**Coral reef health response to chronic and acute changes in water quality in St.
Thomas, United States Virgin Islands**

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Abstract

It is suspected that land cover alteration on the southern coast of St. Thomas, USVI has increased runoff, degrading nearshore water quality and coral reef health. Chronic and acute changes in water quality, sediment deposition, and coral health metrics were assessed in three zones based upon perceived degree of human influence. Chlorophyll ($p < 0.0001$) and turbidity ($p = 0.0113$) were significantly higher in nearshore zones and in the high impact zone during heavy precipitation. Net sediment deposition and terrigenous content increased in nearshore zones during periods of greater precipitation and port activity. Macroalgae overgrowth significantly increased along a gradient of decreasing water quality ($p < 0.0001$). Coral bleaching in all zones peaked in November with a regional thermal stress event ($p < 0.0001$). However, mean bleaching prevalence was significantly greater in the most impacted zone compared to the offshore zone ($p = 0.0396$), suggesting a link between declining water quality and bleaching severity.

Keywords: United States Virgin Islands, water quality, sediment deposition, coral bleaching, macroalgae interactions, chronic and acute stressors

1. Introduction

Coral reefs form the foundation of one of the most diverse marine ecosystems on the planet (Hoegh-Guldberg 1999; Guerra-García and Koonjul 2005; Larsen and Webb

2009). They are an invaluable element in the economies of small, tropical and subtropical island nations, as the tourism and recreational activities associated with coral reefs can account for up to 80% of total island income (Hoegh-Guldberg 1999; Jeffrey et al. 2005; Carbery et al. 2006). However, increased runoff associated with development and land-use changes in the coastal zone has degraded nearshore water quality, threatening the health and persistence of coral reefs (Mora 2008; Haapkylä et al. 2011; Maina et al. 2011; Dadhich and Nadaoka 2012).

Sediment and nutrients are arguably the most influential components of runoff and have been shown to have largely negative impacts on coral reef ecosystems. Direct deposition of sediment on corals can cause burial, smothering, and mortality (Rogers 1990; Dubinsky and Stambler 1996; Nemeth and Nowlis 2001). Land-based sediment particles can also act as vectors for coral disease agents (Larsen and Webb 2009; Haapkylä et al. 2011), while nutrient enrichment in the coastal environment can intensify disease impacts (Dubinsky and Stambler 1996; Bruno et al. 2003). Light reduction due to suspended sediment particles or nutrient-induced eutrophication and phytoplankton growth in the water column increases turbidity, preventing sufficient light from reaching photosynthetic benthic organisms (Hallock and Schlager 1996; Fabricius 2005; Anthony 2006; Haynes et al. 2007; Larsen and Webb 2009). Elevated nutrient concentrations can also favor the competitive ability of macroalgae over corals, leading to overgrowth and community shifts from coral to macroalgae dominance (Szmant 2002; Fabricius 2005; Haynes et al. 2007; Silverman et al. 2007; De'Ath and Fabricius 2010). Increased sediment and nutrient loading may also be associated with a higher prevalence of coral

bleaching (Nemeth and Nowlis 2001). However, it has also been suggested that sediment and nutrients may have positive effects on coral growth and resistance to stress (Fabricius 2005) and that some corals can exhibit heterotrophic plasticity to utilize excess sediment particles as an additional source of energy (Anthony and Fabricius 2000; Anthony 2006; Larsen and Webb 2009).

Both the amount of development in the coastal zone and the volume of pollutants entering the nearshore environment can influence the severity of the impacts of increased runoff. Recently-developed watersheds are a source of elevated turbidity, total suspended solids, and chlorophyll a concentrations in nearshore waters, but these variables tend to decrease with lessening human influence in watersheds (Hertler et al. 2009). In the United States Virgin Islands (USVI), Oliver et al. (2011) demonstrated that distance from human activity was associated with healthier coral reef communities, as coral colony size, density, and species richness were negatively correlated with watershed landscape development around the island of St. Croix. Additionally, sedimentation rates and coral bleaching prevalence have been found to be higher in nearshore environments of the USVI compared to offshore areas and to decrease with distance from shore (Smith et al. 2008).

These findings refer to chronic impacts of low-level sedimentation or nutrient input over extended periods of time; however, acute impacts of heavy sedimentation or nutrient input on water quality and coral reef health have been less frequently documented. In tropical regions, acute events are natural phenomena that occur on a

regular basis in association with seasonal storm activity. However, more intense, frequent storms may be likely due to global climate change (Webster et al. 2005; Knutson et al. 2010), potentially making the impacts of acute events more relevant to coral reef health in the near future. Immediately following a disturbance event, like a large influx of sediment, phytoplankton in the water column can achieve maximal growth rates (Furnas et al. 2005), leading to light reduction to the benthic environment. In laboratory experiments, zooxanthellae within corals exposed to short-term, large volumes of sediment, exhibited photosynthetic stress (Philipp and Fabricius 2003). Additionally, it has been suggested that while some coral species may be more tolerant of low-level, chronic water quality impacts, others could exhibit greater stress under short-term influxes of large volumes of runoff (Philipp and Fabricius 2003). However, field studies of the impacts of acute events on coral reef health are not well documented, and individual species responses to impacts of acute events have tended to be highly variable (Bythell et al. 1993).

In the USVI, water quality is declining, most likely due to rapid development in recent years and poor land-use planning and management (Nemeth and Nowlis 2001; Brooks et al. 2007; Rothenberger et al. 2008). The economy of the territory was approximately 70% tourism based in 2005, increased to 80% in 2010, and development is likely to increase as this industry continues to expand (Jeffrey et al. 2005; van Beukering et al. 2011). Additionally, almost half of surveyed visitors claimed their reason for visiting the USVI was related to coral reefs and the majority would return if the reefs remained at their current status; however, the percent of return visitors drops by almost

half if coral reef quality declines (van Beukering et al. 2011). Therefore, it is essential to assess the impacts of declining water quality on the coral reefs of the USVI because their loss would severely hurt the territory's main source of income. The USVI are also subject to tropical cyclone activity for about five months out of the year (July-November), which could substantially increase the amount of runoff entering the nearshore environment as acute pulses (Rothenberger et al. 2008). A better understanding of the impacts of development and storm activity on coral reef ecosystems is of particular concern in St. Thomas, the most populous of the three islands (U.S. Census Bureau 2011), as it is the most heavily visited.

The southwestern region of St. Thomas contains two, extensively-altered areas where major port activities related to shipping, tourism, and chandlery are concentrated. Additionally, this area has the highest percentage of urban land cover and, historically, had one of the greatest rates of increase in urban cover in St. Thomas (The Cadmus Group 2011). Therefore, this region was targeted to investigate potential impacts of both chronic and acute changes in water quality on coral reef communities across varying levels of human impact. In this study, chronic changes refer to low-level, continuous influxes of runoff whereas acute changes refer to high-volume, transient events on the order of days often associated with tropical storm activity. We hypothesized that acute terrestrial runoff events and chronic impacts from port activities are having negative impacts on coral reefs in this region. Specifically, we hypothesized that sediment loading and nutrient concentrations would be chronically higher in developed nearshore areas and would experience more dramatic increases during acute runoff events, compared to the

offshore region. Additionally, we hypothesized that coral health parameters, such as disease, bleaching, and mortality, in nearshore waters would be more prevalent during both chronic and acute time frames, compared to the offshore area. The results of this study are applicable to other areas in the USVI, in addition to many other areas in the Caribbean, and could potentially aid in the formation or refinement of management actions regarding land-based pollution and port activities.

2. Methods

2.1 Study location

Shallow water coral reefs (less than 30m) in the USVI most commonly form fringing or patch reefs, accounting for about 60% of shallow water substrates (Rothenberger et al. 2008). The most populous area of St. Thomas (83 km²) is the Charlotte Amalie subdistrict (18,481 residents) on the south-central coast (20.1 km² – density of ~920 people/km²; Fig. 1; Jeffrey et al. 2005; U.S. Census Bureau 2011). This area also encompasses the primary ports of St. Thomas, located in Crown Bay and Charlotte Amalie Harbor. The coastal waters adjacent to this sub-district are most likely experiencing the greatest pressure from land-based and marine-based activities on all of St. Thomas due to this context. Therefore, this study includes the nearshore waters associated with this subdistrict, extending south to Flat Cay, Saba Island, and Frenchman's Reef, to examine how gradients in water quality affect coral reef community health (Fig. 1).

Within the study area, three zones containing six sites each were established based upon perceived level of anthropogenic impact (Fig. 1). Perceived level of impact was determined based upon aerial images of the island to locate coastal areas with large amounts of development in addition to personal knowledge of port activities within both the Charlotte Amalie Harbor and Crown Bay. Of the six sites within a zone, four sites were associated with coral reef or coral communities on hardbottom and two sites were located in open water to represent the remaining zone area not associated with targeted reef habitat. The majority of coral monitoring sites were known because of their previous or continued use in other studies. The remaining coral monitoring sites were located by snorkeling areas that appeared to be coral habitat from both aerial imagery and benthic habitat maps (see Fig. 1), and areas were deemed acceptable if estimated coral density was a minimum of 7-8 colonies per square meter between 5 – 10 m depth. Zone I was a nearshore, heavily-impacted pair of embayments encompassing both the Charlotte Amalie Harbor and Crown Bay. Zone II was an intermediately-impacted nearshore zone that included the embayments of Brewers and Perseverance Bay. Zone III was a lower impact zone located immediately offshore of Zones I and II, but on the insular shelf (Fig. 1).

Each zone was sampled for both water quality and coral community parameters from August 2013 to February 2014 with sampling done on August 5-23, September 19-October 1, November 13-16, December 2-14, and February 4-20. Sampling in November and December coincided with acute rain events, defined in this study as an accumulation

of at least 2.5 cm of rain within a 24-hour period. Rainfall accumulation was recorded by a weather station at the Cyril E. King Airport, St. Thomas, USVI (NOAA National Centers for Environmental Information). Water quality and coral reef sampling began within one week after each acute event.

2.2 Water quality sampling

Water quality sampling occurred at all six sites within each zone. Nutrient and total suspended solids (TSS) samples were taken simultaneously at a depth of approximately 1 m below the water's surface following previous methodology (Honisch 2012). Salinity, temperature, dissolved oxygen, pH, turbidity, and chlorophyll were also simultaneously measured using a Conductivity, Temperature, and Depth (CTD) sensor lowered approximately 1 m below the water's surface (Seabird 25 Sealogger CTD, Sea-Bird Electronics, Bellevue, WA, USA). Nutrient samples were analyzed using an autoanalyzer (Astoria Analyzer, Astoria-Pacific, Clackamas, OR, USA) for nitrite, nitrate, orthophosphate, ammonium, total nitrogen, and total phosphorus content. Both nutrient and TSS samples were stored and analyzed following established standard operating procedures of the Environmental Analysis Laboratory (EAL) at the University of the Virgin Islands (EAL 2011; 2012a; 2012b; 2012c; 2014a; 2014b). Nutrient and TSS samples were collected in September, November, and February. Water quality measurements with the CTD sensor were taken in all sampling months but August due to a lack of availability of the instrument. TSS results are not presented as there was not a significant difference among zones ($df = 2/15$, $f = 1.9812$, $p = 0.1724$). Temperature,

dissolved oxygen, conductivity, and pH data are not shown because, although values significantly changed among zones and through time, these variables are related to seasonality. Nitrite ($df = 4/16$, $f = 0.9287$, $p = 0.4719$), nitrate ($df = 4/16$, $f = 0.7535$, $p = 0.5702$), phosphate ($df = 4/16$, $f = 2.2980$, $p = 0.1038$), and ammonium ($df = 4/16$, $f = 1.7693$, $p = 0.1844$) did not show significant differences among any of the treatment levels and are not presented here.

2.3 Sediment deposition

Net sediment deposition was assessed during each sampling month with the deployment of sediment pods (SedPods; Field et al. 2013). SedPods are flat topped, concrete cylinders designed to mimic a coral surface and measure net sediment deposition rather than the total sediment accumulation of conventional traps. Four clean SedPods were deployed at each coral reef site for short, two-day intervals, as it was determined that variance among SedPods within a site increases with time of deployment (R. Ennis and J. Kisabeth, unpublished preliminary data). Collected sediment was filtered, dried, and weighed to determine net sediment deposition, then burned in a muffle furnace to determine the organic, carbonate, and terrestrial compositions (Heiri et al. 2001). Although organic (mean = 67.57%) and carbonate (mean = 30.30%) material made up the majority of bulk material collected, net sediment deposition and the terrestrial component are most relevant to land-based runoff and are the only data included here. Since SedPod surfaces are open to water flow, Plaster of Paris® clod cards were attached to reef substrates at each coral reef site in August and September to

account for any impacts of water flow on deposition. A comparison of clod card weight pre- and post-deployment to before deployment provided an estimate of water flow at each site (Doty 1971; Jokiel and Morrissey 1993; Thompson and Glenn 1994; Boizard and DeWreede 2006). Clod card weights did not significantly differ among zones ($df = 2$, $f = 5.8322$, $p = 0.0541$), so these data are not presented.

2.4 Benthic community assessment

At each coral reef site, four semi-permanently marked 10 m transects were haphazardly established between 5 – 10 m depth to remain on reef structure and maintain depth. A full assessment of the benthic community was performed in August 2013 along all transects using video (Rogers et al. 2001). Video transects were analyzed using Coral Point Count with Excel extensions (CPCe) with random point assignment to establish benthic cover (coral, macroalgae, epilithic algae community, calcareous algae, sponge, gorgonian, cyanobacteria; Kohler and Gill 2008). Potential changes in transient benthic cover (i.e. macroalgae) at each coral reef site were tracked for the remaining sampling months using point intercept methodology to identify cover every 10 cm along each transect using the same cover categories as the video analysis.

2.5 Coral health assessment

Each coral reef site was rapidly assessed during sampling months for coral size, bleaching, disease, partial mortality, and coral-species interactions following established

methodology (Smith et al. 2008; Smith et al. 2013) based on the Atlantic-Gulf Rapid Reef Assessment (Kramer et al. 2005). A coral-species interaction was defined as the presence of another species or entity touching, covering, or growing over live coral tissue. All four semi-permanently marked transects were surveyed as belts of 1 m width. All coral colonies, or up to 75, were recorded on each transect for a total of at least 300 colonies surveyed per site. This number of colonies is able to detect the presence of at least 1% prevalence of a coral health variable at the 95% confidence interval and 1% prevalence is a common level for rare conditions such as coral disease (Calnan et al. 2008). If 75 colonies were recorded prior to finishing a complete transect, the transect was terminated and its length recorded. Complete coral health surveys including colony size, partial mortality, and bleaching were assessed along two of the four transects, while the two remaining transects were assessed solely for the presence of coral disease. Colonies on these transects were identified and those exhibiting signs of disease were sized, the disease identified (Kramer et al. 2005; Bruckner 2007), and the extent (as a percentage) of the coral affected estimated. Partial colony mortality did not significantly differ among zones ($df = 8/18$, $f = 1.3333$, $p = 0.2895$) so these data are not included here.

2.6 Data Analyses

Monthly averages by zone were calculated for all water quality parameters ($n=6$ per zone per month). Due to low concentrations, nutrient data that were measured below the detection limit of the autoanalyzer were set at the minimum detection limit (MDL) of

the instrument. The weight of sediment collected on SedPods was converted to a measure of deposition per SedPod surface area per day of deployment (mg sediment/cm^2 SedPod/day deployment). Burned sediment fractions were converted to percentages of the total composition. Monthly averages by site were calculated for all sediment characteristics ($n=4$ per site per month). All benthic community cover types were calculated by transect as the number of points identified as a cover type out of the total number of points evaluated and expressed as percentages. Coral health metrics were converted to prevalence of the metric in the surveyed population and expressed as percentages. Benthic cover ($n=4$ per site per month) and coral health metrics ($n=2$ per site per month) were converted to monthly averages by site.

When the assumptions of ANOVA were met, Repeated-Measures ANOVA and Tukey HSD post hoc tests, when applicable, were used to determine differences in all water quality parameters among zones and through time. If the assumptions of ANOVA could not be met, non-parametric Friedman's Rank and Wilcoxon pairwise post-hoc tests, when applicable, were used to determine differences among zones and through time. A potential nested effect of site was added to this statistical design to determine differences among zones and through time for all sediment characteristics, benthic cover types, and coral health metrics. Results were considered significant with a p-value less than 0.05. Potential coral community structure and overall benthic cover differences among zones were examined with non-metric multidimensional scaling (nMDS) and similarity percentage analysis (SIMPER) using Primer 6 software (Clarke and Gorley 2006). All data calculations were performed in Microsoft Excel (Microsoft 2011). All statistical

analyses were performed using JMP® 10 Software (SAS Institute Inc.) and Primer 6 (Clarke and Gorley 2006). All figures were created in SigmaPlot 12.3 (Systat Software, San Jose, CA, USA) and Primer 6 (Clarke and Gorley 2006).

3. Results

3.1 Water quality

There were significant interactions of zone and time for the water quality variables total nitrogen, total phosphorus, chlorophyll, and turbidity, which indicated that differences among zones were dependent on the sampling period (Table 1). This pattern may be partly related to periods of heavy rainfall and runoff prior to sampling (Fig. 2). Total nitrogen concentrations tended to increase in the zone of higher potential water quality impact, with Zone I having higher concentrations than the offshore Zone III (Fig. 3a); however, this pattern was influenced by sampling period and was only significant in the month of September, two weeks after heavy rainfall (Fig. 3a). Nearshore zones tended to have higher total phosphorus concentrations than the offshore zone (Fig. 3b), but this was not significant as individual time points varied (Fig. 3b).

Chlorophyll *a* concentrations also followed a nearshore-offshore gradient; however, there was an interaction between zone and time indicating that chlorophyll *a* concentrations depended on the sampling period (Table 1, Fig. 4a). After an acute rainfall event in December (12.45 cm of precipitation between November 30, 2013 and

December 1, 2013; Fig. 2), chlorophyll a concentrations were significantly higher in Zone I compared to Zone III, whereas Zone II had intermediate values (Fig. 4a). Turbidity followed a nearshore-offshore water quality gradient and had a similar interaction between zone and time to chlorophyll a (Table 1). In November and December, turbidity was significantly greater in the nearshore high impact zone than the offshore zone, coinciding with large rain events in those months (Fig. 2, Fig. 4b). Turbidity also significantly increased immediately following a rainfall event totaling 8.92 cm from November 2-3, 2013 (Fig. 4b).

3.2 Sediment deposition

Despite a significant nested effect of site accounting for about 70% of the total variance, all sediment characteristics varied significantly among zones and through time (Table 1). Net sediment and terrigenous material deposition to SedPods tended to not only follow a nearshore-offshore gradient, but was also on average greatest in the predicted higher impact Zone I (Table 1, Fig. 5a and b). Individual time points were variable for both parameters, but net sediment deposition and terrigenous material were greatest in the month of November following that month's acute rainfall event (Table 1, Fig. 5, Fig. 2) and in February coinciding with high wave action from the southeast (average wave height for this study = 1.15 m, February = 1.33 m; <http://www.caricoos.org>) and cruise ship traffic (average ships in port for this study = 1.74, February = 2.57; http://m.cruisett.com/p/US_Virgin_Islands/620-Saint_Thomas).

Sediment deposition and terrigenous sediment content did not vary significantly through time in the offshore low impact zone (Table 1, Fig. 5).

3.3 Benthic cover

All zones were dominated by high cover of macroalgae and epilithic algal communities, leading to poor zone separation in a Bray-Curtis similarity matrix, as indicated by low values of dissimilarity (Table 2). Macroalgae cover was greater in nearshore zones (I and II), significantly so in November, even though a significant nested effect of site was present accounting for about 87% of the total variance (Table 1, Fig. 6a).

Mean coral cover was $16.17\% \pm 0.58\%$ SE and did not significantly differ among zones ($df = 2$, $F = 2.1504$, $p = 0.1190$). However, coral cover diversity (Shannon-Wiener Diversity Index) significantly increased as level of impact in each zone decreased (Table 1, Fig. 6b). There was a significant effect of time on coral cover ($df = 4$, $F = 21.7527$, $p < 0.0001$) and diversity (Table 1), with August having significantly different cover and diversity than all other sampling months. This could potentially be due to differences in sampling methods as August was the only month recorded by video. Although all zones had high abundances of the weedy coral species *Siderastrea siderea* and *Porites astreoides* (characterized by quick growth under sub-optimal conditions; Knowlton 2001; Edmunds 2010; Supplemental Table 1), these species largely contributed to the differentiation of the nearshore high impact zone from the remaining zones (Table 2; Fig.

7a and b). Zone II shared species with both Zone I and III, but was characterized by the addition of high abundances of the longer-lived species *Orbicella annularis* and *Orbicella franksi* (Bak and Engel 1979; Hughes and Tanner 2000; Fig. 7c), as well as branching *Porites* spp. (Table 2, Supplemental Table 1). The offshore low impact zone was differentiated from the nearshore high impact zone by the higher abundance of *Millepora* spp., *Acropora cervicornis*, *O. annularis*, and *Dendrogyra cylindrus* at many of the sites (Table 2, Supplemental Table 1; Fig. 7d).

3.4 Coral reef health

Coral bleaching prevalence was significantly greater in Zone I compared to Zone III (Table 1, Fig. 8a). Coral bleaching prevalence in all zones followed a consistent temporal pattern, significantly increasing in November ($df = 4$, $F = 10.8264$, $p < 0.0001$), immediately following an acute rainfall event and the peak of annual heat stress on October 28, 2013 at 5.26 Degree Heating Weeks, a value sufficient to stimulate the early stages of coral bleaching (<http://coralreefwatch.noaa.gov/vs/data/usvi.txt>).

Zones I and II had significantly more total macroalgae interactions with live coral tissue than Zone III (Table 1, Fig. 8b). There was no significant effect of time on total macroalgae interaction prevalence (Table 1). The nearshore high impact Zone I had a significantly higher prevalence of sediment deposited on coral tissue than the other zones (Table 1, Fig. 8c). There was no difference in the prevalence of sediment deposition on coral tissue through time (Table 1).

4. Discussion

Water quality and coral reef health in the nearshore environment associated with the Charlotte Amalie subdistrict, St. Thomas, USVI, are both chronically and acutely impaired. Total nitrogen concentrations, chlorophyll concentrations, and turbidity were highest in the nearshore high impact zone, but decreased as level of human impact lessened, extending further offshore. This is consistent with previous work that shows that more turbid water and higher chlorophyll concentrations are associated with large amounts of new development in coastal watersheds (Hertler et al. 2009).

Net sediment deposition was also higher in both nearshore zones than the offshore zone exhibiting a strong nearshore-offshore gradient, which has been well documented in both the US Virgin Islands (Rogers 1990; Rothenberger et al. 2008; Smith et al. 2008) and around the world (Haynes et al. 2007; Haapkylä et al. 2011; Dadhich and Nadaoka 2012). Additionally, deposition of total sediments and terrigenous sediments on SedPods increased with human impact in the nearshore waters, most likely attributed to land development. The presence of greater terrigenous sediment content in the nearshore high impact zone supports the suggestion that a combination of poor management practices are contributing to declines in water quality. Land development and planning in the USVI is governed by a two-tier system, dividing the narrow coastal zone (Tier 1) from the steeply-sloped upland areas (Tier 2; Virgin Islands Coastal Zone Management Act). Development regulations differ between tiers and may be more strictly applied within

Tier 1, despite Tier 2 containing the areas naturally more susceptible to soil erosion (WRI and NOAA 2005; Rothenberger et al. 2008). For example, Nemeth and Nowlis (2001) illustrate the lack of enforcement of building practices in Tier 2. Although sediment retention practices had been implemented initially, there was little or no maintenance over the course of the development project rendering them ineffective. Additionally, the development project was poorly planned to begin at the start of the rainy season during peak erosion potential (Nemeth and Nowlis 2001). The coastal area of the high impact Zone 1 (Charlotte Amalie) is located down-slope from an area of similar erosivity, contained the highest percent of impervious land cover, a facilitator of runoff movement (Rothenberger et al. 2008), and was estimated to have the highest potential of erosion due to roads (WRI and NOAA 2005). During periods of heavy rainfall, net sediment deposition, terrigenous sediment content, turbidity, and chlorophyll concentrations substantially increased in both nearshore zones, especially in Zone I, the area of greatest human impact. However, the period of sampling after acute rainfall varied from immediately after the event to up to two weeks, which may have contributed to some of the variability in the response of water quality, such as TN in September, chlorophyll in December, and turbidity in November and December.

The results of this study corroborate previous work documenting the negative impacts of chronic water quality impairment on the health of coral reef ecosystems. Chronic nearshore water quality impairment appears to contribute to nearshore coral reef health decline, as evidenced by increased macroalgae overgrowth, increased sediment deposition on coral tissue, increased coral bleaching prevalence, and decreased coral

diversity. Additionally, these results support previous work suggesting that short-term heavy sediment loads, like those experienced in Zone I, can have impacts on corals equivalent to long-term chronic sedimentation (Fabricius 2005; Weber et al. 2012; Philipp and Fabricius 2003). It also indicates that acute events could in fact be more detrimental to coral reef health, as the coral bleaching stress response was more severe after heavy rainfall than that observed during chronic water quality impairment.

Higher total nitrogen concentrations could be contributing to the higher macroalgae cover and prevalence of overgrowth of corals in the nearshore zones, as nutrient enrichment favors macroalgae growth (Szmant 2002; Fabricius 2005). However, the significant increase in chlorophyll concentrations during acute events could indicate that excess nutrients were instead rapidly taken up and utilized by phytoplankton in the water column (Furnas et al. 2005). A strong positive relationship between sediment loading, macroalgae abundance, and herbivore grazing has been documented previously (Rasher et al. 2012). Therefore, the higher sediment loads to the nearshore zones observed in this study could be a main factor contributing to higher macroalgae cover and overgrowth of coral.

Sediment deposition onto coral tissue and water column turbidity was most prevalent in the nearshore high impact zone and decreased extending offshore. Coral bleaching prevalence prior to and during thermal stress followed the same pattern. Thus, direct deposition of sediment on coral tissue and reduced light availability may also be contributing to the impaired coral reef health state by increasing levels of coral bleaching,

which has been well documented (Nemeth and Nowlis 2001; Fabricius 2005). It has also been suggested that corals exposed to chronic local stressors (i.e. runoff) are unable to recover as rapidly as unexposed corals following a major thermal event (Carilli et al. 2009). Additionally, Sabine et al. (2015) found that tissue regeneration rates of corals at Ruperts Rock, St. Thomas, USVI, located within the high impact Zone I of this study, were about three times slower than sites less impacted by impaired water quality, located within the offshore low impact Zone III of this study. This could indicate that the chronic runoff to the nearshore high impact zone is also affecting the reefs' abilities to recover after stress events.

Climate change impacts, such as increased seawater temperatures, have already contributed to coral reef health decline in the USVI (Miller et al. 2009; Smith et al. 2013). The chronically more turbid and nutrient-enriched water in the nearshore high impact zone may be indirectly contributing to further increased prevalence of coral bleaching. Corals can attempt to compensate for light reduction by increasing endosymbiont density or nutrient enrichment may stimulate higher endosymbiont density; however, it has been suggested that this phenomenon may be detrimental to corals under thermal stress by increasing their susceptibility to bleaching (Cunning and Baker 2012). Corals in the nearshore high impact Zone I exhibited higher bleaching prevalence both prior to and during periods of thermal stress. Peak thermal stress was observed in November which coincided with an acute rainfall event, peak water column turbidity, and peak coral bleaching prevalence, potentially indicating that corals exposed

to impaired water quality are more susceptible to temperature increases associated with climate change.

It has been suggested that as disturbance increases in nearshore environments, only certain coral species will be able to survive the change (Green et al. 2008; Edmunds 2010). Although all sites had equal coral cover, the higher prevalence of inherently hardier coral species and lack of rarer species, such as the threatened species *Acropora* spp. and *Dendrogyra cylindrus*, in the nearshore, high-impact zone could indicate that species composition changes have already occurred in response to the degraded water quality. Additionally, it was noted during diver surveys of the nearshore, highly-impacted sites that there was a large amount of dead *Orbicella* spp. skeleton being overgrown with weedy species, further supporting the suggestion that these reefs have already experienced decline. Furthermore, the analyses of coral compositions among zones indicated that it was, in fact, the prevalence of weedier coral species and lack of *Orbicella* spp. and more diverse communities that distinguished the high impact Zone I from the remaining zones. Therefore, an examination of coral community structure in addition to coral cover and water quality variables may be a more appropriate indicator of coral reef health.

Over long monitoring periods, chronically elevated nutrient concentrations and sediment deposition both contribute to impaired coral reef health and are equally important for monitoring purposes. During heavy rainfall, sediment loading appears to be more influential on coral reef health, as nutrients seemed to be rapidly taken up by

phytoplankton in the water column and may not directly impact the benthic environment. Although the results of this study demonstrate the negative impact of acute events, additional studies focusing solely on the effects of acute rainfall events could provide a more complete picture, as there were only two such events in this study. Additionally, it is suggested that acute event sampling take place as soon as possible after the event has taken place, which was not always feasible in this study and contributed to the low number of acute event samplings. Prevention of excess sediment loading to the nearshore environment should be considered a priority for management agencies in the territory and elsewhere, especially in upland areas on steep slopes most susceptible to erosion. Development restrictions or improved enforcement of existing regulations during the rainy season could also alleviate the severity of acute events during periods of heavy rainfall or tropical storm activity. Considering St. Thomas is one of the most visited ports in the Caribbean, an evaluation of port activity in the Charlotte Amalie Harbor and Crown Bay would also be beneficial to understanding the contribution of cruise ships and similar traffic to changes in water quality and coral reef health (Kisabeth 2014).

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Figure Captions

Figure 1. The southwestern side of the island of St. Thomas, USVI. All watersheds of interest are outlined in bold. Major guts, or streams, are indicated by white lines. Land cover is shown for watersheds of interest and coral reef and colonized hardbottom habitat are shown for the area. Land cover and benthic habitat maps were obtained from NOAA. NOAA land cover classes were grouped into five major categories: impervious surface, natural vegetation (grassland/herbaceous, deciduous forest, evergreen forest, scrub/shrub), no vegetation (unconsolidated shore, bare land), unnatural vegetation (developed open space), and wetland (palustrine forested wetland, palustrine emergent wetland, estuarine forested wetland, estuarine scrub/shrub wetland). Sites in Zone I are

contained within Charlotte Amalie Harbor or Crown Bay Marina [Rupert's Rock (RR), Hassel Island (HI), Hassel Point (HP), Water Island (WI), Charlotte Amalie Harbor (CA), East Gregorie Channel (EG)]. Zone II sites are within Brewers Bay or Perseverance Bay [Brewer's Bay (BB), Black Point (BP), Perseverance Bay East (PE), Perseverance Bay West (PW), Perseverance Bay (PB), Brewers Reference (BR)]. Zone III sites are located in the remaining offshore area within the insular shelf [Frenchman's Reef (FR), Porpoise Rocks (PR), Flat Cay (FC), Saba Island (SI), Porpoise (PO), Saba-Flat (SF)]. The color version of this figure can be found in the online publication.

Figure 2. Rainfall in cm during the study period from August 2013 to February 2014.

Sampling points are represented by triangles. Rainfall data was collected at the Cyril E.

King Airport by the NOAA National Centers for Environmental Information.

Figure 3. Average nutrient concentrations ($\pm$ SEM) among zones and through time. Zones are as follows: I – high impact nearshore, II – intermediate impact nearshore, III –low impact offshore. Letters represent significant differences among all zones and time points as determined by Wilcoxon pairwise tests.

Figure 4. Average chlorophyll *a* and turbidity ($\pm$ SEM) among zones and through time.

Zones are as follows: I – high impact nearshore, II – intermediate impact nearshore, III – low impact offshore. Letters represent significant differences among all zones and time points as determined by Wilcoxon pairwise tests.

Figure 5. Average 2-day SedPods net sediment deposition and terrigenous fraction ($\pm$ SEM) among zones and through time. Zones are as follows: I – high impact nearshore, II – intermediate impact nearshore, III – low impact offshore. Letters represent significant differences among all zones and time points as determined by Tukey HSD tests.

Figure 6. Average macroalgae cover and coral species diversity ($\pm$ SEM) among zones and through time. Zones are as follows: I – high impact nearshore, II – intermediate impact nearshore, III –low impact offshore. Letters represent significant differences among all zones and time points (macroalgae) or among zones (diversity) as determined by Tukey HSD tests.

Figure 7. Non-metric multidimensional scaling (nMDS) plots of coral cover (A). Cover of weedy coral species (*Porites astreoides* and *Siderastrea siderea*) (B), *Orbicella* spp. (C) and *Millepora* spp. (D) are also shown, as they were found to be important in similarity percentages analysis. Bubbles sizes represent percent benthic cover. Site codes as in Figure 1.

Figure 8. Average coral bleaching, total macroalgae overgrowth, and coral-sediment interaction ($\pm$ SEM) prevalence among zones and through time. Zones are as follows: I – high impact nearshore, II – intermediate impact nearshore, III – low impact offshore. Letters represent significant differences among zones as determined by Tukey HSD (sediment) and Wilcoxon pairwise (bleaching, total macroalgae) tests.

Tables

Table 1. Results of statistical analyses testing differences in all parameters among zones, through time, and their interaction. * indicates significance.

Variable	Level	df	F-value	p-value
Total Nitrogen ^b	Zone	2	2.2835	0.1213
	Time	2	54.6582	<0.0001*
	Zone*Time	4	3.8662	0.0131*
Total Phosphorus ^a	Zone	2/9	1.8060	0.2191
	Time	2/8	23.2514	0.0005*
	Zone*Time	4/16	3.9316	0.0208*
Chlorophyll a ^b	Zone	3	26.0641	<0.0001*
	Time	2	7.9796	0.0014*
	Zone*Time	6	5.1417	0.0007*
Turbidity ^a	Zone	2/9	7.6840	0.0113*
	Time	3/7	23.3166	0.0005*
	Zone*Time	6/14	7.4384	0.0010*
Deposition ^a	Zone	2/23	38.6670	<0.0001*
	Site[Zone]	9/33	13.0396	<0.0001*
	Time	4/30	34.3168	<0.0001*
	Zone*Time	8/60	4.9523	<0.0001*
Terrigenous ^a	Zone	2/31	13.7925	<0.0001*
	Site[Zone]	9/31	4.4284	0.0009*
	Time	4/28	12.9657	<0.0001*
	Zone*Time	8/56	2.2752	0.0349*
Macroalgae ^a	Zone	2/36	10.5120	0.0003*
	Site[Zone]	9/36	18.1325	<0.0001*
	Time	4/33	24.7377	<0.0001*

	Zone*Time	8/66	19.3057	<0.0001*
Diversity ^a	Zone	2/33	5.3039	0.0101*
	Site[Zone]	9/33	3.2358	0.0064*
	Time	4/30	32.2920	<0.0001*
	Zone*Time	8/60	1.9854	0.0637
Bleaching ^b	Zone	2	3.3403	0.0396*
	Site[Zone]	9	2.0814	0.0385*
	Time	4	10.8264	<0.0001*
	Zone*Time	8	1.2635	0.2717
Interaction – Macroalgae ^b	Zone	2	29.7629	<0.0001*
	Site[Zone]	9	9.3308	<0.0001*
	Time	4	2.3438	0.0602
	Zone*Time	8	0.9064	0.5146
Interaction – Sediment ^a	Zone	2/12	4.7897	0.0296*
	Site[Zone]	9/12	1.6541	0.2052
	Time	4/9	1.6554	0.2431
	Zone*Time	8/18	0.5378	0.8131

^a Repeated measures ANOVA

^b Friedman's rank test

Table 2. Similarity percentages (SIMPER) matrix between zones for overall benthic cover and coral cover.

Test	Benthic		Coral	
Strata	Zone I	Zone II	Zone I	Zone II
Zone II	21.20		48.78 ^{A, C, D}	
Zone III	29.52	26.54	55.50 ^{B, C, D}	60.12 ^{A, B, D}

Superscripts represent the coral species that contributed most to dissimilarity in sequentially decreasing importance.

A Orbicella annularis

B Millepora alcicornis

C Siderastrea siderea

D Porites astreoides

Supplemental Information

Table 1. Coral community composition at each site. Composition was calculated as number of corals of each species from permanently established video transects at the beginning of the study period.

Species	HI	HP	RR	WI	BB	BP	PE	PW	FC	FR	PR	SI
<i>Acropora cervicornis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	1.25
<i>A. palmata</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
<i>A. agaricites</i>	0.10	0.23	0.08	0.00	0.23	0.05	0.03	0.00	0.05	0.10	0.03	0.00
<i>Agaricia</i> spp.	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Colpophyllia natans</i>	0.03	0.00	0.35	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00
<i>Dendrogyra cylindrus</i>	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.15	0.30	0.88	0.05
<i>Diploria labyrinthiformis</i>	0.03	0.13	0.00	0.00	0.08	0.08	0.00	0.00	0.18	0.00	0.10	0.05
<i>Pseudodiploria strigosa</i>	0.03	0.43	0.00	0.00	0.08	0.00	0.13	0.08	0.08	0.05	0.18	0.13
<i>Dichocoenia stokesii</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00
<i>Eusmilia fastigiata</i>	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.03	0.00	0.00	0.00	0.00
<i>Manicina areolata</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
<i>Madracis decactis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
<i>M. formosa</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
<i>M. mirabilis</i>	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.28	0.03	0.08	0.00	0.00
<i>Meandrina meandrites</i>	0.03	0.10	0.00	0.03	0.00	0.05	0.10	0.08	0.05	0.00	0.03	0.00
<i>Montastraea cavernosa</i>	0.70	0.48	0.03	0.03	0.00	0.15	0.10	0.03	0.13	0.05	0.23	0.35
<i>Orbicella annularis</i>	0.08	0.25	0.23	0.10	5.10	0.60	0.00	1.05	1.45	0.10	0.23	0.03
<i>O. annularis</i> species complex	0.00	0.00	0.00	0.00	0.03	0.13	0.00	0.03	0.03	0.00	0.03	0.00
<i>O. faveolata</i>	0.13	0.08	0.05	0.05	0.18	0.18	0.08	0.00	0.00	0.00	0.00	0.00
<i>O. franksii</i>	0.28	0.00	0.43	0.15	0.38	0.48	0.08	0.53	0.13	0.03	0.03	0.05
<i>Porites astreoides</i>	0.73	1.48	1.50	0.78	1.53	1.10	0.73	1.45	0.55	0.53	1.35	0.18
<i>P. branneri</i>	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.03	0.00	0.00	0.00
<i>P. divaricata</i>	0.00	0.00	0.00	0.10	0.08	0.15	0.48	0.15	0.08	0.05	0.00	0.00
<i>P. furcata</i>	0.05	0.00	0.00	0.00	0.05	0.00	0.18	0.05	0.13	0.05	0.00	0.00
<i>P. porites</i>	0.35	0.00	0.38	0.23	0.43	0.33	0.30	0.20	0.08	0.05	0.03	0.03
Branching <i>P.</i> spp.	0.05	0.00	0.00	0.00	0.08	0.05	0.15	0.18	0.10	0.08	0.00	0.00
<i>Siderastrea radians</i>	0.03	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.08	0.08
<i>S. siderea</i>	1.05	2.70	1.73	0.58	0.40	0.63	1.50	0.45	1.13	1.68	1.10	0.60
<i>Stephanocoenia intersepta</i>	0.03	0.00	0.05	0.00	0.03	0.03	0.00	0.03	0.03	0.05	0.00	0.00
<i>Millepora alcicornis</i>	0.00	1.18	0.00	0.00	0.05	0.05	0.13	0.45	2.40	0.38	1.70	0.58

<i>M. complanata</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.40	0.03
Coral spp.	0.00	0.00	0.03	0.00	0.03	0.00	0.00	0.03	0.03	0.00	0.00	0.00