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Optimization of Light Irradiance During the Early Life of Sexually-Produced Porites astreoides and Agaricia agaricites Recruits

Nicholas J. McMahon
Nova Southeastern University, nick.mcmahon15@gmail.com

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Nicholas J. McMahon

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Approved:
Thesis Committee

Major Professor: Joanna Figueiredo, Ph. D

Committee Member: Brian Walker, Ph. D

Committee Member: Bernhard Riegl, Ph. D

Committee Member: Charlie Gregory, DVM

NOVA SOUTHEASTERN UNIVERSITY

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

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Abstract

Current solutions of coral restoration rely mainly on fragmentation. Though a reliable technique, this asexual form of reproduction does not benefit the genetic diversity of the coral reef. With many global and local stressors threatening corals' existence, the resiliency of corals to future ocean conditions depends highly on sexual reproduction to produce new genotypes. New technology allows coral spawning/larval release, larval settlement and rearing to be carried out in an aquarium system. Many of the techniques necessary to maintain coral recruits are well-established, however the effects of light intensity remain to be studied for these early life stages. Newly settled corals have been found on vertical surfaces and the undersides of ledges and crevices, suggesting full solar irradiance is detrimental to their health. Newly settled *Porites astreoides* and *Agaricia agaricites* recruits were placed under varying irradiance levels to test their survivorship, growth and pigmentation. In the first four weeks post-settlement, growth was significantly different between recruits under a PAR of 10 µmol quanta m^{-2} s^{-1} and 240 µmol quanta m^{-2} s^{-1}. In a separate experiment, growth curves were significantly different between six different irradiance increase regimens in the first 14 weeks post-settlement. This study shows, for the first time, a definitive preference by newly settled coral recruits to lower intensity irradiance, devoid of ultraviolet radiation, in the first four weeks post-settlement, and that *Porites astreoides* recruits can acclimatize to higher intensities at a rate of ~ 11 µmol quanta m^{-2} s^{-1} per week for up to 15 weeks.

Keywords: coral, recruits, juveniles, irradiance.

Introduction

Reef-building corals produce the largest living structures on planet Earth and serve as habitat to one-fourth of all marine organisms (Spalding et al., 2001; Conservation International, 2008). Scleractinian corals are animals that accrete calcium carbonate skeletons, and together form a solid reef structure. This structure provides a habitat that benefits an estimated 9 million species of plants and animals (Knowlton et al., 2001). This includes humans, as over 39% of the world's population lives within 100 km of the coastline (Cesar et al., 2003). Large human populations depend on the coral reefs for their livelihood, nutrition and the protection they provide from coastal erosion and high energy waves (Moberg & Folke, 1999; Cesar et al., 2003).

Despite the high value of reef resources, anthropogenic stressors impose tremendous pressure on coral reefs worldwide, and have led to the decline of most reefs. Destructive fishing techniques including dynamite and cyanide poisoning reduce corals' ability to produce and maintain their three-dimensional structure thereby reducing available niches for many reef inhabiting organisms (MacArthur and MacArthur, 1961; Jones & Hoegh-Guldberg 1999; Fox & Caldwell, 2006). Coastal land development activities, such as waterfront construction, beach renourishment, and dredging often lead to the loss of mangrove and seagrass communities that normally act as land stabilizers thus contributing to reef degradation in the form of increased sedimentation (Rogers, 1990). High sedimentation can alter larval settlement and survival of benthic organisms and ultimately change the overall distribution of reef organisms, specifically corals (Rogers, 1990). Rising levels of CO_2 in the atmosphere are leading to increased ocean temperatures and acidification (IPCC 2014). These are serious issues for many marine species, as the rates of temperature and pH change may be too rapid for many organisms to adapt (Doney et al., 2011). Exposure to higher temperatures and acidification may compromise the coral larval settlement, skeletal accretion and their symbiotic relationship with algae. Corals grow by the accretion of calcium carbonate skeletons. Energy for calcification is provided by the photosynthesis of a symbiotic algae (*Symbiodinium*) within the coral's tissues. Photosynthesis is inhibited by increased temperature, high solar irradiance, and the elevated free-radical oxygen molecules, which are toxic

byproducts of photosynthesis (Lesser, 1997; Reynaud et al., 2003; Abrego, 2008; Baird et al., 2009). Under stress, *Symbiodinium* will leave the coral tissue, a process known as bleaching. Bleached corals suffer increased susceptibility to opportunistic diseases, which can compromise the health of individual coral colonies and entire coral reefs (Muller & van Woesik, 2012; Precht et al., 2016). Caribbean corals have suffered greatly from major disease outbreaks which have decimated coral cover in recent years (Muller & van Woesik, 2012; Precht et al., 2016, Walton et al., 2018). Additionally, acidification and warming can affect coral recruitment. Crustose coralline algae (CCA), a calcareous macroalgae, acts as a cue for coral larvae to settle on the substrate and metamorphose (Heyward & Negri, 1999; Price, 2010). When CCA is exposed to elevated CO_2 for an extended period, coral larval settlement and metamorphosis can be drastically reduced (Webster et al., 2013). Coupled with severe losses of herbivorous fishes and invertebrates, these effects contribute to ecological shifts from coral-dominated to algae-dominated reefs, making reefs less suitable for coral recruitment and juvenile coral growth over the past 30 years (Levitan, 1988; Hughes, 1994; McClanahan et al., 2002; Hughes et al., 2007). The loss of coral in the Caribbean has led to reduced architectural complexity and decreased reef biodiversity (MacArthur & MacArthur, 1961; Alvarez-Filip et al., 2009). This has heightened the need for coral restoration efforts in the Caribbean.

Current solutions to restore corals to the reefs are based on coral fragmentation - an asexual mode of coral reproduction. In the wild, corals can reproduce via fragmentation when pieces of adult colonies are broken off from physical or mechanical stress, and the pieces subsequently reattach to the substrate forming a new colony (Tunnicliffe, 1981; Highsmith, 1982). For restoration purposes, adult colonies are cut into fragments and placed in coral nurseries to be grown in a process commonly referred to as “coral gardening” (Levy et al., 2009). These nurseries are most commonly located in nearshore ocean-based facilities or land-based aquaculture facilities (Levy et al., 2009). Nearshore nurseries are usually installed in areas protected from disturbance and take many shapes and forms. Coral “trees” are a common form in which branches of PVC pipes radiate from a central stem, with multiple fragments dangling from a single monofilament line connected to the branch (Nedimyer et al., 2011). Rope nurseries hang

fragments from long plastic ropes or nets between vertical ropes attached to subsurface buoys (Levy et al., 2009). These structures allow corals to grow in all directions unabated by mechanical stress from wave action and less susceptible to parasitism, predation, sedimentation, and/or algal competition (Nedimyer et al., 2011). Once these fragments reach an acceptable size, they can be out-planted to a disturbed reef (Rinkevich 2005; Levy et al., 2010). This technique utilizes mostly branching corals, such as Acroporids. A relatively new technique called micro-fragmentation allows for restoration and grow-out of mounding, plating and boulder corals, employing tiny coral fragments of 1-3 cm^2 spread evenly over ceramic tiles (Forsman et al., 2015). After being cut, these fragments will continue to grow over the tile in all directions until they reach one another, then fuse together to become a single larger colony in a process called microfusion. This increased colonial growth rate decreases the amount of time required to reach sexual maturity (Forsman et al., 2015). Coral recruits typically allocate energy exclusively to growth, and only after attaining a certain size start allotting energy to reproduction; coral colony age is less determinant than size in regard to reproductive capability (Szmant 1991; Soong 1993). Therefore, microfragmentation and microfusion techniques allow the production of young but large colonies that reach maturity very quickly and are essential to reduce generation intervals.

Fragmentation has proven to be an effective restoration technique; however, it can only at best maintain existing genotypes. Asexual reproduction, "cloning", can lead to founder effects, more commonly known as genetic bottlenecking, because it does not allow for genetic recombination. Bottlenecking occurs when wild populations become unnaturally reduced to a few genotypes (Baums, 2008). Transplanted organisms may have a reduced contribution to population growth due to low initial genotypic diversity, which reduces fertilization success between genetically similar organisms (Williams, 2001; Baums, 2008).

Sexual reproduction alleviates the issues of asexual reproduction by producing new genotypes and contributing to the dispersal of the species to other locations during the larval stage. Corals can be gonochoric, i.e. separate sexes, or hermaphroditic, i.e. have both sexes in the same individual/polyp (Szmant, 1986). Their reproductive cycles

rely on annual external cues such as temperature, lunar cycle and day length (Harrison et al., 1984; Keith et al., 2016) with most species spawning only once annually on a highly synchronized event (Szmant, 1986). Brooding species release larvae that are ready to settle, while broadcast spawners release gametes into the water column where fertilization and larval development occur. Depending on the species, coral larvae can be ready to settle within a few hours or can delay for up to a week. When they are ready to settle, or "competent", larvae will follow settlement cues towards the reef substrate and metamorphose into a polyp. One of the most important cues for settlement of coral larvae is bacterial biofilms on reef substrate (Tran and Hadfield, 2011). Crustose coralline algae (CCA) also play a major role in settlement (Birrell et al., 2008; Price et al., 2010). Short wavelength light in the UV spectrum can be harmful to corals and planula and influences larval swimming behavior (avoidance) and settlement preference on surfaces (Gleason and Wellington, 1995; Gleason et al., 2006).

To use sexually-produced coral recruits for restoration purposes, one can collect gametes during the natural spawning events and then rear and settle the larvae in a laboratory. During natural spawning events, coral gametes or larvae can be collected by placing tent-like structures over or around the colonies which funnel them into a collection cup for transport back to land-based culture tanks (Lillis et al., 2016). However, this is only effective for species with buoyant eggs or egg/sperm bundles, otherwise sperm can be collected by syringe, or negatively buoyant larvae can be collected by netting the entire spawning colony. Another method includes collecting wild adult colonies and placing them in aquaria a few days prior to the expected spawning date where they will spawn in standing water (Mundy and Babcock, 1998; Drenkard et al., 2013; Reich et al., 2017). For broadcast spawners, sperm must be diluted to an appropriate concentration, typically 10^6 mL^{-1}, and then mixed with eggs to induce and maximize fertilization, and minimize polyspermy (Oliver and Babcock, 1992). The major advantage of being manually crossed is to ensure genetic diversity. For brooders, the larvae can be collected immediately. New technologies in aquarium husbandry have allowed researchers to induce corals which have been kept in aquaria long-term to spawn in captivity by mimicking natural temperature and lighting regimens (Craggs et al., 2017). Coral embryos/larvae can be reared in standing water bowls kept at adequate

temperature and salinity; larvae are lecithotrophic so they do not require food. Settlement of the planktonic larvae can be induced using pre-conditioned ceramic tiles, i.e. tiles that have been placed in the ocean for 1-2 months for the accumulation of bacterial biofilms and CCA (Heyward et al., 2002). Techniques for growing newly settled juveniles are not as well developed because the environmental conditions necessary to guarantee survival and healthy growth have not yet been optimized, and/or the juveniles are difficult to maintain in recirculating systems. As with most marine species, corals require a relatively stable temperature and salinity, and low ammonia levels which requires the use of sophisticated/expensive equipment such as chillers, heaters, protein skimmers and biological filtration (Carlson, 1999). Additionally corals require maintenance of high levels of alkalinity and calcium to facilitate skeleton accretion (calcification) which can be accomplished through supplementation (Carlson, 1999). Corals typically feed on zooplankton and thus require at least some level of feeding (Goreau et al., 1971). More importantly, corals have an obligatory symbiosis with algae of the genus (formerly known as) *Symbiodinium* and require adequate lighting.

While light is essential for the survival and growth of both recruits and adult corals, the optimal irradiance needs of newly settled corals seem to differ from the adults. The corals' algal symbionts provide carbon (food) to the coral host, and the coral provides a source of nutrients to the algae, but algae also require light for photosynthesis (Muscatine & Porter, 1977; Falkowski et al., 1984). On coral reefs, values of solar irradiance can vary widely depending on latitude, depth, and turbidity. For example, in the Dry Tortugas, Florida, irradiance varies from 2100 µmol quanta m^{-2} s^{-1} at noon on the surface, to 400 µmol quanta m^{-2} s^{-1} at 10 m depth (just below where most corals occur), to 25 µmol quanta m^{-2} s^{-1} at 18m depth (Lesser et al., 2000), while in the more turbid waters of Broward County, FL, irradiance at 6-8m is 150 µmol quanta m^{-2} s^{-1} (Ashton Galarno, M.S. thesis). Light levels on the coral reef at Magnetic Island, on the Great Barrier Reef, vary from 50 – 300 µmol quanta m^{-2} s^{-1} (Abrego, 2012). However, juvenile corals *Porites astreoides* suffered high mortality when directly exposed to irradiance levels of 240 µmol quanta m^{-2} s^{-1} (Fourney & Figueiredo, 2017). Interestingly, coral recruits are most often found on vertical or downward facing surfaces in shallow waters, but typically face upwards in deeper areas (Bak & Engel, 1979; Birkeland et al. 1981;

Rogers, 1984; Sato, 1985; Babcock & Mundy, 1996). It has been hypothesized by previous studies that this is to avoid sedimentation, while the potential avoidance of solar irradiance has been mostly overlooked (Bak & Engel, 1979; Rogers et al., 1984; Sato, 1985; Price, 2010). I hypothesize that normal irradiance levels, similar to high temperatures, may be detrimental to newly settled recruits by increasing oxidative stress in the coral and its algal symbiont. High temperatures increase the potency of reactive oxygen species (ROS) and increase levels of certain antioxidants (Yakovleva et al., 2004). Larvae with *Symbiodinium* display higher levels of antioxidants, but still suffer higher mortality than *Symbiodinium*-free larvae (Yakovleva et al., 2004). Since newly settled coral juveniles of *A. millepora* and *A. tenuis* reared under lower light displayed higher pigmentation than juveniles reared at higher light (~390 µmol quanta m^{-2} s^{-1}), it is possible that high light irradiance also leads to oxidative stress, hampering the establishment of symbionts and leading to mortality (Abrego et al. 2012). This would also explain why coral recruits settle under ledges and in crevices, away from full light intensities. This evidence suggests that newly settled corals cannot tolerate the same light irradiance levels as adult corals.

As corals grow to become fully tolerant of high light irradiance, tolerance to high levels of irradiance must increase over time. The time at which tolerance to high levels of light irradiance is attained remains unknown, but we hypothesize that it is related to increased density of *Symbiodinium* and/or ability to feed (i.e. having well-developed tentacles) and therefore provide nutrients to the algae. Before corals are able to feed heterotrophically, exposure of *Symbiodinium* to high light may be deleterious to corals by forcing them to metabolize energy reserves. This study seeks to raise corals under laboratory conditions using multiple light irradiances with the intention of determining optimal light levels for the period immediately after settlement, and to determine more precisely when coral recruits are initially able to tolerate high light levels. Light irradiance will be manipulated to produce light regimens where irradiance increases at different time points and rates. Pigmentation, growth, and mortality of the coral recruits will be measured and compared amongst treatments. This study aims to contribute to improvement of current "grow-out" methods for sexually-produced corals in captivity.

Objectives

1. Determine the optimal light irradiance for newly settled *Porites astreoides* coral recruits (i.e. during the first days/week post-settlement)
2. Determine the optimal rate of increase in light irradiance during the early life of *Porites astreoides* coral recruits (first 3 months after settlement) to minimize the time necessary to fully establish symbiosis, while maximizing survival and growth.
3. Determine the optimal rate of increase in light irradiance during the early life of *Agaricia agaricites* coral recruits (first 3 months after settlement) to minimize the time necessary to fully establish symbiosis, while maximizing survival and growth.

Methods

Figure 1. A. Adult Porites astreoides colony. The "mustard hill" coral. B. Adult Agaricia agaricites colony, the "Lettuce coral".

Coral species

Porites astreoides is a mounding/encrusting type coral, found abundantly on shallow reef flats throughout South Florida and the Caribbean in < 10 m depth (Chiappone and Sullivan, 1996; McGuire, 1998, Green et al., 2008; Figure 1). *P. astreoides* can survive high levels of sedimentation and sub-optimal environmental conditions, which makes it a good model species for conservation efforts (Burns 1985; Gleason, 1998; Green et al., 2008, Walton et al., 2018). Colonies display two color

morphotypes: green/yellow and brown (Gleason, 1998). This species is a simultaneous hermaphroditic brooder; during its sexual reproduction, it will release live larvae into the water column (Szmant, 1986; Chornesky and Peters, 1987). The peak event for larval release is during/after the new moon in April, but the species continues releasing through June, and occasionally July through September (Chornesky and Peters, 1987; McGuire, 1998).

Table 1: Broward county coral nursery collection sites

Site ID	Latitude	Longitude
1	26° 9.420′ N	-80° 5.309′ W
2	26° 9.120′ N	-80° 5.340′ W
3	26° 9.127′ N	-80° 5.810′ W
4	26° 8.735′ N	-80° 5.782′ W
5	26° 8.872′ N	-80° 5.916′ W

Agaricia agaricites is another common scleractinian coral found on the Florida Reef Tract and throughout the Caribbean (Picture 2). Their depth distribution ranges from 3 – 45 m, and colony morphology is highly variable between depths (Goreau & Wells, 1967; Bak & Engel, 1979; Helmuth & Sebens, 1993). Colonies can take many shapes, including plates, blades or bifacial plates, and encrusting forms (Helmuth & Sebens, 1993). This coral is also a simultaneous hermaphroditic brooder, releasing fully competent larvae into the water column during the spring and summer months near the full moon (Van Moorsel, 1983). Larval release occurs between the months of March and October a few hours after sunset (Van Moorsel, 1983; Allan Anderson, M.S Thesis).

Collecting adult corals

Twenty-four adult coral colonies of *P. astreoides* were collected four days before the time of the new moon on April 9th, 2018 for experiment 1. Another group of twenty-four *P. astreoides* and twenty *A. agaricites* adults were collected on May 9th for experiments 2 and 3, six days before the new moon. Colonies were collected from multiple sites in the Broward county coral nursery (Table 1) on the Florida Reef Tract (FRT) with permission granted by a Florida Fish and Wildlife Commission special activities license. Collection was accomplished on SCUBA using hammers and chisels. Colonies were collected at sizes of 10-15 cm in diameter, for both species, to ensure sexual maturity (Van Moorsel, 1983; McGuire, 1998). The corals were wrapped in bubble wrap and placed in coolers to avoid physical and temporal stress and direct

sunlight as they were brought back to Nova Southeastern University's Oceanographic Center outdoor tanks. Regular water changes were carried out on the boat every 20-30 min during transportation. Parent colonies were placed in outdoor recirculating tanks with a sump containing bio-balls, a protein skimmer and an average system flow rate of ~ 1.3 L/min. Tanks are located under a series of sun shades to reduce direct solar irradiance and equipped with heaters and a chiller for temperature control.

Larval release

Larval release of *P. astreoides* occurred the night of April 9th, and every subsequent night until April 17th, the night of the new moon. For experiment 2, larval release began on the night of May 9th and collection lasted until May 17th, two days after the new moon. *Agaricia* larval collection began a few days before the full moon on May 25th, but larvae for this experiment were collected between June 1st and June 4th. At night, adults were placed into bowls with a continual overflow spout draining into separate larval collection containers. Collection containers are constructed of a small piece of PVC piping fitted with plankton mesh (100 µm) to allow passage of water through the mesh and retention of larvae in the container. Corals were checked daily for larval release. Tanks were kept out of reach of anthropogenic light to ensure the corals' perception of photoperiod and moonlight was not misguided. The species of interest are brooding species, and larval release typically begins around midnight and continues to a few hours before sunrise (Sharp et al., 2012). Parent colonies remained in their bowls until the following morning, and then moved back into the recirculating system until the next night.

Larval Settlement

Collected larvae were added to polystyrene containers with 30-35 ceramic settlement tiles and seawater. To encourage settlement, crustose coralline algae (CCA) was removed from rocks collected in the field and pulverized into a fine dust. This CCA dust was stirred into a bowl of salt water until the water turned a light pink hue, and then poured over the ceramic settlement tiles. The polystyrene containers were placed into temperature baths and kept at local spring-time ocean temperatures of 25.5º C. Larvae were checked once every 24 h for settlement on the ceramic tiles. The side of the tile

with the most recruits was designated the upward-facing side for the experiment, and any recruits that settled on the bottom were not used for experimental purposes. Once settled, the new recruits were photographed, numbered for reference, and placed into the experimental system.

Experimental System

The experimental system was a recirculating system consisting of two 453 L fiberglass raceways, (240 x 60 x 30 cm) connected to a common sump with approximately 486 additional liters, and a flow rate of approximately 350 L/h (Figure 2). The sump will contain two 25-W Pentair ultraviolet sterilization units, one per raceway, a protein skimmer, bioballs for biological filtration, aerator discs, a phosphate reactor and a calcium reactor. The system temperature was controlled by multiple Eheim® Jager submersible heaters and one Aqua Logic® Cyclone Water 1/4 horsepower chiller, each connected to temperature controllers. The temperature was maintained at ambient local temperatures for experiment 1 – beginning at 25ºC and increasing to 25.5ºC on April 17, and again to 26.1ºC on May 1. Temperature was held at 26.6˚C for the duration of experiment 2 & 3. A salinity of 35 was maintained by addition of reverse osmosis water to accommodate for evaporation and measured with a refractometer. Partial water changes of at least 340 L were implemented once every month to remove detritus and any undesired growth (i.e. algae and *Aiptasia* anemones) from the tanks. Water quality was monitored weekly for accumulation of major nutrients: ammonia, nitrites, nitrates, and phosphates, as well as copper, using Hach® test kits. Snails of the Families *Cerithiidae* and *Turbiniidae* were used in the raceways for algae removal. Coral recruits were fed once a week using a combination of rotifers, when available, and Reef Roids® coral food.

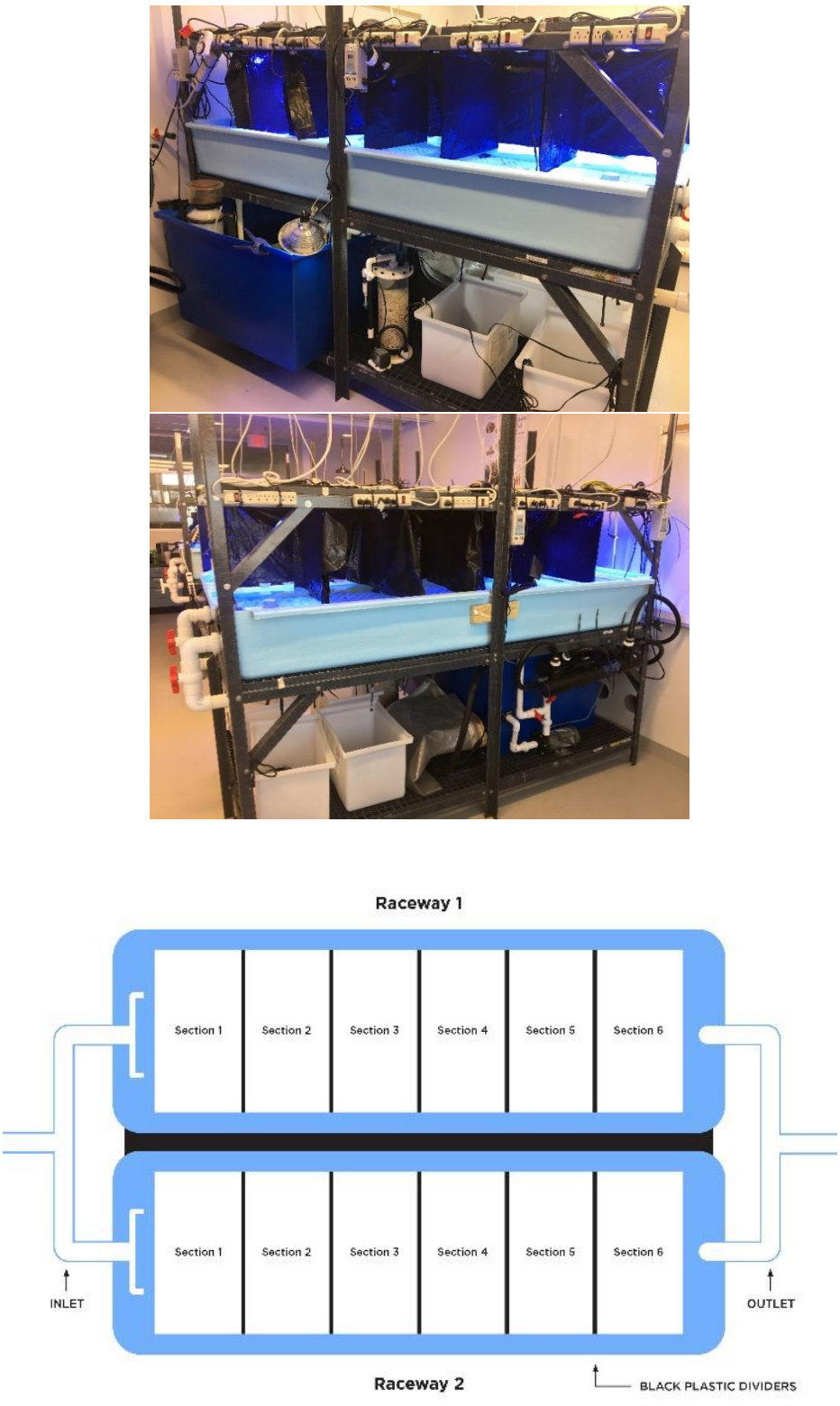

Figure 2. (Clockwise from top left) Pictures of the experimental system, and top-down representation of the experimental system.

Experiment 1: Optimizing initial light irradiance immediately after settlement

Each raceway was lit by six Aqua Illumination Hydra 26 HD LEDs. The light spread of each fixture is approximately 60 x 60 cm. Each raceway was subdivided into 6 sections approximately 36 x 60 cm using black plastic bags to eliminate the possibility of light scattering between sections. Both raceways shared the same water and had the same flow. Treatments were assigned randomly to a section in each raceway and were replicated in both raceways. Each section only contained one treatment, which was replicated in the other raceway to minimize any potential confounding or deleterious effects. The lighting schedule for all experiments maintained a 12:12 light:dark regimen – lights "on" between 6:00 and 18:00 hours, and a ramp up/down time (sunrise/sunset) of 4 hours. The ultraviolet and green channels on these LEDs were kept at 0% for all treatments to maximize coral growth and maximize the capability of the fixture to reach the higher photosynthetically active radiation (PAR) outputs. An Apogee MQ-510 full spectrum underwater LED PAR meter was used to measure and set irradiance levels.

Newly settled juveniles were exposed to one of six light irradiance levels: 10, 30, 60, 90, 120, 240 µmol quanta m^{-2} s^{-1}. The number of replicates of recruits was determined by the amount of larvae released from adult colonies and the amount of larvae that settled. Replicate numbers of tiles ranged from 6 – 11 tiles per treatment, due to large numbers of recruits settling on single tiles near the end of the larval mass settlement process. Total number of recruits was 263. Recruits that were released on different days were distributed as evenly as possible throughout the different experiments to ensure that each treatment was composed of a similar mix of larval quality (Cumbo et al., 2012). Recruits were placed into the experimental system near precisely placed marker tiles. The marker tiles designated areas of accuracy within +/- 5 µmol quanta m^{-2} s^{-1} of the desired irradiance value for each treatment, at each setting. This allowed for precision when replacing tiles after weekly measurements. Recruit survival and growth were evaluated weekly for 4 weeks post-settlement.

Recruits were measured, scored for survival (0 – alive, 1 – dead), and number of polyps per recruit were counted once a week at a magnification of 1.2x. Length and width diameter (d) measurements of the recruits were made manually by using the scale

incorporated into the eyepiece of the scope itself. These measurements, subsequently converted to mm^2, were used to estimate the area of the juvenile as an ellipse (Area = $\pi(d_1/2) \times (d_2/2)$. Overall growth was calculated by subtracting the initial size of the recruit from its final size.

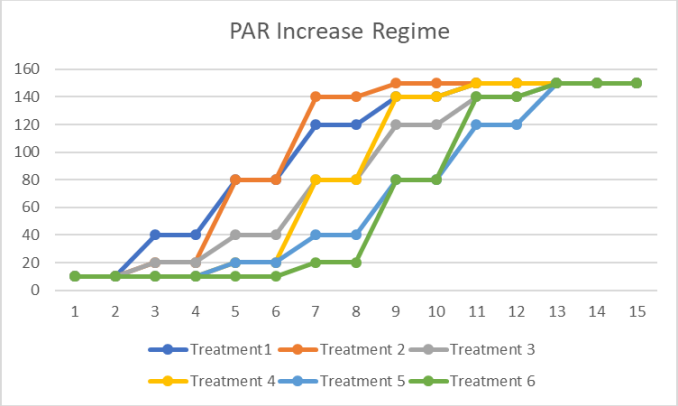

Figure 3. Irradiance treatment regimens for experiment 2 & 3. Week number on the x-axis and PAR values on the y-axis. PAR was measured in µmol quanta m^{-2} s^{-1}. Treatments 4, 5, & 6 also contained Agaricia agaricites recruits introduced on week 3.

Table 2. Light irradiance (µmol quanta m^{-2} s^{-1}) regimens in all treatments. Colors are coordinated to match their respective treatment on Figure 3 (above). Rows shaded blue correspond to the day/week the light irradiance level was increased. Rows shaded gray indicate no data collection.

Date	Week		Treatment 1	Treatment 2	Treatment 3	Treatment 4	Treatment 5	Treatment 6
	Agaricia	*Porites*						
		0	10	10	10	10	10	10
18-May		1	10	10	10	10	10	10
		2	10	10	10	10	10	10
1-Jun	0	3	40	20	20	10	10	10
	1	4	40	20	20	10	10	10
15-Jun	2	5	80	80	40	20	20	10
	3	6	80	80	40	20	20	10
29-Jun	4	7	120	140	80	80	40	20
	5	8	120	140	80	80	40	20
13-Jul	6	9	140	150	120	140	80	80
	7	10	140	150	120	140	80	80
27-Jul	8	11	150	150	140	150	120	140
	9	12	150	150	140	150	120	140
10-Aug	10	13	150	150	150	150	150	150
	11	14	150	150	150	150	150	150
24-Aug	12		150	150	150	150	150	150

Experiment 2: Determining the optimal rate of increase of light irradiance for Porites astreoides.

Each replicate treatment contained 30-35 recruits, totaling 372 recruits. During the first three weeks (weeks 0-2), all recruits were kept at the most effective irradiance level (10 µmol quanta m^{-2} s^{-1}) as determined by experiment 1 (Figure 3 & Table 2). Treatments were randomized in each raceway replicate to ameliorate potential for any deleterious or confounding effects.

Procedures for weekly assessments of survival and growth follow those explained for experiment 1. Pigmentation scores were also assigned to each individual recruit weekly using the "Coral Colour Reference Card" developed by Siebeck et al., 2006 (Figure 4). The chart was scaled to a size that would fit on the bottom of a small plastic bowl, allowing for submersion of recruits while measurements were taken. Magnification was changed as needed to allow for the most accurate assignment of pigmentation score.

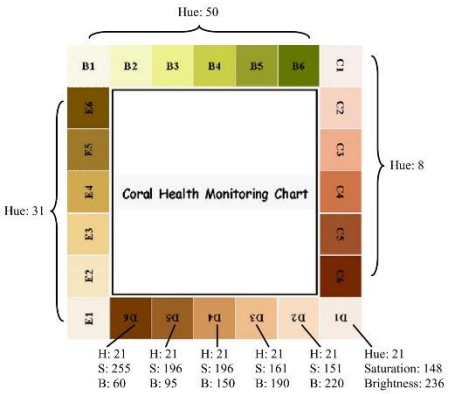

Figure 4. Coral Colour Reference Card (Siebeck et al., 2006) used for assigning pigmentation scores to recruits.

Experiment 3: Determining rate of increase in tolerance to higher light irradiance – Agaricia agaricites.

Recruits of *A. agaricites* were added to treatments 4, 5 and 6 during week 3 (Figure 3 & Table 2). These treatments were chosen to allow the corals to start the experiment at 10 µmol quanta m^{-2} s^{-1} as per experiment 1. Procedures for weekly assessments of survival, growth and pigmentation follow those explained for experiment 2. Each replicate treatment contained 8-11 recruits totaling 55 recruits.

Data analysis

To determine which light was optimal immediately after settlement, the effects of light on juvenile mortality, growth, and pigmentation were compared between treatments. Survival between treatments was compared using a survival analysis (event of interest: Mortality). Survival curves were plotted using the Kaplan-Meier estimator, and

compared using Mantel-Haenszel (log rank) tests. Overall growth for experiments 1 and 2 was assessed using a One-way ANOVA, or corresponding non-parametric Kruskal Wallis. When overall growth was found to significantly differ between treatments, a post-hoc multiple comparison test was used. To estimate and compare growth curves between treatments, we first determined which non-linear model (exponential, power, asymptotic) best described the change in surface area over time, regardless of treatment. Then, the fitness of this treatment-independent model was compared to the models fit to each of the treatments (i.e. where parameters were specific for each treatment) using a loglikelihood ratio test.

Pigmentation scores were compared using frequency analyses, specifically a contingency table to test the association between time (weeks) and coral pigmentation level for each treatment.

All statistical tests were performed in software R version 3.5.1.

Results

Experiment 1: Optimizing initial light irradiance immediately after settlement for Porites astreoides

Mortality during the first 4 weeks was not significantly different among the six irradiance levels (p-value = 0.0956; Figure 5). All treatments had a greater than 90% probability of survival.

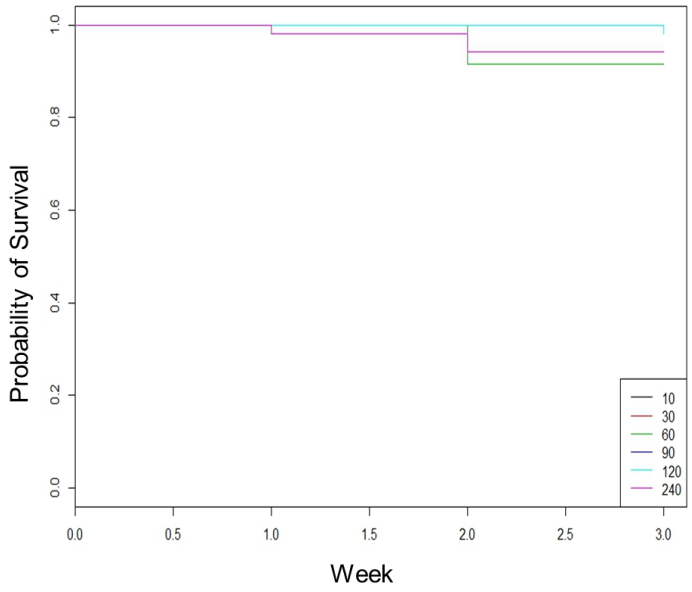

Figure 5. Recruit mortality for Porites astreoides recruits in experiment 1. Survival was not significantly different between treatments (p-value = 0.0956).

Overall growth was significantly different (p-value = 0.0003832) for irradiances 10 and 240 µmol quanta m^{-2} s^{-1} using Tukey's HSD *post hoc* test (Figure 6). Individuals under the lowest irradiance level, 10 µmol quanta m^{-2} s^{-1}, were significantly larger than those kept under the highest values of 240 µmol quanta m^{-2} s^{-1} (Figure 6). In the last week of the experiment, the average size of individuals under the highest irradiance was 2.131 mm^2, while those under the lowest irradiance averaged 3.642 mm^2.

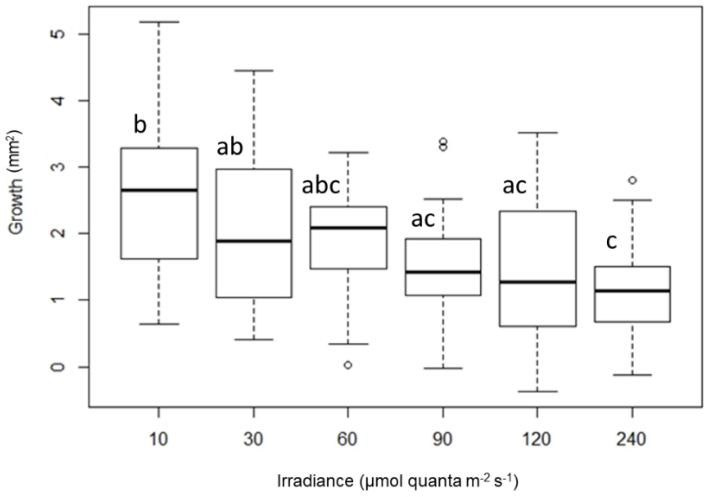

Figure 6. Overall growth of Porites astreoides recruits in experiment 1 (4 weeks). Letters represent significant groups.

Experiment 2: Determining the optimal rate of increase of light irradiance in Porites astreoides.

Mortality was initially found to be significant between treatments (p-value = 0.0317); however, a post-hoc multiple comparisons test did not reveal any treatment to be significantly different from any other. Probability of survival in this experiment exceeded 95% (Figure 7). High water quality and regular monthly water changes certainly contributed to the success of these juveniles. Only one incident of high phosphate was measured in week 6. Subsequently the phosphate removal media was changed, and within two weeks levels were unmeasurable. Alkalinity maintained an average of ~ 160 ppm. Snails from the Families *Turbinidae* and *Cerithiidae* had a very pivotal role in removal of macroalgae. If algae became problematic, snails were even placed directly on tiles with profuse algal cover and removed a large majority of the algae and leaving recruits undisturbed.

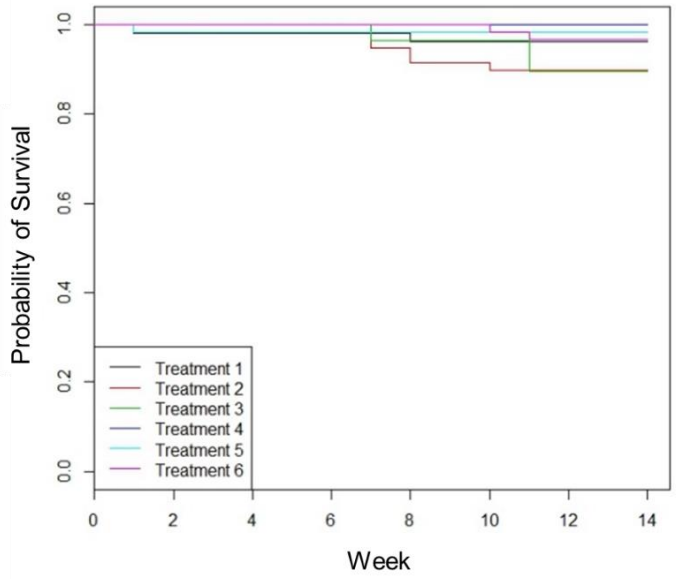

Figure 7. Recruit mortality for Porites astreoides recruits in experiment 2. Survival was not significantly different between treatments (p-value = 0.0317).

Overall growth was found to be significantly different between treatments (p=0.004512, Kruskal Wallis test; Figure 8). Treatments 3 & 4 showed significantly better overall growth compared to treatment 6, which maintained 10 µmol quanta m^{-2} s^{-1} for the first 7 weeks before increasing to only 20 µmol quanta m^{-2} s^{-1} for the two

consecutive weeks. Coral recruit growth was best fit with an exponential model (Figure 9). The growth models where the parameters were treatment-dependent led to a considerably better fit ($p=1.9x10^{-70}$). Treatment 3 produced the fastest growth, followed very closely by treatment 4 (Figure 9). The average growth rate in treatment 3 was 0.4297 mm^2/week. For treatment 6, growth rate averaged 0.2742 mm^2/week. The combined results of both experiments 1 & 2 suggest that during the first three to five weeks 10 µmol quanta m^{-2} s^{-1} is sufficient to significantly increase growth in this species.

Pigmentation changed significantly over time within each treatment (all p-values = 2.2×10^{-16}, Figure 10 A-F). All juveniles displayed pigmentation on the "E" scale of the Coral Colour Reference card (Figure 4), a brownish-yellow coloration. No corals were found pale enough to be designated an "E1" score.

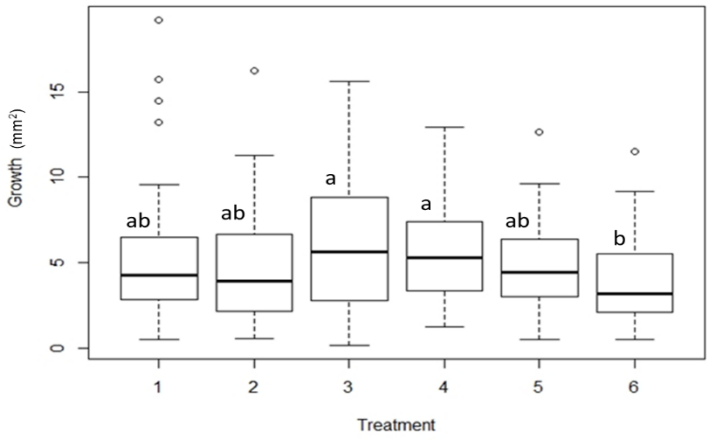

Figure 8. Overall growth of Porites astreoides recruits in experiment 2 (14 weeks). Letters represent significant groups.

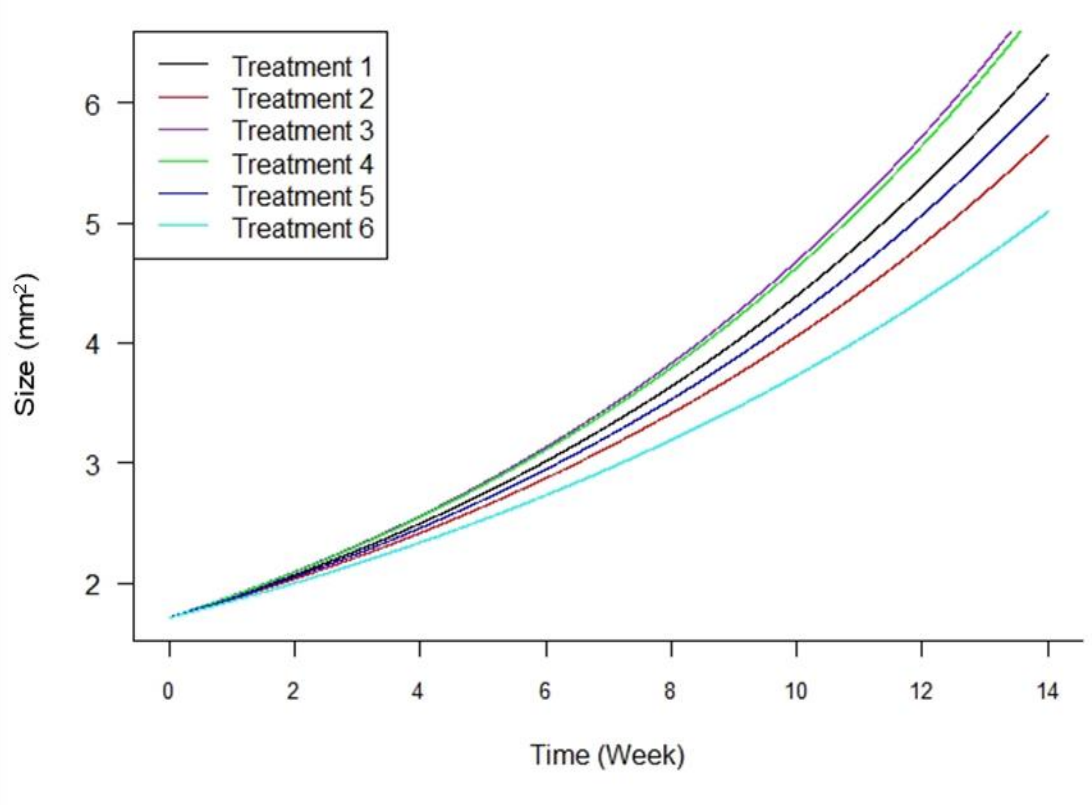

Figure 9. Growth curves fitted to an exponential model for Porites astreoides recruits in experiment 2.

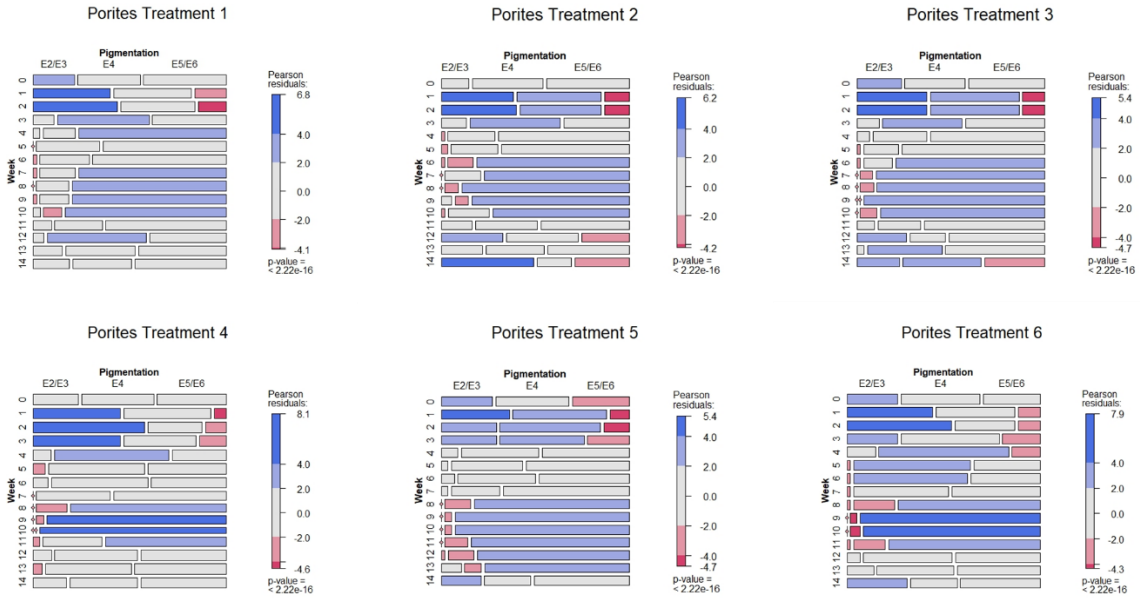

Figure 10 (A-F). Frequency analyses of pigmentation for Porites astreoides recruits throughout experiment 2 for all treatments.

Experiment 3: Determining rate of increase in tolerance to higher light irradiance – Agaricia agaricites.

Survival of *A. agaricites* did not significantly differ between treatments (p = 0.508) and was > 96% at the end of 12 weeks - only two of 55 individuals were lost. Overall growth was also not significantly different between treatments (p-value = 0.191, Kruskal Wallis test). Newly settled recruits had an average surface area of 2.72 mm^2, and by week 12 they averaged 13.947 mm^2, thus average growth rate was 0.9356 mm^2/week. Maximum size recorded at week 12 was 34.885 mm^2 and minimum size was 1.374446 mm^2.

Pigmentation differed significantly over time within all treatments (p-value = 2.2 x 10^{-16}). Similar to *P. astreoides*, the recruits of *A. agaricites* responded to unfavorable light intensities with changes in pigmentation (Figure 11 A-C). Light that was too intense elicited a loss of coral pigmentation, whereas light that was too dim caused an increase in pigmentation.

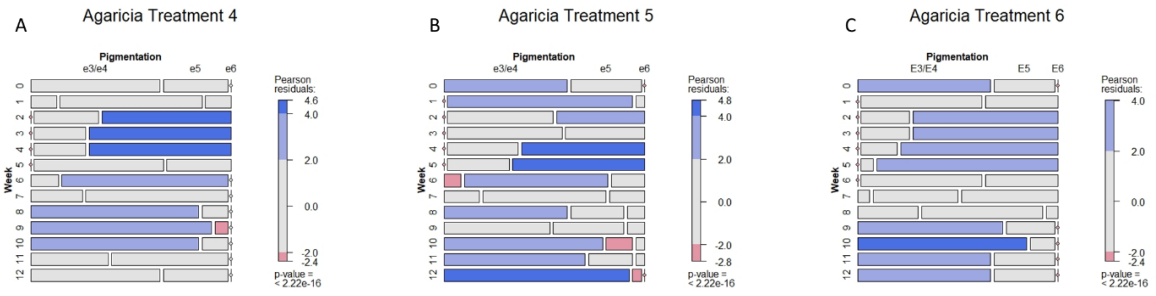

Figure 11 (A-C). Frequency analyses of pigmentation for Agaricia agaricites recruits throughout experiment 3.

Discussion

Porites astreoides recruits were resilient to higher light irradiances, even within the first four weeks post-settlement. Survival of *P. astreoides* and *A. agaricites* recruits in all experiments was extremely high (> 90%), regardless of light irradiance for both species. However, earlier on, growth of *P. astreoides* was negatively impacted by high light intensities: in the first 3-4 weeks after settlement, *P. astreoides* recruits grew more at the lowest light irradiance, 10 µmol quanta m^{-2} s^{-1}, but beyond that point lower irradiance levels restricted their growth. These results suggest that after an initial period

at low light the optimal increase in light intensity for *P. astreoides* is ~11 µmol quanta m^{-2} s^{-1} per week for up to 15 weeks post-settlement, gradually increasing to ~130 µmol quanta m^{-2} s^{-1}. Results for *Agaricia agaricites* suggest recruits require only 2 weeks at low irradiance and an optimal increase of ~ 13 µmol quanta m^{-2} s^{-1} per week up to week 11, remaining at 130 µmol quanta m^{-2} s^{-1} thereafter. In both species pigmentation was reduced under high light and increased under low light.

During the first 4 weeks post-settlement, *P. astreoides* recruits grew the most (highest median) and were significantly larger in the lowest irradiance, 10 µmol quanta m^{-2} s^{-1}, than recruits grown under 90, 120 and 240 µmol quanta m^{-2} s^{-1} (Figure 6). Coral recruits have been reported to settle on the underside of surfaces in shallow depth ranges, but exhibit increasing preference to topside surfaces with increasing depth (Bak & Engel, 1979; Birkeland et al., 1981; Rogers et al., 1984; Sato, 1985; Price, 2010). Though sedimentation in shallow water has been suggested as a culprit, the potential effect of light as a driving force for this settlement behavior has never been investigated. Adult corals, along with other organisms that rely on photosynthesis, can suffer negative effects from excessive light, whereby their overwhelmed algal symbionts undergo a reduction of overall photosynthetic quantum yield – a process known as photoinhibition (Long et al., 1994; Hoegh-Guldberg & Jones, 1999). Ultimately, this limits the amount of carbon fixed by photosynthetic machinery and therefore the transfer of nutrition to the coral host, decreasing the growth rate. The results of this study could imply that *Symbiodinium* in larvae and post-metamorphic juveniles have a substantially lower photoinhibitory threshold, thereby driving larvae to settle in areas with lower light intensities, and inhibiting growth during this life stage.

Differing growth rates between recruits in low- and high-intensity maybe also be explained by photodamage experienced by the host. Perhaps larvae and recruits lack pathways for control of compounds that aid in stress regulation in adults, such as mycosporine-like amino acids (MAAs), antioxidants, heat shock proteins, and other oxygen scavenging mechanisms like superoxide dismutase (SOD) (Hoegh-Guldberg & Jones, 1999; Baird et al., 2009). Antioxidants SOD and catalase (CAT) have been found in aposymbiotic cnidarian host tissues, and even increase concentrations under increased

irradiance (Dykens & Shick, 1984; Levy et al., 2006). Perhaps larvae and juvenile corals lack these antioxidants, or do not possess a sufficient quantity in the first 3-5 weeks to sustain high growth under high irradiance. MAAs are widely viewed as UV-absorbing compounds but can be stimulated by white light lacking UV and blue light and some also act as antioxidants (Shick & Dunlap, 2002; Yakovleva et al., 2004; Furla et al., 2005). The production pathways for MAAs are not present in animals and are provided by the symbiont (Banaszak & Trench, 1995; Shick & Dunlap, 2002; Furla et al., 2005). Interestingly, MAA concentrations are higher in host tissues than in symbiont tissues (Shick and Dunlap, 2002; Furla et al., 2005). A high concentration of MAAs in host tissues, particularly the ectoderm, protects both the symbiont and the host from high irradiance, however the mechanism of translocation of MAAs to the host is unknown (Garcia-Pichel, 1994; Furla et al, 2005). Production of these compounds has also been suggested to be carried out by prokaryotic sources in the tissues of asymbiotic corals (Yakovleva & Baird, 2005). Some MAAs, which are found only in cultured symbionts, can be synthesized by the symbiont in host tissues followed by the production of multiple secondary types not found outside the host (Shick and Dunlap, 2002; Furla et al., 2005). This suggests some form cellular communication between the symbiont and the coral host is necessary for the production of these molecules. It is possible that these early stages of symbiosis, this relationship between coral host and algal symbiont is not yet well established, and these molecules are not present in a sufficient quantity or diversity to allow the coral to withstand high light intensities, even those lacking UV radiation (i.e. this experiment). Moreover, since the tentacles used for feeding are not fully developed within the first weeks post-settlement, heterotrophic feeding at this stage is much more difficult, and exposure to higher light may require recruits to provide the algae with some of their energy reserves for photosynthesis.

Interestingly, MacKichan et al. (2003) found that 20-day old *P. astreoides* recruits had as much as 9-10x higher concentrations of MAAs compared to larvae. This time scale is intriguing when considered along with findings in the present study, in which recruits required higher intensity light after 3-5 weeks. If recruits have a lower concentration of MAAs in the first 2 weeks, it is possible that this would cause a more frequent occurrence of photoinhibition, even in the absence of UV, and thereby

encourage slower growth rates. As previously discussed, recruits may not have the appropriate mechanisms to generate higher concentrations of MAAs and may need more time after settlement to sequester or accumulate MAAs from the necessary source, whether algal or prokaryotic. In order to help understand why recruits grow slower under high intensity irradiance, future studies should investigate the source, production, and accumulation rates of these compounds in coral larvae and recruits.

Recruits of *Agaricia agaricites* are commonly found at shallow depths, but larger colonies are more abundant in deeper waters (Bak & Engel, 1979). Adults for this study were collected in shallow water, approximately 5 – 6 m, increasing likelihood that larvae collected for this experiment were born with relatively higher amounts of MAA compounds for defense against damaging light in shallow waters, and therefore increasing their likelihood of survival pre- and post-settlement (Gleason & Wellington, 1995). In early stages, this species also has higher quantities of MAAs than other species, such as *P. astreoides* (Gleason & Wellington, 1995; MacKichan et al., 2003). Agariciid corals have previously been reported to grow very slowly in shallow water (Bak & Engel, 1979; Van Moorsel, 1985), however recruits in this experiment grew rapidly in all circumstances.

Pigmentation in recruits was reduced following an intensification of light irradiance, implying that light was too intense for the previous density of photopigments in the recruit's symbionts. Pigmentation is regulated by the *Symbiodinium*, which in turn are speculated to be regulated by the coral host (Falkowski & Dubinski, 1981; Kleppel et al., 1989; Baird et al., 2009). Logically, a decrease in symbiont density would inherently decrease the overall pigmentation of the coral. During the first few weeks, all treatments had more individuals than expected with lighter pigmentation levels, suggesting lower symbiont densities. The inverse relationship between the concentration of pigments contained inside the symbionts and total irradiance is consistent with what has already been described been described in coral adults (Falkowski & Dubinksi, 1981; Kleppel et al., 1989; Fabricius, 2006; Abrego et al., 2012). *Porites astreoides* larvae released by adults in shallow water (2-5 m) have been demonstrated to have lower *Symbiodinium* densities than larvae released from adults in deeper areas (Goodbody & Gringley, 2018).

The adult colonies collected for this experiment came from a similar depth range (~5-7 m), and it is possible that this is evident in the first three weeks of this study based on the pigmentation trend of recruits in every treatment (Figure 10). This study suggests that the symbiont densities and/or pigments in coral recruits adapt to varying light conditions in a similar manner to adult colonies. Corals can be light- or shade-adapted as an entire colony, and they also exhibit inter-colonial gradient of multiple algal symbiont phylotypes (Falkowski and Dubinski, 1981; Rowan et al., 1997). Larvae of brooding corals such as *P. astreoides* and *A. agaricites* are given symbionts from their parent colony and are released as fully competent larvae. Larvae therefore have a similar consortium of symbionts as their parents, but after one month juveniles have been shown to have reduced diversities of symbionts (Reich et al., 2017). Since symbionts are responsible for production and translocation of MAAs to the host coral, a decrease in diversity of symbionts could affect the production rate, diversity and/or relative abundance of MAAs available in host tissues. This could also potentially limit the production of certain secondary MAAs only produced by symbionts within host tissues. Lower abundances of these compounds would reduce the absorption of short-wavelength and high intensity radiation in the first month post-settlement, which could have a profound effect on growth during this period.

Until week 3, the majority of *Porites astreoides* recruits displayed lower pigmentation values. Beginning in weeks 6-8 and lasting until weeks 10-11, depending on the treatment, most corals were darker pigmented, indicating light may have not been strong enough. In treatment 6, more corals than expected were pale in color until week 7, suggesting rather high irradiance levels for those corals. Between weeks 8 – 11, however, more individuals than expected were dark-pigmented, suggesting that the irradiance levels were not high enough. Weeks 12-14, pigmentation scores were nearly equal suggesting an acceptable range of irradiance for that age. This treatment (6) had significantly lower overall growth than treatments 3 and 4. This could potentially be explained by weeks 8-11, when pigmentation scores E5 and E6 occurred more often than expected for most individuals. Perhaps the low intensity light was inhibiting their growth, not maximizing their photosynthetic yield. Based on these analyses, a recommendation for an ideal light regime is possible, and is shown in Table 3. The data

suggest that an irradiance near 10 µmol quanta m^{-2} s^{-1} for the first three weeks is sufficient, followed by an increase to 20 µmol quanta m^{-2} s^{-1} for two weeks. In the fifth week light could be increased to 40 µmol quanta m^{-2} s^{-1}, followed by a change to 80 µmol quanta m^{-2} s^{-1} for weeks 6-7, 120 for weeks 8 – 12 and 130 for week 13 onward.

Table 3. Suggested irradiance values (µmol quanta m^{-2} s^{-1}) for Porites astreoides recruits during first 14 weeks post-settlement.

Week	Irradiance
0-2	10
3-4	20
5	40
6-7	80
8-12	120
13+	130

Agaricia agaricites recruits thrived all treatments. As expected the corals became darker to compensate for lower light intensities, until intensities reached the 140-150 µmol quanta m^{-2} s^{-1} range, and pigmentation dropped drastically (Figure 11 A-C). In weeks 2-5, recruits of *A. agaricites* were extremely dark pigmented. This time period corresponded to intensities of 10-80 µmol quanta m^{-2} s^{-1} and implies that this species has the ability to withstand higher irradiances starting their third week of life, potentially even higher than 80 µmol quanta m^{-2} s^{-1}. During weeks 10-12 more recruits were lighter pigmented than expected, indicating irradiance could have been lower. Based on these analyses, it seems *Agaricia agaricites* recruits could have grown faster by increasing light more rapidly in the first five weeks; increased to 80-90 µmol quanta m^{-2} s^{-1} by week 4 for example (Table 4). Irradiance subsequently could be raised to 120 µmol quanta m^{-2} s^{-1} on week 6 and held at this value until the 11^{th} week, and then raised again to 130 µmol quanta m^{-2} s^{-1}. This regimen would satisfy the recruits' metabolic needs and ideally avoid photoinhibition. Increasing water movement within the experimental system concomitantly with increased irradiances can help alleviate photoinhibition, especially at higher PAR values.

Table 4. Suggested irradiance values (µmol quanta m^{-2} s^{-1}) for Agaricia agaricites recruits during first 12 weeks post-settlement.

Week	Irradiance
0-1	10
2	40
3-5	80
6-10	120
11+	130

Regardless of light intensity, mortality was very low in all experiments for both species. *Porites astreoides* and *Agaricia agaricites* have been previously described as "weedy" species, able to tolerate wider ranges of environmental stressors. Recruits of these species have demonstrated resilience to eutrophic settlement sites, low pH conditions, and high sedimentation (Tomascik 1991; Hunte & Wittenberg 1992; Albright et al., 2008; Fourney and Figueiredo, 2017). Over the past 30+ years in the Caribbean, *Porites astreoides* and *Agaricia agaricites* have shown relatively higher recruitment rates, increased relative abundances and, in some locations, increased absolute cover and colony density (Rogers et al., 1984; Green et al., 2011; Walton et al., 2018). In 2016 on the Southeast Florida Reef Tract (SEFRT), *Porites astreoides* recruits comprised 46.7% of the total scleractinian recruits across 12 survey sites (Leah Harper, M.S. Thesis). Along the SEFRT many coral species have suffered immense population declines over the last 6 years due to White Syndrome, one species as high as 95% (Walton et al., 2018). Despite the overwhelming prevalence of this disease, *Porites astreoides* and *Agaricia agaricites* have shown significant increases in colony density throughout the region from 2012 to 2016 (Walton et al., 2018).

In order to restore coral reefs, sexual reproduction must be made a priority, as genetic diversity is the best weapon corals have to ensure population resilience. New techniques and technology allow corals to be spawned, raised, and fragmented/fused to accelerate growth rates for nearly mature adults – all in artificial environments (Forsman et al., 2015; Craggs et al., 2017). Using temperature controllers and modified light schedules, corals can even be triggered to spawn at selected times during the year in controlled aquarium systems (Craggs et al., 2017), followed by manual crossing of gametes to ensure genetic diversity. However, the production of viable coral larvae *ex*

situ is only one part in the restoration process - it is necessary to optimize laboratory procedures for larval and juvenile rearing in terms of efficient growth and maximum survival for eventual outplanting to depauperate reefs. Coral sexual maturity is determined by size, rather than age, so expediting recruit and juvenile growth as much as possible is critical to effective restoration (Szmant 1991; Soong 1993). This study has shown that utilizing the correct lighting regime can boost growth rate of coral recruits. Optimizing growth in this early stage can ultimately help reduce the overall time to reach sexual maturity and allow for earlier out-planting onto the reef. Future studies are needed to lengthen the examination period of these lighting regimens and determine optimal irradiances for other species, especially major reef-builders. Future studies are also necessary to investigate potential sources for antioxidants and MAAs in newly settled juveniles in order to avoid photoinhibition in the early stages post-settlement. This study has shown that utilizing the correct lighting regimen can boost growth rate of coral recruits. Optimizing growth in this early stage can ultimately help reduce the overall time to reach sexual maturity and allow for earlier out-planting onto the reef. The mounting pressures of widespread disease and climate change add immense haste to reef restoration efforts.

Literature cited

Abrego, D., Ulstrup, K. E., Willis, B. L., & van Oppen, M. J. (2008). Species–specific interactions between algal endosymbionts and coral hosts define their bleaching response to heat and light stress. *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1648): 2273-2282.

Abrego, D., Willis, B. L., & van Oppen, M. J. (2012). Impact of light and temperature on the uptake of algal symbionts by coral juveniles. PLoS One, 7(11): e50311.

Albright, R., Mason, B., & Langdon, C. (2008). Effect of aragonite saturation state on settlement and post-settlement growth of *Porites astreoides* larvae. Coral Reefs, 27(3), 485-490.

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., & Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society of London B: Biological Sciences* 276(1669); 3019-3025.

Babcock, R., and Mundy, C. (1996) Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. *Journal of Experimental Marine Biology and Ecology* 206.1-2: 179-201.

Baird, A. H., Bhagooli, R., Ralph, P. J., & Takahashi, S. (2009). Coral bleaching: the role of the host. *Trends in Ecology & Evolution*, 24(1): 16-20.

Bak, R. P. M., and Engel, M. S. (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Marine Biology* 54(4): 341-352.

Banaszak, A. T., & Trench, R. K. (1995). Effects of ultraviolet (UV) radiation on marine microalgal-invertebrate symbioses. II. The synthesis of mycosporine-like amino acids in response to exposure to UV in *Anthopleura elegantissima* and *Cassiopeia xamachana*. Journal of Experimental Marine Biology and Ecology, 194(2), 233-250.

Banks, K. W., Riegl, B. M., Richards, V. P., Walker, B. K., Helmle, K. P., Jordan, L. K., Phipps, J., Shivji, M.S., Spieler, R.E., & Dodge, R. E. (2008). The reef tract of continental southeast Florida (Miami-Dade, Broward and Palm Beach counties, USA). Coral Reefs of the USA, 175-220.

Baums, I.B. (2008) A restoration genetics guide for coral reef conservation. *Molecular Ecology* 17(12): 2796-2811.

Birrell, C. L., McCook, L. J., Willis, B. L., & Harrington, L. (2008). Chemical effects of macroalgae on larval settlement of the broadcast spawning coral *Acropora millepora*. *Marine Ecology Progress Series*, 362: 129-137.

Birkeland, C., Rowley, D., & Randall, R. H. (1981). Coral recruitment patterns at Guam. In Proc 4th Int Coral Reef Symposium, 2: 339-344.

Burke, L., Selig, L., and Spalding, L. (2002) Research report: reefs at risk in South Asia. *World Resources Institute, Washington, DC*.

Burns, T. P. (1985). Hard-coral distribution and cold-water disturbances in South Florida: variation with depth and location. *Coral Reefs*, *4*(2): 117-124.

Carlson, B. A. (1999). Organism responses to rapid change: what aquaria tell us about nature. *American Zoologist*, 39(1): 44-55.

Chiappone, M., & Sullivan, K. M. (1996). Distribution, abundance and species composition of juvenile scleractinian corals in the Florida reef tract. *Bulletin of Marine Science*, *58*(2), 555-569.

Chornesky, E. A., & Peters, E. C. (1987). Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. The Biological Bulletin, 172(2): 161-177.

Cesar, H., Burke, L., and Pet-Soede, L. (2003) The economics of worldwide coral reef degradation. Cesar environmental economics consulting (CEEC).

Conservation International. (2008). Economic Values of Coral Reefs, Mangroves, and Seagrasses: A Global Compilation. Center for Applied Biodiversity Science, Conservation International, Arlington, VA, USA.

Coles, S. L., & Jokiel, P. L. (1977). Effects of temperature on photosynthesis and respiration in hermatypic corals. Marine biology, 43(3), 209-216.

Craggs, J., Guest, J. R., Davis, M., Simmons, J., Dashti, E., & Sweet, M. (2017). Inducing broadcast coral spawning ex situ: Closed system mesocosm design and husbandry protocol. *Ecology and evolution*.

Cumbo, V. R., Fan, T. Y., & Edmunds, P. J. (2012). Physiological development of brooded larvae from two pocilloporid corals in Taiwan. Marine biology, 159(12), 2853-2866.

Doney, S.C., Ruckelshaus, M., Duffy, J.E., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalas, N.N., Sydeman, W.J., Talley, L.D. (2011) Climate change impacts on marine ecosystems, Annu. Rev. Mar. Sci, 4: 11-37.

Drenkard, E.J., et al. (2013) Calcification by juvenile corals under heterotrophy and elevated CO2. *Coral Reefs* 32(3): 727-735.

Fabricius, K.E. (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50(2): 125-146.

Fabricius, K. E. (2006). Effects of irradiance, flow, and colony pigmentation on the temperature microenvironment around corals: implications for coral bleaching? Limnology and Oceanography, 51(1), 30-37.

Falkowski, P.G., et al. (1984) Light and the bioenergetics of a symbiotic coral. *Bioscience* 34(11): 705-709.

Falkowski, P. G., & Dubinsky, Z. (1981). Light-shade adaptation of Stylophora pistillata, a hermatypic coral from the Gulf of Eilat. Nature, 289(5794), 172.

Forsman, Z.H., et al. (2015) Growing coral larger and faster: micro-colony-fusion as a strategy for accelerating coral cover. *PeerJ* 3: e1313.

Fourney, F., & Figueiredo, J. (2017). Additive negative effects of anthropogenic sedimentation and warming on the survival of coral recruits. Scientific Reports, 7(1): 12380.

Fox, H.E., and Caldwell, R.L. (2006) Recovery from blast fishing on coral reefs: a tale of two scales. *Ecological Applications* 16(5): 1631-1635.

Gates, R. D., Hoegh-Guldberg, O., McFall-Ngai, M. J., Bil, K. Y., & Muscatine, L. (1995). Free amino acids exhibit anthozoan" host factor" activity: They induce the release of photosynthate from symbiotic dinoflagellates in vitro. Proceedings of the National Academy of Sciences, 92(16), 7430-7434.

Garcia-Pichel, F. 1994. A model for internal self-shading in planktonic organisms and its implications for the usefulness of ultra-violet sunscreens. Limnol. Oceanogr. 39:1704–1717.

Gleason, D. F., and Wellington, G. M. (1995) Variation in UVB sensitivity of planula larvae of the coral *Agaricia agaricites* along a depth gradient. *Marine Biology* 123(4): 693-703.

Gleason, D. F. (1998). Sedimentation and distributions of green and brown morphs of the Caribbean coral Porites astreoides Lamarck. *Journal of Experimental Marine Biology and Ecology*, *230*(1), 73-89.

Gleason, D.F., Edmunds, P.J., and Gates, R.D. (2006) Ultraviolet radiation effects on the behavior and recruitment of larvae from the reef coral *Porites astreoides*. *Marine Biology* 148(3): 503-512.

Goodbody-Gringley, G., Wong, K. H., Becker, D. M., Glennon, K., & de Putron, S. J. (2018). Reproductive ecology and early life history traits of the brooding coral, *Porites astreoides*, from shallow to mesophotic zones. *Coral Reefs*, *37*(2), 483-494.

Green, D.H., Edmunds, P.J., and Carpenter, R.C. (2008) Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Marine Ecology Progress Series* 359: 1-10.

Goreau, T. F., Goreau, N. I., & Yonge, C. M. (1971). Reef corals: autotrophs or heterotrophs? *The Biological Bulletin*, 141(2): 247-260.

Goreau, T. F., & Wells, J. W. (1967). The shallow-water Scleractinia of Jamaica: revised list of species and their vertical distribution range. *Bulletin of Marine Science*, *17*(2), 442-453.

Harper, L.M. (2017). Variation in Coral Recruitment and Juvenile Distribution Along the Southeast Florida Reef Tract. Master's thesis. Nova Southeastern University. Retrieved from NSUWorks. (458)

Harrison, P. L., Babcock, R. C., Oliver, J. K., Bull, G. D., Wallace, C. C., & Willis, B. L. (1984). Mass spawning in the tropical reef corals. *Science*, 223(4641): 1186-1189.

Helmuth, B., & Sebens, K. (1993). The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus). J. Exp. Mar. Biol. Ecol, 165, 251-278.

Heyward, A. J., and Negri, A. P. (1999) Natural inducers for coral larval metamorphosis. *Coral Reefs* 18(3): 273-279.

Heyward, A. J., Smith, L. D., Rees, M., & Field, S. N. (2002). Enhancement of coral recruitment by in situ mass culture of coral larvae. *Marine Ecology Progress Series*, 230(7): 113-118.

Highsmith, R. C. (1982). Reproduction by fragmentation in corals. *Marine Ecology Progress Series*, 7: 207-226.

Hoegh-Guldberg, O., & Jones, R. J. (1999). Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. Marine Ecology Progress Series, 183, 73-86.

Hughes, T.P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265 (5178): 1547-1551.

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Practchett, M.S., Steneck, R.S., & Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, 17(4): 360-365.

Humanes, A., Ricardo, G. F., Willis, B. L., Fabricius, K. E., & Negri, A. P. (2017). Cumulative effects of suspended sediments, organic nutrients and temperature stress on early life history stages of the coral *Acropora tenuis*. *Scientific Reports*, 7: 44101.

Huston, M. A. (1985) Patterns of species diversity on coral reefs. Ann. Rev. Ecol. Syst. 16:149-177.

Hunte, W., & Wittenberg, M. (1992). Effects of eutrophication and sedimentation on juvenile corals. Marine Biology, 114(4), 625-631.

IPCC 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability.

Jones, R.J., and Hoegh-Guldberg, O. (1999) Effects of cyanide on coral photosynthesis: implications for identifying the cause of coral bleaching and for assessing the environmental effects of cyanide fishing. *Marine Ecology Progress Series, 177, 83-91*

Keith, S. A., Maynard, J. A., Edwards, A. J., Guest, J. R., Bauman, A. G., Van Hooidonk, R., ... & Rahbek, C. (2016). Coral mass spawning predicted by rapid seasonal rise in ocean temperature. In Proc. R. Soc. B, 283(1830): 20160011. The Royal Society.

Kleppel, G. S., Dodge, R. E., & Reese, C. J. (1989). Changes in pigmentation associated with the bleaching of stony corals. *Limnology and Oceanography*, *34*(7), 1331-1335.

Knowlton, N. (2001) Coral reef biodiversity--habitat size matters. *Science* 292(5521): 1493-1495.

Leal, M. C., Ferrier-Pagès, C., Petersen, D., & Osinga, R. (2016). Coral aquaculture: applying scientific knowledge to ex situ production. Reviews in Aquaculture, 8(2): 136-153.

Lesser, M. P. (1997). Oxidative stress causes coral bleaching during exposure to elevated temperatures. Coral reefs, 16(3): 187-192.

Lesser, M. P. L., Mazel, C., Phinney, D., & Yentsch, C. S. (2000). Light absorption and utilization by colonies of the congeneric hermatypic corals *Montastraea faveolata* and *Montastraea cavernosa*. Limnology and Oceanography, 45(1): 76-86.

Lessios, H.A., Robertson, D. R., and Cubit, J. D. (1984) Spread of *Diadema* mass mortality through the Caribbean. *Science* 226.4672: 335-337.

Levitan, D.R. (1988) Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at Saint John, US Virgin Islands. Journal of Experimental Marine Biology and Ecology 119(2): 167-178.

Levy, O., Achituv, Y., Yacobi, Y. Z., Stambler, N., & Dubinsky, Z. (2006). The impact of spectral composition and light periodicity on the activity of two antioxidant enzymes (SOD and CAT) in the coral *Favia favus*. Journal of Experimental Marine Biology and Ecology, 328(1), 35-46.

Levy, G., Shaish, L., Haim, A., & Rinkevich, B. (2010). Mid-water rope nursery—Testing design and performance of a novel reef restoration instrument. Ecological Engineering, 36(4): 560-569.

Long, S. P., Humphries, S., & Falkowski, P. G. (1994). Photoinhibition of photosynthesis in nature. Annual review of plant biology, 45(1), 633-662.

Lillis, A., Bohnenstiehl, D., Peters, J. W., & Eggleston, D. (2016). Variation in habitat soundscape characteristics influences settlement of a reef-building coral. PeerJ, 4: e2557.

MacArthur, R.H., and MacArthur, J.W. (1961) On bird species diversity. *Ecology* 42(3): 594-598.

MacKichan, C. A. (2003). Effects of Ultraviolet Radiation on Newly Settled Recruits of the Reef-building Coral *Porites astreoide*.

Mason, B., M. Beard, and M. W. Miller. (2011) Coral larvae settle at a higher frequency on red surfaces. *Coral Reefs* 3(3): 667-676.

McClanahan, T.R., and Kaunda-Arara, B. (1996) Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology* 10(4): 1187-1199.

McClanahan, T. R., B. A. Cokos, and Sala, E. (2002) Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize. *Marine Pollution Bulletin* 44(6): 441-451.

McGuire, M. P. (1998). Timing of larval release by *Porites astreoides* in the northern Florida Keys. Coral Reefs, 17(4): 369-375.

Mendes, J. M., and Woodley, J.D. (2002) Timing of reproduction in *Montastraea annularis*: relationship to environmental variables. *Marine Ecology Progress Series* 227: 241-251.

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

Muller, E.M., and Woesik, R. (2012) Caribbean coral diseases: primary transmission or secondary infection? *Global Change Biology* 18(12): 3529-3535.

Mundy, C. N., and Babcock, R. C. (1998) Role of light intensity and spectral quality in coral settlement: implications for depth-dependent settlement? *Journal of Experimental Marine Biology and Ecology* 223(2): 235-255.

Muscatine, L., and Porter, J.W. (1977) Reef corals: mutualistic symbioses adapted to nutrient-poor environments. *Bioscience* 27(7): 454-460.

Nedimyer, K., Gaines, K., and Roach, S. (2011) Coral tree nursery: an innovative approach to growing corals in an ocean-based field nursery. *AACL Bioflux* 4(4): 442-446.

Precht, W.F., et al. (2016) Unprecedented disease-related coral mortality in Southeastern Florida. *Scientific reports* 6: 31374.

Price, N. (2010) Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. *Oecologia* 163(3): 747-758.

de Putron, S. J., Lawson, J. M., White, K. Q., Costa, M. T., Geronimus, M. V., & MacCarthy, A. (2017). Variation in larval properties of the Atlantic brooding coral *Porites astreoides* between different reef sites in Bermuda. *Coral Reefs*, *36*(2), 383-393.

Randall, C. J., and R. van Woesik. (2017) Some coral diseases track climate oscillations in the Caribbean. *Scientific Reports* 7(1): 5719.

Reich, H.G., Deborah L. Robertson, and Gretchen Goodbody-Gringley. (2017) Do the shuffle: Changes in *Symbiodinium* consortia throughout juvenile coral development. *PloS one* 12(2): e0171768.

Reynaud, S., Leclercq, N., Romaine-Lioud, S., Ferrier-Pagés, C., Jaubert, J., & Gattuso, J. P. (2003). Interacting effects of CO2 partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. Global Change Biology, 9(11): 1660-1668.

Rinkevich, B. (2005) Conservation of coral reefs through active restoration measures: recent approaches and last decade progress. *Environmental Science & Technology*, 39(12): 4333-4342.

Rogers, C. S., Fitz, H. C., Gilnack, M., Beets, J., & Hardin, J. (1984). Scleractinian coral recruitment patterns at salt river submarine canyon, St. Croix, US Virgin Islands. *Coral Reefs*, 3(2): 69-76.

Rogers, C.S. (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine ecology progress series*, 62: 185-202.

Rowan, R., Knowlton, N., Baker, A., & Jara, J. (1997). Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. Nature, 388(6639), 265.

Sato, M. (1985) Mortality and growth of juvenile coral *Pocillopora damicornis* (Linnaeus). Coral Reefs 4:27–33.

Serrano X, Baums IB, Smith TB, Jones RJ, Shearer TL, Baker AC. Long distance dispersal and vertical gene flow in the Caribbean brooding coral *Porites astreoides*. Sci Rep. 2016; 6.

Sharp, K. H., Distel, D., & Paul, V. J. (2012). Diversity and dynamics of bacterial communities in early life stages of the Caribbean coral *Porites astreoides*. The ISME journal, 6(4): 790-801.

Shick, J. M., Romaine-Lioud, S., Ferrier-Pages, C., & Gattuso, J. P. (1999). Ultraviolet-B radiation stimulates shikimate pathway-dependent accumulation of mycosporine-like amino acids in the coral Stylophora pistillata despite decreases in its population of symbiotic dinoflagellates. *Limnology and Oceanography*, *44*(7), 1667-1682.

Shick, J. M., & Dunlap, W. C. (2002). Mycosporine-like amino acids and related gadusols: biosynthesis, accumulation, and UV-protective functions in aquatic organisms. Annual review of Physiology, 64(1), 223-262.

Siebeck, U. E., Marshall, N. J., Klüter, A., & Hoegh-Guldberg, O. (2006). Monitoring coral bleaching using a colour reference card. Coral Reefs, 25(3), 453-460.

Spalding, M. D., and A. M. Grenfell. (1997) New estimates of global and regional coral reef areas. *Coral Reefs* 16(4): 225-230.

Spalding, M. D., Ravilious, C., & Green, E. P. (2001). World Atlas of Coral Reefs.

Steneck, R. S., and F. G. Walton Smith. (1994) Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean reef systems (1978–1988). Oceanographic Literature Review, 9(42): 778-779.

Soong, K. (1993) Colony size as a species character in massive reef corals. *Coral reefs* 12(2): 77-83.

Szmant, A. M. (1986) Reproductive ecology of Caribbean reef corals. *Coral Reefs* 5.1: 43-53.

Szmant, A. M. (1991) Sexual reproduction by the Caribbean reef corals *Montastrea annularis* and *M. cavernosa*. *Marine Ecology Progress Series*:74, 13-25.

Tran, C., and Michael G. Hadfield. (2011) Larvae of *Pocillopora damicornis* (Anthozoa) settle and metamorphose in response to surface-biofilm bacteria. *Marine Ecology Progress Series* 433: 85-96.

Tomascik, T. (1991). Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies. Marine ecology progress series. Oldendorf, 77(2), 261-269.

Tunnicliffe, V. (1981). Breakage and propagation of the stony coral *Acropora cervicornis*. Proceedings of the National Academy of Sciences, 78(4): 2427-2431.

Van Moorsel, G. W. N. M. (1983). Reproductive strategies in two closely related stony corals (*Agaricia*, Scleractinia). *Mar Ecol Prog Ser*, *13*, 273-283.

Van Moorsel, G. W. N. M. (1985). Disturbance and growth of juvenile corals (*Agaricia humilis* and *Agaricia agaricites*, Scleractinia) in natural habitats on the reef of Curacao. *Mar Ecol Prog Ser*, *24*, 99-112.

Vermeij, M. J., Bakker, J., Hal, N. V. D., & Bak, R. P. (2011). Juvenile coral abundance has decreased by more than 50% in only three decades on a small Caribbean island. Diversity, 3(3): 296-307.

Walton, C. J., Hayes, N. K., & Gilliam, D. S. (2018). Impacts of a Regional, Multi-Year, Multi-Species Coral Disease Outbreak in Southeast Florida. *Frontiers in Marine Science*, *5*, 323.

Webster, N. S., Uthicke, S., Botté, E. S., Flores, F., & Negri, A. P. (2013). Ocean acidification reduces induction of coral settlement by crustose coralline algae. Global Change Biology, 19(1): 303-315.

Williams, S. L. (2001) Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. *Ecological Applications* 11.5: 1472-1488.

Yakovleva, I., Bhagooli, R., Takemura, A., & Hidaka, M. (2004). Differential susceptibility to oxidative stress of two scleractinian corals: antioxidant functioning of mycosporine-glycine. Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology, 139(4): 721-730.

Yakovleva, I. M., & Baird, A. H. (2005). Ontogenetic change in the abundance of mycosporine-like amino acids in non-zooxanthellate coral larvae. Coral Reefs, 24(3), 443-452.