Exposure to nutrient-enriched sediments mitigates the negative impacts of sedimentation on coral growth in the Caribbean corals *Porites astreoides* and *Siderastrea siderea*

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Abstract. Sedimentation is a major source of disturbance to coral reefs. However, the documentation of healthy coral communities in areas with high sediment and nutrient inputs suggests that an enhanced heterotrophic environment may allow corals to thrive under marginal conditions. Here, we document the effects of sedimentation on the survivorship and growth of *Porites astreoides* and *Siderastrea siderea* to evaluate whether the higher nutrient content of enriched sediments can be utilized to offset the negative impacts of sedimentation.

P. astreoides and *S. siderea* showed high tolerance to chronic sedimentation that reduced light levels and covered corals daily for three weeks. Limited tissue losses were observed, but total mortality was not recorded. Coral growth was significantly influenced by the addition of sediments. For *P. astreoides*, control corals had the fastest growth rates, followed by corals from the enriched nutrient treatment, non-enriched sediment treatment, and the shading treatment. For *S. siderea*, growth rates were highest for control corals, followed by corals in the enriched sediments treatment, the shading treatment, and the non-enriched sediment treatment. The enhanced growth of *Porites astreoides* and *Siderastrea siderea* exposed to nutrient-enriched sediments shows that corals are able to offset the negative impacts of sedimentation by assimilating sediment nutrients.

Key words: Sedimentation, coral growth, nutrient assimilation

Introduction

The impacts of sedimentation are regarded as an increasing threat to coral reefs worldwide (Bryant et al. 1998; McCulloch et al. 2003; Fabricius 2005). Rapid population growth, changes in land-use patterns, and watershed modifications have all increased terrestrial runoff to coastal habitats (Devlin and Brodie 2005). Moreover, urban development and activities such as beach nourishment and dredging have also resulted in increased sedimentation patterns on nearshore coral reef habitats with significant detrimental effects on coral abundance, diversity, and distribution (Wilkinson 2004; Fabricius 2005).

Most sedimentation-related research on coral reefs has focused on direct and indirect stress pathways that include reduced light, abrasion, smothering, burial, toxicity (Fabricius 2005; Sanders and Baron-Szabo 2005), and associated impacts that include reduced photosynthesis (Riegl and Branch 1995; Phillips and Fabricius 2003), partial or complete tissue mortality (Rogers 1983; Nugues and Roberts 2003), reduced growth (Rice and Hunter 1992), and reduced fertilization, larval survivorship, and recruitment (Gilmour 1999; Babcock and Smith

2000). However, recent studies indicate that reef habitats exposed to sedimentation, suspended particulate matter, and nutrient inputs have access to an enhanced heterotrophic environment that may allow corals to survive and thrive under conditions often considered as marginal for coral growth and reef development (Anthony 1999, 2000, 2006; Anthony and Fabricius 2000). Increased availability of heterotrophic energy and nutrient sources in nearshore coastal habitats has been linked to higher coral growth rates (Edinger et al. 2000), increased energy storage (Anthony 2006), and increased resilience to disturbance (Grottoli et al. 2006).

The role of sediments as a potential source of nutrition for corals has been documented in studies that showed that organic matter from sediments can be transferred to the coral tissue (Rosenfeld et al. 1999), and that corals can selectively extract food particles from sediments (Mills and Sebens 1997) and assimilate the N available in sediments (Mills and Sebens 2004). In this study, we document experimentally the effects of high sedimentation on the short-term (i.e., 3 weeks) growth of two Caribbean coral species, *Porites astreoides* and

Siderastrea siderea, and evaluate whether the higher nutrient content of enriched sediments can be utilized by corals to offset the negative impacts of sedimentation.

Methods

Porites astreoides and *Siderastrea siderea* are among the most abundant species in both inshore and offshore reefs of the Florida Reef Tract (Lirman and Fong 2007) and are commonly found in areas with high sedimentation (Rogers 1990). Fragments (2-3 cm in diameter) of *P. astreoides* and *S. siderea* were extracted from a single colony of each species, thus ensuring genetic uniformity of fragments. The coral colonies were collected from a mid-channel patch reef in the northern section of the Florida Reef Tract. Mean water nutrient levels for the area where the colonies were collected were 0.6 μM DIN and 0.03 μM SRP (Lirman and Fong 2007). Nutrient levels in the seawater used in this study had higher DIN (2.1 μM) and similar levels of SRP (0.04 μM; data provided by the NOAA/AOML/South Florida Program.

The fragments were attached to the PVC platforms used to measure coral growth using underwater epoxy and, after an acclimation period of two months, were placed into the 5-L aquaria used as experimental units. Coral fragments were randomly assigned to the following treatments: (1) controls; (2) non-enriched sediments; (3) enriched sediments; and (4) shading. Replicates for each treatment were 9 fragments for *P. astreoides* and 4 fragments for *S. siderea*.

Air was supplied with air stones and seawater was added continuously at a turnover rate of approximately 6-8 times every 24 hr. A barrier constructed of plankton netting material was glued to the top of the aquaria to trap sediments as the water flowed out of the aquaria. Corals were kept in a aereated, flow-through system (as opposed to a static system) to ensure that any changes in pH, dissolved oxygen, carbonate chemistry, and water nutrients due to the addition of sediments would be transient, thus isolating the impacts of sedimentation and sediment nutrients from these other potentially confounding factors. Measurements of pH, dissolved oxygen, and salinity inside the experimental aquaria before and after the addition of sediments did not show any significant impacts of sediment addition on these parameters. However, water nutrient levels were not measured after sediment addition. While we believe that the use of a flow-through system limits the influence of nutrients transferred from the sediments to the water column as a factor in this study, the lack of nutrient readings precludes a full separation

between the potential effects of sediment nutrients and elevated water nutrients.

Similarly, the seawater supplied was filtered using a set of 10 μm and 1 μm canister filters to minimize the amount of external particles available to the corals. The aquaria were placed within flow-through holding tanks for temperature control and light was supplied by compact fluorescent bulbs on a 12-hour light and dark cycle. The aquaria were cleaned and repositioned at random within the holding tanks once a week. The amount of light reduction caused by sedimentation was measured with a LiCor sensor placed inside an aquarium where levels of PAR were measured at 10 min-intervals after sediment addition.

The sediments used in this study were collected from the top layer (< 5 cm in depth) at a reef from Key Largo, Florida. Mean particle size, calculated with a Coulter Particle Size Analyzer, was 176 μm (S.D. = ± 34, n = 4 samples). The sediments were placed in two aerated 10-gal aquaria filled with seawater one week prior to the start of the experiment. Nutrients were added to one of the aquaria to create an enriched sediment treatment. NO_3 and PO_4 were added to the seawater to achieve enrichment levels of approximately 20 μM N and 2 μM P above ambient (Fong et al. 2003). At the end of the experiment, five samples were collected from the control and enriched sediments and the nutrient content of sediments was measured by the Nutrient Analytical Services Laboratory of the University of Maryland.

Each day, sediments were added to the experimental aquaria at a concentration of approximately 1000 mg DW L^{-1}. The mean sedimentation rate within aquaria was 53 mg DW cm^{-2} d^{-1} (S.D. = ± 17). These high concentrations were within the range of values reported to cause significant negative impacts on coral physiology and were similar to the sedimentation values obtained for Biscayne Bay, a coastal lagoon adjacent to the city of Miami (Rogers 1990; Lirman et al. 2003; Fabricius 2005; Weber et al. 2006). Finally, to evaluate the effects of light reduction on coral growth, corals were kept under shade-cloth that reduced available light levels by 62.5 % throughout the experiment.

Coral growth was measured using a Keyence© high accuracy CCD micrometer that measures the height profile of corals mounted on PVC platforms with micron-accuracy (Fig. 1). An aluminum pin cemented into each platform provides a standard against which coral height can be accurately measured. By measuring the height profile of each fragment repeatedly, linear extension rates can be determined as the difference in height between measurement intervals. Reported vertical linear extension rates are the average extension rate over the

entire surface of the colony. Differences in growth rates were compared among treatments using ANOVA.
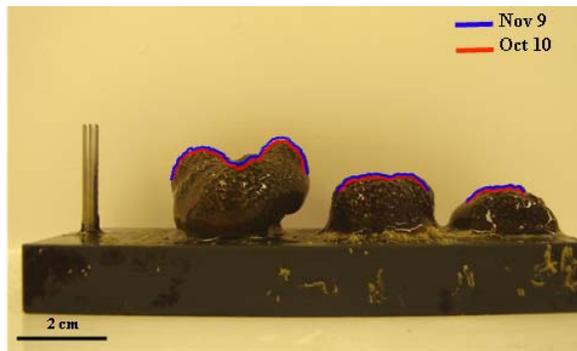

Figure 1: Photograph of the PVC platform used to measure vertical coral growth with a Keyence© high-accuracy CCD micrometer. Vertical growth along the coral contour was measured as the difference in height between intervals.

Results

Immediately after sediment addition, light levels inside aquaria were reduced to < 10 % of ambient levels but returned to pre-sedimentation levels (250 – 315 μE m^{-2} sec^{-1}) within 1.5 - 2 hr as the suspended sediments settled on the coral surface and the bottom of the aquaria. The light levels recorded after the sensor was completely covered by accumulated sediments were < 5 % of ambient levels. After addition, sediments were deposited rapidly over the coral surface and corals were covered completely within 45 min. The removal of sediments from the coral surface took up to 6 hr. Mean nutrient content was 10.3 μg g DW^{-1} (S.D. = ± 1.5) N and 2.1 μg g DW^{-1} (0.4) P for the control, non-enriched sediments, and 176.2 μg g DW^{-1} (± 62.2) N and 3.8 μg g DW^{-1} (0.4) P for the enriched sediments. The mean content of both N and P was significantly higher in the enriched sediments (t-test, $p < 0.05$). Total C (organic and inorganic) content (8 - 10 % DW) was not different between the sediment treatments (t-test, $p > 0.05$). The nutrient content of the sediments used in this experiment were similar to those values obtained from reef sediments in the Florida Reef Tract by Szmant and Forrester (1996). Enriched sediments used in this study had N values higher than those recorded for inshore reef habitats (25-140 μg g^{-1}) of the Florida Keys and P values within the range (2 -6 μg g^{-1}) observed for these habitats (Szmant 2002).
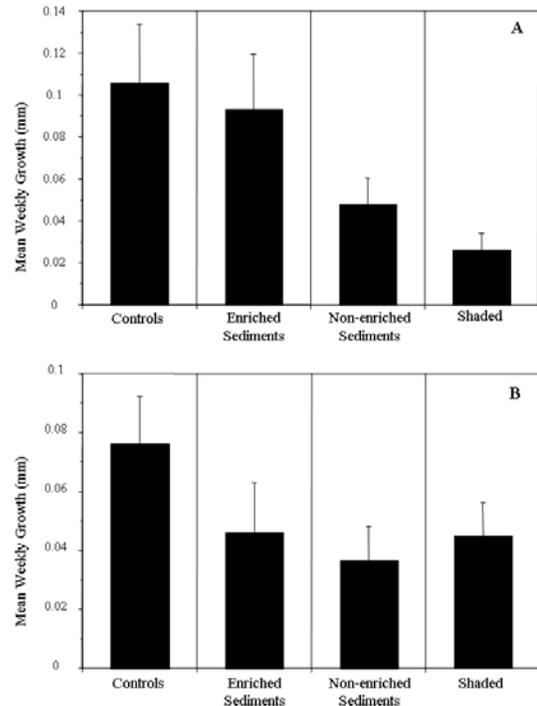

Figure 2: Growth of coral fragments of (A) *P. astreoides* and (B) *S. siderea* exposed to enriched sediments, non-enriched sediments, and shading treatments for a period of three weeks.

The growth of *P. astreoides* and *S. siderea* was significantly influenced by the addition of sediments. For *P. astreoides*, control corals had the fastest growth rates, followed by corals from the enriched nutrient treatment, non-enriched sediment treatment, and, finally, the shading treatment (Fig. 2A). No significant differences in growth rates were documented between control corals and corals exposed to enriched sediments. These two groups had growth rates significantly higher than those recorded for shaded corals and corals exposed to non-enriched sediments, which were not significantly different from each other (ANOVA, $p < 0.05$, Tukey HSD test).

For *S. siderea*, growth rates were highest for control corals, followed by corals in the enriched sediments treatment, the shading treatment, and the non-enriched sediment treatment (Fig. 2B). Significant differences were only documented between control corals and corals exposed to non-enriched sediments (ANOVA, $p < 0.05$, Tukey HSD test). Finally, some tissue losses were observed in the perimeter of the colonies, but none of the small fragments used in this study exhibited total mortality.

Discussion

Corals in marginal environments frequently encounter high levels of sedimentation and nutrients, and their

ability to maintain a positive energy balance and sustain growth under sub-optimal conditions are crucial to their persistence in these habitats (Anthony and Fabricius 2000; Lirman and Manzello 2009). The enhanced growth of *Porites astreoides* and *Siderastrea siderea* exposed to nutrient-enriched sediments shows that corals are able, at least in part, to offset the negative impacts of sedimentation by assimilating sediment nutrients. The ability of corals to assimilate nutrients and food particles contained in sediments has been previously documented by Rosenfeld et al. (1999) and Mills and Sebens (1997, 2004), but this is the first study to show a relationship between coral growth and the nutrient content of sediments. Future studies on the nutrient uptake of sediment nutrients by corals are needed to determine the nutrient pathways within the coral holobiont.

The response of corals to turbidity and sedimentation is influenced by species-specific light requirements and sediment rejection characteristics (Rogers 1983, 1990; Stafford-Smith 1993; Fabricius 2005). The present study showed a high tolerance of both *P. astreoides* and *S. siderea* to chronic high sedimentation levels that significantly reduced light levels and covered corals on a daily basis for three weeks. The ability to shed sediments and continue to grow under reduced light levels without significant tissue mortality correlates well with the high abundance of these two species throughout the Florida Reef Tract, even in areas with reduced water quality (Lirman and Fong 2007). Shading had the largest impact on the growth of *P. astreoides*, but the impact of light reduction in the absence of sediments was not significant for *S. siderea*. The green morph of *P. astreoides* used in this study is commonly found in shallow reef habitats (Gleason 1998) and may have a restricted depth distribution based on its higher light requirements.

In the Florida Reef Tract, a cross-shelf gradient in coral growth and mortality contrary to what was expected based on water quality patterns was documented by Lirman and Fong (2007). Corals from inshore habitats with higher nutrients and turbidity levels showed faster growth rates and lower rates of partial mortality compared to corals from similar habitats with lower nutrient and turbidity levels further away from shore. These findings led to the hypothesis that inshore habitats may provide an expanded heterotrophic niche for corals not available to offshore corals (Lirman and Fong 2007). This hypothesis is supported by research from Australia's GBR where corals in high-turbidity habitats are able to thrive due to particle feeding and nutrient assimilation (Anthony 1999, 2000, 2006; Anthony and Fabricius 2000). The higher growth rate of corals exposed to nutrient-enriched sediments compared to corals exposed to non-enriched sediments supports the hypothesis that the assimilation of nutrients from sediment sources may be partly responsible for the high growth rates documented for *P. astreoides* and *S. siderea* on inshore reefs where the highest levels of interstitial nutrients and N content of sediments are present (Szmant and Forrester 1996).

Finally, while enriched sediments can provide an additional source of nutrients for corals, sedimentation still remains one of the most significant sources of stress to corals worldwide. The balance between the negative impacts of sedimentation and the potential for enhanced heterotrophic sources of nutrition will depend on the frequency and intensity of sedimentation stress as well as species-specific tolerance patterns. Extensive research is still needed to fully understand the thresholds associated with sedimentation stress, but it is clear that prolonged exposure to sediments that exceed the shedding capability of corals can result in reduced growth, colony mortality, and significant modifications to coral abundance and community composition (Rogers 1990; Fabricius 2005; Dikou and van Woesik 2006). Moreover, while corals may be able to partly mitigate the cost of increased turbidity and the energy expended in clearing deposited sediments through nutrient assimilation, high organic and nutrient levels within fine sediments can cause tissue mortality through the increased activity of harmful microbial communities and the development of anoxic conditions (Weber et al. 2006).

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