



Using community-wide recruitment and succession patterns to assess sediment stress on Jamaican coral reefs



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ABSTRACT

Sedimentation resulting from the direct and indirect effects of coastal development is an increasing threat to Caribbean coral reefs. This study investigated taxonomic diversity, percent cover and successional patterns of recruited organisms over a period of 30 months to understand the community-wide consequences of increased coastal development and sediment supply along the northern coast of Jamaica. Terra cotta tiles were secured to the reef and the communities inhabiting both the cryptic and exposed sides of the tiles were monitored. The location with the highest sediment supply had the lowest Shannon diversity (H' ; 1.37–1.41) and percent cover of organisms inhabiting the cryptic tile sides after 30 months (bare space was between 37 and 40%). The cryptic communities at each of the locations were similar in composition of organisms after 30 months; however, the cryptic community trajectories (analyzed using the second-stage nMDS ordination) varied and two distinct clusters were found, with the most impacted location differing from the other locations in the deep depth strata. The exposed communities at all locations were primarily composed of macroalgae, turf and encrusting algae; the location with the highest sediment supply had higher diversity of algae and lower amounts of turf than the other locations. This study provides evidence that differences in sediment supply between these locations may play a subtle role in structuring communities.

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1. Introduction

Coastal development (and the associated changes to sediment supply) is an increasingly prominent threat to reef ecosystems, as population growth continues to expand on island nations in the Caribbean (Fabricius, 2005; Rogers, 1990). In Jamaica, the island's residential population has been steadily increasing over the past few decades, but the exponential growth in tourism (Alleyne and Boxill, 2003) is primarily responsible for the development of resorts and hotels that have dramatically altered the natural shoreline. Resort and highway construction and the subsequent creation of beaches in areas previously composed of limestone terrace (Land, 1973), have resulted in increased small-grained (<63 μm), terrigenous sediment supply to adjacent reefs in northern Jamaica (Stubler et al., 2015; Westfield, 2008).

Many reef organisms are affected directly and indirectly by increased suspended and settling sediments, which may lead to divergent community structure and assemblages in areas experiencing sedimentation (McClanahan and Obura, 1997). Adult organisms may be adversely affected by sediment stress, but it is often the juvenile and early developmental stages that are the most susceptible.

Coral recruits, for example, have a much lower sediment tolerance threshold than more mature or adult stages (Babcock and Smith, 2002; Fabricius et al., 2003; Phillipp and Fabricius, 2003). When exposed to elevated sediment deposition, coral juveniles exhibit higher mortality and are found in lower abundances (Babcock and Smith, 2002; Gilmour, 1999; Wittenberg and Hunte, 1992). The resultant adult community tends to be dominated by corals that mature quickly and have high reproductive output (Hunte and Wittenberg, 1992; Wittenberg and Hunte, 1992).

While understanding the effects of sedimentation stress on the recruitment patterns, survival, and community structure of hermatypic corals is important, non-coral taxa are becoming increasingly dominant on coral reefs (Bell et al., 2013; Norström et al., 2009). These sessile organisms, such as ascidians, polychaetes, and sponges may also be negatively affected by sedimentation. Some ascidian species exhibit reduced oxygen consumption when exposed to increased sediment concentrations (Torre et al., 2012). Heavy sediment loads may clog the aquiferous system of sponges as they filter feed; to prevent this, many sponges have physiologically adapted and are able to close their intake ostioles and suspend feeding during periods of sediment stress (Ilan and Abelson, 1995; Nickel, 2004). Sponge communities exposed to seasonal or long-term sedimentation will shift and form different assemblages in areas of high and low sedimentation (Maldonado et al., 2008). Other sessile invertebrates may be affected as well, such as polychaetes,

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which have significantly reduced survival in areas of high sedimentation (Irving and Connell, 2002).

In addition to the direct effects of sedimentation on individual organisms within the community, there are several indirect effects that can cascade throughout the ecosystem. Sediment stress may change the competitive advantage of organisms. This has been observed between freshwater rotifers and cladocerans exposed to siltation; cladocerans usually outcompete rotifers in food acquisition but when concentrations of total suspended solids are increased, rotifers gain a competitive advantage and dominate the zooplankton community (Kirk, 1991). While specific changes in competition between benthic organisms are more difficult to observe in the reef environment due to the multiple and complex interactions that occur, it is easy to envision a scenario where alteration of competitive vigor may have detrimental cascading effects. For example, by affecting the growth and survival of many sessile invertebrates, sedimentation may also reduce spatial competition, thereby promoting the growth of sediment-trapping macroalgae (reviewed in Fabricius, 2005). As macroalgae trap sediments, it further increases localized sediment accumulation, and subsequently negatively influences the recruitment of corals—a necessary component of a healthy reef (Birrell et al., 2005; Box and Mumby, 2007; Rogers, 1990). It is therefore crucial to understand how sedimentation impacts the recruitment and succession of reef organisms.

Community succession and development have been studied for decades; traditionally observational, these studies sought to describe the basic recruitment and replacement processes that form communities (Clements, 1936; Connell and Slayter, 1977; Odum, 1969; Underwood, 1994). Odum's (1969) successional theory posited that communities begin simply and acquire complexity in an orderly process of development and that the growth of an initial community will physically alter the environment and therefore facilitate the colonization of superseding organisms until a final, climax community is achieved. Classic successional studies of marine ecosystems were undertaken in accessible, yet highly disturbed, physically unstable environments, such as the rocky intertidal (e.g. Foster, 1975; Sousa, 1979).

As the scientific community endeavored to understand modern reef dynamics in the 1960s, 1970s and 1980s, successional studies of coral reef ecosystems also gained momentum. Many of these studies focused exclusively on the succession of hard corals (e.g., Grigg and Maragos, 1974; Hughes, 1985; Loya, 1976; Pearson, 1981; Tanner et al., 1994), largely ignoring other non-coral invertebrates (Jackson and Winston, 1982; Winston and Jackson, 1984). Today, while the literature is replete with studies of coral—and more recently macroalgae—colonization dynamics (Ceccarelli et al., 2011; Fricke et al., 2011; McClanahan, 1997), there remain few studies investigating the multitude of ancillary colonizers populating the successional spectrum in coral reefs (e.g., sponges, bryozoans, ascidians). Even within the studies that focus on the recruitment and replacement patterns for other reef organisms (Ceccarelli et al., 2011; Fairfull and Harriott, 1999), the motivation behind the research often remains coral-centric.

Perhaps even more nascent, is the idea proposed abstractly by Odum (1969) but expanded upon and championed by Sandin and Sala (2012) that community succession may be a way to monitor the status and health of an ecosystem in the face of anthropogenic disturbances and alteration. Recognizing the difficulty in assigning and subsequently measuring one indicator of an ecosystem's health (which is often measured by the performance of a single species; see Zacharias and Roff, 2001), Sandin and Sala (2012) suggested that succession may be used as a barometer of the overall functionality of an ecosystem. Building upon decades of research on successional theory, they proposed that successional indicators could be used to resolve where an ecosystem lies on the scale of degradation, such as inferring the 'maturity' of a community by discerning the prevalence of r-selected (fast-growing, indicative of an immature community) vs. K-selected organisms (slow-growing,

therefore indicative of a mature community). This method, which evaluates the response of the whole community, may be a more effective way to evaluate stressors that may not have an equal impact on all organisms, affect certain life stages of organisms, or have time-lagged effects on organism development.

The study presented aimed to utilize successional theory, along with traditional metrics used to characterize communities, such as percent cover and Shannon diversity (H'), to understand the impacts of anthropogenic sedimentation and coastal development on community-wide recruitment and succession patterns on coral reefs in northern Jamaica. Exposed and cryptic community succession was monitored after 6, 18 and 30 months on settlement tiles at three locations with different degrees of coastal development and sedimentation rates. Previous investigations of cryptic community recruitment at these locations showed that post-settlement mortality events seem to be higher for sessile organisms at the location with the highest degree of coastal development (Stubler, 2015); therefore, the present study aimed to determine whether the community assemblages and trajectory of successional development would differ between locations. Specifically, this study sought to determine whether the early-stage cryptic communities would be less diverse and exhibit a higher percentage of bare space on the tiles at the location with the highest adjacent development, and whether this would translate into an altered community trajectory (successional development) compared to the locations with less development. The succession of macroalgae and epibionts recruiting to the exposed (top) sides of tiles was also investigated; the expectation was that macroalgae would dominate communities at the location with highest sediment supply, while locations with lower sedimentation would have lower macroalgae coverage but higher coverage of crustose coralline algae (CCA).

2. Materials and methods

2.1. Description of study locations

This study was conducted on the northern coast of Jamaica, West Indies at three locations, each representing different degrees of coastal development and sediment deposition (Stubler et al., 2015; Westfield, 2008): Pear Tree (N 18.465, W 77.343), Discovery Bay fore reef (N 18.473, W 77.412) and Dairy Bull (N 18.471, W 77.379) (Fig. 1a). Pear Tree, the easternmost location in this study, was directly adjacent to a large resort that was constructed in 2005, which resulted in approximately 25,000 m² of artificially created and filled beaches (Westfield, 2008)—a 42% increase in beach area—along less than 2 km of shoreline. Approximately 4 km to the west of Pear Tree, Dairy Bull has the least amount of adjacent coastal development of the three locations. Finally, the Discovery Bay location was on the forereef just west of the Discovery Bay inlet; this location was considered moderately developed due to its proximity to several residential and commercial developments within Discovery Bay. Bathymetrically, the study locations were very similar with large spur and groove reef tracts present less than 1 km from the shoreline. Full characterization of the environmental parameters at each of the study locations is described by Stubler et al. (2015); temperature, salinity, dissolved oxygen and chlorophyll *a* were found to be statistically similar among locations. Light levels measured at 8–10 m and 15–18 m at each location did not statistically vary among locations (Stubler et al., 2015).

Sediment trap data previously collected at these locations (Stubler et al., 2015; Fig. 1A) found that rates of sediment accumulation were related to wind events. During low wind events ($<10 \text{ m s}^{-1}$), no differences in sedimentation rates among locations were found; however, when sustained wind speeds were high ($>10 \text{ m s}^{-1}$), Pear Tree experienced significantly higher rates of sediment accumulation compared to Discovery Bay and Dairy Bull (Stubler et al., 2015). Sediments accumulating at Discovery Bay and Dairy Bull were primarily carbonate-based

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