Marine Pollution Bulletin 95 (2015) 253–264

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Environmental conditions influence tissue regeneration rates in scleractinian corals

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ARTICLE INFO

Article history:
Received 17 October 2014
Revised 5 April 2015
Accepted 10 April 2015
Available online 13 May 2015

Keywords:
Coral lesions
Tissue regeneration
Water flow
Turbidity
U.S. Virgin Islands
Orbicella annularis

ABSTRACT

Natural and anthropogenic factors may influence corals' ability to recover from partial mortality. To examine how environmental conditions affect lesion healing, we assessed several water quality parameters and tissue regeneration rates in corals at six reefs around St. Thomas, US Virgin Islands. We hypothesized that sites closer to developed areas would have poor water quality due to proximity to anthropogenic stresses, which would impede tissue regeneration. We found that water flow and turbidity most strongly influenced lesion recovery rates. The most impacted site, with high turbidity and low flow, recovered almost three times slower than the least impacted site, with low turbidity, high flow, and low levels of anthropogenic disturbance. Our results illustrate that in addition to lesion-specific factors known to affect tissue regeneration, environmental conditions can also control corals' healing rates. Resource managers can use this information to protect low-flow, turbid nearshore reefs by minimizing sources of anthropogenic stress.

1. Introduction

Coral reefs are increasingly affected by natural and anthropogenic processes that cause partial mortality in scleractinian corals (Gardner et al., 2003; Hughes, 1984; Rogers and Miller, 2006; Smith et al., 2008). Both acute and prolonged stresses acting on a reef can cause lesions, including storm damage (Rogers et al., 1982), diseases (Brandt et al., 2013), predation (Rotjan and Lewis, 2008), algal overgrowth (Jompa and McCook, 2002), sedimentation (Bak and Engel, 1979; Rogers, 1983), and boat groundings (Lirman, 2000). The resulting lesions are characterized by the loss of tissue and exposure of skeleton, which may also be damaged depending on the severity of the injury (van Woesik, 1998). The ability of corals to recover from partial mortality has been documented in early experiments by Bak et al. (1977), Bak and Steward-Van Es (1980), and Hughes (1984). These studies as well as more recent papers (e.g., van Woesik, 1998; Fisher et al., 2007) demonstrated that the rate and degree of healing can vary under the influence of a number of intrinsic and extrinsic factors. Regeneration rates are known to be species-specific and can also be affected by lesion size, shape, and position (Bak et al., 1977; Meesters et al., 1992, 1996, 1997; Hall, 1997; Cróquer et al., 2002).

While this information has been confirmed by several studies, less is known about the potential effects of environmental conditions on lesion regeneration. The few studies that have investigated associations between environmental factors and lesion recovery rates have targeted only one specific variable rather than a suite of water quality parameters. For example, coral colonies located in areas with high sedimentation rates have been observed to recover from lesions slower than those in areas with low sediment accumulation (Meesters et al., 1992; Rogers, 1983; Cróquer et al., 2002; Nugues and Roberts, 2003). Sediment deposition can slow lesion recovery by increasing stress on corals through hypoxia and bleaching (Wesseling et al., 2001; Fabricius, 2005). Small terrigenous particles are particularly easily trapped in corals' mucous layers and can prevent light from reaching corals, impairing photosynthesis and hindering tissue regeneration (Weber et al., 2006). However, the effects of sediment deposition can vary with coral species, as some species are more adept than others at rejecting particles and may not suffer from reduced regeneration rates when covered with sediment (Meesters et al., 1992).

Aside from the effects of sedimentation on lesion recovery, much remains unknown about how environmental factors affect tissue regeneration, as results from studies on the subject have

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http://dx.doi.org/10.1016/j.marpolbul.2015.04.006
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been inconsistent. Algal colonization of lesion area has been shown to have negative effects on lesion recovery in some cases (Kramarsky-Winter and Loya, 2000; Fisher et al., 2007) but no effect in others (Bak et al., 1977; Rogers et al., 1982; van Woesik, 1998; Vermeij et al., 2010). Furthermore, it is unknown whether impacts such as habitat degradation and anthropogenic pollution are reliable indicators of regeneration potential at a site. Fisher et al. (2007) found that corals regenerated tissue significantly faster at protected reefs than at reefs located near developed, urbanized areas that had high input of pollution and nutrients. In contrast, Lester and Bak (1985) found the opposite: corals regenerated lesions faster at a site that received industrial discharge from a power plant than at a pristine reef with minimal anthropogenic disturbance. These results ran contrary to their expectations, and a temperature difference between the two sites was cited as a possible explanation. Inconsistencies in corals' regenerative capabilities in different environments emphasize the need for further research into how tissue regeneration is influenced by environmental conditions.

Lesions can impair corals' growth and reproductive activity and can increase their susceptibility to bleaching and disease (Hughes and Connell, 1987; Jayewardene, 2010; Meesters et al., 1994). Furthermore, corals that sustain lesions are more vulnerable to receiving repeated injuries in the future (Hughes, 1984). Lesions can even reduce genetic diversity by causing complete mortality or fission, whereby the growing lesion causes the coral to subdivide into genetically identical colonies (Hughes, 1984; Hughes and Jackson, 1985). Additionally, areas of partial mortality are susceptible to colonization by macroalgae or bioeroding organisms such as boring sponges that can weaken the coral skeleton and cause further fragmentation (Meesters and Bak, 1993; McCook et al., 2001). With corals facing such severe threats, it is of the utmost importance that we fully understand the specific controls affecting their ability to return to a healthy state. This information will facilitate the work of natural resource managers in mitigating potential stressors to foster better water quality in which corals can thrive. Reefs that are identified as highly threatened or having low resilience can then be managed more appropriately to improve tissue regeneration rates in corals.

The boulder star coral *Orbicella annularis* (formerly *Montastraea annularis*) is a dominant framework-building species in the U.S. Virgin Islands (USVI) and the wider Caribbean (Goreau, 1959; Sheppard, 1982; Smith et al., 2008). Yet this important species is in decline in the USVI (Edmunds and Elahi, 2007; Miller et al., 2009) and was recently listed as threatened under the Endangered Species Act (ESA) of 1973, as amended (Anonymous, 2014). In the past few years, over 60% of corals surveyed in the Territorial Coral Reef Monitoring Program in the USVI exhibited some degree of partial mortality, with 10–15% showing signs of recent mortality that occurred within the past year (Smith et al., 2013). It is clear that corals in this region are suffering from what is likely a combination of stresses causing lesions on coral surfaces. The goal of the present study was to assess how the environment affects recovery of coral lesions in the primary ecosystem engineer *O. annularis* in the USVI. A water quality gradient exists around St. Thomas, with sedimentation and macroalgal cover decreasing following a nearshore to offshore gradient (Smith et al., 2008). Coral cover and coral health generally increase along this gradient, with lower incidence of bleaching and partial mortality observed at sites farther from shore (Smith et al., 2008). This study used a total of six research locations, including nearshore and offshore reefs. It was hypothesized that the nearshore study sites would be characterized by poorer water quality due to their proximity to land-based anthropogenic stresses, and that this would slow recovery of coral lesions at these sites.

2. Materials and methods

2.1. Study area

The study was conducted from November 2012 to January 2013 at reefs located on the south side of St. Thomas, USVI (18°20′N, 64°55′W, Fig. 1). The six sites represented a variety of environmental conditions and levels of water quality around the island, including varying distances from shore and along a longitudinal gradient. All sites were shallow fringing reefs (maximum depth of 7–10 m) dominated by the reef-building scleractinian corals *O. annularis*, *O. faveolata*, and *O. franksi*. Three sites were nearshore locations (<0.25 km from shore): Brewers Bay (BB), Perseverance Bay (PB), and Rupert's Rock (RR); and three were reefs adjacent to uninhabited rocks or cays ("offshore" sites, 3–5 km from shore): Flat Cay (FC), Porpoise Rocks (PR), and Saba Island (SI). Coral cover at these sites ranges from 12% to 24% and is not significantly different among sites (Ennis, 2014). FC and SI are frequented by several of the SCUBA diving companies on St. Thomas; moorings present at these locations make them popular diving destinations. Additionally, FC is located downstream of a busy commercial port and sewage outflow (Smith et al., 2012). The third offshore site was PR, an area of high surge with waves commonly breaking over the rocks. RR is located adjacent to a cruise ship dock in Charlotte Amalie Harbor. The dock can hold up to four cruise ships at a time, which have been observed to churn up sediment in the harbor, making the water very turbid (authors, unpub. observations). Of the other two nearshore sites, BB is more sheltered from wave action but is fronted by a beach that is highly frequented with many visitors and high traffic. PB is more exposed to wind and waves to the east and can experience moderately strong currents, but the beach at PB is not easily accessible and is not as developed as BB.

2.2. Coral lacerations

Experimental lesions were created on 10 *O. annularis* colonies at least 10 cm in maximum diameter (mean diameter 14.5 ± 3.7 cm,

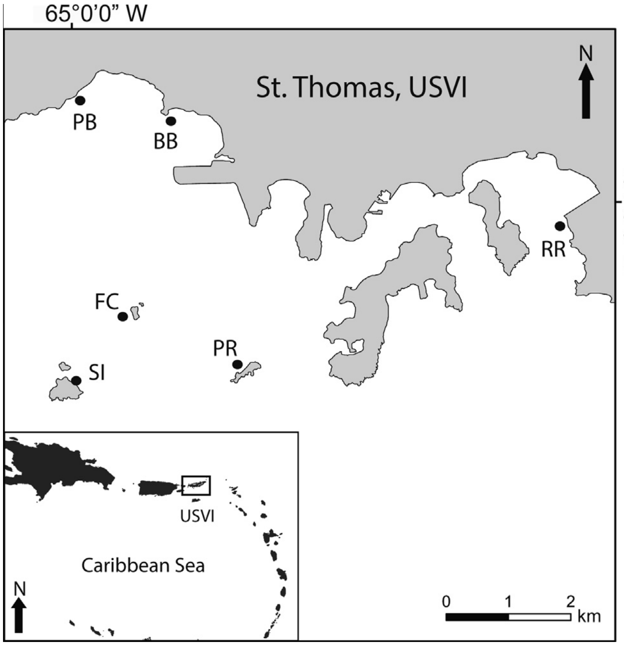

Fig. 1. Locations of study sites around St. Thomas, US Virgin Islands: Brewers Bay (BB), Flat Cay (FC), Perseverance Bay (PB), Porpoise Rocks (PR), Rupert's Rock (RR), and Saba Island (SI). Sites were varying distances from shore and were exposed to different levels of water quality and levels of impact.

mean ± SE) at a depth of 6 m at each site. No colonies had any visible signs of bleaching, disease, or other negative health impacts, and all were located at least 1 m apart from each other. The corals were photographed using a Canon G12 camera fitted with an underwater housing. Colony size in a planar view was assessed from these initial photographs using image analysis software. A scraping laceration was inflicted on each colony using a 1.5 cm diameter chisel to remove a roughly circular area of tissue about 3 mm deep down to the skeleton. Mean initial lesion area was 3.7 ± 0.09 cm^2 (hereafter, mean ± SE), which resulted in removal of polyps to the skeleton. Mean ratio of lesion area to overall colony area was 2.9 ± 0.22%. Mean lesion perimeter was 7.23 ± 0.10 cm. All lesions were created in the center of the colony and were completely surrounded by living tissue. Colonies were re-photographed on days 3, 8, 14, 20, 31, 40, 48, and 64 after initial lesion creation, using a ruler in the frame for scale. Any algae or sediment that settled in the lesion areas was not disturbed during the surveys. Photographs were analyzed using NIH ImageJ 1.45s software, where the lesion borders were traced and areas and perimeters were calculated. Lesion recovery was observed to be a multi-step process, involving growth of new tissue in the site of the injury, formation of new complete corallites and polyps, and return of pigmentation.

2.3. Environmental characterization

2.3.1. Water flow

Clod cards were used to determine water current strength at each site (McClanahan et al., 2011). This technique is based on the principle that water motion causes molded calcium sulfate "clods" to dissolve to a fraction of their initial weight due to oscillatory flow and unidirectional current. Clods were made following the methodology of Doty (1971), which involved mixing 50 g of plaster of paris (DAP) for every 45 ml of water, resulting in clods that were 80 ± 1 g. The clods were glued to 5 × 7 cm plastic cards with waterproof contact cement and attached to lead weights. Experimental clods were arranged on reef substrate near each transect; control clods were placed in a weighted and covered 20 L bucket that was tied down to the substrate, preventing water flow from acting on the controls. A 1 cm diameter hole was drilled through the side of each bucket to maintain temperature and salinity of the water inside and to allow dissolved material to exit, preventing saturation of the water (Jokiel and Morrissey, 1993). The clods were retrieved after 24 h. No evidence of abrasion or predation was seen on the clods.

Dry weight lost by the clods was converted to a percentage of the initial weight to account for the small differences in starting weights. Dissolution values were obtained by determining differences in loss between clods exposed to water flow and clods in calm-water (control) conditions, allowing water movement to be compared across sites (Doty, 1971). Three batches of clods were created using identical methods, and one trial was deployed each month that the lesion recovery study was conducted.

2.3.2. Sedimentation

Three sediment traps were installed at each site to measure trap accumulation as a proxy for sedimentation rates. The PVC cups (height = 20.3 cm, aperture = 5.0 cm) were suspended 50 cm above the substrate and were changed every three to four weeks. Upon collection, loss-on-ignition analysis was conducted using a muffle furnace to combust samples first at 550 °C and then at 950 °C, to determine percent composition of organic, carbonate, and terrestrial material (Heiri et al., 2001). Weights of each component were converted to flux rates by taking into account the size of the traps and duration of collection period.

2.3.3. Water quality measurements

Water quality parameters were measured approximately every two weeks using a CTD Profiler (Sea-bird Electronics Sealogger, Model SBE 25) with a sampling rate of 8 Hz. Variables measured were temperature (SBE 3F), conductivity (SBE 4C), pressure (SBE 29), and dissolved oxygen (SBE 43), with chlorophyll and turbidity measured fluorometrically with an attached fluorometer (WETLabs Model ECO-FLU). Conductivity and pressure served as proxies for salinity and depth, respectively. The instrument was deployed from the boat to the depth of the reef to record a full profile from surface to substrate. The data were clipped to analyze the bottom meter (approximately 4.5–5.5 m depth), to represent the portion of the water column directly affecting the corals.

2.4. Data analyses

Statistical analysis was performed using JMP Version 10.0 (SAS Institute) with alpha = 0.05 for all tests. Site differences in lesion perimeter and ratio of lesion size to coral size were tested via one-way ANOVAs. Lesion recovery rates ($mm^2\,d^{-1}$) were determined by dividing the amount of tissue recovered for each lesion by the number of days between each successive set of measurements. Repeated-measures ANOVA (RM ANOVA) tested for differences in recovery rates among sites over time, considering lesion perimeter and the ratio of initial lesion area: colony area as covariates (Sokal and Rohlf, 1995). After running the repeated-measures analysis, a two-way ANOVA model was run looking at the site $*$ time interaction with a post hoc Tukey Honestly Significant Difference (HSD) test.

Sediment flux was divided into its components of organic, carbonate, and terrestrial flux. Accumulation of each component was compared across sites and sampling periods using RM ANOVA. A two-way ANOVA with a Tukey HSD test served as a post hoc analysis. Differences in mean clod card dissolution were analyzed in the same manner. Site differences in water quality parameters measured by the CTD were tested via one-way ANOVAs with Tukey HSD and nonparametric Kruskal–Wallis tests for post hoc analyses. A Principal Components Analysis (PCA) was also run, including all environmental parameters. The first two principal components were analyzed to determine which parameters contributed most to water quality differences among sites. Pearson's partial correlation analysis was performed to test for significant correlations between all pairs of variables. Finally, multiple regression examined the effects of environmental variables on lesion regeneration rates. In this analysis, effects of the variables that contributed most strongly to site differences were examined. Total sediment flux was used rather than the individual components to summarize each site.

3. Results

3.1. Environmental data

The PCA (Fig. 2) revealed that carbonate and terrestrial sediment flux contributed the most to Principal Component (PC) 1, and that water flow and dissolved oxygen were the strongest contributors to PC 2. These two PCs accounted for 88% of the variance ($p < 0.05$). Several pairs of variables were significantly correlated (Table 1). These included temperature with each component of sediment flux; chlorophyll with water flow; dissolved oxygen with organic flux; and salinity with terrestrial flux. Additionally, when overall sediment flux was substituted for the three individual flux components, there was no significant correlation between this parameter and the rest of the variables ($r = 0.49$; $p = 0.3245$). Overall sediment flux was used to summarize each site in the

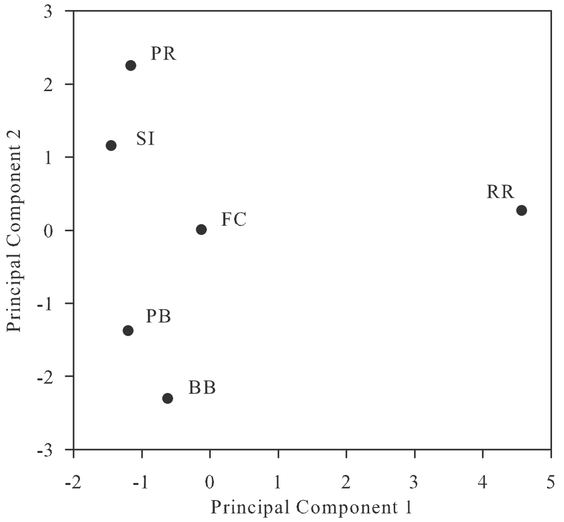

Fig. 2. Results of the Principal Components Analysis (PCA) showing separation of study sites due to environmental factors. Carbonate and terrestrial sedimentation contributed most strongly to the first principal component, and water flow and dissolved oxygen contributed the strongest to the second principal component.

Table 1
Pairwise correlation analysis of environmental variables.

Variable 1	Variable 2	Correlation	*P*
Chlorophyll	Temperature	−0.3791	0.4586
Turbidity	Temperature	−0.5415	0.2671
Turbidity	Chlorophyll	0.5822	0.2254
Salinity	Temperature	−0.6508	0.1616
Salinity	Chlorophyll	0.6453	0.1664
Salinity	Turbidity	0.6939	0.1262
Dissolved oxygen	Temperature	−0.6707	0.1448
Dissolved oxygen	Chlorophyll	−0.3199	0.5366
Dissolved oxygen	Turbidity	−0.1079	0.8388
Dissolved oxygen	Salinity	0.0241	0.9639
Organic flux	Temperature	−0.9519	0.0034*
Organic flux	Chlorophyll	0.1431	0.7868
Organic flux	Turbidity	0.387	0.4485
Organic flux	Salinity	0.4173	0.4104
Organic flux	Dissolved oxygen	0.8455	0.0340*
Carbonate flux	Temperature	−0.991	0.0001*
Carbonate flux	Chlorophyll	0.2831	0.5866
Carbonate flux	Turbidity	0.4594	0.3594
Carbonate flux	Salinity	0.6238	0.1857
Carbonate flux	Dissolved oxygen	0.7222	0.1050
Carbonate flux	Organic flux	0.9548	0.0030*
Terrestrial flux	Temperature	−0.8616	0.0274*
Terrestrial flux	Chlorophyll	0.2426	0.6432
Terrestrial flux	Turbidity	0.6784	0.1385
Terrestrial flux	Salinity	0.8117	0.0498*
Terrestrial flux	Dissolved oxygen	0.4785	0.3370
Terrestrial flux	Organic flux	0.7666	0.0754
Terrestrial flux	Carbonate flux	0.8682	0.0249*
Water flow	Temperature	0.241	0.6455
Water flow	Chlorophyll	−0.8532	0.0307*
Water flow	Turbidity	−0.7967	0.0578
Water flow	Salinity	−0.526	0.2838
Water flow	Dissolved oxygen	0.4147	0.4137
Water flow	Organic flux	−0.0609	0.9087
Water flow	Carbonate flux	−0.1161	0.8266
Water flow	Terrestrial flux	−0.2253	0.6678

* Indicates significant correlation ($p < 0.05$).

Table 2
Results of multiple regression examining effects of environmental variables on lesion recovery rates, including Variance Inflation Factor (VIF) scores.

Effect	*F*	*P*	VIF
Whole model	3216.21	0.0132*	.
Water flow	7123.27	0.0075*	5.88
Dissolved oxygen	1910.40	0.0146*	4.66
Turbidity	429.58	0.0307*	3.99
Total sediment flux	24.05	0.1281	5.98

* Indicates significant result ($p < 0.05$).

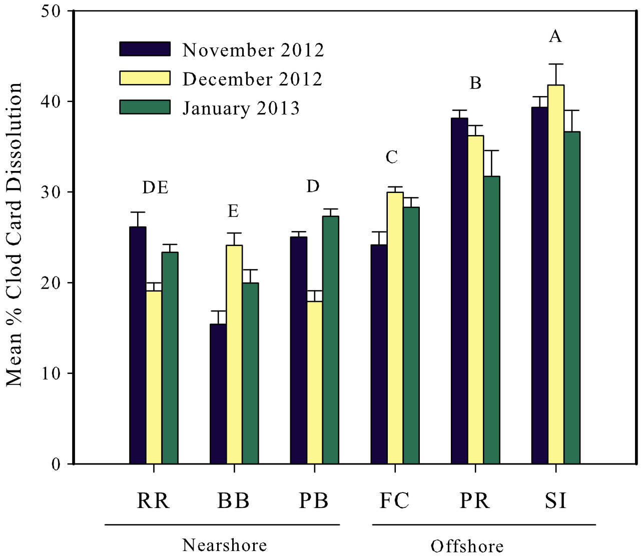

Fig. 3. Mean clod card dissolution as a percentage of original clod card weight ± SE for each month. Means labeled with the same letter are not significantly different (Tukey HSD post hoc test). $N = 5$ clod cards for each trial at each site.

multiple regression analysis, as carbonate and terrestrial fluxes contributed almost equally to the first PC. The regression considered the effects of water flow, sedimentation, and turbidity, which were significantly different among sites, and dissolved oxygen, which also contributed strongly to site differences along the second PC. Water flow, turbidity, and dissolved oxygen were significantly associated with lesion recovery rates across sites, with water flow accounting for most of the variance ($R^2 = 0.99$, $p < 0.05$, Table 2); however, there was no significant association between lesion healing rates and sedimentation. Variance Inflation Factor (VIF) scores were also analyzed for each of the independent variables in the multiple regression. High VIFs (>10) indicate collinearity among variables. All independent variables included in the model had low VIF scores (<10), indicating that these parameters did not have a strong degree of collinearity with each other.

Water flow increased along a nearshore to offshore gradient (Fig. 3). Clod card dissolution differed by site ($F_{5,24} = 92.63$, $p < 0.0001$) but not by trial. Only PB and BB showed an effect of an interaction of site $*$ trial on dissolution ($F_{9.6,46.2} = 7.20$, $p < 0.0001$), each having one trial different than the other two. This indicates that all three offshore sites are consistently well flushed due to constant exposure to the prevailing wind and current direction, while RR has consistently low flow due to a high level of protection within the inner harbor.

RR had the highest total sedimentation regime, showing the greatest accumulation of terrestrial as well as carbonate material (Fig. 4). However, terrestrial flux at SI was not significantly lower than RR due to the high variance associated with the latter site. Organic flux did not differ by site (Table 3). Total sediment, terrestrial, and organic accumulation increased with time at all sites (Table 4). Indicative of resuspension activity, carbonate made up the greatest proportion of sediment collected at each site and increased with time to varying degrees across sites.

Turbidity was the only water quality parameter measured by the CTD that was significantly different among sites, being highest at RR and lowest at SI and FC (Tables 5 and 6). Turbidity remained relatively constant throughout the study.

3.2. Lesion recovery rates

Lesions began to show signs of healing within three days after infliction. During the first week, a layer of new white tissue accumulated at a rate of 11.1 ± 0.88 $mm^2 d^{-1}$ (mean ± SE). These initial rates varied by site, from 5.0 ± 1.44 $mm^2 d^{-1}$ at RR to 17.5 ± 1.06 $mm^2 d^{-1}$ at SI, a difference of a factor of 3.5. Over the following weeks, recovery slowed as the tissue began to take shape and new corallites developed. Many of the corallites formed in the same locations that previous corallites had been positioned. However, in some instances new corallites were observed to form wherever there was sufficient space and, as Meesters et al. (1992) observed, these had a different orientation than the neighboring corallites (Fig. 5). Corallite development was followed by the return of pigmentation. The time elapsed for complete lesion regeneration ranged from two weeks to over two months, with 85% of lesions having completely regenerated tissue by the end of the study. The healing process generally occurred from the outside to the inside, toward the center of the injury, though in some cases settlement of sediment particles or algae colonization

Table 3
Results of repeated-measures ANOVA examining variations in sediment accumulation among sites and sampling months.

Component	Effect	NumDF	DenDF	*F*	*P*
Total					
	Site	5	9	21.38	0.0001*
	Time	1.13	10.19	63.23	0.0001*
	Site* time	5.66	10.19	2.78	0.0742
Terrestrial					
	Site	5	9	24.93	0.0001*
	Time	2	18	7.11	0.0053*
	Site* time	10	18	1.21	0.3465
Organic					
	Site	5	9	1.77	0.2162
	Time	1.13	10.19	27.22	0.0003*
	Site* time	5.66	10.19	0.91	0.5231
Carbonate					
	Site	5	9	18.76	0.0002*
	Time	1.18	10.67	74.56	0.0001*
	Site* time	5.92	10.67	4.01	0.0239*

* Indicates significant result ($p < 0.05$).

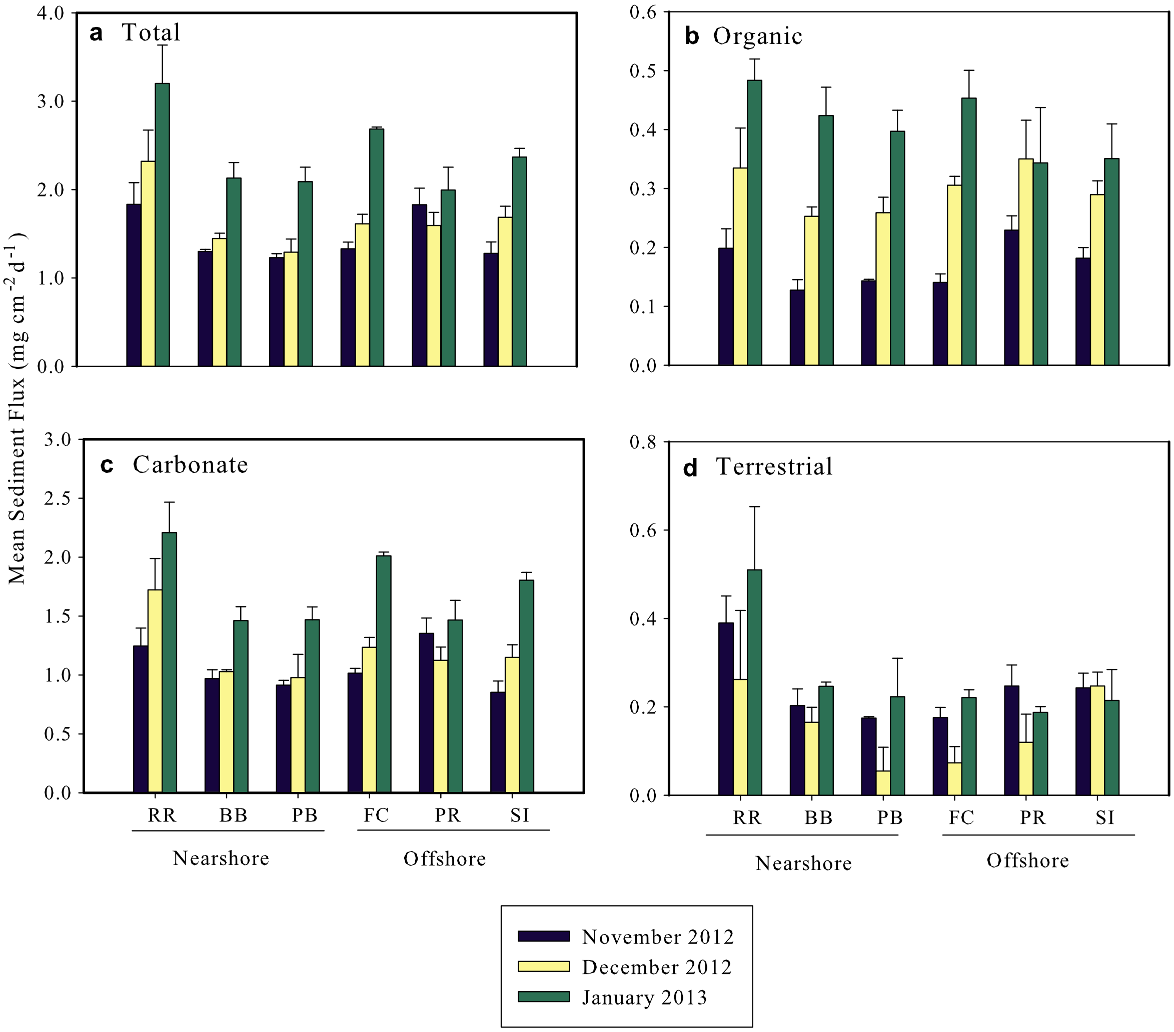

Fig. 4. Mean total, organic, carbonate, and terrestrial sediment accumulation ± SE for each site. $N = 3$ for each month at each site.

Table 4
Results of repeated-measures ANOVA post hoc tests of differences in sediment accumulation by site and over time (site codes as in Fig. 1). Uppercase letters signify differences among months; lowercase letters signify differences among sites. Blanks indicate no significant difference among factors.

Sediment component	Month	Time comparisons	Site comparisons					
			RR	BB	PB	FC	PR	SI
Total			a	b	b	b	b	b
	November 2012	B						
	December 2012	B						
	January 2013	A						
Terrestrial			a	ab	b	b	b	ab
	November 2012	A						
	December 2012	B						
	January 2013	A						
Organic								
	November 2012	C						
	December 2012	B						
	January 2013	A						
Carbonate								
	November 2012		cde	e	e	de	bcde	e
	December 2012		abcd	de	e	cde	cde	cde
	January 2013		a	bcde	bcde	ab	bcde	abc

Table 5
Results of statistical analyses comparing CTD parameters across sites.

Parameter	N	$F(\chi^{2a})$	P
Temperature	24	0.26[a]	0.9983
Salinity	18	1.53[a]	0.9086
Dissolved oxygen	24	0.10	0.9910
Chlorophyll	24	1.97	0.1320
Turbidity	18	7.77	0.0018[*]

[a] Indicates where Kruskal-Wallis (χ^2) test was performed rather than one-way ANOVA (F). Degrees of freedom were 5 for all comparisons.
[*] Indicates significant result ($p < 0.05$).

appeared to prevent tissue expansion in certain parts of the lesion area. A mixture of green turf algae and filamentous algae colonized some lesions beginning 1–3 weeks into the study, affecting nine lesions among the corals at the nearshore sites. Complete recovery was prevented in five of these injuries (56%); the remaining four lesions were able to recover despite the presence of algae.

Some lesions initially grew larger before beginning to recover, as the tissue bordering the injury retracted before the area stabilized. This occurred in 12 lesions (20%) beginning on day 3 after lesions were created. However, the lesion growth was temporary and by the end of the second week, 11 of those 12 lesions had begun to shrink. The exception was one lesion at PR that expanded and after 3 weeks was 64% larger than its initial size. A thick layer of turf algae colonized the area and trapped sediment particles, shading the surrounding healthy polyps and appearing to cause their mortality. Because this lesion expanded instead of recovering, it was excluded from the tissue regeneration analysis.

There were notable site differences in percentage of completely healed lesions and degree of recovery, with 0% of lesions fully healed at RR (36% total recovered area) and 70% completely regenerated at SI (83% total recovered area). Lesion recovery rates were significantly different between SI (6.43 ± 0.95 $mm^2\ d^{-1}$) and RR (2.34 ± 0.18 $mm^2\ d^{-1}$), while the other sites were not different from either of these sites or each other (Fig. 6). Additionally, regeneration was fastest during the first three days at all sites, after which rates dropped and remained steady similarly across all sites (Table 7, Fig. 7).

Although the ratio of initial lesion area to colony area differed significantly among sites ($F_{5,53} = 4.88$, $p = 0.0009$), this parameter did not significantly affect lesion recovery rates when considered in the analysis ($p > 0.05$). Initial lesion perimeter also varied significantly with site ($F_{5,53} = 10.24$, $p < 0.0001$), being largest at RR, PR, and SI and smallest at FC. Lesion perimeter did significantly affect lesion recovery rates in the RM ANOVA analysis ($F_{1,44} = 27.02$, $p < 0.0001$, Table 7). There was also a significant interaction between time and initial lesion perimeter, as perimeter had a positive effect which was strongest in the first three days and lower thereafter, except during days 14–20, during which it had a negative effect ($F_{7,38} = 5.09$, $p = 0.0004$).

4. Discussion

4.1. Effects of water quality on lesion recovery rates

Anthropogenic activities leading to reduced water quality cause substantial stress to reefs in the USVI (Rogers, 1990; Gray et al., 2008). Development in upland areas disturbs soils and results in high volumes of eroded material running down steep slopes and unpaved roads to marine areas, especially during heavy rainfall (Ramos-Scharron and MacDonald, 2005). High input of such land-based sources of pollution has been shown to degrade health of nearshore reefs, with impact tapering off with increasing

Table 6
Means of water quality parameters (±SE) measured by CTD for each sampling period.

Parameter	Time 1 1 November 2012	Time 2 15 November 2012	Time 3 3 December 2012	Time 4 17 January 2013
Temperature (°C)	29.3 (0.03)	28.9 (0.03)	28.6 (0.02)	26.1 (0.06)
Salinity (PSU)	35.4 (0.001)	35.0 (0.01)	35.0 (0.01)	N/A
Dissolved oxygen ($ml\ l^{-1}$)	6.0 (038)	5.4 (0.21)	7.7 (0.48)	6.5 (0.03)
Chlorophyll ($\mu g\ m^{-3}$)	0.23 (.014)	0.19 (0.01)	0.23 (0.14)	0.18 (0.02)
Turbidity (NTU)	0.66 (0.31)	0.72 (0.38)	0.75 (0.25)	N/A

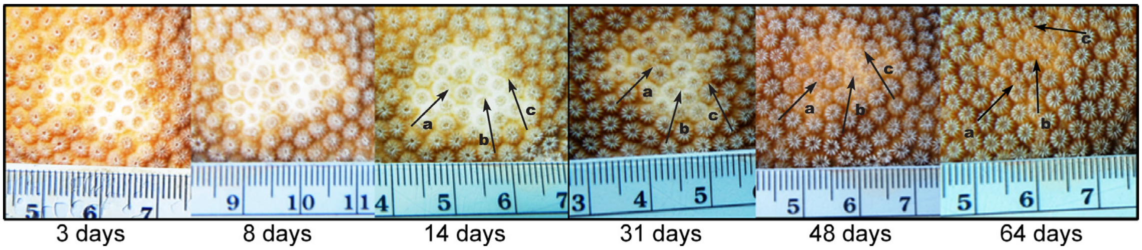

Fig. 5. Recovery of a lesion beginning 3 days after initial creation showing deposition of new tissue and return of pigmentation. Arrows indicate formation of new corallites in locations where corallites did not originally exist.

distance from shore (Brooks et al., 2007; Fisher et al., 2007; Smith et al., 2012). Several of the measured water quality parameters varied along a nearshore to offshore gradient in this study, likely due to the level of development occurring around the sites. Despite this, lesion recovery rates were only different between the two sites that were most strikingly different from each other: the slowest recovery at RR was associated with greater environmental stress represented by high turbidity and sediment accumulation, whereas SI, located relatively far from shore, had positive environmental qualities and rapid lesion recovery rates associated with a more pristine reef. However, many pairs of parameters were correlated, demonstrating the complex nature of assessing water quality. It would not be appropriate to include all variables in the regression analysis, since the statistical test would not be able to detect which variable in a correlated pair to attribute significance to, due to the overlap. For this reason, we included in the multiple regression variables that were not correlated with each other (water flow, turbidity, and overall sediment flux). The exception, dissolved oxygen, was included because it was only weakly correlated with one other parameter, organic flux, which we grouped with the other sediment flux components. Additionally, DO contributed strongly to the second PC along with water flow, a variable with which it was not correlated. Carbonate flux being highly correlated with the other components suggests that it may have only been necessary to measure organic and terrestrial flux, or to just measure total flux which would account for all components and simplify the data collection. Temperature was also highly correlated with each sediment component, so it was not necessary to include this variable in the final analysis since it overlapped so strongly. Since it is not possible to discern which variables may end up being correlated with each other in a given setting, it may still be useful to measure as many as possible. Then, variables that are identified as highly correlated with each other may be excluded from certain analyses to eliminate the redundancy which may cloud the data analyses and results.

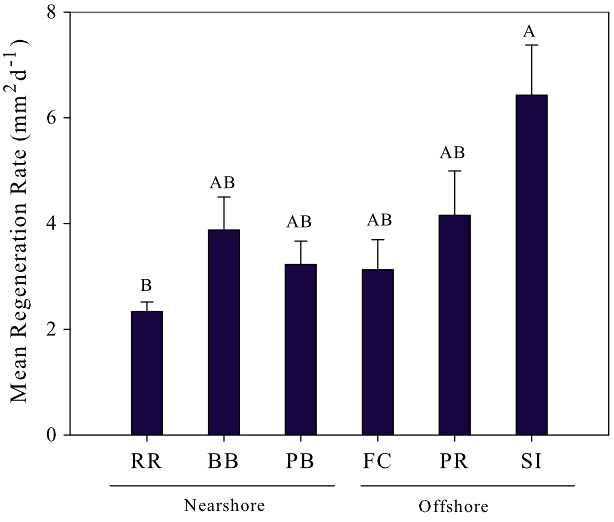

Fig. 6. Mean overall daily tissue regeneration rates ± SE by site. Means labeled with the same letters are not significantly different (Tukey HSD post hoc test).

Gradients of varying strength were observed in the water quality analysis. While temperature, salinity, and dissolved oxygen did not differ across sites and total sediment accumulation was similar at five of the sites, variables including water flow and turbidity followed clearer nearshore to offshore gradients. The exposed offshore sites (SI and PR) tended to experience high water flow and low turbidity, and are thus likely to benefit from less sediment deposition on corals and fewer associated impacts such as abrasion and anoxia, as well as rapid recovery from bleaching and rapid coral growth due to enhanced transport of nutrients and food to colonies (Rogers, 1983; Nakamura and van Woesik, 2001; Fabricius, 2005). In contrast, the nearshore sites experienced lower flow due to less exposure, higher turbidity, and slightly higher chlorophyll levels. The increased turbidity suggests that there is considerable runoff of terrestrial matter or high primary productivity at these sites, as input of sediment and particulate organic matter shades the water column (Fabricius and Wolanski, 2000). RR in particular lies in close proximity to the densely populated town of Charlotte Amalie, which delivers runoff of sediment, wastewater, and other pollutants to the coastal waters. Additionally, the high levels of commercial development and the steep slopes characterizing the land facilitate runoff into the harbor around RR, contributing to heightened turbidity in this region. Similarly, the elevated chlorophyll levels at this site are representative of phytoplankton biomass that is stimulated by the introduction of nutrients from such terrestrial sources as fertilizers or leaky septic systems (Furnas et al., 2005), the latter of which are prevalent on St. Thomas (authors, unpub. obs.). An added consideration for RR is that passing cruise ships can also agitate sediment, causing resuspension and further reducing water clarity. High turbidity may produce long-term effects such as increased algal growth, reduced species diversity, and reduced coral growth and recruitment (Fabricius, 2005). This may ultimately lead to a shift in the benthic community structure toward higher abundance of small,

Table 7
Results of ANCOVA with repeated measures assessing the effects of time, site, initial lesion area:colony area, and initial lesion perimeter on lesion recovery rates.

Effect	NumDF	DenDF	*F*	*P*
Time	7	38	3.89	0.0027*
Site	5	44	7.51	<0.0001*
Initial lesion area: colony area	1	44	0.97	0.3299
Initial lesion perimeter	1	44	27.02	<0.0001*
Time* site	2.79	162.28	2.79	<0.0001*
Time* initial lesion area: colony area	7	38	0.27	0.9617
Time* initial lesion perimeter	7	38	5.09	0.0004*

* Indicates significant result ($p < 0.05$).

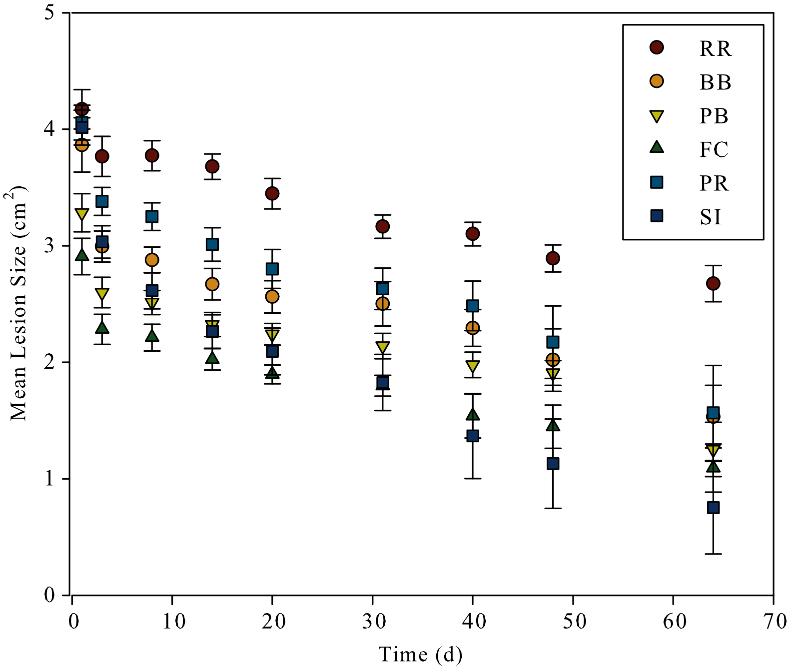

Fig. 7. Mean lesion size over time ± SE for each site.

weedy species and macroalgal dominance of substrate (Fabricius, 2005). It is also likely that corals on turbid reefs exhibit reduced photosynthesis due to the enhanced light attenuation when compared with clearer offshore sites (Anthony and Fabricius, 2000). If this is true, it is possible that corals tend toward greater heterotrophic feeding to compensate for the lower photosynthetic energy production at these nearshore sites (Fabricius, 2005). In addition, higher concentrations of total nitrogen and total phosphorus have been found at nearshore sites around St. Thomas when compared to offshore sites including SI, PR, and FC (Ennis, 2014). These data further emphasize the water quality differences among study sites and support the conclusion that the nearshore zone is subjected to land-based sources of pollution, in contrast to the offshore sites which are removed from anthropogenic stresses by distances of 3–5 km. This distance buffers the sites from sources of terrestrial sediment and nutrients, while the more rapid water flow characteristic of these exposed sites facilitates their dispersal.

Previous analyses of sediment accumulation in USVI waters have found that reefs fringing developed watersheds had significantly greater sedimentation than reefs in less developed areas (Gray et al., 2008). While sediment flux in our study was highest at RR, the most highly developed watershed, our results strayed from those of other researchers (i.e. Brooks et al., 2007; Gray et al., 2008) in that we did not observe overall sediment flux and terrestrial flux to clearly and regularly decrease with increasing distance from shore. This may be due to the site with the second highest terrestrial flux being located in front of a small island, despite being situated the farthest from mainland St. Thomas. This small island is likely the source of the terrestrial sediment collected. Overall sediment flux, however, was significantly higher at RR and lower at all other sites. This was similar to the trend observed with turbidity, which was highest at RR and lowest at SI and FC. Despite this similarity, no correlation was observed between turbidity and any of the sediment fluxes, and there was a lack of collinearity between turbidity and overall sediment flux in the multiple regression model, suggesting no significant relationship between these variables. This may be due to the fact that turbidity decreased more gradually, being moderate at three of the sites compared with five sites that had non-significantly different sediment fluxes. The lack of relationship may also be explained by the fundamental differences in what these two variables measure. The sediment fluxes recorded represent an accumulated response of sedimentation, including large components that do not remain suspended in the water column. Meanwhile, turbidity is a point measurement that measures all suspended materials such as plankton, algae, microbes, and other material which may be a result of primary productivity occurring in the water column.

We must consider that trap accumulation was measured in this study, which may not accurately reflect the amount of sediment that is settling and remaining on the benthos. Trap accumulation is affected by a number of variables, including trap shape and size, current velocity, particle size, and particle settlement speed (Baker et al., 1988; Bothner et al., 2006; Storlazzi et al., 2009; Storlazzi et al., 2011). Bloesch and Burns (1979) determined that cylindrical containers with appropriate aspect ratios are less likely to overtrap or undertrap particles than designs such as funnels, wide- or narrow-mouthed jars, or trays. The aspect ratio of the traps we used (4:1 height to diameter ratio) was similar to the ideal ratios proposed (3:1–10:1, Bloesch and Burns, 1979; Storlazzi et al., 2009); however, it is still suspected that the containers overtrapped sediments when considering our intention for using the traps. Once sediment falls in the traps it is not easily removed due to the highly retentive trap walls, while sediment landing on corals can be dislodged by even low amounts of turbulence and rejected by the corals themselves using their cilia or mucus as a defense (Rogers, 1990; Storlazzi et al., 2011). It is probable that sediment deposition is less of a problem affecting the offshore reefs than our results suggest, as the high water motion at those locations can clear corals of debris. While the various methods used to quantify sedimentation each have their flaws, an alternate technique may have suited our needs better for investigating sediment accumulation on corals. For instance, sediment pods, which are rough flat-topped devices rather than open containers that trap particles, would better represent coral surfaces and likely provide a more accurate measure of the amount and type of sediment affecting coral colonies (Field et al., 2013). Fine particles remain trapped in the cylindrical PVC tubes but are easily resuspended from the benthos by turbulence, for example (Storlazzi et al., 2011). It is possible that if the sediment pod method had been used, sediment deposition would have more accurately mirrored the natural processes acting on reefs. It follows that this parameter also may have varied along a stronger nearshore to offshore trend similar to other variables measured, and thus may have made a greater contribution to site differences in lesion recovery rates.

Another possible explanation for why sedimentation did not significantly affect lesion recovery rates is that corals may have adapted to the conditions at their respective sites, making it difficult to detect differences. For example, corals at RR may have grown accustomed to the higher levels of sediment deposition that is typical of this site and have adapted to deal with it, only suffering during severe atypical events such as acute storm events. *O. annularis* has shown variable particle rejection rates, and has been documented as being both more efficient than species such as *A. palmata* and *Diploria strigosa* in some cases (i.e., Abdel-Salam and Porter, 1988) and less efficient than them in others (Loya, 1976; Rogers, 1990). In order to handle the relatively high sediment accumulation, *O. annularis* colonies at RR may have improved their efficiency at dislodging particles using movement of their tentacles and cilia, or by maintaining a continuously high production of mucus, which prevents sediment settlement by trapping particles and later sloughing off the colony (Abdel-Salam and Porter, 1988; Stafford-Smith and Ormond, 1992).

A final consideration to note when drawing conclusions from the results of our water quality analysis is that while spread from west to east and ranging from 0.1 to 5 km offshore, the reefs sampled in this study cover a relatively small area of the USVI. Sampling alternate sites that are spread across a larger area with more extreme differences might yield varying results. If additional sites such as deep mesophotic reefs or reefs not adjacent to cays had been studied, it is possible that other environmental parameters would most strongly contribute to differences in lesion recovery rates, depending on the degree of water quality differences among those sites. This may be particularly true for sedimentation, since the five sites that had similar sediment fluxes, which were grouped along the first principal component in the PCA, have similar geographic locations. The small differences in longitudinal positioning of these sites potentially weakened the resolution needed to detect significant effects. Increasing the spatial distribution of study locations may provide more power to detect statistically significant differences in sedimentation among sites and more power to assess its potential influence on tissue regeneration rates, an important consideration for future studies.

4.2. Effects of biological interactions on lesion recovery

Lesions began recovering in as little as a few days. Initial recovery rates measured during the first eight days were 5–17.5 $\text{mm}^2\,\text{d}^{-1}$, which is in the range reported in other studies on this species (Meesters and Bak, 1993; Meesters et al., 1997). Many authors reported exponentially decreasing recovery rates with time (e.g., Bak and Steward-Van Es, 1980; Meesters et al., 1997; Cróquer et al., 2002). We observed the fastest recovery during the first three to eight days, after which rates of healing remained fairly constant. These observed differences may be due to differences in techniques used to inflict the lesions among the various studies. For example, many of the aforementioned studies employed mechanical methods such as using grinding stones attached to a pneumatic drill (Bak et al., 1977; Meesters et al., 1992, 1997; Nagelkerken et al., 1999). In contrast, we used a chisel to create our lesions by hand, which may have impacted the corals differently and may have led to varying degrees of uniformity among lesions. Additionally, the sizes of our lesions were fairly consistent since we were not primarily investigating the effect of lesion size on recovery rates, and our lesions were relatively small in relation to the colony sizes. This is in contrast to several of the studies that documented exponentially decreasing recovery rates, which created and analyzed much larger lesions (e.g., Lirman, 2000; Oren et al., 1997).

At the conclusion of our study, several lesions had yet to completely regenerate new tissue. Unhealed lesions are susceptible to colonization by turf algae and filamentous cyanobacteria (Bak et al., 1977; van Woesik, 1998), various species of foliose macroalgae (McCook et al., 2001; Aronson and Precht, 2006), and bioeroding organisms such as sponges or zoanthids (Bak et al., 1977; Bak and Steward-Van Es, 1980). We observed growth of cyanobacteria which created algal turfs that trapped sediment on some lesions, similar to Bak et al. (1977), but we did not observe colonization by foliose macroalgae or other invertebrates that could potentially cause structural damage to the corals. At the slowest healing rate observed at RR, these unhealed lesions could be expected to be fully healed in 61 ± 12 d (mean ± SE; range 18–124 d) in the absence of colonization by algae or bioeroding organisms.

In addition, several fish species are frequently observed impacting *O. annularis* reefs around the USVI, including stoplight and redband parrotfish (*Sparisoma viride* and *S. aurofrenatum*, respectively) and threespot and dusky damselfish (*Stegastes planifrons* and *S. adustus*, respectively) (authors, unpub. observations). These species can cause partial mortality through corallivory and creation of territorial algal gardens on corals (Bythell et al., 1993). Fish predation and damselfish territoriality have shown the greatest impact on protected nearshore reefs with many colonies exhibiting several scars (Garzon-Ferreira et al., 2005). This suggests another factor potentially hindering tissue regeneration in nearshore areas, as corals with multiple lesions have been found to recover slower (Henry and Hart, 2005). Meesters et al. (1992) reported that several lesions in their study did not regenerate, either remaining the same size or enlarging, likely as a result of fish grazing. Fish bites were commonly observed at the nearshore sites of BB and PB in our study, and could have slowed regeneration rates at these sites by causing additional stress to the corals. Furthermore, predation by fish and other corallivorous invertebrates is a widespread cause of lesions in scleractinian corals and can cause damage to otherwise healthy colonies, in addition to hindering recovery from other injuries. Predation on corals can slow growth rates and reduce reproduction potential, while increasing susceptibility to bleaching, disease vectors, and additional stressors (Meesters et al., 1992; Rotjan et al., 2006; Rotjan and Lewis, 2008; Shantz et al., 2011). If the proportion of fish bites that is unable to heal is the same as what we observed in our study (approx. 15% of lesions), this indicates that predation may be extremely detrimental toward coral health and reef resilience, as predation is so abundant on reefs around the world (Rotjan and Lewis, 2008).

4.3. Lesion characteristics

Some studies have suggested correlations between lesion recovery rates and parameters such as injury shape and size, lesion perimeter, and colony size (e.g., Meesters et al., 1997; Oren et al., 1997; van Woesik, 1998). We found mixed results when investigating potential effects of these parameters. Our lesions were a small range of sizes with small standard errors for both area and perimeter. Other studies that showed an effect of injury extent on healing rates grouped lesions into size classes of wider ranges to specifically investigate how lesion size influences recovery (e.g., 0–5 cm^2, 5–10 cm^2, and 10–20 cm^2, Lirman, 2000). The size differences among our lesions were not large enough to have any effect on recovery rates. Furthermore, by calculating the ratio of lesion area to colony area, we accounted for the parameter of coral size. Statistical analysis found that this ratio did not affect tissue regeneration rates, indicating that colony size is inconsequential for the size range of corals used in this study. Similarly, Bak and Steward-Van Es (1980) and Fisher et al. (2007) found that lesion recovery rates were not affected by colony size. However, while our goal was to create consistent, uniform lesions, we found that initial lesion perimeter did vary by site. Additionally, we observed that lesion perimeter did have a significant effect on regeneration rates, which was strongest in the initial three days of the study and diminished over time. These results support the idea that energy for the recovery process is drawn from the polyps immediately surrounding the lesion rather than the entire colony (Oren et al., 2001). However, it is important to note that the two sites with the fastest and slowest recovery rates (SI and RR, respectively), had non-significantly different initial perimeters, indicating that perimeter alone was not responsible for the observed differences in tissue regeneration rates.

A related consideration is lesion depth, which may have affected recovery rates since it was difficult to control depth while inflicting the injuries. It is possible that not all lesions were precisely the same depth, and thus that some lesions suffered more skeletal damage while others primarily only had tissue removed. It is thus a possibility that these lesions recovered at different rates. On one hand, deeper injuries result in more surface area needing to be repaired, which may slow recovery rates by increasing the size of the lesion and requiring regrowth of more material, as several authors have found (Bak and Steward-Van Es, 1980; Hall, 1997; Meesters et al., 1997). On the other hand, Bak et al. (1977) examined differences in regeneration rates of tissue vs. skeletal lesions of the same size in *O. annularis* and found that the skeletal injuries healed faster than the lesions that had only suffered tissue damage. Based on this conflicting information, it is not possible to say with certainty how small variations in lesion depth affected our results.

The lesions inflicted in this study can represent lacerations caused by storm damage, predation including parrotfish and damselfish bites, disease, or other types of physical injuries (Bak and Steward-Van Es, 1980; Hall, 1997; Brandt and McManus, 2009). The artificial lesions we created appeared especially similar to fish predation injuries that characterize reefs in the USVI, as parrotfish bites have been observed to recover in a similar time frame of 1–2 months (Bythell et al., 1993). Additionally, while typically only causing tissue damage rather than affecting the coral skeleton, coral diseases are increasing in frequency and remain a rapid and widespread mechanism of inducing partial mortality, as disease lesions are often very large (Miller et al., 2009). Regardless of the cause of lesions, it is expected that regrowth of tissue from naturally caused partial mortality would follow the trends observed in this study. It is likely that such injuries would also heal faster at offshore sites where there is higher water flow and lower anthropogenic impact that at nearshore sites where water flow is lower and sedimentation and turbidity are higher.

With many reefs in a state of decline around the Caribbean, it is essential to understand how the environment affects partial mortality in corals. This study showed that both natural and anthropogenic parameters influence tissue regeneration in corals, in addition to the lesion-specific factors already known to affect recovery. Nine lesions that we created failed to show significant signs of recovery, an important number as this represents 15% of injured corals in our study. The remaining healing time that we calculated for the unclosed lesions, ranging from 18 to 124 d, is long enough that there is time for ambient conditions to change and prevent the slower-healing lesions from recovering. There is no guarantee that these remaining lesions would heal completely as there are many extrinsic factors unable to be controlled, such as colonization by bioeroding organisms, potential bleaching events, predation, or disease outbreaks. This is noteworthy, as partial mortality can negatively affect coral colonies and reef health on both small and large scales. Lesions have been linked to decreased coral reproduction, reduced photosynthesis and growth, and algal overgrowth of corals (Van Veghel and Bak, 1994; Oren et al., 2001; Bruckner, 2002). High prevalence and slow recovery of such injuries contribute to declining reef health, shifting population demographics toward more tolerant species and smaller colonies, and reductions in reef resilience. If 15% of injured corals are unable to recover from damage that is so abundant across reefs, partial mortality may be a valuable parameter to measure when assessing reef health, as it may be indicative of biological and ecological degradation. We can see from this study that low-flow, nearshore reefs are likely to be the least resilient. Additionally, the tendency of sites like Rupert's Rock to heal lesions slowly suggests that reefs subjected to such conditions will recover slowly from other disturbances such as bleaching or disease outbreaks as well. Since it would be a challenge to change the rate of water flow at a site, management efforts might be best focused on minimizing anthropogenic impacts in order to improve environmental conditions on these reefs.

Further study should look at recovery from a wider range of injuries, such as coral diseases, algal overgrowth, and predation from a variety of organisms, as healing rates may depend upon the type of the injury as well as the length of exposure to the stressor. Furthermore, measuring additional variables could reveal effects of other stresses on lesion healing rates that were not considered in this study. For example, while none of the sampled corals exhibited signs of bleaching or disease, it is possible that these negative health impacts characterize nearby colonies, causing corals to have compromised or weakened immune systems that would slow their healing abilities (Fine et al., 2002; Ritchie, 2006). Additionally, genetic variability within and among sites may have influenced differences in recovery rates. *O. annularis* can fragment, resulting in close distributions of genetically identical colonies on a single reef. No genetic studies of *O. annularis* were performed at these specific sites during this study; however, colonies sampled were separated by at least one meter and showed variability in color and morphology. No indication of previous connectivity among the colonies, such as rubble between colonies, was found. Assessing these additional variables would provide a more comprehensive view of how rapidly corals around the USVI can be expected to recover from various disturbances. Other threatened species should also be studied, including *Acropora palmata* and *A. cervicornis*, to expand the current state of knowledge of these primary reef-building corals so they can be managed effectively. Looking at added sites in this region would serve to identify further local differences in water quality and coral health and shed more insight into the processes characterizing the ecologically important reefs of the USVI.

Author contribution

AM Sabine conducted the research and prepared the manuscript.

ME Brandt assisted with fieldwork and design of analysis. ME Brandt, TB Smith, and DE Williams contributed to project design and manuscript preparation.

All authors have approved the final article.

Conflict of interest

The Virgin Islands Experimental Program to Stimulate Competitive Research and the US National Science Foundation financially supported this research. Neither group had any

influence in project design, data analysis, writing the manuscript, or deciding to submit for publication.

Acknowledgements

This work was supported by Virgin Islands Experimental Program to Stimulate Competitive Research (VI-EPSCoR) Grant #0814417 as well as a US National Science Foundation Scholarship in Science, Technology, Engineering, and Mathematics. We would like to thank M. Kammann for providing field assistance and for offering helpful comments in a review of the manuscript. We also thank Z. Whitener, R. Brewer, L. Conlon, B. Honisch, V. Brandtneris, V. Wright, J. Gyory, I. Byrne, and S. Prosterman for providing field and logistical assistance. Finally, we would like to thank two anonymous reviewers for providing a helpful critique of the manuscript. Any opinions, findings, conclusions, or recommendations expressed in the material are those of the authors and do not necessarily reflect the views of the granting agencies. This is contribution #98 from the UVI Center for Marine and Environmental Studies at the University of the Virgin Islands.

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