Effects of anthropogenic stressors on tropical sponge ecology

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Amber Dawn Stubler

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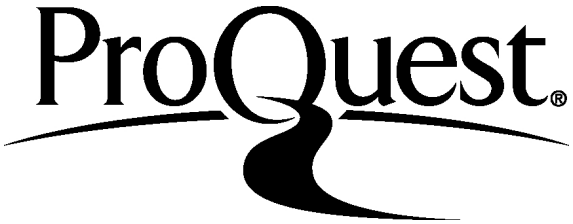

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Abstract of the Dissertation

Effects of anthropogenic stressors on tropical sponge ecology

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The impacts of coastal development, ocean acidification, and temperature increases on sponge ecology were investigated, with an emphasis on community-wide impacts. At three locations with varying degrees of coastal development and sediment supply, field surveys were used to assess existing sponge abundance, diversity, species richness and community composition in Jamaica. Sediment accumulation rate, total suspended solids and other water quality parameters were quantified. The community-wide consequences of coastal development and increased sediment supply were also investigated by monitoring the annual and seasonal recruitment, as well as community succession over 6 years and 30 months, respectively. Of the adult (existing) populations surveyed, the location with the lowest degree of coastal development and sediment supply had higher sponge abundance, diversity, species richness and a distinct community composition than the other two locations with higher coastal development. Sponge seasonal recruitment was similar in diversity and percent cover across all locations; however, the diversity and percent cover of sponges assessed annually was lowest at the location with the most coastal development and sediment supply, suggesting that post-settlement mortality was higher at this location. After 30 months, the location with the highest sediment supply had statistically more bare space, which is indicative of an overall lack of recruitment; this provides further evidence that post-settlement mortality is occurring and propagating community trajectory changes. Although the exact mechanism is unclear, this study provides correlative

evidence that even moderate coastal development is influencing sponge communities on reefs along the northern coast of Jamaica

To determine the effects of industrialization and increasing atmospheric CO_2 on sponges, two studies were performed to evaluate how 1) ocean acidification affects the interactions between a bioeroding sponge, *Cliona varians,* and a coral, *Porites furcata* and 2) how increasing temperature and decreasing pH affect sponge erosion of living and dead coral substrate. The results of the first study indicated that acidification had no negative physiological impacts on *C. varians*, and no significant impact on the survival of either coral or sponges. However, exposure to end-of-century levels of pH reduced calcification in *P. furcata* and led to a significant increase in sponge-mediated erosion. The second study provided a more comprehensive evaluation of the relevant interactions between sponges and living corals and evaluated the differential impacts of bioeroders on living and dead coral substrate under acidification and warming scenarios. The findings of this study suggest differential impacts of temperature, pH and sponge bioerosion for living and dead corals. Living coral calcification was significantly reduced by temperature and sponge treatments, with no significant effect of pH, while dead coral dissolution was primarily driven by pH, regardless of sponge presence or seawater temperature. The results of this study suggests that future acidification and warming studies should include ecologically relevant time scales, adequate acclimation periods, interactions, and multiple levels of community organization to better understand and predict ecosystem-level response to future environmental conditions. This dissertation represents an effort to understand how anthropogenic stressors are affecting sponge communities, and the subsequent implications for reef community structure and function.

Dedication Page

"Tell me, what is it you plan to do
With your one wild and precious life?"
-Mary Oliver, "The Summer Day"

I would like to dedicate this dissertation to my family, who never doubted or questioned that the path I had chosen was the right path for me. For their love and support, I am eternally grateful.

Frontispiece

Table of Contents

List of Figures

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

List of Tables

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

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Chapter 1
Introduction

Background

Marine sponges are animals belonging to the phylum Porifera, with the majority of sponges (~90%) classified as demosponges (Phylum Porifera, Class Demospongiae). Sponges are found in benthic communities throughout the polar, temperate and tropical latitudes, however they are particularly abundant in tropical ecosystems (Diaz and Rützler 2001). Habitats such as coral reefs, mangroves and even seagrass beds host a large diversity and abundance of sponges. Often, sponges are as diverse and abundant as other important organisms such as corals. In the Caribbean, there are >300 known sponge species, compared to approximately 70 species of hard corals (see Diaz and Rützler 2001 for coral-sponge richness comparisons). In some coral reefs, sponges can occupy a quarter of the available hard substrate (Diaz and Rützler 2001) and dominate the biomass and volumetric space on many reefs (Wilkinson and Evans 1989; Diaz and Rützler 2001). While sponges are already prevalent on coral reefs, there is growing evidence that sponge growth may be outpacing coral growth on Caribbean reefs (McMurray et al. 2010), potentially shifting reefs from coral to sponge dominance (Bell et al. 2013).

Tropical sponges, while highly diverse themselves, also enhance the diversity of other organisms by providing key micro- and macrohabitat structure and complexity. The extensive variations in sponge morphology provide habitats and have cultivated several symbioses in tropical habitats. Zoanthids, crustose coralline algae, shrimp, crustaceans, bivalves, amphipods, and other sponge species are just some of the groups that are known to associate with sponges. In addition to these associations, there are numerous organisms that utilize sponges as microhabitat; for example over 2200 organisms, representing 75 different species, were found in 19 specimens of the sponge *Mycale microsigmatosa* in Brazil (Ribeiro et al. 2003). Sponges also harbor microbial communities; microbes inhabiting the mesohyl are more taxonomically varied and may include cyanobacteria, proteobacteria (α and γ), actinobacteria, and many others. Photosynthetic cyanobacteria and dinoflagellates can also live within the outer sponge pinacoderm and generally have a relationship analogous to the well-known mutualism between corals and zooxanthellae (Hill 1996; Erwin and Thacker 2008).

Sponges also contribute to the macrohabitat in an ecosystem. In coral reefs, sponges are capable of reef creation, stabilization, and substrate consolidation (Wulff 1984). Reef stabilization by sponges is particularly important after large disturbances such as hurricanes;

fragments of sponges can attach to rubble and temporarily stabilize the reef framework until crustose coralline algae recruits can more permanently cement the reef structure (Wulff 1984). The cryptic and sub-cryptic sponge species found in the interstitial spaces between rubble may also help to bind and stabilize the substrate (Bell 2008).

Besides modifying and providing biogenic structure, some sponges have the ability to reshape carbonate frameworks by physically removing and chemically dissolving calcium carbonate (Pomponi 1980). These sponges are interchangeably referred to as boring, eroding or excavating sponges throughout the literature and are found predominantly in temperate and tropical environments (Cerrano et al. 2001 McClintock et al. 2005). Excavating sponges are important, particularly in coral reef environments (Rützler 1975; MacGeachy 1977; Rützler 2002) where they can reshape whole coral colonies (Goreau and Hartman 1963), create new space for settlement, and ease spatial competition among benthic organisms (Williams et al. 1999; Lopez-Victoria and Zea 2005). While excavating sponges play a vital role in reef ecosystems, their abundance on coral reefs has steadily increased with water quality declines (i.e. nutrient enrichment, pollution and sediment run-off) (Rose and Risk 1985; Holmes 2000; Ward-Paige et al. 2005). Facilitated by wide-spread decline in coral health due to a suite of anthropogenic stressors, excavating sponges have exploited the reduced defensive capabilities of stressed corals and steadily increased in abundance (Rose and Risk 1985; Holmes 2000).

Additional ecological functions of sponges include the creation of nursery habitat, providing an important food source to animals such as angelfish and turtles, and shaping community structure through competitive interactions. Sponges also contribute to water filtration, carbon and nitrogen cycling (Fiore et al. 2010), and may help control phytoplankton blooms (Peterson et al. 2006). As filter-feeders that pump and filter seawater to fulfill their nutritional and gas exchange requirements (Reiswig 1971; Southwell et al. 2008), their ability to consume phytoplankton, bacteria, particulate organic matter (POM), viruses (Reiswig 1971; Hadas et al. 2009; Hadas et al. 2006), dissolved organic matter (DOM) (de Goeij et al. 2013) and dissolved organic carbon (DOC) (Mueller et al. 2014) contribute to nutrient cycling (Fiore et al. 2010) and control of phytoplankton blooms (Wall et al. 2012; Peterson et al. 2006) on coral reefs. Sponges can be an important economic resource for many small developing countries; in

some parts of the world, sponges are still harvested for use as bath sponges (Duckworth and Wolff 2007).

While we have begun to recognize the importance of sponges in coastal ecosystems, the impacts of human stressors, although well studied for many other key organisms, are still largely unknown for sponges. Sponges have traditionally been considered auxiliary species in many ecosystems, yet as the main foundational species in areas such as coral reefs are degraded, sponges are becoming more prominent in their contributions to community structure and function (Diaz and Rützler 2001). Considering the varied ecosystem functions provided by sponges, an understanding of how certain human-induced stressors are affecting sponges is important to understanding how benthic marine communities will respond to future conditions. The immediate impacts on sponge communities from human development, such as sedimentation, as well as longer term impacts, such as ocean acidification and temperature rise, are all integral parts to understanding how humans impact and change ecosystems.

Sedimentation and Sponges

Sponges are filter-feeding organisms that must pump and filter seawater to obtain the majority of their nutrition (Reiswig, 1971; Southwell et al., 2008). This lifestyle leaves sponges highly susceptible to increased sediment loads because their filtering and sorting structures are easily congested. Some sponges are able to temporarily suspend feeding (Gerrodette and Flechsig 1979; Tompkins-MacDonald and Leys 2008) or control the size of (or close) their incurrent openings when particle concentrations suddenly increase to avoid becoming congested with unwanted sediment particles (Bell 2004). Some sponge species are also capable of reversing water flow thereby expelling sediments from their intake ostioles and unclogging themselves (Nickel 2004). Other species have the ability to secrete a mucus layer that will act as a trap for sediment and can then be discarded along with any silt (Turon et al. 1999). These temporary acclimation strategies are useful only during short periods of increased sedimentation, since arresting pumping rates for long periods of time retards their ability to feed and results in an internal oxygen debt.

Based on the feeding strategy of sponges, it would seem that some are unlikely to be found in areas where suspended sediment levels are high. However, there are sponges that have physiologically adapted to living under conditions where there is constant sediment stress. Morphological alterations such as branching or a strategic positioning/angling of incurrent openings can reduce the amount of sediment encountered by the sponge (Bell and Barnes 2000). Separation of the incurrent and excurrent flows can also help reduce the amount of sediment ingested by the sponge (Bell et al. 2002). The cellular plasticity of demosponges allows them to reorganize their cell structure to accommodate new environmental situations. These physiological modifications enable some sponges to inhabit areas where sediment concentrations would normally be intolerable.

Despite these multiple abilities, there are limits to sponge tolerance of suspended and settling sediment. The negative impacts of sedimentation on sponge growth, reproduction and survival may ultimately translate into broad-scale sponge distribution and community composition changes.

Ocean Acidification, Temperature Rise and Sponges

Sponges also experience indirect anthropogenic impacts, such as those resulting from increased CO_2 emissions due to industrialization. Current levels of atmospheric CO_2 fluctuate around 400 ppm and continue to rise (Kleypas 1999; Sabine and al. 2004; Orr et al. 2005; Guinotte and Fabry 2008); projected scenarios indicate that atmospheric CO_2 levels will approach 750-1000 ppm by 2100 (Caldeira and Wickett 2005; Gattuso and Lavigne 2009). The resultant increase in dissolved seawater CO_2 is expected to reduce surface ocean pH by 0.3-0.4 units, substantially altering the carbonate chemistry of coastal marine ecosystems (Caldeira and Wickett 2003; Caldeira and Wickett 2005; Doney et al. 2009). These changes will affect the physiological ability of organisms to precipitate calcium carbonate ($CaCO_3$) (Orr et al. 2005) and will therefore disproportionately impact ecosystems relying on the formation of carbonate biogenic structure, such as coral reefs.

While ocean acidification will negatively affect reef-building corals (Anthony et al. 2008; Jokiel et al. 2008; Kurihara 2008), the potential effects on non-calcifying organisms are still

largely unknown (Przeslawski et al. 2008; Duckworth et al. 2012). Duckworth et al. (2012) found that several common reef sponges were unaffected by increased temperature and lowered pH, however this study did not include boring sponges. Boring sponges may benefit from lowered pH because $CaCO_3$ dissolution would be favored and reduced calcification rates may increase bioerosion efficiency (Wisshak et al. 2012). A recent study examining the bioerosion of scallop shells by *Cliona celata* found that boring rates are enhanced in acidified waters (Duckworth and Peterson 2012). In addition, although increases in sea surface temperature will negatively affect corals, and other foundational organisms, sponges seem to be relatively unaffected by temperature increases (Duckworth et al. 2012). This suggests that the combined effects of warmer, more acidic waters may greatly increase sponge growth/expansion and boring activity, which could negatively impact ecosystems relying on calcium carbonate biogenic structures.

Objectives

The aim of this dissertation was to evaluate how three different anthropogenically-induced stressors (sedimentation, acidification, and warming) affect aspects of sponge ecology. Both field and laboratory experiments were performed with the objectives of testing the effects of each stressor at both the individual and community level. Understanding the immediate impacts of human development, such as sedimentation, as well as the longer-term impacts, such as ocean acidification and temperature rise, on sponge ecosystem function is essential to predict how benthic marine communities will respond to future conditions.

The following hypotheses were addressed:

1. Sediment deposition will result in 1) reduced species richness and abundance, 2) lower diversity, 3) distinct community composition, and 4) differences in the dominant morphology and size distribution of sponges. (Chapter 1)
2. Increased sediment supply will lead to 1) lower sponge recruitment, 2) reduced overall epibiont diversity and 3) decreased cover (%) of recruited organisms. As a result of these expected changes, the successional patterns will be altered, leading to divergent community development. (Chapters 2 and 3)

3. Acidification will result in higher substrate erosion rates and alter the competitive interactions occurring between a common excavating sponge (*Cliona varians*) and coral (*Porites furcata*) in favor of the sponge. (Chapter 4)
4. Elevated temperature and decreased pH will amplify sponge (*Cliona varians*) erosional activity; however, bioerosion rates will be different on living and dead corals. (Chapter 5)

References

Anthony KR, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences USA* 105:17442-17446

Bell JJ (2004) Evidence for morphology-induced sediment settlement prevention on the tubular sponge Haliclona urceolus. *Marine Biology* 146:29-38

Bell JJ (2008) The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science* 79:341-353

Bell JJ, Barnes DKA (2000) The distribution and prevalence of sponges in relation to envrionmental gradients within a temperate sea lough: vertical cliff surfaces. *Diversity and Distributions* 6:283-303

Bell JJ, Barnes DJ, Turner J (2002) The importance of micro and macro morphological variation in the adaptation of a sublittoral demosponge to current extremes. *Marine Biology* 140:75-81

Bell JJ, Davy SK, Jones T, Taylor MW, Webster NS (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology* 19:2613-2624

Caldeira K, Wickett M (2003) Oceanography: Anthropogenic carbon and ocean pH. *Nature* 425:365

Caldeira K, Wickett M (2005) Ocean Model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *Journal of Geophysical Research* 110:np

Cerrano C, Bavestrello G, Calcinai B, Cattaneo-Vietti R, Chiantore M, Guidetti M, Sara A (2001) Bioerosive processes in Antarctic seas. *Polar Biology* 24:790-792

de Goeij JM, van Oevelen D, Vermeij MJ, Osinga R, Middelburg JJ, de Goeij AF, Admiraal W (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science* 342:108-110

Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean reefs. *Bulletin of Marine Science* 69:535-546

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean Acidification: The Other CO2Problem. *Annual Review of Marine Science* 1:169-192

Duckworth AR, Wolff C (2007) Bath sponge aquaculture in Torres Strait, Australia: Effect of explant size, farming method and the environment on culture success. *Aquaculture* 271:188-195

Duckworth AR, Peterson BJ (2012) Effects of seawater temperature and pH on the boring rates of the sponge Cliona celata in scallop shells. *Marine Biology* 160:27-35

Duckworth AR, West L, Vansach T, Stubler A, Hardt M (2012) Effects of water temperature and pH on growth and metabolite biosynthesis of coral reef sponges. *Marine Ecology Progress Series* 462:67-77

Erwin PM, Thacker RW (2008) Phototrophic nutrition and symbiont diversity of two Caribbean sponge-cyanobacteria symbioses. *Marine Ecology Progress Series* 362:139-147

Fiore CL, Jarett JK, Olson ND, Lesser MP (2010) Nitrogen fixation and nitrogen transformations in marine symbioses. *Trends in Microbiology* 18:455-463

Gattuso J-P, Lavigne H (2009) Technical Note: Approaches and software tools to investigate the impact of ocean acidification. *Biogeosciences* 6:2121-2133

Gerrodette T, Flechsig AO (1979) Sediment-induced reduction in the pumping rate of the tropical sponge Verongia lacunosa. *Marine Biology* 55:103-110

Goreau T, Hartman WD (1963) Boring sponges as controlling factors in the formation and maintenance of reefs. In: RF S (ed) Mechanisms of hard tissue destruction. *American Association for the Advancement of Science* 25-54

Guinotte JM, Fabry VJ (2008) Ocean acidification and its potential effects on marine ecosystems. *Annals of the New York Academy of Sciences* 1134:320-342

Hadas E, Marie D, Shpigel M, Ilan M (2006) Virus predation by sponges is a new nutrient-flow pathway in coral reef food webs. *Limnology and Oceanography* 51:1548-1550

Hadas E, Shpigel M, Ilan M (2009) Particulate organic matter as a food source for a coral reef sponge. *Journal of Experimental Biology* 212:3643-3650

Hill MS (1996) Symbiotic zooxanthellae enhance boring and growth rates of the tropical sponge Anthosigmella varians forma varians. *Marine Biology* 125:649-654

Holmes KE (2000) Effects of eutrophication on bioeroding sponge communities with the description of a new West Indian sponges, Cliona spp. (Porifera: Hadromerida: Clionidae). *Invertebrate Biology* 119:125-138

Jokiel PL, Rodgers KS, Kuffner IB, Andersson AJ, Cox EF, Mackenzie FT (2008) Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs* 27:473-483

Kleypas JA (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284:118-120

Kurihara H (2008) Effects of CO_2-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series* 373:275-284

Lopez-Victoria M, Zea S (2005) Current trends of space occupation by encrusting excavating sponges on Colombian coral reefs. *Marine Ecology* 26:33-41

MacGeachy J (1977) Factors controlling sponge boring in Barbados reef corals. *Proceedings of the 3rd International Coral Reef Symposium* 2:477-483

McClintock JB, Amsler CD, Baker BJ, van Soest RWM (2005) Ecology of Antarctic marine sponges: An overview. *Integrative and Comparative Biology* 45

McMurray SE, Henkel TP, Pawlik JR (2010) Demographics of increasing populations of the giant barrel sponges Xestospongia muta in the Florida Keys. *Ecology* 91:560-570

Mueller B, de Goeij JM, Vermeij MJ, Mulders Y, van der Ent E, Ribes M, van Duyl FC (2014) Natural diet of coral-excavating sponges consists mainly of dissolved organic carbon (DOC). *Plos One* 9:E90152

Nickel M (2004) Kinetics and rhythm of body contractions in the sponge Tethya wilhelma (Porifera: Demospongiae). *Journal of Experimental Biology* 207:4515-4524

Orr JC, Fabry V, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishida A, Joos F (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681-686

Peterson BJ, Chester CM, Jochem FJ, Fourqurean JW (2006) Potential role of sponge communities in controlling phytoplankton blooms in Florida Bay. *Marine Ecology Progress Series* 328:93-103

Pomponi S (1980) Cytological mechanisms of calcium carbonate excavation by boring sponges. *International Review of Cytology* 65:301-319

Przeslawski R, Ahyong S, Byrne M, WÖRheide G, Hutchings PAT (2008) Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. *Global Change Biology* 14:2773-2795

Reiswig H (1971) Particle feeding in natural populations of three marine Demosponges. *Biological Bulletin* 141

Ribeiro SM, Omena EP, Muricy G (2003) Macrofauna associated to Mycale microsigmatosa (Porifera, Demospongiae) in Rio de Janeiro State, SE Brazil. *Estuarine, Coastal and Shelf Science* 57:951-959

Rose CS, Risk MJ (1985) Increase in Cliona deletrix infestation of Montastrea cavernosa heads on an oragnically polluted portion of the Grand Cayman fringing reef. *Marine Ecology* 6:345-363

Rützler K (1975) The role of burrowing sponges in bioerosion. *Oecologia* 19:203-216

Rützler K (2002) Impact of crustose Clionid sponges on Caribbean reef corals. *Acta Geologica Hispanica* 37:61-72

Sabine C, al. e (2004) The oceanic sink for anthropogenic CO_2. *Science* 305:367

Southwell M, Weisz JB, Martens CS, Lindquist N (2008) In situ fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. *Limnology and Oceanography* 53:986-996

Tompkins-MacDonald GJ, Leys SP (2008) Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. *Marine Biology* 154:973-984

Turon X, Uriz M-J, Willenz P (1999) Cuticular linings and remodelisation processes in *Crambe crambe* (Demospongiae: Poecilosclerida). *Memoirs of the Queensland Museum* 44:617-625

Wall CC, Rodgers BS, Gobler CJ, Peterson BJ (2012) Responses of loggerhead sponges *Spechiospongia vesparium* during harmful cyanobacterial blooms in a sub-tropical lagoon. *Marine Ecology Progress Series* 451:31-43

Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. *Marine Pollution Bulletin* 51:570-579

Wilkinson CR, Evans E (1989) Sponge distribution across Davies Reef, Great Barrier Reef, relative to location, depth, and water movement. *Coral Reefs* 8:1-7

Williams E, Bartels P, Bunkley-Williams L (1999) Predicted disappearance of coral-reef ramparts: a direct result of major ecological disturbances. *Global Change Biology* 5:839-845

Wisshak M, Schönberg CHL, Form A, Freiwald A (2012) Ocean acidification accelerates reef bioerosion. *Plos One* 7

Wulff JL (1984) Sponge-mediated coral reef growth and rejuvenation. *Coral Reefs* 3:157-163

Chapter 2

The effects of coastal development on sponge abundance, diversity, and community composition on Jamaican coral reefs

Abstract

Over the past decade, development along the northern coast of Jamaica has accelerated, resulting in elevated levels of sedimentation on adjacent reefs. To understand the effects of this development on sponge community dynamics, surveys were conducted at three locations with varying degrees of adjacent coastal development to quantify species richness, abundance and diversity at two depths (8-10 m and 15-18 m). Sediment accumulation rate, total suspended solids and other water quality parameters were also quantified. The sponge community at the location with the least coastal development and anthropogenic influence was often significantly different from the other two locations, and exhibited higher sponge abundance, richness, and diversity. Sponge community composition and size distribution were statistically different among locations. This study provides correlative evidence that coastal development affects aspects of sponge community ecology, although the precise mechanisms are still unclear.

Introduction

Caribbean reef ecosystems have undergone a series of alterations, both natural and anthropogenic, during the last several decades. Overfishing (Munro 1983, Hardt 2008), hurricanes (Woodley et al. 1981; Kjerfve et al. 1986), echinoid disease (Lessios et al. 1984; Hughes et al. 1985; Liddell and Ohlhorst 1986) and other human activities (Hughes 1994) have led to large-scale deterioration of nearshore coral reef ecosystems (Goreau 1992; Liddell and Ohlhorst 1992; Hughes 1994). The overall ecosystem health of Caribbean reefs has been substantially reduced during the modern era (Pandolfi et al. 2003) and continues to decline on many reefs due to overfishing and the myriad effects of coastal development.

One third of Caribbean reefs are directly threatened by coastal development and the associated impacts (Burke et al. 2004). For many islands in the Caribbean, long-term growth in the domestic population has contributed to mounting environmental pressure; however, anthropogenic activities directly impacting island resources have risen most recently due to increased tourism. Proximity of the United States and Canada has resulted in dramatically increased tourism to Caribbean nations over the past 30-40 years. For example, the number of annual visitors to Jamaica was just under 400,000 in 1977 (Alleyne and Boxill 2003) compared to 3.3 million in 2012 (Jamaica Tourist Board 2012). The resultant economic boom has fueled large-scale coastal development and alteration, removing important coastal habitats and transforming them into resorts and beaches. While these activities can have a variety of damaging impacts to marine ecosystems, one of the most ubiquitous threats of coastal development is elevated sedimentation resulting from construction, artificial beach creation, and run-off (Fabricius 2005).

Suspended and settled sediment negatively affects many reef organisms, particularly many coral species. Experimental manipulations have demonstrated that many corals are physiologically distressed by increased sediment deposition and suspension (Riegl and Branch 1995; Gilmour 1999; Phillipp and Fabricius 2003; Weber et al. 2006). High amounts of suspended sediments decrease light availability to the benthos and reduce the photosynthetic yield of zooxanthellae within hermatypic corals (Phillipp and Fabricius 2003). Shading experiments designed to mimic light attenuation in turbid waters (Rogers 1979) demonstrated that hard corals experienced bleaching and a decrease in community metabolism after five weeks

of limited light. Reduced coral recruitment, changes in the size, diversity and abundance of coral colonies, and reduced community diversity have all been reported as effects of increased run-off and sedimentation (Cortés and Risk 1985).

While understanding the effects of sediment deposition on hermatypic corals has been a priority in the past, many modern reef environments are biogenically dominated by non-hermatypic invertebrates, most notably gorgonians and sponges (Norström et al. 2009; González-Rivero et al. 2011; Bell et al. 2013). In the Caribbean, there are >300 known sponge species, compared to approximately 70 hard coral species (Diaz and Rützler 2001), with growing evidence that sponge population growth may be outpacing corals on Caribbean reefs (McMurray et al. 2010), potentially shifting reefs toward sponge dominance (Bell et al. 2013). There is a growing need, therefore, to understand the impacts of sedimentation on the physiology, ecology and distribution of sponges in the Caribbean (Bell et al. 2015).

Sponges are filter-feeding organisms that rely on processing large volumes of water to obtain the majority of their nutrition (Reiswig 1971; Southwell et al. 2008). Sponges are able to efficiently retain particles within the size range of 0.3-50 μm (Reiswig 1971); however, this particle size range partially overlaps with that of silts and clays (< 63 μm). To prevent their aquiferous system (internal canal network) from becoming congested with unwanted sediment particles, many sponges can temporarily close or reduce the size of their incurrent openings (ostia) during times of increased turbidity (Ilan and Abelson 1995; Nickel 2004; Leys and Meech 2006). Alternatively, sponges may cease to pump water if suspended sediment concentrations become intolerable. Gerrodette and Flechsig (1979) demonstrated that the reef sponge, *Aplysina lacunosa* (formerly known as *Verongia lacunosa*) reduced its pumping rate after just 4 hours of exposure to suspended sediment concentrations greater than 11 mg L^{-1}, and chronic exposure (4 days) resulted in a continuous decline in pumping rates. Similar effects of sediment exposure on pumping rates were found in glass sponges (Tompkins-MacDonald and Leys 2008). Settled sediments can also affect sponge feeding by smothering and clogging ostia. Some sponge species are capable of reversing water flow in an effort to expel deposited sediments from their ostia (Nickel 2004), while others are able to trap settling sediments within a mucus layer that can be discarded (Turon et al. 1999).

For sponges that acquire a portion of their nutrition from photosynthetic symbionts (hereafter referred to as phototrophic sponges), suspended and settled sediments may have negative consequences for both the symbionts and sponge hosts (reviewed by Bell et al. 2015). Light reductions, such as those found in constantly turbid environments, may suppress symbiont photosynthetic rates (Cheshire et al. 1995) and alter the amount of symbiont-derived carbon transferred to host sponges (Freeman and Thacker 2011). While differences in light availability caused by increased turbidity negatively affect phototrophic sponges, Pineda et al. (2015) showed that exposure to a single pulse of sediments (meant to mimic dredging activity) did not alter the overall microbial assemblages in seven sponge species. Observational studies of phototrophic sponge distributions have shown lower abundances in turbid areas compared to less turbid environments (Wilkinson and Cheshire 1989; Bannister et al. 2010), providing correlative evidence that suspended sediments negatively impact phototrophic sponge communities.

While various physiological and morphological adaptations allow sponges to cope with short-term increases in suspended or settled sediment (Bell et al. 2015), persistent or intense sediment stress may have severe impacts on sponge health, survival and reproduction. Lohrer et al. (2006) determined that even sponge species adapted to living in environments with elevated suspended sediment loads (e.g. *Aaptos* sp.) were still negatively affected by experimental deposition of terrigenous sediment (77% silts and clays, 23% sands). Three weeks after application of sediment, sponges exhibited reduced clearance rates, decreased oxygen consumption and significantly lower indices of condition in treatments where sediment was applied (Lohrer et al. 2006). In an experimental manipulation of sediment deposition over a 125-day period, Maldonado and colleagues (2008) demonstrated that sponge survival was greatly reduced in areas of high sediment accumulation. Bannister et al. (2012) showed that sponges living in environments with higher sedimentation rates do so at a substantial metabolic cost, ultimately reducing reproductive output and growth. And finally, Maughan (2001) differentiated between the effects of light reduction and sedimentation on sponge recruitment by using clear covers over settlement panels; sponge recruitment was lowest on tiles exposed to sediment deposition, regardless of light exposure.

The negative impacts on individual sponge physiology, health, reproduction and survival associated with suspended and settled sediments may translate into broad-scale sponge

distribution and community composition changes. As vulnerable species succumb to sediment stress, communities may transform in unexpected ways. Carballo (2006) found that seasonal differences in sedimentation shifted the sponge community from a morphologically (and taxonomically) diverse community to one dominated almost exclusively by low-relief morphologies, such as encrusting and boring sponges. In Indonesia, the distribution, abundance and diversity of sponges were directly related to depth, sedimentation and substrate angle (Bell and Smith 2004). Also in Indonesia, Powell et al. (2014) found that sponges were consistently the dominant organisms in highly sedimented reefs, yet sponge diversity was lower when compared to sites with less sedimentation. Bannister et al. (2012) found a correlation between the abundance of *Rhopaloeides odorabile* on the Great Barrier Reef and the level of sedimentation; abundance was lower on inshore reefs where terrigenous, fine-grained sedimentation occurred than on outer reefs with less sediment.

This study aimed to characterize sponge communities at three locations experiencing different stages of coastal development along the northern coast of Jamaica. I sought to understand the effects of sediment deposition that have been linked to development activities (Westfield 2008) on sponge community metrics. Based on previous studies of sponge community response to sedimentation, I hypothesized that higher rates of sediment deposition would impact the sponge community and result in 1) reduced species richness and abundance, 2) lower diversity, 3) distinct community composition, and 4) differences in the dominant morphology and size distribution of sponges.

Methods

Study Locations

Three study locations along the northern coast of Jamaica, West Indies were chosen, representing different intensities of coastal development and direct shoreline alteration (Westfield 2008): Dairy Bull (N 18.471, W 77.379), Discovery Bay fore reef (N 18.473, W 77.412), and Pear Tree (N 18.465, W 77.343) (Figure 1). The Dairy Bull reef location lacks any recent coastal development and the shoreline is composed of hardened Falmouth Limestone (Land 1973) that has not undergone any anthropogenic alterations. Sediment accumulation occurring at Dairy Bull is primarily autochthonous reef material (e.g. *Halimeda* debris, foraminiferan particles, and sediments from the adjacent sandy groove). Discovery Bay fore reef is located north of the reef crest, just west of the inlet, and experiences low levels of sediment disturbance despite the moderate residential and industrial (bauxite mining and distribution facility) development occurring within the bay.

Pear Tree, the easternmost location, has the most residential and commercial development of the three study reefs. Pear Tree is located adjacent to a large resort that was constructed in 2005 (Figure 1, inset), despite environmental concerns from the Jamaican government (NEPA Environmental Impact Assessment 2005). The creation of this resort resulted in a 42% enlargement of the beach area (additional 25,000 m^2) along less than 2 km of shoreline (Westfield et al. 2008). At the same time that the resort was built, expansion of the main highway, which comes within 50 m of the shoreline, occurred. Using geochemical fingerprinting, Westfield et al. (2008) identified the construction activities associated with the highway and resort construction (e.g. dredging and run-off) and the episodic erosion of the resort's beaches as primary causes of elevated sediment deposition on Pear Tree reefs.

The three locations, which provide a gradient in coastal development intensity, were each divided into two sites, an eastern and western, separated by approximately 500 m to create a level of replication within locations. A depth element was also of interest, as suspended sediment concentration and the amount of sediment deposition are affected by wave energy, distance from shore, and depth of water column. Two distinct depth strata within each site nested within location, 8-10 m and 15-18 m, were used in all surveys and sampling.

Sediment collection and characterization

The study locations were chosen based on a geochemical fingerprinting and sediment source study by Westfield (2008); however, to compare the relative sediment accumulation rate at the chosen survey locations, sediment traps were deployed with a diameter to height ratio of 3:1, as recommended by Gardner (1980) for low flow environments. Sediment traps have been used for decades to measure sedimentation rate on reefs, but there has been some controversy as to whether they effectively estimate the sediment accumulation experienced by the benthos (Storlazzi et al. 2011). Despite their pitfalls (see Storlazzi et al. (2011) for full review), sediment traps are still a relevant and useful method of obtaining relative trap accumulation rates in areas with low flow/horizontal currents (such as our study locations), provided that traps are designed correctly and values reported appropriately (Jordan et al. 2010; Storlazzi et al 2011). Three sediment accumulation traps were placed 20-25 m apart at each site/depth combination (n=36 total; n=12 at each location) approximately 0.5 m above the benthos for 5-9 days in August 2010, January 2010, January 2011 and January 2012. After collection, trap sediment was rinsed with distilled water, lyophilized or dried at 60 °C for 36 hours and weighed. Sediment mass was standardized to the trap collection area and number of days to calculate trap accumulation rate (g m^{-2} day^{-1}). Analysis of the grain-size distribution and proportion of insoluble (non-carbonate) sediments was performed for the January 2012 trap samples. Mesh sieves (500 μm and 63 μm) were used to separate coarse sand and gravel (>500 μm) from coarse sand and very fine sand (63-500 μm) and silts and clays (<63 μm) (Krumbein 1938). After sediments were sieved, sediment fractions were weighed and then digested in 10% HCl following recommended U.S. Geological Survey procedures (Poppe et al. 2000) to dissolve the soluble material (e.g. calcium carbonate) from each size class within the samples. The remaining insoluble sediments were rinsed with deionized water 5 times, dried to a constant weight at 60°C and re-weighed. Additionally, ~20 L of surface seawater was collected at each location in January 2012 and filtered through pre-weighed Millipore ® glass fiber filters to quantify total suspended solids (n=5; 4 L per filter). Filters were immediately dried for 24 hours at 60 °C and re-weighed.

Environmental parameters

Using a YSI-6600EDS, measurements of salinity, temperature and dissolved oxygen were made continuously from the surface to 15 m depth over a time period of 30 minutes at each

location in January and August 2010, January 2011 and 2012. An optional chlorophyll sensor was used to measure the relative fluorescence units (RFU) (YSI6025; resolution: 0.1 µg/L or 0.1% RFU). Additionally, at each site and depth combination, HOBO® pendant temperature/light data loggers were secured alongside the sediment traps to stainless steel rods 0.5 m above the seafloor. Data loggers recorded temperature and light every 15 minutes during the same duration that sediment traps were deployed (i.e. 5-9 days); the analysis of light data was restricted to a 6-hour period of peak and direct light intensity (09:30-15:30 h). Data logger light measurements are reported as photometric units (lux=lumens m^{-2}). Wind data was obtained from the Sangster International Airport database of atmospheric conditions in Montego Bay, the closest official weather reporting station.

Survey Protocol

Sponges were surveyed using 20-m belt transects at two distinct depths, 8-10 m and 15-18 m at each site nested within locations. Five transects were surveyed per site/depth combination for a total of 20 transects at each location (n=10 in shallow, n=10 in deep, per location). Transect surveys were performed randomly in August 2009, January 2010 and August 2010 to ensure that each location/depth was sampled at different times and seasons. Belt transects were laid out haphazardly by two divers; divers worked from both ends to count and measure sponges (to the nearest 1 cm) found within 1 m of one side of the transect tape (20 m^2). For all sponges, volume was estimated based on the general morphology of each species. For example, several height, width and length measurements were taken for massive and bulbous sponges, and the volume was modeled by a series of rectangles; branching species were best modeled by a series of cylinders, therefore the length and circumference of each branch was recorded. Due to the difficulty in measuring the interior height and diameter of smaller tube sponges, all tube sponges were modeled as solid cylinders. The giant barrel sponge, *Xestospongia muta*, was best represented by a semi-hollow frustum of a cone (McMurray et al. 2008). Encrusting sponges that were less than 1 cm in height were measured using surface area alone. The more complex the sponge, the greater the number of measurements taken to create an appropriate series of geometric models for calculation of volumes. It is important to note that due to the simplicity of geometric shapes used to model sponges (e.g. solid cylinders, spheres, cubes,

frustums, etc.), the calculated sponge volumes are not estimates of biomass, and are used only to compare relative sizes across locations and depths within this study.

Divers visually identified and photographed sponges *in situ*. For any unknown sponge, a small sample was collected and analyzed (e.g. through spicule characteristics) to determine its species. Only sponges living exposed on the substrate were surveyed, as it was not possible due to diving limitations to count and measure any cryptic sponges living under or in substrate (e.g. crevices, holes). Sponges were also classified morphologically (Zea et al. 2014) as branching, tube, fan/lobate, massive, encrusting, bushy or spherical to compare abundance and diversity of growth forms among locations.

Data Analysis

For all data analyses, no differences between sites (western vs. eastern) were found within each location, therefore site data were combined for each location, and only location and depth were used as factors. All analyses were performed using R 2.15.1 (R Development Core Team 2008).

After appropriate transformation, water quality parameters were compared using multiple one-way ANOVAs where the parameter of interest (e.g. salinity, chlorophyll *a* or dissolved oxygen) was compared between locations. To dampen the effects of season and depth, light data from HOBO ® loggers were analyzed using depth and sampling period-specific anomalies as a metric (season*depth specific means were subtracted from the means of each logger over the corresponding sampling period); a one-way ANOVA of anomalies by location was performed for each parameter to determine whether there were differences by location. Trap sediment accumulation rates (g m^2 d^{-1}) from each date were analyzed using a two-way ANOVA on ranked data for differences in location and depth. Sediment grain size proportions and proportion of insoluble material were each analyzed using a two-way ANOVA for differences between location and depths. Total suspended solids (TSS) were analyzed using a one-way ANOVA to evaluate differences among locations. For all ANOVA models run, the Tukey HSD test was used when a significant main effect or interaction term was found to differentiate treatment levels.

Because the assumptions of ANOVA (equal variance and normality) were not met, the over-dispersed abundance data were fit to a quasipoisson-distributed generalized linear model

(GLM) to test whether sponge abundance was related to location and depth; an analysis of deviance table was computed for the GLM using the F test. Multiple comparisons for the GLM were calculated using the Tukey HSD test in the *glht* function in the *multcomp* package of R. Proportion of sponges that were phototrophic were analyzed using a two-way ANOVA with depth and location as factors. A two-way ANOVA was used to determine location and depth differences in the proportion of boring sponges (Family Clionaidae), which may be more common on impacted reefs. Differences in species richness due to location and depth were assessed with a two-way ANOVA on ranks (a non-parametric test) after data failed to meet the assumptions of equal variance and normality. Species diversity was calculated using both the Shannon and Simpson's diversity indices and each was analyzed using a two-way ANOVA of diversity with location and depth as factors. To determine whether there were differences in the diversity of sponge morphologies a two-way ANOVA was used to test the main and interactive effects of location and depth on morphological diversity (Shannon index only). Sponge volumes were log-transformed and a two-way ANOVA was used to determine location and depth differences. Pairwise sponge size frequency distributions were compared among locations using a two-sample Kolmogorov-Smirnov test.

Prior to ordination by non-metric multidimensional scaling (nMDS), species community composition data (species counts) were log (x+1) transformed to reduce the importance of rare species. The Bray-Curtis dissimilarity matrices of sponge communities were analyzed against 999 null permutations with the *ADONIS* function in the R package *vegan*, to test the effects of location and depth. The *ADONIS* function is a non-parametric multivariate analysis of variance (MANOVA) using distance matrices, which is considered more robust than an analysis of similarity (ANOSIM) (Anderson 2001).

Results

Sediment accumulation and water quality

Overall sediment trap accumulation rates varied significantly by collection date ($F_{(2,115)}$=76.397; P<0.001). Tukey HSD post-hoc analysis showed that January 2010 and 2012 traps were not statistically different from one another and had significantly higher rates of trap sediment accumulation (g m^{-2} day^{-1}) than August 2010 and January 2011. To simplify subsequent analyses, these two time points—January 2010 and January 2012—were combined and analyzed together. Traps deployed during these two periods, January 2010 and 2012 captured sediment accumulation during high-wind events; the weather database from Sangster International Airport in Montego Bay reported that the highest sustained wind speed in 2010 occurred in January (13.4 m s^{-1}) and January 2012 experienced sustained winds between 8-10.3 m s^{-1} during trap deployment (Table 1). The January 2010 and 2012 trap accumulation rates were significantly different by location ($F_{(2,36)}$=10.551, P<0.001), however, depth was not significant ($F_{(1,36)}$=3.645, P=0.06) and no significant interaction term was found. During these collection periods, overall mean trap accumulation rates (± 1SD; g m^{-2} d^{-1}) at Pear Tree were an order of magnitude higher than the other two locations (Pear Tree: 139.6 ± 180.5, Discovery Bay: 11.0 ± 6.6, Dairy Bull: 9.9 ± 5.3). Trap accumulation rates for the other time-points, August 2010 and January 2011, were not statistically different by location or depth. Mean sediment accumulation for the January 2011 and August 2010 sampling periods did not exceed 3.0 g m^{-2} d^{-1} at any of the locations or depths (Table 1).

Grain size analysis from January 2012 traps revealed that Pear Tree sediments had a significantly higher proportion of silts and clays (<63 μm) than both Dairy Bull and Discovery Bay ($F_{(2,21)}$=8.207, P=0.002); depth was not a significant factor. Within the <63 μm size class, the mean proportion of insoluble material was significantly higher at Pear Tree ($F_{(2,24)}$=12.4, P<0.001) than at the other locations. Proportion of sediments classified as sand (63-500 μm) were significantly different by location ($F_{(2,21)}$=6.136, P=0.008), but not depth. Dairy Bull had the highest proportion of sediments that fell between 63 and 500 μm (70%; Figure 2) and was significantly different than Pear Tree (Tukey HSD: P=0.006) but not Discovery Bay. Sediments that were over 500 μm were not statistically analyzed, since they were likely autochthonous reef debris (*Halimeda*, foraminiferans, etc.) that were too large to negatively impact sponges. The

mean ratio of insoluble to soluble sediment collected in traps at Pear Tree was 0.153 for 63 µm and 0.135 for 63-500 µm size classes; ratios were 0.033 and 0.08 for Discovery Bay and 0.088 and 0.071 at Dairy Bull, respectively for the same size classes.

No differences in salinity, dissolved oxygen or chlorophyll *a* were found between locations. Mean water temperature in August was 30.1 ± 0.2℃ and January 27.0 ± 0.6℃; no statistical differences among locations were found. No statistical differences in light (lumens m^{-2}) were found among locations; however, overall Pear Tree light values were 18% lower than Dairy Bull and Discovery Bay in the shallow depth strata. At the deeper depth strata, overall light reaching the bottom at Pear Tree was 8% lower than Dairy Bull and 32% lower than Discovery Bay. Total suspended solids (TSS; mg L^{-1}) measurements at the surface of the water ranged from 3.5 to 13.5 mg L^{-1}; mean TSS was highest at Pear Tree (9.23 ± 2.73 mg L^{-1}) compared to Discovery Bay (6.63 ± 2.41 mg L^{-1}) and Dairy Bull (7.65 ± 1.99 mg L^{-1})(Table 1).Total suspended solids (TSS; mg L^{-1}) were statistically different by location ($F_{(2,43)}$=4.99; P=0.01); Pear Tree differed significantly from Discovery Bay (Tukey HSD: P=0.01) but no pairwise differences were found between Discovery Bay and Dairy Bull or Pear Tree and Dairy Bull.

Sponge abundance, species richness, diversity and size distribution

A total of 4,046 sponges were sampled throughout the 60 surveys, representing 67 species, belonging to 27 families (Table 2). An overall species accumulation curve was constructed and a distinct asymptote was reached, suggesting that further surveys were not warranted (Figure 3). Of the total number of sponges encountered during the surveys, 63% (2,555 individuals) were found at Dairy Bull, while Pear Tree and Discovery Bay had only 16% and 21% of the total sponges, respectively. Mean (± 1SD) sponges densities (m^{-2}) at the deep depth of all locations were 1.82 ± 0.60, 2.65 ± 1.3 and 7.04 ± 0.75 for Pear Tree, Discovery Bay and Dairy Bull, respectively (see Table 3 for full abundance summaries). Mean sponge density in the shallows was slightly less: Pear Tree: 1.34 ± 0.53, Discovery Bay: 1.91 ± 0.54 and Dairy Bull: 5.49 ± 1.12. Overall sponge abundance and density were significantly higher in the deep than in the shallow strata ($F_{(1,56)}$=15.36; P<0.001, Table 4D). Abundance was also significantly different among locations ($F_{(2,57)}$=142.99, P<0.001; Table 4D), with lower mean abundance found at Pear Tree and Discovery Bay; no significant interaction between location and depth was found (Table

4D). No significant differences in the proportion abundance of either boring sponges (clionaids) or phototrophic sponges were found between locations or depths.

Mean and cumulative species richness were lower at Pear Tree and Discovery Bay than at Dairy Bull (Table 3). While species richness was consistently higher at the 15-18 m depth, this was not statistically significant; however, location was significant ($F_{(2,54)}$=125.646, P<0.001, Table 4C) with the highest species richness recorded at Dairy Bull. Sponge diversity, calculated using both the Simpson's and Shannon indices, was significantly higher at Dairy Bull regardless of which indices the two-way ANOVA was run on (Simpson's: $F_{(2,54)}$=9.353, P<0.001 and Shannon: $F_{(2,54)}$= 26.039, P<0.001; see Table 3 for full summary of diversity values and Table 4A,B for statistical summary). The main effect of location was significant for the analysis of Shannon morphological diversity ($F_{(2,54)}$= 4.164, P=0.02), although Tukey post hoc pairwise comparisons revealed that only Dairy Bull and Discovery Bay were significantly different (Tukey HSD adjusted P=0.02). The largest morphological contributors at Discovery Bay were massive (29%), encrusting (19%) and branching (18%) sponges. Dairy Bull was dominated by branching (27.5%) and massive sponges (25%), and Pear Tree was dominated by encrusting (27%) and massive (25%) morphologies (see Table 4 for depth-specific morphological breakdown).

Median and mean sponge volumes found along the surveys were calculated (Table 3). Mean sponge volume can be greatly skewed by a few extremely large (e.g. *Xestospongia muta*) or small individuals, therefore in a sponge community where sizes can span several orders of magnitude, median sponge volume may be a more appropriate descriptor of the size distribution. Median sponge volumes were under or around 200 cm^3, and Dairy Bull consistently had the lowest median volume at each depth (Table 3). Volume differences among location and depth combinations were analyzed using a two-way ANOVA on log-transformed data to reduce the influence of extremely large or small individuals; there was a main effect of location on volume ($F_{(2,4160)}$=47.059, P<0.001), but not depth, with a significant interaction term ($F_{(2,4160)}$=16.731, P<0.001). The volume of sponges was significantly different among locations according to Tukey HSD post hoc tests (Discovery Bay vs. Dairy Bull: P<0.001; Discovery Bay vs. Pear Tree: P=0.02; Dairy Bull vs. Pear Tree: P<0.001). Although Dairy Bull had the highest abundance of sponges, these sponges were also the least voluminous, on average.

Pairwise comparisons of size frequency distributions compared between the three locations using the Kolmogorov-Smirnov test were significant, indicating that size distribution was different at each location (Dairy Bull vs. Pear Tree: D=0.08, $P<0.001$; Dairy Bull vs. Discovery Bay: D=0.15, $P<0.001$; Discovery Bay vs. Pear Tree: D=0.095, $P=0.002$); refer to Figure 4 for log-transformed size distributions. Untransformed size distributions at Pear Tree and Discovery Bay were both negatively skewed, with a greater number of large individuals, whereas Dairy Bull was positively skewed, with many small individuals. Dairy Bull had the largest range of sizes represented; the largest individual sponge volume recorded in any of the surveys at Pear Tree was only 86,016 cm^3, whereas the largest individuals at Discovery Bay and Dairy Bull were 372,738 cm^3 and 1,113,425 cm^3, respectively.

Community Composition

Species community composition patterns were visualized using an nMDS ordination (Figure 5); however, the stress level was high (>.20), indicating that the 2D-plot was not an accurate portrayal of the data in high-dimensional space. The *ADONIS* analysis, which runs in high dimensional space and is therefore able to statistically interpret the non-metric dimensional scaling, indicated that there were significant differences in community composition between locations and depths. The *ADONIS* output indicated that clustering was significant; although the relative contribution of the location and depth factors were generally low – location explained just 19% ($F=6.908$, $R^2= 0.1902$, $P= 0.001$) of the variation and depth 4.3% ($F=3.091$, $R^2= 0.0426$, $P=0.002$).

Discussion

Sedimentation

This study compared the relative sedimentation rates at three locations with different intensities of coastal development along the north coast of Jamaica and found that sediment accumulation was variable and influenced by wind events. During four periods of sediment monitoring, January 2010, August 2010, January 2011, and January 2012, two wind and wave energy events were captured (January 2010 and January 2012, Table 1) and it was only during these times that Pear Tree, the most developed study location, had statistically higher rates of gross sediment deposition than the other two locations. Sediment deposition at Pear Tree was highest when mean wind speeds were >3.5 m s^{-1} and maximum sustained wind speed exceeded 10 m s^{-1}; these conditions occurred 184 times between 2008 and 2014, an average of 26.1 ± 21.6 occasions $year^{-1}$, indicating that sediment deposition at Pear Tree is primarily wind-driven, and therefore a chronic, yet episodic event.

The mean trap accumulation rates at Pear Tree during the wind events in January 2010 and 2012 were an order of magnitude higher than the accumulation rates at Discovery Bay and Dairy Bull (Table 1). While caution should be used when comparing sedimentation studies using different methods/trap designs (Storlazzi et al. 2011), the overall sediment accumulation rates at Discovery Bay and Dairy Bull remained at or below the range of sediment accumulation previously reported as typical or 'natural' (<10 g m^{-2} day^{-1}) on reefs not subjected to stress (Rogers 1990) even when they experienced high wind energy. Mean trap accumulation rates at Pear Tree exceeded this 10 g m^{-2} day^{-1} threshold during periods of high wave activity, and therefore would be categorized as experiencing periodically 'high' levels of sedimentation by Rogers (1990). It is important to note that this threshold (Rogers 1990) may not be an accurate measure of whether sedimentation is 'high' on reefs, as it was based on various sedimentation studies using multiple trap designs (Storlazzi et al. 2011). Previous work in the Discovery Bay lagoon by Dodge et al. (1974) reported trap accumulation rates ranging from 0.5-1.1 g m^{-2} day^{-1}, which are comparable to the accumulation rates found in this study during periods of low wind.

Not only is the rate of sediment accumulation higher at Pear Tree, but there is also a significant difference in the proportion of sediments that are classified as silts and clays (<63

μm). Additionally, the amount of insoluble silts and clays was significantly higher at Pear Tree than at the other two locations. Westfield (2008) found that sediments collected from Pear Tree exhibited a higher proportion of smaller grain sizes and insoluble sediments than Dairy Bull and Discovery Bay, and attributed the increase in insoluble residue to the runoff from the construction of the resort and expansion of the Queen's Highway in 2005-2007.

Westfield (2008) found no geochemical evidence that the Pear Tree Bottom River, which discharges into an embayment approximately 2 km west of Pear Tree, contributed to the sediments found at the Pear Tree location. Due to the easterly long-shore currents, this small river does not typically influence our study locations. During the January 2012 wind event, a gradient was found of TSS (e.g. silts and clays) from east to west, which suggests that the river may alter the amount of suspended material during wind/wave events at the survey locations. No differences in surface salinity were found among the locations at any sampling period; however, the fluvial signal may have been lost in January 2012 due to heavy wind mixing. An alternative explanation for the elevated suspended solids and sediment accumulation may be the wind and wave-driven erosion of a small dry canal filled with terrigenous sediment that is located approximately 500 m east of the Pear Tree location (Westfield 2008). This may be a more likely explanation of the elevated TSS and higher levels of insoluble silts and clays found at Pear Tree than the river, given the easterly long-shore currents and lack of salinity differences found.

Sponge community

Several differences in the sponge communities were found among the three locations, although in many ways Dairy Bull, the location with the least coastal development, was the atypical location. Sponge abundance was significantly different among locations, with the number of sponges found at Dairy Bull an order of magnitude higher than at Discovery Bay and Pear Tree. Dairy Bull also had significantly higher sponge species richness and diversity than Discovery Bay and Pear Tree. While size distributions of sponges were statistically distinct among all locations, Dairy Bull had the smallest mean and median sponge volume of the three locations.

The literature is replete with studies focused on the ecological (biotic) and physical (abiotic) factors influencing sponge abundance, richness and diversity. Ecologically, patterns are

attributed to factors such as predation (Wulff 2000; Pawlik 1998) and food availability (Lesser 2006; Lesser and Slattery 2013; Pawlik et al. 2013). Major sponge predators in the Caribbean include spongivorous fish, (Pawlik 1995), the Hawksbill sea turtle (Meylan 1988), and sea stars (Wulff 2000). While previous studies have suggested that spongivory structures tropical sponge assemblages (Pawlik 1995), it is unlikely that predation resulted in the sponge distribution patterns observed in this study. No sponge tissue damage or predation scars indicative of sea turtle or fish predation were recorded in the surveys; additionally, spongivorous fish are almost completely absent along the north coast of Jamaica (Loh and Pawlik 2014) due to heavy fishing pressure.

Whether Caribbean sponges are, or can be, food limited has been hotly contested (e.g. Lesser and Slattery 2013; Pawlik et al. 2013), yet growing evidence suggests that bottom-up processes on reefs do not limit sponge abundance or distribution (see review by Pawlik et al. 2015). Regardless, no evidence that chlorophyll *a* concentrations varied among our study locations was found, suggesting that phytoplankton abundance is not contributing to the observed differences in sponge communities. Further, recent evidence suggests that sponges are able to utilize DOM and DOC (de Goeij et al. 2013; Mueller et al. 2014) and are unlikely to be limited by phytoplankton abundance. Additionally, many of the species found in the surveys are known to contain high abundances of photosynthetic symbionts (Erwin and Thacker 2007) and would therefore not depend solely on allochthonous food sources in the water column for nutrition and growth. In their review of the evidence of food limitation in sponges, Pawlik and colleagues (2015) proposed that phototrophic sponges should dominate Caribbean communities, as they do in the Great Barrier Reef, if food availability were a problem. No significant differences in the proportion of phototrophic sponges among locations or depths were found, further supporting the assumption that food availability or light did not structure sponge communities at the locations in this study.

Abiotic, or physical, factors affecting sponge distribution are more complex; environmental factors such as light/depth (Wilkinson and Cheshire 1989), water flow (Bell and Barnes 2000a,b), water quality (Rose and Risk 1985; Holmes 2000), and sedimentation (Bell and Smith 2004) have all been credited with structuring sponge communities. Among the three locations no statistical difference in light was found; water flow, although not measured, did not

differ qualitatively between locations. Water quality—specifically, the concentration of nutrients—was not assessed directly; however, chlorophyll *a* concentration, an indicator of water quality that is sensitive to nutrient loading (Boyer et al. 2009), did not differ among locations, suggesting that nutrient differences were either minimal or not exploited by the phytoplankton.

Evidence that Caribbean sponge distributions can be affected by eutrophication is largely limited to boring sponges, with significant increases in clionaid infestation found at sites with elevated land-based nutrients (Ward-Paige et al. 2005), organic pollution (Rose and Risk 1985) and eutrophication (Holmes 2000). Interestingly, the abundance of boring sponges was not significantly different between the locations. The analysis of clionaid abundance indicated that the proportion of this bioeroding sponge family was higher at Pear Tree (13%) than at either Discovery Bay or Dairy Bull (7% each), yet these differences were not significant.

Sediment stress has previously been implicated in structuring the species composition and size distributions of sponges. Carballo (2006) found that tropical sponge assemblages in the Mexican Pacific were significantly impacted by seasonal changes in sediment accumulation, both in terms of abundance and distribution, but also size. When sediment disturbance was highest, a shift from large-bodied to small-bodied species occurred (Carballo 2006), reducing the overall sponge biomass. Volumetric response at the study locations displayed no obvious pattern that corresponded with sedimentation. Although size distributions were statistically distinct among all locations, Pear Tree and Discovery Bay had negatively skewed sponge size distributions, while Dairy Bull had a positively skewed population. The negatively skewed distributions at Discovery Bay and Pear Tree suggest that recruitment rates are low and/or mortality of small individuals is high. The positively skewed sponge distribution and wide range of sponge sizes at Dairy Bull indicates a healthy population with high recruitment, which has been shown in coral and sponge populations (Meesters et al. 2001; Duckworth et al. 2009).

Sediment deposition was found to negatively affect the overall sponge community assemblages in several studies (Carballo 2006; Nava and Carballo 2013; Bell and Smith 2004). This study found differences in the multivariate community composition among locations and depths (Figure 5). There were several noticeable differences in sponge species found within the communities (Table 2), such as the absence of *Chondrilla caribensis* at Dairy Bull. *C. caribensis* (formerly referred to as *Chondrilla nucula*) is gaining notoriety as an indicator of degraded

systems. *C. caribensis* has been reported rapidly colonizing areas where corals have been damaged and, in areas, becoming the dominant component of the benthos (Aronson et al. 2002; Norström et al. 2009). Several other common reef species were conspicuously absent from the Pear Tree surveys, such as *Xestospongia muta*, *Ectyoplasia ferox, Mycale laxissima* and *Verongula gigantea*, all of which are large, long-lived species. Nineteen species were found at either Discovery Bay or Dairy Bull, but were absent from Pear Tree, whereas the number of species absent at Dairy Bull but found elsewhere was only six (Table 2). Although many of these species may make up a much smaller (in terms of abundance and biomass) proportion of the community, there is still a notable absence of commonly occurring species at Pear Tree.

Overall, there seem to be no distinct patterns that implicate sedimentation from coastal development as the driver of sponge community differences among locations. Accounts of sponge abundance and species composition (both qualitative and quantitative) through the 1990s suggest that these sponge communities were once very similar (Lehnert and Fischer 1999; Lehnert and van Soest 1998). However, since this time few studies of sponge community structure along the north shore of Jamaica have been published (but see Loh and Pawlik 2014). Therefore, the exact timeline of sponge community divergence between these locations is unknown. During the surveys, there were subtle differences between some, but not all, of these locations. Discovery Bay was most similar to Pear Tree (diversity, species richness), while Dairy Bull was distinct, or all locations were statistically different from each other (abundance, community composition, size distribution). Our inability to attribute these differences between communities to one particular environmental factor may have been because the differences between the sponge communities were subtle enough that eliciting a statistical difference between all three locations was not possible.

While we are beginning to recognize the importance of sponges in coral reef ecosystems, the impacts of coastal development are still largely unknown for sponges. Overall, Dairy Bull, the location with no coastal development, had higher sponge abundance, diversity and a wider range of size distributions than the other two locations. Although the exact mechanism is unclear, this study provides correlative evidence that even moderate coastal development is influencing sponge communities on reefs along the northern coast of Jamaica.

References

Alleyne D, Boxill I (2003) The impact of crime on tourist arrivals in Jamaica. *International Journal of Tourism Research* 5:381-391

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46

Aronson RB, Precht WF, Toscano M, Koltes K (2002) The 1998 bleaching event and its aftermath on a coral reef in Belize. *Marine Biology* 141:435-447

Bannister RJ, Battershill CN, de Nys R (2010) Demographic variability and long-term change in a coral reef sponge along a cross-shelf gradient of the Great Barrier Reef. *Marine and Freshwater Research* 61:389-396

Bannister RJ, Battershill CN, de Nys R (2012) Suspended sediment grain size and mineralogy across the continental shelf of the Great Barrier Reef: Impacts on the physiology of a coral reef sponge. *Continental Shelf Research* 32:86-95

Bell JJ, Barnes DJ (2000a) The influences of bathymetry and flow regime upon the morphology of sublittoral sponge communities. *Journal of the Marine Biological Association of the United Kingdom* 80:707-718

Bell JJ, Barnes DKA (2000b) The distribution and prevalence of sponges in relation to envrionmental gradients within a temperate sea lough: vertical cliff surfaces. *Diversity and Distributions* 6:283-303

Bell JJ, Davy SK, Jones T, Taylor MW, Webster NS (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology* 19:2613-2624

Bell JJ, McGrath E, Biggerstaff A, Bates T, Bennett H, Marlow J, Shaffer M (2015) Sediment impacts on marine sponges. *Marine Pollution Bulletin*, http://dx.doi.org/10.1016/j.marpolbul.2015.03.030

Bell JJ, Smith D (2004) Ecology of sponge assemblages (Porifera) in the Wakatobi region, south-east Sulawesi, Indonesia: richness and abundance. *Journal of the Marine Biological Association of the UK* 84:581-591

Boyer JN, Kelble CR, Ortner PB, Rudnick DT (2009). Phytoplankton bloom status: Chlorophyll a biomass as an indicator of water quality condition in the southern estuaries of Florida, USA. *Ecological indicators* 9:S56-S67

Burke L et al. (2004) Reefs at Risk in the Caribbean. World Resources Institute

Washington, D.C. http://www.wri.org/publication/reefs-risk-caribbean

Carballo JL (2006) Effect of natural sedimentation on the structure of tropical rocky sponge assemblages. *Ecoscience* 13:119-130

Cheshire AC, Butler AJ, Westphalen G, Rowland B, Stevenson J, Wilkinson CR (1995) Preliminary study of the distribution and photophysiology of the temperate phototrophic sponge *Cymbastela* sp. from South Australia. *Marine and freshwater research* 46:1211-1216

Cortés J, Risk MJ (1985) A reef under siltation stress: Cahuita, Costa Rica. *Bulletin of Marine Science* 36:339-356

de Goeij JM, van Oevelen D, Vermeij MJ, Osinga R, Middelburg JJ, de Goeij AF, Admiraal W (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science* 342:108-110

Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean coral reefs. *Bulletin of Marine Science* 69:535-546

Dodge RE, Aller RC, Thomson J (1974) Coral growth related to resuspension of bottom sediments. *Nature* 247:574-577

Duckworth AR, Wolff CW, Luter H (2009) Patterns of abundance and size across varying spatial scales for the coral reef sponge *Coscinoderma matthewsi*. *Marine Ecology Progress Series* 396:27-33

Erwin PM, Thacker RW (2007) Incidence and identity of photosynthetic symbionts in Caribbean coral reef sponge assemblages. *Journal of the Marine Biological Association of the UK* 87:1683-1692

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50:125-146

Freeman CJ, Thacker RW (2011) Complex interactions between marine sponges and their symbiotic microbial communities. *Limnology and Oceanography 56:*1577-1586

Gardner WD (1980) Field assessment of sediment traps. *Journal of Marine Research* 38: 41-52

Gerrodette T, Flechsig AO (1979) Sediment-induced reduction in the pumping rate of the tropical sponge *Verongia lacunosa*. *Marine Biology* 52:103-110

Gilmour J (1999) Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. *Marine Biology* 135:451-462

González-Rivero M, Yakob L, Mumby PJ (2011) The role of sponge competition on coral reef alternative steady states. *Ecological Modelling* 222:1847-1853

Goreau TJ (1992) Bleaching and reef community change in Jamaica 1951-1991. *American Zoologist* 32:683-695

Hardt MJ (2008) Lessons from the past: the collapse of Jamaican coral reefs. *Fish and Fisheries* 10:1-16

Holmes KE (2000) Effects of eutrophication on bioeroding sponge communities with the description of a new West Indian sponges, *Cliona* spp. (Porifera: Hadromerida: Clionaidae). *Invertebrate Biology* 119:125-138

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547-1551

Hughes TP, Keller BD, Jackson JBC, Boyle MJ (1985) Mass mortality of the echinoid *Diadema antillarum* Phillipi in Jamaica. *Bulletin of Marine Science* 36:377-384

Ilan M, Abelson A (1995) The life of a sponge in a sandy lagoon. *Biological Bulletin* 189:363-369

Jamaica Tourist Board (2012) Annual Travel Statistics. www.visitjamaica.com

Jordan LK, Banks KW, Fisher LE, Walker BK, Gilliam DS (2010) Elevated sedimentation on coral reefs adjacent to a beach nourishment project. *Marine Pollution Bulletin* 60:261-271

Kjerfve B, Magill KE, Porter JW, Woodley JD (1986) Hindcasting of hurricane characteristics and observed damage on a fringing reef, Jamaica, West Indies. *Journal of Marine Research* 44:119-148

Krumbein WC (1938) Size frequency distributions of sediments and the normal phi curve. *Journal of Sedimentary Petrology* 8:84-90

Land LS (1973) Holocene meteoric dolomitization of Pleistocene limestones, North Jamaica. *Sedimentology* 20:411-424

Lehnert H, Fischer H. (1999) Distribution patterns of sponges and corals down to 107m off North Jamaica. *Memoirs-Queensland Museum* 44:307-316

Lehnert H, Van Soest RW (1998) Shallow water sponges of Jamaica. *Beaufortia*, *48*.

Lesser MP, Slattery M (2013) Ecology of Caribbean sponges: are top-down or bottom-up processes more important? *PloS one* 8:e79799

Lesser MP (2006) Benthic–pelagic coupling on coral reefs: feeding and growth of Caribbean sponges. *Journal of Experimental Marine Biology and Ecology* 328:277-288.

Lessios HA, Robertson DR, Cubit JD (1984) Spread of *Diadema* mass mortality through the Caribbean. *Science* 226:335-337

Leys SP, Meech RW (2006) Physiology of coordination in sponges. *Canadian Journal of Zoology* 84:288-306

Liddell WD, Ohlhorst SL (1986) Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. *Journal of Experimental Marine Biology and Ecology* 95:271-278

Liddell WD, Ohlhorst SL (1992) Ten years of disturbance and change on a Jamaican fringing reef. In *Proceedings of the 7th International Coral Reef Symposium, Guam* (pp.149-155)

Loh TL, Pawlik JR (2014) Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. *Proc Natl Acad Sci USA* 111:4151-4156

Lohrer AM, Hewitt JE, Thrush SF (2006) Assessing far-field effects of terrigenous sediment loading in the coastal marine environment. *Marine Ecology Progress Series* 315:13-18

Maldonado M, Giraud K, Carmona C (2008) Effects of sediment on the survival of asexually produced sponge recruits. *Marine Biology* 154:631-641

Maughan BC (2001) The effects of sedimentation and light on recruitment and development of a temperate, subtidal, epifaunal community. *Journal of Experimental Marine Biology and Ecology* 256:59-71

McMurray SE, Blum JE, Pawlik JR (2008) Redwood of the reef: growth and age of the giant barrel sponge Xestospongia muta in the Florida Keys. *Marine Biology* 155:159-171

McMurray SE, Henkel TP, Pawlik JR (2010) Demographics of increasing populations of the giant barrel sponges Xestospongia muta in the Florida Keys. *Ecology* 91:560-570

Meesters EH, Hilterman M, Kardinaal E, Keetman M, de Vries M, Bak RPM (2001) Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. *Marine Ecology Progress Series* 209:43-54

Meylan A (1988). Spongivory in hawksbill turtles: a diet of glass. *Science* 239:393-395.

Mueller B, de Goeij JM, Vermeij MJ, Mulders Y, van der Ent E, Ribes M, van Duyl FC (2014) Natural diet of coral-excavating sponges consists mainly of dissolved organic carbon (DOC). *Plos One* 9:E90152

Munro JL (1983) The composition and magnitude of trap catched in Jamaican waters. In: J.L. M (ed) *Caribbean Coral Reef Fishery Resources. International Center for Living Aquatic Resources Managment* (ICLARM), Manila

Nava H, Carballo JL (2013) Environmental factors shaping boring sponge assemblages at Mexican Pacific coral reefs. *Marine Ecology* 34:269-279

NEPA Environmental Impact Assessment (2005) Bahia Principe Hotel Resort Development, Pear Tree Bottom, St. Ann. Jamaica. National Environmental and Planning Agency, Kingston, Jamaica

Nickel M (2004) Kinetics and rhythm of body contractions in the sponge *Tethya wilhelma* (Porifera: Demospongiae). *Journal of Experimental Biology* 207:4515-4524

Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Marine Ecology Progress Series* 376:295-306

Pandolfi J, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955-958

Pawlik JR (1995) Defenses of Caribbean sponges against predatory reef fish, I: chemical deterrency. *Marine Ecology Progress Series* 127:183-194

Pawlik JR (1998) Coral reef sponges: Do predatory fishes affect their distribution? *Limnology and Oceanography* 43:1396-1399

Pawlik JR, Loh TL, McMurray SE, Finelli CM (2013) Sponge communities on Caribbean coral reefs are structured by factors that are top-down, not bottom-up. *PloS one* 8:e62573

Pawlik JR, McMurray SE, Erwin P, Zea S (2015) A review of evidence for food limitation of sponges on Caribbean reefs. *Marine Ecology Progress Series* 519:265-283

Phillipp E, Fabricius KE (2003) Photophysiological stress in scleractinian corals in response to short-term sedimentation. *Journal of Experimental Marine Biology and Ecology* 287:57-78

Pineda MC, Duckworth A, Webster N (2015) Appearance matters: sedimentation effects on different sponge morphologies. *Journal of the Marine Biological Association of the United Kingdom*, 1-12

Poppe LJ, Eliason AH, Fredericks JJ, Rendigs RR, Blackwood D, Polloni CF (2000) Grain size analysis of marine sediments: methodology and data processing. *US Geological Survey East Coast sediment analysis: procedures, database, and georeferenced displays.* US Geological Survey Open File Report 00-358. http://pubs.usgs.gov/of/2000/of00-358

Powell A, Smith DJ, Hepburn LJ, Jones T, Berman J, Jompa J, Bell JJ (2014) Reduced diversity and high sponge abundance on a sedimented Indo-Pacific reef system: implications for future changes in environmental quality. *Plos One* 9:e85253

R Development Core Team (2008) R: A language and environment for statistical computing In: Computing RFfS (ed), Vienna, Austria

Reiswig H (1971) Particle feeding in natural populations of three marine Demosponges. *Biological Bulletin* 141:568-591

Riegl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *Journal of Experimental Marine Biology and Ecology* 186:259-275

Rogers C (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62:185-202

Rogers CS (1979) The effect of shading on coral reef structure and function. *Journal of Experimental Marine Biology and Ecology* 41:269-288

Rose CS, Risk MJ (1985) Increase in *Cliona deletrix* infestation of *Montastrea cavernosa* heads on an oragnically polluted portion of the Grand Cayman fringing reef. *Marine Ecology* 6:345-363

Southwell M, Weisz JB, Martens CS, Lindquist N (2008) *In situ* fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. *Limnology and Oceanography* 53:986-996

Storlazzi CD, Field ME, Bothner MH (2011) The use (and misuse) of sediment traps in coral reef environments: theory, observations, and suggested protocols. *Coral Reefs* 30:23-38

Tompkins-MacDonald GJ, Leys SP (2008) Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. *Marine Biology* 154:973-984

Turon X, Uriz M-J, Willenz P (1999) Cuticular linings and remodelisation processes in *Crambe crambe* (Demospongiae: Poecilosclerida). Memoirs of the Queensland Museum 44:617-625

Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. *Marine Pollution Bulletin* 51:570-579

Weber M, Lott C, Fabricius KE (2006) Sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, organic and geochemical properties. *Journal of Experimental Marine Biology and Ecology* 336:18-32

Westfield I (2008) Geochemical fingerprinting of sediments on the Pear Tree Bottom Reef, near Runaway Bay, Jamaica. Master of Science, Baylor University

Westfield I, Dworkin S, Bonem R, Lane E (2008) Identification of sediment sources using geochemical fingerprinting at Pear Tree Bottom Reef, Runaway Bay, Jamaica. *Abstracts of the 11th International Coral Reef Society*, p. 137

Wilkinson CR, Cheshire AC (1989) Patterns in the distribution of sponge populations across the central Great Barrier Reef. *Coral Reefs* 8:127-134

Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe CM, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749-755

Wulff, J. L. (2000). Sponge predators may determine differences in sponge fauna between two sets of mangrove cays, Belize barrier reef. *Atoll Res Bull 477:*251-263

Zea S, Henkel TP, Pawlik JR (2014) The Sponge Guide: a picture guide to Caribbean sponges. 3rd Edition. www.spongeguide.org

Figures and Tables

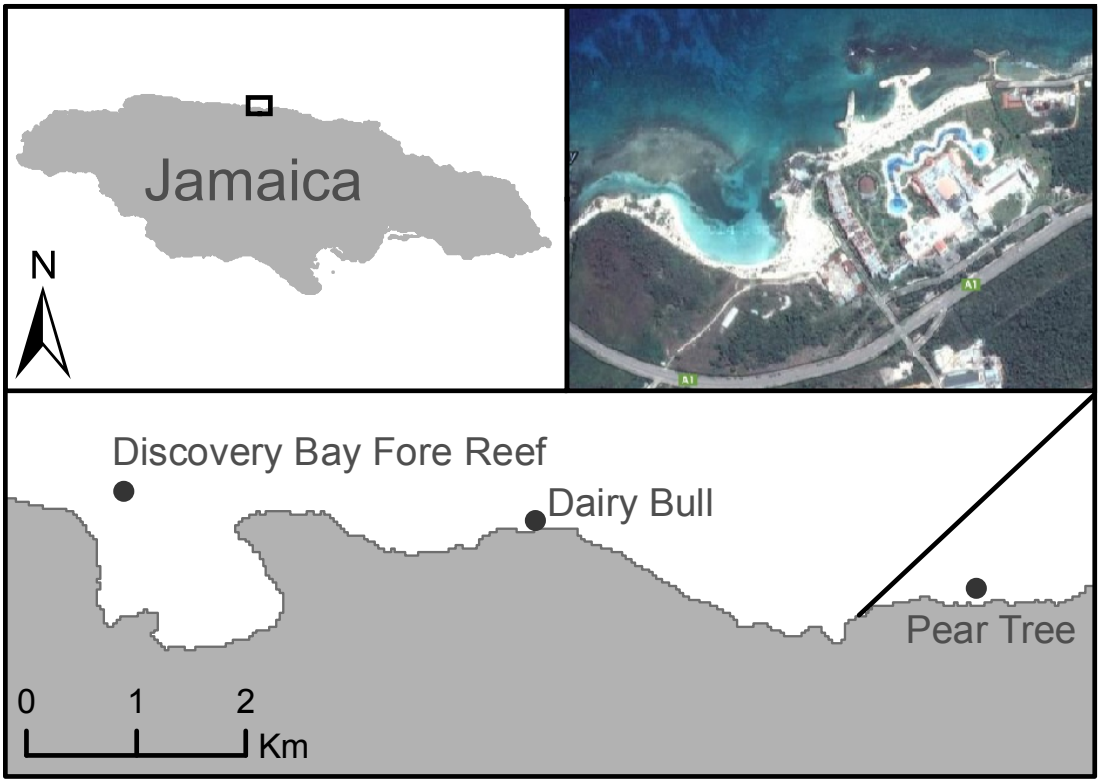

Figure 1. Upper left inset: The island of Jamaica, West Indies; the small black box indicates the specific region where the surveys took place. Study locations are denoted by circles on the expanded coastal map. Upper right inset: The resort adjacent to the Pear Tree location.

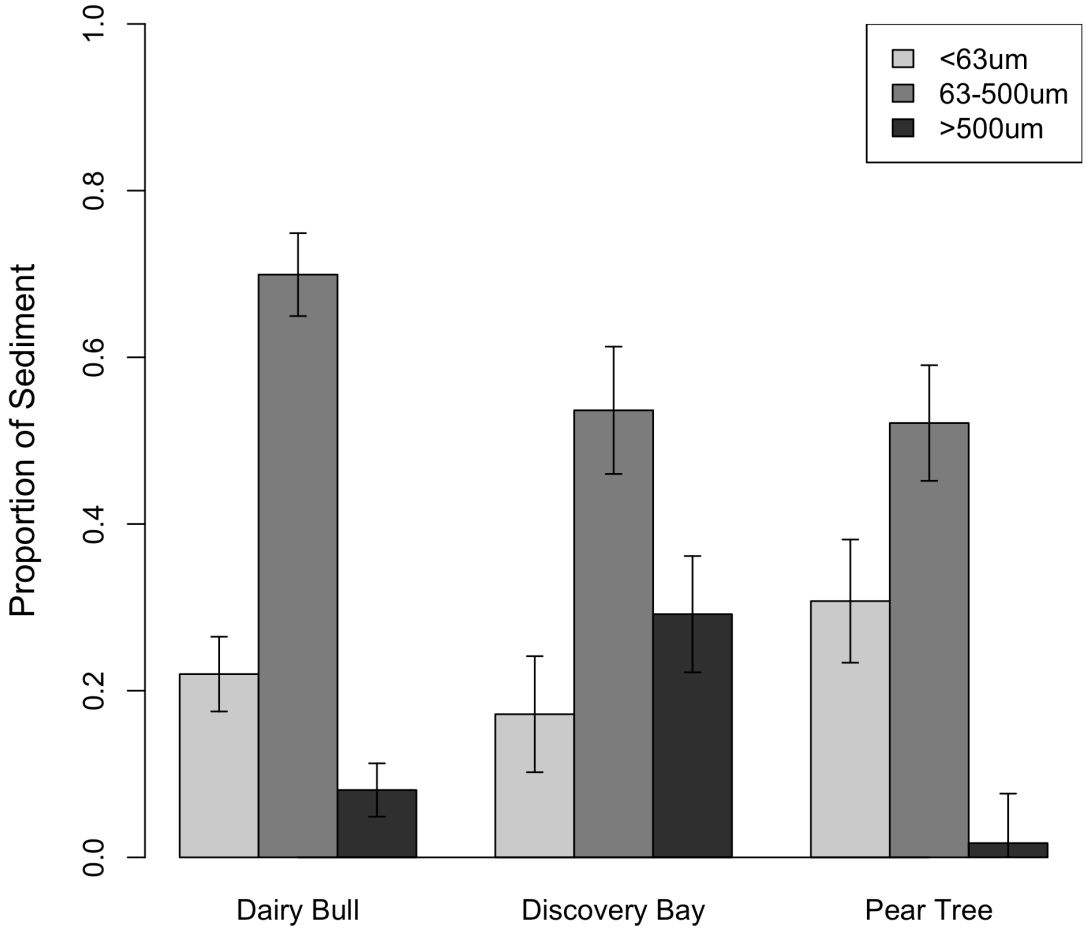

Figure 2: Mean proportion of sediments (± standard error) within each size class measured (>500um, 63-500um and <63um).

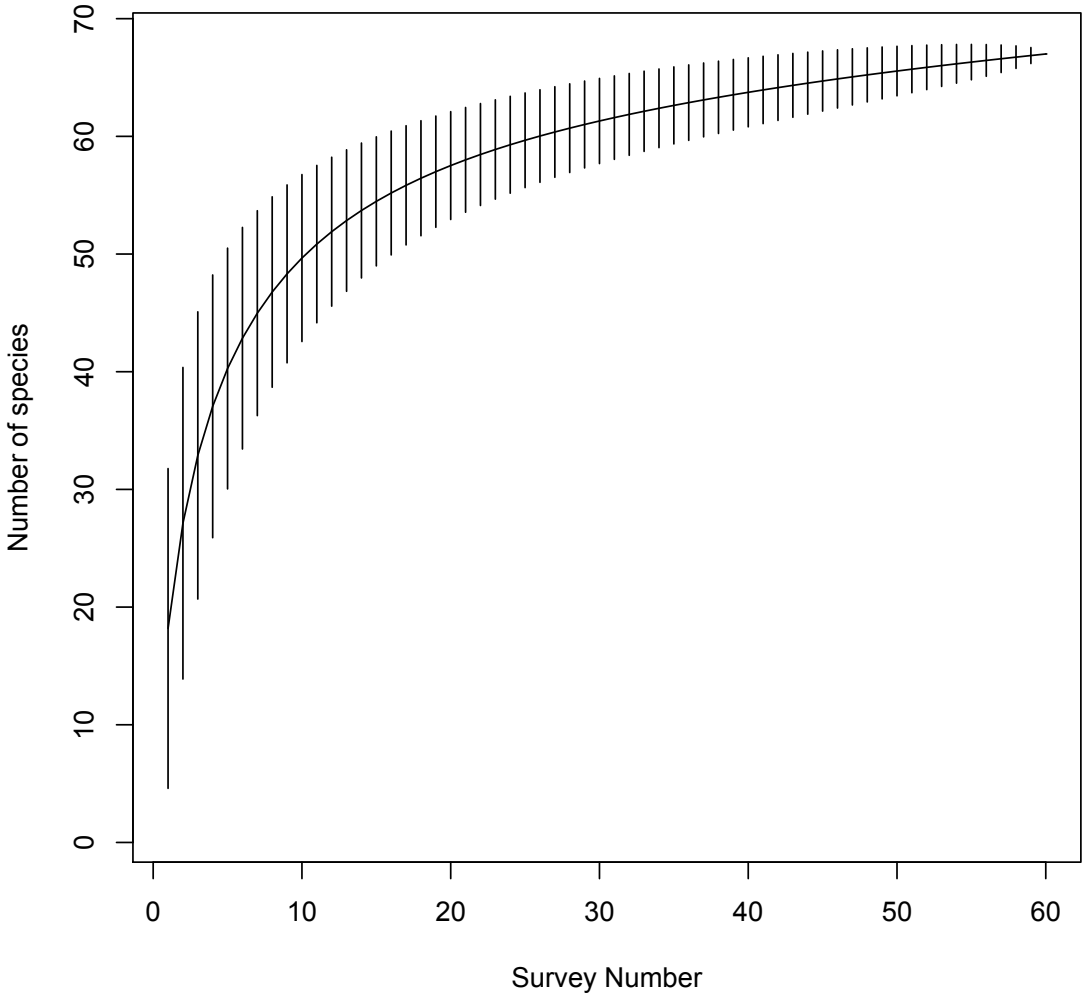

Figure 3: Species accumulation curve for all locations. A total of 60 transects were completed.

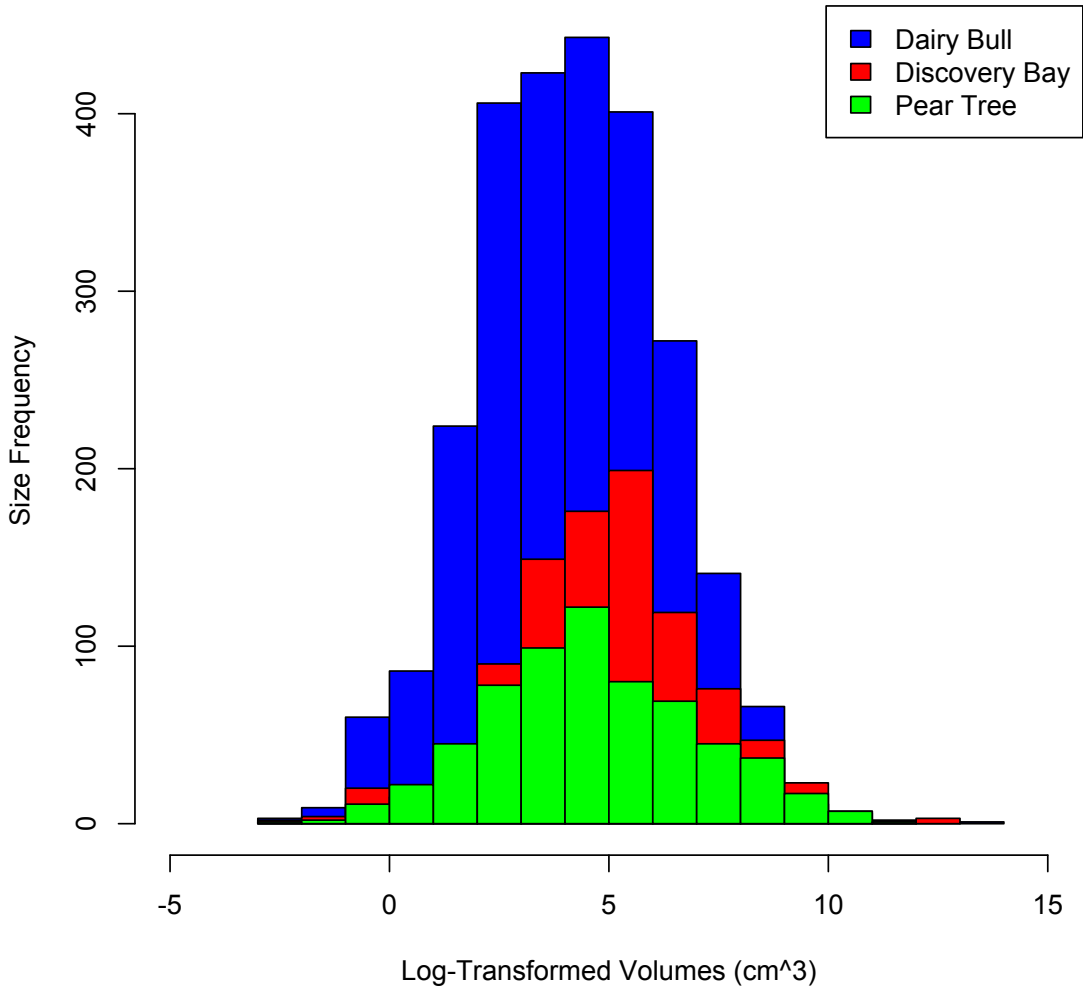

Figure 4: Size frequency distribution of log-transformed sponge volumes at each location.

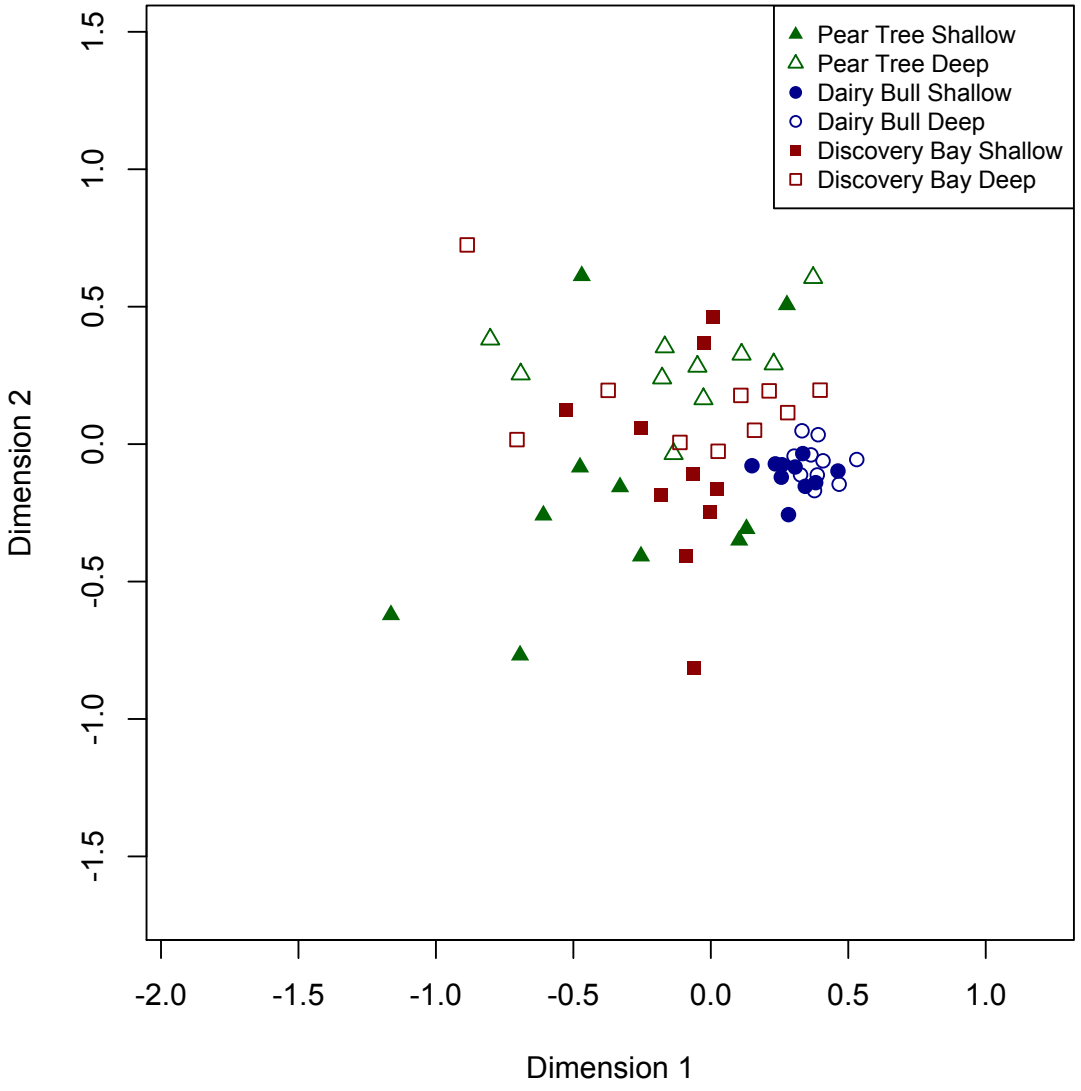

Figure 5: Two-dimensional nMDS ordination (stress >0.20) of species community composition at both depths of Pear Tree, Discovery Bay and Dairy Bull. Closed geometric shapes represent the shallow depth (8-10 m), open geometric shapes are deep strata (15-18 m) within each location.

Table 1. Trap accumulation rates (g m^2 d^{-1}) over four collection periods from January 2010-January 2012 at all locations and depths. Mean total suspended solids (TSS; mg L^{-1}), collected in January 2012 from the surface of the water, are reported for each location. Wind speeds (m s^{-1}) were obtained from weather records at Sangster International Airport in Montego Bay, Jamaica. All values are means; standard deviations are denoted where applicable.

	Maximum Sustained Wind Speed (m s^{-1})	Mean Wind Speed (m s^{-1})	Pear Tree		Discovery Bay		Dairy Bull	
			Shallow (g m^2 d^{-1})	Deep (g m^2 d^{-1})	Shallow (g m^2 d^{-1})	Deep (g m^2 d^{-1})	Shallow (g m^2 d^{-1})	Deep (g m^2 d^{-1})
January 2010	13.4	4.18 ± 1.51	365.8 ± 132.5	323.2 ± 173.9	16.9 ± 4.7	11.4 ± 6.1	---	---
August 2010	9.0	2.33 ± 0.63	0.8 ± 0.8	2.2 ± 1.8	1.2 ± 1.0	0.9 ± 0.5	0.8 ± 0.2	0.7 ± 0.4
January 2011	9.3	3.25 ± 1.02	1.5 ± 1.6	2.0 ± 2.2	0.9 ± 0.4	2.2 ± 2.7	2.6 ± 2.2	1.1 ± 0.3
January 2012	10.3	4.22 ± 1.15	30.6 ± 22.8	14.5 ± 4.7	10.2 ± 7.4	4.8 ± 3.0	11.4 ± 4.9	7.0 ± 5.8
TSS (mg L^{-1})	---	---	9.2 ± 2.7 (surface)		6.6 ± 2.4 (surface)		7.7 ± 2.0 (surface)	

Table 2. Sponge species identified at each of the study locations in Jamaica. Check marks indicate whether a species was found at each location.

Family	Species	Pear Tree	Discovery Bay	Dairy Bull
Agelisidae				
	Agelas clathrodes	✓	✓	✓
	Agelas citrina	✓	✓	✓
	Agelas conifera		✓	✓
	Agelas dispar	✓	✓	✓
	Agelas sceptrum		✓	
	Agelas sventres	✓		
	Agelas tubulata		✓	✓
	Agelas wiedenmayeri		✓	✓
Aplysinidae				
	Aiolochroia crassa	✓	✓	✓
	Aplysina cauliformis	✓	✓	✓
	Aplysina fulva			✓
	Aplysina insularis	✓	✓	✓
	Aplysina lacunosa	✓	✓	✓
	Aplysina fistularis	✓	✓	✓
	Verongula rigida	✓	✓	✓
	Verongula gigantea		✓	✓
Axinellidae				
	Axinella corrugata	✓	✓	
	Ptilocaulis walpersii	✓	✓	✓
Callyspongidae				
	Callyspongia fallax	✓	✓	✓
	Callyspongia plicifera			✓
Chalinidae				
	Haliclona sp. (?)			✓
Chondrillidae				
	Chondrilla caribensis	✓	✓	✓
	Chondrosia sp.	✓		
Clionaidae				
	Cliona aprica	✓		✓
	Cliona caribbaea	✓	✓	✓
	Cliona delitrix	✓	✓	✓

	Cliona laticavicola (?)	✓	✓	✓
	Cliona varians	✓	✓	✓
Desmacellidae				
	Neofibularia nolitangere	✓	✓	✓
Dictyonellidae				
	Scopalina ruetzleri	✓	✓	✓
	Svenzea tubulosa	✓		✓
Dysideidae				
	Dysidea sp.			✓
Geodiidae				
	Erylus bahamensis		✓	✓
Heteroxyidae				
	Myrmekioderma sp.	✓	✓	✓
Hymedesmiidae				
	Phorbas amaranthus	✓	✓	✓
Iotrochotidae				
	Iotrochota birotulata	✓	✓	✓
Irciniidae				
	Ircinia campana		✓	
	Ircinia felix	✓	✓	✓
	Ircinia strobilina	✓	✓	✓
Microcionidae				
	Clathria venosa	✓	✓	✓
	Pandaros acanthifolium	✓	✓	✓
Mycalidae				
	Mycale laxissima			✓
	Mycale laevis	✓	✓	✓
Niphatidae				
	Amphimedon compressa	✓	✓	✓
	Amphimedon viridis			✓
	Cribrochalina sp.		✓	✓
	Niphates alba	✓	✓	✓
	Niphates digitalis	✓	✓	✓
	Niphates erecta		✓	✓
Oscarellidae				
	Pseudocorticium sp.			✓
Petrosiidae				
	Neopetrosia carbonaria	✓	✓	✓

	Neopetrosia subtriangularis	✓	✓	
	Petrosia sp.		✓	✓
	Xestospongia muta		✓	✓
Plakinidae				
	Plakortis sp.	✓	✓	✓
Raspailiidae				
	Ectyoplasia ferox		✓	✓
Spirastrellidae				
	Spirastrella coccinea	✓	✓	✓
	Spirastrella hartmani	✓	✓	✓
Spongiidae				
	Spongia sp.			✓
Suberitidae				
	Aaptos sp.	✓	✓	✓
Tetillidae				
	Cinachyrellla sp.	✓	✓	✓
Thorectidae				
	Smenospongia aurea	✓	✓	✓
	Smenospongia conulosa	✓	✓	✓
	Hyrtios sp.		✓	✓

Table 3. Mean sponge density, abundance, richness, diversity and volumes (median is also presented) at each location and depth. Reported values are per transect (20 m^{-2}) unless otherwise stated and are reported as mean (or median) ± 1 standard deviation where applicable.

	Pear Tree (8-10m)	Pear Tree (15-18m)	Discovery Bay (8-10m)	Discovery Bay (15-18m)	Dairy Bull (8-10m)	Dairy Bull (15-18m)
Sponge density (m^{-2})	1.34 ± 0.53	1.82 ± 0.60	1.91 ± 0.54	2.65 ± 1.3	5.49 ± 1.12	7.04 ± 0.75
Sponge abundance (20 m^{-2})	26.7 ± 10.6	36.4 ± 11.9	38.1 ± 10.7	52.9 ± 25.9	109.7 ± 22.3	140.8 ± 15.0
Species richness	13 ± 3.1	15 ± 3.7	14.3 ± 2.7	17.8 ± 5.3	26.5 ± 2.3	28.1 ± 2.2
Cumulative species richness	38	42	41	50	53	56
Shannon Diversity (H')	2.24 ± 0.28	2.35 ± 0.26	2.26 ± 0.23	2.56 ± 0.32	2.83 ± 0.16	2.79 ± 0.12
Simpson's Diversity	0.87 ± 0.04	0.88 ± 0.03	0.87 ± 0.04	0.90 ± 0.04	0.9 2± 0.02	0.91 ± 0.02
Morphological diversity (H')	1.65 ± 0.19	1.70 ± 0.20	1.59 ± 0.20	1.71 ± 0.10	1.8 ± 0.13	1.73 ± 0.09
Mean Sponge Volume (cm^3)	958.5 ± 3473.3	1541.1 ± 5888.3	3012.3 ± 21109.2	1406.2 ± 15598.3	404.1 ± 3256.5	1492.3 ± 29868.2
Median Sponge Volume (cm^3)	67.3	112.7	201.1	108.0	57.5	72.0

Table 4. Results of a two-way ANOVA testing the effects of location and depth on a) the Shannon diversity (H'), b) the Simpson's diversity, c) and ranked species richness of sponges. Abundance data was fitted to a quasi-poisson distributed generalized linear model (GLM) and an analysis of deviance table was computed for the GLM using the F-test (d).

A	**ANOVA**	**df**	**SS**	**MS**	***F*-value**	***P***	
Diversity (Shannon Index, H')							
Location		2	2.937	1.468	26.039	<0.001	
Depth		1	0.218	0.218	3.869	0.0543	
Location * Depth		2	0.300	0.150	2.664	0.0789	
Residuals		54	3.045	0.056	---	---	
B	ANOVA	df	SS	MS	*F*-value	*P*	
Diversity (Simpson's Index)							
Location		2	0.0203	0.0102	9.353	0.0003	
Depth		1	0.0031	0.0031	2.853	0.097	
Location * Depth		2	0.006	0.003	2.762	0.072	
Residuals		54	0.0587	0.0012			
C	ANOVA	df	SS	MS	*F*-value	*P*	
Richness							
Location		2	2034.5	1017.3	125.65	<0.001	
Depth		1	6.7	6.7	0.823	0.368	
Location * Depth		2	13.3	6.7	0.823	0.444	
Residuals		54	437.2	8.1	---	---	
D	GLM	df	Deviance	Residual df	Residual Deviance	*F*-value	P
Abundance							
Location		2	1427.44	57	360.14	143.0	<0.001
Depth		1	76.65	56	283.5	15.36	0.0003
Location * Depth		2	1.21	54	282.28	0.121	0.886
Residuals		---	---	59	1787.6	---	---

Chapter 3

Seasonal and annual assessment of sponge and epibiont recruitment along the north coast of Jamaica

Abstract

Coastal development along the northern coast of Jamaica has increased over the past few decades, resulting in increased sediment supply to adjacent reefs. To understand the effects of sediment supply on sponge recruitment patterns, the seasonal and annual recruitment of sponge, as well as epibiont, communities were monitored over five years at three locations with varying degrees of coastal development. From photos, the percent cover and Shannon diversity (H') of sponges and epibionts on the cryptic undersides of ceramic settlement tiles were calculated and analyzed. When assessed seasonally, differences in sponge recruit diversity and coverage were found between depths, but not location or season. No differences in sponge diversity or coverage, as well as bare space on tiles, were found among locations in the seasonal monitoring periods, suggesting that larval supply was similar among locations. Annual assessment revealed significant differences in the percent cover and diversity of sponges among locations, indicating that post-settlement mortality events may be an important factor structuring sponge communities, although the exact contributor is still unknown. This study provides correlative evidence that sediment supply differences associated with coastal development may play a role in post-settlement mortality, although an experimental investigation and/or continued monitoring is necessary to explicitly link sediment stress to differences in sponge communities along the northern coast of Jamaica

Introduction

Increases in resident and tourist populations on many Caribbean islands over the past 30-40 years have placed undue pressure on local resources and ecosystems (Cincotta et al. 2000). As a result, many marine environments in the Caribbean suffer from degradation caused by overfishing (Hardt 2008), land-use changes (both agricultural and commercial), and increased nutrient loading (eutrophication) (Burke et al. 2004; Mora 2008; Wilkinson 1999). Coastal development, and associated activities, can directly affect the concentration of suspended solids in the water column and benthic sediment deposition rates (Burke et al. 2004; Fabricius 2005). Residential and commercial construction activities may lead to elevated suspended and settled sediments on reefs due to run-off and erosion (Fabricius 2005; Westfield 2008). Removal of important buffering habitats, such as mangroves (Alongi 2002) or seagrasses (Harbone et al. 2006), and alteration of natural shoreline composition (Westfield 2008) can reduce wave attenuation and result in increased coastal erosion, further reducing water quality and increasing sedimentation (Dahdouh-Guebas et al. 2005; Granek and Ruttenberg 2007).

Elevated suspended solids and sedimentation rates are detrimental to many reef organisms (Rogers 1990), but filter-feeding animals, such as sponges, may be particularly vulnerable (Bell et al. 2015). Sponges are a prominent component of tropical reefs (Diaz and Rützler 2001, Bell et al. 2013) providing structure, water filtration, and nutrient cycling to reef environments. However, sponges must process large volumes of water to meet their nutritional needs (Reiswig 1971, Southwell et al. 2008), which leaves them inherently sensitive to suspended and settling sediments that may clog their internal canals or smother their exterior. Many sponges are able to acclimate to short episodes of increased water column sediment loads by closing or narrowing the size of their incurrent openings (Ilan and Abelson 1995, Nickel 2004, Leys and Meech 2006). When sediment deposition occurs, sponges may reverse water flow to expel sediments (Nickel 2004) or trap and discard sediments within a mucus layer (Turon et al. 1999). These short-term physiological adaptations reduce, but may not completely eliminate, the harmful effects of suspended and settling sediments on sponges. For example, Tompkins-MacDonald and Leys (2008) exposed glass sponges to suspended sediments and found that despite cessation of pumping activities many of the smaller canals in the aquiferous system were still partially or completely obstructed by clays and fine sediments.

Persistent or intense sedimentation stress may have severe impacts on sponge health, survival and reproduction, even for species capable of living in highly sedimented environments. Lohrer et al. (2006) found that direct application of terrigenous sediment negatively affected sponge clearance rates, oxygen consumption and condition (tissue weight relative to body size) after just three weeks of exposure. A reduction in sexual reproductive output of sponges was reported along an *in situ* gradient of suspended sediment concentrations (Whalan et al. 2007, Bannister et al. 2012) as well as in experimental manipulations of sediment deposition over 13 weeks (Roberts et al. 2006). Additionally, sediment deposition reduced the survival and recruitment of small, asexually produced (fragmented) sponges (Maldonado et al. 2008).

Reductions in reproductive output and recruitment success as a result of sediment stress may eventually lead to changes in the sponge community. Few studies have analyzed the recruitment and development of tropical sponge communities in relation to environmental stressors such as sedimentation (Bell et al. 2015). Maughan (2001) attempted to tease apart the covarying effects of sedimentation and light attentuation and found that sponge recruitment was lowest on tiles exposed to siltation, regardless of their light exposure. Carballo (2006) found that a seasonal increase in sediment deposition rate resulted in a loss of morphological and taxonomic diversity and decreased the maturity of sponge assemblages. However, these relatively short-term assessments do not capture the cascading changes that might occur in future sponge populations as a result of increased sedimentation and further investigations of the long-term impacts on sponge communities are necessary (Bell et al. 2015).

To understand the effects of increased sediment supply on sponge recruitment processes, this study monitored seasonal and annual recruitment over five years at three locations known to have varying degrees of coastal development and sedimentation supply (Chapter 1). Diversity, percent cover, abundance and multivariate community composition of sponges and other sessile epibionts were evaluated to determine whether recruiting communities differed among locations. Sedimentation is thought to negatively affect sponge reproduction (Whalan et al. 2007, Bannister et al. 2012) and survival of recruits (Maldonado et al. 2008); therefore, I expected that the recruiting sponge diversity and percent cover would be reduced at the location experiencing the highest amount of sediment deposition. Previous surveys of sponge communities at the chosen study locations have shown that sponge diversity, richness and abundance vary along a gradient

of coastal development (Chapter 1). I hypothesized, therefore, that the diversity and percent cover of all recruiting organisms would follow a similar pattern to that of the adults.

Methods

Study Locations

Recruitment was monitored at three locations along the northern coast of Jamaica, West Indies. Each location represented different amounts of human impact and sedimentation (Westfield 2008; Chapter 1). Pear Tree (N 18.465, W 77.343), the easternmost location, is directly adjacent to a large resort (Figure 1). The resort was constructed in 2005, and resulted in approximately 25,000 m^2 of artificially created and filled beaches—a 42% increase in beach area—along less than 2 km of shoreline (Westfield et al. 2008). Sediment deposition at Pear Tree is variable and seems to be highest during wind events (Chapter 1). The concentration of total suspended solids (TSS) measured at all three locations during a high wind event (>10 m s^{-1}) was highest at Pear Tree, although only statistically different than Discovery Bay (Chapter 1). Approximately 4 km to the west, Dairy Bull (N 18.471, W 77.379) experiences the least amount of coastal development of the three locations. The previous chapter found low sediment accumulation rates at Dairy Bull regardless of wind speeds. Finally, Discovery Bay (N 18.473, W 77.412) is located north of the reef crest, just west of the inlet near the Discovery Bay Marine Lab and is surrounded by moderate coastal development. Low rates of sediment deposition were recorded at Discovery Bay despite its proximity to a bauxite mining and distribution facility located within the bay (Chapter 1), although there is evidence that past sedimentation might have been higher when mining activities were heightened and less regulated by the authorities (Perry and Taylor 2004, Macdonald and Perry 2003).

All three locations are generally comparable with respect to geologic structure, distance from shore, and water flow/currents (NEPA Environmental Impact Assessment 2005). Previous water quality assessments at these locations found no significant differences in seawater temperature, salinity, dissolved oxygen levels, nutrient or chlorophyll *a* concentrations (see Chapter 1 for methods). Light levels, although not statistically different, were 18% lower at Pear Tree than both Dairy Bull and Discovery in the shallow depth strata. At the deeper depth strata, overall light reaching the bottom at Pear Tree was 8% lower than Dairy Bull and 32% lower than Discovery Bay (Chapter 1).

Experimental design

At each of the locations, recruitment was monitored for six consecutive seasonal periods (spring/summer and fall/winter), followed by three consecutive annual (12-month) periods. Each location was divided into two sites, east and west, separated by approximately 500 m. To test the effect of depth, tiles were placed at two depth strata, 8-10 m and 15-18 m (hereafter referred to as shallow and deep) within each site at each location (Figure 2).

For the seasonal recruitment monitoring period (January 2009-January 2012), unglazed terra cotta recruitment tiles (12 cm x 12 cm) with a hole (1 cm diameter) drilled through the middle were oriented parallel to the reef floor using permanent baseplates as suggested by Mundy (2000) for coral recruitment studies. The baseplates, which were corrosion resistant steel plates fastened to coralline rock with plastic screw anchors, were fitted with an upward-facing screw that allowed a single tile to be easily mounted 3-5 cm above the benthos using nylon wingnuts and removed later (Duckworth et al. 2008 Figure 3). Each site at each location had 15 tiles placed in the shallow (8-10 m) and deep strata (15-18 m; n=30 at each site), for a total of 60 tiles at each location (n=180 total). Within each site and depth stratum, tiles were divided into three groups of replicates. Tile groups consisted of 5 tiles that were each separated by a minimum of 1 m, and tile groups were separated from one another by at least 25 m (Figure 2).

The experiment began in January 2009 when clean, unconditioned tiles were attached to all baseplates. Tiles were left undisturbed until the first sampling period in August 2009. During sampling periods, the wingnuts were carefully unscrewed and tiles were removed from the baseplates. To minimize disturbance to organisms, *in situ* photographs (Sony Cybershot DSC-T900 housed within a Sony Cybershot Marinepack; 12.1 megapixels) were immediately taken of the undersides (cryptic) and top side (exposed) of each tile using a custom-made camera frame that held tiles at a fixed distance of 28 cm. After photographs were taken, tiles were carefully placed into crates and brought to the Discovery Bay Marine Lab for further examination. New terra cotta tiles were secured to the baseplates and sampling procedures were repeated every six months over a period of three years (August and January, 2009-2012). Once back at the lab, fouled tiles were kept in flow-through seawater tables until voucher samples of all sponges and any unknown organisms were obtained and preserved. After the initial 3-year seasonal recruitment monitoring period, tiles were reduced to n=5 per depth/site stratum (n=20 per

location) and annual recruitment was monitored from January 2012 to January 2015. Tiles were photographed, collected and replaced as described above every January during this period.

Image Analysis

All tile photos (seasonal and annual samples) were processed in the same manner. Only the cryptic sides of tiles were analyzed because the majority of organisms recruited to the undersides of the tiles, likely due to the negative phototactic and positive geotactic tendencies of recruiting organisms (Carleton and Sammarco 1987, Maida et al. 1994, Maldonado and Young 1996). To eliminate potential edge effects, photographs were first scaled and then cropped using ImageJ (Abramoff et al. 2004) to remove the outer 1.2 cm of the tiles, resulting in a 9.6 cm x 9.6 cm (92.16 cm^2) section of the original 12 cm x 12 cm area. These edited photos were then imported into Coral Point Count with Excel extensions (CPCe) (Kohler and Gill 2006), and scaled once more. Each organism was traced to determine areal coverage and identified to the lowest possible taxonomic level. Due to the broad range of organisms that recruited to the tiles, many of the organisms were classified only to broad taxonomic categories (e.g. bryozoans, ascidians, macroalgae). Only sponge individuals were identified to a lower taxonomic level. However, sub-adult sponges, or small recruits, often lack a full complement of spicules and are difficult to accurately identify (Zea 1993); therefore, only order or family-level assignments were made, when possible. Sponge spicules were prepared following common methods for examination and identification (Hooper and van Soest 2002). In cases where certain organisms (e.g., serpulid worms) were too abundant (>100 individuals) to be accurately and efficiently traced in Coral Point Count, the total area covered by the organism was measured using the Color Threshold tool in ImageJ. The Color Threshold tool allows areal measurement of features that are difficult to trace by selecting all pixels that fall within a user-specified range of color intensity and measuring the area. All other organisms on the tile were traced as individuals.

Data analysis

All data were analyzed using R, a free statistical software (R Development Core Team 2008), unless otherwise specified. Individual tiles (n=5) within each tile group served as pseudoreplicates of one another (Hurlbert 1984), and were therefore averaged to obtain tile group means at each time-point, which were subsequently used for all analyses. Variables of interest

were analyzed separately for seasonal and annual tiles. Sponge and overall taxonomic diversity of cryptic tile sides were calculated using the Shannon diversity index (H') for each sampling time point. Analyses of seasonal and annual sponge diversity, percent sponge cover, taxonomic diversity and percent bare space were all completed using a generalized linear model (GLM) with Gaussian distribution and location, depth and time-point (season or year) as factors; only seasonal sponge diversity, percent sponge and bare space coverage required transformations (square-root, fourth-root and arcsine, respectively) to achieve normality. When no significant interaction term was found, the non-interactive GLM was re-run and results were reported from this model. When a significant main effect was found, post hoc tests of pairwise Tukey comparisons were run using the glht function in the R package multcomp.

Results

Seasonal Sponge Recruitment

Recruited sponge diversity was significantly different by season ($F_{(2,105)}$=5.69, P=0.019, Table 1a). The highest diversity of sponge recruits was found during the August sampling period (Figure 4a, b), indicating that the majority of sponge reproduction and settlement occurs between January and August in Jamaica. There was no significant difference in sponge diversity among locations or depths (Table 1a). In August, mean (± SD) sponge Shannon diversity (H') was 0.17 ± 0.12, whereas in January it was 0.12 ± 0.11. There were 53 visually unique sponges observed over all tiles, of which 32 were classified into 10 orders (likely 16 families), and 21 remain unclassified (Table 3). Mean number of sponges recruiting per tile between January and August was 3.4 (±1 SD: ± 4.4), and between August and January was 1.4 (± 2.2). Seasonal sponge percent cover was not significantly different among locations or depths, but season was found to be a significant factor ($F_{(1,103)}$=4.209, P=0.043; Table 1b). Sponges made up a mere 2% of areal coverage at Pear Tree and 4% areal coverage at Discovery Bay and Dairy Bull.

Seasonal Epibiont Recruitment

Shannon diversity (H') of the entire epibiont community during the seasonal sampling period was significantly different by location, depth and season (Table 1c), with a significant interaction between location*depth ($F_{(2,101)}$=4.3365, P=0.016). Shallow depths had the highest epibiont diversity ($F_{(1,104)}$=18.0576, P<0.001); tiles collected at the August time-points also had consistently higher diversity ($F_{(1,103)}$=86.0285, P<0.001). Diversity was statistically different among locations ($F_{(2,105)}$=6.1540, P=0.003); Pear Tree had significantly lower epibiont diversity than both Dairy Bull and Discovery Bay (adjusted-P=0.036 and P=0.003, respectively), which were not statistically different from one another (see Figure 5a,b for comparison of diversity among locations). Analysis of the percent bare space on cryptic undersides of tiles showed that only the main effects of depth and season were significant ($F_{(1,104)}$=22.09, P<0.001; $F_{(1,103)}$=49.20, P<0.001, respectively). Significantly less areal coverage of organisms was found on tiles at the January time-point resulting in more bare space (76 ± 11%) than in August when mean bare space was 65 ± 14%. This indicates that the majority of recruitment and growth occurs during the spring/summer months. Mean (± SD) bare space was significantly higher in the

deep (74 ± 10%) than in the shallow strata (65 ± 14%). The taxonomic groups contributing the largest percent areal coverage during the seasonal sampling periods were ascidians (4-6%), polychaetes (5-8%) and bryozoans (6%). Coral spat abundance ranged from 0-95 spat per tile, with a mean of 4.7 (± 8.6) spat per tile—the equivalent of roughly 500 spat m^{-2}.

Annual Sponge Recruitment

Annual sponge recruitment diversity did not vary by year or depth, however location was shown to be a significant factor ($F_{(2,33)}$=6.67, P=0.004; Table 2a). Post hoc Tukey pairwise contrasts revealed that Pear Tree had significantly lower sponge diversity than Dairy Bull (adjusted-P= 0.001) and Discovery Bay (adjusted-P=0.026). Mean (± 1 SD) Shannon diversity (H') of sponges at Pear Tree was 0.18 ± 0.09, compared with 0.28 ± 0.11 and 0.32 ± 0.13 at Discovery Bay and Dairy Bull, respectively (see Figure 4c for location and depth diversity). Mean number of sponges per tile for the annual sampling periods was 5.1 (± 5.3), with 11 orders and 20 families recorded on annual tiles (Table 3) and 26 visually unique sponges remaining unclassified. Percent cover of sponges was significantly different by location ($F_{(2,33)}$=5.498, P=0.009, Table 2b) with mean (± SD) sponge cover of 15.3 ± 7.4% at Dairy Bull, 15.5 ± 9.0% at Discovery Bay, and 6.6 ± 4.9% at Pear Tree. Post hoc Tukey pairwise comparisons indicated that Pear Tree had lower sponge cover than the other two locations (Pear Tree vs. Dairy Bull: adjusted-P=0.013; Pear Tree vs. Discovery Bay: adjusted-P=0.01; Dairy Bull vs. Discovery Bay: adjusted-P=0.99).

Annual Epibiont Recruitment

Sponges dominated annual epibiont communities at Discovery Bay and Dairy Bull (15.2 and 14.8% respectively); Pear Tree had 11.5% sponge cover. Bryozoans were the second most dominant organism and covered 12% of tile surfaces at all three locations (Figure 6). Annual coral spat abundance was similar to seasonal abundance with a mean of 4.1 (± 5.8) spat per tile, although the range was lower (0-43 spat $tile^{-1}$). Bare space was significantly different by location and depth ($F_{(2,33)}$=6.13, P=0.006; $F_{(1,32)}$=5.17, P=0.03, respectively; Table 2d). Mean bare space at Pear Tree was 56.5 ± 11.1% while Dairy Bull (44.0 ± 10.2%) and Discovery Bay (44.4 ± 10.6%) had significantly lower amounts of bare space (adjusted-P= 0.006 and 0.008), respectively. Shallow depths also had significantly less bare space—mean bare space was 44.5 ±

13.1% compared to 52.1 ± 9.4% at deep strata. Annual epibiont diversity was not significantly different by location, depth or year (Table 2c).

Discussion

Given the difficulty in measuring the settlement of organisms in the field, recruitment is often used to infer settlement after a specified time period (Zea 1993; Booth and Brosnan 1995). Seasonal recruitment (settled organisms surviving after 6 months) and annual recruitment (settled organisms surviving after 12 months) of sponges and the entire epibiont community were monitored at three locations with different degrees of coastal development and sediment supply (Figure 1). Previous studies have found that sponge reproductive output (number of gametes released) is negatively impacted by sedimentation (Roberts et al. 2006; Whalan et al. 2007); therefore, lower sponge recruitment was anticipated for Pear Tree where sediment accumulation rate was highest during wind events (Figure 1; but also Chapter 1). Surprisingly, no differences in sponge diversity or percent sponge cover were found among locations during the seasonal sampling periods (Table 1a,b). However, when evaluated annually, the percent cover and diversity of sponge recruits was significantly different among locations (Table 2a,b); sponge diversity and percent cover was lower at Pear Tree compared to Discovery Bay and Dairy Bull.

Recruitment patterns are determined primarily by larval supply (Lewin 1986; Roughgarden et al. 1987; Underwood and Fairweather 1989) and/or post-settlement mortality (Connell 1985). The detection of differences in sponge recruit diversity and percent cover during annual, but not seasonal, monitoring periods suggests that post-settlement mortality, rather than limited larval supply, may be playing an important role in structuring these sponge communities. Had larval supply been a critical factor, differences among locations should have been apparent during the seasonal sampling periods, which are more reflective of recent reproductive activity (and settlement) than the annual sampling periods. The similarities in sponge diversity or percent cover during the seasonal sampling periods suggest that larval supply (and larval habitat selection; Jenkins 2005) was equivalent at all three locations. The number of sponges recruiting was similar in magnitude to those found by Zea (1990), suggesting that sponge recruitment in Jamaica was comparable to other sites in the Caribbean.

While larval supply did not necessarily reflect the distribution of adults (fewer adult sponges were found at Discovery Bay and Pear Tree in Chapter 1), it is unlikely that sponge recruitment at the study locations was driven by supply from an outside larval source (see review by Maldonado 2006). Sponge larvae are generally poor swimmers, and many are considered

anchiplanic, spending only minutes to days in the water column before entering the site-selection phase (Maldonado 2006). During this phase, larvae crawl along the bottom until a suitable substrate is found and settlement occurs (Maldonado and Young 1996). This strategy results in short dispersal distances (less than a few meters; Zea 1993) and high larval retention within the immediate environment, particularly in areas of low current—such as the chosen study locations—where hydrologic factors are minimal (Mariani et al. 2006; Maldonado and Young 1996). Previous studies have shown that sponge recruitment reflects the abundance, maturity, and diversity of the immediate reproductive sponge community (Zea 1993, Maldonado and Young 1996). Therefore, although differences in the adult sponge communities were found between the three locations (Chapter 1), they were likely similar in their reproductive activity. That there were no differences in either percent cover or diversity of sponges during the seasonal samplings suggests that larval supply is not the main driver of differences between communities.

Differences in sponge diversity and percent cover emerged when tiles were evaluated annually, rather than seasonally (Table 2a,b). Annual assessment of sponge recruitment revealed that Pear Tree had lower sponge diversity and percent cover than both Dairy Bull and Discovery Bay. This pattern was also found in the percent cover of epibionts recruiting (based on analysis of bare space): no differences in the percentage of bare space were found seasonally among locations (Table 1d), but annual sampling periods showed significant differences in bare space among locations (Table 2d) driven by a percentage of bare space at Pear Tree (Figure 6). This suggests that post-settlement mortality is propagating differences in sponge and epibiont recruitment at Pear Tree, perhaps driven by differing environmental conditions such as increased sediment suspension and accumulation during wind events (Figure 1; Chapter 1).

Suspended and settling sediments can negatively affect small or juvenile sponge survival due to scouring, burial or clogging of the aquiferous system (Maldonado et al. 2008; Bell et al. 2015). Maldonado et al. (2008) compared survival between sponges exposed to direct sediment deposition and sponges that were ‘shielded’ from direct sediment deposition by small plates. Direct sediment deposition reduced the survival of small sponge fragments compared to those under protective plates (Maldonado et al. 2008). It is important to point out that the tiles in this study, by design, shielded recruits found on the cryptic sides of tiles from the effects of any direct sediment accumulation. Therefore, only the resultant effects of existing in an environment

experiencing occasionally elevated sediment accumulation (e.g. scouring, difficulty filtering water) would have contributed to mortality for recruited sponges. In addition to shielding sponges from direct sediment stress, the tiles may have also protected recruited organisms from fish predation and/or physical disturbances such as urchin movement. The protection of sponge and epibiont communities provided by the tiles may have resulted in higher survival and artificially inflated recruitment over what might have occurred if organisms were not protected.

While there are many potential contributors to post-settlement mortality in recruitment communities, identifying a specific stressor and linking it to mortality is often very difficult (Wilson and Harrison 2005; Hunt and Scheibling 1997). Many post-settlement mortality events (predation, physiological or physical stress, storm disturbance) may occur over short time periods (minutes to days), but other stressors, such as competition, overgrowth, and long-term environmental changes (e.g. siltation, temperature stress, acidification), may occur gradually and deleterious affects may not be apparent for weeks to months (see review by Hunt and Scheibling 1997). Additionally, more complex interactions may be occurring at different rates between recruited organisms, such as allelopathic interactions. Some organisms, most notably sponges, exude allelochemicals (biochemical compounds) that have been shown to facilitate (Bingham and Young 1991; Bakus and Kawaguchi 1984) or inhibit (Porter and Targett 1988; Bingham and Young 1991) the recruitment, growth and survival of other organisms. In an *a posteriori* regression analysis there was no evidence found that allelopathic facilitation or inhibition was occurring between sponges and the epibiont community on the tiles during either seasonal or annual recruitment monitoring periods. However, any allelopathic interactions occurring over a time period shorter than 6 months would have been missed due to our sampling strategy, and thus, allelopathic interactions cannot be excluded as a potential contributor to post-settlement mortality.

Regardless of the stressor, this study found that a realistic timeframe might be a year or more for observing changes at the community-level, given that the effects of post-settlement mortality may not be apparent at the seasonal scale. Further, the explicit link between sedimentation (or any stressor) and recruitment patterns is often problematic because sedimentation associated with coastal development is difficult to source, may be episodic (e.g. terrestrial run-off increases during rainstorms), and can be relatively short-lived over large

temporal scales (e.g. increased sedimentation during dredging or construction) (Rogers 1990; McClanahan and Obura 1997; Babcock and Smith 2000). The differences in sedimentation found at the three study locations were minimal during low wind events, and only differed during high wind events (Figure 1; Chapter 1). Given these subtle and periodic differences, it is likely that sedimentation is just one of many factors contributing to the differences found in sponge communities in Chapter 1 and the present study. There are many confounding variables that may co-occur with sedimentation, such as light attenuation (Maughan 2001) and enhanced nutrients (Fabricius 2005), further complicating the unequivocal establishment of sedimentation as a direct causative agent of subsequent community change, except in very extreme sediment regimes (Rogers 1990).

Taxonomically, sponge recruitment seemed to represent the surrounding adult sponge communities. Although a direct comparison between adult and recruited sponge species could not be made due to the difficulty in identifying juvenile sponges (Zea 1993), the sponge orders and families that recruited to the tiles were generally similar to those adults surveyed in Chapter 1 (see Table 3). However, there were several differences between the adult sponge communities found in Chapter 1 that were not reflected in the current evaluation of sponge recruitment. Specifically, the abundance, species richness and diversity of sponges were reduced at Discovery Bay and Pear Tree compared to Dairy Bull (the location with the least coastal development). Sponge recruits at Pear Tree had significantly lower diversity and percent cover, but unlike the adult sponge communities (Chapter 1), sponge recruits at Discovery Bay did not display reduced diversity and percent cover compared to Dairy Bull. Instead, sponge recruitment at Discovery Bay and Dairy Bull were most similar with higher diversity and percent cover (and also less bare space) than Pear Tree. While sedimentation could be an explanation of the recruitment patterns observed in this study, the patterns of adult and recruited sponges differ, at Discovery Bay in particular, pointing to an additional, albeit unknown, driver of sponge community composition.

Conclusions

The potential for sedimentation and coastal development to structure recruiting sponge communities was investigated here by monitoring sponge recruitment over a five-year period. While seasonal differences between recruiting sponge communities were limited, during annual samplings reduced sponge diversity, sponge percent cover and increased bare space were

observed at the location with the highest sedimentation (Pear Tree). While there may have been other unmeasured environmental parameters that differentiated the three study locations, sediment accumulation rate was the only measured parameter that differed significantly (Chapter 1). This study provides correlative evidence that sediment associated with coastal development may play a role in structuring sponge communities along the northern coast of Jamaica. It is imperative that an experimental investigation and/or continued monitoring should be undertaken to explicitly link these community-level changes directly to sedimentation derived from coastal development projects.

References

Abramoff MD, Magalhaes PJ, Ram SJ (2004) Image processing with ImageJ. *Biophotonics International* 11:36-42

Alongi DM (2002) Present state and future of the world's mangrove forests. *Environmental Conservation* 29: 331-349

Babcock R, Smith, L (2002) Effects of sedimentation on coral settlement and survivorship. In *Proceedings of the Ninth International Coral Reef Symposium, Bali, 23-27 October 2000* 1:245-248

Bakus GJ, Kawaguchi M (1984) Toxins from marine organisms: studies on antifouling. In: Bolis L, Zadunaisky J, Gilles R (eds.) *Toxins, drugs, and pollutants in marine animals*. Springer-Verlag, Berlin.

Bannister RJ, Battershill CN, de Nys R (2012) Suspended sediment grain size and mineralogy across the continental shelf of the Great Barrier Reef: Impacts on the physiology of a coral reef sponge. *Continental Shelf Research* 32:86-95

Bell JJ, Davy SK, Jones T, Taylor MW, Webster NS (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology* 19:2613-2624

Bell JJ, McGrath E, Biggerstaff A, Bates T, Bennett H, Marlow J, Shaffer M (2015). Sediment impacts on marine sponges. *Marine Pollution Bulletin*, http://dx.doi.org/10.1016/ j.marpolbul.2015.03.030

Bingham BL, Young CM (1991) Influence of sponges on invertebrate recruitment: a field test of allelopathy. *Marine Biology* 109:19-26

Booth DJ, Brosnan DM (1995) The role of recruitment dynamics in rocky shore and coral reef fish communities. *Advances in Ecological Research* 26:309-385.

Burke et al. (2004) Reefs at Risk in the Caribbean. World Resources Institute

Washington, D.C. http://www.wri.org/publication/reefs-risk-caribbean

Carballo JL (2006) Effect of natural sedimentation on the structure of tropical rocky sponge assemblages. *Ecoscience* 13:119-130

Carleton JH, Sammarco PW (1987) Effects of substratum irregularity on success of coral settlement: quantification by comparative geomorphological techniques. *Bulletin of Marine Science* 40:85-98

Cincotta RP, Wisnewski J, Engelman R (2000) Human population in the biodiversity hotspots. *Nature* 404:990-992

Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 93:11-45

Dahdouh-Guebas F, Jayatissa LP, Di Nitto D, Bosire JO, Seen DL, Koedam N (2005) How effective were mangroves as a defense against the recent tsunami? *Current biology* 15:R443-R447

Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean reefs. *Bulletin of Marine Science* 69:535-546

Duckworth AR, Wolff C, Evans-Illidge E, Whalan S, Lui S (2008) Spatial variability in community structure of Dictyoceratida sponges across Torres Strait, Australia. *Continental Shelf Research* 28:2168-2173

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50:125-146

Granek E, Ruttenberg BI (2008) Changes in biotic and abiotic processes following mangrove clearing. *Estuarine, Coastal and Shelf Science* 80:555-562

Harborne AR, Mumby PJ, Micheli F, Perry CT, Dahlgren CP, Holmes KE, Brumbaugh DR (2006) The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. *Advances in marine biology* 50:57-189

Hardt MJ (2008) Lessons from the past: the collapse of Jamaican coral reefs. *Fish and Fisheries* 10:1-16

Hooper JNA, van Soest RWM (2002) Systema Porifera: A guide to the classification of sponges. Springer USA

Hunt HL, Scheibling RE (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Marine Ecology Progress Series* 155:269-301

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological monographs* 54:187-211

Ilan M, Abelson A (1995) The life of a sponge in a sandy lagoon. *Biological Bulletin* 189:363-369

Jenkins SR (2005) Larval habitat selection, not larval supply, determines settlement patterns and adult distribution in two chthamalid barnacles. *Journal of Animal Ecology*, 74:893-904

Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences* 32:1259-1269

Lewin R (1986) Supply-side ecology. *Science* 234:25-27

Leys SP, Meech RW (2006) Physiology of coordination in sponges. *Canadian Journal of Zoology* 84:288-306

Lohrer AM, Hewitt JE, Thrush SF (2006) Assessing far-field effects of terrigenous sediment loading in the coastal marine environment. *Marine Ecology Progress Series* 315:13-18

Macdonald IA, Perry CT (2003) Biological degradation of coral framework in a turbid lagoon environment, Discovery Bay, north Jamaica. *Coral Reefs* 22:523-535

Maida M, Coll JC, Sammarco PW (1994) Shedding new light on scleractinian coral recruitment. *Journal of Experimental Marine Biology and Ecology* 180:189-202

Maldonado M, Young CM (1996) Effects of physical factors on larval behavior, settlement and recruitment of four tropical demosponges. *Marine Ecology Progress Series* 138:169-180

Maldonado M (2006) The ecology of the sponge larva. *Canadian Journal of Zoology* 84:175-194

Maldonado M, Giraud K, Carmona C (2008) Effects of sediment on the survival of asexually produced sponge recruits. *Marine Biology* 154:631-641

Mariani S, Uriz MJ, Turon X, Alcoverro T (2006) Dispersal strategies in sponge larvae: integrating the life history of larvae and the hydrologic component. *Oecologia* 149:174-184

Maughan BC (2001) The effects of sedimentation and light on recruitment and development of a temperate, subtidal, epifaunal community. *Journal of Experimental Marine Biology and Ecology* 256:59-71

McClanahan TR, Obura D (1997) Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology* 209:103-122

Mora C (2008) A clear human footprint in the coral reefs of the Caribbean. *Proc Biol Sci* 275:767-773

Mundy CN (2000) An appraisal of methods used in coral recruitment studies. *Coral Reefs* 19:124-131

NEPA Environmental Impact Assessment (2005) Bahia Principe Hotel Resort Development, Pear Tree Bottom, St. Ann. Jamaica. National Environmental and Planning Agency, Kingston, Jamaica

Nickel M (2004) Kinetics and rhythm of body contractions in the sponge *Tethya wilhelma* (Porifera: Demospongiae). *Journal of Experimental Biology* 207:4515-4524

Perry CT, Taylor KG (2004) Impacts of bauxite sediment inputs on a carbonate-dominated embayment, Discovery Bay, Jamaica. *Journal of Coastal Research* 1070-1079

Porter JW, Targett NM (1988) Allelochemical interactions between sponges and corals. *Biological Bulletin* 175:230-239

R Development Core Team (2008) R: A language and environment for statistical computing In: Computing RFfS (ed), Vienna, Austria

Reiswig H (1971) Particle feeding in natural populations of three marine Demosponges. *Biological Bulletin* 141:568-591

Roberts DE, Davis AR, Cummins SP (2006) Experimental manipulation of shade, silt, nutrients and salinity on the temperate reef sponge *Cymbastela concentrica. Marine Ecology Progress Series* 307:143-154

Rogers C (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62:185-202

Roughgarden J, Gaines SD, Pacala SW (1987) Supply side ecology: the role of physical transport processes. In *Symposium of the British Ecological Society*.

Southwell M, Weisz JB, Martens CS, Lindquist N (2008) In situ fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. *Limnology and Oceanography* 53:986-996

Tompkins-MacDonald GJ, Leys SP (2008) Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. *Marine Biology* 154:973-984

Turon X, Uriz M-J, Willenz P (1999) Cuticular linings and remodelisation processes in Crambe crambe (Demospongiae: Poecilosclerida). *Memoirs of the Queensland Museum* 44:617-625

Underwood AJ, Fairweather PG (1989) Supply-side ecology and benthic marine assemblages. *Trends in Ecology and Evolution* 4:16-20

Westfield I (2008) Geochemical fingerprinting of sediments on the Pear Tree Bottom Reef, near Runaway Bay, Jamaica. Master of Science, Baylor University.

Whalan S, Battershill C, de Nys R (2007) Variability in reproductive output across a water quality gradient for a tropical marine sponge. *Marine Biology* 153:163-169

Wilkinson CR (1999) Global and local threats to coral reef functioning and existence: review and predictions. *Marine and Freshwater Research* 50:867-878

Wilson J, Harrison P (2005) Post-settlement mortality and growth of newly settled reef corals in a subtropical environment. *Coral Reefs* 24:418-421

Zea S (1990) Distribution, cover and recruitment of demosponges (Porifera, Demospongiae) in rocky and reefal habitats of Santa Marta, Colombian Caribbean. PhD Dissertation. The University of Texas at Austin, Austin, 154pp.

Zea S (1993) Recruitment of Demosponges (Porifera, Demospongiae) in rocky and coral reef habitats of Santa Marta, Colombian Caribbean. *Marine Ecology* 14:1-21

Figures and Tables

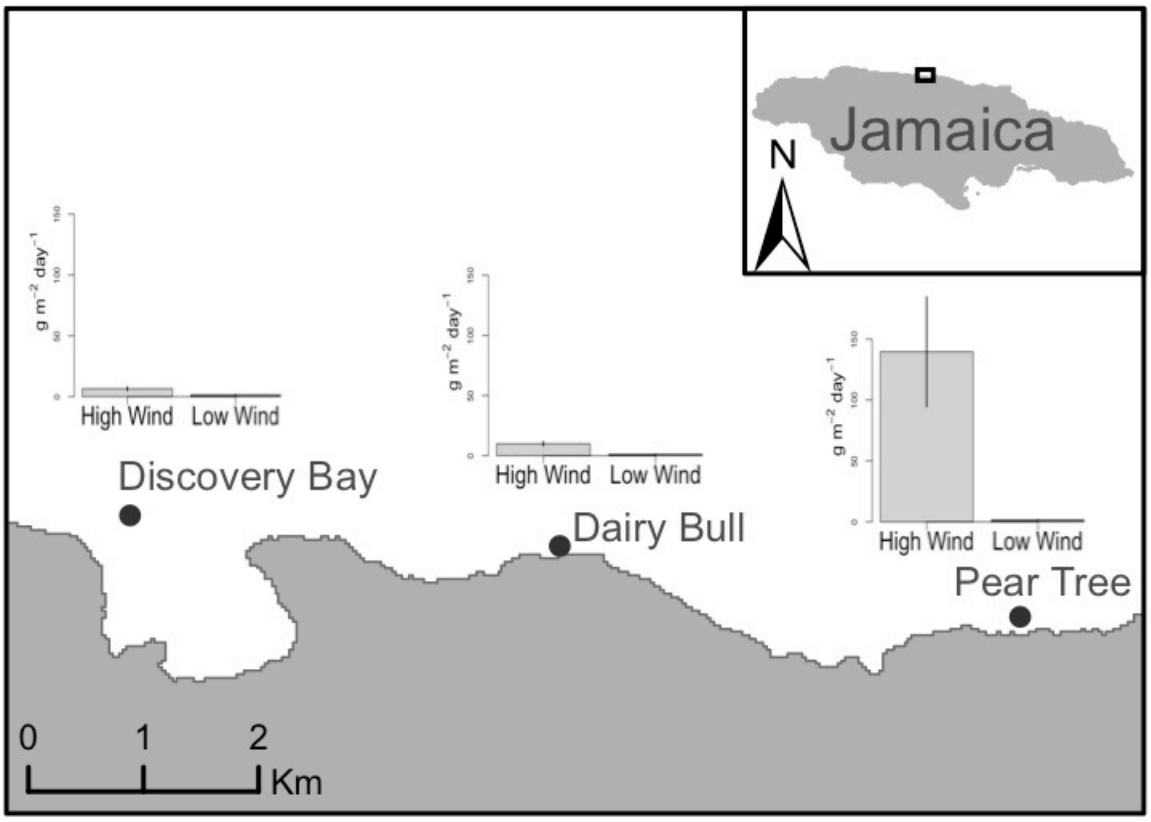

Figure 1. Map of study locations. Upper right inset: The island of Jamaica, West Indies; the small black box indicates the specific area where recruitment monitoring took place. The three study locations are denoted by circles; the corresponding levels of sediment accumulation rates (g m^{-2} day^{-1}) during high (> 10 m s^{-1}) and low wind events (< 10 m s^{-1}) are provided directly above each location. The y-axis has the same scale in all three graphs; error bars represent standard error of the mean.

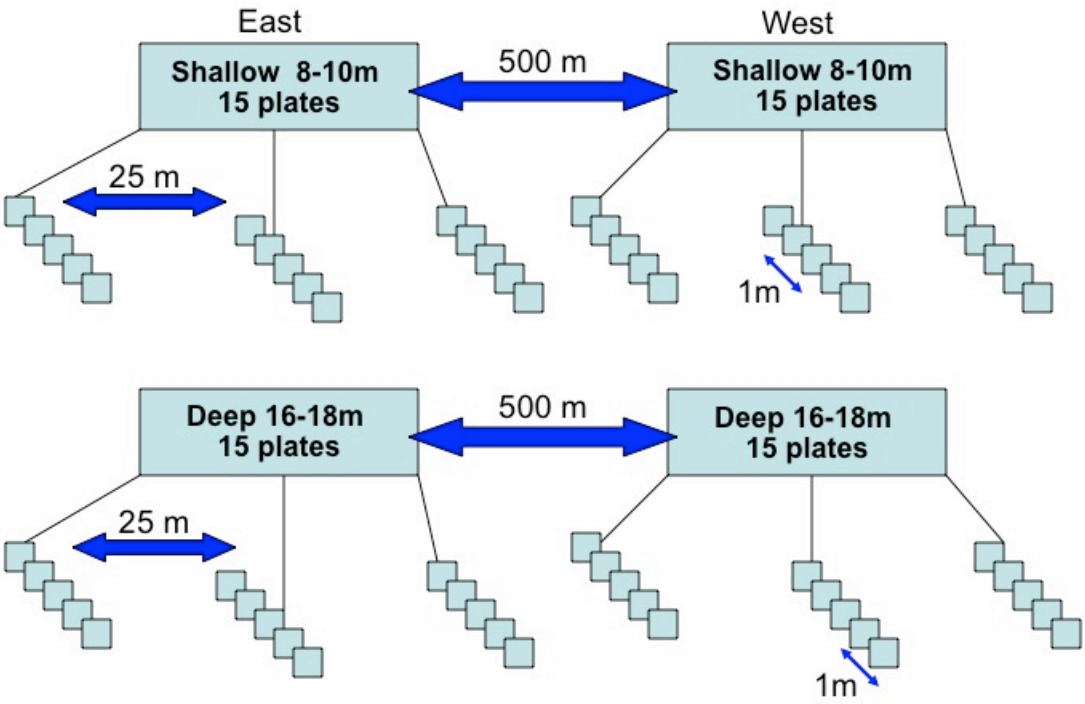

Figure 2. Tile layout at each location; locations were each divided into an eastern and western site, which were further divided into shallow and deep strata. Three replicate tile groups (n=5 tiles) were placed at each site/depth combination (n=15); tile groups were separated by a minimum of 25 m. Total number of tiles at each location was n=30 for the shallow, and n=30 for deep.

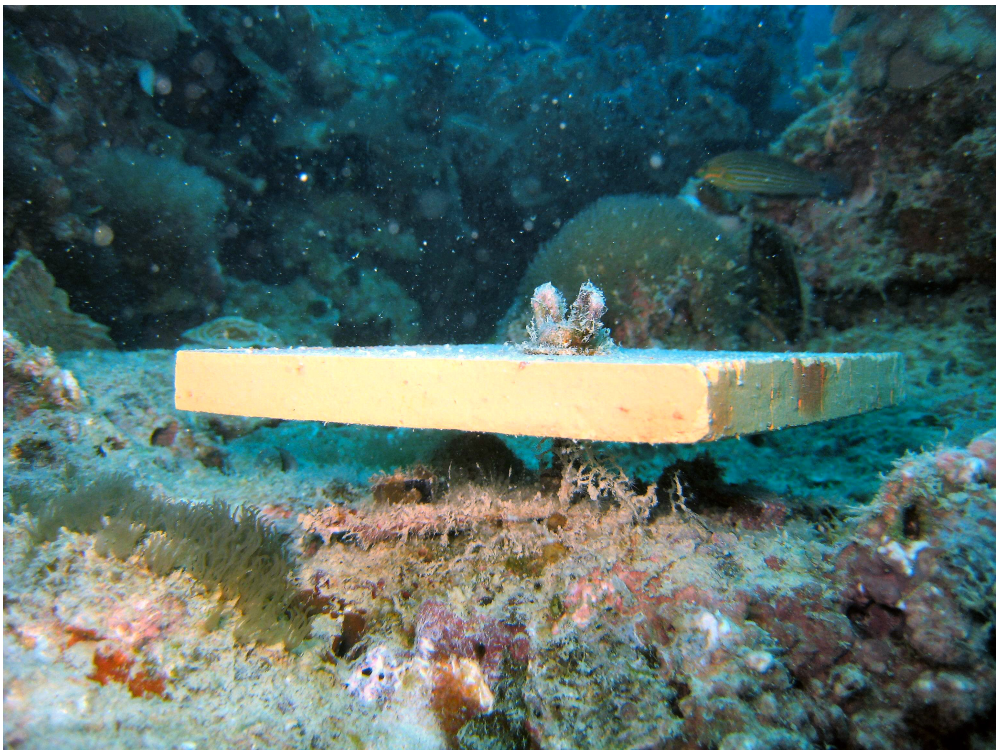

Figure 3. Ceramic settlement tile mounted to baseplate; an example of one tile mounted to the baseplate and secured using a nylon wingnut. The distance between the substrate and tile is approximately 3-5 cm.

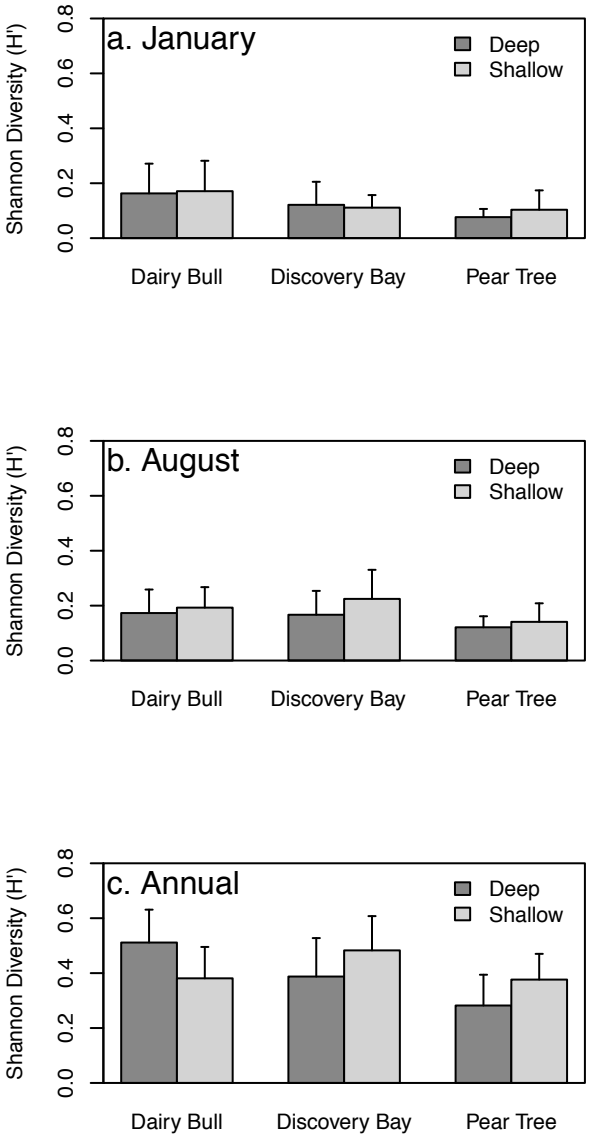

Figure 4. Mean Shannon diversity (H') of sponges recruited to the seasonal (a,b) and the annual tiles (c) are presented for the deep and shallow depths at each location. Error bars represent the standard deviation of the mean.

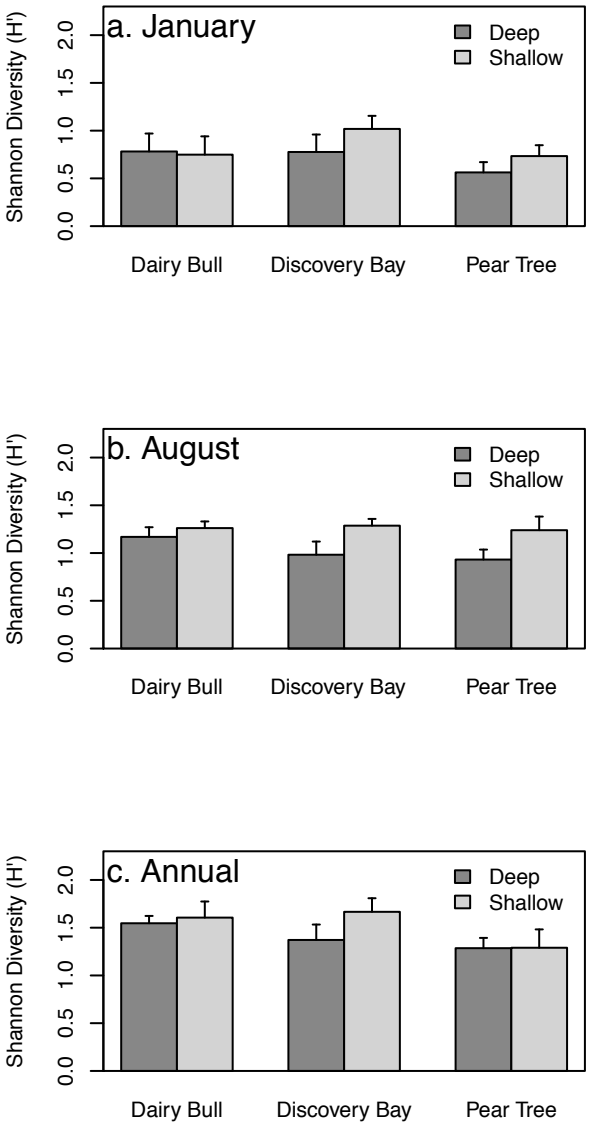

Figure 5. Mean (±SD) Shannon diversity (H') of epibionts recruited to the seasonal (a,b) and the annual tiles (c) are presented for the deep and shallow depths at each location.

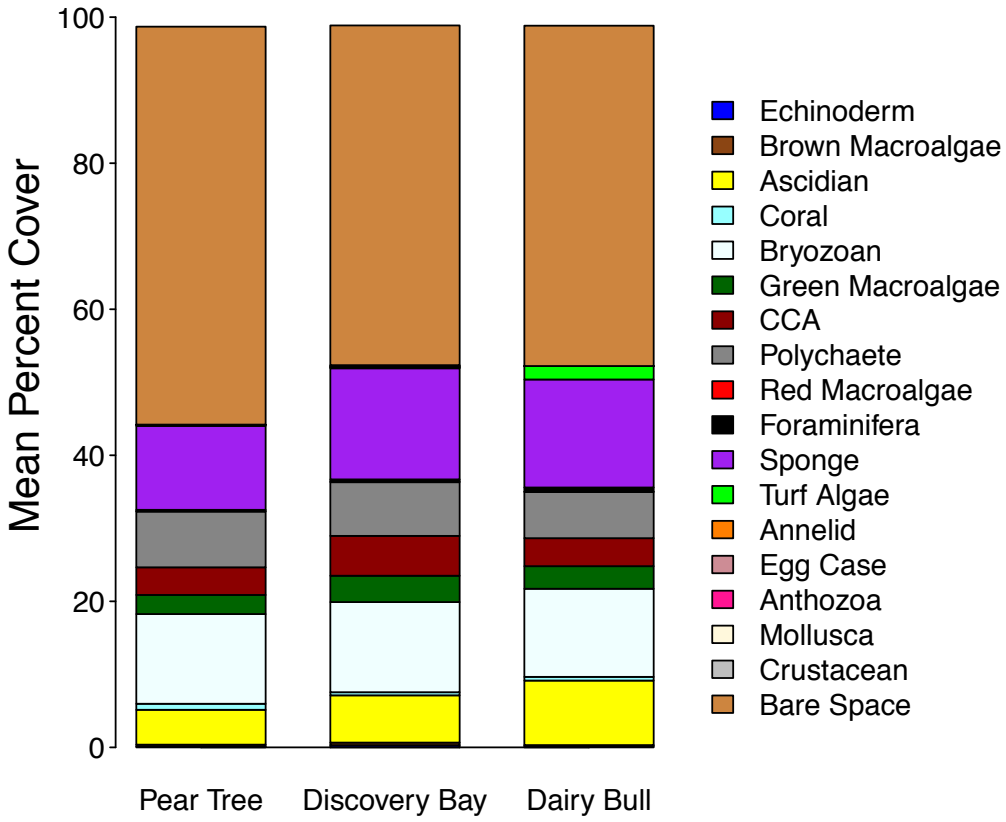

Figure 6. Percent cover of each major taxonomic category on tiles sampled annually at each location.

Table 1. Results from the generalized linear models (GLM) for a) seasonal sponge diversity, b) seasonal sponge percent cover, c) seasonal epibiont diversity and d) seasonal percent cover of bare space, formatted as an analysis of deviance table using the F-test. Asterisks (***) indicate a statistically significant factor.

a) GLM	df	Deviance	Residual df	Residual Deviance	*F*-value	P
Seasonal Sponge Diversity						
Location	2	0.023210	105	1.1458	1.1010	0.336
Depth	1	0.000153	104	1.1456	0.0145	0.904
Season	1	0.059938	103	1.0857	5.6864	0.019***
Residuals	---	---	107	1.1690	---	---
b) GLM	df	Deviance	Residual df	Residual Deviance	*F*-value	P
Seasonal Sponge Percent Cover						
Location	2	0.031264	105	1.5138	1.1071	0.334
Depth	1	0.000016	104	1.5137	0.0012	0.973
Season	1	0.059426	103	1.4543	4.2088	0.043***
Residuals	---	---	107	1.545	---	---
c) GLM	df	Deviance	Residual df	Residual Deviance	*F*-value	P
Seasonal Epibiont Diversity						
Location	2	0.27355	105	4.7716	6.1540	0.003***
Depth	1	0.40134	104	4.3702	18.0576	<0.001***
Season	1	1.91204	103	2.4582	86.0285	<0.001***
Location * Depth	2	0.19276	101	2.2654	4.3365	0.016***
Location * Season	2	0.10663	99	2.1588	2.3989	0.096
Depth * Season	1	0.02388	98	2.1349	1.0744	0.303
Location * Depth * Season	2	0.00126	96	2.1337	0.0283	0.972
Residuals	---	---	107	5.0451	---	---
d) GLM	df	Deviance	Residual df	Residual Deviance	*F*-value	P
Seasonal Bare Space Percent Cover						
Location	2	0.09989	105	3.5395	2.4593	0.091
Depth	1	0.44856	104	3.0909	22.0877	<0.001***
Season	1	0.99921	103	2.0917	49.2028	<0.001***
Residuals	---	---	107	3.6394	---	---

Table 2. Results from the generalized linear models (GLM) for a) annual sponge diversity, b) annual sponge percent cover, c) annual epibiont diversity and d) annual percent cover of bare space, formatted as an analysis of deviance table using the F-test. Asterisks (***) indicate a statistically significant factor.

a) GLM	df	Deviance	Residual df	Residual Deviance	*F*-value	P
Annual Sponge Diversity						
Location	2	0.168678	33	0.39378	6.6686	0.004***
Depth	1	0.000084	32	0.39370	0.0066	0.936
Year	1	0.001633	31	0.39206	0.1291	0.722
Residuals	---	---	35	0.56246	---	---
b) GLM	df	Deviance	Residual df	Residual Deviance	*F*-value	P
Annual Sponge Percent Cover						
Location	2	0.062353	33	0.17661	5.4980	0.009***
Depth	1	0.000007	32	0.17660	0.0012	0.973
Year	1	0.000813	31	0.17579	0.1433	0.708
Residuals	---	---	35	0.23896	---	---
c) GLM	df	Deviance	Residual df	Residual Deviance	*F*-value	P
Annual Epibiont Diversity						
Location	2	0.143144	33	0.87806	2.8190	0.075
Depth	1	0.058026	32	0.82003	2.2855	0.141
Year	1	0.032976	31	0.78706	1.2988	0.263
Residuals	---	---	35	1.02120	---	---
d) GLM	df	Deviance	Residual df	Residual Deviance	*F*-value	P
Annual Bare Space Percent Cover						
Location	2	0.123142	33	0.37549	6.1291	0.006***
Depth	1	0.051935	32	0.32356	5.1699	0.030***
Year	1	0.012142	31	0.31142	1.2087	0.280
Residuals	---	---	35	0.49863	---	---

Table 3. Sponge orders and families identified on recruitment tiles during seasonal and annual assessment are noted by an "X"; presence of sponges found Chapter 1 are also included for comparison. Unidentified sponges (no order or family assignment was possible) are not included.

Order	Family	Seasonal	Annual	Sponges encountered in Chapter 1
Agelasida	Agelasida	X	X	X
	Astroscleridae	X		
Astrophorida	Geodiidae			X
	Pachostrellidae	X	X	
Chondrosida	Chondrillidae	X	X	X
Clathrinida	Clathrinidae		X	
	Leucaltidae	X	X	
Dictyoceratida	Dysideidae	X	X	X
	Irciniidae	X	X	X
	Spongiidae			X
	Thorectidae	X		X
Hadromerida	Clionaidae			X
	Spirastrellidae	X	X	X
	Suberitidae			X
Halichondrida	Axinellidae			X
	Dictyonellidae			X
	Heteroxyidae			X
Haplosclerida	Callyspongidae			X
	Chalinidae	X	X	X
	Niphatidae		X	X
	Petrosiidae	X	X	X
	Phloeodictyidae		X	
Homosclerophorida	Plakinidae	X	X	X
Poecilosclerida	Crambeidae		X	
	Desmacellidae			X
	Hymedesmiidae			X
	Iotrochotidae	X	X	X
	Merliidae		X	
	Microcionidae	X	X	X
	Mycalidae	X	X	X
	Raspailiidae			X
Spirophorida	Tetillidae		X	X
Verongida	Aplysinidae	X	X	X
	TOTAL	16	20	26

Chapter 4

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

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 succession 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. No clear patterns in diversity and percent bare space were found among locations that indicated sediment is the primary driver of community differences. The location with the highest sediment supply had lower diversity and percent cover of organisms inhabiting the cryptic tile sides after 6 months. This pattern did not hold after 18 months when no differences were found by location, and after 30 months, the location with the highest sediment supply was statistically similar in cryptic community diversity and percent cover bare space to the location considered to be the most pristine. 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, although no definite relation to sediment or coastal development was established. The exposed communities were primarily macroalgae, turf and encrusting algae; the location with the highest sediment supply had higher diversity of algae types and lower amounts of turf than the other locations. Although sediment supply differences between these locations may play some role in structuring communities, additional uninvestigated factors are likely influencing the community development at these locations.

Introduction

Coastal development (and the associated change in sediment supply) is an increasingly prominent threat to reef ecosystems, as population growth continues to expand on island nations in the Caribbean (Rogers 1990; Fabricius 2005). In Jamaica, our chosen study region, 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, terrigenous sediment supply to adjacent reefs in northern Jamaica (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, but it is often the juvenile and early developmental stages that are the most susceptible to sediment stress. 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 (Wittenberg and Hunte 1992; Gilmour 1999; Babcock and Smith 2002). 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 corals is important, species other than corals are becoming increasingly dominant on coral reefs (Norström et al. 2009; Bell et al. 2013). 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, 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 (Rogers 1990; Box and Mumby 2007; Birrell et al. 2005). It is therefore crucial to understand how sedimentation impacts the recruitment and succession of reef organisms.

Ecosystem succession and development have been studied for decades. Traditionally observational, these studies have sought to describe the basic successional processes that form communities (Clements 1936; Odum 1969; Connell and Slayter 1977; 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. 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 Margaros 1974; Loya 1976; Pearson 1981; Hughes 1985; 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 (McClanahan 1997; Ceccarelli et al. 2011; Fricke et al. 2011), 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 (Fairfull and Harriott 1999; Ceccarelli et al. 2011), 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, affects certain life stages of organisms, or have time-lagged effects on organism development.

In the study presented here, I 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 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; I hypothesized that the community assemblages and trajectory of successional development would differ between locations as a result. Specifically, I posited that 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 that 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. I expected 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).

Materials and Methods

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 (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) (Figure 1a). Large spur and groove reef tracts are present at each location and begin less than 1 km from the shore, leaving reef organisms susceptible to shoreline alterations and sedimentation. Sediment trap data previously collected at these locations (see Chapter 1; Table 1) demonstrated that Dairy Bull and Discovery Bay experienced low sediment accumulation rates (<3.0 g m^{-2} d^{-1}) regardless of wind speeds; sediment accumulating at these locations was also shown to be primarily carbonate-based material with grain sizes >63 μm, likely derived from resuspension, *Halimeda* debris, foraminiferan particles, and sediment from adjacent sandy grooves. The third location, Pear Tree, is located near a village and tourist resort; sediment accumulation rates were variable depending on the wind speeds (Chapter 1). During low wind events (<10 m s^{-1}), Pear Tree experienced similar sedimentation rates to Dairy Bull and Discovery Bay; however, when wind speeds exceeded 10 m s^{-1}, rates of sediment accumulation on the adjacent reef were two orders of magnitude higher (Chapter 1; Table 1). Sediment deposited at Pear Tree was found to have a significantly higher proportion of insoluble (non-carbonate) material than Discovery Bay and Dairy Bull as well as a higher proportion of silts and clays (grain sizes < 63 μm) (Chapter 1; Westfield 2008). For this study, each location (Pear Tree, Discovery Bay and Dairy Bull) was divided into two sites, an eastern and western, separated by 500 m to create replication within each location; sites within each location were further divided into two distinct depths, 8-10 m and 15-18 m (Figure 1b).

Succession Tiles

Unglazed terra cotta recruitment tiles (12 cm x 12 cm x 1 cm) with a hole (1 cm diameter) drilled through the middle, were oriented horizontally parallel to the reef floor using permanent baseplates as suggested by Mundy (2000). The baseplates, which were corrosion resistant steel plates fastened to coralline rock with plastic screw anchors, had an upward-facing

screw that allowed a single tile to be mounted 3-5 cm above the substrate (Duckworth and Wolff 2008; Chapter 2). Each location had 20 tiles placed in the shallow and in the deep; tiles were distributed between the eastern and western sites (n=10 at each site/depth). Within each site and depth stratum, tiles were divided into three groups. Tile groups were randomly assigned to include either 3 or 4 baseplates that were each separated by a minimum of 1 m; care was taken to ensure that the tile groups were separated from one another by at least 25 m (Figure 1b). The experiment began in early August 2011 when clean, unconditioned tiles were attached to the baseplates and left undisturbed until the first sampling time point six months later (January 2012). During sampling time points, tiles were removed and placed in a custom-made camera frame; *in situ* photographs (Sony Cybershot DSC-T900 housed within a Sony Cybershot Marinepack; 12.1 megapixels) were immediately taken of both sides (exposed = top, cryptic = underside) of each tile. After photographs were taken, tiles were carefully replaced onto their original baseplates in the same orientation and photographed again in the same manner after 18 and 30 months (January 2013 and 2014, respectively).

Image Analysis

To eliminate potential edge effects, photographs were first scaled and then cropped using ImageJ (Abramoff et al. 2004) to remove the outer 1.2 cm of the tiles, resulting in a 9.6 cm x 9.6 cm (92.16 cm^2) section from the original 12 cm x 12 cm surface. These edited photos were then imported into Coral Point Count with Excel extensions (CPCe) (Kohler and Gill 2006), and scaled once more. Each organism was traced to determine area coverage and then identified and grouped into broad taxonomic groups (n=16 categories: bare space, coral, bryozoan, ascidian, sponge, polychaetes worms, other annelids, macroalgae, encrusting algae, turf algae, egg case, echinoderm, foraminifera, crustacean, anthozoa (non-coral), mollusk). In cases where certain taxa (e.g., polychaete worms) were too abundant to be accurately and efficiently traced, all other organisms were traced and the photograph was then re-imported into ImageJ, rescaled and the total area of the overly abundant organism was measured using the Color Threshold tool (see Chapter 2 for detailed image analysis methods).

Data Analysis

For all data analyses, no differences between sites (western vs. eastern) were found within each location; therefore, site data for each location were combined, and only location and depth were used as factors. Additionally, for all analyses of exposed and cryptic sides of tiles that incorporated the 30-month time point, one deep tile group (n=3 tiles) was removed from the Dairy Bull location because an adjacent sand bar shifted onto the tile group between the 18 and 30 month sampling periods, scouring the surface of the tiles and visibly altering the community structure. All univariate analyses were performed using R 2.15.1 (R Development Core Team 2008).

Taxonomic diversity of cryptic and exposed sides of individual tiles was calculated using the Shannon index of diversity (H') for each time point. While the cryptic sides were analyzed at all time points, the exposed sides of tiles were only analyzed at the 18- and 30-month time points because the photos from the 6-month time point were corrupted. After appropriate transformations, analysis was performed for the exposed and cryptic tile sides separately using a two-way ANOVA of diversity as a function of location and depth for each time point to understand overall differences in diversity at 6, 18 and 30 months. Percent cover of major taxa of each of the tile sides was similarly assessed at each time point for differences in location and depth.

Using the software PRIMER 6 (Clarke and Gorley 2006), percent cover data of sessile taxa on the cryptic sides of tiles were fourth-root transformed and a Bray-Curtis dissimilarity matrix was created for differences among sampling time points at each location and depth and these were assessed using a second-stage MDS ordination. The second-stage MDS ordination was constructed by creating a dissimilarity matrix of all the first-stage dissimilarity matrices (Somerfield and Clarke 1995); this technique incorporated the community trajectory throughout all samplings into a single profile and therefore accommodated the repeated measures experimental design (Clarke et al. 2006). A two-way analysis of similarity (ANOSIM) test was then applied to the second-stage similarities (Chapman 2003). The exposed tile sides were not assessed in this manner due to the lack of a 6-month time point; end-stage community differences (30 months) were assessed for the exposed sides by calculating the Bray-Curtis dissimilarity matrix and visualized using an nMDS ordination. The effects of location and depth were tested using a two-way ANOSIM for the exposed sides of tiles.

Results

Cryptic Recruitment Patterns

The most common groups recruiting to the cryptic sides of tiles after 6 months were polychaetes, sponges, bryozoans and macroalgae (Table 3), which each contributed less than 12% to the total areal coverage. Bare space dominated the tiles after only 6 months (Figure 2a); mean bare space at each location ranged from 63.0-81.9% (Table 3). Both location and depth were significant factors affecting percent cover of bare space after 6 months (Table 5a: $F_{(2,112)}$=3.905, P=0.023; $F_{(1,112)}$=9.164, P=0.003, respectively); deep tiles were found to have significantly more bare space than shallow. Pear Tree had significantly more bare space than Discovery Bay (adjusted-P=0.02), but not Dairy Bull (adjusted-P=0.11) at this early stage. The main effects of location and depth were also significant for the diversity of the cryptic community (Table 4a: $F_{(2,112)}$=5.339, P=0.006; $F_{(1,112)}$=11.285, P=0.001, respectively). Tukey HSD pairwise contrasts showed that Pear Tree had significantly lower diversity than Discovery Bay (adjusted-P=0.007) and Dairy Bull (adjusted-P=0.04).

After 18 months, the mean percentage of bare space decreased and ranged from 30-48% across locations and depths (Figure 2b). No significant differences in percent cover of bare space were found among locations (Table 5b); however, depth was a significant factor ($F_{(1,108)}$=14.264, P<0.001). The primary contributors to the shallow community on the cryptic sides after 18 months were sponges (15.4-16.6%), bryozoans (13.6-18.7%), encrusting algae (7.7-13.2%), followed by ascidians (7.7-8.8%) and polychaetes (5.2-8.2%)(Table 3). The deep cryptic community was dominated by sponges (11.9-15.1%), encrusting algae (7.7-10.1%), ascidians (5.3-10.0%), polychaetes (8.2-9.6%) and bryozoans 6.9-9.1%) (Table 3). Overall, diversity increased between the 6-month and 18-month time points but did not statistically differ among locations at this stage; diversity was significantly different by depth after 18 months (Table 4b; $F_{(1,108)}$=12.191, P<0.001), with higher diversity found in the shallows (Table 2).

Few changes in percent cover and diversity occurred between the 18- and 30-month time points, although bare space continued to decrease (Figure 2c), and sponges and bryozoans increased to 17.7-24.8% and 12.2-27.7% cover, respectively (Table 3). Percent cover of bare space was significantly different by location, but not depth, after 30 months ($F_{(2,103)}$=8.284,

P<0.001). Mean (±SD) bare space at Pear Tree was 40.5 ± 18.8% in the shallows and 37.0 ± 16.0% in the deep stratum. Location effects were found in the analysis of cryptic diversity at the 30-month sampling point ($F_{(2,103)}$=4.175, P=0.018, Table 4c); Pear Tree exhibited lower diversity (Table 2), although this was only statistically different from Discovery Bay (adjusted-P=0.014). Throughout many of the sampling periods, mean bare space by location was higher at Pear Tree as compared to the other locations (Figure 2), indicating that overall epibiont recruitment at Pear Tree was lowest. Depth also affected overall recruitment; more bare space remained on tiles positioned at the deep (15-18 m) depth stratum as compared to the shallow (8-10 m) stratum during the 6- and 18-month, although this statistical significance was not found at the final 30-month sampling period.

In general, coral recruitment was low, however there were differences by depth, but not location. No difference in coral recruitment was found after only 6 months, but after 18 and 30 months coral recruitment was significantly higher in the shallow depths (18 months: $F_{(1,108)}$=4.644, P=0.03; 30 months: $F_{(1,103)}$=6.172, P=0.01). Encrusting algae (including CCA), displayed a difference in percent cover at depth during the 6-month time point (shallow was higher; $F_{(1,112)}$=22.849, P<0.001), however no further differences in percent cover were found due to either location or depth at the 18 or 30 month time points. Bryozoan coverage varied by time interval; location was significant at the 6- and 30-month time points (6 months: $F_{(2,112)}$=11.497, P<0.001; 30 month: $F_{(2,103)}$=4.973, P=0.009), but not at 18 months and depth was significant only at the 18-month time point ($F_{(1,108)}$=11.491, P<0.001). Interestingly, no difference in percent cover of turf algae, ascidians or sponges was found at any of the locations and depths at any of the time intervals.

Exposed Surface Succession Patterns

The major taxonomic groups covering the exposed surface of tiles after 18 months was largely limited to turf algae (10.7-61.0%), encrusting algae (21.6-56.9%), and macroalgae (1.6-18.4%); polychaetes also colonized the exposed sides but contributed less than 2.2% to tile cover. Bare space was much lower on the exposed sides of tiles compared to the cryptic sides, largely due to the high percentage of colonization by photosynthetic organisms. The percent cover of bare space (Figure 3a) was statistically different by depth at the 18-month sampling period ($F_{(1,102)}$=15.034, P<0.001, Table 7a) but the main effect of location was not significant;

there was also a significant interaction between location and depth for the percent cover of bare space ($F_{(2,102)}$=5.685, P=0.005, Table 7a). Diversity of the exposed sides of tiles was significantly different by location and depth (Table 6a); exposed tiles at Dairy Bull, which were primarily colonized by turf algae (shallow: 61.0% and deep: 39.3%) after 18 months had significantly lower diversity than tiles at Discovery Bay and Pear Tree (Tukey HSD: P<0.001 for both; see Table 2 for mean diversity values). Tiles in the deep (15-18 m) depth strata had higher diversity after 18 months than those in the shallow (8-10 m) depths ($F_{(1,102)}$=4.378, P=0.039) (see Table 2 for diversity values).

After 30 months, patterns in percent cover of bare space on exposed sides remained similar to those at 18 months (Figure 3b). The main effect of depth was significant ($F_{(1,99)}$=19.844, P<0.001); bare space was lowest overall in the shallows where means ranged from 0.0-9.1% (Table 3). A significant interaction between location and depth was also found ($F_{(2,99)}$=5.018, P=0.008) (Table7b). The dominant organisms on the exposed tiles were, once again, encrusting algae (52.9-73.9%), turf algae (0.0-40.7%) and macroalgae (1.9-17.9%); sponges, polychaetes and coral were also found (one large *Siderastrea siderans* colony was found on a single Pear Tree tile) (Table 3). Dairy Bull tiles had significantly higher turf algae coverage (11.0-41.7%) compared to Discovery Bay (0-14.4%) and Pear Tree (0.6-22.4%) (Tukey HSD: P=0.002 and P=0.02, respectively). Diversity was different among locations ($F_{(2,99)}$=4.257, P=0.017) but not depth (Table 6b); Pear Tree diversity was significantly higher diversity than Dairy Bull (Tukey HSD: P=0.012) but not Discovery Bay (Tukey HSD: P=0.39).

After 30 months, encrusting algae (including CCA) was the dominant spatial colonizer of the exposed tile sides at all locations, means ranged from 52.9-73.9% (Table 3). Macroalgae were the next most dominant group on tiles (Table 3); after 30 months, percent cover of macroalgae was significantly lower at Dairy Bull than either Pear Tree or Discovery Bay (Tukey HSD: P<0.001 and P=0.024, respectively). Dairy Bull had the highest amount of turf coverage at both time points compared with Discovery Bay and Pear Tree (18 months: Tukey HSD: P<0.001 and P=0.002 and 30 months: Tukey HSD: P=0.002 and P=0.015, respectively); turf coverage was significantly higher in the shallows after 30 months ($F_{(1,99)}$=22.469, P<0.001) than in the deeper strata. Polychaete cover was significantly different by location ($F_{(2,102)}$=4.544, P=0.013) and depth ($F_{(1,102)}$=12.365, P<0.001) at the 18-month time point, but only depth was significant

at 30 months ($F_{(1,99)}$=8.734, P=0.004). No differences by depth or location were found for encrusting algae, sponges, or corals at the final sampling time point (30 months). An example of succession on the cryptic and exposed sides of individual tiles after 6, 18, and 30 months placed in the shallows of Discovery Bay is shown in Figure 4.

Multivariate Community Analysis

The cryptic community assemblages were compared at each location and depth through time using second-stage nMDS ordination (Somerfield and Clarke 1995; Clarke et al. 2006); ANOSIM revealed that the cryptic community trajectory for the Pear Tree deep tiles were significantly different than all other locations and depths (R=1.0, P<0.05). Consequently, two distinct clusters of cryptic community development were identified (one-way ANOSIM, R=1.0, P<0.001; Figure 5a); one cluster was composed only of the Pear Tree deep tile groups and one Pear Tree shallow tile group. Exposed community composition was visualized using a first-stage nMDS ordination at the 30-month sampling time point (Figure 5b) and an ANOSIM revealed that the deep Pear Tree exposed community was significantly different (R=0.514, P=0.01) than the other tile communities.

Discussion

In general, the patterns of succession were consistent at all locations. Fast-growing, colonial organisms such as ascidians, bryozoans and sponges, along with polychaetes, rapidly colonized the cryptic sides of tiles after just 6 months. After 18 months, bare space on the cryptic sides had decreased by roughly 50% from the 6-month time point (Figure 2b), and was largely replaced by sponges and bryozoans. One particularly striking difference among the locations was the amount of bare space still remaining on the cryptic sides of tiles after 30 months at Pear Tree (40.5 ± 18.8%; Figure 2c). Turf algae, encrusting algae, and macroalgae dominated the exposed sides with very few invertebrates present even after 30 months (Table 3). Few slow-growing species, such as corals or gorgonians, were found on any of the settlement tiles regardless of location, even after 30 months, indicating that these communities are still considered developmentally 'immature' and may not have achieved climax communities.

Cryptic Community Succession

Although successional patterns for sessile reef organisms have not been evaluated as widely as coral and macroalgae, the trends in our data are similar to those reported in other studies. In a successional study of a sub-tropical reef in southwestern Australia, Fairfull and Harriott (1999) determined that bryozoans dominated (>50% coverage) the cryptic undersides of tiles during the first 6 months. In their study, bryozoans, which maintained over 40% coverage at all times, decreased on the cryptic sides and were replaced by hydrozoans, ascidians and sponges after 9 months; this pattern held until the termination of their experiment at 29 months (Fairfull and Harriott 1999). Comparison of recruitment on a natural and artificial reef in the Red Sea showed that, again, bryozoans and serpulid worms were the most abundant recruits to experimental substrata during each of the 6-, 12- and 18-month monitoring time points (Perkol-Finkel and Benayahu 2007). Bryozoans dominated in our study as well (Table 3); however, sponges were equally adept at colonizing and maintaining spatial coverage on the tiles regardless of location or depth.

In their classic studies, Jackson and Winston (1982) observed cryptic communities inhabiting the undersides of foliaceous corals in Jamaica. They found a similar composition of organisms described in this study; however, the percent coverage of bare space was less than 1%

on the corals examined in their study (Jackson and Winston 1982). In a follow-up study of recruitment over three years, Winston and Jackson (1984) found that sponges and bryozoans, which together accounted for 25% coverage of tiles at 18 months in this study, were either absent or had very low percent cover (<10%) on their fouling plates after 18 months. They suggested this discrepancy in sponge and bryozoan coverage between the observed cryptic community composition (where sponges covered 18-51% and bryozoans 5-25%; Jackson and Winston 1982) and the 3-year recruitment study (Winston and Jackson 1984) was evidence that the two taxa are adept spatial competitors, and as such are expected to be highly abundant on older substrata (such as the coral), but relatively absent on younger substrata (recruitment tiles). Our studies do not reflect the same delay in spatial dominance, as bryozoans and sponges together cover ~10% of the available space after just 6 months, between 20-30% after 18 months and nearly 50% after 30 months on cryptic sides (Table 3). The differences in bryozoan and sponge cover between the 3-year recruitment study performed by Winston and Jackson in 1984 and the present study may be an artifact of the different tile substrates used; Winston and Jackson (1984) used asbestos-cement sheeting, while the current study used unglazed ceramic terra cotta tiles. The comparison of recruitment tile substrates has been well evaluated in the literature (Harriot and Fisk 1987; Mundy 2000; Field et al. 2007) and although no individual study has compared asbestos concrete (likely because asbestos is no longer added to concrete) and terra cotta tiles, several studies have found that ceramic terra cotta tiles impart a smaller recruitment bias (Harriot and Fisk 1987; Field et al. 2007, Burt et al. 2009) than concrete, bricks, and coral slabs.

Exposed Community Succession

Studies of algal succession on reefs are more common than studies that investigate sessile invertebrate community development. Unfortunately, the lack of a 6-month time point in this study for the exposed sides of tiles limited our ability to make direct comparisons to other studies, except in the late-stage successional time points. This limitation in our data also prevented the detection of important patterns that might have occurred in the initial colonization stages (e.g. any differences in initial settlement and larval supply may have been missed), decreasing our ability to discern differences between locations and depths in these early-stage communities. After 30 months, macroalgae coverage (such as *Sargassum* sp., *Lobophora* sp. and *Dictyota* sp.) was highest at Pear Tree, followed by Discovery Bay and Dairy Bull. In contrast,

higher turf algae coverage was found at Dairy Bull compared to Discovery Bay and Pear Tree; no location differences were found for the encrusting algae (mostly CCA).

In a previous study of algal succession in Curacao, Fricke et al. (2011) found that communities were largely dominated by cyanobacteria (~50% cover) and the red alga, *Herposiphonia* sp. after 333 days. While the algae was not identified to the taxonomic level that Fricke and colleagues did, there were no cyanobacteria mats found on the exposed tiles at any of our sampling periods. Another study compared algal succession in Kenyan reefs outside of and within marine parks (McClanahan 1997). McClanahan (1997) found that in marine parks where herbivorous fish were present in high abundance, early algal succession was comprised almost entirely of turf algae, but over time encrusting algae (primarily CCA) increased in coverage, while turf decreased. In contrast, reefs that were heavily fished and primarily grazed by sea urchins had consistent coverage of turf algae throughout all six time-points sampled in the 450-day study.

A survey of reef fish by Loh and Pawlik (2014) along the north coast of Jamaica found that fish abundances are similar, albeit severely depressed, at all three of our selected locations. McClanahan (1997) presented evidence that herbivores (fish vs. urchins) influence algal succession on reefs; however, on overfished reefs with low urchin abundance, such as those in Jamaica (Moses and Bonem 2001), algal succession is likely driven by alternate environmental factors, such as nutrient loading, light availability, or sedimentation. In an analysis of the molar ratio of carbon to nitrogen (C:N) in *Sargassum* sp. tissues (n=5 collected at each location and depth), there were no differences in the C:N ratio among locations and/or depths. The similar C:N ratios suggest that there were no differences in *Sargassum* sp. tissue nitrogen enrichment, an indicator of elevated allochthonous nutrients in the water column that has previously been used in Jamaica (LaPointe 1997).

Chapter 1 found no statistical differences in light among locations at each depth, although differences in total suspended solids were found in January 2012, with Pear Tree exhibiting the highest concentrations, followed by Dairy Bull and finally Discovery Bay. Working in the Great Barrier Reef, Schaffelke et al. (2005) found that turbid areas had higher abundances of *Sargassum* sp. than areas with less turbidity. At the location with the highest sediment supply in this study (Pear Tree), higher macroalgal growth and lower cover of turf algae (but not

significantly higher than Discovery Bay, which has low sedimentation) were observed. Diversity of organisms (primarily various algae types) was highest at Pear Tree compared to Dairy Bull after both 18 and 30 months. No difference in the coverage of encrusting algae (56-72%) was found among the locations and depths. Although increased sedimentation has been correlated with higher coverage of macroalgae in previous studies (Scheffelke et al. 2005), there may be additional, unidentified differences driving the composition of algae in this study. Moreover, since no initial settlement data from the 6-month time point was analyzed, propagule supply cannot be eliminated as a driver of differences in algal communities on the exposed tile sides.

Community Composition

At each location, the cryptic community assemblages and their relative contribution to percent cover were similar between the 18 and 30-month samplings, indicating that, once established, the organisms and their communities do not rapidly change. This may also suggest that the climax community has been achieved, despite being composed primarily of fast-growing, r-selected organisms, which are not typically characteristic of climax communities (Odum 1969). However, there is evidence that the prevalence of r-selected organisms may be symptomatic of damaged reefs. Jessen et al. (2014) experimentally simulated a eutrophied, overfished reef in the Red Sea and found that fast-growing colonizers such as bryozoans, bivalves and polychaetes monopolized caged recruitment tiles exposed to increased nutrients. Alternatively, 30 months may be too short a duration to achieve a climax community even under ideal environmental conditions and the stabilization of the space occupiers that was observed may have remained asymptotic for years until lower probability recruitment of slow-growing, K-selected organisms occurred. For example, Tanner et al. (1994) modeled reef community dynamics and succession and found that while species diversity peaked after 2-6 years, the community equilibrium was not achieved until 10-15 years.

The most striking difference among locations was the amount of bare space remaining on the cryptic undersides of tiles over the course of 30 months. Space is a limited resource on coral reefs and yet the cryptic sides of tiles remained largely uncolonized (37-40.5%) at Pear Tree (Figure 2c). This suggests that the organisms in this area may not be reproducing at rates similar to the other locations, that post-settlement mortality was higher (as posited in Chapter 2), or some small-scale inhibitory process (such as allelopathy) was occurring. Our sampling times

(separated by 6 and 12 months) and style (*in situ* photographs only, no laboratory/stereoscope inspection) did not allow us to discern specific mortality rates; however, in Chapter 2, post-settlement mortality was implicated as a likely driver of recruitment differences. Another explanation may be that the elevated macroalgal growth on the exposed sides led to reduced recruitment on the cryptic sides of tiles. Many macroalgae have been shown to have detrimental impacts on invertebrate settlement (Kuffner et al. 2006; Box and Mumby 2007; Arnold et al. 2010) due to allelopathic interactions, physical interruption of settling, or other unidentified inhibitory effects. The amount of macroalgae on the exposed sides of tiles does not seem to be related to the amount of bare space on the cryptic sides. The exposed sides of tiles in the shallows at Discovery Bay and Pear Tree have similar macroalgal coverages after 30 months (16-17%), yet bare space on the cryptic sides is 22.2% at Discovery Bay and 40.5% at Pear Tree (Table 3), suggesting that macroalgae cover on the exposed tile side was not related to recruitment on the cryptic sides.

The overall trajectory of community change may be a symptom of underlying differences in environmental stressors among different locations. The community trajectory could not be evaluated for the exposed tile communities, but differences were found among the cryptic community trajectories. Pear Tree deep tiles had a different community trajectory than the other locations and depths over the course of 30 months (Figure 5a), and while there may be multiple explanations for differing community development, I hypothesized that these differences may be attributable to sedimentation. To support this hypothesis, I took advantage of the natural sedimentation event that occurred during our study when a sand bar shifted and engulfed one of the Dairy Bull deep tile groups and reanalyzed the data incorporating this tile group. Interestingly, the resulting community of the 'sedimented' Dairy Bull tile group is more closely related to those tiles found at 15-18 m in Pear Tree (Figure 6). However, two of the shallow Pear Tree cryptic communities, despite also experiencing episodic sediment deposition, do not group with the Pear Tree deep tiles and 'sedimented' Dairy Bull tile; this strongly suggests that although sediment may play some role in altering communities, additional uninvestigated factors are likely influencing the community development at these locations.

Recruitment and succession are just one aspect of community health, and while they are not the only components that can be measured to determine whether a stressor is impacting the

current and future reef communities, they are often more integrative than surveys of older, preexisting populations. This study focused on the community development as well as the diversity and percent cover of organisms over a period of 30 months to resolve whether sedimentation is impacting the overall ecosystem health at 3 locations along the north coast of Jamaica. No definitive patterns of diversity, percent cover or community trajectory for either the exposed or cryptic tile sides were found to suggest that sedimentation is the primary driver of differences in community development at these locations.

References

Abramoff MD, et al. (2004) Image processing with ImageJ. *Biophotonics International* 11:36-42

Alleyne D, Boxill I (2003) The impact of crime on tourist arrivals in Jamaica. *International Journal of Tourism Research* 5:381-391

Arnold SN, et al. (2010) Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology Progress Series* 414:91-105

Babcock R, Smith L (2002) Effects of sedimentation on coral settlement and survivorship. In: Kasim Moosa MK, Soemodihardjo S, Nontji A, Soegiarto A, Romimohtarto K, Sukarno, Suharsono (Eds.) *Proceedings of the Ninth International Coral Reef Symposium, Bali, Indonesia, October 23–27, 2000*. *Ministry of Environment, the Indonesian Institute of Sciences and the International Society for Reef Studies*, pp. 245–248

Bell JJ, et al. (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology* 19:2613-2624

Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin* 51:408-414

Burt J, Bartholomew A, Bauman A, Saif A, Sale PF (2009) Coral recruitment and early benthic community development on several materials used in the construction of artificial reefs and breakwaters. *Journal of Experimental Marine Biology and Ecology* 373:72-78

Box SJ, Mumby PJ (2007) Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Marine Ecology Progress Series* 342:139-149

Ceccarelli DM, et al. (2011) Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. *Journal of Experimental Marine Biology and Ecology* 399:60-67

Chapman MG (2003) The use of sandstone blocks to test hypotheses about colonization of intertidal boulders. *Journal of the Marine Biological Association of the UK* 83:415-423

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Clarke KR, et al. (2006) Exploring interactions by second-stage community analyses. *Journal of Experimental Marine Biology and Ecology* 338:179-192

Clements FE (1936) Nature and structure of the climax. *Journal of Ecology* 24:252-284

Connell JH, Slayter RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 1119-1144

Duckworth AR, Wolff CWW (2008) Ecological role and potential value of sponges to Torres Strait. *Annual Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre and Australian Institute of Marine Science*. 49 p.

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50:125-146

Fabricius KE, et al. (2003) Effects of transparent exopolymer particles and muddy terrigenous sediments on the survival of hard coral recruits. *Estuarine, Coastal and Shelf Science* 57:613-621

Fairfull SJL, Harriott VJ (1999) Succession, space and coral recruitment in a subtropical fouling community. *Marine and Freshwater Research* 50:235-242

Field SN, Glassom D, Bythell J (2007) Effects of artificial settlement plate materials and methods of deployment on the sessile epibenthic community development in a tropical environment. *Coral Reefs* 26:279-289

Fricke A, et al. (2011) Succession patterns in algal turf vegetation on a Caribbean coral reef. *Botanica Marina* 54:111-126

Gilmour J (1999) Experimental investigation into the effects of suspended sediment on fertilisation, larval survival, and settlement in a scleractinian coral. *Marine Biology* 135:451-462

Grigg RW, Maragos JE (1974) Recolonization of hermatypic corals on submerged lava flows in Hawaii. *Ecology* 55:387-395

Harriott VJ, Fisk DA (1987) A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. *Marine Ecology Progress Series* 37:201-208

Hughes TP (1985) Life histories and population dynamics of early successional corals. In: Gabrie C, Salvat B (Eds.) *The Fifth International Coral Reef Congress, ICRS*, pp.101-106

Hunte W, Wittenberg M (1992) Effects of eutrophication and sedimentation on juvenile corals II. Settlement. *Marine Biology* 114:625-631

Ilan M Abelson A (1995) The life of a sponge in a sandy lagoon. *Biological Bulletin* 189:363-369

Irving AD, Connell SD (2002) Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages. *Marine Ecology Progress Series* 245:83-91

Jackson JBC, Winston JE (1982) Ecology of cryptic coral reef communities. I. Distribution and abundance of major groups of encrusting organisms. *Journal of Experimental Marine Biology and Ecology* 57:135-147

Jessen C et al. (2014) *In situ* effects of simulated overfishing and eutrophication on settlement of benthic coral reef invertebrates in the Central Red Sea. *PeerJ* 2:e339; DOI 10.7717/peerj.339

Kirk KL (1991) Inorganic particles alter competition in grazing plankton: the role of selective feeding. *Ecology*, 915-923

Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences* 32:1259-1269

Kuffner IB, et al. (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series* 323:107-117

Land LS (1973) Holocene meteoric dolomitization of Pleistocene limestones, North Jamaica. *Sedimentology* 20:411-424

Lapointe BE (1997) Nutrient thresholds for bottom‑up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography* 42:1119-1131

Loh TL, Pawlik JR (2014) Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. *Proceedings of the National Academy of Sciences* USA 111:4151-4156

Loya Y (1976) Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology* 57: 278-289

Maldonado M, et al. (2008) Effects of sediment on the survival of asexually produced sponge recruits. *Marine Biology* 154:631-641

McClanahan TR (1997) Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. *Journal of Experimental Marine Biology and Ecology* 218:77-102

McClanahan TR, Obura D (1997) Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology* 209:103-122

Moses CS, Bonem RM (2001) Recent population dynamics of *Diadema antillarum* and *Tripneustes ventricosus* along the north coast of Jamaica, W.I. *Bulletin of Marine Science* 68:327-336

Mundy CN (2000) An appraisal of methods used in coral recruitment studies. *Coral Reefs* 19:124-131

Nickel M (2004) Kinetics and rhythm of body contractions in the sponge *Tethya wilhelma* (Porifera: Demospongiae). *Journal of Experimental Biology* 207:4515-4524

Norström AV, et al. (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Marine Ecology Progress Series* 376:295-306

Odum EP (1969) The strategy of ecosystem development. *Science* 164:262-270

Pearson RG (1981) Recovery and recolonization of coral reefs. *Marine Ecology Progress Series* 4:105-122

Perkol-Finkel S, Benayahu Y (2007) Differential recruitment of benthic communities on neighboring artificial and natural reefs. *Journal of Experimental Marine Biology and Ecology* 340:25-39

Phillipp E, Fabricius KE (2003) Photophysiological stress in scleractinian corals in response to short-term sedimentation. *Journal of Experimental Marine Biology and Ecology*. 287:57-78

R Development Core Team (2008) R: A language and environment for statistical computing In: Computing RFfS (ed), Vienna, Austria

Rogers C (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62:185-202

Sandin SA, Sala E (2012) Using successional theory to measure marine ecosystem health. *Evolutionary Ecology* 26:435-448

Schaffelke B, et al. (2005) Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. *Marine Pollution Bulletin* 51:279-296

Somerfield PJ, Clarke K R (1995) Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series* 127:113-119

Sousa WP (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49:227-254

Tanner JE, et al. (1994) Species coexistence, keystone species, and succession: a sensitivity analysis. *Ecology* 75:2204-2219

Torre L, et al. (2012) Respiratory responses of three Antarctic ascidians and a sea pen to increased sediment concentrations. *Polar Biology* 35:1743-1748

Underwood A (1994) Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. *Journal of the Marine Biological Association of the UK* 74:563-584

Westfield I (2008) Geochemical fingerprinting of sediments on the Pear Tree Bottom Reef, near Runaway Bay, Jamaica. Masters Thesis, Department of Geology, Baylor University, Waco, TX, USA

Winston JE, Jackson JBC (1984) Ecology of cryptic coral reef communities. IV. Community development and life histories of encrusting cheilostome byrozoa. *Journal of Experimental Marine Biology and Ecology* 76:1-21

Wittenberg M, Hunte W (1992) Effects of eutrophication and sedimentation on juvenile corals I. Abundance, mortality and community structure. *Marine Biology* 112:131-138

Zacharias MA, Roff JC (2001) Use of focal species in marine conservation and management: a review and critique. *Aquatic Conservation: Marine and Freshwater Ecosystems* 11:59-76

Figures and Tables

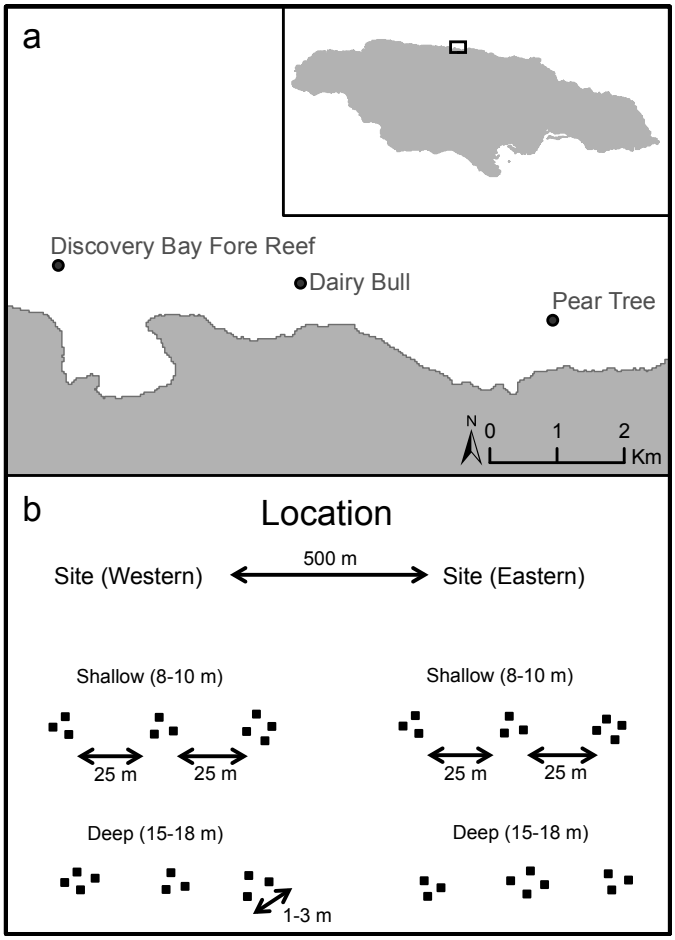

Figure 1 a) Map of the three study locations along the north coast of Jamaica. Filled circles denote locations: Discovery Bay fore reef (N 18.473, W 77.412), Dairy Bull (N 18.471, W 77.379) and Pear Tree (N 18.465, W 77.343). b) Schematic of the tile layout at one location. Each location was divided into two sites, an eastern and western, that were separated by >500 m; sites were further divided into two depths, shallow: 8-10 m and deep: 15-18 m. At each depth, there were three tile groups, which were >25 m apart from one another. Each tile group had either 3 or 4 tiles, for a total of 10 tiles at each site/depth combination. Filled squares denote individual tiles; at each of the locations there were a total of 40 tiles.

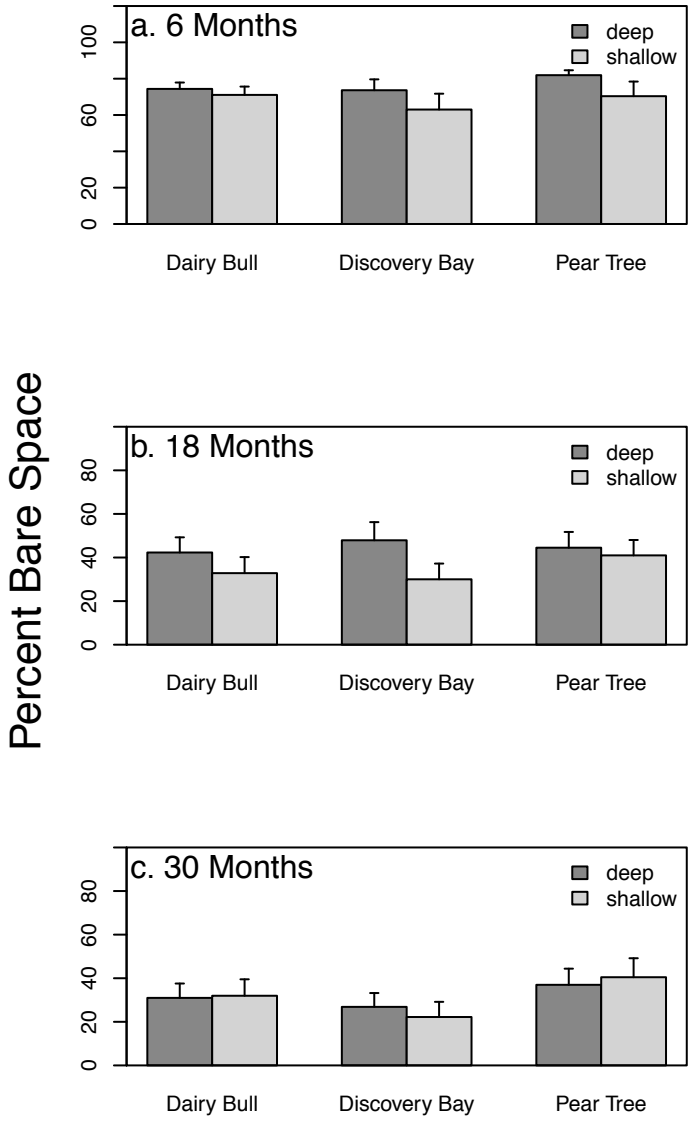

Figure 2. Mean percent bare space (error bars represent 1 standard deviation of the mean) on the cryptic tiles at each location and depth combination after a) 6 months b) 18 months and c) 30 months.

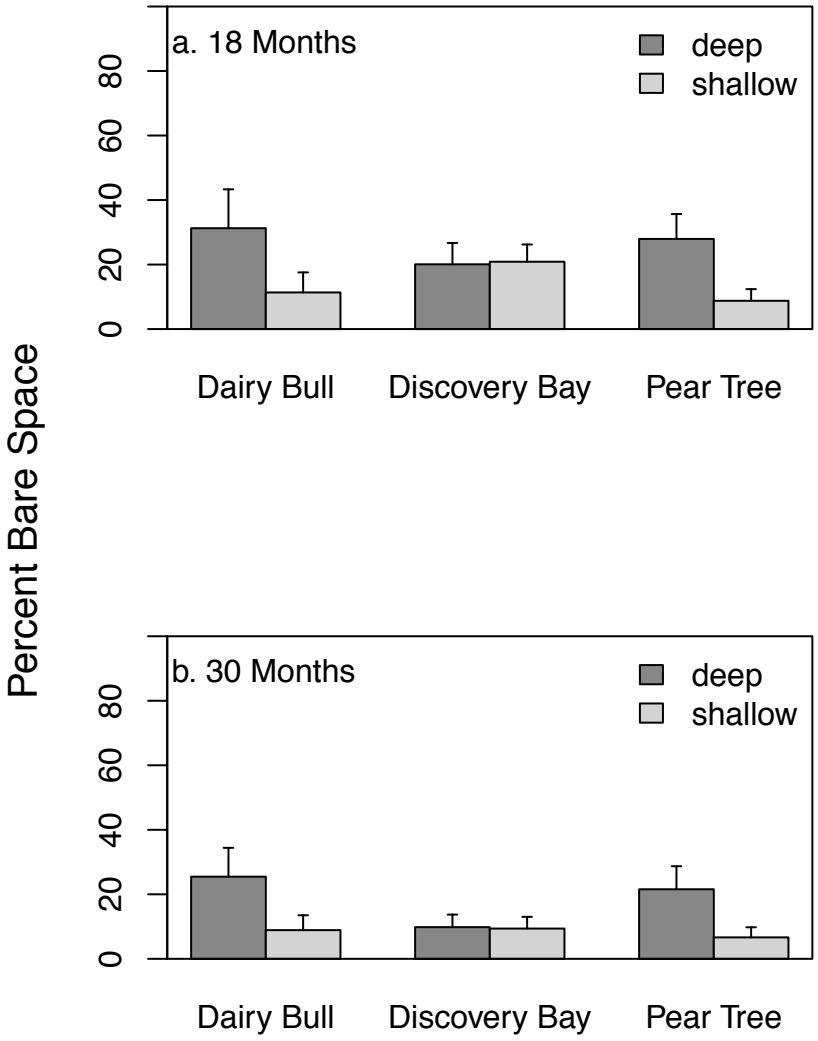

Figure 3. Mean percent bare space (error bars represent 1 standard deviation of the mean) on the exposed tile sides at each location and depth combination after a) 18 months and b) 30 months.

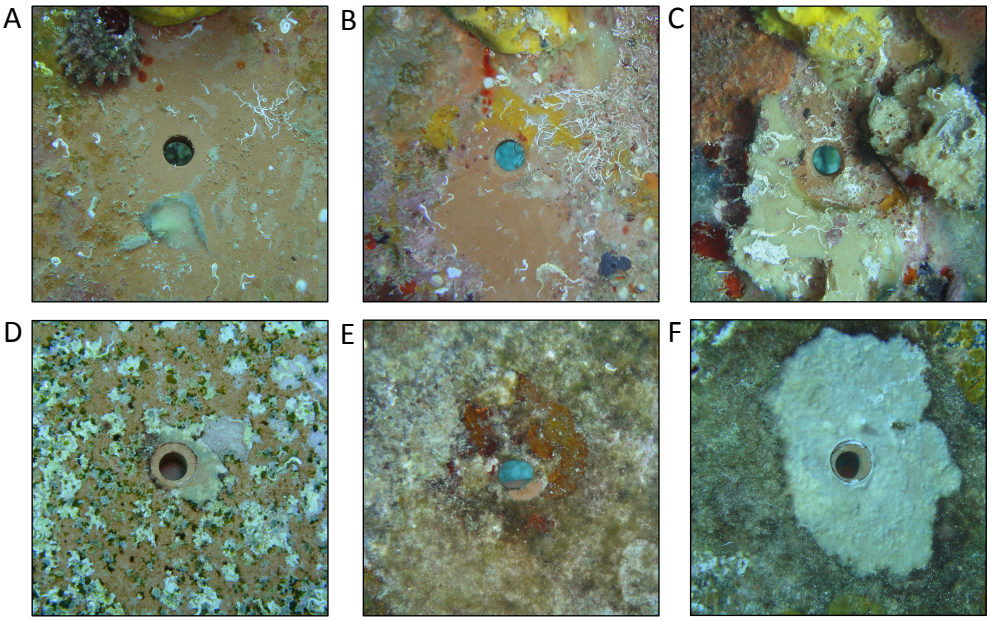

Figure 4. A-C: Succession of cryptic community at Discovery Bay in the shallow depth (8-10m); photos are of an individual tile after A) 6 months, B) 18 months, and C) 30 months. D-F: Successional changes of the exposed community at Discovery Bay in the shallow depth (8-10 m); photos are of an individual tile after D) 6 months, E) 18 months, and F) 30 months.

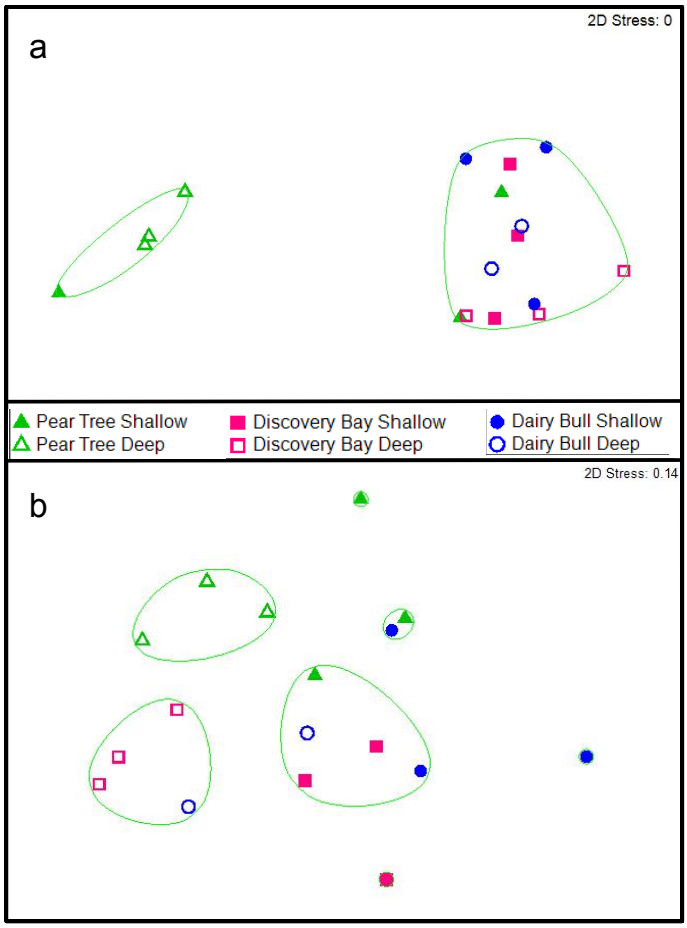

Figure 5 a) Second-stage MDS ordination of the pairwise similarities between first-stage matrices of Bray-Curtis dissimilarities (Clarke et al. 2006) of percent cover of taxonomic groups on tile groups found at each location and depth. Each point represents the profile of one tile group over all three sampling periods compressed into one point (second-stage). Lines around points indicate 0.9 correlation between tile groups. b) A first-stage nMDS plot of Bray-Curtis dissimilarities of exposed tile assemblages after 30 months at Pear Tree (triangles), Discovery Bay (squares) and Dairy Bull (circles). Lines around points indicate 80% (0.8) similarity between tile groups. Each point represents a group of tiles, which consisted of either 3 or 4 tiles; one Dairy Bull tile group from the deep is not represented due to an unplanned sedimentation event that required its removal from the analysis.

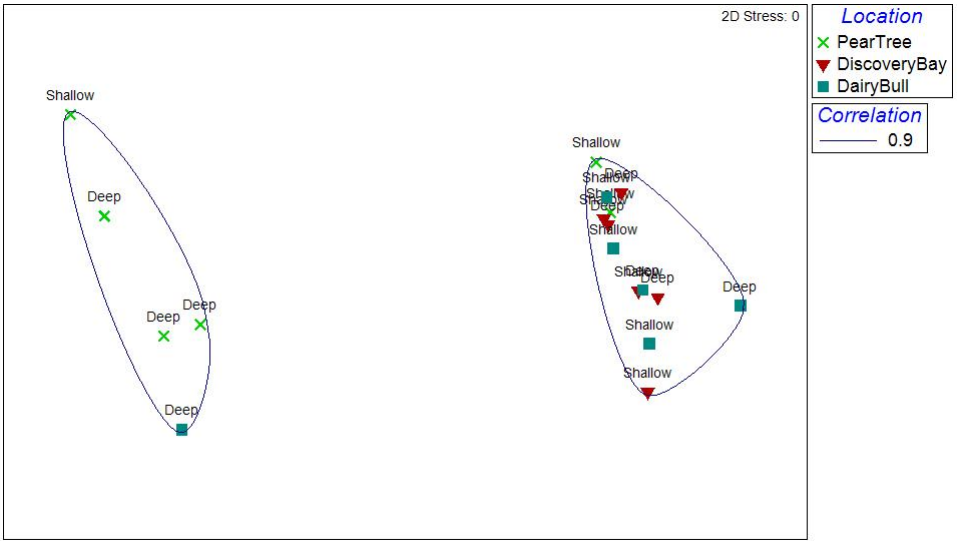

Figure 6. Second-stage MDS ordination of the pairwise similarities between first-stage matrices of Bray-Curtis dissimilarities (Clarke et al. 2006) of percent cover of taxonomic groups on tile groups found at each location and depth. The deep Dairy Bull tile group that was subjected to an unplanned sedimentation event when a sandbar shifted onto it was included in this analysis and clusters significantly with the Pear Tree deep tiles (and one shallow Pear Tree tile group). Lines around points include 0.9 correlation between tile groups.

Table 1. Sediment accumulation and size fractionation data from January 2012 at each of the three study locations. Sediment traps (n=3) were placed at each site/depth combination per location (n=12 total at each location). Mean (± 1 SD) sediment accumulation (g m^{-2} d^{-1}) are shown for each location, and the fraction of each size class is given in mean percentage of total sample (± 1 SD). Table adapted from Chapter 1.

		Pear Tree		Discovery Bay		Dairy Bull	
		Shallow (8-10 m)	Deep (15-18 m)	Shallow (8-10 m)	Deep (15-18 m)	Shallow (8-10 m)	Deep (15-18 m)
Total Sediment Accumulation (g m^{-2} d^{-1})		30.6 ± 22.8	14.5 ± 4.7	10.2 ± 7.4	4.8 ± 3.0	11.4 ± 4.9	7.0 ± 5.8
Size Fractionation of Sediment	<63µm	49.8 ± 21.9 %	48.3 ± 24.0 %	30.7 ± 19.7 %	3.7 ± 5.7 %	22.0 ± 13.5 %	19.7 ± 9.7 %
	63-500µm	47.7 ± 21.2 %	36.7 ± 16.9 %	44.9 ± 9.6 %	62.4 ± 28.1 %	63.4 ± 16.6 %	78.0 ± 8.2 %
	>500µm	2.4 ± 1.1 %	14.9 ± 18.0 %	24.5 ± 12.8 %	33.9 ± 26.2 %	12.7 ± 10.7 %	2.3 ± 3.3 %

Table 2. Mean (± 1 SD) Shannon diversity index (H') values for each location/depth combination over all three sampling time points for the cryptic and exposed sides of tiles. The 6-month time point for the exposed tiles is missing due to corrupted data files.

Side	Location	Depth	6 months	18 months	30 months
Cryptic	Pear Tree	8-10 m	0.90 ± 0.37	1.57 ± 0.30	1.37 ± 0.42
		15-18 m	0.63 ± 0.16	1.49 ± 0.23	1.41 ± 0.21
	Discovery Bay	8-10 m	1.06 ± 0.32	1.61 ± 0.25	1.54 ± 0.31
		15-18 m	0.89 ± 0.35	1.37 ± 0.31	1.57 ± 0.25
	Dairy Bull	8-10 m	0.97 ± 0.25	1.48 ± 0.39	1.46 ± 0.44
		15-18 m	0.88 ± 0.21	1.40 ± 0.28	1.50 ± 0.24
Exposed	Pear Tree	8-10 m	--	0.93 ± 0.21	0.89 ± 0.40
		15-18 m	--	1.02 ± 0.21	0.99 ± 0.26
	Discovery Bay	8-10 m	--	0.94 ± 0.32	0.88 ± 0.34
		15-18 m	--	1.00 ± 0.14	0.81 ± 0.31
	Dairy Bull	8-10 m	--	0.55 ± 0.35	0.64 ± 0.36
		15-18 m	--	0.72 ± 0.27	0.81 ± 0.27

Table 3. Mean (± 1 SD) percent cover of major taxonomic groupings from the cryptic and exposed sides of tiles.

Side	Time Point	Location	Depth	Bare Space	Coral	Ascidian	Sponge	Polychaetes	Macroalgae	Encrusting Algae	Bryozoan	Turf Algae	Other
Cryptic	6 months	Pear Tree	8-10 m	70.4 ± 18.4	0.38 ± 0.61	3.2 ± 5.3	6.3 ± 13.8	10.5 ± 7.3	4.5 ± 4.2	1.4 ± 2.4	2.2 ± 3.9	0 ± 0	0.01 ± 0.03
			15-18 m	81.9 ± 6.0	0.1 ± 0.12	1.4 ± 2.3	1.0 ±1.9	11.7 ± 6.1	1.7 ± 2.5	0.6 ± 0.8	0.6 ± 1.2	0 ± 0	0.06 ± 0.24
		Discovery Bay	8-10 m	63.0 ± 19.4	0.5 ± 0.84	2.6 ± 5.8	7.0 ± 20.0	6.6 ± 4.7	8.5 ± 9.2	3.4 ± 3.3	6.9 ± 7.4	0 ± 0	0.4 ± 1.4
			15-18 m	73.6 ± 13.7	0.31 ± 0.7	3.0 ± 4.1	5.6 ± 8.2	7.9 ± 4.2	4.6 ± 5.6	0.2 ± 0.4	3.6 ± 4.8	0 ± 0	0.01 ± 0.02
		Dairy Bull	8-10 m	71.1 ± 10.4	0.3 ± 0.6	2.2 ± 4.4	4.2 ± 7.6	8.3 ± 3.9	4.0 ±5.2	2.4 ± 3.0	6.1 ± 7.1	0.2 ± 0.7	0.07 ± 0.1
			15-18 m	74.4 ± 8.0	0.3 ± 0.4	1.8 ± 3.4	2.7 ± 4.9	10.0 ± 3.6	3.2 ± 4.2	1.0 ± 1.4	5.0 ± 5.1	0 ± 0	0.7 ± 3.1
	18 months	Pear Tree	8-10 m	40.1 ± 14.9	1.4 ± 2.4	7.7 ± 5.3	16.6 ± 19.5	5.2 ± 2.9	4.2 ± 2.8	7.7 ± 6.8	13.6 ± 11.1	0.3 ± 0.7	1.2 ± 0.9
			15-18 m	44.4 ± 16.5	0.26 ± 0.4	9.6 ± 9.4	12.1 ± 13.2	8.2 ± 2.8	4.7 ± 5.6	9.8 ± 8.2	9.1 ± 9.1	0 ± 0	0.6 ± 1.3
		Discovery Bay	8-10 m	30.0 ± 16.1	0.42 ± 0.43	8.7 ± 8.5	15.4 ± 17.6	6.7 ± 4.1	5.6 ± 6.8	10.7 ± 8.3	18.7 ± 17.2	0.07 ± 0.3	2.3 ± 2.1
			15-18 m	47.9 ± 19.0	0.34 ± 1.0	5.3 ± 5.5	15.1 ± 17.5	9.3 ± 4.8	4.8 ± 7.1	7.7 ± 9.1	7.3 ± 7.6	0 ± 0	1.1 ± 1.2
		Dairy Bull	8-10 m	32.8 ± 16.8	0.31 ± 0.46	8.8 ± 10.7	16.0 ± 23.7	8.2 ± 5.8	2.4 ± 2.9	13.2 ± 16.0	14.3 ± 12.9	0 ± 0	2.6 ± 1.9
			15-18 m	44.5 ± 15.1	0.43 ± 0.45	10.0 ± 12.3	11.9 ± 18.4	9.6 ± 4.6	2.8 ± 2.6	10.1 ± 15.0	6.9 ± 8.9	0 ± 0	2.8 ± 4.6
	30 months	Pear Tree	8-10 m	40.5 ± 18.8	0.49 ± 0.7	6.8 ± 7.1	21.7 ± 27.8	5.6 ± 3.4	1.2 ± 2.8	8.6 ± 8.2	12.2 ± 10.7	0.4 ± 1.1	1.3 ± 1.4
			15-18 m	37.0 ± 16.0	1.0 ± 0.16	6.6 ± 6.8	17.7 ± 20.9	7.6 ± 4.4	2. 9 ± 3.9	5.5 ± 5.6	21.9 ± 18.9	0 ± 0	6.1 ± 1.7
		Discovery Bay	8-10 m	22.2 ± 14.2	0.13 ± 0.19	8.4 ± 8.9	21.8 ± 20.7	5.9 ± 5.9	3.4 ± 4.6	6.5 ± 5.9	27.7 ± 17.9	0.5 ±1.0	2.3 ± 2.7
			15-18 m	26.0 ± 14.1	0.13 ± 0.29	7.9 ± 8.8	22.3 ± 18.9	9.2 ± 14.8	2.9 ± 4.2	6.2 ± 4.6	22.0 ± 14.8	0.5 ± 2.0	1.0 ± 1.1
		Dairy Bull	8-10 m	31.9 ± 17.2	0.24 ± 0.3	6.5 ± 6.3	22.8 ± 24.8	9.8 ± 12.4	1.9 ± 2.7	7.4 ± 6.6	15.3 ± 17.5	0 ± 0	2.8 ± 2.1
			15-18 m	31.0 ± 14.3	0.13 ± 0.25	12.9 ± 13.8	24.8 ± 17.3	8.3 ± 5.7	1.5 ± 2.0	4.8 ± 4.1	14.4 ± 14.7	0.01 ± 0.05	1.0 ± 1.1
Exposed	18 months	Pear Tree	8-10 m	8.8 ± 7.4	0 ± 0	0 ± 0	0 ± 0	0.4 ± 0.7	18.4 ± 24.5	45.0 ± 33.4	0 ± 0	27.4 ± 31.2	0.2 ± 0.5
			15-18 m	27.8 ± 17.4	0 ± 0	0 ± 0	0 ± 0	2.1 ± 2.6	12.3 ± 12.8	40.6 ± 15.6	0 ± 0	17.3 ± 24.8	0 ± 0
		Discovery Bay	8-10 m	20.1 ±11.3	0 ± 0	0 ± 0	0 ± 0	0.9 ± 1.0	5.7 ± 6.3	51.0 ± 23.8	0 ± 0	21.4 ± 29.9	0 ± 0
			15-18 m	18.4 ± 18.9	0 ± 0	0 ± 0	0 ± 0	2.2 ± 2.5	11.8 ± 20.0	56.9 ± 28.1	0 ± 0	10.7 ± 22.7	0 ± 0
		Dairy Bull	8-10 m	5.6 ± 28.0	0 ± 0	0 ± 0	0 ± 0	0.4 ± 0.7	1.6 ± 4.0	31.3 ± 33.5	0 ± 0	61.0 ± 40.0	0.2 ± 0.8
			15-18 m	26.8 ± 35.9	0 ± 0	0 ± 0	0 ± 0	0.6 ± 0.6	11.7 ± 16.9	21.6 ± 19.4	0 ± 0	39.3 ± 44.0	0.06 ± 0.2
	30 months	Pear Tree	8-10 m	6.6 ± 6.4	0 ± 0	0 ± 0	0.01 ± 0.04	0.36 ± 0.4	17.5 ± 21.9	52.9 ± 30.0	0 ± 0	22.4 ± 24.9	0.1 ± 0.5
			15-18 m	21.6 ± 15.9	0.31 ± 0.13	0 ± 0	0 ± 0	1.0 ±1.5	17.9 ± 19.4	58.9 ±21.3	0 ± 0	0.6 ± 2.3	0 ± 0
		Discovery Bay	8-10 m	9.1 ± 7.9	0 ± 0	0 ± 0	0.8 ± 3.2	0.3 ± 0.6	9.5 ± 16.1	65.8 ± 28.5	0 ± 0	14.4 ± 25.2	0.1 ± 0.5
			15-18 m	9.3 ± 9.2	0 ± 0	0 ± 0	0 ± 0	0.7 ± 0.1	16.1 ± 14.4	73.9 ±16.2	0 ± 0	0 ± 0	0.02 ± 0.09

	Dairy Bull	8-10 m	0.0 ± 32.0	0 ± 0	0 ± 0	1.2 ± 5.2	0.2 ± 0.3	1.9 ± 4.4	56.1 ± 45.9	0 ± 0	40.7 ± 40.2	0 ± 0
		15-18 m	25.3 ± 19.1	0 ± 0	0 ± 0	0 ± 0	0.9 ± 1.0	4.9 ± 8.3	58.0 ± 23.5	0 ± 0	11.0 ± 22.9	0 ± 0

Table 4. Univariate analyses of variance (ANOVA) of the cryptic diversity at a) 6 months, b) 18 months and c) 30 months; 18- and 30-month ANOVAs were on rank-transformed data.

a) **ANOVA**	**df**	**Sum of Squares**	**Mean Sum of Squares**	***F*-value**	**P**
Cryptic Diversity (6 months)					
Location	2	0.882	0.4410	5.339	0.006
Depth	1	0.932	0.9322	11.285	0.001
Location * Depth	2	0.162	0.0811	0.982	0.378
Residuals	112	9.252	0.0826	---	---
b) **ANOVA (ranked)**	**df**	**Sum of Squares**	**Mean Sum of Squares**	***F*-value**	**P**
Cryptic Diversity (18 months)					
Location	2	1584	792	0.792	0.455
Depth	1	12183	12183	12.191	<0.001
Location * Depth	2	1762	881	0.881	0.417
Residuals	108	107925	999	---	---
c) **ANOVA (ranked)**	**df**	**Sum of Squares**	**Mean Sum of Squares**	***F*-value**	**P**
Cryptic Diversity (30 months)					
Location	2	8061	4030	4.175	0.018
Depth	1	242	242	0.251	0.618
Location * Depth	2	161	80	0.083	0.9202
Residuals	103	99446	965	---	---

Table 5. Univariate analysis of variance (ANOVA) of the percent cover of bare space on the cryptic undersides of tiles at a) 6 months, b) 18 months, and c) 30 months. All ANOVA were performed on rank-transformed data to meet the assumptions of normality.

a)	**ANOVA (ranked)**	**df**	**Sum of Squares**	**Mean Sum of Squares**	***F*-value**	**P**
Cryptic Percent Cover Bare Space (6 months)						
Location		2	8191	4096	3.905	0.023
Depth		1	9611	9611	9.164	0.003
Location * Depth		2	1654	827	0.788	0.457
Residuals		112	117454	1049	---	---
b)	**ANOVA (ranked)**	**df**	**Sum of Squares**	**Mean Sum of Squares**	***F*-value**	**P**
Cryptic Percent Cover Bare Space (18 months)						
Location		2	1485	743	0.773	0.464
Depth		1	13697	13697	14.264	<0.001
Location * Depth		2	4562	2281	2.375	0.098
Residuals		108	103708	960	---	---
c)	**ANOVA (ranked)**	**df**	**Sum of Squares**	**Mean Sum of Squares**	***F*-value**	**P**
Cryptic Percent Cover Bare Space (30 months)						
Location		2	14860	7430	8.284	<0.001
Depth		1	4	4	0.004	0.947
Location * Depth		2	664	332	0.370	0.691
Residuals		103	92382	897	---	---

Table 6. Univariate analyses of variance (ANOVA) of the exposed side diversity at a) 18 months and b) 30 months.

a) ANOVA	df	Sum of Squares	Mean Sum of Squares	*F*-value	P
Exposed Diversity (18 months)					
Location	2	2.930	1.4648	22.150	<0.001
Depth	1	0.290	0.2895	4.378	0.039
Location * Depth	2	0.055	0.0273	0.413	0.663
Residuals	102	6.745	960.066	---	---
b) ANOVA	**df**	**Sum of Squares**	**Mean Sum of Squares**	***F*-value**	**P**
Exposed Diversity (30 months)					
Location	2	0.902	0.4512	4.257	0.017
Depth	1	0.128	0.1280	1.207	0.275
Location * Depth	2	0.259	0.1294	1.221	0.299
Residuals	99	10.493	0.1060	---	---

Table 7. Univariate analyses of variance (ANOVA) of the exposed side percent bare space after a) 18 months and b) 30 months. Prior to analysis, percent cover data at 18 months was square root transformed and 30-month data was ranked to force normality.

a) ANOVA	df	Sum of Squares	Mean Sum of Squares	*F*-value	P
Exposed Percent Cover Bare Space (18 months)					
Location	2	3.4	1.71	0.490	0.614
Depth	1	52.4	52.37	15.034	<0.001
Location * Depth	2	39.6	19.80	5.685	0.005
Residuals	102	355.3	3.48	---	---
b) ANOVA	**df**	**Sum of Squares**	**Mean Sum of Squares**	***F*-value**	**P**
Exposed Percent Cover Bare Space (30 months)					
Location	2	2201	1101	1.506	0.227
Depth	1	14501	14501	19.844	<0.001
Location * Depth	2	7333	3667	5.018	0.008
Residuals	99	72342	731	---	---

Chapter 5

Effects of pH on the interaction between an excavating sponge, *Cliona varians,* and a hermatypic coral, *Porites furcata*.

Abstract

Ocean acidification is a mounting threat to coral reef ecosystems. While the biological and physiological impacts of acidification are well documented for many hermatypic corals, the potential effects on bioerosion processes remain largely unknown. Decreases in pH are likely to modify the direct interactions between corals and bioeroders, such as excavating sponges, with broad implications for the balance between biologically mediated deposition and erosion of carbonate in reef communities. This study investigated the effects of three levels of pH on the direct interaction between a bioeroding sponge, *Cliona varians,* and a Caribbean coral, *Porites furcata*. Decreased seawater pH had no effect on the attachment rates of *C. varians* to the corals, and did not significantly impact the survival of either the coral or sponges. However, exposure to end-of-century levels of pH significantly reduced calcification in *P. furcata* and led to a significant increase in sponge-mediated erosion of *P. furcata*. These findings demonstrate that acidification can enhance erosional efficiency without impacting survival or competitive vigor (attachment rates) in these two species. While few studies have considered the influence of acidification on the competitive interactions between corals and other reef organisms, our study suggests that assessing the impacts of changing pH on species interactions is crucial to adequately predict ecosystem-level responses in the future.

Introduction

Currently, atmospheric CO_2 levels fluctuate around 390ppm and continue to rise (Caldeira and Wickett 2003; Caldeira and Wickett 2005); projected scenarios indicate that levels will approach 450-600ppm by 2050 and 750-1000ppm by the end of the 21st century (IPCC 2007; Gattuso and Lavigne 2009). The resultant increase in dissolved seawater CO_2 is expected to reduce surface ocean pH by 0.3-0.4 units, substantially altering the carbonate chemistry of coastal marine ecosystems (Kleypas 1999; Guinotte and Fabry 2008; Doney et al. 2009). These changes in seawater chemistry, collectively known as acidification, will affect the physiological ability of organisms to precipitate calcium carbonate ($CaCO_3$) (Feely 2004; Orr et al. 2005) and will therefore disproportionately impact ecosystems relying on the formation of biogenic carbonate structure, such as coral reefs (Hoegh-Guldberg et al. 2007; Andersson and Gledhill 2013).

Tropical studies investigating the effects of acidification have primarily focused on the biological responses of calcifying species, particularly the calcification processes of hermatypic corals and coralline algae (Gattuso et al. 1997; Kuffner et al. 2007; Anthony et al. 2008; Jokiel et al. 2008; Kurihara 2008; Albright and Langdon 2011; Diaz-Pulido et al. 2012). Based on the results of these studies, it is now widely accepted that decreases in pH will reduce calcification rates across a range of taxa, and therefore directly impact the net growth, stabilization and carbonate accretion processes on reefs. Acidification also intensifies the rate of erosional processes by physically and chemically weakening existing $CaCO_3$ structures (Kleypas 1999), thereby facilitating the biologically mediated erosion of carbonate substrates (Tribollet et al. 2009; Duckworth and Peterson 2012; Wisshak et al. 2012; Fang et al. 2013; Reyes-Nivia et al. 2013).

Biological erosion, or bioerosion, is carried out by a suite of reef organisms, such as urchins (Asgaard and Bromley 2008), fish (Bruggemann et al. 1996), algae (Reyes-Nivia et al. 2013), microbes (Tribollet et al. 2009), polychaetes (Hutchings 2008), mollusks (Kleeman 2008), and excavating sponges. Natural rates of bioerosion vary greatly among taxa; however, sponges are often regarded as the dominant (Perry 1998) and most destructive in terms of $CaCO_3$ removal on coral reefs (Neumann 1966; MacGeachy 1977; Rützler 2002; Schönberg 2002). Calcium carbonate removal rates for tropical excavating sponges can range from 0.84-23.0 kg $CaCO_3$ m^{-2}

year^{-1} (Hill 1996; Zundelevich et al. 2007; Nava and Carballo 2008), with some of the highest rates reported for *Cliona varians* (Hill 1996) and *Cliona lampa* (Neumann 1966) at 22.8 kg calcite m^{-2} year^{-1} and 22.0-23.0 kg CaCO3 m^{-2} yr^{-1}, respectively. Excavating sponges are important to healthy reef ecosystems, and perform vital functions such as recycling minerals, restructuring coral colonies (Goreau and Hartman 1963), creating new space for settlement and easing spatial competition among benthic taxa (Williams et al. 1999). In recent years, however, there has been a global increase in the prevalence of excavating sponges on threatened and impacted reefs, likely facilitated by wide-spread declines in coral health (Rose and Risk 1985; Holmes 2000; Rützler 2002; Lopez-Victoria and Zea 2004; Ward-Paige et al. 2005; Schönberg and Ortiz 2008; Carballo et al. 2013).

The increase in excavating sponge abundance, coupled with the detrimental effects of acidification on accretion processes, may cause net reef bioerosion to increase in the near future. Recent studies by Wisshak et al. (2012) and Fang et al. (2013) have shown that the Indo-Pacific sponge *Cliona orientalis*, a member of the *'Cliona viridis* species complex' (Schönberg 2000), increases its boring rates on pre-infested dead coral skeleton when exposed to projected future pCO_2 conditions, while experiencing little to no direct negative impacts on its own physiology. Members of the '*Cliona viridis* species complex' are known to be particularly efficient bioeroders, as this group of sponges harbor symbiotic zooxanthellae that both accelerate boring rates and necessitate direct spatial competition with corals for light (Hill 1996). Studies demonstrating that erosional processes are affected by decreased pH (Duckworth and Peterson 2012) and increased pCO_2 (Wisshak et al. 2012; Fang et al. 2013, Wisshak et al. 2014) are important for understanding how future changes will affect substrate erosion; however, a direct evaluation of the spatial interactions and competitive outcomes between corals and excavating sponges must also be undertaken.

Cliona varians, a member of the '*Cliona viridis* species complex', is a prominent bioeroder on Caribbean reefs and a direct spatial competitor (Vicente 1978) with hermatypic corals (Hill 1996; Perry 1998; Rützler 2002), simultaneously overgrowing living coral tissue while eroding the skeleton beneath. To determine how acidification affects this living coral-sponge interaction, we used *C. varians*, and the coral, *Porites furcata*, an abundant, opportunistic branching coral, commonly colonized by *C. varians* on shallow (<5 m) Caribbean reefs (pers

obs: Bocas del Toro, Panama). The effect of three levels of pH on the ability of *C. varians* to spatially compete with and subsequently erode living *P. furcata* was examined. Hypothesizing that *C. varians* would exhibit greater success attaching to and eroding *P. furcata* in seawater with higher acidification, I expected that a simultaneous reduction in *P. furcata* calcification and defense from pH stress would lead to an increase in attachment efficiency of *C. varians* and therefore an increase in erosional activity in treatments with decreased pH.

Materials and methods

Study species collection

Approximately 30 *Porites furcata* colonies from a continuous reef system on Isla Pastores, Panama (9° 13.551' N, 82° 19.538' W) served as donors for the experiment. After collection, coral specimens were placed in flow-through seawater tables; while submerged, the growing tips from healthy branches were excised to create smaller fragments (3-6 cm in length). Any fragments exhibiting necrotic tissue, bleaching, disease or an infestation of excavating sponges or other bioeroders were discarded. After one week of recovery, each *P. furcata* fragment was tagged, and initial buoyant weights were determined following methods of Jokiel et al. (1978) and Davies (1989). Fifteen large *Cliona varians* forma *incrustans* individuals (each >300 cm^2 surface area) were also collected at Isla Pastores; standard spicule preparations were used to confirm species identification. Sponges were cut into smaller explants (~8 cm^3) taking care to include approximately 4 cm^2 of the choanosome layer where the zooxanthellae reside. Explants were allowed a 3-day recovery period to ensure that all sponges had healed, before being loosely secured to coral fragments with cable ties (Schönberg 2002). *P. furcata* fragments serving as controls (no sponge attached) were also supplied a cable tie to partially account for any abrasion or shading artifacts. Fragments of corals, with (n=5) and without sponges (n=5) were placed into experimental aquaria (n=30). All coral fragments were elevated off the bottom using plastic 'egg crate' material to prevent contact with any accumulated sediment or detritus.

Flow-through system and experimental design

Using the outdoor unfiltered, seawater system at the Smithsonian Tropical Research Institute's Bocas del Toro Laboratory, a flow-through pH-stat system was constructed with 3 reservoirs (200L each) that each fed 10 aquaria (30L). These reservoirs allowed for three levels of pH manipulation that corresponded with current as well as projected levels of acidification for mid and end-of-century (based on the SRES A2 emissions scenario; IPCC 2007). Target pH values for this system were 8.00 (ambient), 7.80 (mid-century) and 7.60 (end-of-century). In each reservoir, pH was monitored continuously using a pH controller (Reef Fanatic; resolution: 0.01, accuracy: 0.1%) connected to a CO_2 regulator (Milwaukee MA957); whenever pH levels exceeded the target values of 7.80 and 7.60 for the moderate and high acidification treatments,

respectively (Anthony et al. 2008; Duckworth et al. 2012), the controller opened a valve that delivered CO_2 gas to the reservoir until target values were achieved again. No CO_2 manipulations occurred in the ambient pCO_2 reservoir. All reservoirs, regardless of treatment, were also bubbled with ambient air to ensure that dissolved oxygen levels were adequate. Each reservoir received water from the open flow-through system at a rate of 30L min^{-1} and supplied 10 aquaria with treatment water at a rate of roughly 3L min^{-1}; seawater residence time in each aquarium was ~10 minutes. Within the aquaria, *in situ* temperature, salinity, and pH (calibrated daily using NIST/NBS traceable standards) were monitored daily with a hand-held YSI 85 and Oakton 35-series pH meter. In addition, HOBO loggers continuously monitored temperature (°C) and light (photons) conditions in the aquaria. Finally, temperature, salinity and pH were sampled hourly during one 24-hour period in all aquaria to monitor fluctuations over the course of an entire tidal and daylight cycle. The experiment ran for 51 days (October-December 2011); during this time, weekly measurements of temperature, salinity, pH were also taken at the field collection site, Isla Pastores, for comparison.

Response variables

Survival was monitored weekly for both *P. furcata* and *C. varians* individuals. To understand whether the competitive interaction between *C. varians* and *P. furcata* was affected by pH, *C. varians* attachment to corals was assessed weekly for each coral-sponge pair by visually inspecting and gently prodding the sponge explant (Duckworth et al. 2012). Calcification was quantified using the percent change in skeletal weight of individual corals, obtained from the initial and final buoyant weights (Jokiel et al. 1978; Davies 1989) and hereafter referred to as percent net calcification. Percent net calcification, rather than absolute weight change, was used exclusively in data analyses due to the variation in fragment size and surface area. Coral fragments with sponges were similarly assessed, although here, changes in skeletal mass were a function of both coral calcification and sponge-mediated bioerosion. At the conclusion of the experiment, *C. varians* were removed from *P. furcata* fragments, and corals were immersed in a 10% bleach solution for 24 hours to remove live tissue (sponge or coral). The fragments were then rinsed with deionized water, dried at 60°C for 24 hours and reweighed. Micro-scale sponge-induced erosion and cleavage patterns in *P. furcata* individuals with attached *C. varians* (n=6; 2 from each treatment) were evaluated qualitatively using a scanning electron

microscope (SEM); photos were taken at 225x magnification beneath the sponge attachment site and at an area distal to the coral-sponge interaction.

Data Analysis

The hierarchical design of the experiment required the use of tank means (n=30) in the analysis of all response variables. All data were assessed for normality using the Shapiro-Wilk test; no transformations were necessary for survival or attachment data. Mean survival (days) for *P. furcata* fragments in each tank was analyzed using a two-way ANOVA to test for the main and interactive effects of sponge presence and pH on survival. Attachment times, represented as days until sponge attachment, were used to compare competitive competence in *C. varians* between pH treatments using a one-way ANOVA. Percent net calcification was negatively skewed and leptokurtic, and so these data were rank-transformed; only those tanks with 2 or more individuals alive at the close of the experiment were included in this analysis. A two-way analysis of variance (ANOVA) on ranked data was used to test for the main and interactive effects of pH and sponge presence on percent net calcification. When significant main effects were identified, Tukey's honestly significant difference (HSD) tests were used to determine treatment differences. All analyses were performed using the open-source statistical software, R version 2.13.2 (R Core Team 2012).

Results

Water parameters

The reservoir pH-stat system was successful at producing significantly different acidification treatments ($F_{(2,22)}$=223.5, P<0.001; Table 1). Other conditions, such as flow rate, temperature and salinity did not vary among pH treatments. Seawater parameters that were measured within the aquaria and at the field collection site are summarized in Table 1. It is important to note that pH was measured on the NBS scale, rather than the preferred total or seawater scale. Hourly monitoring of the temperature, salinity and pH over a 24-hour period within each aquarium showed that fluctuations in the flow-through treatment system paralleled natural fluctuations due to tidal and light cycles (Figure 1). Unfortunately, no further carbonate chemistry was calculated.

Survival and attachment

No *C. varians* individuals died during the experiment. Survival for *P. furcata* fragments (mean ± 1 standard deviation) in the highest acidification treatment was 31.0 ± 6.9 days (n=10 tanks, n=43 coral individuals) and 30.2 ± 12.0 days (n=10 tanks, n=43 coral individuals) for corals with and without sponges, respectively. Comparatively, survival in the ambient treatment was 32.9 ± 12.6 days (n=10 tanks, n=44 coral individuals) and 37.8 ± 10.2 days (n=10 tanks, n=46 coral individuals) for corals with and without sponges, respectively. No significant difference in coral survival was observed between or within any of the treatment combinations. The time-to-attachment of *C. varians* was independent of pH treatment, with no significant difference between treatments observed. The mean days until attachment of *C.varians* to *P. furcata* was 12.1 ± 7.1 days.

Calcification and erosion

The full ANOVA model found a significant main effect of pH on percent net calcification. A *post hoc* Tukey's HSD revealed that there was no statistically significant difference between the moderate and high acidification treatments. The impact of pooling the moderate and high treatments on the magnitude of the F-statistic for sponge presence (two-way ANOVA) was tested using a resampling technique (10,000 permutations, with replacement) that

preserved the original sampling balance. This approach indicated that there was no statistically significant difference between the original high and resampled composite moderate-high treatments (P>0.124). Therefore, only the results of a two-way interactive model comparing the percent net calcification of corals using two pH levels (ambient and high acidification levels * sponge presence; Table 2) are presented.

The percent net calcification was significantly affected by pH ($F_{(1,28)}$=24.846, P<0.001) and sponge presence ($F_{(1,28)}$=4.690, P=0.04). Further exploration using Tukey's HSD showed that these significant main effects were driven by the significantly lower net calcification of coral fragments with *C. varians* in the highest acidification treatment compared to corals with or without *C. varians* in the ambient treatments (Tukey HSD; P<0.001 and P<0.001, respectively; Table 2). Net calcification decreased with decreasing pH levels, and this decline in calcification was exacerbated in the coral fragments with sponges, due to increased bioerosion (Figure 2), particularly in the highest acidification level. An increase in erosional scars in the highest acidification levels was qualitatively confirmed using the SEM photographs (Figure 3).

Discussion

The results of this study suggest that decreasing pH altered some, but not all, interactions between *P.furcata* and *C. varians*. Coral survival was not statistically related to pH treatments. It is widely assumed that future increases in temperature, rather than pH, will be the primary determinant of coral survivorship (Hoegh-Guldberg 1999; Fine and Tchernov 2007; Hoegh-Guldberg et al. 2007). While corals may be able to recover from a lack of growth and/or calcification (Fine and Tchernov 2007), recovery from temperature-induced bleaching is unlikely (see Hoegh-Guldberg 1999 and references within). Although corals without sponges tended to live a few days longer than corals with sponges at ambient and moderate acidification conditions, these differences were not statistically, and most likely not ecologically, significant. Additionally, no sponge mortality was observed. Aerts (1998) and Aerts and van Soest (1997) described sponge/coral interactions on reefs and showed that the majority of interactions between coral and *C. varians* were limited to peripheral contact, not complete overgrowth. In our experiment, the induced colonization of *P. furcata* by *C. varians* led to coral polyp death directly underneath the attachment site; however, no further overgrowth of the coral was observed over the 51-day study period.

Unexpectedly, the time until attachment for sponges was not statistically related to pH treatment. If corals had exhibited a reduction in defensive vigor as a result of acidification, as has been posited under most climate change scenarios (Fabry et al. 2008), we would have expected *C. varians* to exploit the stressed corals and attach at rates positively related to acidification. It remains possible, though, that the corals were not sufficiently stressed or that *C. varians* was affected in some unmeasured way that differentially limited attachment capacity across pH treatments. In a similar species, *Cliona celata*, attachment to bivalve shells was slower in reduced pH treatments, and survival slightly depressed (Duckworth and Peterson 2012); however, this study lowered pH using hydrochloric acid, not by injecting CO_2. It is possible that the reduced pH might have had a negative physiological effect on the sponges themselves, although there was no observed sponge mortality in this study, and others have reported limited impacts of acidification on sponge physiology (Duckworth et al. 2012; Wisshak et al. 2012; Fang et al. 2013). Despite no significant differences in attachment rates among treatments, sponge

bioerosion was significantly increased in the low pH treatments. Thus, we might conservatively expect that this sponge-coral interaction will continue to intensify in the future.

Percent net calcification in corals with attached *C. varians* was significantly reduced in the highest acidification treatment as compared to the ambient treatment. These findings are consistent with other studies that have investigated changes in bioerosion efficiency of excavating sponges (albeit on non-living biogenic substrate) to lowered pH (Duckworth and Peterson 2012) and increased pCO_2 (Wisshak et al. 2012; Fang et al. 2013). No difference in net calcification was found between coral fragments with and without sponges in ambient pH treatments, indicating that the accretion and erosion processes were still in balance at this acidification level.

The limited response of the corals with and without sponges to the moderate acidification treatment (Figure 2) may be related to the biotic history of the corals. Putnam and Edmunds (2011) and Dufault (2012) demonstrated that corals from sites that experienced large daily fluctuations in temperature or pCO_2 were often unaffected by elevated levels of these parameters in experimental conditions. The *P. furcata* fragments used in this experiment were collected from a reef tract on Isla Pastores that, like most reefs inside the archipelago of Bocas del Toro, Panama, lies directly adjacent to a large mangrove habitat (<10 m distance). Mangrove habitats typically experience large diel variations in pH, pCO_2 and temperature due to the shallow waters and high levels of organic matter decomposition within the sediments (Borges 2003; Zablocki et al. 2011). CO_2-enriched seawater from mangrove habitats is then tidally exported to adjacent environments before being mixed and diluted. Zablocki et al. (2011) found that the maximum diel range of pH in mangrove habitats of Bermuda was from 7.51-8.01 (NBS scale pH), which is beyond the range experienced in this controlled experiment designed to manipulate pH at certain target levels. The measured pH values at Isla Pastores only ranged from 7.96-8.01; however, measurements were taken weekly during the mid-morning hours, and therefore a full diel range is not represented by these data. It may be that the coral used in this experiment had already been acclimated to large fluctuations in pH and that the calcification responses were therefore dampened in all but the highest experimentally altered level of acidification.

The precise mechanisms underlying the observed increase in sponge-mediated erosion in high acidification treatment are still unclear. Excavating sponges remove coralline substrate

through a combination of chemical (etching agents are used to weaken the $CaCO_3$ matrix) and mechanical (etching cells physically chip away at the substrate) erosion, although the exact contributions of each process are not fully understood (Hatch 1980; Pomponi 1980; Zundelevich et al. 2007; Nava and Carballo 2008). The possibility remains that increased sponge erosion was (1) an opportunistic response to an overall weaker coral skeleton, (2) a response to a decreased dissolution gradient between the surrounding seawater and the sponge-substrate interface that lowered the metabolic cost of excavation (Wisshak et al. 2012; Fang et al. 2013) or (3) a synergistic response of acidified water augmenting the sponges' natural exudates, easing substratum resistance to etching cells without additional metabolic costs. Determining which of these might be responsible for the observed increase in bioerosion was beyond the scope of this study and warrants future consideration. The result, however, was plainly evident: the erosion efficiency of *C. varians* increased in the lowest pH treatment, which represented projections for the end of the century in the SRES A2 scenario (IPCC 2007).

Previous studies have independently shown that (1) excavating sponges are increasing in abundance (Rose and Risk 1985; Ward-Paige et al. 2005; Chiappone et al. 2007), (2) bioerosion efficiency of dead substrate increases with increasing acidification (Wisshak et al. 2012; Fang et al. 2013) and (3) across-taxa reductions in calcification occur with decreased pH (Anthony et al. 2008; Andersson and Gledhill 2013). However, none of these studies have taken into account the ability of interspecific interactions to amplify detrimental effects of decreasing pH. This is the first study that has used living coral and excavating sponges in tandem to assess how future changes in pH may affect this common reef interaction. This study established that competitive outcomes between *P. furcata* and *C. varians* do not change under different acidification regimes and that the bioerosion efficiency of *C. varians* increases with decreasing pH, despite the stress of constant peripheral interaction with a living coral. This suggests that as pH declines in shallow coastal waters, the mode and efficiency of *C. varians* invasion will remain the same, while a simultaneous reduction in coral calcification and an increase in sponge-mediated bioerosion will accelerate reef structural degradation and net erosion. Further investigations of this interaction that include temperature manipulations are necessary, as many excavating sponges grow faster in higher temperatures (Siegrist et al. 1992), which may further exacerbate their ability to overgrow corals. I demonstrate here and further argue that assessing the impact of changing pH on species interactions is crucial to adequately predict ecosystem-level responses in the future.

References

Aerts L (1998) Sponge/coral interactions in Caribbean reefs: analysis of overgrowth patterns in relation to species identity and cover. *Marine Ecology Progress Series* 175:241-249

Aerts L, van Soest RWM (1997) Quantification of sponge/coral interactions in a physically stressed reef community, NE Colombia. *Marine Ecology Progress Series* 148:125-134

Albright R, Langdon C (2011) Ocean acidification impacts multiple early life history processes of the Caribbean coral *Porites astreoides*. *Global Change Biology* 17:2478-2487 doi:10.1111/j.1365-2486.2011.02404.x

Andersson AJ, Gledhill D (2013) Ocean acidification and coral reefs: effects on breakdown, dissolution and net ecosystem calcification. *Annual Review of Marine Science* 5:321-348

Anthony KR, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Science* USA 105:17442-17446 doi:10.1073/pnas.0804478105

Asgaard U, Bromley RG (2008) Echinometrid sea urchins, their trophic styles and corresponding bioerosion. In: Wisshak M, Tapanila L (eds) Current Developments in Bioerosion. Springer-Verlag, Berlin, pp 279-304

Borges AV (2003) Atmospheric CO_2 flux from mangrove surrounding waters. *Geophysical Research Letters* 30:1558-1562 doi:10.1029/2003gl017143

Bruggemann JH, van Kessel AM, van Rooij JM, Breeman AM (1996) Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series* 134:59-71

Caldeira K, Wickett M (2003) Oceanography: Anthropogenic carbon and ocean pH. *Nature* 425:365

Caldeira K, Wickett M (2005) Ocean Model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *Journal of Geophysical Research* 110:np

Carballo JL, Bautista E, Nava H, Cruz-Barraza JA, Chavez JA (2013) Boring sponges, an increasing threat for coral reefs affected by bleaching events. *Ecology and Evolution* 3:872-886 doi:10.1002/ece3.452

Chiappone M, Rutten LM, Miller SL, Swanson DW (2007) Large-scale distributional patterns of the encrusting and excavating sponge *Cliona deletrix* Pang on Florida Keys coral substrates. *Porifera Research: Biodiversity, Innovation and Sustainability*:255-263

Davies PS (1989) Short-term growth measurements of corals using an accurate buoyant weight technique. *Marine Biology* 101:389-395

Diaz-Pulido G, Anthony KRN, Kline DI, Dove S, Hoegh-Guldberg O (2012) Interactions between ocean acidification and warming on the mortality and dissolution of coralline algae. *Journal of Phycology* 48:32-39 doi:10.1111/j.1529-8817.2011.01084.x

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO_2 problem. *Annual Review of Marine Science* 1:169-192 doi:10.1146/annurev.marine.010908.163834

Duckworth AR, Peterson BJ (2012) Effects of seawater temperature and pH on the boring rates of the sponge *Cliona celata* in scallop shells. *Marine Biology* 160:27-35 doi:10.1007/s00227-012-2053-z

Duckworth AR, West L, Vansach T, Stubler A, Hardt M (2012) Effects of water temperature and pH on growth and metabolite biosynthesis of coral reef sponges. *Marine Ecology Progress Series* 462:67-77 doi:10.3354/meps09853

Dufault AM, Cumbo VR, Fan TY, Edmunds PJ (2012) Effects of diurnally oscillating pCO_2 on the calcification and survival of coral recruits. *Proceedings of the Royal Society B: Biological Sciences* 279:2951-2958. doi:10.1098/rspb.2011.2545

Fang JK, Mello-Athayde MA, Schönberg CH, Kline DI, Hoegh-Guldberg O, Dove S (2013) Sponge biomass and bioerosion rates increase under ocean warming and acidification. *Global Change Biology* 19:3581-3591 doi:10.1111/gcb.12334

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero,FJ (2004) Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science* 305:362-366

Fine M, Tchernov D (2007) Scleractinian coral species survive and recover from decalcification. *Science* 315:1811

Gattuso J-P, Frankignoulle M, Bourge I, Romaine S, Buddemeier RW (1997) Effect of calcium carbonate saturation of seawater on coral calcification. *Global and Planetary Change* 18:37-46

Gattuso J-P, Lavigne H (2009) Technical Note: Approaches and software tools to investigate the impact of ocean acidification. *Biogeosciences* 6:2121-2133

Guinotte JM, Fabry VJ (2008) Ocean acidification and its potential effects on marine ecosystems. *Annals of the New York Academy of Sciences* 1134:320-342

Hatch W (1980) The implication of carbonic anhydrase in the physiological mechanism of penetration of the carbonate substrata by the marine burrowing sponge *Cliona celata* (Demospongiae). *Biological Bulletin* 159:135-147

Hill MS (1996) Symbiotic zooxanthellae enhance boring and growth rates of the tropical sponge *Anthosigmella varians* forma *varians*. *Marine Biology* 125:649-654

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50:839-866

Hoegh-Guldberg O et al. (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737-1742. doi:10.1126/science.1152509

Holmes KE (2000) Effects of eutrophication on bioeroding sponge communities with the description of a new West Indian sponges, *Cliona* spp. (Porifera: Hadromerida: Clionidae). *Invertebrate Biology* 119:125-138

Hutchings P (2008) Role of polychaetes in bioerosion of coral substrates. In: Wisshak M, Tapanila L (eds) Current Developments in Bioerosion. Springer-Verlag, Berlin, pp 249-264

IPCC (2007) Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambirdge University Press, Cambridge.

Jokiel PL, Maragos JE, Franzisket L (1978) Coral growth: buoyant weight technique. UNESCO *Monographs of Oceanographic Methodology* 5:529-542

Jokiel PL, Rodgers KS, Kuffner IB, Andersson AJ, Cox EF, Mackenzie FT (2008) Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs* 27:473-483

Kleeman K (2008) *Parapholas quadrizonata* (Spengler, 1792), dominating dead-coral boring bivalve from the Maldives, Indian Ocean. In: Wisshak M, Tapanila L (eds) Current Developments in Bioerosion. Springer-Verlag, Berlin, pp 265-278

Kleypas JA (1999) Geochemical Consequences of Increased Atmospheric Carbon Dioxide on Coral Reefs. *Science* 284:118-120 doi:10.1126/science.284.5411.118

Kuffner IB, Andersson AJ, Jokiel PL, Rodgers KS, Mackenzie FT (2007) Decreased abundance of crustose coralline algae due to ocean acidification. *Nature Geosciences* 1:114-117 doi:10.1038/ngeo100

Kurihara H (2008) Effects of CO_2-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series* 373:275-284 doi:10.3354/meps07802

Lopez-Victoria M, Zea S (2004) Storm-mediated coral colonization by an excavating Caribbean sponge. *Climate Research* 26:251-256

MacGeachy J (1977) Factors controlling sponge boring in Barbados reef corals. *Proceedings of the 3rd International Coral Reef Symposium* 2:477-483

Nava H, Carballo JL (2008) Chemical and mechanical bioerosion of boring sponges from Mexican Pacific coral reefs. *Journal of Experimental Biology* 211:2827-2831 doi:10.1242/jeb.019216

Nava H, Carballo JL (2013) Environmental factors shaping boring sponge assemblages at Mexican Pacific coral reefs. *Marine Ecology* 34:269-279 doi:10.1111/maec.12012

Neumann AC (1966) Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*. *Limnology and Oceanography* 11:92-108

Orr JC, et al. (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681-686

Perry CT (1998) Macroborers within coral framework at Discovery Bay, north Jamaica: species distribution and abundance, and effects on coral preservation. *Coral Reefs* 17:277-287

Pomponi S (1980) Cytological mechanisms of calcium carbonate excavation by boring sponges. *International Review of Cytology* 65:301-319

Putnam HM, Edmunds PJ (2011) The physiological response of reef corals to diel fluctuations in seawater temperature. *Journal of Experimental Marine Biology and Ecology* 396:216-223. doi:10.1016/j.jembe.2010.10.026

R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Reyes-Nivia C, Diaz-Pulido G, Kline D, Ove Hoegh G, Dove S (2013) Ocean acidification and warming scenarios increase microbioerosion of coral skeletons. *Global Change Biology* 19:1919-1929 doi:10.1111/gcb.12158

Riebesell U, Fabry VJ, Hansson L, Gattuso J-P (2011) Guide to best practices for ocean acidification research and data reporting. Publications Office of the European Union, Luxembourg

Rose CS, Risk MJ (1985) Increase in *Cliona deletrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of the Grand Cayman fringing reef. *Marine Ecology* 6 (4):345-363

Rützler K (2002) Impact of crustose Clionid sponges on Caribbean reef corals. *Acta Geologica Hispanica* 37:61-72

Sabine CL, et al. (2004) The oceanic sink for anthropogenic CO_2. *Science* 305:367

Schönberg CHL (2000) Sponges of the *'Cliona viridis* complex' - a key for species identification. *Proceedings of the 9th International Coral Reef Symposium* (Bali, Indonesia)

Schönberg CHL (2002) Substrate effects on the bioeroding Demosponge *Cliona orientalis*. 1. Bioerosion rates. *Marine Ecology* 23:313-326

Schönberg CHL, Ortiz J-C (2008) Is sponge bioerosion increasing? In: Proceedings of the 11th International Coral Reef Symposium, Fort Lauderdale, FL, USA, 2008. pp 527-530

Siegrist HG, Bowman RG, Randall RH, Stifel PB (1992) Diagenetic effects related to hot-water effluent in a modern reef on Guam. *Pacific Science* 46:379

Tribollet A, Godinot C, Atkinson M, Langdon C (2009) Effects of elevated pCO_2 on dissolution of coral carbonates by microbial euendoliths. *Global Biogeochemical Cycles* 23(3) doi:10.1029/2008gb003286

Veron JE, et al. (2009) The coral reef crisis: the critical importance of <350 ppm CO_2. *Marine Pollution Bulletin* 58:1428-1436 doi:10.1016/j.marpolbul.2009.09.009

Vicente VP (1978) An ecological evaluation of the West Indian Demosponge *Anthosigmella varians* (Hadromerida: Spirastrellidae). *Bulletin of Marine Science* 28:771-777

Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. *Marine Pollution Bulletin* 51:570-579 doi:10.1016/j.marpolbul.2005.04.006

Wisshak M, Schönberg CHL, Form A, Freiwald A (2012) Ocean acidification accelerates reef bioerosion. *PLoS ONE* 7(9):e45124

Wisshak, M., C. H. L. Schönberg, A. Form, and A. Freiwald (2014) Sponge bioerosion accelerated by ocean acidification across species and latitudes? *Helgoland Marine Research*: 1-10.

Zablocki JA, Andersson AJ, Bates NR (2011) Diel aquatic CO_2 system dynamics of a Bermudian mangrove environment. *Aquatic Geochemistry* 17:841-859 doi:10.1007/s10498-011-9142-3

Zundelevich A, Lazar B, Ilan M (2007) Chemical versus mechanical bioerosion of coral reefs by boring sponges--lessons from *Pione* cf. *vastifica*. *Journal of Experimental Biology* 210:91-96 doi:10.1242/jeb.02627

Figures and Tables

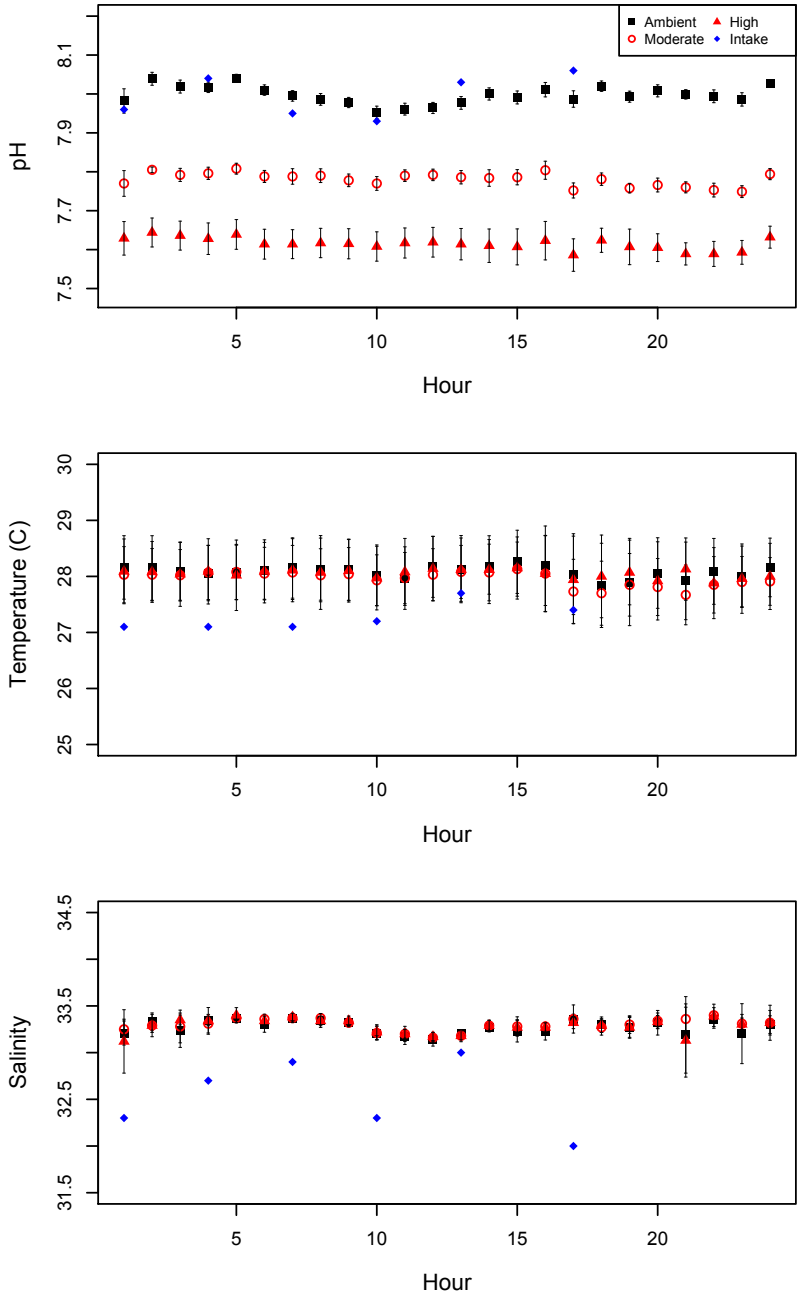

Figure 1. Hourly monitoring of pH, temperature, and salinity within aquaria and adjacent bay water (intake) during one 24-hour period (November 12th, 2011). Intake water was measured intermittently due to difficulty accessing the intake point in the adjacent bay.

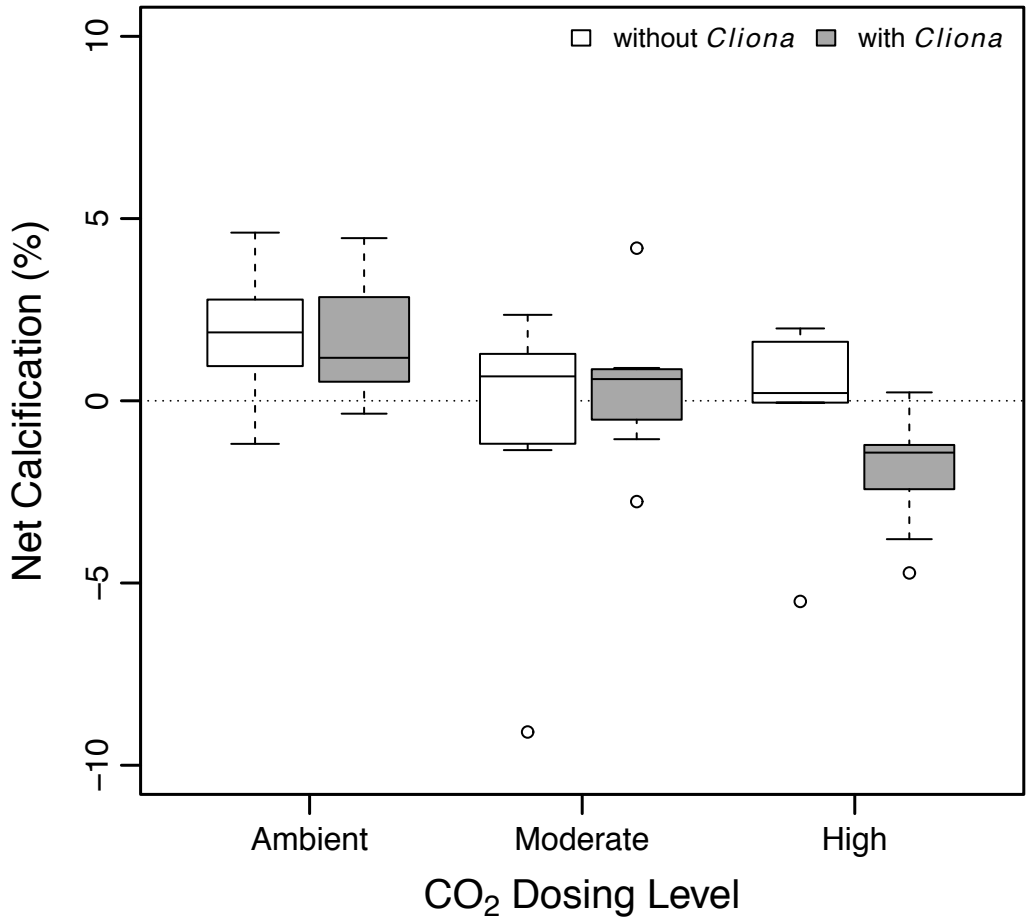

Figure 2. Change in percent net calcification of *Porites furcata* over the 51-day experimental period in specimens with (gray) and without (white) *Cliona varians* present. Boxplots mark median values with a central bar, the 1st and 3rd quartiles with a box, the ±1.5 interquartile ranges with 'Tukey whiskers' and outliers with open circles

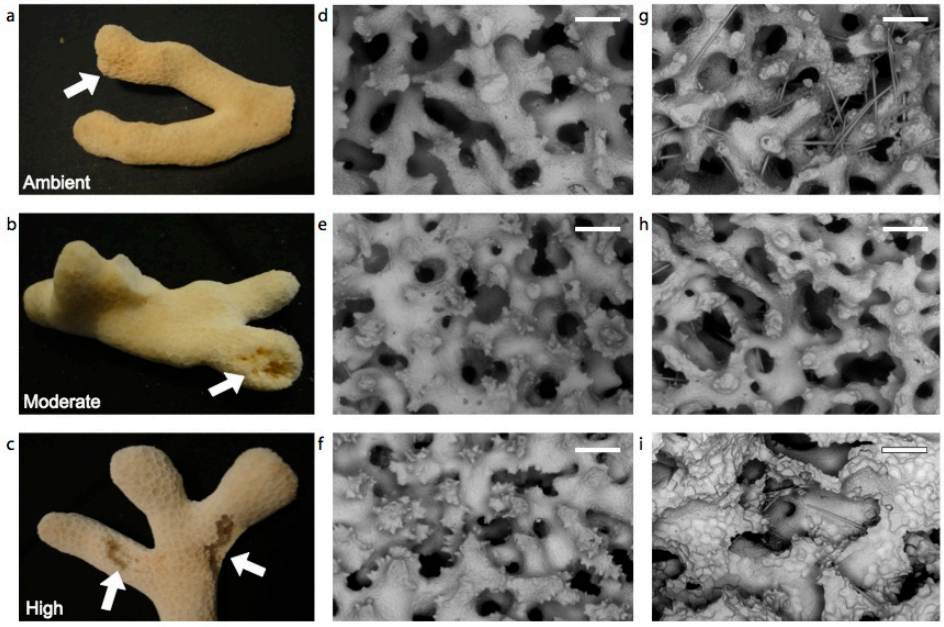

Figure 3. Macro and SEM images of *Porites furcata* specimens from ambient, moderate and high acidification treatments. a-c, *P. furcata* fragment used in subsequent SEM imaging from each of the three pH treatment levels; arrows indicate regions of *Cliona varians* attachment and erosion. SEM images (d-f) are of *P. furcata* skeletal regions that were free of *C. varians* infestation throughout the entirety of the experiment. g-i, SEM images of *C. varians* attachment sites and sponge erosional scars on *P. furcata* from each pH level, as previously indicated by arrows in a-c (sponge removed for imaging purpose). Scale bars from all SEM images (d-i) are 250μm

Table 1. Summary of water parameters measured at the field collection site (Isla Pastores; weekly from Oct. 5th-Nov 1st, 2011), and within aquaria for each pH treatment (see text for sampling frequency). Measured values were pH (NBS scale), temperature, and salinity.

Variable	Isla Pastores	Ambient	Moderate	High
Temperature (°C)	30.4 ± 0.3	28.8 ± 0.6	28.8 ± 0.5	28.7 ± 0.6
Salinity	32.3 ± 0.01	31.8 ± 0.04	31.8 ± 0.13	31.8 ± 0.04
pH (NBS scale)	7.99 ± 0.02	7.97 ± 0.03	7.77 ± 0.03	7.58 ± 0.05

Table 2. Results of the analysis of variance (two-way ANOVA on ranks) of percent net coral calcification due to pH and sponge presence, followed by the results of the *post hoc* Tukey's HSD pairwise comparisons.

ANOVA	**df**	**SS**	**MS**	***F*-value**	***P***
pH	1	1144.5	1144.5	24.846	<0.0001
Sponge presence	1	216.0	216.0	4.690	0.039
pH * Sponge	1	77.7	77.7	1.687	0.205
Residuals	28	1289.8	46.1	---	---

Tukey's HSD	**Diff**	**Lower 95% Conf. Interval**	**Upper 95% Conf. Interval**	**Adjusted *P* value**
Low pH vs. Ambient pH	-11.98	-16.91	-7.06	<0.0001
No *Cliona* vs. *Cliona*	5.16	0.24	10.09	0.0405
Low pH: *Cliona* vs. Ambient pH: *Cliona*	-14.21	-23.21	-5.20	0.001
Ambient pH: no *Cliona* vs. Ambient pH: *Cliona*	2.35	-6.66	11.35	0.892
Low pH: no *Cliona* vs. Ambient pH: *Cliona*	-5.54	-15.55	4.47	0.444
Ambient pH: no *Cliona* vs. Low pH: *Cliona*	16.56	7.82	25.29	<0.0001
Low pH: no *Cliona* vs. High pH: *Cliona*	8.67	-1.10	18.43	0.096
Low pH: no *Cliona* vs. Ambient pH: no *Cliona*	-7.89	-17.66	1.88	0.146

Chapter 6

Sponge erosion under acidifcation and warming scenarios: differential impacts on living and dead coral

Abstract

Ocean acidification will disproportionately impact calcifying organisms in coral reef ecosystems, as calcium carbonate ($CaCO_3$) dissolution becomes favored. Simultaneously, sponge bioerosion rates have been shown to increase as seawater pH decreases. A 20-week experiment was conducted that included a 4-week acclimation period with a high number of replicate tanks (N=144) and a fully orthogonal design with two levels of temperature, three levels of pH and two levels of sponge (present and absent) to account for differences in sponge attachment and bioerosion for both living and dead coral substrate. Net calcification/dissolution, coral survival, sponge attachment, sponge growth, and sponge symbiont health were evaluated. Additionally, the empirical observations of individual coral-sponge interactions were used to develop a stochastic simulation of carbonate change for small coral clusters (i.e., simulated reefs). Our findings suggest differential impacts of temperature, pH and sponge bioerosion for living and dead corals. Net coral calcification was significantly reduced by increased temperatures and sponge erosion, with no significant effect of acidification, while net dissolution of dead coral skeletons was primarily driven by pH, regardless of sponge presence or seawater temperature. A reevaluation of the current paradigm of bioerosion under future acidification and warming scenarios should include ecologically relevant time scales, interactions, and community organization to more accurately predict ecosystem-level response to future conditions.

Introduction

Global atmospheric CO_2 (CO_{2atm}) has risen at an unprecedented rate, bypassing the forewarned tipping point of 350 ppm (Veron et al. 2009) and nearly exceeding 400 ppm. This increase in CO_{2atm}, largely driven by anthropogenic emissions, has already begun to disturb climate patterns, raise mean global temperatures, and alter ocean chemistry (Bates et al. 2014; IPCC 2013). The ocean has warmed by approximately 0.5 °C since the 1970s and is projected to increase an additional 1.8-4 °C by the end of the century (IPCC 2013). The partial pressure of CO_2 in seawater (pCO_2) at multiple ocean observatories has increased by 1.28-2.95 μatm since 1984, with corresponding decreases of 0.0013-0.0026 pH units (Bates et al. 2014). The projected decreases in surface ocean pH by the end of the century range from 0.06-0.32 (15-109% increase in acidity; IPCC 2013), with serious implications for marine calcifying organisms as the aragonite saturation state ($\Omega_{aragonite}$) will be simultaneously reduced.

Decreases in seawater pH and subsequent reductions in $\Omega_{aragonite}$, known as ocean acidification (OA), will disproportionately impact calcifying organisms as available carbonate ion (CO_2^{3-}) concentrations decrease (Orr et al. 2005; Zeebe and Wolf-Gladrow 2001), thereby increasing the metabolic cost of calcification. This will have substantial consequences for ecosystems engineered by calcifying organisms, such as coral reefs. Coral reefs are one of the most vulnerable ecosystems to predicted seawater chemistry changes, with reduced calcification rates reported across a range of coral taxa exposed to experimentally altered pH and pCO_2 levels (e.g. Anthony et al. 2008; Anthony et al. 2011; Hoegh-Guldberg et al. 2007). While species vary in degree of vulnerability, the effect of acidification on coral health, calcification, survival, and reproduction/settlement has been shown to be overwhelmingly negative (Anthony et al. 2011; Dufault et al. 2012; Marubini et al. 2008; McCulloch et al. 2012; Nakamura et al. 2011).

Concurrent inflation of sea surface temperatures as a result of elevated CO_{2atm} will directly impact coral calcification and survival on reefs. Many coral species are residing close to, or at the limits of their physiological thermal tolerance (Goreau and Hayes 1994) and may experience reductions in calcification rates as temperatures rise (Jokiel and Coles 1977). Additionally, corals harboring symbiotic zooxanthellae are uniquely sensitive, as many clades of zooxanthellae are unable to tolerate short term anomalous temperature increases (or decreases) and will disassociate themselves from the corals if conditions deteriorate. This expulsion or loss

of zooxanthellae, termed coral bleaching, often results in coral mortality (Hoegh-Guldberg 1999). As shallow coastal waters experience record-breaking summer temperature maxima at a higher frequency and for longer durations (Erez et al. 2011; Hoegh-Guldberg 1999), corals will undoubtedly incur reductions in calcification and survival (Hoegh-Guldberg et al. 2007).

As coral calcification rates are reduced by acidification and temperature increases, reef accretion rates are expected to decline, slowing the overall growth rate of reefs and reducing the resilience of these ecosystems. Simultaneously, the antagonistic processes to reef accretion (bioerosion, physical and chemical breakdown of carbonate) may be accelerated as reefs are subjected to stressors (e.g. rising temperatures) that result in elevated coral mortality and reduced coral cover (DeCarlo et al. 2014). Wide-spread declines in coral coverage facilitate increased bioeroder abundance (Carballo et al. 2013; Holmes 2000; Lopez-Victoria and Zea 2004; Rose and Risk 1985), and may result in reefs shifting from net accretion to net erosion (Enochs et al. 2015).

Increases in bioerosion rates under acidification scenarios have been reported for several bioeroding taxa, including algae (Tribollet et al. 2009), polychaetes, lithophagid bivalves (DeCarlo et al. 2014), and sponges (Fang et al. 2013; Stubler et al. 2014; Wisshak et al. 2012). Sponges are often regarded as the most effective taxonomic group of bioeroders in terms of the amount of $CaCO_3$ removed from coral reefs (Glynn 1997; MacGeachy 1977; Neumann 1966; Rützler 2002; Schönberg 2002), which can range from 0.84-23.00 kg $CaCO_3$ m^{-2} $year^{-1}$ (Hill 1996; Nava and Carballo 2008; Zundelevich et al. 2007). Recent studies have shown that boring rates of an Indo-Pacific sponge, *Cliona orientalis,* increase in pre-infested dead coral skeleton when exposed to predicted future pCO_2 conditions, with no direct negative impacts on the sponge reported (Wisshak et al. 2012; Fang et al. 2013). In the Caribbean, Stubler et al. (2014) induced *Cliona varians* colonization of living *Porites furcata* and found increased erosion rates of *C. varians* under elevated pCO_2 levels.

Bioerosion studies incorporating increased temperature, have found a variety of sponge bioerosion responses. Fang et al. (2013) observed increases in *C. orientalis* bioerosion rates under acidification and warming, however the design was not fully orthogonal (temperature increased in tandem with increasing pCO_2), therefore the individual effects of temperature and acidification were not assessed. A fully crossed design was used by Wisshak et al. (2013) to

evaluate sponge erosion at four levels of pCO_2 and temperature, with limited impacts of temperature on bioerosion reported over an experimental period of 72 h. Unfortunately, the main and interactive effects of increased temperature and acidification on sponge bioerosion rates have not yet been thoroughly evaluated at a temporal scale that allows sponges to physiologically adapt, rather than merely acclimate, to environmental changes.

Additionally, many studies investigating tropical sponge bioerosion have used pre-infested dead substrate and do not account for changes in competitive interactions between sponges and living corals, such as colonization successes (attachment) (but see Stubler et al. 2014). Excavating sponges that harbor zooxanthellae, such as members of the '*Cliona viridis* species complex' (Schönberg 2000) must engage in a direct spatial interaction with corals as they compete for light and space on the reef (Hill 1996). Stubler et al. (2014) found no difference in *Cliona varians* attachment rates to a common Caribbean coral, *Porites furcata*, as pH decreased and concluded that the competitive interaction between these two species will remain unchanged with projected future pH conditions. However, the effects of temperature increases were not evaluated, despite evidence that suggests the competitive vigor of clionaid sponges increases with temperature (Rützler 2002; Siegrist et al. 1992).

The present study investigated the bioerosion rates and competitive interactions (attachment) occurring between the excavating sponge *Cliona varians* (Duchassaing and Michelotti 1864), a prominent Caribbean member of the '*Cliona viridis* species complex,' and a common, hermatypic coral*, Porites furcata* (Lamarck 1816). *C. varians* is commonly found overgrowing and/or eroding *P. furcata,* as well as other hermatypic corals (Hill 1996; Rützler 2002), throughout the Caribbean region. Gamma-stage (massive growth form) *C. varians* individuals are abundant space occupiers in shallow back-reef environments (Diaz 2005; Wiedenmayer 1977) and are considered competitively superior to most coral species (Vicente 1978). These two taxa are therefore ideal study organisms for investigating the effects of acidification and warming on bioerosion and spatial competition.

To accomplish this, a fully orthogonal design was employed with two levels of temperature (ambient and +1°C), three pH levels (ambient: 8.1, moderate: 7.8 and high: 7.6) and two levels of sponge (present and absent). Sponge attachment, growth, bioerosion rate and symbiont health were evaluated for sponges interacting with dead and living coral substrate at

each of the crossed temperature and pH levels. I predicted that the interactive effects of increased acidification and temperature would amplify the erosional activity of *C. varians* and lead to a more rapid degradation of bare coralline substrate. Under the same pH and temperature treatments, we induced sponge colonization of a living coral and measured coral and sponge survival, sponge attachment, erosion rate, and sponge symbiont parameters to quantify the effects of acidification and warming on the sponge-coral interaction. I anticipated that sponge bioerosion would be matched by coral growth, despite stressful environments, and that bioerosion would only outpace net calcification at the extreme pCO_2 and temperature levels.

To integrate the findings of our controlled experiments into the context of the entire reef and further interpret the results of the study, empirical observations of individual coral-sponge interactions were used to develop a stochastic simulation of carbonate change for small coral clusters (i.e., simulated reefs). This approach used estimates of coral survival, sponge presence, attachment, and calcification of both living and dead corals, obtained under our full suite of treatment conditions, to simulate future scenarios of reef development, providing a holistic assessment of growth, survival and competitive dynamics between *Porites furcata* and *Cliona varians*.

Methods and Materials

Flow-through System and Treatments

The experiment began in July 2013 and ran for a total of 20 weeks. This included a 4-week acclimation period, followed by 16-weeks of full-treatment conditions. Using the outdoor unfiltered, seawater system at the Smithsonian Tropical Research Institute's Bocas del Toro Station in Panama, a flow-through pH-stat system was constructed using 12 reservoirs (200 L each) that each fed 12 aquaria (1.8 L). Aquaria (n=144) were gravity-fed treated seawater at a rate of roughly 0.2 L min^{-1}; seawater residence time in each aquarium was ~10 minutes. Reservoirs were randomly assigned pH and temperature treatments, although some modification of temperature treatment assignment was necessary to accommodate position of electrical outlets. Aquariums connected to reservoirs were randomly positioned and assigned sponge treatments (present or absent).

Three acidification treatments were employed; target pH values (NBS scale) were 8.1, 7.8 and 7.6 (hereafter: ambient, moderate, and high acidification, respectively). These values correspond with ambient pCO_2 and the projected levels of pCO_2 for the years 2100 and 2300 guided by the IPCC A1FI/RCP8.5 emissions scenario (IPCC 2007; Meinshausen *et al.* 2011) and models by Caldeira and Wickett (2003). In each reservoir, pH was regulated continuously using a pH controller (Reef Fanatic) connected to a CO_2 regulator (Milwaukee MA957); whenever reservoir pH levels exceeded the target values for the moderate and high acidification treatments, the controller opened a valve that delivered CO_2 gas until target values were restored (Anthony *et al.* 2008; Stubler *et al.* 2014). Calibration of the pH controllers occurred every 2-3 days using NIST standards to ensure minimal drift. No direct CO_2 manipulations occurred for the ambient pH treatments.

Two dynamic levels of temperature were applied, ambient (no temperature alteration) and increased (+1°C over ambient). While tropical water temperatures are expected to rise 1-3°C by the end of the century (multi-model ensemble; IPCC 2001), a conservative temperature increase of only 1°C above ambient was used. Temperature increases were achieved by placing two 800W titanium heaters connected to a temperature controller within the appropriate reservoirs. Due to limitations in electrical supply to the facility, the heat treatments could only be applied to

3 reservoirs (n=12 aquaria at each acidification level), and the remaining reservoirs (n=9) were held at ambient temperature (n=36 aquaria at each acidification level acidification). The flow-through system allowed experimental temperature treatments to mirror the diurnal and seasonal (rainy vs. dry) temperature variations occurring the in the bay where the seawater was drawn, therefore temperature ranged from 28.0-30.71 °C and 29.38-31.64°C for the ambient and increased temperature treatments, respectively. Sponge treatments (present or absent) were applied within the aquariums directly; aquaria were designated as either sponge treatments or non-sponge treatments.

Daily measurements of pH (NBS scale), temperature, salinity, and dissolved oxygen were recorded within each aquarium. HOBO® temperature loggers were placed in one representative aquaria from each reservoir to continuously record temperatures. To characterize full water chemistry parameters of treatments, discrete water samples (300 ml) were taken monthly from each reservoir following NOAA's dissolved inorganic carbon (DIC) sampling protocols. Water samples were immediately preserved by adding 200 µl of a saturated mercuric chloride ($HgCl_2$) solution and stored at 4°C. DIC measurements were made using an EGM-4 Environmental Gas Analyzer ® (PP Systems) after acidification and separation of the gas phase from seawater using a LiquiCel ® Membrane (Membrana). The instrument was calibrated using standards made from sodium bicarbonate and provided a full recovery of Dr. Andrew Dickson's (UCSD, Scripps Institute of Oceanography) certified reference material for total inorganic seawater (Batch 135: 2036 µmol DIC kg seawater^{-1}). Levels of pCO_2, total alkalinity, and $\Omega_{aragonite}$ were calculated by the CO2SYS program based on measured levels of dissolved inorganic carbon, pH (NBS scale), temperature, and salinity using the GEOSECS constants (designed for pH measured on the NBS scale).

Acclimation Period

To minimize stress attributable to sudden pH and temperature changes and reduce physiological shock, a 4-week acclimation period was used to slowly bring subject organisms to full treatment conditions. Once organisms were placed in their respective treatment tanks, the reservoir pH was reduced by 0.1 units per week for all pCO_2 treatments; pH reductions were

staggered by treatment intensity to simultaneously reach targeted values at the same rate (e.g. reductions for the high acidification treatment began immediately to reduce the pH from ambient to 7.6 over 4 weeks, followed by moderate which was reduced during the last 2 weeks of the acclimation period from ambient to 7.8). Temperature treatments were elevated biweekly by 0.5°C, regardless of acidification treatment.

Study species

Approximately 30 small colonies of *Porites furcata* were collected from a continuous reef system on Isla Pastores, Panama (9° 13.551' N, 82° 19.538' W); colonies were separated by a minimum distance of 5 m to increase the likelihood of obtaining multiple genets. After collection, coral specimens were placed in flow-through seawater tables; while submerged, the growing tips from healthy branches were excised to create smaller fragments (3-6 cm in length). Any fragments exhibiting necrotic tissue, bleaching, disease or infestations of bioeroders were discarded, although the complete exclusion of euendolithic microbioeroders living symbiotically within corals (Gutner-Hoch and Fine 2011) was not possible due to the difficulty in visually detecting their presence deep within the carbonate material. After one week of recovery, each *P. furcata* fragment was tagged, and attached to a glass microscope slide using CorAffix® ethyl cyanoacrylate glue. Corals were randomly distributed across treatment tanks (n=7 per aquaria) during the 4-week acclimation period. Thirty large gamma-stage *Cliona varians* forma *varians* individuals (each >300 cm^2 surface area) were also collected at Isla Pastores; standard spicule preparations confirmed species identification. Sponge tissues (no carbonate material was included) were cut into smaller explants (~8 cm^3) taking care to include approximately 4 cm^2 of the ectosome where the majority of zooxanthellae reside, as well as a portion of the choanosome. Explants were allowed a 7-day recovery period in a large raceway to ensure that all sponges were healed before being assigned treatment tanks. Aquaria designated as sponge treatments (n=72 aquaria) were supplied 10 sponge explants. Sponges were placed in the same tanks as corals; however, during the acclimation period sponges and coral units were segregated within treatment tanks to prevent premature interactions from occurring.

To determine differences in sponge bioerosion rates of living and dead corals, skeletal corals were also included within each tank. Skeletal specimens of *P. furcata* were collected from the reef system along Isla Pastores, Panama. Skeletal corals were soaked in a 10% sodium

hypochlorite (bleach) solution for 3 days to remove any coral tissue and epibiota. Skeletal fragments were then soaked in deionized water (DIW) for 24 h, rinsed, and dried to a constant mass at 60 °C. Fragments were tagged with unique IDs and dry weights recorded. All coral and sponge fragments were elevated off the bottom using plastic grating and aquaria were siphoned every 3 days to remove any accumulated sediment or debris; any algal growth was also dislodged and removed by siphoning. Aquaria and tubing were cleaned as necessary to maintain consistent water flow and light levels throughout the experiment.

After the acclimation period, initial buoyant weights of the living corals and sponges were determined following methods of Jokiel et al. (1978) and Davies (1989). Sponges were then loosely secured to coral fragments with cable ties (Schönberg and Wilkinson 2001) and returned to designated treatment tanks. *P. furcata* fragments serving as controls (no sponge attached) were also supplied a small marker cable tie that mimicked the contact area of sponges (3.75 cm^2) to partially account for any abrasion or shading artifacts. Skeletal fragments were not assigned to or placed in tanks until after the acclimation period was over to prevent premature carbonate dissolution. Once acclimation was completed, the skeletal fragments were placed in treatment tanks (n=3 per aquaria); fragments assigned to sponge treatments had sponges attached while fragments designated as controls received a cable tie as a procedural control.

Calcification

Living corals were buoyant weighed before and after the experiment to determine net change in calcium carbonate, hereafter referred to as net calcification. After obtaining final buoyant weights, corals were bleached in 10% sodium hypochlorite solution for a minimum of 24 h, or until all tissue was removed, and skeletal buoyant weights were obtained for tissue correction (Davies 1989). Corals were then soaked overnight in DIW, and triple rinsed before being placed in the drying oven for 72 h at 60 °C. Dry weights were obtained for each coral. To quantify surface area of corals, a standard paraffin wax-dipping procedure was used (Holmes 2008; Stimson and Kinzie 1991), which is an accurate and efficient method for processing large quantities of corals (Veal et al. 2010). Net calcification (mg $CaCO_3$) was then standardized to surface area and number of days the coral spent in the experiment.

Sponge biomass and symbiont health

Prior to experimental breakdown, an underwater pulse amplitude modulated (PAM) fluorometer (Walz, Germany) was used to assess photosynthetic yield of sponges across all pCO_2 and temperature treatments. Photosynthetic yield (*Fv*/*Fm*) measurements were taken at midnight so that sponges were unobtrusively dark-adapted for ~6 h. After PAM measurements were completed, sponges were removed from corals and buoyant weighed to determine biomass changes. After weighing, two small portions were excised (approximately 0.25 g) from the surface of the sponge for zooxanthellae and chlorophyll *a* analysis. Each portion was gently blotted and wet weighed; the chlorophyll *a* portion was placed in a small, labeled foil packet and immediately frozen at -20 °C. Samples were then lyophilized for 24 h and dry weights recorded. Dried sponge pieces were added to aluminum-wrapped vials containing 10 ml of 90% acetone and stored at 4 °C overnight. After 18 h, each sample was centrifuged and the absorbance of the supernatant was measured at wavelengths 630, 647, 664, and 750 nm on a scanning spectrophotometer (SpectraMax® Plus 384). Concentrations of chlorophyll *a* were calculated based on equations provided by Parsons et al. (1984) and standardized to both sponge dry mass and blotted wet weights.

The second sponge portion was used to quantify the density of zooxanthellae. Blotted wet weights were recorded and each sponge piece was immediately homogenized using a mortar and pestle and centrifuged at 2000 rpm for 5 minutes. Supernatant was discarded and 5 ml of filtered seawater was added to re-suspend the pellet; 1 ml of homogenized, re-suspended fluid was removed and 200 µl of Lugol's solution was then added for cell staining and preservation. Zooxanthellae densities were counted under the microscope using a hemocytometer and counts (5 replicates) were normalized to wet tissue weights (cells g^{-1} sponge tissue). The amount of chlorophyll per zooxanthellae cell was calculated by normalizing the chlorophyll *a* concentration to wet mass and dividing by the number of cells found in one gram of wet sponge tissue (µg $cell^{-1}$).

Stochastic Simulation Study

To fully integrate the data from the living and dead corals and to understand how our results might translate to the reef level, empirical values obtained from individual corals within the experiment were used to simulate a series of reef replicates exposed to the future conditions. The simulation incorporated the following values for all treatment combinations obtained from

the actual experiment: number of days of coral survival, net calcification rates for living coral (with and without sponges present), net dissolution rates for dead coral (with and without sponges present), and proportion of successful attachment in sponge treatments. The simulation incorporated data that was not included in the analysis of the mesocosm data, such as the net calcification of corals in the sponge treatments that did not experience any erosion because the sponge never attached. Input values were from individual corals (living/dead), rather than tank means. Miniature reefs (hereafter, 'trays'), consisted of 10 corals initialized at a standardized weight (600 mg) and surface area (25 cm^2). Change in calcium carbonate of trays (n=10 replicate trays per treatment) was simulated under a fully orthogonal combination of temperature, pCO_2, and sponge treatment for 113 days (the duration of the mesocosm experiment from which empirical values were drawn). All simulated corals within the trays began as living corals and were assigned a daily calcification rate sampled with replacement from all calcification rates recorded during the experiment (mg cm^{-2} day^{-1}) for that treatment combination; therefore calcification rates varied daily for each of the modeled corals. Each coral within the trays was randomly appointed a number of days to survive (based on actual survival data), if corals were slated to expire before the end of the model period, corals were then assigned a randomly sampled daily dissolution rate appropriate for the specific treatment combination. A final, tray-wide change in carbonate was then calculated and compared between each treatment combination. Note that because the simulation was based on empirical values obtained from the mesocosm experiments, this model cannot logistically capture new sponge recruitment to corals that were not interacting with a sponge (which may occur in a real-world scenario, but could not occur in our mesocosm experiments). The goal of the simulation was to integrate our survival and sponge attachment data with different calcification/dissolution rates observed between living and dead corals under experimental conditions of temperature, pH and sponge presence, thereby providing insight into how these effects might propagate to higher levels of organization (i.e., the community).

Data Analysis

All data analysis was performed using R statistical software (R Development Core Team 2008). In summary, 1008 living corals and 432 skeletal corals were distributed across 144 tanks (7 live corals per tank and 3 skeletal corals per tank); 72 tanks were designated as sponge

treatments, and 504 sponges were attached to live corals and 216 sponges attached to skeletal corals. The experimental design required the analysis of tank means (n=144), rather than individual coral/sponge units (which served as pseudoreplicates of each other). Due to the imbalance of the design (n=12 aquaria per increased temperature/acidification treatment; n=36 aquaria per ambient temperature/acidification treatments), survival of corals (number of days in experiment) and net calcification/dissolution (mg $CaCO_3$ cm^{-2} day^{-1}) of dead and living corals, were analyzed by permutation of the residuals (n=5000, without replacement) in a three-way analysis of variance with three fixed factors (temperature, pH, sponge) following the guidelines of Anderson and ter Braak (2003). Only corals that had sponges that successfully attached (as opposed to merely cable-tied on, but not attached) were considered in the analysis of sponge treatments for survival and calcification response. Homogeneity of variances were tested for each term using the non-parametric Fligner-Killeen test prior to permutation tests, as this is the only assumption of permutation tests. Sponge biomass changes, photosynthetic yield, zooxanthellae density, and chlorophyll *a* (μg $cell^{-1}$) were analyzed by permutation of the residuals (n=5000, without replacement) in a two-way analysis of variance with the fixed factors, temperature and pH (Anderson and ter Braak 2003). To determine whether attachment was a response to the treatments, the proportion of sponges that were attached to corals in each tank was calculated, and tank means were used to assess attachment for each treatment. The mean proportion of sponges attached to corals was analyzed using a binomial generalized linear model with permutation test (package: glmperm) with temperature and pH as factors. Water chemistry parameters that were not directly measured were calculated using the CO2SYS package and a two-way ANOVA was used to confirm that unique treatments were established.

Simulated data from the stochastic model was analyzed using regression with empirical variable selection (REVS) that uses a branch-and-bound all-subsets regression to quantify the empirical support for predictor variables (Goodenough et al. 2012). This model is more effective than stepwise, full or all-subsets regression models (Goodenough et al. 2012) because it selects models by the amount of empirical support, rather than systematically adding or removing variables based on AIC or p-values. The REVS model was run using the *leaps* function in R following the code provided by Goodenough et al. (2012). Mean tray carbonate change from the simulated data was the dependent variable and parameters included as predictor variables were temperature, pH, sponge presence, and coral survival. Because survival was directly related to

carbonate loss (due to very different empirical living coral calcification and dead coral dissolution rates), the mean of the lower quartile of days coral survived from each tray was used to represent the tray-wide survival in the regression model. Once the best fit model was determined, tests were run to check the assumptions of 1) normality for the dependent variable and residuals, 2) multicollinearity, 3) homogeneity of variance, 4) independence of the residuals. After failing to meet the assumptions of homogeneity of variance and normality of the residuals, the *avas* function in the R package acepack was used to fit additive, variance-stabilized models (AVAS) to the optimally transformed dependent variable so that the additive model fits well and has constant variance. Transformed predictor variables were then once again tested for all aforementioned assumptions.

Results

Water Chemistry and Treatment Parameters

Mean temperature (± SD) of the ambient temperature treatment aquaria was 29.7 ± 0.4 °C (range was 28.0-30.71 °C) and 30.7 ± 0.5 °C in the elevated heat treatment (range was 29.38-31.64°C) over the 16-week experimental period. Temperature changes tracked natural fluctuations in ambient water temperatures and were consistently ~ 1 °C higher than ambient values. Mean (± SD) pH (NBS scale) was 8.13 ± 0.01, 7.77 ± 0.02, and 7.57 ± 0.03 for the ambient, moderate and high acidification treatments, which corresponded to mean pCO_2 of 539 ± 48 µatm, 1294 ± 107 µatm, and 2245 ± 263 µatm. Seawater carbonate chemistry parameters for each treatment can be found in Table 1. It is worth noting that ambient pCO_2, total alkalinity and DIC values are slightly higher than expected for coral reef ecosystems; this is likely due to the influence of mangroves surrounding the bay where the seawater intake lies for the flow-through system (Zablocki et al. 2011).

Survival

All sponges survived the duration of the experiment. In general, moderate mortality was observed for the corals, with 64% of all corals surviving until the end of the experiment. Permutation of the residuals from a three-way ANOVA analyzing coral survival as a function of sponge presence, temperature and pH, revealed that temperature and sponge both significantly affected the number of days of coral survival; no interactions were found (Table 2). Surprisingly, higher temperatures increased the mean survival of corals from 85.3 days (± 29.4) to 103.1 (± 15.9) ($F_{(1,98)}$=10.422, P<0.001). Sponge presence also positively affected coral survival ($F_{(1,98)}$: 4.62, P=0.03); mean days survived was 85.4 (± 28.7) when no sponge was present, and 98.0 (± 23.8) when sponge was present and attached.

Attachment

Within sponge treatments, *C. varians* colonization of *P. furcata* was induced; however, successful attachment did not always occur. Some sponges readily attached to corals (24% experiment-wide attachment success), while the remainder did not attach and existed as free-living individuals. All donor sponges were gamma-stage individuals, which may have

predisposed the explants to exist independent of substrate. The proportion of sponges successfully attached to living corals was not significantly affected by pH or temperature. The high acidification treatment had the highest mean percent attached, at 30%, and the increased temperature treatment also had a higher percentage attached at 33%. The lowest attachment was found in the moderate acidification treatments, which was less than 20% regardless of temperature. Sponge attachment to dead coral skeletons was not significantly different among treatments, with similar patterns found to the live coral (see Table 3 for summary).

Calcification

Living coral calcification (mg $CaCO_3$ cm^{-2} day^{-1}) was significantly affected by temperature and sponge presence ($F_{(1,100)}$=7.68, P=0.007 and $F_{(1,100)}$=11.26, P=0.001, respectively; Table 2). When sponges were attached, sponge presence resulted in greater loss of $CaCO_3$ for living corals (Figure 1). Temperature also resulted in greater $CaCO_3$ loss; no significant interactions were found. Interestingly, pH did not affect calcification (P=0.38) for living corals. For corals without sponges attached, the highest mean calcification rate was found in the ambient temperature*high acidification treatment (0.22 ± 0.16 mg $CaCO_3$ cm^{-2} day^{-1}), and the lowest was found in the increased temperature*ambient acidification treatment (0.08 ± 0.12 mg $CaCO_3$ cm^{-2} day^{-1}; Table 3). For corals with attached sponges, the greatest loss of $CaCO_3$ was found in the increased temperature*moderate acidification treatment (-0.13 ± 0.22 mg $CaCO_3$ cm^{-2} day^{-1}). Dead coral skeletons performed as expected, with a significant effect of acidification ($F_{(2,92)}$=4.80, P=0.007), however neither sponge nor temperature were significant (Figure 2). Mean carbonate loss was 63% greater in the moderate and high acidification treatments than the ambient. Mean carbonate loss was -0.015 (± 0.02) mg $CaCO_3$ cm^{-2} day^{-1} in ambient, -0.041 (± 0.06) in moderate and -0.039 (± 0.03) for the high acidification treatments (Table 3).

Living corals continued to accrete carbonate at ambient temperatures, regardless of pH levels or sponge presence; however, when temperatures and acidification simultaneously increase, as is expected in the future, sponge erosion outpaces coral growth. The net loss of $CaCO_3$ at elevated temperatures when sponges are actively eroding at moderate and high levels of acidification is -0.02 (± 0.31) kg $CaCO_3$ m^{-2} $year^{-1}$ and -0.46 (± 0.82) kg $CaCO_3$ m^{-2} $year^{-1}$, respectively. This implies that sponge bioerosion rates of living corals will be amplified by pH changes in the future, but only if temperature increases simultaneously, which seems to play a

key role in tipping the balance from net accretion to net erosion. However, erosion of non-living carbonate is primarily a result of corrosive seawater, whether bioerosion is occurring or not.

Sponge Biomass Changes

Throughout the course of the experiment, sponges elongated, receded and overall altered their original standardized size (2 cm^3). To determine whether sponges achieved an overall net growth in temperature or pH treatments, sponge biomass changes were calculated from the difference between initial and final buoyant weights (Lesser, 2006). For sponges interacting with living corals, sponge biomass was not significantly different in either increased temperatures or pH treatments. Sponges on dead coral fragments, however, were significantly impacted by temperature, with a significant interaction between pH and temperature ($F_{(1,54)}$: 7.58, P=0.009 and $F_{(2,54)}$: 3.99, P=0.02, respectively). Overall growth was low, regardless of treatments (Table 4).

Sponge symbiont parameters

Zooxanthellae densities (cells g^{-1} sponge tissue) of sponges attached to living corals did not differ significantly by either temperature or acidification. The amount of chlorophyll extracted was standardized to number of zooxanthellae cells (ug $cell^{-1}$); there was no significant difference between treatments. Sponges attached to skeletal fragments showed no significant difference in density of zooxanthellae or chlorophyll *a* content per zooxanthellae cell. There was a significant main effect of acidification on photosynthetic yield (Fv/Fm) of sponges attached to living corals ($F_{(2,59)}$=4.72, P=0.01); there was also a significant interaction between pH and temperature ($F_{(2,59)}$=5.37, P=0.008). In the ambient temperatures, photosynthetic yield plateaued between moderate and high acidification levels, however with increased temperatures, the highest yield was in the high pCO_2 treatment. For the dead corals, only the main effect of pH was significant ($F_{(2,63)}$=3.771, P=0.03), with photosynthetic yield of the symbionts increasing with acidification, regardless of temperature. See Table 4 for mean values (± 1 SD) of all symbiont parameters in each treatment combination.

Simulation Model

The regression model that met all assumptions and best explained reef-level carbonate change ($\Delta CaCO_3$) included temperature and coral survival as predictor variables (adjusted R^2 = 0.14, $P<0.001$). Temperature played an important role in reducing calcification of living corals in the mesocosm experiment; it is therefore intuitive that within the simulated data, temperature along with the amount of time a coral survived, ultimately dictated $\Delta CaCO_3$ at the reef level. Temperature also resulted in statistically higher survival days in the mesocosms (Table 2), therefore the relationship between temperature and survival lends itself to complicated results. The maximum $\Delta CaCO_3$ of any tray with all corals surviving until the end of the simulation in an increased temperature treatment was 23% less than the maximum $\Delta CaCO_3$ in a tray in ambient temperature with all coral surviving until the end of the simulation. In trays where coral survival was <100%, $\Delta CaCO_3$ was 56% lower in the increased temperature trays, as compared to the ambient temperature (although caution should be used when interpreting this value, as only n=2 trays in the increased temperature treatments experienced less than 100% survival). Averaging over all treatments, when survival was <100%, calcification was 17% lower. Mean values of $\Delta CaCO_3$ in each treatment remained positive and experienced net accretion over the modeled 113-day period, however, the $\Delta CaCO_3$ was lowest in the increased temperature*high acidification*sponge treatment, which was an order of magnitude less than any other treatment, even though survival was 100% for all trays. When compared to the ambient temperature*ambient acidification *sponge treatment, coral trays exhibited 90% less calcification, indicating that, although not statistically significant, the combination of high temperatures, acidification and sponge erosion will reduce calcification even if all corals survive.

Discussion

This study tested the relative contributions of the main and interactive effects of acidification and temperature on sponge-mediated bioerosion of living and dead *P. furcata* fragments. Previous studies of clionaid bioerosion rates using pre-infested carbonate substrate found a positive relationship with acidification and warming but did not aim to include the direct interactions (attachment and subsequent erosion) occurring between living coral and boring sponges (e.g. Wisshak et al. 2012; Fang et al. 2013). One previous study investigated changes in sponge attachment rates to coral under experimentally altered pH conditions, yet no differences were found, prompting Stubler et al. (2014) to suggest that the interaction between *P. furcata* and *C. varians,* will remain unchanged at acidification levels expected this century, although no temperature increases were assessed. The data presented here demonstrate differential impacts of sponge bioerosion and attachment for living and dead corals under acidification and warming scenarios.

Experimental manipulation of acidification, warming and sponge presence

The effects of acidification and warming on the bioerosion rates and interaction between *P. furcata* and *C. varians* were evaluated over an experimental period of 16 weeks (following a 4-week acclimation period). Temperature, rather than acidification, had the most dramatic impact on net coral calcification. A temperature increase of 1°C over ambient resulted in reduced coral calcification and corresponded with increased sponge bioerosion (Table 3). Coral calcification typically follows a Gaussian distribution, with calcification increasing until an optimal temperature, generally 25-28°C, is achieved and then declining (Coles and Jokiel 1978; Jokiel and Coles 1977; Marshall and Clode 2004). Corals inhabiting areas where mean temperatures are below the optimal calcification range will experience increasing calcification with temperature (Bessat and Buigues 2001; Cooper et al. 2012; Lough and Barnes 2000), whereas those already residing within or beyond this range may experience reductions in calcification as temperatures increase (e.g. De'Ath et al. 2009). In this study, temperatures were consistently >28 °C which is representative of the mean ambient water temperatures in the region, therefore reported *P. furcata* calcification rates are assumed to have been representative of those *in situ*. While some studies have observed increased coral calcification at temperatures exceeding 28 °C (Edmunds et

al. 2012; *Porites rus*), it is likely that the addition of 1 °C over ambient caused temperatures to exceed the optimal temperature range of *P. furcata* and resulted in reduced calcification rates.

Surprisingly, acidification did not have a significant effect on net coral calcification despite the $\Omega_{aragonite}$ approaching undersaturation in the highest acidification treatments. Stubler *et al.* (2014) reported reduced calcification of *P. furcata* after 8 weeks of exposure to elevated pCO_2 (~750 μatm). Potential explanations for the differences in calcification response to acidification between this study and that of Stubler et al. (2014) may be that the present study incorporated a longer experimental duration (16 weeks), an acclimation period (4 weeks), and a large number of experimental units (n=144 tanks), derived from 1008 coral fragments. The acclimation period may have allowed the corals to physiologically adapt and alter their response to pH changes. There is currently no consensus as to whether an acclimation period should be standard procedure for acidification studies; however, the contrariety in the response of *P. furcata* to acidification between Stubler et al. (2014) and this study suggest that the use of an acclimation period may alter coral calcification response. Previous studies of congeners have shown both resilience (*Porites rus*; Edmunds et al. 2012) and sensitivity (*Porites lobata*, Anthony *et al.* 2008) to acidification and warming.

The literature is replete with discrepancies of coral calcification response to pH changes, McCulloch et al. (2012) related this to the species-specific ability of corals to control the pH of their internal calcifying fluid. Active transport of Ca^{2+}, DIC and H^+ ions enables corals to alter the pH of their internal calcifying fluid, which facilitates coral calcification even when ambient seawater carbonate chemistry is less than favorable, albeit at an increased metabolic cost. Corals harboring zooxanthellae may be able to up-regulate pH more readily due to the excess energy supplied by photosynthetic symbionts, which may benefit from increased CO_2 availability (McCulloch et al. 2012). While the calcifying fluid pH has not been measured for *P. furcata*, two other *Porites* species exhibit low gradients between the calcifying fluid and seawater pH, suggesting that the genera may expend less energy calcifying relative to other coral genera (McCulloch et al. 2012). The species-specific physiology may be one reason why the corals in this experiment did not exhibit large reductions in calcification, even at high pCO_2 levels.

Sponge bioerosion resulted in decreased net calcification rates compared to control corals in the same treatments (Figure 1, Table 3), reducing the overall $CaCO_3$ accretion of *P. furcata*.

Despite sponge presence, net calcification remained positive in all treatment combinations except when acidification treatments were crossed with elevated temperatures (Table 3), suggesting that temperature may be an important factor affecting *C. varians* erosion. On the contrary, sponge bioerosion did not increase the net dissolution of dead coral skeletons. This finding differs from prior studies examining the effects of sponge erosion on carbonate substrate under combined treatments of increasing temperature and acidification. Previous studies of tropical (*C. orientalis*) and temperate (*C. celata*) sponge erosion of carbonate substrate show that acidification leads to increased bioerosion rates over time scales ranging from 72 hours to 8 weeks (Duckworth and Peterson 2012; Fang et al. 2013; Wisshak et al. 2012; Wisshak et al. 2013; Wisshak et al. 2014), however *C. varians* did not follow the same pattern. This study found that acidification alone influenced dissolution rates of dead corals, whether a sponge was attached and eroding or not.

One explanation may be that the elevated levels of pCO_2 used in our study were much higher than those used in other studies and were sustained for almost double the time used in prior analogous experiments. At more moderate pCO_2 increases (500-750 μatm), sponge erosion increased with increasing pCO_2, and was found to be a significant driver in bioerosion of carbonate material (Fang et al. 2013; Wisshak et al. 2013). Our study, which used pCO_2 treatments of ~1200 and 2200 μatm, found that net dissolution of coral skeletons was primarily driven by passive carbonate dissolution, and relatively unaffected by sponge-mediated erosion.

Many microborers, like the ubiquitous *Ostreobium* sp., inconspicuously exist within carbonate material and could have contributed to the net dissolution of coral skeletons. The dead coral skeletons were bleached prior to experimental manipulation, which effectively removed all living organisms; however, 16 weeks is ample time for colonization by endolithic microborers such as algae, cyanobacteria or fungi (Grange et al. 2014). Measurable rates of biogenic carbonate dissolution due to endolithic organisms have been reported under elevated pCO_2 and temperature scenarios (Reyes-Nivia et al. 2013; Tribollet et al. 2009), and may have contributed to the changes that were attributed to passive dissolution in dead coral skeletons. While no visible signs of microbioerosion or infestations by endoliths were found in our live corals, the possibility that they contributed to the net calcification cannot be discounted. Regardless, net calcification was not significantly different by pH treatment, suggesting that microbioerosion was negligible and did not impart any bias in the interpretation of results.

Changes in sponge biomass displayed no clear patterns between living and dead corals. The sponge biomass was underestimated for attached sponges since some portion of the sponge could not be sufficiently removed from within the carbonate material. This likely affected the final biomass values, resulting in artificially inflated negative growth rates reported for attached sponges (Table 3). Biomass changes are notoriously difficult to measure for excavating sponges due to their morphological plasticity and tendency to grow within carbonate substrate (Fang et al. 2013). Buoyant weight changes (which primarily measure spicule mass) may not have been the best method to capture nuanced differences in the sponge tissue growth and spicule generation in *C. varians* (Fang et al. 2013).

Other studies have shown that bleaching in zooxanthellate sponges (Fang et al. 2013; Wisshak et al. 2013) is amplified by increases in temperature and pCO_2, however this was not the case in our study. Sponge symbiotic zooxanthellae did not exhibit significant changes in population density or chlorophyll *a* concentrations in any of the treatment combinations. The photosynthetic yield of the symbionts, however, was positively affected by acidification, and a significant interaction between acidification and temperature was found for sponges attached to dead corals. Photosynthetic response of zooxanthellae symbionts to acidification varies widely among invertebrates such as corals, anemones and sponges, with negative (Iguchi et al. 2012), positive (Langdon and Atkinson 2005) and null (Kroeker et al. 2010) effects being reported; the reasons for the wide variation in photosynthetic yield are unclear.

Attachment, which represented one form of direct competitive interaction that can occur between *C. varians* and *P. furcata,* was not affected by either temperature or acidification; number of sponges attached to dead coral skeletons was independent of treatments. Experiment-wide attachment was low (24%), however the values observed in this study were similar to those found by Schönberg and Wilkinson (2001) who attempted to induce *C. orientalis* colonization of several *Porites* species and achieved a 25-30% success rate for sponge infestation. In a similar study, Stubler et al. (2014) monitored weekly attachment rates between *C. varians* and *P. furcata* and found no differences due to acidification. Our results suggest that no alteration of the interaction between *C. varians* and *P. furcata* occurs as a result of acidification and/or warming. Our original hypothesis that coral survival would be negatively affected by sponge presence was unsupported by our results. On the contrary, sponge presence increased the mean days of

survival for *P. furcata* by 21% across all treatments. While the reason for increased coral survival is unclear, interpretation at a larger reef-scale should be cautiously approached as further overgrowth and shading of coral tissue will undoubtedly result in coral mortality.

In addition to sponge presence, temperature positively impacted the survival of *P. furcata*. The increased temperature treatment was 30.7 ± 0.5 °C; however, the corals were collected from a very shallow reef that frequently experiences water temperatures in excess of 30 °C in the dry season. Perhaps the corals (and their zooxanthellae) were already adapted to higher temperatures and were therefore unaffected by the heat stress imposed during the experiment, a phenomenon observed in corals inhabiting shallow lagoons in Indonesia (Hoeksema 1991; Rowan 2004). An alternative hypothesis is that the corals may have responded to the temperature stress by shifting their energy towards maintenance and survival, which may also explain the reduced calcification and growth.

Modeling future reef erosion

The experimental portion of this study looked at sponge erosion of living and dead coral in elevated temperature and acidification scenarios, however it did not evaluate impacts at the reef level. Therefore a stochastic model was developed to empirically simulate the response of a reef system allowed to experience growth, bioerosion, death and dissolution. The results of our simulation study were used as a tool to quantitatively guide the interpretation and discussion of the observed sponge and coral responses to warming and acidification from the controlled experiment, given the divergent importance of each factor for living and dead coral substrates.

Our simulation showed that temperature and the demographic survival response of corals to global climate change might be the most important factors in determining net calcification on future coral reefs. Temperature reduced calcification for the simulated *P. furcata* reef; however, survival was 22% higher in elevated temperatures than in ambient. Caribbean reefs have already begun (and will continue) to experience temperature increases related to climate change (Kuffner et al. 2014), therefore understanding the relative impact of temperature is paramount. Our study indicates that for *P. furcata* reefs that survive temperature increases, net calcification may not be as detrimentally impacted by acidification or bioerosion as previously postulated. Reef-wide changes in calcification will be largely dependent on direct temperature effects and the ability of

P. furcata to survive these changes, rather than as a function of reduced calcification rates or acidification *per se*.

The relatively short time period of the mesocosm study and the use of a single coral species from which empirical values were drawn does not take into consideration the long-term or species-specific responses to elevated physiological stress or its impact on reproductive effort and recruitment success. McCulloch et al. (2012) modeled the future response of several coral species to warming (+ 2 °C) and acidification (~1000 μatm) and found a slight calcification increase, despite acidification, for coral species that are able to up-regulate pH. This suggests that if species capable of up-regulating pH are able to maintain up-regulation without unforeseen physiological consequences, then acidification and warming may not directly inhibit calcification. However, any species unable to maintain, or up-regulate internal calcifying fluid pH will likely succumb to decreases in calcification and growth as temperature and pCO_2 increase; further, the intrinsic capacity of corals and zooxanthellae for long-term adaptation is still unknown.

The simulation was parameterized with empirical data from our experimental manipulation and is not meant to be a predictive model; therefore, we caution against extrapolation beyond the scope of the experimental parameters. Additionally, the low adjusted-R^2 (0.14) may suggest that additional important parameters were absent from our investigation; I argue against this interpretation as alternative models provided better adjusted-R^2 values (from 0.20 to 0.61), however these models were discounted as they failed one or more assumptions. The model that explained the most variance (R^2=0.61) included temperature, coral survival and sponge presence, however, the assumptions of homogeneity of variance and normality of the residuals could not be met.

The sponge presence treatment in the simulation study included all coral calcification data even when a sponge did not attach to a coral, therefore all coral-sponge interactions—even those that did not lead to bioerosion—were incorporated. This resulted in a wide range of calcification responses to sponge presence, but added in an important scenario that was necessarily excluded from the mesocosm experiment analysis. Unfortunately, the addition of the sponge term resulted in the increased heterogeneity of variance and a subsequent diagnostic rejection of the model explaining the most variance. Ecologically, sponge contribution may

become increasingly important, even if bioerosion is not amplified, as abundance and prevalence of boring sponges increase on reefs (Schönberg and Ortiz 2008).

According to Glynn (1997), increases in bioerosion occur when 1) conditions causing coral death become more frequent or 2) when conditions favor bioeroders over calcifying organisms. Unfortunately, both of these criteria will be increasingly met under projected future scenarios; the challenge lies in determining the relative contribution of each to the overall decline in reef functioning. While there is growing evidence that the abundance of bioeroders and their carbonate removal rates, will increase under future conditions, this study demonstrates the need to expand our understanding of the interactions between bioeroders and hermatypic organisms.

References

Anderson M, ter Braak C (2003) Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* 73:85-113

Anthony KR, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America* 105:17442-17446

Anthony KRN, Maynard JA, Diaz-Pulido G, Mumby PJ, Marshall PA, Cao L, Hoegh-Guldberg OVE (2011) Ocean acidification and warming will lower coral reef resilience. *Global Change Biology* 17:1798-1808

Bates N, Astor Y, Church M *et al.* (2014) A time-series view of changing ocean chemistry due to ocean uptake of anthropogenic CO_2 and ocean acidification. *Oceanography* 27:126-141

Bessat F, Buigues D (2001) Two centuries of variation in coral growth in a massive *Porites* colony from Moorea (French Polynesia): a response of ocean-atmosphere variability from south central Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* 175:381-392

Caldeira K, Wickett M (2003) Oceanography: Anthropogenic carbon and ocean pH. *Nature* 425:365

Carballo JL, Bautista E, Nava H, Cruz-Barraza JA, Chavez JA (2013) Boring sponges, an increasing threat for coral reefs affected by bleaching events. *Ecology and Evolution* 3:872-886

Coles SL, Jokiel PL (1978) Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Marine Biology 43:*209-216

Cooper TF, O'leary RA, Lough JM (2012) Growth in Western Australia corals in the Anthropocene. *Science* 335:593-596

Davies PS (1989) Short-term growth measurements of corals using an accurate buoyant weight technique. *Marine Biology* 101:389-395

De'ath G, Lough JM, Fabricius KE (2009) Declining coral calcification on the Great Barrier Reef. *Science* 323:116-119

DeCarlo TM, Cohen AL, Barkley HC *et al.* (2014) Coral macrobioerosion is accelerated by ocean acidification and nutrients. *Geology*. doi:10.1130/G36147.1

Diaz MC (2005) Common sponges from shallow marine habitats from Bocas del Toro region, Panama. *Caribbean Journal of Science* 41:465-475

Duckworth AR, Peterson BJ (2012) Effects of seawater temperature and pH on the boring rates of the sponge Cliona celata in scallop shells. *Marine Biology* 160:27-35

Dufault AM, Cumbo VR, Fan TY, Edmunds PJ (2012) Effects of diurnally oscillating pCO_2 on the calcification and survival of coral recruits. *Proceedings. Biological sciences / The Royal Society* 279:2951-2958

Edmunds PJ, Brown D, Moriarty V (2012) Interactive effects of ocean acidification and temperature on two scleractinian corals from Moorea, French Polynesia. *Global Change Biology* 18:2173-2183

Enochs IC, Manzello DP, Carlton RD, Graham DM, Ruzicka R, Colella MA (2015) Ocean acidification enhances the bioerosion of a common coral reef sponge: implications for the persistence of the Florida Reef Tract. *Bulletin of Marine Science* 91

Erez J, Reynaud S, Silverman J, Schneider K, Allemand D (2011) Coral calcification under ocean acidification and global change. In *Coral reefs: an ecosystem in transition* (pp. 151-176). Springer Netherlands.

Fang JK, Mello-Athayde MA, Schönberg CH, Kline DI, Hoegh-Guldberg O, Dove S (2013) Sponge biomass and bioerosion rates increase under ocean warming and acidification. *Global Change Biology* 19:3581-3591

Fang JK, Schönberg CH, Kline DI, Hoegh‐Guldberg O, Dove S (2013) Methods to quantify components of the excavating sponge Cliona orientalis Thiele, 1900. *Marine Ecology* 34:193-206

Grange J, Rybarczyk H, Tribollet A (2014) Successions of Microbioeroding Communities over a Year Period with a Monthly Resolution: Impact on Biogenic Dissolution in Dead Corals (New Caledonia). *2014 Ocean Science Meeting*.

Glynn PW (1997) Bioerosion and coral reef growth: a dynamic balance. In: *Life and Death of Coral Reefs.* (ed Birkeland C) pp 68-95. New York, Chapman & Hall.

Goodenough AE, Hart AG, Stafford R (2012) Regression with empirical variable selection: description of a new method and application to ecological datasets. *Plos One* 7: e34338

Goreau TJ, Hayes RL (1994) Coral bleaching and ocean "hot spots". *Ambio,* 23, 176-180.

Gutner-Hoch E, Fine M (2011) Genotypic diversity and distribution of *Ostreobium quekettii* within scleractinian corals. *Coral reefs* 30:643-650

Hill MS (1996) Symbiotic zooxanthellae enhance boring and growth rates of the tropical sponge *Anthosigmella varians* forma *varians*. *Marine Biology* 125:649-654

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50:839-866

Hoegh-Guldberg O, Mumby PJ, Hooten AJ *et al.* (2007) Coral Reefs Under Rapid Climate Change and Ocean Acidification. *Science* 318:1737-1742

Hoeksema BW (1991) Controls of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy. *Marine Ecology Progress Series* 74:225-237

Holmes G (2008) Estimating three-dimensional surface areas on coral reefs. *Journal of Experimental Marine Biology and Ecology* 365:67-73

Holmes KE (2000) Effects of eutrophication on bioeroding sponge communities with the description of a new West Indian sponges, *Cliona* spp. (Porifera: Hadromerida: Clionidae). *Invertebrate Biology* 119:125-138

Iguchi A, Ozaki S, Nakamura, T, et al. (2012) Effects of acidified seawater on coral calcification and symbiotic algae on the massive coral *Porites australiensis*. *Marine Environmental Research* 73:32-36

IPCC (2007) Climate Change 2007: Synthesis Report. (ed Change IPOC) pp 26-73, Valencia, Spain.

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In: *IPCC.* (eds Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM) pp 1535, Cambridge.

Jokiel PL, Coles SL (1977) Effects of temperature on the mortality and growth of Hawaiian reef corals. *Marine Biology 43*:201-208

Jokiel PL, Maragos JE, Franzisket L (1978) Coral growth: buoyant weight technique. *UNESCO Monographs on Oceanographic Methodology* 5:529-542

Kroeker,KJ, Kordas RL, Crim RN, Singh GG (2010) Meta‐analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology letters* 13:1419-1434

Kuffner IB, Lidz BH, Hudson JH, Anderson JS (2014) A century of ocean warming on Florida Keys coral reefs: historic in situ observations. *Estuaries and Coasts,*10.1007/s12237-014-9875-5

Langdon C, Atkinson MJ (2005) Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *Journal of Geophysical Research: Oceans (1978–2012)*, 110 (C9).

Lesser MP (2006) Benthic–pelagic coupling on coral reefs: Feeding and growth of Caribbean sponges. *Journal of Experimental Marine Biology and Ecology* 328:277-288

Lopez-Victoria M, Zea S (2004) Storm-mediated coral colonization by an excavating Caribbean sponge. *Climate Research* 26:251-256

Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology* 245:225-243

Macgeachy J (1977) Factors controlling sponge boring in Barbados reef corals. *Proceedings of the 3rd International Coral Reef Symposium* 2:477-483

Marshall AT, Clode P (2004) Calcification rate and the effect of temperature in a zooxanthellate and an azooxanthellate scleractinian reef coral. *Coral Reefs* 23:218-224

Marubini F, Ferrier-Pagès C, Furla P, Allemand D (2008) Coral calcification responds to seawater acidification: a working hypothesis towards a physiological mechanism. *Coral Reefs* 27:491-499

McCulloch M, Falter J, Trotter JA, Montagna P (2012) Coral resilience to ocean acidification and global warming through pH up-regulation. *Nature Climate Change* 2:623-627

Meinshausen M, *et al.* (2011) The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic change* 109:213-241

Nakamura M, Ohki S, Suzuki A, Sakai K (2011) Coral larvae under ocean acidification: survival, metabolism, and metamorphosis. *Plos One* 6:e14521

Nava H, Carballo JL (2008) Chemical and mechanical bioerosion of boring sponges from Mexican Pacific coral reefs. *The Journal of Experimental Biology* 211:2827-2831

Neumann AC (1966) Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*. *Limnology and Oceanography* 11:92-108

Orr JC, *et al.* (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681-686

Parsons TR, Maita Y, and CM Lalli (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, New York.

R Development Core Team (2008) R: A language and environment for statistical computing (ed Computing RFFS), Vienna, Austria.

Reyes‐Nivia C, Diaz‐Pulido G, Kline D, Hoegh-Guldberg O, Dove S (2013) Ocean acidification and warming scenarios increase microbioerosion of coral skeletons. *Global Change Biology* 19:1919-1929

Rose CS, Risk MJ (1985) Increase in *Cliona deletrix* infestation of *Montastrea cavernosa* heads on an oragnically polluted portion of the Grand Cayman fringing reef. *Marine Ecology* 6:345-363

Rowan R (2004) Thermal adaptation in reef coral symbionts. *Nature* 430:742

Rützler K (2002) Impact of crustose Clionid sponges on Caribbean reef corals. *Acta Geologica Hispanica* 37:61-72

Schönberg CHL (2000) Sponges of the *'Cliona viridis* complex' - a key for species identification. *Proceedings of the 9th International Coral Reef Symposium*.

Schönberg CHL (2002) Substrate effects on the bioeroding Demosponge *Cliona orientalis*. 1. Bioerosion rates. *Marine Ecology* 23:313-326

Schönberg CHL, Ortiz J-C (2008) Is sponge bioerosion increasing? In: *Proceedings of the 11th International Coral Reef Symposium.* pp 527-530, Fort Lauderdale, FL, USA.

Schönberg CHL, Wilkinson CR (2001) Induced colonization of corals by a clionid bioeroding sponge. *Coral Reefs* 20:69-76

Siegrist HG, Bowman RG, Randall RH, Stifel PB (1992) Diagenetic effects related to hot-water effluent in a modern reef on Guam. *Pacific Science* 46:379

Stimson J, Kinzie Iii RA (1991) The temporal pattern and rate of release of zooxanthellae from the reef coral Pocillopora damicornis (Linnaeus) under nitrogen-enrichement and control conditions. *Journal of Experimental Marine Biology and Ecology* 153:63-74

Stubler AD, Furman BT, Peterson BJ (2014) Effects of pCO_2 on the interaction between an excavating sponge, *Cliona varians*, and a hermatypic coral, *Porites furcata*. *Marine Biology* 161:1851-1859

Tribollet A, Godinot C, Atkinson M, Langdon C (2009) Effects of elevated pCO_2 on dissolution of coral carbonates by microbial euendoliths. *Global Biogeochemical Cycles* 23: doi:10.1029/2008GB003286.

Veal CJ, Holmes G, Nunez M, Hoegh-Guldberg O, Osborn J (2010) A comparative study of methods for surface area and three-dimensional shape measurements of coral skeletons. *Limnology and Oceanography: Methods* 8:241-253

Veron JE, Hoegh-Guldberg O, Lenton TM *et al.* (2009) The coral reef crisis: the critical importance of <350 ppm CO_2. *Marine Pollution Bulletin* 58:1428-1436

Vicente VP (1978) An ecological evaluation of the West Indian demosponge *Anthosigmella varians* (Hadromerida: Spirastrellidae). *Bulletin of Marine Science* 28:771-779

Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. *Marine Pollution Bulletin* 51:570-579

Wiedenmayer F (1977) Shallow-water sponges of the Western Bahamas. Basel: Birkhauser, Verlag.

Wisshak M, Schönberg CHL, Form A, Freiwald A (2012) Ocean acidification accelerates reef bioerosion. *Plos One* 7:e45124

Wisshak M, Schönberg CHL, Form A, Freiwald A (2013) Effects of ocean acidification and global warming on reef bioerosion—lessons from a clionaid sponge. *Aquatic Biology* 19:111-127

Wisshak M, Schönberg CHL, Form A, Freiwald A (2014) Sponge bioerosion accelerated by ocean acidification across species and latitudes? *Helgoland Marine Research*.

Zablocki JA, Andersson AJ, Bates NR (2011) Diel aquatic CO_2 system dynamics of a Bermudian mangrove environment. *Aquatic Geochemistry* 17:841-859

Zeebe RE, Wolf-Gladrow DA (2001) CO2 in seawater: equilibrium, kinetics, isotopes (Vol. 65). *Gulf Professional Publishing.*

Zundelevich A, Lazar B, Ilan M (2007) Chemical versus mechanical bioerosion of coral reefs by boring sponges--lessons from *Pione* cf. *vastifica*. *The Journal of Experimental Biology* 210:91-96

Figures and Tables

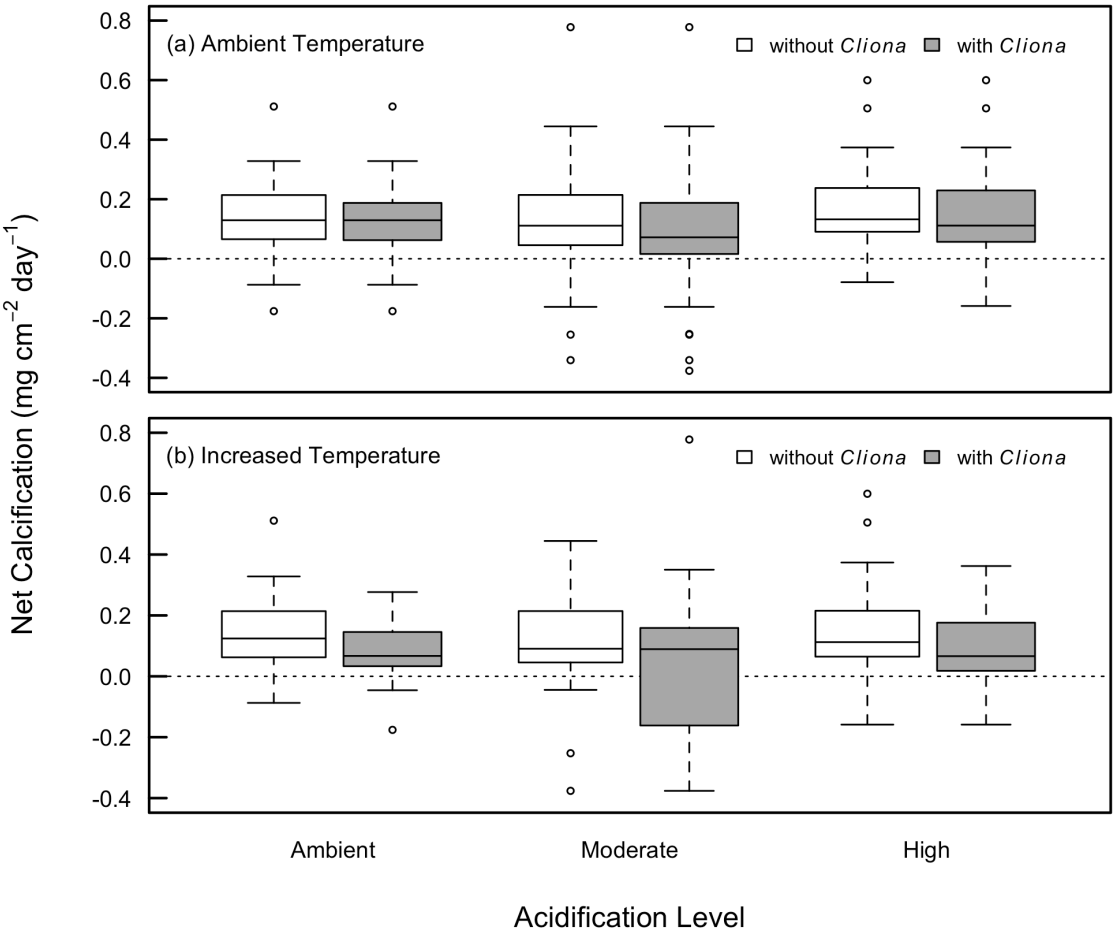

Figure 1. Net calcification (mg cm^{-2} day^{-1}) in living *Porites furcata* at a) ambient and b) increased temperatures in each acidification level over the 113-day experimental period. Corals with and without *Cliona varians* present are denoted in gray and white, respectively. Boxplots mark median values with a central bar, the 1st and 3rd quartiles with a box, the ±1.5 interquartile ranges with 'Tukey whiskers' and outliers with open circles.

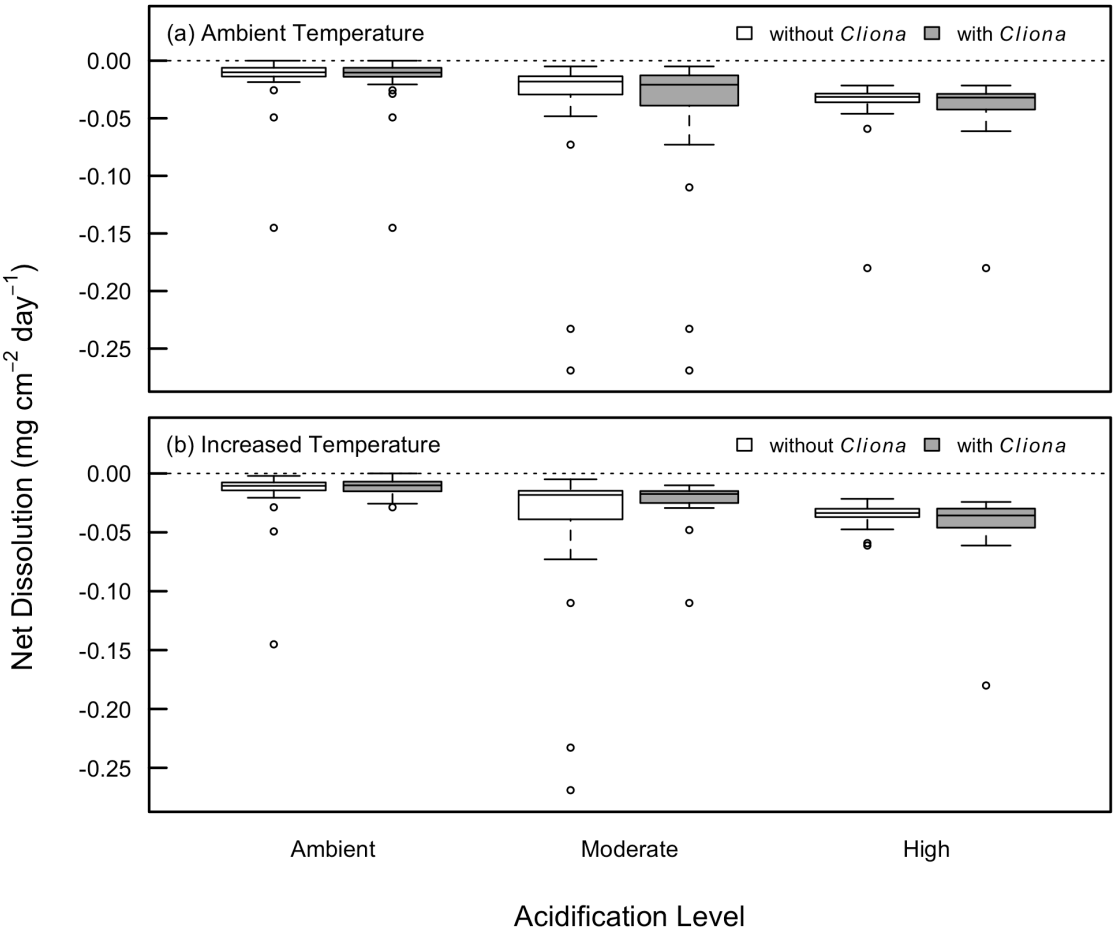

Figure 2. Net dissolution (mg $CaCO_3$ cm^{-2} day^{-1}) in dead *Porites furcata* skeletons at a) ambient and b) increased temperatures in each acidification level over the 113-day experimental period. Skeletons with and without *Cliona varians* present are denoted in gray and white, respectively. Boxplots mark median values with a central bar, the 1st and 3rd quartiles with a box, the ±1.5 interquartile ranges with 'Tukey whiskers' and outliers with open circles.

Table 1. Summary of measured (*) and calculated (**) seawater chemistry parameters represented as means ± 1 standard deviation. Reported values of temperature, salinity and pH (NBS scale) were measured daily in aquaria. Total scale pH, and carbonate chemistry values were calculated from preserved DIC samples and represent the mean values from treatment reservoirs at three time-points collected mid-day at the beginning, middle and end of the experiment.

	Ambient Temperature			Increased Temperature		
	Ambient Acidification	Moderate Acidification	High Acidification	Ambient Acidification	Moderate Acidification	High Acidification
Temperature (°C)*	29.77 ± 0.4	29.76 ± 0.4	29.76 ± 0.4	30.67 ± 0.5	30.79 ± 0.5	30.62 ± 0.4
Salinity*	33.38 ± 0.5	33.35 ± 0.6	33.34 ± 0.6	33.35 ± 0.5	33.29 ± 0.5	33.37 ± 0.5
pH (NBS scale)*	8.14 ± 0.01	7.78 ± 0.02	7.56 ± 0.03	8.13 ± 0.01	7.76 ± 0.04	7.58 ± 0.03
pH(Total scale)**	8.04 ± 0.01	7.68 ± 0.04	7.48 ± 0.04	8.03 ± 0.01	7.66 ± 0.05	7.50 ± 0.04
Total Alkalinity ** (μmol kg^{-1} seawater)	2724 ± 209	2535 ± 162	2595 ± 156	2612 ± 131	2538 ± 113	2704 ± 214
DIC * (μmol kg^{-1} seawater)	2438 ± 190	2448 ± 152	2578 ± 154	2338 ± 114	2448 ± 110	2679 ± 215
pCO_2**(μatm)	540 ± 54	1284 ± 90	2253 ± 232	534 ± 14	1337 ± 185	2234 ± 328
$\Omega_{aragonite}$ **	3.4 ± 0.2	1.56 ± 0.18	1.04 ± 0.11	3.26 ± 0.03	1.56 ± 0.16	1.13 ± 0.11

Table 2. Results of permutation tests; the interactive and main effects of temperature, pH and sponge are evaluated for a) living coral calcification (mg cm^{-2} day^{-1}), b) dead coral dissolution (mg cm^{-2} day^{-1}), c) coral survival (days). Significant factors are indicated by asterisks (***).

A ANOVA	df	SS	MS	*F*-value	*P* (perm)
Net Calcification					
Temperature	1	0.20	0.20	7.68	0.007***
pH	2	0.05	0.03	0.98	0.38
Sponge	1	0.29	0.29	11.26	0.001***
Temp * pH	2	0.01	0.004	0.15	0.86
Temp * Sponge	1	0.02	0.02	0.81	0.37
pH * Sponge	2	0.03	0.01	0.37	0.59
Temp * pH * Sponge	2	0.04	0.02	0.59	0.45
Residuals	100	2.56	0.03	---	---
B ANOVA	df	SS	MS	*F*-value	*P* (perm)
Net Dissolution					
Temperature	1	0.0001	0.0001	0.085	0.78
pH	2	0.014	0.007	4.803	0.007***
Sponge	1	0.0001	0.0001	0.084	0.77
Temp * pH	2	0.0003	0.0001	0.093	0.91
Temp * Sponge	1	0.003	0.003	1.995	0.16
pH * Sponge	2	0.002	0.001	0.689	0.50
Temp * pH * Sponge	2	0.009	0.004	2.901	0.07
Residuals	92	0.138	0.0014	---	---
C ANOVA	df	SS	MS	*F*-value	*P* (perm)
Coral Survival					
Temperature	1	6932.5	6932.5	10.42	<0.001***
pH	2	319.3	159.6	0.24	0.80
Sponge	1	3075.4	3075.4	4.62	0.03***
Temp * pH	2	1783.0	891.5	1.34	0.27
Temp * Sponge	1	839.8	839.8	1.26	0.26
pH * Sponge	2	3961.9	1981.0	2.98	0.054
Temp * pH * Sponge	2	458.1	229.1	0.34	0.72
Residuals	98	65186.9	665.2	---	---

Table 3. Coral survival, net calcification and dissolution rates, as well as the proportion of sponges attached and change in sponge biomass are reported for living and dead corals (mean ± 1 standard deviation).

		Ambient Temperature			Increased Temperature		
		Ambient Acidification	Moderate Acidification	High Acidification	Ambient Acidification	Moderate Acidification	High Acidification
Living Corals, Sponge Present	Coral survival (days)	85.2 ± 30.1	105.8 ± 17.3	106.0 ± 17.8	97.2 ± 27.0	112.8 ± 0.5	98.5 ± 24.0
	Net Calcification (mg $CaCO_3$ cm^{-2} day^{-1})	0.10 ± 0.12	0.05 ±0.35	0.12 ± 0.11	0.05 ± 0.07	-0.13 ± 0.22	-0.005 ± 0.085
	Proportion Attached	0.23 ± 0.25	0.16 ± 0.2	0.22 ± 0.26	0.28 ± 0.27	0.17 ± 0.14	0.54 ± 0.25
	Attached Sponge Biomass Change (mg day^{-1})	-0.97 ± 1.1	-1.4 ± 1.3	-0.06 ± 3.5	1.37 ± 5.6	-1.7 ± 2.3	-0.2 ± 0.75
	N (tanks)	12	8	9	4	4	6
Living Corals, Sponge Absent	Coral survival (days)	83.4 ± 28.3	80.1 ± 33.3	82.8 ± 32.6	108.3 ± 7.6	110.3 ± 12.2	92.1 ± 27.0
	Net Calcification (mg $CaCO_3$ cm^{-2} day^{-1})	0.17 ± 0.14	0.15 ± 0.13	0.22 ± 0.16	0.08 ± 0.12	0.15 ± 0.13	0.12 ± 0.15
	N (tanks)	18	18	17	4	6	6
Dead Coral Skeletons, Sponge Present	Net Dissolution (mg $CaCO_3$ cm^{-2} day^{-1})	-0.01 ± 0.01	-0.02 ±0.01	-0.05 ± 0.06	-0.02 ± 0.01	-0.11 ± 0.01	-0.04 ± 0.01
	Proportion Attached	0.33 ± 0.34	0.17 ± 0.26	0.19 ± 0.3	0.22 ± 0.27	0.05 ± 0.14	0.46 ± 0.36
	Attached Sponge Biomass Change (mg day^{-1})	-0.48 ± 1.62	-0.75 ± 0.83	-0.82 ± 1.24	-0.3 ± 0.36	-0.04 ± 2.0	0.84 ± 1.66
	N (tanks)	11	6	7	3	2	5
Dead Coral Skeletons, Sponge Absent	Net Dissolution (mg $CaCO_3$ cm^{-2} day^{-1})	-0.02 ± 0.03	-0.05 ± 0.07	-0.03 ± 0.01	-0.01 ± 0.004	-0.02 ± 0.001	-0.03 ± 0.004
	N (tanks)	18	18	17	6	5	6

Table 4. Tank means (± 1 SD) of symbiont parameters for sponges attached to living or dead corals in each of the treatment combinations.

		Ambient Temperature			Increased Temperature		
		Ambient Acidification	Moderate Acidification	High Acidification	Ambient Acidification	Moderate Acidification	High Acidification
Sponges Attached to Living Corals	Zooxanthellae Density (cells g^{-1} wet tissue)	$6.1 \times 10^5 \pm 3.4 \times 10^5$	$5.5 \times 10^5 \pm 3.1 \times 10^5$	$6.1 \times 10^5 \pm 4.6 \times 10^5$	$4.4 \times 10^5 \pm 2.8 \times 10^5$	$6.9 \times 10^5 \pm 2.9 \times 10^5$	$6.5 \times 10^5 \pm 4.4 \times 10^5$
	Chlorophyll *a* (ug g^{-1} wet tissue)	80.5 ± 56.8	59.2 ± 28.4	57.0 ± 31.7	60.9 ± 27.9	65.2 ± 38.9	66.8 ± 29.9
	Chlorophyll *a* (ng $cell^{-1}$)	0.019 ± 0.02	0.017 ± 0.01	0.02 ± 0.03	0.018 ± 0.01	0.01 ± 0.008	0.018 ± 0.02
	Fv/Fm (Photosynthetic Yield)	0.67 ± 0.06	0.69 ±0.05	0.69 ± 0.05	0.67 ± 0.05	0.67 ± 0.04	0.71 ± 0.03
Sponges Attached to Dead Coral Skeletons	Zooxanthellae Density (cells g^{-1} wet tissue)	$6.3 \times 10^5 \pm 3.7 \times 10^5$	$8.6 \times 10^5 \pm 5.7 \times 10^5$	$5.8 \times 10^5 \pm 3.3 \times 10^5$	$4.9 \times 10^5 \pm 4.3 \times 10^5$	$8.0 \times 10^5 \pm 4.7 \times 10^5$	$7.2 \times 10^5 \pm 3.6 \times 10^5$
	Chlorophyll *a* (ug g^{-1} wet tissue	79.6 ± 39.7	65.2 ± 44.7	63.9 ± 28.7	51.3 ± 22.6	60.6 ± 23.9	65.3 ± 23.4
	Chlorophyll *a* (ng $cell^{-1}$)	0.017 ± 0.01	0.015 ± 0.02	0.014 ± 0.01	0.016 ± 0.01	0.01 ± 0.002	0.012 ± 0.01
	Fv/Fm (Photosynthetic Yield)	0.68 ± 0.04	0.69 ± 0.05	0.70 ± 0.03	0.68 ± 0.05	0.69 ± 0.03	0.71 ± 0.02

Chapter 7
Conclusions

Conclusions

While often overlooked, sponges are a fundamental component of coral reefs, exhibiting greater diversity and biomass than corals (Diaz and Rützler 2001), creating and destroying habitat (Butler et al. 1995), contributing to nutrient and carbon cycling (Hutchings 1986; de Goeij et al. 2013; Mueller et al. 2014) and aiding in water filtration (Peterson et al. 2006, Southwell et al. 2008). Growing evidence suggests that anthropogenic impacts are reducing the resilience of coral reef ecosystems; however, since many reef studies are largely coral and macroalgal-centric, the potential impacts to sponges have received less attention. Correlative and experimental evidence that environmental stressors may be influencing sponge ecology exists (Butler et al. 1995; Bannister et al. 2010; Duckworth et al. 2012; Fang et al. 2013), but are still woefully limited in comparison to studies of anthropogenic effects on other reef organisms. This discontinuity in understanding reef ecology inhibits our ability to truly comprehend the resultant ecological perturbations rendered by the anthropogenic era.

Sedimentation and sponges

Sedimentation has been shown to negatively affect the distribution (Bell and Smith 2004), abundance (Powell et al. 2014), size and reproductive output (Whalan et al. 2007, Bannister et al. 2010, Bannister et al. 2012) of sponges. The length of time that sedimentation occurs, as well as the rate and intensity of sediment accumulation, have been evaluated at several scales. Experimental studies of sponge response to sedimentation have opted to either expose sponges to constantly suspended sediment (Gerrodette and Flechsig 1979; Tompkins-MacDonald and Leys 2008) or directly apply a specified amount of sediment to sponge subjects (Lohrer et al. 2006; Pineda et al. 2015). These types of studies have occurred over a period of hours (Tompkins-MacDonald and Leys 2008; Bannister et al. 2012), days (Gerrodette and Flechsig 1979), or weeks (Pineda et al. 2015; Bannister et al. 2012) and included a wide variety of sediment ranges. Field observations and correlative studies on the effects of sediment typically involve a survey investigation (Bannister et al. 2010; Bell and Smith 2004) or monitoring the performance of individuals and/or communities (Carballo 2006; Maldonado et al. 2008) in an attempt to link differences in sponge demographics to sedimentation regimes. While generally conducted over a longer period of time than experimental studies, these studies do not occur at timescales associated with observing true community change (years).

In the studies presented here, the rate of sediment accumulation was not constant among all locations, but rather, was elevated during high wind events at Pear Tree, the location closest to recent and ongoing coastal development. During wind events, greater amounts of silts and clays were found at Pear Tree, with a higher proportion of insoluble sediments in this size class (Chapter 1). Although not currently experiencing elevated sedimentation, Discovery Bay was previously subjected to higher rates of fine-grained sedimentation when the adjacent bauxite mine was more productive and not subjected to the more stringent environmental regulations that currently govern its operations (MacDonald and Perry 2003; Perry and Taylor 2004). Due to this legacy of sedimentation, as well as a higher degree of coastal development, Discovery Bay is considered an intermediate location despite not currently experiencing elevated levels of sedimentation. While the direct link between sedimentation and sponge community change is difficult to establish, the adult sponge population (Chapter 1), initial recruiting sponge community (Chapter 2) and community succession (Chapter 3) were monitored to identify if sponge communities differed among locations experiencing a sedimentation gradient.

Chapters 1-3 present evidence that coastal development and episodic sedimentation result in subtle differences among Jamaican sponge communities and that future shifts in communities may occur. Of the adult (existing) populations surveyed (Chapter1), Dairy Bull (low sediment supply and coastal development) consistently had higher sponge abundance, diversity, species richness and a more distinct community composition from the other two locations, Pear Tree (elevated sediment, high coastal development) and Discovery Bay (currently low sediment, moderate coastal development). Other than sedimentation, there were no parameters measured that differed between these three locations (which historically had similar sponge communities), yet Discovery Bay, despite experiencing low sedimentation, was often more closely related to Pear Tree, rather than Dairy Bull. While unexpected, the patterns found in the adult sponge population at Discovery Bay may be a remnant of previous human impacts and sediment disturbance, or a result of some other unmeasured difference between locations. Although similar to Pear Tree in sponge diversity and several other ecological measures of community structure (Table 1), Discovery Bay did not lack the conspicuous species that were absent at Pear Tree, nor did it exhibit reduced morphological diversity. It is likely that the Discovery Bay community represents an intermediate between Dairy Bull and Pear Tree, however, the gradient observed

between Pear Tree and Dairy Bull may not have been extreme enough to elicit a statistically distinct intermediate community type.

Regardless of the differences noted in adult sponge populations (Chapter 1), sponge settlement (monitored every spring/summer and fall/winter over a three year period) was similar in diversity and percent cover across all locations (Chapter 2). The lack of measurable differences between sponge diversity and percent cover at these locations suggests that sponge settlement is not limited by larval supply. While sponge settlement was similar across all locations (seasonal sampling), differences emerged between the three locations when sponge recruitment was evaluated annually (annual sampling), namely Pear Tree exhibited reduced diversity and percent cover when compared to Dairy Bull and Discovery Bay (Table 1). Given the similarities between initial sponge settlement, the distinct reduction in diversity and sponge cover of successfully recruited sponges at Pear Tree seems to implicate post-settlement mortality as a primary driver in distinguishing these communities (Chapter 2).

To further understand long-term community development, succession was monitored over 30 months at the same locations. The focus of Chapter 3, however, was primarily on overall community trajectories, not just sponge species. Pear Tree was distinguished from the Discovery Bay and Dairy Bull communities by lower recruitment after 30 months, as indicated by statistically higher amounts of bare space at Pear Tree, which is indicative of an overall lack of recruitment. This provides further evidence that post-settlement mortality is occurring at Pear Tree and propagating community trajectory changes. The higher amount of bare space and reduced recruitment of all organisms at Pear Tree is concerning, and indicates that sedimentation, likely along with other ecological stressors, had a negative impact on the survival and development of the cryptic community.

In conclusion, the information garnered from Chapters 1-3 suggests that the direct and indirect effects of sedimentation and coastal development have detrimental affects on the existing adult populations (Chapter 1), newly settled and recruited sponges (Chapter 2) and developing benthic communities (Chapter 3). Our results suggest that monitoring vulnerable groups, such as sponges, may be a productive way to gauge the impact of sedimentation; however, time periods of monitoring must be longer than 6 months, as community differences don’t begin to emerge until at least 12 months. This has important implications for groups active

in assessing coral reef ecosystems; our studies indicate that yearlong monitoring periods are essential for ensuring that anomalous events do not drive our understanding of a system. Sedimentation is generally thought of as a constant stressor, but these studies show that even periodic sedimentation may play a role in structuring community ecology.

Table 1. Light grey shading indicates that the location was statistically different from other locations in post-hoc pairwise comparisons, whereas dark grey shading signifies statistical similarity with the other locations shaded in dark grey. Trajectories are indicated by words describing the direction of differences found, where relevant. Note that Discovery Bay often aligns itself with Pear Tree in the surveys of adult populations (Chapter 1), however the ecological patterns of settlement/recruitment at Discovery Bay are more similar to Dairy Bull than Pear Tree (Chapter 2).

Sediment Accumulation Rate			
	Pear Tree	Discovery Bay	Dairy Bull
HIGH wind events	high		
LOW wind events			
Chapter 1: Surveys of Existing Sponge Populations			
Abundance	low	intermediate	high
Species Richness			
Diversity			
Sponge Size/Volume			
Community Composition			
Chapter 2: Seasonal and Annual Recruitment			
SEASONAL Sponge Diversity			
SEASONAL Sponge Percent Cover			
SEASONAL Sponge Community Composition			
ANNUAL Sponge Diversity	low		
ANNUAL Sponge Percent Cover	low		
ANNUAL Sponge Community Composition			

Ocean acidification, warming, and sponges

Sponges are thought to be generally tolerant of the temperature and acidification changes predicted for the upcoming century (Duckworth et al. 2012; Bell et al. 2013; Lee 2012). Bioeroding or boring sponges have been of particular interest in the context of acidification due to their ability to physically and chemically break down carbonate material. The possibility that these boring sponges will work in tandem with acidification is of interest, and the desire to understand feedbacks that could accelerate acidification effects has been heightened, particularly as evidence increases that boring sponges are increasing in prevalence on reefs (e.g. Rose and Risk 1985; Ward-Paige et al. 2005).

There have been several studies of sponge erosion using the Pacific species *Cliona orientalis*, a member of the zooxanthellate '*Cliona viridis* complex'. However, all of these studies investigated the response of the sponge eroding dead, previously infested substrate under acidification scenarios. This particular group of boring sponges, characterized by their symbiotic zooxanthellae, must compete for space and light on the reef and often directly interact with coral species, yet there have been no previously published studies of boring sponge/living coral interactions in the face of acidification. The studies conducted here focused on the effects of acidification (Chapter 4) and the combined effects of acidification and warming (Chapter 5) on the interaction between a Caribbean member of the '*Cliona viridis* complex', *Cliona varians*, and the coral, *Porites furcata*.

Chapter 4 sought to determine whether a forced interaction between *C. varians* and a living coral in the presence of acidification would result in increased sponge erosion efficiency, as was previously reported for congeners interacting with dead coral. Interestingly, sponge competitive viability (measured by the rate of attachment), was neither unaffected by acidification. Survival of corals and sponges was also unaffected by acidification, even at the highest level of pCO_2. However, decreased coral calcification and increased sponge erosion efficiency were found at anticipated end-of-century pCO_2 levels. This study was the first to examine living coral and sponge interactions under future acidification scenarios and further supported the need to assess species interactions under changing conditions.

While acidification is expected to occur at a faster rate in the near future, temperature changes (particularly anomalously high temperature events) have already begun to occur in many tropical ecosystems as a result of elevated atmospheric carbon dioxide. Chapter 5 expanded upon the research reported in Chapter 4 and evaluated the interactive effects of temperature and acidification on the interaction between *C. varians* and *P. furcata*, including a comparison between sponge erosion of dead and living substrate. The study incorporated a longer experimental period (16 weeks) and applied several methodological advances, such as an acclimation period (4 weeks), to create a more comprehensive study with broader relevance to ecosystems worldwide. The empirical, individual-level data from the experiment were then used to quantitatively integrate the relative importance of temperature, acidification and coral mortality on sponge erosion and carbonate change at the community or reef level in a stochastic simulation model. Chapter 5 suggests differential impacts of temperature, pCO_2 and sponge bioerosion for living and dead corals. Living coral calcification was significantly reduced by temperature and sponge treatments, with no significant effect of pCO_2, while dead coral dissolution was primarily driven by pCO_2, regardless of sponge presence or seawater temperature. This study challenged the rapidly materializing paradigm that sponge erosion is heightened by ocean acidification and that bioerosion may trump the erosive capabilities of acidic seawater. While this may be true for dead substrate, this study presented the first evidence that sponge erosion of living coral substrate may not occur in the manner originally predicted. In conclusion, this study suggests that future acidification and warming studies should include ecologically relevant time scales, adequate acclimation periods, interactions, and multiple levels of community organization to better understand and predict ecosystem-level response to future environmental conditions.

Anthropogenic impacts and sponges

Sponges are the primary biogenic habitat and structure on many tropical reefs, and may be increasing in both abundance and overall contribution to ecological functioning (Goreau 1992; Bell et al. 2013; Schönberg and Fromont 2012). Anecdotally, tropical sponges are thought to be more resilient to physical stress (e.g. storms, damage from predation) than other reef organisms, such as coral, due to their ability to rapidly regenerate and recover from fractionation.

However, our understanding of sponge stressors, such as predation, light attenuation, temperature, pH/pCO_2, and degraded water quality, has been advanced in recent years by experimental studies directly evaluating sponge response to each stressor. From these studies, it is apparent that, just like corals, some sponge species and communities are sensitive while others are more resilient. For almost any stressor, examples of negative *and* positive (and occasionally neutral) sponge responses can be found within the literature; for example, decreasing light (Thacker 2005; Maughan 2001), algal blooms (Wall et al. 2012; Peterson et al. 2006), sedimentation (e.g. Lohrer et al. 2006; Carballo 2006; Powell et al. 2014), temperature change and acidification (Duckworth and Peterson 2012; Fang et al. 2014; Wisshak et al. 2012; Chapter 5; Chapter 6; Bell et al. 2013). The variability of species-specific responses to stressors further demands that more intense investigations be made for a variety of species and at the community level to better understand the response of sponge communities to environmental changes. The consequences of anthropogenic environmental alteration to sponge ecology are, therefore, of increasing importance and should be incorporated into management and monitoring programs whenever possible. This dissertation represents an effort to understand how anthropogenic changes have and will affect the ecology, biology and functional roles of sponges on ecologically relevant timescales.

References

Bannister RJ, Battershill CN, de Nys R (2010) Demographic variability and long-term change in a coral reef sponge along a cross-shelf gradient of the Great Barrier Reef. *Marine and Freshwater Research* 61:389-396

Bannister RJ, Battershill CN, de Nys R (2012) Suspended sediment grain size and mineralogy across the continental shelf of the Great Barrier Reef: Impacts on the physiology of a coral reef sponge. *Continental Shelf Research* 32:86-95

Bell JJ (2008) The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science* 79:341-353

Bell JJ, Davy SK, Jones T, Taylor MW, Webster NS (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology* 19:2613-2624

Bell JJ, Smith D (2004) Ecology of sponge assemblages (Porifera) in the Wakatobi region, south-east Sulawesi, Indonesia: richness and abundance. *Journal of the Marine Biological Association of the UK* 84:581-591

Butler MJ, Hunt JH, Herrnkind WF, Childress MJ, Bertelsen R, Sharp W, Matthews T, Field JM, Marshall HG (1995) Cascading distubances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. *Marine Ecology Progress Series* 129:119-125

Carballo JL, Bautista E, Nava H, Cruz-Barraza JA, Chavez JA (2013) Boring sponges, an increasing threat for coral reefs affected by bleaching events. *Ecology and Evolution* 3:872-886

Colvard NB, Edmunds PJ (2011) Decadal-scale changes in abundance of non-scleractinian invertebrates on a Caribbean coral reef. *Journal of Experimental Marine Biology and Ecology* 397:153-160

de Goeij JM, van Oevelen D, Vermeij MJ, Osinga R, Middelburg JJ, de Goeij AF, Admiraal W (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science* 342:108-110

Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean reefs. *Bulletin of Marine Science* 69:535-546

Duckworth, A. R. and B. J. Peterson. 2012. Effects of seawater temperature and pH on the boring rates of the sponge *Cliona celata* in scallop shells. *Marine Biology* 160:27-35.

Duckworth AR, West L, Vansach T, Stubler A, Hardt M (2012) Effects of water temperature and pH on growth and metabolite biosynthesis of coral reef sponges. *Marine Ecology Progress Series* 462:67-77

Fang JK, Mello-Athayde MA, Schönberg CH, Kline DI, Hoegh-Guldberg O, Dove S (2013) Sponge biomass and bioerosion rates increase under ocean warming and acidification. *Global Change Biology* 19:3581-3591

Gerrodette T, Flechsig AO (1979) Sediment-induced reduction in the pumping rate of the tropical sponge *Verongia lacunosa*. *Marine Biology* 55:103-110

Goreau TJ (1992). Bleaching and reef community change in Jamaica: 1951–1991. *American Zoologist* 32: 683-695.

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas JA, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929-933

Hutchings P (1986) Bioerosion of coral reefs. *Oceanus* 29:71

Lee S (2012) Adaptive tolerance to ocean acidification in the marine sponge *Chondrilla nucula.* Masters Thesis. University of Mississippi.

Lohrer AM, Hewitt JE, Thrush SF (2006) Assessing far-field effects of terrigenous sediment loading in the coastal marine environment. *Marine Ecology Progress Series* 315:13-18

Maughan BC (2001). The effects of sedimentation and light on recruitment and development of a temperate, subtidal, epifaunal community. *Journal of Experimental Marine Biology and Ecology* 256: 59-71

Mora C (2008) A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society B: Biological Sciences* 275:767-773

Mueller B, de Goeij JM, Vermeij MJ, Mulders Y, van der Ent E, Ribes M, van Duyl FC (2014) Natural diet of coral-excavating sponges consists mainly of dissolved organic carbon (DOC). *Plos One* 9:E90152

Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Marine Ecology Progress Series* 376:295-306

Pandolfi J, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955-958

Peterson BJ, Chester CM, Jochem FJ, Fourqurean JW (2006) Potential role of sponge communities in controlling phytoplankton blooms in Florida Bay. *Marine Ecology Progress Series* 328:93-103

Pineda MC, Duckworth A, Webster N (2015) Appearance matters: sedimentation effects on different sponge morphologies. *Journal of the Marine Biological Association of the United Kingdom*:1-12

Powell A, Smith DJ, Hepburn LJ, Jones T, Berman J, Jompa J, Bell JJ (2014) Reduced Diversity and High Sponge Abundance on a Sedimented Indo-Pacific Reef System: Implications for Future Changes in Environmental Quality. *Plos One* 9:e85253

Rose CS, Risk MJ (1985) Increase in *Cliona deletrix* infestation of *Montastrea cavernosa* heads on an oragnically polluted portion of the Grand Cayman fringing reef. *Marine Ecology* 6:345-363

Schönberg CHL, Fromont J (2012). Sponge gardens of Ningaloo Reef (Carnarvon Shelf, Western Australia) are biodiversity hotspots. *Hydrobiologia*, 687:143-161

Schönberg CHL, Ortiz J-C Is sponge bioerosion increasing? *Proceedings of the 11th International Coral Reef Symposium*

Schutte VGW, Selig ER, Bruno JF (2010) Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Marine Ecology Progress Series* 402:115-122

Southwell M, Weisz JB, Martens CS, Lindquist N (2008) In situ fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. *Limnology and Oceanography* 53:986-996

Thacker RW (2005) Impacts of shading on sponge-cyanobacteria symbioses: A comparison between host-specific and generalist associations. *Integrative and Comparative Biology* 45:369-376

Tompkins-MacDonald GJ, Leys SP (2008) Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. *Marine Biology* 154:973-984

Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. *Marine Pollution Bulletin* 51:570-579

Whalan S, Battershill C, Nys R (2007) Variability in reproductive output across a water quality gradient for a tropical marine sponge. *Marine Biology* 153:163-169

Wisshak, M., C. H. L. Schönberg, A. Form, and A. Freiwald. 2012. Ocean acidification accelerates reef bioerosion. *Plos One* **7**.

Wall CC, Rodgers B, Gobler CJ, Peterson BJ (2012) Responses of loggerhead sponge, Spechiospongia vesparium during harful cyanobacterial blooms in a sub-tropical lagoon. *Marine Ecology Progress Series* 451:31-43

References

Abramoff MD, et al. (2004) Image processing with ImageJ. *Biophotonics International* 11:36-42

Aerts L (1998) Sponge/coral interactions in Caribbean reefs: analysis of overgrowth patterns in relation to species identity and cover. *Marine Ecology Progress Series* 175:241-249

Aerts L, van Soest RWM (1997) Quantification of sponge/coral interactions in a physically stressed reef community, NE Colombia. *Marine Ecology Progress Series* 148:125-134

Albright R, Langdon C (2011) Ocean acidification impacts multiple early life history processes of the Caribbean coral *Porites astreoides*. *Global Change Biology* 17:2478-2487 doi:10.1111/j.1365-2486.2011.02404.x

Alleyne D, Boxill I (2003) The impact of crime on tourist arrivals in Jamaica. *International Journal of Tourism Research* 5:381-391

Alongi DM (2002) Present state and future of the world's mangrove forests. *Environmental Conservation* 29: 331-349

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46

Anderson M, ter Braak C (2003) Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* 73:85-113

Andersson AJ, Gledhill D (2013) Ocean acidification and coral reefs: effects on breakdown, dissolution and net ecosystem calcification. *Annual Review of Marine Science* 5:321-348

Anthony KR, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America* 105:17442-17446

Anthony KRN, Maynard JA, Diaz-Pulido G, Mumby PJ, Marshall PA, Cao L, Hoegh-Guldberg OVE (2011) Ocean acidification and warming will lower coral reef resilience. *Global Change Biology* 17:1798-1808

Arnold SN, et al. (2010) Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology Progress Series* 414:91-105

Aronson RB, Precht WF, Toscano M, Koltes K (2002) The 1998 bleaching event and its aftermath on a coral reef in Belize. *Marine Biology* 141:435-447

Asgaard U, Bromley RG (2008) Echinometrid sea urchins, their trophic styles and corresponding bioerosion. In: Wisshak M, Tapanila L (eds) Current Developments in Bioerosion. Springer-Verlag, Berlin, pp 279-304

Babcock R, Smith, L (2002) Effects of sedimentation on coral settlement and survivorship. In *Proceedings of the Ninth International Coral Reef Symposium, Bali, 23-27 October 2000* 1:245-248

Bakus GJ, Kawaguchi M (1984) Toxins from marine organisms: studies on antifouling. In: Bolis L, Zadunaisky J, Gilles R (eds.) *Toxins, drugs, and pollutants in marine animals*. Springer-Verlag, Berlin.

Bannister RJ, Battershill CN, de Nys R (2010) Demographic variability and long-term change in a coral reef sponge along a cross-shelf gradient of the Great Barrier Reef. *Marine and Freshwater Research* 61:389-396

Bannister RJ, Battershill CN, de Nys R (2012) Suspended sediment grain size and mineralogy across the continental shelf of the Great Barrier Reef: Impacts on the physiology of a coral reef sponge. *Continental Shelf Research* 32:86-95

Bates N, Astor Y, Church M *et al.* (2014) A time-series view of changing ocean chemistry due to ocean uptake of anthropogenic CO_2 and ocean acidification. *Oceanography* 27:126-141

Bell JJ (2004) Evidence for morphology-induced sediment settlement prevention on the tubular sponge Haliclona urceolus. *Marine Biology* 146:29-38

Bell JJ (2008) The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science* 79:341-353

Bell JJ, Barnes DKA (2000a) The distribution and prevalence of sponges in relation to envrionmental gradients within a temperate sea lough: vertical cliff surfaces. *Diversity and Distributions* 6:283-303

Bell JJ, Barnes DJ (2000b) The influences of bathymetry and flow regime upon the morphology of sublittoral sponge communities. *Journal of the Marine Biological Association of the United Kingdom* 80:707-718

Bell JJ, Barnes DJ, Turner J (2002) The importance of micro and macro morphological variation in the adaptation of a sublittoral demosponge to current extremes. *Marine Biology* 140:75-81

Bell JJ, Smith D (2004) Ecology of sponge assemblages (Porifera) in the Wakatobi region, south-east Sulawesi, Indonesia: richness and abundance. *Journal of the Marine Biological Association of the UK* 84:581-591

Bell JJ, Davy SK, Jones T, Taylor MW, Webster NS (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology* 19:2613-2624

Bell JJ, McGrath E, Biggerstaff A, Bates T, Bennett H, Marlow J, Shaffer M (2015) Sediment impacts on marine sponges. *Marine Pollution Bulletin*, http://dx.doi.org/10.1016/j.marpolbul.2015.03.030

Bessat F, Buigues D (2001) Two centuries of variation in coral growth in a massive *Porites* colony from Moorea (French Polynesia): a response of ocean-atmosphere variability from south central Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* 175:381-392

Bingham BL, Young CM (1991) Influence of sponges on invertebrate recruitment: a field test of allelopathy. *Marine Biology* 109:19-26

Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin* 51:408-414

Booth DJ, Brosnan DM (1995) The role of recruitment dynamics in rocky shore and coral reef fish communities. *Advances in Ecological Research* 26:309-385.

Borges AV (2003) Atmospheric CO_2 flux from mangrove surrounding waters. *Geophysical Research Letters* 30:1558-1562 doi:10.1029/2003gl017143

Box SJ, Mumby PJ (2007) Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Marine Ecology Progress Series* 342:139-149

Boyer JN, Kelble CR, Ortner PB, Rudnick DT (2009). Phytoplankton bloom status: Chlorophyll a biomass as an indicator of water quality condition in the southern estuaries of Florida, USA. *Ecological indicators* 9:S56-S67

Bruggemann JH, van Kessel AM, van Rooij JM, Breeman AM (1996) Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series* 134:59-71

Burke et al. (2004) Reefs at Risk in the Caribbean. World Resources Institute Washington, D.C. http://www.wri.org/publication/reefs-risk-caribbean

Burt J, Bartholomew A, Bauman A, Saif A, Sale PF (2009) Coral recruitment and early benthic community development on several materials used in the construction of artificial reefs and breakwaters. *Journal of Experimental Marine Biology and Ecology* 373:72-78

Caldeira K, Wickett M (2003) Oceanography: Anthropogenic carbon and ocean pH. *Nature* 425:365

Caldeira K, Wickett M (2005) Ocean Model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *Journal of Geophysical Research* 110:np

Carballo JL (2006) Effect of natural sedimentation on the structure of tropical rocky sponge assemblages. *Ecoscience* 13:119-130

Carballo JL, Bautista E, Nava H, Cruz-Barraza JA, Chavez JA (2013) Boring sponges, an increasing threat for coral reefs affected by bleaching events. *Ecology and Evolution* 3:872-886 doi:10.1002/ece3.452

Carleton JH, Sammarco PW (1987) Effects of substratum irregularity on success of coral settlement: quantification by comparative geomorphological techniques. *Bulletin of Marine Science* 40:85-98

Ceccarelli DM, et al. (2011) Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. *Journal of Experimental Marine Biology and Ecology* 399:60-67

Cerrano C, Bavestrello G, Calcinai B, Cattaneo-Vietti R, Chiantore M, Guidetti M, Sara A (2001) Bioerosive processes in Antarctic seas. *Polar Biology* 24:790-792

Chapman MG (2003) The use of sandstone blocks to test hypotheses about colonization of intertidal boulders. *Journal of the Marine Biological Association of the UK* 83:415-423

Cheshire AC, Butler AJ, Westphalen G, Rowland B, Stevenson J, Wilkinson CR (1995) Preliminary study of the distribution and photophysiology of the temperate phototrophic sponge *Cymbastela* sp. from South Australia. *Marine and freshwater research* 46:1211-1216

Chiappone M, Rutten LM, Miller SL, Swanson DW (2007) Large-scale distributional patterns of the encrusting and excavating sponge *Cliona deletrix* Pang on Florida Keys coral substrates. *Porifera Research: Biodiversity, Innovation and Sustainability*:255-263

Cincotta RP, Wisnewski J, Engelman R (2000) Human population in the biodiversity hotspots. *Nature* 404:990-992

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Clarke KR, et al. (2006) Exploring interactions by second-stage community analyses. *Journal of Experimental Marine Biology and Ecology* 338:179-192

Clements FE (1936) Nature and structure of the climax. *Journal of Ecology* 24:252-284

Coles SL, Jokiel PL (1978) Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Marine Biology 43*:209-216

Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 93:11-45

Connell JH, Slayter RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 1119-1144

Cooper TF, O'leary RA, Lough JM (2012) Growth in Western Australia corals in the Anthropocene. *Science* 335:593-596

Cortés J, Risk MJ (1985) A reef under siltation stress: Cahuita, Costa Rica. *Bulletin of Marine Science* 36:339-356

Dahdouh-Guebas F, Jayatissa LP, Di Nitto D, Bosire JO, Seen DL, Koedam N (2005) How effective were mangroves as a defense against the recent tsunami? *Current biology* 15:R443-R447

Davies PS (1989) Short-term growth measurements of corals using an accurate buoyant weight technique. *Marine Biology* 101:389-395

De'ath G, Lough JM, Fabricius KE (2009) Declining coral calcification on the Great Barrier Reef. *Science* 323:116-119

DeCarlo TM, Cohen AL, Barkley HC *et al.* (2014) Coral macrobioerosion is accelerated by ocean acidification and nutrients. *Geology*. doi:10.1130/G36147.1

de Goeij JM, van Oevelen D, Vermeij MJ, Osinga R, Middelburg JJ, de Goeij AF, Admiraal W (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science* 342:108-110

Diaz MC (2005) Common sponges from shallow marine habitats from Bocas del Toro region, Panama. *Caribbean Journal of Science* 41:465-475

Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean reefs. *Bulletin of Marine Science* 69:535-546

Diaz-Pulido G, Anthony KRN, Kline DI, Dove S, Hoegh-Guldberg O (2012) Interactions between ocean acidification and warming on the mortality and dissolution of coralline algae. *Journal of Phycology* 48:32-39 doi:10.1111/j.1529-8817.2011.01084.x

Dodge RE, Aller RC, Thomson J (1974) Coral growth related to resuspension of bottom sediments. *Nature* 247:574-577

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean Acidification: The Other CO2Problem. *Annual Review of Marine Science* 1:169-192

Duckworth AR, Wolff C (2007) Bath sponge aquaculture in Torres Strait, Australia: Effect of explant size, farming method and the environment on culture success. *Aquaculture* 271:188-195

Duckworth AR, Wolff CWW (2008) Ecological role and potential value of sponges to Torres Strait. *Annual Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre and Australian Institute of Marine Science*. 49 p.

Duckworth AR, Wolff C, Evans-Illidge E, Whalan S, Lui S (2008) Spatial variability in community structure of Dictyoceratida sponges across Torres Strait, Australia. *Continental Shelf Research* 28:2168-2173

Duckworth AR, Wolff CW, Luter H (2009) Patterns of abundance and size across varying spatial scales for the coral reef sponge *Coscinoderma matthewsi*. *Marine Ecology Progress Series* 396:27-33

Duckworth AR, Peterson BJ (2012) Effects of seawater temperature and pH on the boring rates of the sponge Cliona celata in scallop shells. *Marine Biology* 160:27-35

Duckworth AR, West L, Vansach T, Stubler A, Hardt M (2012) Effects of water temperature and pH on growth and metabolite biosynthesis of coral reef sponges. *Marine Ecology Progress Series* 462:67-77

Dufault AM, Cumbo VR, Fan TY, Edmunds PJ (2012) Effects of diurnally oscillating pCO_2 on the calcification and survival of coral recruits. *Proceedings of the Royal Society B: Biological Sciences* 279:2951-2958. doi:10.1098/rspb.2011.2545

Edmunds PJ, Brown D, Moriarty V (2012) Interactive effects of ocean acidification and temperature on two scleractinian corals from Moorea, French Polynesia. *Global Change Biology* 18:2173-2183

Enochs IC, Manzello DP, Carlton RD, Graham DM, Ruzicka R, Colella MA (2015) Ocean acidification enhances the bioerosion of a common coral reef sponge: implications for the persistence of the Florida Reef Tract. *Bulletin of Marine Science* 91

Erez J, Reynaud S, Silverman J, Schneider K, Allemand D (2011) Coral calcification under ocean acidification and global change. In *Coral reefs: an ecosystem in transition* (pp. 151-176). Springer Netherlands.

Erwin PM, Thacker RW (2007) Incidence and identity of photosynthetic symbionts in Caribbean coral reef sponge assemblages. *Journal of the Marine Biological Association of the UK* 87:1683-1692

Erwin PM, Thacker RW (2008) Phototrophic nutrition and symbiont diversity of two Caribbean sponge-cyanobacteria symbioses. *Marine Ecology Progress Series* 362:139-147

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50:125-146

Fabricius KE, et al. (2003) Effects of transparent exopolymer particles and muddy terrigenous sediments on the survival of hard coral recruits. *Estuarine, Coastal and Shelf Science* 57:613-621

Fairfull SJL, Harriott VJ (1999) Succession, space and coral recruitment in a subtropical fouling community. *Marine and Freshwater Research* 50:235-242

Fang JK, Mello-Athayde MA, Schönberg CH, Kline DI, Hoegh-Guldberg O, Dove S (2013) Sponge biomass and bioerosion rates increase under ocean warming and acidification. *Global Change Biology* 19:3581-3591

Fang JK, Schönberg CH, Kline DI, Hoegh‐Guldberg O, Dove S (2013) Methods to quantify components of the excavating sponge *Cliona orientalis* Thiele, 1900. *Marine Ecology* 34:193-206

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero,FJ (2004) Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science* 305:362-366

Field SN, Glassom D, Bythell J (2007) Effects of artificial settlement plate materials and methods of deployment on the sessile epibenthic community development in a tropical environment. *Coral Reefs* 26:279-289

Fine M, Tchernov D (2007) Scleractinian coral species survive and recover from decalcification. *Science* 315:1811

Fiore CL, Jarett JK, Olson ND, Lesser MP (2010) Nitrogen fixation and nitrogen transformations in marine symbioses. *Trends in Microbiology* 18:455-463

Freeman CJ, Thacker RW (2011) Complex interactions between marine sponges and their symbiotic microbial communities. *Limnology and Oceanography 56:*1577-1586

Fricke A, et al. (2011) Succession patterns in algal turf vegetation on a Caribbean coral reef. *Botanica Marina* 54:111-126

Gardner WD (1980) Field assessment of sediment traps. *Journal of Marine Research* 38: 41-52

Gattuso J-P, Frankignoulle M, Bourge I, Romaine S, Buddemeier RW (1997) Effect of calcium carbonate saturation of seawater on coral calcification. *Global and Planetary Change* 18:37-46

Gattuso J-P, Lavigne H (2009) Technical Note: Approaches and software tools to investigate the impact of ocean acidification. *Biogeosciences* 6:2121-2133

Gerrodette T, Flechsig AO (1979) Sediment-induced reduction in the pumping rate of the tropical sponge Verongia lacunosa. *Marine Biology* 55:103-110

Gilmour J (1999) Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. *Marine Biology* 135:451-462

Glynn PW (1997) Bioerosion and coral reef growth: a dynamic balance. In: *Life and Death of Coral Reefs.* (ed Birkeland C) pp 68-95. New York, Chapman & Hall.

González-Rivero M, Yakob L, Mumby PJ (2011) The role of sponge competition on coral reef alternative steady states. *Ecological Modelling* 222:1847-1853

Goodenough AE, Hart AG, Stafford R (2012) Regression with empirical variable selection: description of a new method and application to ecological datasets. *Plos One* 7: e34338

Goreau T, Hartman WD (1963) Boring sponges as controlling factors in the formation and maintenance of reefs. In: RF S (ed) Mechanisms of hard tissue destruction. *American Association for the Advancement of Science* 25-54

Goreau TJ, Hayes RL (1994) Coral bleaching and ocean "hot spots". *Ambio,* 23, 176-180.

Goreau TJ (1992) Bleaching and reef community change in Jamaica 1951-1991. *American Zoologist* 32:683-695

Granek E, Ruttenberg BI (2008) Changes in biotic and abiotic processes following mangrove clearing. *Estuarine, Coastal and Shelf Science* 80:555-562

Grange J, Rybarczyk H, Tribollet A (2014) Successions of Microbioeroding Communities over a Year Period with a Monthly Resolution: Impact on Biogenic Dissolution in Dead Corals (New Caledonia). *2014 Ocean Science Meeting*.

Grigg RW, Maragos JE (1974) Recolonization of hermatypic corals on submerged lava flows in Hawaii. *Ecology* 55:387-395

Guinotte JM, Fabry VJ (2008) Ocean acidification and its potential effects on marine ecosystems. *Annals of the New York Academy of Sciences* 1134:320-342

Gutner-Hoch E, Fine M (2011) Genotypic diversity and distribution of *Ostreobium quekettii* within scleractinian corals. *Coral reefs* 30:643-650

Hadas E, Marie D, Shpigel M, Ilan M (2006) Virus predation by sponges is a new nutrient-flow pathway in coral reef food webs. *Limnology and Oceanography* 51:1548-1550

Hadas E, Shpigel M, Ilan M (2009) Particulate organic matter as a food source for a coral reef sponge. *Journal of Experimental Biology* 212:3643-3650

Harborne AR, Mumby PJ, Micheli F, Perry CT, Dahlgren CP, Holmes KE, Brumbaugh DR (2006) The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. *Advances in marine biology* 50:57-189

Hardt MJ (2008) Lessons from the past: the collapse of Jamaican coral reefs. *Fish and Fisheries* 10:1-16

Harriott VJ, Fisk DA (1987) A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. *Marine Ecology Progress Series* 37:201-208

Hatch W (1980) The implication of carbonic anhydrase in the physiological mechanism of penetration of the carbonate substrata by the marine burrowing sponge *Cliona celata* (Demospongiae). *Biological Bulletin* 159:135-147

Hill MS (1996) Symbiotic zooxanthellae enhance boring and growth rates of the tropical sponge Anthosigmella varians forma varians. *Marine Biology* 125:649-654

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50:839-866

Hoegh-Guldberg O et al. (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737-1742. doi:10.1126/science.1152509

Hoeksema BW (1991) Controls of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy. *Marine Ecology Progress Series* 74:225-237

Holmes G (2008) Estimating three-dimensional surface areas on coral reefs. *Journal of Experimental Marine Biology and Ecology* 365:67-73

Holmes KE (2000) Effects of eutrophication on bioeroding sponge communities with the description of a new West Indian sponges, Cliona spp. (Porifera: Hadromerida: Clionidae). *Invertebrate Biology* 119:125-138

Hooper JNA, van Soest RWM (2002) Systema Porifera: A guide to the classification of sponges. Springer USA

Hughes TP (1985) Life histories and population dynamics of early successional corals. In: Gabrie C, Salvat B (Eds.) *The Fifth International Coral Reef Congress, ICRS*, pp.101-106

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547-1551

Hughes TP, Keller BD, Jackson JBC, Boyle MJ (1985) Mass mortality of the echinoid *Diadema antillarum* Phillipi in Jamaica. *Bulletin of Marine Science* 36:377-384

Hunt HL, Scheibling RE (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Marine Ecology Progress Series* 155:269-301

Hunte W, Wittenberg M (1992) Effects of eutrophication and sedimentation on juvenile corals II. Settlement. *Marine Biology* 114:625-631

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological monographs* 54:187-211

Hutchings P (2008) Role of polychaetes in bioerosion of coral substrates. In: Wisshak M, Tapanila L (eds) Current Developments in Bioerosion. Springer-Verlag, Berlin, pp 249-264

Iguchi A, Ozaki S, Nakamura, T, et al. (2012) Effects of acidified seawater on coral calcification and symbiotic algae on the massive coral *Porites australiensis*. *Marine Environmental Research* 73:32-36

Ilan M Abelson A (1995) The life of a sponge in a sandy lagoon. *Biological Bulletin* 189:363-369

IPCC (2007) Climate Change 2007: Synthesis Report. (ed Change IPOC) pp 26-73, Valencia, Spain.

IPCC (2007) Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambirdge University Press, Cambridge.

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In: *IPCC.* (eds Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM) pp 1535, Cambridge.

Irving AD, Connell SD (2002) Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages. *Marine Ecology Progress Series* 245:83-91

Jackson JBC, Winston JE (1982) Ecology of cryptic coral reef communities. I. Distribution and abundance of major groups of encrusting organisms. *Journal of Experimental Marine Biology and Ecology* 57:135-147

Jamaica Tourist Board (2012) Annual Travel Statistics. www.visitjamaica.com

Jenkins SR (2005) Larval habitat selection, not larval supply, determines settlement patterns and adult distribution in two chthamalid barnacles. *Journal of Animal Ecology*, 74:893-904

Jessen C et al. (2014) *In situ* effects of simulated overfishing and eutrophication on settlement of benthic coral reef invertebrates in the Central Red Sea. *PeerJ* 2:e339; DOI 10.7717/peerj.339

Jokiel PL, Coles SL (1977) Effects of temperature on the mortality and growth of Hawaiian reef corals. *Marine Biology 43*:201-208

Jokiel PL, Maragos JE, Franzisket L (1978) Coral growth: buoyant weight technique. *UNESCO Monographs on Oceanographic Methodology* 5:529-542

Jokiel PL, Rodgers KS, Kuffner IB, Andersson AJ, Cox EF, Mackenzie FT (2008) Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs* 27:473-483

Jordan LK, Banks KW, Fisher LE, Walker BK, Gilliam DS (2010) Elevated sedimentation on coral reefs adjacent to a beach nourishment project. *Marine Pollution Bulletin* 60:261-271

Kirk KL (1991) Inorganic particles alter competition in grazing plankton: the role of selective feeding. *Ecology*, 915-923

Kjerfve B, Magill KE, Porter JW, Woodley JD (1986) Hindcasting of hurricane characteristics and observed damage on a fringing reef, Jamaica, West Indies. *Journal of Marine Research* 44:119-148

Kleeman K (2008) *Parapholas quadrizonata* (Spengler, 1792), dominating dead-coral boring bivalve from the Maldives, Indian Ocean. In: Wisshak M, Tapanila L (eds) Current Developments in Bioerosion. Springer-Verlag, Berlin, pp 265-278

Kleypas JA (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284:118-120

Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences* 32:1259-1269

Kroeker,KJ, Kordas RL, Crim RN, Singh GG (2010) Meta‐analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology letters* 13:1419-1434

Krumbein WC (1938) Size frequency distributions of sediments and the normal phi curve. *Journal of Sedimentary Petrology* 8:84-90

Kuffner IB, et al. (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series* 323:107-117

Kuffner IB, Andersson AJ, Jokiel PL, Rodgers KS, Mackenzie FT (2007) Decreased abundance of crustose coralline algae due to ocean acidification. *Nature Geosciences* 1:114-117 doi:10.1038/ngeo100

Kuffner IB, Lidz BH, Hudson JH, Anderson JS (2014) A century of ocean warming on Florida Keys coral reefs: historic in situ observations. *Estuaries and Coasts,*10.1007/s12237-014-9875-5

Kurihara H (2008) Effects of CO_2-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series* 373:275-284

Land LS (1973) Holocene meteoric dolomitization of Pleistocene limestones, North Jamaica. *Sedimentology* 20:411-424

Langdon C, Atkinson MJ (2005) Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *Journal of Geophysical Research: Oceans (1978–2012)*, 110 (C9).

Lapointe BE (1997) Nutrient thresholds for bottom‐up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography* 42:1119-1131

Lehnert H, Fischer H. (1999) Distribution patterns of sponges and corals down to 107m off North Jamaica. *Memoirs-Queensland Museum* 44:307-316

Lehnert H, Van Soest RW (1998) Shallow water sponges of Jamaica. *Beaufortia*, *48*.

Lesser MP (2006) Benthic–pelagic coupling on coral reefs: feeding and growth of Caribbean sponges. *Journal of Experimental Marine Biology and Ecology* 328:277-288.

Lesser MP, Slattery M (2013) Ecology of Caribbean sponges: are top-down or bottom-up processes more important? *PloS one* 8:e79799

Lessios HA, Robertson DR, Cubit JD (1984) Spread of *Diadema* mass mortality through the Caribbean. *Science* 226:335-337

Lewin R (1986) Supply-side ecology. *Science* 234:25-27

Leys SP, Meech RW (2006) Physiology of coordination in sponges. *Canadian Journal of Zoology* 84:288-306

Liddell WD, Ohlhorst SL (1986) Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. *Journal of Experimental Marine Biology and Ecology* 95:271-278

Liddell WD, Ohlhorst SL (1992) Ten years of disturbance and change on a Jamaican fringing reef. In *Proceedings of the 7th International Coral Reef Symposium, Guam* (pp.149-155)

Loh TL, Pawlik JR (2014) Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. *Proc Natl Acad Sci USA* 111:4151-4156

Lohrer AM, Hewitt JE, Thrush SF (2006) Assessing far-field effects of terrigenous sediment loading in the coastal marine environment. *Marine Ecology Progress Series* 315:13-18

Lopez-Victoria M, Zea S (2004) Storm-mediated coral colonization by an excavating Caribbean sponge. *Climate Research* 26:251-256

Lopez-Victoria M, Zea S (2005) Current trends of space occupation by encrusting excavating sponges on Colombian coral reefs. *Marine Ecology* 26:33-41

Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology* 245:225-243

Loya Y (1976) Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology* 57: 278-289

Macdonald IA, Perry CT (2003) Biological degradation of coral framework in a turbid lagoon environment, Discovery Bay, north Jamaica. *Coral Reefs* 22:523-535

Macgeachy J (1977) Factors controlling sponge boring in Barbados reef corals. *Proceedings of the 3rd International Coral Reef Symposium* 2:477-483

Maida M, Coll JC, Sammarco PW (1994) Shedding new light on scleractinian coral recruitment. *Journal of Experimental Marine Biology and Ecology* 180:189-202

Maldonado M (2006) The ecology of the sponge larva. *Canadian Journal of Zoology* 84:175-194

Maldonado M, Young CM (1996) Effects of physical factors on larval behavior, settlement and recruitment of four tropical demosponges. *Marine Ecology Progress Series* 138:169-180

Maldonado M, Giraud K, Carmona C (2008) Effects of sediment on the survival of asexually produced sponge recruits. *Marine Biology* 154:631-641

Mariani S, Uriz MJ, Turon X, Alcoverro T (2006) Dispersal strategies in sponge larvae: integrating the life history of larvae and the hydrologic component. *Oecologia* 149:174-184

Marshall AT, Clode P (2004) Calcification rate and the effect of temperature in a zooxanthellate and an azooxanthellate scleractinian reef coral. *Coral Reefs* 23:218-224

Marubini F, Ferrier-Pagès C, Furla P, Allemand D (2008) Coral calcification responds to seawater acidification: a working hypothesis towards a physiological mechanism. *Coral Reefs* 27:491-499

Maughan BC (2001) The effects of sedimentation and light on recruitment and development of a temperate, subtidal, epifaunal community. *Journal of Experimental Marine Biology and Ecology* 256:59-71

McClanahan TR (1997) Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. *Journal of Experimental Marine Biology and Ecology* 218:77-102

McClanahan TR, Obura D (1997) Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology* 209:103-122

McClintock JB, Amsler CD, Baker BJ, van Soest RWM (2005) Ecology of Antarctic marine sponges: An overview. *Integrative and Comparative Biology* 45

McCulloch M, Falter J, Trotter JA, Montagna P (2012) Coral resilience to ocean acidification and global warming through pH up-regulation. *Nature Climate Change* 2:623-627

McMurray SE, Blum JE, Pawlik JR (2008) Redwood of the reef: growth and age of the giant barrel sponge Xestospongia muta in the Florida Keys. *Marine Biology* 155:159-171

McMurray SE, Henkel TP, Pawlik JR (2010) Demographics of increasing populations of the giant barrel sponges Xestospongia muta in the Florida Keys. *Ecology* 91:560-570

Meesters EH, Hilterman M, Kardinaal E, Keetman M, de Vries M, Bak RPM (2001) Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. *Marine Ecology Progress Series* 209:43-54

Meinshausen M, *et al.* (2011) The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic change* 109:213-241

Meylan A (1988). Spongivory in hawksbill turtles: a diet of glass. *Science* 239:393-395.

Mora C (2008) A clear human footprint in the coral reefs of the Caribbean. *Proc Biol Sci* 275:767-773

Moses CS, Bonem RM (2001) Recent population dynamics of *Diadema antillarum* and *Tripneustes ventricosus* along the north coast of Jamaica, W.I. *Bulletin of Marine Science* 68:327-336

Mueller B, de Goeij JM, Vermeij MJ, Mulders Y, van der Ent E, Ribes M, van Duyl FC (2014) Natural diet of coral-excavating sponges consists mainly of dissolved organic carbon (DOC). *Plos One* 9:E90152

Mundy CN (2000) An appraisal of methods used in coral recruitment studies. *Coral Reefs* 19:124-131

Munro JL (1983) The composition and magnitude of trap catched in Jamaican waters. In: J.L. M (ed) *Caribbean Coral Reef Fishery Resources. International Center for Living Aquatic Resources Managment* (ICLARM), Manila

Nakamura M, Ohki S, Suzuki A, Sakai K (2011) Coral larvae under ocean acidification: survival, metabolism, and metamorphosis. *Plos One* 6:e14521

Nava H, Carballo JL (2008) Chemical and mechanical bioerosion of boring sponges from Mexican Pacific coral reefs. *The Journal of Experimental Biology* 211:2827-2831

Nava H, Carballo JL (2013) Environmental factors shaping boring sponge assemblages at Mexican Pacific coral reefs. *Marine Ecology* 34:269-279

NEPA Environmental Impact Assessment (2005) Bahia Principe Hotel Resort Development, Pear Tree Bottom, St. Ann. Jamaica. National Environmental and Planning Agency, Kingston, Jamaica

Neumann AC (1966) Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*. *Limnology and Oceanography* 11:92-108

Nickel M (2004) Kinetics and rhythm of body contractions in the sponge Tethya wilhelma (Porifera: Demospongiae). *Journal of Experimental Biology* 207:4515-4524

Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Marine Ecology Progress Series* 376:295-306

Odum EP (1969) The strategy of ecosystem development. *Science* 164:262-270

Orr JC, Fabry V, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishida A, Joos F (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681-686

Pandolfi J, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955-958

Parsons TR, Maita Y, and CM Lalli (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, New York.

Pawlik JR (1995) Defenses of Caribbean sponges against predatory reef fish, I: chemical deterrency. *Marine Ecology Progress Series* 127:183-194

Pawlik JR (1998) Coral reef sponges: Do predatory fishes affect their distribution? *Limnology and Oceanography* 43:1396-1399

Pawlik JR, Loh TL, McMurray SE, Finelli CM (2013) Sponge communities on Caribbean coral reefs are structured by factors that are top-down, not bottom-up. *PloS one* 8:e62573

Pawlik JR, McMurray SE, Erwin P, Zea S (2015) A review of evidence for food limitation of sponges on Caribbean reefs. *Marine Ecology Progress Series* 519:265-283

Pearson RG (1981) Recovery and recolonization of coral reefs. *Marine Ecology Progress Series* 4:105-122

Perkol-Finkel S, Benayahu Y (2007) Differential recruitment of benthic communities on neighboring artificial and natural reefs. *Journal of Experimental Marine Biology and Ecology* 340:25-39

Perry CT (1998) Macroborers within coral framework at Discovery Bay, north Jamaica: species distribution and abundance, and effects on coral preservation. *Coral Reefs* 17:277-287

Perry CT, Taylor KG (2004) Impacts of bauxite sediment inputs on a carbonate-dominated embayment, Discovery Bay, Jamaica. *Journal of Coastal Research* 1070-1079

Peterson BJ, Chester CM, Jochem FJ, Fourqurean JW (2006) Potential role of sponge communities in controlling phytoplankton blooms in Florida Bay. *Marine Ecology Progress Series* 328:93-103

Phillipp E, Fabricius KE (2003) Photophysiological stress in scleractinian corals in response to short-term sedimentation. *Journal of Experimental Marine Biology and Ecology* 287:57-78

Pineda MC, Duckworth A, Webster N (2015) Appearance matters: sedimentation effects on different sponge morphologies. *Journal of the Marine Biological Association of the United Kingdom*, 1-12

Pomponi S (1980) Cytological mechanisms of calcium carbonate excavation by boring sponges. *International Review of Cytology* 65:301-319

Poppe LJ, Eliason AH, Fredericks JJ, Rendigs RR, Blackwood D, Polloni CF (2000) Grain size analysis of marine sediments: methodology and data processing. *US Geological Survey East Coast sediment analysis: procedures, database, and georeferenced displays.* US Geological Survey Open File Report 00-358. http://pubs.usgs.gov/of/2000/of00-358

Porter JW, Targett NM (1988) Allelochemical interactions between sponges and corals. *Biological Bulletin* 175:230-239

Powell A, Smith DJ, Hepburn LJ, Jones T, Berman J, Jompa J, Bell JJ (2014) Reduced diversity and high sponge abundance on a sedimented Indo-Pacific reef system: implications for future changes in environmental quality. *Plos One* 9:e85253

Przeslawski R, Ahyong S, Byrne M, WÖRheide G, Hutchings PAT (2008) Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. *Global Change Biology* 14:2773-2795

Putnam HM, Edmunds PJ (2011) The physiological response of reef corals to diel fluctuations in seawater temperature. *Journal of Experimental Marine Biology and Ecology* 396:216-223. doi:10.1016/j.jembe.2010.10.026

R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

R Development Core Team (2008) R: A language and environment for statistical computing (ed Computing RFFS), Vienna, Austria.

Reiswig H (1971) Particle feeding in natural populations of three marine Demosponges. *Biological Bulletin* 141:568-591

Reyes‐Nivia C, Diaz‐Pulido G, Kline D, Hoegh-Guldberg O, Dove S (2013) Ocean acidification and warming scenarios increase microbioerosion of coral skeletons. *Global Change Biology* 19:1919-1929

Ribeiro SM, Omena EP, Muricy G (2003) Macrofauna associated to Mycale microsigmatosa (Porifera, Demospongiae) in Rio de Janeiro State, SE Brazil. *Estuarine, Coastal and Shelf Science* 57:951-959

Riebesell U, Fabry VJ, Hansson L, Gattuso J-P (2011) Guide to best practices for ocean acidification research and data reporting. Publications Office of the European Union, Luxembourg

Riegl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *Journal of Experimental Marine Biology and Ecology* 186:259-275

Roberts DE, Davis AR, Cummins SP (2006) Experimental manipulation of shade, silt, nutrients and salinity on the temperate reef sponge *Cymbastela concentrica. Marine Ecology Progress Series* 307:143-154

Rogers CS (1979) The effect of shading on coral reef structure and function. *Journal of Experimental Marine Biology and Ecology* 41:269-288

Rogers C (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62:185-202

Rose CS, Risk MJ (1985) Increase in *Cliona deletrix* infestation of *Montastrea cavernosa* heads on an oragnically polluted portion of the Grand Cayman fringing reef. *Marine Ecology* 6:345-363

Roughgarden J, Gaines SD, Pacala SW (1987) Supply side ecology: the role of physical transport processes. In *Symposium of the British Ecological Society*.

Rowan R (2004) Thermal adaptation in reef coral symbionts. *Nature* 430:742

Rützler K (1975) The role of burrowing sponges in bioerosion. *Oecologia* 19:203-216

Rützler K (2002) Impact of crustose Clionid sponges on Caribbean reef corals. *Acta Geologica Hispanica* 37:61-72

Sabine C, al. e (2004) The oceanic sink for anthropogenic CO_2. *Science* 305:367

Sandin SA, Sala E (2012) Using successional theory to measure marine ecosystem health. *Evolutionary Ecology* 26:435-448

Schaffelke B, et al. (2005) Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. *Marine Pollution Bulletin* 51:279-296

Schönberg CHL (2000) Sponges of the *'Cliona viridis* complex' - a key for species identification. *Proceedings of the 9th International Coral Reef Symposium* (Bali, Indonesia)

Schönberg CHL (2002) Substrate effects on the bioeroding Demosponge *Cliona orientalis*. 1. Bioerosion rates. *Marine Ecology* 23:313-326

Schönberg CHL, Wilkinson CR (2001) Induced colonization of corals by a clionid bioeroding sponge. *Coral Reefs* 20:69-76

Schönberg CHL, Ortiz J-C (2008) Is sponge bioerosion increasing? In: Proceedings of the 11th International Coral Reef Symposium, Fort Lauderdale, FL, USA, 2008. pp 527-530

Siegrist HG, Bowman RG, Randall RH, Stifel PB (1992) Diagenetic effects related to hot-water effluent in a modern reef on Guam. *Pacific Science* 46:379

Somerfield PJ, Clarke K R (1995) Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series* 127:113-119

Sousa WP (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49:227-254

Southwell M, Weisz JB, Martens CS, Lindquist N (2008) In situ fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. *Limnology and Oceanography* 53:986-996

Stimson J, Kinzie Iii RA (1991) The temporal pattern and rate of release of zooxanthellae from the reef coral Pocillopora damicornis (Linnaeus) under nitrogen-enrichement and control conditions. *Journal of Experimental Marine Biology and Ecology* 153:63-74

Storlazzi CD, Field ME, Bothner MH (2011) The use (and misuse) of sediment traps in coral reef environments: theory, observations, and suggested protocols. *Coral Reefs* 30:23-38

Stubler AD, Furman BT, Peterson BJ (2014) Effects of pCO_2 on the interaction between an excavating sponge, *Cliona varians*, and a hermatypic coral, *Porites furcata*. *Marine Biology* 161:1851-1859

Tanner JE, et al. (1994) Species coexistence, keystone species, and succession: a sensitivity analysis. *Ecology* 75:2204-2219

Tompkins-MacDonald GJ, Leys SP (2008) Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. *Marine Biology* 154:973-984

Torre L, et al. (2012) Respiratory responses of three Antarctic ascidians and a sea pen to increased sediment concentrations. *Polar Biology* 35:1743-1748Tribollet A, Godinot C, Atkinson M, Langdon C (2009) Effects of elevated pCO_2 on dissolution of coral carbonates by microbial euendoliths. *Global Biogeochemical Cycles* 23(3) doi:10.1029/2008gb003286

Turon X, Uriz M-J, Willenz P (1999) Cuticular linings and remodelisation processes in *Crambe crambe* (Demospongiae: Poecilosclerida). Memoirs of the Queensland Museum 44:617-625

Underwood A (1994) Seasonal and temporal aspects of recruitment and succession in an intertidal estuarine fouling assemblage. *Journal of the Marine Biological Association of the UK* 74:563-584

Underwood AJ, Fairweather PG (1989) Supply-side ecology and benthic marine assemblages. *Trends in Ecology and Evolution* 4:16-20

Veal CJ, Holmes G, Nunez M, Hoegh-Guldberg O, Osborn J (2010) A comparative study of methods for surface area and three-dimensional shape measurements of coral skeletons. *Limnology and Oceanography: Methods* 8:241-253

Veron JE, et al. (2009) The coral reef crisis: the critical importance of <350 ppm CO_2. *Marine Pollution Bulletin* 58:1428-1436 doi:10.1016/j.marpolbul.2009.09.009

Vicente VP (1978) An ecological evaluation of the West Indian Demosponge *Anthosigmella varians* (Hadromerida: Spirastrellidae). *Bulletin of Marine Science* 28:771-777

Wall CC, Rodgers BS, Gobler CJ, Peterson BJ (2012) Responses of loggerhead sponges *Spechiospongia vesparium* during harmful cyanobacterial blooms in a sub-tropical lagoon. *Marine Ecology Progress Series* 451:31-43

Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. *Marine Pollution Bulletin* 51:570-579

Weber M, Lott C, Fabricius KE (2006) Sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, organic and geochemical properties. *Journal of Experimental Marine Biology and Ecology* 336:18-32

Westfield I (2008) Geochemical fingerprinting of sediments on the Pear Tree Bottom Reef, near Runaway Bay, Jamaica. Master of Science, Baylor University

Westfield I, Dworkin S, Bonem R, Lane E (2008) Identification of sediment sources using geochemical fingerprinting at Pear Tree Bottom Reef, Runaway Bay, Jamaica. *Abstracts of the 11th International Coral Reef Society*, p. 137

Whalan S, Battershill C, de Nys R (2007) Variability in reproductive output across a water quality gradient for a tropical marine sponge. *Marine Biology* 153:163-169

Wiedenmayer F (1977) Shallow-water sponges of the Western Bahamas. Basel: Birkhauser, Verlag.

Wilkinson CR, Cheshire AC (1989) Patterns in the distribution of sponge populations across the central Great Barrier Reef. *Coral Reefs* 8:127-134

Wilkinson CR, Evans E (1989) Sponge distribution across Davies Reef, Great Barrier Reef, relative to location, depth, and water movement. *Coral Reefs* 8:1-7

Wilkinson CR (1999) Global and local threats to coral reef functioning and existence: review and predictions. *Marine and Freshwater Research* 50:867-878

Williams E, Bartels P, Bunkley-Williams L (1999) Predicted disappearance of coral-reef ramparts: a direct result of major ecological disturbances. *Global Change Biology* 5:839-845

Wilson J, Harrison P (2005) Post-settlement mortality and growth of newly settled reef corals in a subtropical environment. *Coral Reefs* 24:418-421

Winston JE, Jackson JBC (1984) Ecology of cryptic coral reef communities. IV. Community development and life histories of encrusting cheilostome byrozoa. *Journal of Experimental Marine Biology and Ecology* 76:1-21

Wisshak M, Schönberg CHL, Form A, Freiwald A (2012) Ocean acidification accelerates reef bioerosion. *Plos One* 7:e45124

Wisshak M, Schönberg CHL, Form A, Freiwald A (2013) Effects of ocean acidification and global warming on reef bioerosion—lessons from a clionaid sponge. *Aquatic Biology* 19:111-127

Wisshak M, Schönberg CHL, Form A, Freiwald A (2014) Sponge bioerosion accelerated by ocean acidification across species and latitudes? *Helgoland Marine Research*.

Wittenberg M, Hunte W (1992) Effects of eutrophication and sedimentation on juvenile corals I. Abundance, mortality and community structure. *Marine Biology* 112:131-138

Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe CM, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749-755

Wulff JL (1984) Sponge-mediated coral reef growth and rejuvenation. *Coral Reefs* 3:157-163

Wulff, J. L. (2000). Sponge predators may determine differences in sponge fauna between two sets of mangrove cays, Belize barrier reef. *Atoll Res Bull 477:*251-263

Zablocki JA, Andersson AJ, Bates NR (2011) Diel aquatic CO_2 system dynamics of a Bermudian mangrove environment. *Aquatic Geochemistry* 17:841-859

Zacharias MA, Roff JC (2001) Use of focal species in marine conservation and management: a review and critique. *Aquatic Conservation: Marine and Freshwater Ecosystems* 11:59-76

Zea S (1990) Distribution, cover and recruitment of demosponges (Porifera, Demospongiae) in rocky and reefal habitats of Santa Marta, Colombian Caribbean. PhD Dissertation. The University of Texas at Austin, Austin, 154pp.

Zea S (1993) Recruitment of Demosponges (Porifera, Demospongiae) in rocky and coral reef habitats of Santa Marta, Colombian Caribbean. *Marine Ecology* 14:1-21

Zea S, Henkel TP, Pawlik JR (2014) The Sponge Guide: a picture guide to Caribbean sponges. 3rd Edition. www.spongeguide.org

Zeebe RE, Wolf-Gladrow DA (2001) CO2 in seawater: equilibrium, kinetics, isotopes (Vol. 65). *Gulf Professional Publishing.*

Zundelevich A, Lazar B, Ilan M (2007) Chemical versus mechanical bioerosion of coral reefs by boring sponges--lessons from *Pione* cf. *vastifica*. *The Journal of Experimental Biology* 210:91-96