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Environmental conditions influence tissue regeneration rates in scleractinian corals

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A B S T R A C T

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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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,

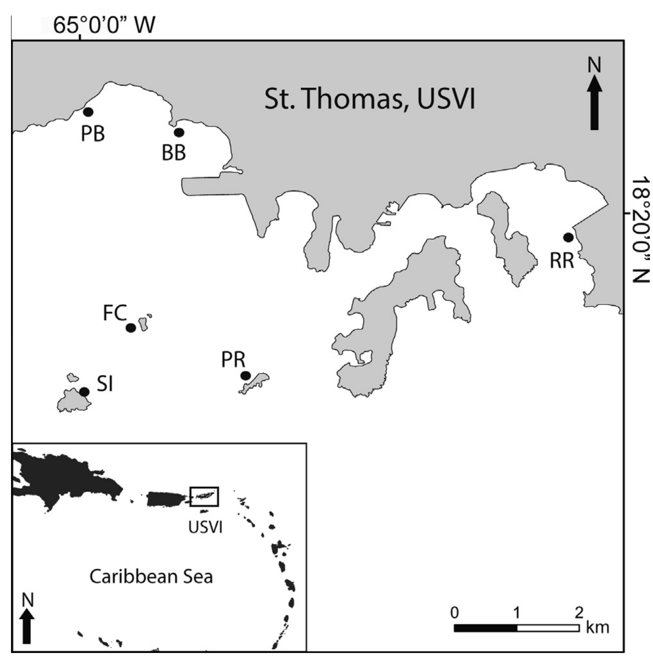

Fig. 1. Locations of study sites around St. Thomas, US Virgin Islands: Brewers Bay (BB), Flat Cay (FC), Perseverance Bay (PB), Porpoise Rocks (PR), Rupert's Rock (RR), and Saba Island (SI). Sites were varying distances from shore and were exposed to different levels of water quality and levels of impact.

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