stressors responsible for greater relative signs of coral health impairment in nearshore coral reefs. However, relative to less degraded midshelf-island reefs, nearshore reefs had five-fold greater sedimentation rates of clay and silt (i.e., <75 μM) and nearly three-fold greater sedimentation rates of all sediment fractions. Furthermore, while caution must be applied to the use of sedimentation thresholds (Rogers, 1990), in nearshore reefs fine sediments and total sediments surpassed 10 mg cm^{-2} d^{-1} in 13%

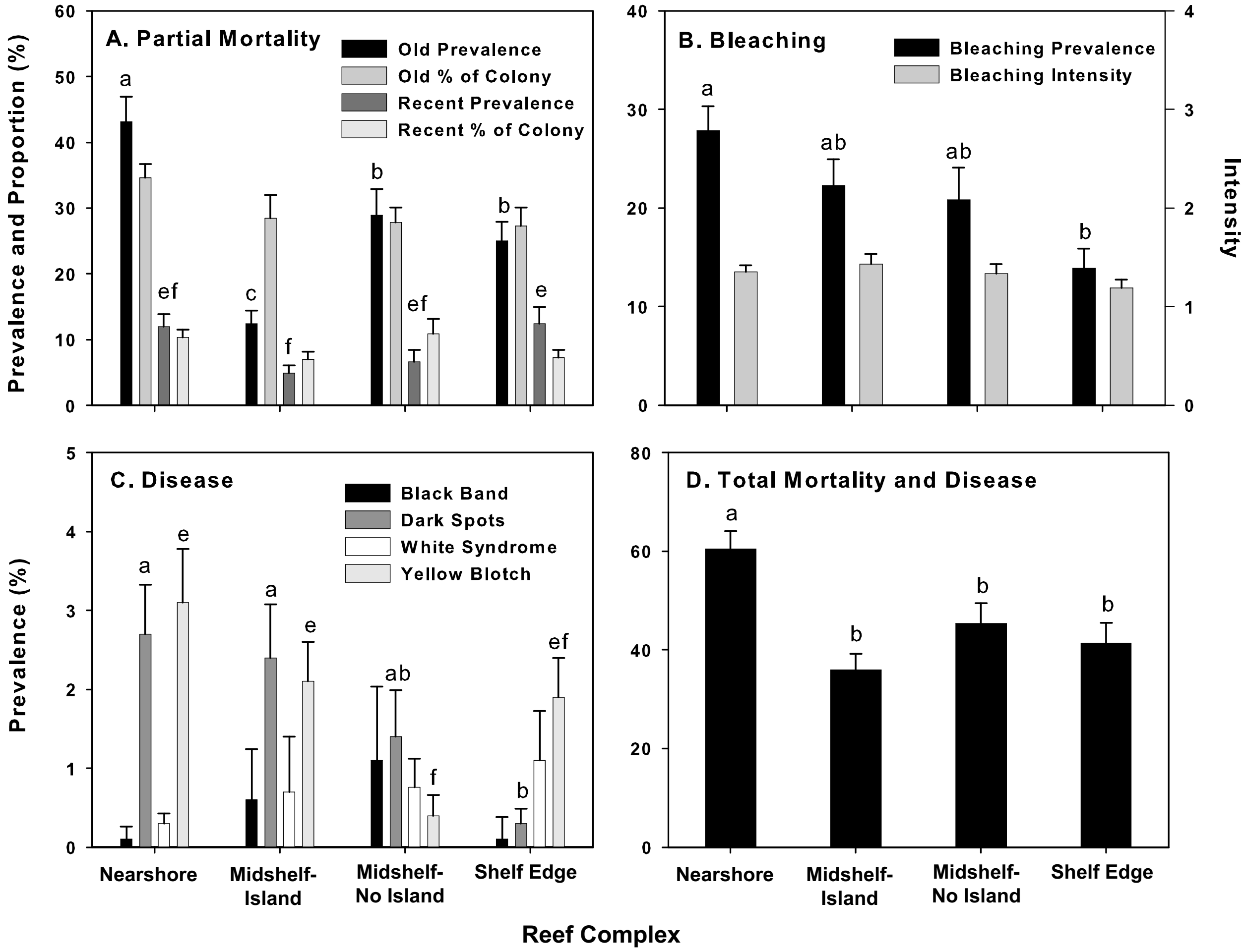

Fig. 4. Indicators of coral health across the nearshore, midshelf-island, midshelf-no island, and shelf edge coral reef complexes. Coral health was evaluated in the categories (A) mean prevalence of coral colonies with old and recent partial mortality and the mean proportion of the colony (%) affected by old and recent partial mortality, (B) prevalence of colonies with bleaching and the intensity of bleaching (see text for details), (C) prevalence of four recognizable coral diseases, and (D) prevalence of colonies displaying at least one sign of partially mortality or disease. Variance bars around means denote standard error. Homogeneous subsets of means are indicated with lowercase letters (Tukey HSD Post Hoc comparison).

(17 of 136) and 35% (48 of 136) of sediment samples, respectively, versus 1% (1 of 86) and 10% (9 of 85) for midshelf sites. This suggests that sedimentation rates in nearshore reefs have the potential to be stressful, and may be one of the primary drivers of coral reef degradation at nearshore sites. This is supported by numerous studies in which sedimentation has been associated with increased partial mortality severity (Wesseling et al., 2001; Nugues and Roberts, 2003) and increased bleaching (e.g., Bak, 1978; Rogers, 1983; Acevedo and Morelock, 1988; Nemeth and Sladek Nowlis, 2001; Philipp and Fabricius, 2003). However, factors that stimulate non-thermal bleaching also include toxins (e.g., Ross, 2004) and pathogens (Kushmaro et al., 1996), which may be co-transported in the run-off that carries sediments and may be linked in ways that makes their effects hard to separate in field studies. Despite uncertainties concerning the exact relationship between elevated sedimentation and coral health in the US Virgin Islands there should not be further delay of increased management of run-off that has clearly been increasing in nearshore environments (MacDonald et al., 1997; Brooks et al., 2007).

The data presented in this study were not able to show a correspondence between lowered water quality (e.g., sedimentation) in nearshore coral reefs and higher prevalence of diseases. We expected that scleractinian coral disease, if linked to local stresses, would be higher in nearshore environments, as a link has been made by local anthropogenic stressors and sea fan and hard coral diseases (Smith et al., 1996; Kaczmarsky et al., 2005; Kuta and Richardson, 2002). The lack of association with nearshore stressors or the spatial distribution of susceptible species suggests other factors were responsible for the prevalence patterns of disease across our study sites.

In addition, detection of the common diseases white plague and black band may not be powerful diagnostic signs in annual monitoring programs because they are often transient or rare. White plague disease and black band disease can cause rapid rates of tissue loss on infected coral colonies (Borger, 2005a). For example, white plague has been shown to spread up to 20 mm a day (Richardson et al., 1998) and black band disease up to 3 mm a day (Rutzler et al., 1983). White plague infections are often active for far less than a year, while black band tends to be more persistent, though not always active and discernable (Miller et al., 2003; Borger, 2005a; Borger and Steiner, 2005). Therefore, these diseases may be missed in annual and semi-annual monitoring programs, particularly if surveys do not coincide with peaks of disease signs and if surveys sample relatively few corals (Calnan et al., 2008). Even at low prevalence both diseases may have large effects on coral faunas (see references above), so efforts should be made to improve their monitoring with intra-annual assessments to understand their relationship, if any, to anthropogenic stressors (Miller et al., 2006).

Persistent signs of reduced coral health may be more useful in coral monitoring and assessment programs. Partial mortality of coral tissue is followed by a systematic progression of stages from bare skeleton to colonization by algae and/or sessile benthic organisms. The results of this research indicate that the old stage of partial mortality, may be a useful indicator of coral health and past disturbance. Old mortality persists after the disturbance that created it and integrates disturbance over time, therefore, it is likely to be a robust and detectable sign of impaired coral health in field monitoring programs (Bythell et al., 1993; Hughes and Jackson, 1985; Nugues and Roberts, 2003). In addition, our data suggest that where sampling effort is constrained, as is normally the case, that the prevalence of all combined forms of coral impairment may allow rapid ranking of sites by disturbance. This measure integrates all available information on coral health, and may allow the greatest possibility of detection of coral health shifts. To our knowledge this is the first time that total measures of impairment have been used to compare different reefs in evaluation of potential impacts from stressors.

Benthic cover may be less useful in attempting to separate areas based on coral health or coral reef disturbance. For example, dead coral covered with turf algae may integrate signs of disturbance over a long period (i.e., the final stage of partial or total coral mortality) and, thus, might be useful as an integrated measure of past disturbance. However, many factors influence non-coral benthic cover and the maintenance of coral-free patches of space and these include a variety of natural disturbance and regenerative processes. In the same way, comparison of coral cover between areas may not always be informative because coral cover is a long-term response to degradation and restoration processes. Benthic cover as an indicator of coral reef health will only be useful in long-term monitoring (decadal) programs that track trajectories of reef development and attempt to discover the processes that influence these trajectories (e.g., Hughes, 1994; Rogers and Miller, 2006). To this end, the benthic cover described across the northern US Virgin Islands among different reef complexes and reefs will be useful as a baseline for effective long-term monitoring.

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