

BENTHIC COMMUNITY RECOVERY FROM SMALL- SCALE DAMAGE ON MARGINAL CARIBBEAN REEFS: AN EXAMPLE FROM PANAMA

Carmen Schlöder, Aaron O'Dea, and Hector M Guzman

ABSTRACT

The frequency of small-scale physical damage to coral reefs is likely to increase as fishing and tourism pressures intensify. Predicting how reefs will respond to the effects of these types of damage requires empirical exploration, especially on reefs that are already heavily degraded. We replicated small-scale damage on four reefs that live close to their ecophysiological tolerance limits in the Bocas del Toro Archipelago of Caribbean Panama and quantified their recovery over 2 yrs. On each reef we cleared five replicate 1 × 1-m plots of all living benthos simulating physical damage by boat grounding, anchoring, or fishing practices. Recovery of the benthic community was quantitatively monitored and compared to adjacent non-cleared plots (treated as a control) every 6 mo. After 2 yrs, only one of the reefs exhibited evidence of recovery of the cleared plots. Poor recruitment of benthos appeared to slow down recovery of cleared plots on another reef. The other two reefs showed unequivocal shifts toward a macroalgae-dominated system, suggesting that small-scale disturbances could have lasting impacts on marginal reefs. We found no clear contemporary or historical environmental signal that could explain the differential dynamics of recovery amongst these reefs.

Reefs are frequently affected by destructive maritime activities such as fishing, boat grounding, and the collection of aquarium goods and building materials. These practices are increasing globally (Aronson and Swanson 1997, McManus et al. 1997, Guzman and Guevara 1998, Rützler 2002, Moulding et al. 2012) and not only destroy reef architecture and kill benthos, but also increase the amount of bare substrate available for colonization by organisms other than coral (Hughes 1994, Connell 1997, McManus et al. 1997, Precht et al. 2001, Dudgeon et al. 2010, Moulding et al. 2012). This may be more manifested on Caribbean reefs that show severely altered baselines (Hughes 1994, McClanahan et al. 1999, Gardner et al. 2003, Pandolfi et al. 2003, Mumby et al. 2007, Knowlton and Jackson 2008).

Large-scale damage to reefs, for example, by hurricanes, destroys swathes of reef architecture, and recovery is dependent upon the viability of recruitment and distance from other, less damaged reefs (Dennis and Bright 1988, Knowlton et al. 1990, Hughes 1994, Aronson and Swanson 1997, Lirman 1999, Hughes et al. 2003). The recovery of small-scale damage, on the other hand, is probably much more limited by the health and recruitment potential of the reef surrounding the damaged patch (Bonin et al. 2011). Therefore, it is likely that reefs that are living close to their ecophysiological tolerance limits will respond unfavorably to small-scale damage.

A patch of reef that has been cleared by disturbance can follow one of three possible trajectories: (1) full recovery back to the original community, (2) failure to recover, or (3) a shift towards an alternative state (Bellwood et al. 2004, Knowlton 2004, Rogers and Miller 2006, Norström et al. 2009). Of the latter, the shift to

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macroalgal domination has been the most pervasive on Caribbean reefs (Hughes 1994, Ostrander et al. 2000, Scheffer et al. 2001, Szmant 2002, Gardner et al. 2003, Scheffer and Carpenter 2003, Knowlton 2004, Mumby et al. 2007, Knowlton and Jackson 2008, Dudgeon et al. 2010).

In the present study, we explore the recovery from small-scale damage on four marginal Caribbean reefs. We investigated if small areas of damage on marginal reefs recovered along similar trajectories or if recovery differed when these reefs were exposed to additional stressors. Two of the reefs were exposed to high runoff and sedimentation due to deforestation, as well as freshwater loads during heavy rains (Guzman and Guevara 1998, Cramer et al. 2012). We hypothesized that these reefs would remain bare, exhibit slower recovery, or shift in their community structure because of the variability of their environment. We hypothesized that the two reefs less affected by sedimentation and runoff would attain a similar benthic community composition to their surrounding areas.

METHODS

STUDY REGION.—The Bocas del Toro archipelago in Panama (Fig. 1) consists of seven medium-sized islands covered by lowland wet tropical forest and fringed by extensive mangrove forests. The mainland vegetation alternates between banana plantations, clear-felled cattle lands, and rainforest (Carruthers et al. 2005, Cramer et al. 2012, Cramer 2013). Two large water bodies that dominate the archipelago are the Chiriquí Lagoon in the southeast and the Bay of Almirante in the northwest (Fig. 1). The two connect through mangrove channels, and both are connected to the open ocean (Carruthers et al. 2005, D’Croz et al. 2005). Almirante Bay shows moderate reef formation to a maximum depth of around 23 m (Guzman and Guevara 1998). Coral growth in the Chiriquí Lagoon is limited (O’Dea et al. 2007), as it is exposed to high levels of runoff from a number of large rivers (Carruthers et al. 2005, D’Croz et al. 2005).

From around 2 Ma until the mid-Holocene and probably even until the last few centuries or decades, *Acropora palmata* (Lamarck, 1816) and *Acropora cervicornis* (Lamarck, 1816) dominated the fringing reef landscape of Bocas del Toro (Aronson et al. 2004, Klaus et al. 2011, Cramer et al. 2012, Cramer 2013, Fredston-Hermann et al. 2013), even in sheltered lagoonal areas. Today, the dominant shallow-water coral in Bocas is *Porites furcata* Lamarck, 1816 (Guzman and Guevara 1998, Schlöder and Guzman 2008). This shift is blamed upon decreasing water quality (Aronson et al. 2004), likely due to increasing sedimentation from deforestation, eutrophication from the banana industry, increasing sewage, and over-fishing (Cramer et al. 2012). Guzman and Guevara (1998) observed that shallow reefs close to rivers in Bocas are frequently covered by a layer of fresh water after heavy rains, suggesting that even the great acroporid reefs of the past may have lived close to their environmental tolerances, and as such were termed “marginal reefs” (Guzman and Guevara 1998).

Marginal reefs are exposed to suboptimal, fluctuating environmental conditions such as acute changes in temperature, salinity, sedimentation, freshwater input, irradiation, and light availability (Bak and Meesters 2000, Perry and Larcombe 2003, Hennige et al. 2010), which push reefs close to the threshold for coral survival. These abrupt changes in conditions are commonly found in Bocas del Toro (Guzman and Guevara 1998) and may reduce species diversity, species composition, and reef development (Hennige et al. 2010). On one hand, marginal reefs may be more resistant to environmental change as they adapt over time to these challenging conditions (Hennige et al. 2010). On the other hand, they could be highly sensitive to additional human stressors, as they usually consist of fewer and more



Figure 1. The Bocas del Toro Archipelago with reefs studied: (1) Gallinazo Point (Reef 1), (2) Cristóbal (Reef 2), (3) Cristóbal Village (Reef 3), and (4) Cayo Agua (Reef 4) in the Chiriquí Lagoon.

tolerant species (Guzman and Guevara 1998, Bak and Meesters 2000), which is important to consider in the face of increasing coastal development.

STUDY SITES.—Four reefs were chosen for study: Gallinazo Point (Reef 1), Cristobal (Reef 2), Cristobal Village (Reef 3), and Cayo Agua (Reef 4) (Fig. 1). Reefs 1–3 are located in the semi-enclosed Bay of Almirante that receives oceanic water from the north at Boca del Drago (D’Croz et al. 2005, Fig. 1). Fifteen years ago, Guzman and Guevara (1998, 1999) observed around 30% coral cover and 20%–45% algal cover in reefs located in Almirante Bay. Reef 4 is located in the eastern sector of the archipelago close to an island in the North of Chiriquí Lagoon. This area was observed to have the highest reef diversity, but lowest living coral cover in the region (Guzman and Guevara 1999). We chose the four reefs based on their different environmental conditions: Reef 1 is downstream of the large river Rio Oeste that can deliver considerable amounts of terrigenous sediment after heavy rains (Guzman and Guevara 1998). Chiriquí Lagoon is naturally more turbid than Almirante Bay, and Reef 4 likely exhibited lower salinity and higher dissolved nutrients due to a larger catchment area, and hence, greater runoff (Carruthers et al. 2005, D’Croz et al. 2005, Cramer et al. 2012). Although sedimentation rates were not quantitatively measured, much of the benthic community was covered by fine sediment particles on Reefs 1 and 4, while Reefs 2 and 3 were apparently not affected by these parameters.

MONITORING CLEARED AND CONTROL REEF COMMUNITIES.—Control plots were established by placing permanent line transects parallel to the shore at 2 m depth with three

Table 1. Categories of sessile living benthos and coral species mapped during the monitoring of control and cleared plots on four reefs in Bocas del Toro.

| Guild | Growth form (examples) |
|--|--|
| Corals (<i>Porites furcata</i> , <i>Agaricia</i> sp., <i>Millepora</i> sp., <i>Porites astreoides</i> , <i>Diploria</i> sp., <i>Siderastrea</i> sp., <i>Colpophyllia</i> sp.) | Branching (e.g., <i>P. furcata</i> , <i>Millepora alcicornis</i> Linnaeus, 1758); flat, round (e.g., <i>juvenile corals</i>); lettuce form, encrusting [e.g., <i>Agaricia tenuifolia</i> Dana, 1846, <i>Agaricia agaricites</i> (Linnaeus, 1758), <i>Agaricia humilis</i> Verrill, 1902]; massive, dome shape [e.g., <i>Diploria strigosa</i> (Dana, 1846)]; massive, round heads [e.g., <i>Siderastrea radians</i> (Pallas, 1766), <i>Siderastrea siderea</i> (Ellis and Solander, 1786), <i>Colpophyllia natans</i> (Houttuyn, 1772)] |
| Filter-feeders (zoanths, sponges, anemones, tunicates) | Dense mats, circular discs (e.g., <i>Zoanthus pulchellus</i> Duchassaing and Michelotti, 1860), encrusting (e.g., <i>Chondrilla nucula</i> Schmidt, 1862, <i>Plakortis</i> sp., <i>Amphimedon</i> sp.); elongated body [e.g., <i>Erylus formosus</i> Sollas, 1886, <i>Calyx podatypa</i> (de Laubenfels, 1934), <i>Xestospongia</i> sp., <i>Ircinia</i> sp.]; flat oral disc with tentacles [e.g., <i>Condylactis gigantea</i> (Weinland, 1860), <i>Stichodactyla helianthus</i> (Ellis, 1768), <i>Actinoporus elegans</i> Duchassaing, 1850, <i>Bartholomea</i> sp.]; erect or globular, thick body [e.g., <i>Polycarpa spongiabilis</i> Traustedt, 1883, <i>Rhopalaea abdominalis</i> (Sluiter, 1898), <i>Phallusia nigra</i> Savigny, 1816] |
| Plants (algae, <i>Thalassia</i> sp.*) | Flattened thalli (e.g., <i>Dictyota</i> sp., <i>Halimeda</i> sp.); elongated oval blades, (e.g., <i>Caulerpa</i> sp.); flat blades (e.g., <i>Thalassia testudinum</i>) |
| Substrate (coral rubble, dead corals†) | n/a |

† only recorded in control plots

* only recorded in cleared plots

replicate 10-m transects, separated by 10 m. Thus, fifteen control plots were monitored per reef and used to compare with cleared plots. These control plots have been part of a long-term monitoring program (STRI-ESP) and follow a standard protocol (<http://stri.si.edu/sites/esp/>). This and our goal to minimize the amount of area destroyed during the study resulted in the uneven number of control and cleared plots (control plots $n = 15$; cleared plots $n = 5$). Control plots were located about 20 m apart from cleared plots at the same depth. To simulate physical damage on cleared plots, we removed all living benthos and coral skeletons from within five 1-m² areas by hand and using metal brushes. After clearing, plots were composed of bare substrate, which in most cases was coral rubble of *P. furcata*. Rugosity was not measured, as all plots were treated in the same way and had flat surfaces after clearing.

All plots (cleared and control) were monitored using a PVC 1-m² frame divided into 100 squares and placed over each plot area to facilitate visually estimating percent coverage of all sessile taxa (Table 1). Corals were identified to species or genus, while other benthos were recorded as major taxonomic groups (Table 1; after Guzman et al. 2005). All plots were monitored with this method every 6 mo for 2 yrs from November 2003 through November 2005.

ANALYSIS.—Community structure through time in both the cleared and control plots was examined with principal components analysis (PCA; Lepš and Šmilauer 2003). Mean relative abundance of the categories *P. furcata*, *P. furcata* juveniles, *Millepora* sp., zoanths, *Porites astreoides* Lamarck, 1816, *Agaricia* sp., tunicates, sponges, anemones, the seagrass *Thalassia* sp., and bare coral rubble in cleared and control plots during each monitoring period were calculated. Mean relative abundances were arcsine-transformed and data from all reefs at all times were analyzed in a single PCA. Resulting sample scores of reefs at each time were plotted separately for each reef, allowing us to observe the relative stability of control plots and the recovery trajectories of cleared plots through time on each of the reefs.

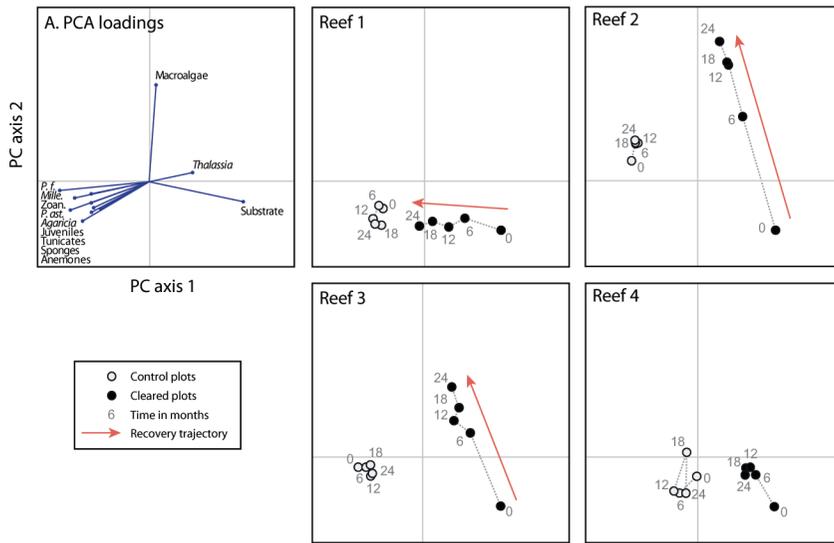


Figure 2. Principal Components Analysis (PCA) performed on relative abundance (% cover) of sessile organisms on four reefs in Bocas del Toro. (A) Taxa/species eigenvectors. (B–E) Independent sample scores for cleared and control plots on Reefs 1–4 with numbers representing time in months revealing trajectories of reef community compositions through time. Grey circles are control plots and black circles cleared plots.

RESULTS

PCA reveals the dynamics of cleared and control communities on the four reefs through the 2-yr study (Fig. 2). The first two axes explain 84.6% of the variation, with 69.5% explained by the first axis and 15.1% by the second.

Control communities on Reefs 1 and 3 were structurally similar, occupying similar PC space, while Reef 2 had greater macroalgae cover and Reef 4 greater bare substrate and *Thalassia*. Community structure in the control plots on all reefs changed little over time (Fig. 2). The cleared plots on all reefs begin at the same location in PC space, being composed of 100% bare substrate. During the 2-yr period, change in community composition in the cleared plots differed on reefs. Reef 1 showed rapid community development on control plots with 43% benthic cover after 2 yrs (Fig. 3A), and after 2 yrs the settling community came close in composition to the control plots (Fig. 2). Cleared plots on Reef 2 also showed rapid development with 55% benthic cover after 2 yrs (Fig. 3A), but the community followed a trajectory away from the control plots and toward a community dominated by macroalgae and turtle grass (*Thalassia testudinum* Banks ex König; Fig. 2). Reef 3 showed a similar trajectory away from the control plots and toward a community dominated by macroalgae and turtle grass, but benthic cover was stunted at 18 mo when it had reached 34%, only to drop to 26% 6 mo later (Fig. 3A). Community development on cleared plots in Reef 4 was slow, with only 14% of the plots covered in benthos after 2 yrs, after which time *Thalassia* was the dominant living organism on Reef 4 (Fig. 2, 3A).

We calculated the percent cover of benthos for each reef over time (Fig. 3B–E), divided into four categories: corals (all species recorded, Table 1), filter feeders

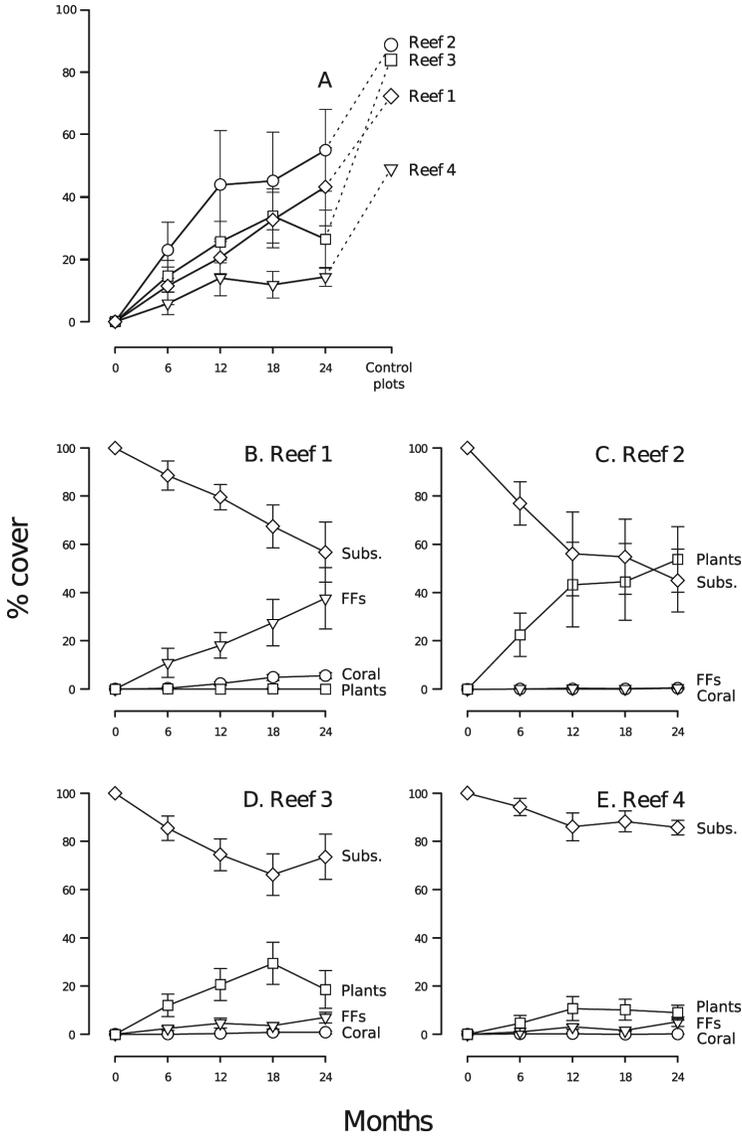


Figure 3. (A) Mean percent cover of all living benthos on four reefs in Bocas del Toro over two years after clearing. The dashed line connects the mean percent cover of benthos from the cleared plots to the mean percent cover of benthos in the control plots. (B–E) Changes in mean percent cover of major benthic groups (coral, FFs = filter feeders, marine plants and Subs = substrate, bare coral rubble) on the cleared plots for Reefs 1–4. Error bars = 95% confidence intervals.

(anemones, tunicates, sponges, zoanthids), plants (macroalgae and *Thalassia*), and substrate (bare coral rubble). The graphs mainly reflect the trends presented in the PCA (Fig. 2), with Reef 1 showing an increase in percent cover of both filter feeders and corals, but not for the plants (Fig. 3B). Macroalgae rapidly covered the bare coral rubble on Reef 2 and reached a total cover of 55% after 2 yrs, while growth of other benthos was minimal (Fig. 3C). Similar patterns were observed on Reef 4, although at a much slower rate (Fig. 3E). The cover of macroalgae on Reef

3 increased until it reached a peak of 29% around 18 mo, then decreased to 19%. Simultaneously, the cover of filter feeders increased from 3.6% after 18 mo to 7% 2 yrs after clearing (Fig. 3D).

DISCUSSION

The four reefs in our study demonstrated strikingly different patterns of recovery following experimental clearing, and the results did not support our hypotheses. Cleared plots did not recover on one of the two reefs that were subjected to higher sedimentation, while cleared plots on the other reef acquired a benthic community similar to the surrounding reef. Cleared plots on the two reefs that were less affected by sedimentation were covered by algae and did not recover.

The lack of recovery at Reef 4 suggests that those aspects of water quality that typically limit coral reef development in Chiriqui Lagoon (e.g., high runoff and sediment loads; Carruthers et al. 2005, D’Croz et al. 2005) may also have limited benthic recovery in our cleared plots. The additional factors that might have influenced recovery at other sites (e.g., altered regimes of sedimentation, herbivory, or recruitment) showed no effect here.

Higher sediment loads and runoff did not inhibit recovery at Reef 1; the cleared plots on this reef recovered a suite of benthic biota similar to the control community over time. Perhaps this reef is the best adapted to sedimentation because of its location just off the mainland, suggesting that “marginal” may be a misleading term to apply to such reef locations. These may actually be quite resistant and resilient reefs, and more capable of withstanding environmental stressors that degrade reefs in environments that are typically considered more favorable (e.g., stable conditions; clear, oligotrophic waters).

Data from Reefs 2 and 3 suggest that something other than sedimentation influenced their recovery trajectories. The dominance of algae in cleared plots on these reefs suggests a lack of herbivory as a control. This result has been seen on many Caribbean reefs since the *Diadema* die-off in 1983. We consistently observed high densities of *Echinometra viridis* (Agassiz, 1863) at Reef 1, but failed to spot any individuals at Reefs 2, 3, or 4 at any time during the study period. Previous studies demonstrate the importance of herbivory for reef health (Lessios 1988, McCook 1999, Jackson et al. 2001, Mumby 2006, Hughes et al. 2007) and show that *E. viridis* can shape communities by controlling macroalgal growth and promoting coral recruitment by providing suitable substrate (Sammarco 1982, Hughes et al. 1987, Aronson and Precht 1997, Aronson and Precht 2006, Lessios 2008). We recognize that its presence could be instrumental in the recovery of damaged plots in Bocas del Toro and future studies should investigate how sea urchins may affect the rate of recovery of coral reef habitats.

Results from our experiment suggest that controls on recovery from small-scale damage are likely multifaceted and that predicting recovery is quite complex. Undoubtedly, the health and status of the surrounding reef plays an essential role in recovery, probably through levels of recruitment and the magnitude of herbivorous grazing. Reduced water quality and increased sedimentation likely affect benthic diversity as well as community composition, and may favor more tolerant species. The structure of available substrate also influences successful recovery of benthos, as studies on reef recovery conducted after several boat groundings

in Florida demonstrated (Precht et al. 2001, Moulding et al. 2012). However, in our study, it does not explain differential responses, since rugosity was consistent across all sites in the cleared plots. Fossil, Holocene, and historical reefs in Bocas del Toro have demonstrably different communities compared to modern reefs (Aronson et al. 2004, Cramer et al. 2012, Fredston-Hermann et al. 2013). It is therefore possible that these reefs exhibited different recovery patterns not only because they were exposed to multiple stressors, but also because of reduced resilience due to long-term historical deterioration (Knowlton et al. 1990, Hughes 1994, Hughes and Connell 1999, Pandolfi et al. 2003, Mora 2008).

Aerts (2000) proposed that small-scale damage may have large impacts on reef systems as it alters competitive interactions among reef members. The implication is that resilience may be lower for damaged reefs compared to those considered “marginal,” particularly when other ecosystem stressors such as reduced grazing pressure and fishing impacts are already in place. Our results were variable and it is not clear how far the synergistic effect of small-scale damage and marginal conditions will affect reefs in the future. This becomes especially important as more reefs will likely be exposed to marginal conditions due to climate change and increasing, human-mediated coastal development. Understanding the susceptibility of marginal reefs to damage and to what we generally consider as “stressful” conditions will guide appropriate management of onshore human activities directed at protecting both nearshore and offshore reefs.

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ADDRESSES: *Smithsonian Tropical Research Institute, Apartado 0843-03092, Panama, Republic of Panama.* CORRESPONDING AUTHOR: (CS) Email: <schloederc@si.edu>, Phone: (507) 212-8700; Fax: (507) 212-8791.



