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Coral vs. Macroalgae: Relative Susceptibility to Sedimentation and Ocean Warming

Ashton J. Galarno
Nova Southeastern University, ajgalarn@g.coastal.edu

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

CORAL VS. MACROALGAE:
RELATIVE SUSCEPTIBILITY TO SEDIMENTATION AND OCEAN WARMING

By:
Ashton Galarno

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ASHTON GALARNO
Nova Southeastern University
Halmos College of Natural Sciences and Oceanography

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Approved:

Thesis Committee:

Major Professor: _____
Joana Figueiredo, Ph.D

Committee Member: _____
Bernhard Riegl, Ph.D

Committee Member: _____
Brian K. Walker, Ph.D

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Abstract

Sedimentation and ocean warming are two major anthropogenic stressors that directly affect coral recruitment and recovery. Many coral-dominated reefs have undergone phase shifts becoming macroalgae-dominated because of the coral population's inability to tolerate these increasing stressors. Predicting these phase shifts requires a determination of the relative susceptibility of coral and macroalgae to these stressors. The objective of this study was to quantitatively assess the synergistic effects of sedimentation and elevated temperature on the survival and growth of *Montastraea cavernosa* newly settled coral juveniles, and fragments of the macroalgae, *Dictyota ciliolata.* A crossed experimental design tested the two temperatures and four sedimentation levels. After 12 weeks, a 2°C increase in temperature did not significantly affect survival of the *M. cavernosa* juveniles or fragments of *D. ciliolata*. *Montastraea cavernosa* juvenile survival was negatively affected by a decrease in sediment. *Dictyota ciliolata* survival was highly sensitive to the increase in sedimentation. The survival and growth of both species appeared to be susceptible to an increase in sedimentation, but in opposite ways. This study demonstrates that both *M. cavernosa* juveniles and *D. ciliolata* fragments may be more vulnerable to light caused by changes in turbidity rather than temperature.

Key Words: Coral, macroalgae, sedimentation, ocean warming, juvenile, survival, growth

1. Introduction

Coral reefs are one of the most biologically diverse and important ecosystems on Earth because they provide essential ecosystem services while maintaining a substantial socioeconomic value. It is estimated that $30 billion of goods and net benefits are derived from coral reef ecosystems annually, including seafood products, mineral oil and gas, and live organisms for the aquarium trade (Moberg & Folke, 1999; Cesar et al., 2003). They can also be considered the Earth's "medicine cabinet" because many pharmaceuticals are derived from coral reef organisms (Conservation International, 2008). Coral reefs protect shorelines from storm surge and erosion and provide millions of jobs to local populations through ecotourism and other recreational activities (Moberg & Folke, 1999; Conservation International, 2008). Reefs are important cultural heritage sites in many regions of the world and many traditions are intimately tied to the reefs (Conservation International, 2008). Even though reefs only span 0.2% of the ocean floor, they are estimated to support more than 25% of all marine life (Spalding et al., 2001). Over 9 million estimated species of plants and animals benefit from the habitats and food provided by the structures formed from coral skeletons (Knowlton, 2001). The alteration of the provision of these ecosystem services can have consequences on the livelihood and development of coral reefs (Norstrom et al., 2009).

The main builders of coral reefs are hermatypic, scleractinian corals. These corals deposit calcium carbonate skeletons that constitute the stony framework and foundation of the reef structure. Coral cover in reefs, a metric of the amount of coral in an area, can be severely diminished by natural and anthropogenic stressors. The space left by dead corals is often proliferated by algae or other benthic organisms (McManus & Polsenberg, 2004). The presence of algae in close proximity (at the order of a few centimeters) of typical coral settlement habitats decreases the recruitment potential of corals (McManus & Polsenberg, 2004; Arnold et al., 2010). This is because the macroalgae impedes larval access to that habitat, inhibits coral facilitating substrates, and increases the mortality of post-settlement juveniles (Arnold et al., 2010). Therefore, an excessive loss of corals and a decrease in settlement success of planulae can potentially induce a community phase shift from coral to macroalgae dominance (McManus & Polsenberg, 2004). In some cases, herbivores can assist in keeping algal cover low and allowing corals to re-colonize

the free space (Mumby, 2006; Ledlie et al., 2007). Corals co-evolved with predators and competitors, thus, in the absence of anthropogenic stressors, the population can recover and remain the dominant species on the reef.

Most local anthropogenic stressors such as overfishing (Jackson, 1997), euthrophication (Dubinsky & Stambler, 1996), primarily affect corals and facilitate macroalgae dominance. Herbivores, such as fish and sea urchins, can control the abundance of macroalgae on reefs (Ledlie et al., 2007; Arnold et al., 2010; Ainsworth & Mumby, 2015), and thus removing herbivores facilitates algal dominance (Bellwood et al., 2004). Increased nutrients from terrestrial run-off and sewage (eutrophication) accelerates the growth of macroalgae (Smith et al., 1981; Sheppard et al., 2009; Burke et al., 2011). Nutrient enrichment can also increase the severity of coral diseases, such as black band and yellow band disease (Kuta & Richardson, 2002; Bruno et al., 2003). Stress and a greater presence of pathogens are hypothesized to reduce the immune system of corals and facilitate the spread of disease (Lafferty & Holt, 2003; Bruno et al., 2007). Vulnerable corals are often more susceptible to disease and warm temperature anomalies can drive disease outbreaks (Bruno et al., 2007). The loss of coral cover is asynchronous and disease is only one of the agents facilitating a phase shift from coral to algae-dominated states.

Sedimentation caused by beach nourishment, coastal construction, and dredging activities is a local anthropogenic stressor that can affect both corals and macroalgae. The increased turbidity caused by finer sediment particles reduces light availability, decreasing photosynthetic efficiency of both the macroalgae and the corals' algal endosymbionts (*Symbiodinium spp.*) (Riegl and Branch, 1995). Deposited sediment can smother both corals and macroalgae. When smothered in sediment, organisms will not have access to light, food nor oxygen and thus often die. Macroalgae responses to sedimentation seem to be species-specific and correlate with reproductive strategies (Eriksson and Johansson, 2005) while sediment load is an important constraint for species distribution and abundance. Species of macroalgae with extended reproductive periods are the most tolerant to increased sedimentation due to their dependency on dispersal by fragmentation or vegetative propagation (Eriksson and Johansson, 2005). Advantageous macroalgal traits in sediment rich habitats include: vegetative

fragmentation (Airoldi, 1998), tough thalli (Daly and Mathiesen, 1977; Johansson et al., 1998), and the ability to regenerate from basal thallus parts that can resist burial (Daly and Mathiesen, 1977). This suggests that high sedimentation rates promote tolerant macroalgae species with physiological and morphological adaptations to external stressors and disturbances (Eriksson and Johansson, 2005). While several studies have investigated the effect of sedimentation on reproduction and community composition, there are few experimental studies that focus on the species-specific susceptibility of macroalgae to increased sedimentation from anthropogenic sources.

The worldwide reduction in coral cover is mainly attributed to ocean warming (Hughes et al., 2003; Hoegh-Guldberg et al., 2007; van Woesik & McCaffrey, 2017). Global warming affects most organisms in the ocean and is directly linked to humans. The burning of fossil fuels releases carbon dioxide into the atmosphere where it gets trapped, creating heat (IPCC, 2014). The ever-growing greenhouse gas emissions has led to a 0.4 - 0.8°C increase in sea surface temperatures in the 20th century, and is predicted to cause the rise of at least another 3°C by the end of this century (IPCC, 2014). Corals are extremely sensitive to changes in temperature as they live very close to the limit of their thermal tolerances. Unusually warm conditions can cause the corals to bleach (Glynn and D'Croz, 1990; Glynn, 1993). Bleaching is a stress response that corals exhibit due to stressful environmental changes, where they expel the *Symbiodinium* from their tissues, leaving the tissue transparent and exposing the calcium carbonate skeleton underneath (Glynn, 1993; Glynn 1996). Bleaching events can be devastating to corals because the *Symbiodinium* can supply more than 75% of their hosts' daily metabolic energy requirements through photosynthesis (Grottoli et al., 2006; Baird et al., 2009). Coral reefs can survive bleaching episodes depending on the duration and level of temperature stress, the level of light irradiance, and other compounding factors. However, even recovered reefs exhibit reduced growth and reproduction (Burke et al., 2011). Bleached corals are left in a fragile condition because their maintenance and growth are severely impacted by the reduction in energy reserves resulting from the loss of their endosymbionts (Grottoli et al., 2004; Anthony et al., 2007). Experts have predicted that bleaching events could become so frequent that corals will not have time to recover even though they have shown some capacity to adapt to the changing environment (Donner et

al., 2005; Baird & Maynard, 2008; van Woesik & McCaffrey, 2017). An increase in water temperatures due to global climate change has shown to enhance algal growth and recruitment (Beardall et al., 1998), however, it also increases metabolic rate thus enhancing grazer activity (Paul et al., 1989). The photosynthetic performance of macroalgae can be reduced by an increase in ultraviolet radiation from holes in the ozone layer, which also damages DNA, alters nutrient uptake, and changes the pigment composition of the algae (Franklin and Forster, 1997; Lotze and Worm, 2002).

Increased anthropogenic sedimentation and elevated temperature undermine the coral population recovery processes. Recovery of coral cover is done through growth of surviving colonies (asexual reproduction) and recruitment (sexual reproduction). The five fundamental steps for coral recovery through recruitment are the production/availability of larvae, dispersal of larvae to disturbed site, ability of larvae to settle (aided by presence of chemical cues to induce settlement), availability of suitable settlement substrate for coral to grow, and survival and growth of newly settled juveniles to maturity stage (Ritson-Williams et al., 2009; Arnold et al., 2010). Newly settled corals are likely more vulnerable to climate change and sedimentation than adults, however they have been poorly studied. An increased sediment load, especially involving fine sediments, often clogs the feeding structures of juvenile corals, reducing their ability to actively feed and depleting their energy stores (Stafford-Smith & Ormond, 1992; Burke et al., 2011; Erftemeijer et al., 2012; Jones et al., 2015), thus reducing their survival (Fourney & Figueiredo, *in preparation*). When the coral is smothered in sediment, anoxic areas surrounding juvenile polyps create an area without proper water flow for oxygen repletion (Erftemeijer et al., 2012). As a result, sedimentation can significantly threaten the replenishment of coral populations and recovery after disturbances. Newly settled corals are also likely more vulnerable to warming because they have less energy reserves than adults (Chua et al.,2012). The recent rapid declines in coral health and cover (30% lost in the past decade) world-wide (Bellwood et al., 2004; Burke et al., 2011) suggest that natural recovery processes are evidently being affected by anthropogenic stressors. Currently, almost 75% of worldwide coral reefs are threatened by anthropogenic stressors with several studies predicting that 60-90% of corals will be lost by 2030 (Hughes et al.,

2003; Burke et al., 2011). The undermining of coral recovery by sedimentation and warming may accelerate the decline and facilitate algal dominance.

When considering the future of coral reef ecosystems, it is critical to assess the relative susceptibility of corals and macroalgae to increased anthropogenic sedimentation and elevated temperature. Measuring the effects of sedimentation and temperature on both juvenile coral and algae helps to generate better predictions of coral-algae balance on reefs. It is important to focus on juvenile corals because recovery of adult coral communities strongly depends on successful recruitment. Due to the vulnerability of small-sized new recruits, it is vital to identify the threshold level of the combined effects of sedimentation and temperature for juvenile coral survival and growth. The first objective of this study was to compare the survival of juvenile corals, *Montastraea cavernosa,* and the macroalgae, *Dictyota ciliolate,* under varying levels of sedimentation and temperature. The second objective was to quantitatively assess the synergistic effects of sedimentation and increased temperature on the growth of juvenile corals and macroalgae.

2. Methods

2.1 *Study Species and Collection*

Montastraea cavernosa (Figure 1) was selected for this study because it is a relatively abundant and structurally important scleractinian coral in South Florida's reefs (Acosta and Zea, 1997; Vargas-Angel, 2006a; Klug & Walker, *in prep*.). *Montastraea cavernosa* is found in Florida, the Gulf of Mexico, Bermuda, the Bahamas, and in the Caribbean (Aronson et al., 2008), with peak abundance between 10 to 30 m (Szmant *et al*. 1997). These corals are gonochoric and reproduce sexually through mass synchronized broadcast spawning events (Acosta and Zea, 1997). Spawning of *M. cavernosa* typically occurs after sunset, one week after the full moon in August or September (Szmant, 1986; Vize et al., 2005; Vargas-Angel et al., 2006b). *Montastraea cavernosa* forms small colonies usually in boulder or dome shapes with large, protruding corallites and can vary extensively in shape, size, and color (Szmant et al., 1997).

Figure 1. Adult colony of *Montastraea cavernosa* in Broward County, FL

The most dominant genus of macroalgae on reefs between 7 and 21 m along the Florida Reef Tract is *Dictyota* (Littler et al., 1986; Beach et al., 2003). *Dictyota ciliolata* (Figure 2) was chosen for this experiment due to its high abundance and association with coral reefs in southern Florida (Beach & Walters, 2000). It is a brown alga that generally forms mats of densely packed leaves, with forked tips, that overgrow the substrate. *Dictyota ciliolata* has been found to contain a variety of chemical compounds that have anti-herbivore and anti-fouling properties (Beach & Walters, 2000). They exhibit a typical alteration of generations between two haploid sexual plants (male and female which constitute gametophytes) and a diploid tetrasporic plant which is regarded as the sporophyte (Foster et al., 1972). Fertilization occurs after both kinds of gametes are released into the water column, which occurs every 14 days after the highest spring tides (Foster et al., 1972). The abundance of *Dictyota* is enhanced by its ability to asexually reproduce via fragmentation (Airoldi, 1998; Beach and Walters, 2000; Herren et al., 2006). Vegetative fragmentation of *Dictyota* occurs with four main steps: disturbance leading to the creation of fragments, settlement or entanglement, attachment, and continued epiphytic growth on benthic biota or substrate (Herren et al., 2006).

Figure 2. *Dictyota ciliolata* from Broward County, FL

Thirty-one healthy corals, roughly 30 cm in diameter, were collected on the day of the full moon (August 18, 2016) from three locations (26° 09.046N, 80° 05.402W; 26° 09.476N, 80° 05.348W; 26° 11.176N, 80° 05.277W) in Broward County, FL (Figure 3). SCUBA divers identified colonies suitable for collection and removed them from the substrate with pry bars and hammers at the base of the colony to prevent tissue damage. The colonies were brought up to the boat in wire dish racks, where the corals were immediately wrapped in bubble wrap and placed in coolers. The coolers were filled with seawater, with water changes performed every 20 minutes to maintain temperature, adequate oxygen, and prevent desiccation. Colonies were transported to Nova Southeastern University's (NSU) Guy Harvey Oceanographic Center (GHOC) and placed in outdoor aquaria. These aquaria contained 1500L recirculating water equipped with biological filtrations, protein skimmers, temperature controlled heaters, a chiller, and shade cloth to mimic natural light conditions. While in the field, temperature (29°C) was measured with a YSI® Pro20 temperature probe and the light irradiance at the sites (average of 153 μmol photons $m^{-2}s^{-1}$) was measured with a Li-Cor® Li-250A light meter at the depth the corals were collected.

Ten clusters, roughly 10 cm in diameter, of *D. ciliolata* were collected from the same sites as the coral colonies (Figure 3). SCUBA divers identified clusters suitable for collection and removed them from the substrate with scissors at the base of the plant to prevent damage. The clusters were brought up to the boat in plastic Ziploc bags, where they were immediately placed in a 5-gallon bucket. The bucket was filled with seawater, with water changes performed every 20 minutes to maintain temperature, adequate

oxygen, and prevent desiccation. The clusters were transported to NSU GHOC and placed in an indoor aquarium. This aquarium was 30L volume equipped with two pumps, a temperature controlled heater, and a LED light to mimic natural light conditions.

Figure 3. Map of the 3 specimen collection sites in Broward County, FL.

2.2 *Coral Spawning, larval rearing, and settlement*

Colonies were monitored for spawning every night starting the day of collection, due to potential alterations in spawning synchronism caused by captivity conditions (e.g. transportation stress). Every night at sunset, each colony was removed from the tank and placed in a separate bucket of seawater for spawning because *M. cavernosa* is gonochoric and the sexes of the colonies were unknown. The colonies were observed for spawning until midnight, after which they were placed back into the recirculating aquaria. After the completion of the spawning event, all adult corals were returned to their collection site and cemented to the reef with an identification tag.

Spawning occurred from August 19 - 29, 2016 and the sex of the colony and time of spawning was recorded each night. Eggs were collected by skimming the surface with a plastic cup and gently transferred to a separate bowl. Sperm was collected with a turkey baster and placed in a separate bowl. The gametes were then combined, with a sperm concentration of 10^6 mL^{-1}, to allow fertilization to occur. One hour after combining the

gametes, a sample of the eggs was observed under the microscope (Olympus LC20 digital camera attached to an Olympus SZ61 dissecting microscope with cellSens® software) for cleavage, i.e. fertilization. After ~80% of the eggs were fertilized, the sperm was removed by a series of dilutions with 1 µm filtered, sterilized seawater. The embryos were then separated into bowls at a density of < 1 embryo/mL and the bowls were placed into water baths kept at ambient temperature (29°C). The water within each bowl was changed daily to ensure good water quality conditions and reduce mortality. Once the planula reached competency (~3 days post-fertilization) they were moved to settlement jars.

Ceramic tiles (2.5 cm diameter, 0.5 cm height) were conditioned in the ocean for 3 months, at the same depth the coral species were collected. It was necessary to condition the tiles to allow for the colonization of bacterial biofilms and crustose coralline algae (CCA), which is a settlement cue for the planula (Babcock et al., 2003). Following the conditioning period, the tiles were collected, checked for the presence of CCA, and placed in the outdoor recirculating aquaria until they were needed for the larval settlement process.

The competent larvae were placed in 200 mL glass jars filled with filtered seawater (20 planula per jar), each containing a pre-conditioned settlement tile. The jars were inspected every 24 h to determine settlement success (metamorphosis to polyp stage). This occurred every day until the desired number of juveniles for each treatment (100+ per treatment) was reached. After the larvae had settled, each tile was observed under the dissecting stereoscope to count and map the settled juveniles. The tiles were photographed, using cellSens®, to record the position and surface area of the juvenile corals. Once initial position and size were recorded, the tiles were distributed evenly and randomly across treatment tanks.

Two hundred and forty (30 per treatment tank) pieces of *D. ciliolata* were cut with dissecting scissors into 1 cm fragments, that were measured with calipers. Twist ties were used to hold the fragments to pre-conditioned settlement tiles and placed back in the aquarium for four days, at which point they had naturally attached to the tiles. Once they were attached, the twist tie was removed and the tiles were randomly distributed into treatment tanks.

2.3 *Sediment Collection*

Sediment was collected from the top 10 - 20 cm of bottom material in the boat basin at NSU's GHOC, located next to Port Everglades via SCUBA diving. The sediment was placed in ramekins and put into a drying oven at 70°C for a minimum of 72 hours to ensure all interstitial organisms were killed and to assure accurate sediment weighing. The sediment composition was assessed according to the Udden-Wentworth US standard classification scale (Wentworth, 1922). The dry sediment was sieved (Sieve Shaker model RX-86) with a series of sieves (500 µm, 180 µm, and 63 µm) to quantify the percentages of different grain sizes. Sedimentation levels used were 0, 30, 60, and 120 mg cm^{-2} of deposited sediment, representing a control, natural rates, double natural rates, and rates found during dredging events respectively (Jordan et al., 2010). Note that the sedimentation levels reflect the amount deposited after one day, not necessarily how much sediment was placed in each tank (sediment was only added on day one; the heaviest sediment settled within one day, while the finer sediment remained suspended due to water flow; with turbidity and settled sediment staying relatively constant afterwards). Prior to the start of the experiment, the quantity of sediment needed to produce these rates in each treatment was tested to account for the amount of sediment that would remain in suspension. Sediment traps were used to determine the sedimentation rate by adding several known amounts of sediment to a 45cm x 30cm x 30cm tank with glass jar lids (25.65 cm^2 openings) as the traps. A linear regression was used to describe the relationship between the quantity of sediment added and the sedimentation rate produced. This relationship was used to determine the correct quantity of sediment necessary to add to produce each treatment (2% >500 µm, 40% 180-500 µm, 42% 63-180 µm, and 15% <63 µm).

2.4 *Temperature and Sedimentation Treatments*

There were 8 treatments comprised of two temperatures and four sedimentations; 29°C and 31°C (current summer ambient seawater temperature and the predicted seawater temperature for the middle of the 21st century, IPCC 2014) and 0, 30, 60, and 120 mg cm^{-2}, respectively. All treatments were replicated to account for a possible tank

effect. There was a total of 1091 coral juveniles and 240 fragments of *D. ciliolata* divided between the treatments (Figure 4). As stated above, the treatment tanks were 45 x 30 x 30cm to ensure viable space for all tiles. The juvenile corals and macroalgae were reared in captivity under the described conditions with survival and growth recorded weekly for 3 months. Once a week, each tile was inspected under the microscope and photographed to track survival and record surface area.

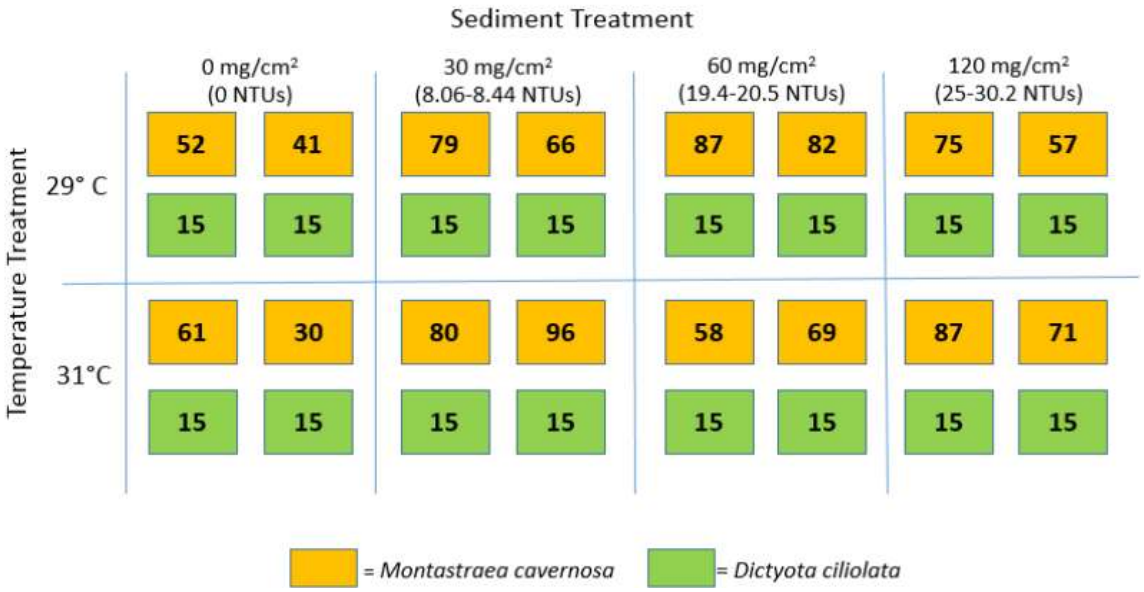

Figure 2. Experimental design where color of box represents species (orange is coral, green is macroalgae). The number inside each box represents the number of individuals in each tank.

2.5 *Treatment Maintenance*

For all treatments, the juvenile corals and algae were kept indoors in tanks equipped with an Aqueon® Pro 250 submersible heater to maintain temperature, with temperature measured daily using a YSI® Pro20 to ensure accuracy. Two SunSun® JP-032 submersible pumps with a flow rate of 350L/h were used to maintain ideal oxygen concentration and keep sediment suspended. Aquaillumination® Hydra26 LED lights with a controllable light intensity were used to create a 12:12h light:dark photoperiod that mimics the daily sun cycle (Babcock et al., 2003). Solar noon irradiance was measured at the bottom of each tank, with a maximum irradiance of 153µmol photons/m^2s, mimicking natural reef levels from the day of specimen collection. Nephlometric Turbidity Units (NTUs) were measured with a turbidimeter (LaMotte 2020we). The salinity of each tank

was maintained at 35ppt and reverse osmosis water was added daily to replace water lost to evaporation. Ammonia, nitrate, nitrite, copper, and phosphate concentrations were monitored and recorded weekly throughout the experiment with 50% water changes implemented every other day to maintain water quality. Excess sediment from each tank was collected during water changes and was redistributed to the corresponding tank to ensure maintenance of the sedimentation concentration. Every week, when the tiles were scoured, 100% water changes were performed and new sediment was introduced to the tank. The day before the 100% water change the juvenile corals were fed ~58,000 rotifers, mimicking the abundance of phytoplankton in a reef environment.

Juvenile corals were provided with *Symbiodinium* by introducing water exposed to sediment (adapted from Cumbo et al., 2013). Natural reef sediment from the top 10 cm was collected from the coral collection sites, brought back to the GHOC, and kept in the outdoor recirculating aquaria. Twice a week, during a water change, natural sediment was washed with filtered seawater and filtered through a 53 µm sieve and then added to each coral juvenile tank. During the weekly assessment of growth and survival, the coral juveniles were observed for symbiont uptake.

2.6 *Data Analysis*

To compare the survival of juvenile corals and macroalgae under different levels of sedimentation and temperature a Kaplan-Meier survival curve was produced for each treatment. The "Cox Model" was used to test the effect of sediment and temperature on juvenile coral and macroalgae survival. Post hoc multiple comparisons were performed with Mantel-Haenszel (log-rank) tests to compare survival between treatments.

The growth data was also explored by modelling change in surface area over time of juvenile corals and macroalgae fragments using a stepwise method informed by the Akaike Information Criteria (AIC). Fitting a regular growth curve to the data would bias growth measurements since some of the juveniles died during the experiment. To avoid this, weekly growth rates of surviving individuals were calculated. For each individual, its actual size measurements were used while it remained alive, then the size of the dead individuals for the following weeks were estimated by randomly selecting one of the growth rates measured that week. The model that best fit (linear or nonlinear) the data to

obtain the growth curve was chosen and its 95% confidence interval was calculated. To determine the effect of temperature and sedimentation on the growth curves, the AIC of temperature and/or sedimentation dependent models were compared with temperature and/or sedimentation independent models. When comparing models, the one with the lower AIC is the model with the better fit.

The statistical software R was used to conduct all analysis.

3. Results

3.1 *Juvenile Coral Survival*

The survival of coral juveniles was significantly affected by sediment ($p < 2.0x10^{-16}$) but was not significantly affected by temperature ($p = 0.537$). Coral survival at 0mg/cm^2 (0 NTUs) was significantly different from all other treatments ($p = 6.56x10^{-6}$, $p < 2.0x10^{-16}$, $p < 2.0x10^{-16}$) with corals being dead by week 7 (Figure 5). There was a significant difference in coral survival between 30mg/cm^2 (8.06-8.44 NTUs) sediment treatments and 60mg/cm^2 (19.4-20.5 NTUs) and 120mg/cm^2 (25-30.2 NTUs) treatments ($p = 2.55x10^{-7}$; $p = 0.000129$; respectively). The mortality of juvenile corals was not significantly different ($p = 0.339$) between 60mg/cm^2 (19.4-20.5 NTUs) and 120mg/cm^2 (25-30.2 NTUs) treatments, and was the lowest of all treatments. Corals in the 30mg/cm^2 (8.06-8.44 NTUs) had an intermediate mortality, while all juvenile corals in the 0mg/cm^2 (0 NTUs) treatment were dead after 7 weeks, leading to the highest mortality of all treatments (Figure 5).

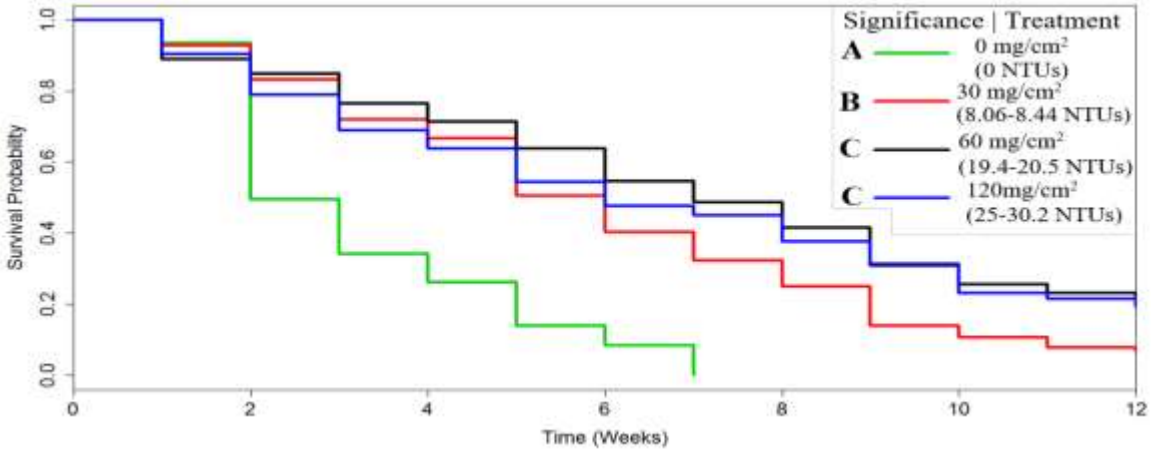

Figure 5. Kaplan-Meier survival curves of juvenile corals in each of the sediment treatments. The colors and line type represent the different sedimentation levels.

3.2 *Juvenile Coral Growth*

The change in surface area over time of *Montastraea cavernosa* juveniles was best fit with an asymptotic model (Figure 6), which shows the fast increase in size in the first week followed by a decrease in growth rate the following weeks. The increase in size in the first week coincides with the spread of the polyps' basal plate, common in all corals. Based on the AIC values, temperature and sediment both significantly affected coral juvenile growth. *Montastraea cavernosa* growth was the greatest at the higher temperature and 60mg/cm^2 (19.4-20.5 NTUs), followed by the ambient temperature with 60mg/cm^2 (19.4-20.5 NTUs). The next highest growth rates in *M. cavernosa* were seen in the 120mg/cm^2 (25-30.2 NTUs) treatments at 31°C followed by 29°C. The lowest growth rate was seen at ambient temperature with no sediment.

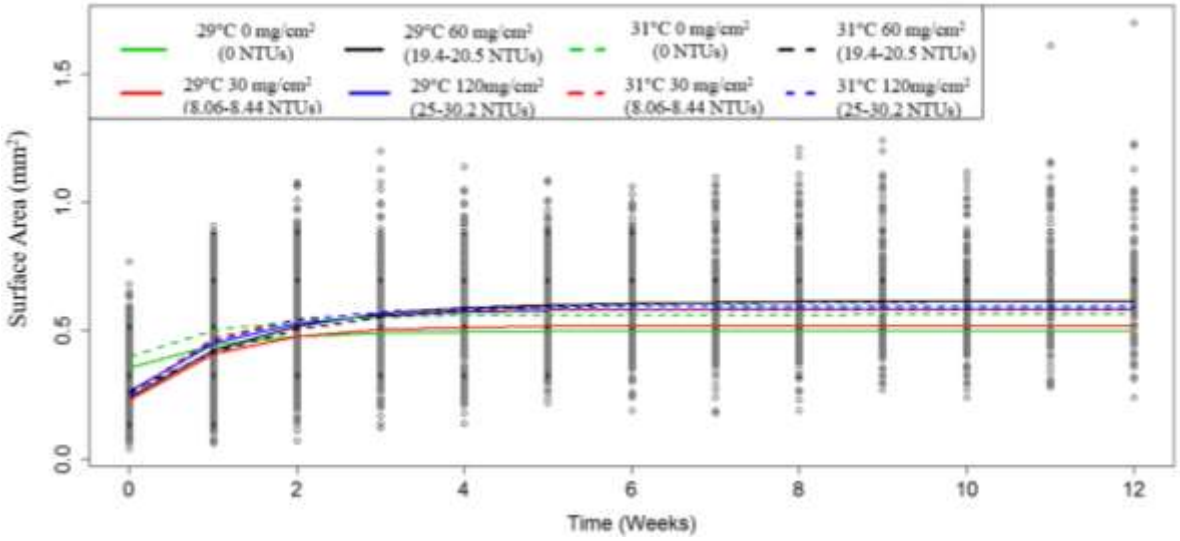

Figure 6. Growth of *Montastraea cavernosa* for all treatments. The colors represent the different sedimentation levels with the solid lines representing ambient temperature (29°C) and the dashed lines representing the elevated temperature (31°C).

3.3 *Macroalgae Survival*

Macroalgae survival was significantly affected by sediment (p = 0.00432) but was not significantly affected by temperature (p = 0.15145). The survival of *D. ciliolata* in the 120mg/cm^2 (25-30.2 NTUs) treatment was significantly different from all other treatments (p = 0.000969, p =)0581, p = 0.0488; 0, 30, and 60 mg/cm^2; respectively). There was not a significant difference (p = 0.219) in macroalgae survival between the

30mg/cm^2 (8.06-8.44 NTUs) sediment treatment and the 60mg/cm^2 (19.4-20.5 NTUs) treatment. The macroalgae in the 120mg/cm^2 (25-30.2 NTUs) treatments had the highest mortality. The *D. ciliolata* fragments in the 0mg/cm^2 (0 NTUs), 30mg/cm^2 (8.06-8.44 NTUs), and 60mg/cm^2 (19.4-20.5 NTUs) treatments had the lowest mortality, however, not a single piece of macroalgae, in any treatment, survived the entire duration of the experiment (Figure 7).

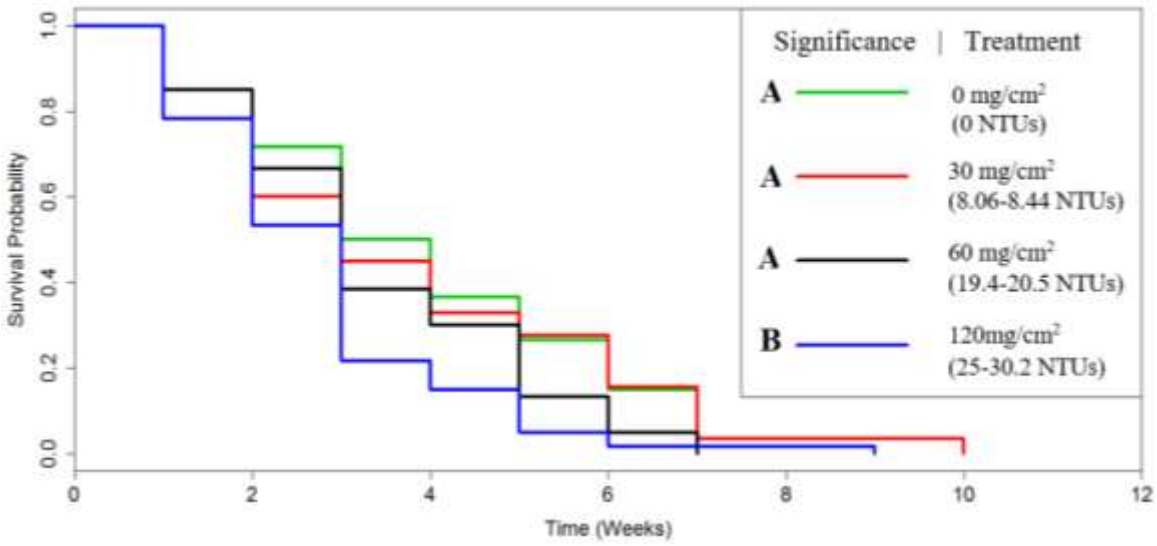

Figure 7. Kaplan-Meier survival curves of macroalgae in each of the sediment treatments. The colors and line type represent the different sedimentation levels.

3.4 *Macroalgae Growth*

The change in surface area over time of *D. ciliolata* fragments was best fit with a linear model (Figure 8). Based on the AIC values, temperature and sediment affected macroalgae growth as well as their combined affects. *Dictyota ciliolata* growth was the greatest at the higher temperature and no sediment, followed by the higher temperature with 30mg/cm^2 (8.06-8.44 NTUs) and 60mg/cm^2 (19.4-20.5 NTUs) respectively. The lowest growth rate was seen at ambient temperature with 60mg/cm^2 (19.4-20.5 NTUs).

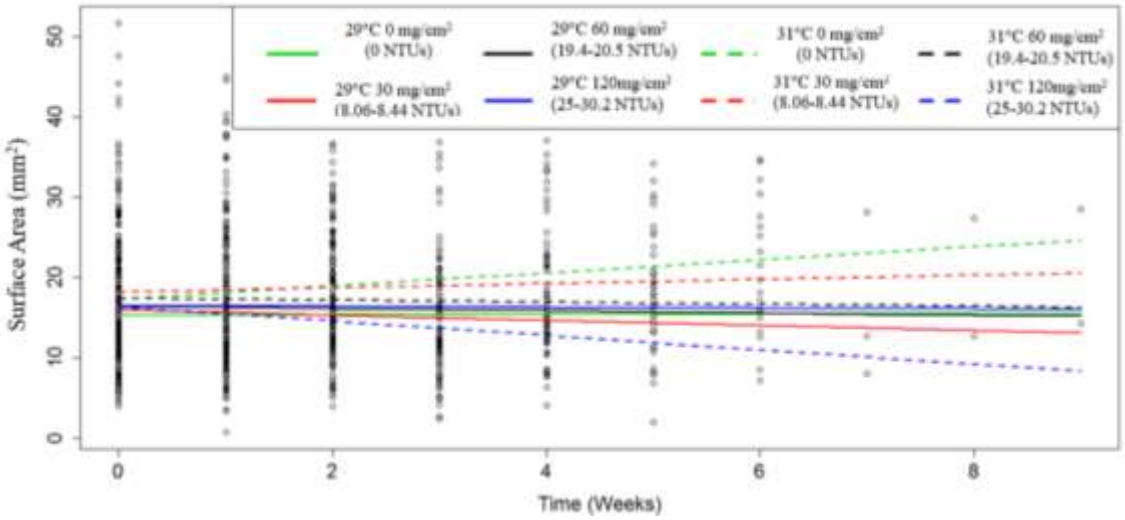

Figure 8. Growth of *Dictyota ciliolata* for all treatments. The colors represent the different sedimentation levels with the solid lines representing ambient temperature (29°C) and the dashed lines representing the elevated temperature (31°C).

4. Discussion

A 2°C increase in temperature did not significantly affect survival of the juvenile *M. cavernosa* corals and fragments of *D. ciliolata*. *Montastraea cavernosa* juvenile survival was lower in the treatments with lower sediment concentration, however this result is likely confounded by higher exposure to light. *Dictyota ciliolata* survival was highly sensitive to the increase in sedimentation. The juvenile corals grew much less and died earlier in the absence of sediment. Temperature and sediment both affected coral juvenile growth and their combined affects were additive. Macroalgae grew faster at higher temperatures but grew less at higher sedimentation, so their combined affects were antagonistic.

An increase in temperature did not have a significant deleterious effect on the survival of *M. cavernosa* juveniles. The newly settled *M. cavernosa* juveniles had yet to acquire symbionts because, like the majority of broadcast spawning species of corals, this species acquires *Symbiodinium* horizontally (Harrison & Wallace, 1990), from a free-swimming reservoir (Baird et al., 2009). In this experiment, the coral juveniles were placed in the predicted future temperature treatments before they acquired symbionts. Corals can switch their symbionts in response to environmental changes, like ocean warming, allowing for the selection of a more thermally tolerant clade (Baker, 2001;

Silverstein et al., 2015; Boulette et al., 2016). As these *M. cavernosa* juveniles were already acclimated to the warmer temperature, they may have selected for more thermally tolerant *Symbiodinium* allowing them to persist in the warmer conditions over time (Abrego et al. 2012). Alternatively, corals in South Florida have suffered bleaching in the three years prior to this study so their offspring may be a little more resistant to warmer conditions (van Woesik & McCaffrey, 2017). It has been suggested that directional selection in a warming ocean may favor the corals that are able to tolerate inshore environments with higher turbidity (van Woesik & McCaffrey, 2017).

Unexpectedly, *M. cavernosa* juvenile survival was positively affected by an increase in sedimentation. Suspended sediment concentration has a direct relationship with turbidity and therefore decreases light availability for corals, which has been shown to negatively impact adult corals (Bak and Elgershuizen, 1976; Dodge and Vaisny, 1977; Erftemiejer et al., 2012). In this experiment, the light irradiance used was one that is optimal for adult corals, reaching its maximum at solar noon. An experiment looking at the orientation of coral settlement dishes that represented different levels of sedimentation and the effect of position on the survival of juvenile corals concluded that downward facing dishes had the highest survival (Sato, 1984). This is commonly interpreted that the corals do not get sediments falling and burying them, so the coral juveniles have a higher probability of survival. However, this dish orientation is also protecting them from excessive light and in this study light was not considered as a factor so the results could be interpreted differently if considering light. It is known that coral juveniles tend to settle in cracks in crevices in the field (Babcock & Mundy, 1996; Mundy & Babcock, 1998) and on the bottom side of tiles in the lab (personal observation) and if the dish orientation is compared to the amount of light available to the corals, the juveniles could also be surviving better because of the lower light intensity. A coral settlement study done in Guam used tile orientation at different depths to determine the settlement preference of coral recruits (Birkeland et al., 1981). At shallow depths, where light intensity was the highest, there were more coral juveniles settled on the bottom of the horizontal tiles and at the deeper depths there were more corals settled on the top of the horizontal tiles. Therefore, it was concluded that light attenuation affects settlement location of coral juveniles (Birkeland et al., 1981). Thus, sediment was seen to

be less problematic than light at this stage of coral development most likely due to juvenile corals preference for settling on cryptic surfaces (Babcock and Mundy, 1996; Mundy and Babcock, 1998) and high light in the early stages of coral development being highly deleterious. To verify this result, optimal light irradiance for juvenile survival and growth would need to be determined and this experiment repeated with the new light levels.

Despite the overwhelming amount of information on the adverse effects of increased sedimentation and turbidity, there are a few potentially advantageous effects of turbidity, particularly to early life stages of coral juveniles. An increase in turbidity can cause light attenuation, oxidative stress, and reduced visibility for predators (Jones et al., 2015). It has been suggested that lower light intensities can reduce the oxidative stress on *Symbiodinium* cells in juvenile corals (Abrego et al., 2012). Under normal conditions *Symbiodinium* are capable of protecting themselves; however, high temperature and high light stress can overwhelm the mechanisms they use to protect themselves (Abrego et al., 2012). Many stressors, including high light intensity, ultra-violet radiation, pollution, and temperature may cause *Symbiodinium* to burden corals in their early life history stages (Yakovleva et al., 2009). Clearly, symbionts are not always a burden for the coral host, as almost all species of scleractinian corals cannot live without their symbionts, so at some point in development, the benefits must outweigh the costs (Yakovleva et al., 2009).

Montastraea cavernosa juvenile growth was maximized at the warmer temperature and higher sedimentation. Metabolic rates accelerate with an increase in temperature thus accelerating cell division allowing for faster growth (O'Connor et al., 2007; Chua et al., 2012). Sediment smothering can cause a decrease in heterotrophy and metabolite exchange in coral juveniles because photosynthesis and heterotrophic feeding can be impaired causing an inability of the coral to replenish its energy reserves, however, this may not have been the major driver of these results (Fitt et al., 2000; Jones et al., 2015). The high light irradiance most likely caused severe oxidative stress to the corals in the non-sediment treatments. These corals may have spent energy surviving the stress caused by high light irradiance while the ones shielded from the light, due to turbidity and burial, may have been able to expend more energy towards growth.

The survival of *D. ciliolata* was not significantly affected by a 2°C increase in temperature while growth was positively affected. The majority of tropical macroalgae exhibit thermal limits ranging from 24-30°C with growth thresholds averaging ~3°C lower, though many species have not been studied (Koch et al., 2013). The thermal range maximum for *D. ciliolata* is 29.9°C (Tronholm et al., 2012). Therefore, the temperatures the macroalgae were exposed to in this study were at the top and above the optimal range, likely causing the low probability of survival. Although the *D. ciliolata* grew better at the higher temperature, the growth rate decreased over time likely due to the macroalgae dedicating more energy to survival than growth. Thermal limits of macroalgae were modelled in South Florida and biomass significantly declined at temperatures greater than 31°C (Biber, 2002).

An increase in sedimentation caused a decrease in *D. ciliolata* survival and growth. An increase in turbidity, due to sedimentation, reduced light availability to the macroalgae and likely resulted in less energy for nutrient uptake, storage, and growth (Rosemond et al.,2000; Clausing and Fong, 2016). Along with the increase in turbidity, sediment smothering may have also played a role in the light and nutrient availability for the *D. ciliolata*. High light irradiance along with an ample supply of nutrients (phosphorous and nitrogen) allows for a rapid growth rate in *Dictyota* (Clausing and Fong, 2016). However, throughout the duration of this experiment, weekly water quality tests determined that nutrient availability was very limited. The macroalgae survived and grew the best in the non-sediment treatments suggesting that light availability for photosynthesis was the main driver for successful growth. Light limitation is common when turbidity and deposited sediment concentration are high (Grobbelaar, 1990; Rosemond et al., 2000; Cloern, 2001). Recent evidence suggests light availability may have dominance over nutrient availability and constrain growth regardless of nutrient supply (Karlsson et al., 2009) as growth of *D. ciliolata* is positively related to increasing light intensity (Cronin & Hay, 1996).

The survival and growth of either species appeared to be susceptible to an increase in sedimentation, but in opposite ways. In terms of survival, the juvenile corals were less susceptible to an increase in sedimentation than the macroalgae. For example, at week two there was 6% decrease in coral survival and a 7% decrease in macroalgae survival.

However, at week four, coral mortality was lower in the high sediment concentration treatments. Considering the known negative effects of sediment on corals (Stafford-Smith & Ormond, 1992; Riegl & Branch, 1995; Burke et al., 2011; Erftemeijer et al., 2012; Jones et al., 2015), this was most likely due the sediment providing a shield from excessive light, which has been shown to be deleterious in earlier stages (Abrego et al., 2012). In contrast, under low light intensity, the macroalgae had a drastic decrease in survival while these *M. cavernosa* juveniles had a higher probability of surviving than the *D. ciliolata*. Then again, the coral juveniles in this experiment were exposed to direct light which they are not usually exposed to in the wild. Therefore, the experiment should be redone using a lower light irradiance (typical of crevices) to see if this pattern will reverse. In terms of growth, these juvenile corals grew better under intermediate and high sedimentation, regardless of temperature while the macroalgae grew better in low sedimentation but high temperature. If the *M. cavernosa* recruit is directly exposed to light and it is on a horizontal position, it is less affected by sedimentation than the *D. ciliolata*. However, it is unclear if this relationship holds when recruits are exposed to lower light irradiance, as they usually are in nature (Babcock & Mundy, 1996; Mundy and Babcock, 1998). Once again, light stress may have played a role in the energy available to allocate towards growth for the juvenile corals and more studies on the synergistic effects of light and sedimentation should be done.

A change in the intensity of a stressor (i.e. sedimentation) can lead to a shift to an alternative stable state that encompasses a change in ecosystem processes, functions, and feedback mechanisms (Knowlton, 1992; Scheffer et al., 2001; Mumby et al., 2007). Reverting to the original state requires the stable variables in the newly shifted system to be restored to levels way beyond the threshold that originally caused the regime shift (O'Neill, 1998; Suding et al., 2004). There is limited evidence of reversals from macroalgae regime shifts back to coral dominance and these recoveries are usually correlated with an increase in herbivorous sea urchin abundance (Carpenter & Edmunds, 2006). Resilience to abrupt disturbances may not always be the issue for corals, but constant stress may push a reef beyond its resistance threshold (McManus & Polsenberg, 2004). Simply removing the stress after the ecosystem has shifted to a new stable state will not automatically result in a recovery of the original system (Norstrom et al., 2009),

making management of future anthropogenic stressors (i.e. dredging) crucial to prevent the regime shift from ever occurring.

Understanding the effects of sedimentation from anthropogenic sources on juvenile corals and macroalgae is needed to better understand future coral-macroalgae competition for space and help guide management decisions. Arguably one of the least studied life history stages of corals is early juvenile, where the small sized (sub-millimeter) polyps start zooplanktivory, gain *Symbiodinium*, and develop secondary polyps (Jones et al., 2015). The tiny size of the newly settled recruits makes them vulnerable to an array of factors and difficult to study and coral reef recovery depends on successful recruitment of coral larvae after disturbances. Although it is not known how long *Dictyota* fragments can remain viable in the water column before attachment, the incessant fragment creation with their rapid attachment rates may continue to contribute to the abundance of macroalgae on reefs if the conditions are right for a regime shift. This study demonstrates that both *M. cavernosa* juveniles and *D. ciliolata* fragments may be more vulnerable to light caused by changes in turbidity rather than temperature. Future studies should investigate how the synergistic effects of light irradiance and sedimentation effect the survival and growth of juvenile coral survival.

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6. Literature Cited

Abrego D, Willis BL & van Oppen MJH (2012). Impact of Light and Temperature on the Uptake of Algal Symbionts by Coral Juveniles. *PLOS ONE, 7*(11), e50311.

Acosta A & Zea S (1997). Sexual reproduction of the reef coral Montastreacavernosa (Scleractinia: Faviidae) in the Santa Marta area, Caribbean coast of Colombia. *Marine Biology, 128*(1), 141-148.

Ainsworth CH & Mumby PJ (2015). Coral–algal phase shifts alter fish communities and reduce fisheries production. *Global Change Biology, 21*(1), 165-172.

Airoldi L (1998). Roles of Disturbance, Sediment Stress, and Substratum Retention on Spatial Dominance in Algal Turf. *Ecology, 79*(8), 2759-2770.

Anthony KRN, Connolly SR & Hoegh-Guldberg O (2007). Bleaching, energetics, and coral mortality risk: Effects of temperature, light, and sediment regime. *Limnology and Oceanography, 52*(2), 716-726.

Arnold SN, Steneck R & Mumby PJ (2010). Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology-Progress Series, 414*, 91.

Aronson RB, Bruckner A, Moore J, Precht B & Weil E (2008). *Montastraea cavernosa*. The IUCN Red List of Threatened Species 2008 e.T133237A3646174.

Babcock R & Mundy C (1996). Coral recruitment: Consequences of settlement choice for early growth and survivorship in two scleractinians. *Journal of Experimental Marine Biology and Ecology, 206*(1), 179-201.

Babcock RC, Baird AH, Piromvaragorn S, Thomson DP & Willis BL (2003). Identification of scleractinian coral recruits from Indo-Pacific reefs. *ZOOLOGICAL STUDIES-TAIPEI-, 42*(1), 211-226.

Baird A & Maynard JA (2008). Coral adaptation in the face of climate change. *Science, 320*(5874), 315-316.

Baird AH Guest JR & Willis BL (2009). Systematic and Biogeographical Patterns in the Reproductive Biology of Scleractinian Corals. *Annual Review of Ecology, Evolution, and Systematics, 40*(1), 551-571.

Bak RPM & Elgershuizen JHBW (1976). Patterns of Oil-Sediment rejection in corals. *Marine Biology, 37*(2), 105-113.

Baker AC (2001). Ecosystems: Reef corals bleach to survive change. *Nature, 411*(6839), 765-766.

Beach K, Walters L, Borgeas H, Smith C, Coyer J & Vroom P (2003). The impact of *Dictyota spp.* on *Halimeda* populations of Conch Reef, Florida Keys. *Journal of Experimental Marine Biology and Ecology, 297*(2), 141-159.

Beach KS & Walters LJ (2000). *Dictyota bloom in the Florida Keys National Marine Sanctuary: fragments and fouling.* Paper presented at the AAUS 20th Symposium.

Beardall J, Beer S & Raven J (1998). Biodiversity of marine plants in an era of climate change: some predictions based on physiological performance. *Botanica Marina, 41*(1-6), 113-124.

Bellwood DR, Hughes TP, Folke C & Nyström M (2004). Confronting the coral reef crisis. *Nature, 429*(6994), 827-833.

Birkeland C, Rowley D & Randall RH (1981). *Coral recruitment patterns at Guam.* Paper presented at the Proc 4th Int Coral Reef Symp.

Bruno JF, Petes LE, Harvell DC & Hettinger A (2003). Nutrient enrichment can increase the severity of coral diseases. *Ecology letters, 6*(12), 1056-1061.

Bruno JF, Selig ER, Casey KS, Page CA, Willis BL, Harvell CD, Sweatman H, Melendy AM (2007). Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biol, 5*(6), e124.

Bruno JF, Sweatman H, Precht WF, Selig ER & Schutte VG (2009). Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology, 90*(6), 1478-1484.

Burke L, Reytar K, Spalding M & Perry A (2011). *Reefs at risk revisited*.

Carpenter RC & Edmunds PJ (2006). Local and regional scale recovery of Diadema promotes recruitment of scleractinian corals. *Ecology letters, 9*(3), 271-280.

Cesar H, Burke L & Pet-Soede L (2003). *The economics of worldwide coral reef degradation*.

Chua CM, Leggat W, Moya A & Baird AH (2013). Temperature affects the early life history stages of corals more than near future ocean acidification. *Marine Ecology Progress Series, 475*, 85-92.

Clausing RJ & Fong P (2016). Environmental variability drives rapid and dramatic changes in nutrient limitation of tropical macroalgae with different ecological strategies. *Coral Reefs, 35*(2), 669-680.

Cloern JE (2001). Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series, 210*, 223-253.

Conservartion International (2008). Economic Values of Coral Reefs, Mangroves, and Seagrasses: A Global Compilation.

Cronin G & Hay ME (1996). Effects of Light and Nutrient Availability on the Growth, Secondary Chemistry, and Resistance to Herbivory of Two Brown Seaweeds. *Oikos, 77*(1), 93-106.

Cumbo VR, Edmunds PJ, Wall CB & Fan TY (2013). Brooded coral larvae differ in their response to high temperature and elevated pCO2 depending on the day of release. *Marine Biology, 160*(11), 2903-2917.

Daly M & Mathieson A (1977). The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Marine Biology, 43*(1), 45-55.

Dodge RE & Vaisnys JR (1977). Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. *Journal of Marine Research, 35*(4), 715-730.

Donner SD, Skirving WJ, Little CM, Oppenheimer M & Hoegh-Guldberg O (2005). Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology, 11*(12), 2251-2265.

Dubinsky Z & Stambler N (1996). Marine pollution and coral reefs. *Global Change Biology, 2*(6), 511-526.

Erftemeijer PLA, Riegl B, Hoeksema BW, & Todd PA (2012). Environmental impacts of dredging and other sediment disturbances on corals: A review. *Marine Pollution Bulletin, 64*(9), 1737-1765.

Eriksson BK, & Johansson G (2005). Effects of sedimentation on macroalgae: species-specific responses are related to reproductive traits. *Oecologia, 143*(3), 438-448.

Fitt WK, McFarland F, Warner ME, & Chilcoat GC (2000). Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnology and Oceanography, 45*(3), 677-685.

Fong P, Katharyn EB, Krista K, & Karleen AB (2003). Influence of initial tissue nutrient status of tropical marine algae on response to nitrogen and phosphorus additions. *Marine Ecology Progress Series, 262*, 111-123.

Foster M, Neushul M, & Chi E (1972). Growth and reproduction of *Dictyota binghamiae* JG Agardh. *Botanica Marina, 15*(2), 96-101.

Franklin L, & Forster R (1997). The changing irradiance environment: consequences for marine macrophyte physiology, productivity and ecology. *European Journal of Phycology, 32*(3), 207-232.

Glynn PW (1993). Coral reef bleaching: ecological perspectives. *Coral Reefs, 12*(1), 1-17.

Glynn PW (1996). Coral reef bleaching: facts, hypotheses and implications. *Global Change Biology, 2*(6), 495-509.

Glynn PW, & D'Croz L (1990). Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs, 8*(4), 181-191.

Grobbelaar JU (1990). Modelling phytoplankton productivity in turbid waters with small euphotic to mixing depth ratios. *Journal of Plankton Research, 12*(5), 923-931.

Grottoli A, Rodrigues L, & Juarez C (2004). Lipids and stable carbon isotopes in two species of Hawaiian corals, *Porites compressa* and *Montipora verrucosa*, following a bleaching event. *Marine Biology, 145*(3), 621-631.

Grottoli AG, Rodrigues LJ, & Palardy JE (2006). Heterotrophic plasticity and resilience in bleached corals. *Nature, 440*(7088), 1186-1189.

Harrison P, & Wallace C (1990). Reproduction, dispersal and recruitment of scleractinian corals. *Ecosystems of the world, 25*, 133-207.

Herren LW, Walters LJ, & Beach KS (2006). Fragment generation, survival, and attachment of Dictyota spp. at Conch Reef in the Florida Keys, USA. *Coral Reefs, 25*(2), 287-295.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K (2007). Coral reefs under rapid climate change and ocean acidification. *Science, 318*(5857), 1737-1742.

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosber R, Hoegh-Guldberg O, Kleypas J (2003). Climate change, human impacts, and the resilience of coral reefs. *Science, 301*(5635), 929-933.

IPCC (2014). *Climate Change 2014–Impacts, Adaptation and Vulnerability: Regional Aspects*: Cambridge University Press.

Jackson JB (1997). Reefs since columbus. *Coral Reefs, 16*(1), S23-S32.

James EC (2001). Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series, 210*, 223-253.

Johansson G, Eriksson BK, Pedersén M, & Snoeijs P (1998). Long-term changes of macroalgal vegetation in the Skagerrak area. *Hydrobiologia, 385*(1), 121-138.

Jones R, Ricardo GF, & Negri AP (2015). Effects of sediments on the reproductive cycle of corals. *Marine Pollution Bulletin, 100*(1), 13-33.

Jordan LKB, Banks KW, Fisher LE, Walker BK, & Gilliam DS (2010). Elevated sedimentation on coral reefs adjacent to a beach nourishment project. *Marine Pollution Bulletin, 60*(2), 261-271.

Karlsson J, Bystrom P, Ask J, Ask P, Persson L, & Jansson M (2009). Light limitation of nutrient-poor lake ecosystems. *Nature, 460*(7254), 506-509.

Klug & Walker BK (2017). *in prepration.*

Knowlton N (1992). Thresholds and Multiple Stable States in Coral Reef Community Dynamics1. *American Zoologist, 32*(6), 674-682.

Knowlton N (2001). The future of coral reefs. *Proceedings of the National Academy of Sciences, 98*(10), 5419-5425.

Koch M, Bowes G, Ross C, & Zhang XH (2013). Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Global Change Biology, 19*(1), 103-132.

Kuta K, & Richardson L (2002). Ecological aspects of black band disease of corals: relationships between disease incidence and environmental factors. *Coral Reefs, 21*(4), 393-398.

Laffert KD, & Holt RD (2003). How should environmental stress affect the population dynamics of disease? : BLACKWELL PUBLISHING LTD.

Ledlie M, Graham N, Bythell J, Wilson S, Jennings S, Polunin N, & Hardcastle J (2007). Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs, 26*(3), 641-653.

Littler MM, Littler DS, & Lapointe BE (1986). *Baseline studies of herbivory and eutrophication on dominant reef communities of Looe Key National Marine Sanctuary*: US Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service.

Lotze HK & Worm B (2002). Complex interactions of climatic and ecological controls on macroalgal recruitment. *Limnology and Oceanography, 47*(6), 1734-1741.

McManus JW, & Polsenberg JF (2004). Coral–algal phase shifts on coral reefs: Ecological and environmental aspects. *Progress in Oceanography, 60*(2–4), 263-279.

Moberg F, & Folke C (1999). Ecological goods and services of coral reef ecosystems. *Ecological economics, 29*(2), 215-233.

Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science, 311*(5757), 98-101.

Mumby PJ, Hastings A, & Edwards HJ (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature, 450*(7166), 98-101.

Mundy CN, & Babcock RC (1998). Role of light intensity and spectral quality in coral settlement: Implications for depth-dependent settlement?1. *Journal of Experimental Marine Biology and Ecology, 223*(2), 235-255.

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.

O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, & Weiss JM (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences, 104*(4), 1266-1271.

O 'Neill RV (1998). Recovery in complex ecosystems. *Journal of Aquatic Ecosystem Stress and Recovery (Formerly Journal of Aquatic Ecosystem Health), 6*(3), 181-187.

Paul RW, Hatch WI, Jordan WP, & Stein MJ (1989). Behavior and respiration of the salt marsh periwinkle, *Littorina irrorata* (Say), during winter. *Marine & Freshwater Behaviour & Phy, 15*(4), 229-241.

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*(2), 259-275.

Ritson-Williams R, Arnold SN, Fogarty ND, Steneck RS, Vermeij MJ, & Paul VJ (2009). New perspectives on ecological mechanisms affecting coral recruitment on reefs. *Smithsonian Contributions to the Marine Sciences*(38), 437.

Rosemond AD, Mulholland PJ, & Brawley SH (2000). Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and

productivity to variation in light, nutrients, and herbivores. *Canadian Journal of Fisheries and Aquatic Sciences, 57*(1), 66-75.

Sato M (1985). Mortality and growth of juvenile coral *Pocillopora damicorni*s (Linnaeus). *Coral Reefs, 4*(1), 27-33.

Scheffer M, Carpenter S, Foley JA, Folke C & Walker B (2001). Catastrophic shifts in ecosystems. *Nature, 413*(6856), 591-596.

Sheppard CR, Davy SK, & Pilling GM (2009). *The biology of coral reefs*: OUP Oxford.

Silverstein RN, Cunning R, & Baker AC (2015). Change in algal symbiont communities after bleaching, not prior heat exposure, increases heat tolerance of reef corals. *Global Change Biology, 21*(1), 236-249.

Smith SV, Kimmerer WJ, Laws EA, Brock RE, & Walsh TW (1981). Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pacific Science, 35*(4), 279-395.

Spalding M, Ravilious C, & Green EP (2001). *World atlas of coral reefs*: Univ of California Press.

Stafford-Smith M, & Ormond R (1992). Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. *Marine and Freshwater Research, 43*(4), 683-705.

Szmant A, Weil E, Miller M, & Colon D (1997). Hybridization within the species complex of the scleractinan coral Montastraea annularis. *Marine Biology, 129*(4), 561-572.

Szmant AM (1986). Reproductive ecology of Caribbean reef corals. *Coral Reefs, 5*(1), 43-53.

Tronholm A, Leliaert F, Sansón M, Afonso-Carrillo J, Tyberghein L, Verbruggen H & De Clerck O (2012). Contrasting Geographical Distributions as a Result of Thermal Tolerance and Long-Distance Dispersal in Two Allegedly Widespread Tropical Brown Algae. *PLOS ONE, 7*(1), e30813.

van Woesik R & McCaffrey KR (2017). Repeated Thermal Stress, Shading, and Directional Selection in the Florida Reef Tract. *Frontiers in Marine Science, 4*(182).

Vargas-Ángel B, Colley SB, Hoke SM & Thomas JD (2006a). The reproductive seasonality and gametogenic cycle of *Acropora cervicornis* off Broward County, Florida, USA. *Coral Reefs, 25*(1), 110-122.

Vargas-Ángel B, Riegl B, Gilliam DS & Dodge RE (2006b). An experimental histopathological rating scale of sedimentation stress in the Caribbean coral *Montastraea cavernosa*.

Vize PD, Embesi JA, Nickell M, Brown DP & Hagman DK (2005). Tight temporal consistency of coral mass spawning at the Flower Garden Banks, Gulf of Mexico, from 1997-2003. *Gulf of Mexico Science, 23*(1), 107-114.

Wentworth CK (1922). A scale of grade and class terms for clastic sediments. *The Journal of Geology, 30*(5), 377-392.

Yakovleva IM, Baird AH, Yamamoto HH, Bhagooli R, Nonaka M & Hidaka M (2009). Algal symbionts increase oxidative damage and death in coral larvae at high temperatures. *Marine Ecology Progress Series, 378*, 105-112.