8-8-2023

The Effect of Water Flow Rates on the Survival and Growth Rates of Three Caribbean Bouldering Coral Species Juveniles in an Indoor versus Outdoor Environment

Ian Michael Johnson
Nova Southeastern University

Thesis of
Ian Michael Johnson

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science
Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

August 2023

Approved:
Thesis Committee

Committee Chair: Joana Figueiredo Ph.D.

Committee Member: Andrew Bauman Ph.D.

Committee Member: Dorothy Ellen Renegar Ph.D.

NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF ARTS AND SCIENCES

The Effect of Water Flow Rates on the Survival and Growth Rates of Three Caribbean Bouldering Coral Species Juveniles in an Indoor Versus Outdoor Environment

By

Ian Michael Johnson

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Science

Nova Southeastern University

August 2023

Abstract

Coral reefs are vital ecosystems for the world's oceans and humanity; however, they are threatened by climate change, disease, and local anthropogenic stressors, and need assistance to recover. Traditional reef restoration efforts (fragmentation and outplanting are helping but are limited in effectiveness by not increasing genetic diversity. *Ex situ* sexual propagation for corals provides new, genetically different coral recruits. However, this process is laborious, expensive and time consuming, especially at the scale required to effectively contribute to the widespread recovery. To lower costs, two key parameters that require optimization to hasten the growth of coral recruits are water flow and tank location. In this study, the combined effects of water flow 0.1 $m.s^{-1}$ versus 0.4 $m.s^{-1}$ and tank location (LEDs indoors versus Natural Sunlight outdoors) were tested to find the optimal regime to raise juveniles of the of the stony coral tissue loss disease sensitive coral species *Montastraea cavernosa, Diploria labyrinthiformis* and *Colpophyllia natans.* It was found that the lower water flow rate was more suitable for the coral recruits' health, survival and growth compared to the higher water flow rate and that the location (indoor vs. outdoor) with natural or artificial light, did not significantly affect the growth and survival of the coral. These results suggest that growing corals indoors or outdoors leads to similar results, but that lower water flow rates may lower time and monetary costs of raising coral recruits until they reach the size suitable for outplanting on the reef.

Keywords: optimization, flow, light, coral recruits, growth

Table of Contents

Introduction

Coral reefs are among the most biodiverse and productive ecosystems in the world. While currently covering less than 0.1% of the world's oceans benthic area (Spalding et al., 2001), they house an estimated 550,000 to 1,330,000 species of multicellular forms of life (Fisher et al., 2015). Coral reefs generate 36 billion USD from tourism worldwide (Spalding et al., 2015); if we add fisheries and the value of the ecosystem services they provide, such as storm surge protection, erosion prevention and building materials (Woodhead et al., 2019), reefs worldwide are worth 375 billion USD (Brander & Beukering, 2013). Reefs and the associated economic activities around them support a multitude of jobs and industries. Coral reefs are mainly built of calcium carbonate skeleton excreting cnidarian anthozoans of the order Scleractinia, commonly known as stony corals.

Tropical and sub-tropical scleractinian corals are made up of individual animals (i.e., polyps) that house photosynthetic dinoflagellate endosymbionts (Symbiodiniaceae), commonly known as zooxanthellae (Stanley, 2003, Blackall et al., 2015). The symbionts are protected from predation and use the waste products of the coral cellular respiration for photosynthesis. In return, the coral host gains access to many of the macro nutrients produced by the algae through photosynthesis. The corals use these nutrients for growth, and they aid in the deposition of the corals' calcium carbonate skeleton (Gattuso et al., 1999, Stat et al., 2006). This partnership however is under severe threat due to huma induced climate change. Corals naturally live near their thermal maximum thresholds. When this thermal threshold is exceeded, the delicate relationship between the coral and their endosymbionts is disrupted and causes the coral to expel their endosymbionts from their tissues, thus losing their main source of food. This event is called coral bleaching (Douglas, 2003, Ruiz-Moreno et al., 2012). While other environmental stressors, such as metal pollution, large salinity changes or algal overgrowth can also cause bleaching (Fisher et al., 2019; Hughes et al., 2018; Woodridge & Done, 2009), rapid changes in water temperature are the main cause (Douglas, 2003; Fitt et al., 2001). If the stressor is short lived, the endosymbionts can be recaptured or pulled from tissue reserves, and slowly recultivated in the coral over time, allowing the coral to survive. However, if the bleaching is prolonged, the coral can starve and die. As greenhouse gas emissions continue to rise, the oceans' temperatures continue to rise, making the frequency, spatial and time spread of bleaching events in the last 100

years double what it. This massive increase in the frequency of bleaching events results in the coral populations not having enough time and energy to recover and leads to coral cover loss (Frieler et al., 2012; Hughes et al., 2018). Coral cover worldwide has declined by 14% worldwide between 2009 and 2018 (Hughes et al., 2018) and it is projected that more than 90% will be lost by 2100 (Souter et al., 2022). In the Caribbean alone, coral cover declined from 17.6% in 1999 to 14.5% in 2019, a loss of 17.8%, and has continued to increase due to diseases (Walton et al., 2018) and other environmental factors (Estrada-Saldivar et al., 2020). This loss of a vital habitat and ecosystem has led to many efforts to restore coral reefs.

Traditional methods for reef restoration include fragmenting coral and outplanting the fragments back on the reef or to further grow them in land-based or offshore nurseries. This technique takes advantage of coral populations' natural adaptations to recover after a storm. Naturally, storms and tidal forces often cause colonies to break into smaller fragments or detach completely and be transported to new areas (Hughes et al., 1992). Some of these coral fragments survive and can reattach and grow into colonies. Coral restoration makes use of this asexual mode of reproduction by collecting whole colonies and breaking them into fragments, which are then reared at an *ex situ* or *in situ* coral nursery, and then once the fragments are large enough, they are fragmented again or outplanted on the reef (Boström-Einarsson et al., 2020; Bowden, 2001; Garrison & Ward 2012). Because propagating corals through fragmentation essentially produces dozens if not hundreds of clones of the same coral genotype, nurseries cultivate many different genotypes. Regardless, as survival, growth rates, and disease resistance differ between coral genotypes, there is always a risk of some genotypes becoming overrepresented in the population. This compromises their ability to sexually reproduce (due to their inability to self-fertilize). Additionally, if this massively propagated genotype is more susceptible to a disease or temperature changes, potentially makes the whole population more vulnerable and prone to more coral cover loss.

To increase genetic diversity, restoration techniques and methods should instead, or at least concurrently, produce corals through sexual reproduction. Coral gametes can be collected in the field during the annual spawning events (Guest et al., 2010: Rada-Osario et al., 2020), be collected in the lab from (sexually-mature) colonies brought to the lab shortly before the predicted spawning (Doropoulos et al., 2019; Guest et al. 2010), or by keeping corals in the

laboratory year-round and mimicking annual temperature, solar and moon light cycles to induce gonad maturation and synchronous spawning (Craggs et al., 2017). Gametes are then mixed for fertilization, larvae are reared and settled, and develop into juveniles which are grown until reaching a suitable size for outplanting on the reef. The production of corals through sexual reproduction can greatly contribute to increase genetic diversity on the reefs and thus increase chances of persistence through climate change (DeFillipo et al., 2022). However, the coral culture methodology needs to be further optimized to be effective at large (reef system) spatial scales.

Growing newly settled corals to a suitable size for outplanting typically requires the precise control of environmental conditions using expensive equipment and trained professionals. The current methodologies to grow newly settled corals to a size suitable for outplanting are still leading to higher mortality and lower growth than desired. The main issues are algae overgrowth, and likely sub-optimal, abiotic conditions, including light, water quality and feeding. Optimizing the conditions juvenile corals are reared in, should result in higher survival and faster growth, lowering the labor, cost, and time required to outplant the coral recruits out to the reef. This reduction in cost would also allow for much larger scale operations in more areas.

Light is key for coral growth. The corals' endosymbionts require light to perform photosynthesis which is the corals' main energy source. In coral aquaculture facilities, there are two possible sources for light: outdoor natural light, and artificial light such as LEDs. The effect of light source, light intensity and spectra on juvenile corals has been shown to impact growth rates and therefore the costs of operations (Rocha et al., 2013). Additionally, artificial lights (LEDs) have been shown to promote similar growth rates to natural sunlight in some coral species (e.g., *Acropora*), albeit with lower photosynthetic efficiency (Slagel et al., 2021). Different light intensities and spectra greatly affect growth rates over time (Schlacher et al., 2007; Schutter et al., 2008). The effects of light on calcification and growth rates are however dependent on water flow rates, with higher flow rates leading to higher calcification rates (Schutter et al., 2011).

Water flow rate can greatly influence coral growth as it determines the delivery of nutrients, such as calcium and nitrogen, as well as prey to the coral. Water flow has also been

demonstrated to mediate in the short term some environmental stressors such as temperature and ocean acidification (Comeau et al., 2014). Natural flow rates vary widely among locations, reef types, and the structures surrounding the reef (Davis et al., 2021; Hench & Rosman, 2013). These variations help drive the spatial distribution of corals within reefs and regions. Studying the effects of different flow rates on coral growth and survival will be essential to create more ideal conditions for coral production in nurseries. Increased water flow conditions have been shown to enhance Pocilloporidae corals fecundity (Mass et al., 2011), enhanced growth rates in *Galaxea fascicularis* (Schutter et al., 2010), boosted recovery rates from bleaching (Nakamura & Yamasaki, 2005) and affected the morphology of multiple coral species (Chindapol et al., 2013). Similarly, elevated water flow aided in reducing photoinhibition in high water temperatures in Acroporidae (Nakamura et al., 2005) and *Agaricia tenuifolia* (Sebens et al., 2003), showing the possible benefits for aquaculture. However, very few studies investigating the effects of water flow rates have been done on the growth and survival of Caribbean brain and bouldering corals. Furthermore, most previous studies on these species focused on the effects of water flow on prey capture (Sebens et al., 1998) rather than growth rate or survival. The effects of water flow on the survival and growth of coral juveniles, with the intent to find the optimal conditions to raise corals in an onshore nursery remain unstudied.

In this study, I will assess the effect of water flow and tank location (with the major difference being light source type) on the survival and growth of sexually produced juveniles of 3 coral species, *Montastraea cavernosa*, *Diploria labyrinthiformis* and *Colpophyllia natans* to determine the optimum grow-out conditions. Brain and bouldering corals are key reef building species in Florida's Coral Reef, susceptible to stony coral tissue loss disease (SCTLD) and thus the target of current restoration efforts. Corals were grown either in outdoor recirculating aquaculture systems (RAS's) or indoor RAS/s using natural light (sunlight) or artificial light (LEDs) and were exposed to; either a high flow rate of 0.4 ± 0.1 m/s, mimicking the levels at an average reef crest or fore reef at 3m depth, or a low flow rate of 0.1 ± 0.1 m/s, mimicking the levels present at the deeper (9m) reef slope or back reef (Adey & Steneck, 2003, Johansen, 2014). Survival and growth data was collected over six months to assist recommendations for optimal cultivation of each species.

Methods and Materials

Outdoor vs Indoor RAS Setup

Coral juveniles of *Montastraea cavernosa, Diploria labyrinthiformis* and *Colpophyllia natans* were maintained in recirculating aquaculture systems (RAS): two separate, but identical systems outdoors, and two raceways of the same indoor system at Nova Southeastern's Oceanographic Campus in Fort Lauderdale, Florida, USA. The two outdoor systems each consist of a 1100 L fiberglass tank, with an attached 400 L sump holding Red Sea® Reefer RSK-900 protein skimmer, 2 Two Little Fishes Inc. PhosBan Phosphate Reactor 550™, one with Brightwell Aquatics™ Purit™ Carbon Media and one with Two Little Fishes Inc PhosBan™ Phosphate Absorption Media, and GEOS Reef® 6x18 calcium reactor, as shown in Figure 1. For biofiltration, live rock, bioballs and Brightwell Aquatics™ BioBricks were kept in the sump. The temperature was maintained by three Eheim® Jager 300-watt submersible heaters, two in the tank, one in the sump, and one in line Aqua Logic® ½ HP water chiller, each controlled by an Aqua Logic, Inc® NEMA 4X digital temperature controller, set to mimic the natural temperature gradient of the southeastern Florida Reef Tract (23 °C in January to 29°C in September) as reported by SECREMP 2007-2018 (excluding bleaching events). Each sump had a 1 m Lifeguard Aquatics High Output Amalgam Germicidal 90-Watt UV sterilizer. The tanks were covered by 3.66m × 1.8m clear tarps and 50% 3.05 × 1.8m My Tarps® shade cloths held down by bungee cords to prevent rainwater and imitate natural light spectrum at reef depth with a peak of ~250 µMol/m^2s.

Figure 1. Outdoor RAS

The indoor system consists of two 450 L fiberglass raceways, connected to a 650 L sump, as shown in Figure 2. The light was generated by a EcoTech Marine® 5th Generation Radion XR30 LED light set to a minimum of 150 µMol/m^{2}s PAR to a peak of 250 µMol/m^{2}s PAR on a schedule that mimics the Fort Lauderdale yearly cycle and insolation curve. The indoor systems followed the same temperature patterns as the outdoor systems, using one Eheim® Jager 150-watt submersible heater per raceway near the inflow and one in the sump. The sump has a Tradewinds© 1/3 HP Drop-in chiller, 2 Two Little Fishes Inc. PhosBan Phosphate Reactor 550™, one with Brightwell Aquatics™ Purit™ Carbon Media and one with Two Little Fishes Inc PhosBan™ Phosphate Absorption Media, and a GEOS Reef® 6x18 calcium reactor. For biofiltration, live rock, bioballs and Brightwell Aquatics™ BioBricks were used. All heating equipment was controlled by a Neptune Systems© Apex system programed to follow the same natural temperature curve as the outdoor systems and the system uses a Neptune Systems© Apex auto water top-off system to help maintain constant salinity.

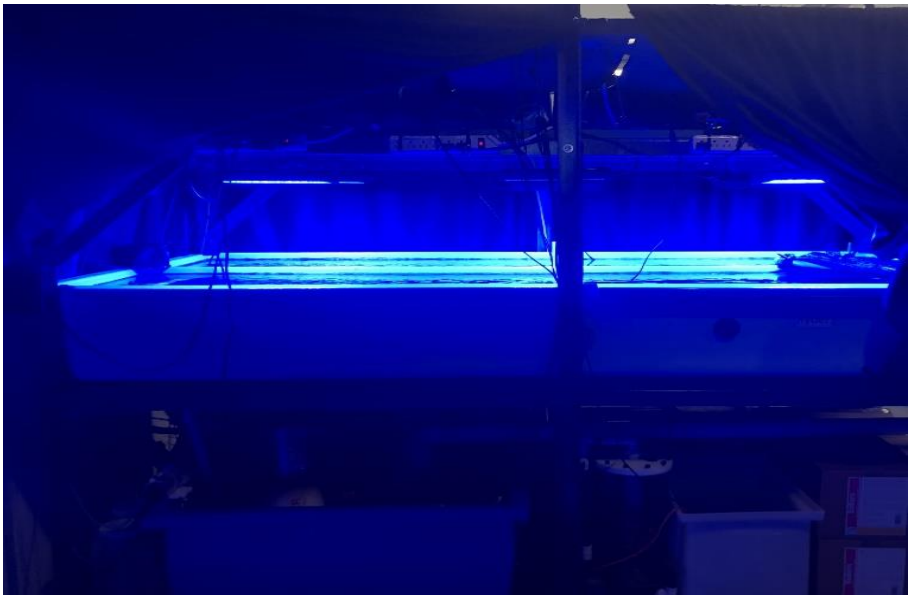


Figure 2. Indoor RAS

Corals in the indoor aquariums were placed on racks made of eggcrate with PVC at a depth of ~22 cm, with the outdoor corals at a depth ~30 cm from the surface, arranged within their treatment group flow rates, as shown in Figure 1, adapted to each individual tank due coral size and their influence on flow behind and around them. All race ways generated additional water flow with an CoralVue® IceCap - 4K Gyre Flow Pump and controlled by the Hydros app.

In general, the high flow treatments were in two close groups of corals, very near the two turbines of the gyre, while the low flow treatments were either in two groups far away from the gyre in the outdoor systems or one wide group at the furthest point from the gyre in the indoor systems. Each cell in Figure 1 represents an eggcrate grid of ~ 1cm. The first corals in the high flow groups were ~10 cm from the front of the gyre. The gyres were set to override flow pattern at max power with an output setting of 50-65% depending upon the system to achieve the two constant flow rates of 0.4 ± 0.1 m/s (hereafter referred to as the high treatment) and 0.1 ± 0.1 m/s (hereafter referred to as the low treatment) within the system. This was adjusted as needed as corals either grew to affect flow, or the equipment began to wear.

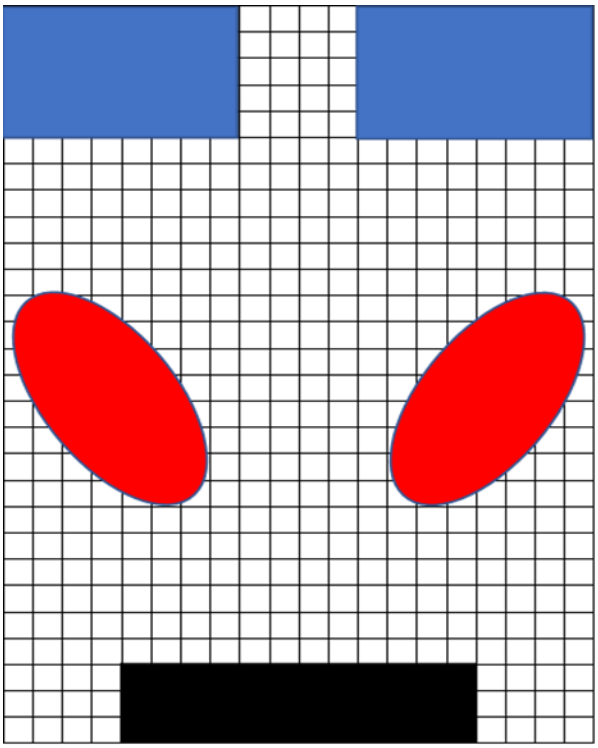


Figure 3. Red is the high flow rate and Blue is the low rate. Black is the Gyre, with two turbines.

All systems used artificial seawater of a salinity of 35 ±1 ppm measured with a Vee Gee® Scientific STX-3 Handheld Refractometer, made from Brightwell™ NeoMarine Salt Blend and reverse osmosis deionized water. Water temperature and salinity were checked daily, using a YSI ProPlus Polarographic DO pH Quatro 4 Meter. weekly for ammonia (0 mg/L), nitrate (0-0.2 mg/L), nitrite (0-0.02 mg/L), phosphate (<0.2 mg/L), using a Hach® DR 900 Multiparameter Portable Colorimeter, alkalinity (~140 ppm), and calcium (~440 ppm), and monthly for

magnesium (~1500 pm), using Hanna Instruments® Checkers. Light levels were measured weekly with an Apogee® MQ-510 Underwater Full-Spectrum Quantum PAR Meter and all parameters were recorded and tracked to assure water quality.

Coral Husbandry

Corals were fed four times a week using a mixture of live rotifers enriched with Rotigrow Plus® algae approximately one hour before being fed to the corals, Reef Nutrition® Oyster Feast, Reef Nutrition ® Real Oceanic Eggs, Brightwell Aquatics™ CoralAminos, Polyp Lab® ReefRoids, Aquatic Foods Inc. Golden Pearls, American Marine Inc Selcon^{TM} and Bene-pets ® Bene-Reef. During the feeding period, the water flow was turned off for 30-60 minutes and the corals were spot fed using a turkey baster. Once a week the corals, the tanks, and their ceramic plugs were cleaned to remove algae and a 15-25% water change was performed to maintain water quality parameters.

Tank and Water Flow Rate Treatment Assignment

Coral juveniles used in this experiment were produced during the 2020 spawning season and have been growing in recirculating aquaculture systems since settlement. Forty *Montastraea cavernosa* juveniles, 32 *Diploria labyrinthiformis* juveniles, and 32 *Colpophyllia natans* juveniles were randomly distributed into 4 groups: two groups in the indoor raceways and two groups in the two outdoor RASs. Within each system, the juveniles were further divided and randomly assigned treatment groups of either a flow rate of 0.1 ±0.1 ms^{-1} (Low flow) or 0.4±0.1 ms^{-1} (High Flow). Each group contained five *M. cavernosa*, four *C. natans* and four *D. labyrinthiformis*, for a total of 13 per treatment group. Each coral will be attached to a ceramic frag plug from Ocean Wonders and labelled on the bottom with the species (M, C or D), the coral number (1-40 for *M. cavernosa*, 1-32 for both *C. natans* and *D. labyrinthiformis*) and the treatment (H for the high rate and L for the lower). Maps of each tank and coral position were generated to ensure corals (see Figure 4 for example map) remain in the same position for the duration of the experiment and each coral was spaced to limit species competition/interactions. These coral species were chosen because they were historically common on the reefs of Southeastern Florida and have been severely affected by pollution, and stony coral tissue disease, making them corals of interest for reef restoration.

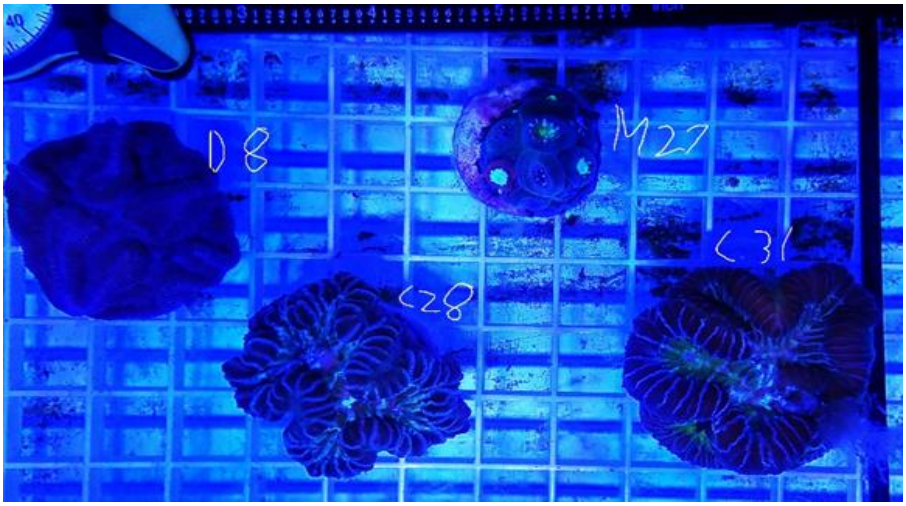


Figure 4 Example of a Coral ID map

Data Collection and Analysis

The flow rate was measured every other week using a Xylem Inc. FP111 Digital Handheld Water Velocity Meter, with an accuracy of ± 0.1 m/s before, during and after the placement of the coral juveniles to ensure treatment conditions are maintained. A basic flow map was created as shown above in Figure 1. When rates were not correct, the output profile of the gyres was adjusted. Corals were photographed every two weeks, using an Olympus camera with a ruler attached for calibration, with photos taken at 30 cm from the coral. Growth was assessed by measuring the coral surface area of the corals in the photos using ImageJ and the attached ruler. The experiment was run for 6 months (6/9/22-12/8/22), for a total of 12 data points for each coral, 480 points for *M. cavernosa*, and 384 for *C. natans* and *D. labyrinthiformis* respectively. The effect of water flow rate, tank location (light source), and the species of coral on growth will be analyzed using a GAMM (Generalized Additive Mixed Model), where tank location (light source), water flow rate, and coral species will be fixed categorical predictors, time is a continuous predictor, with tank and individual coral ID number will be random categorical predictors. A Cox model survival analysis was also conducted, using the survival differential function, due to one treatment having no events. All data analysis was conducted using the R studios software program.

Results

Survival Analysis

Fourteen of the 104 coral juveniles used in this study did not survive, specifically 2 *C. natans*, 3 *M. cavernosa*, and 9 *D. labyrinthiformis*. These were all corals placed into the high water flow treatment (0.4 ± 0.1m/s). The parts of the coral that faced the flow would first exhibit strong polyp retraction. As the experiment progressed, the tissue would begin to recede into the skeleton, towards the mouth of the polyps, eventually leading to the death of the polyp. The exposed skeleton was then often colonized by algae that needed to be removed, as depicted in Figure 5 and 6 with a *D. labyrinthiformis* on Day 0 and Day 70.

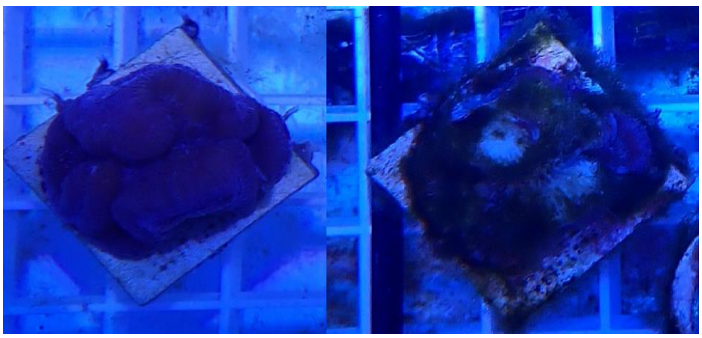


Figure 5 & 6 D. labyrinthiformis on Day 0 and Day 70

The tissue loss would often continue to the other side of the coral that was not directly in the flow and could lead to the total loss of the coral juvenile. While most corals in the high water flow treatment survived, those that did nearly always experienced a net decrease in the total live tissue of the coral recruit or negligible growth. The corals exposed to the low water flow had no mortality and on average increased their surface area. They also required far less cleaning due to algae not having areas to colonize and grow on. The tissue loss in the high flow treatment seemed to stem primarily from the corals being irritated by the pressure from the water. These species' polyps and tissue are normally very extended in captivity, so the additional flow causes the tissue to be injured on the corals' own skeletons. This leads to wounds and eventually tissue death. Survival significantly differed between coral species ($p=0.0109$) and with water flow rate ($p=2\times10^{-8}$), while there was no significant difference between indoor and outdoor systems ($p=0.0958$). (Figure 7)

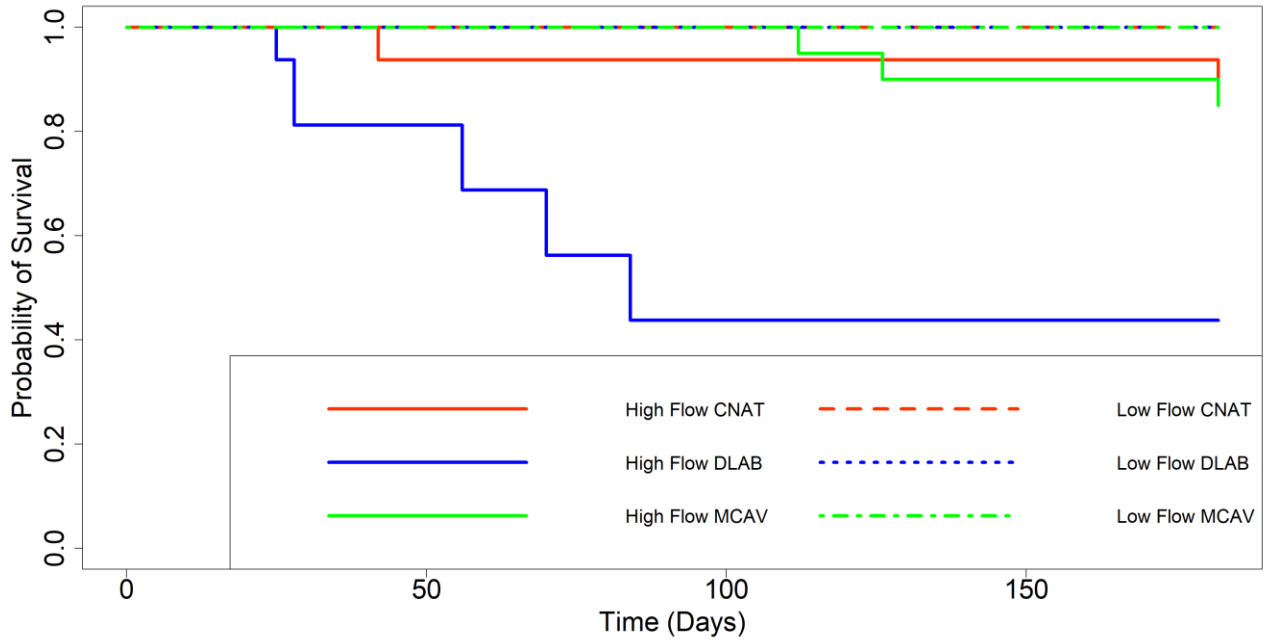


Figure 7 Probability of Survival over Time (Days) by Species

Growth

During the experiment, the effects of the water flow treatment ($p=1.91\times10^{-8}$), coral species ($p=1.34\times10^{-8}$), and time ($p<2\times10^{-16}$) on the growth of juveniles were all found to be significant. (Figures 9-12). However, dissimilar growth was also significantly explained by individual differences between corals. ($p<2\times10^{-16}$). The effect of tank location (light source type) and the random effect of assigned tank were found to be colinear and were not significant ($p=0.978$), and there were no significant interactions. Together, water flow treatment, coral species and the random effect of individual coral explained 93.4% of the variation in growth observed ($R^2=0.934$). The average high water flow treatment corals experienced a loss in total live surface area (Figures 8-11). The recruits that experienced the low water flow on average experienced a positive increase in total surface area. *Diploria labyrinthiformis* were the most negatively affected by the high water flow followed by the *Colpophyllia natans* then *Montastraea cavernosa*. In the low flow treatments, the *M. cavernosa* had the highest growth rate. The average monthly growth rate for *C. natans, D. labyrinthiformis* and *M. cavernosa* was 0.3944 cm^2, 0.1684 cm^2, and 0.5888 cm^2 respectively. Tables 1 & 2 show visual results for each species and flow treatment.

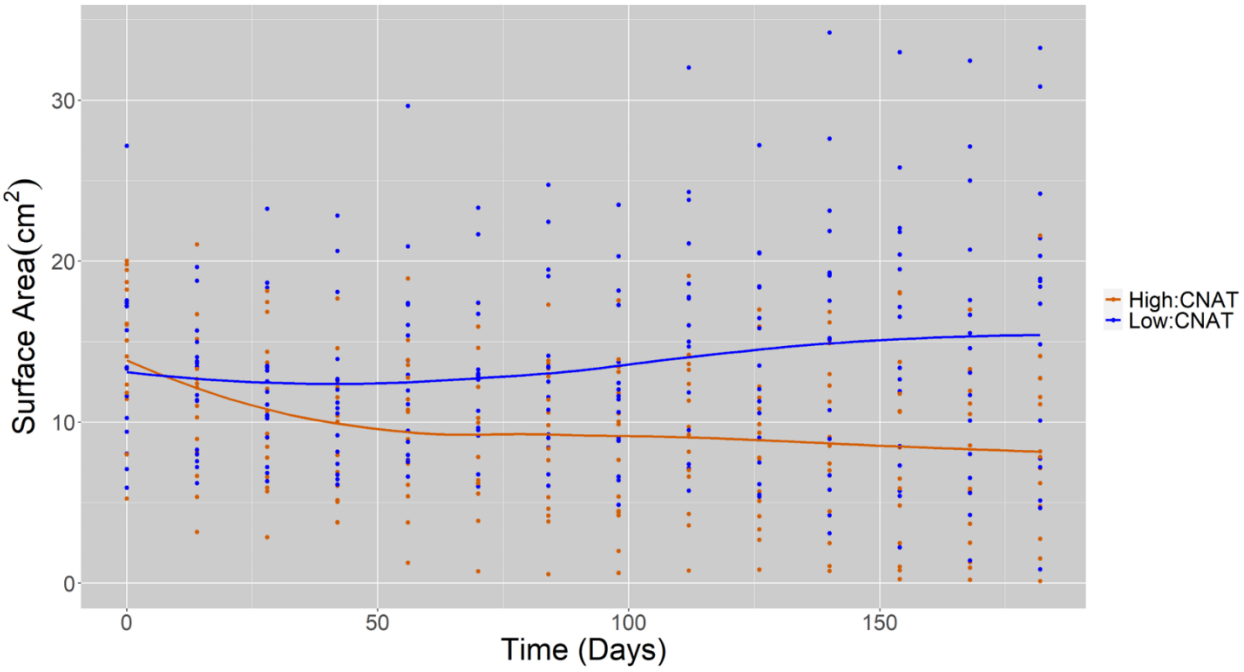


Figure 8. Surface area of C. natans over time by Water Flow Rate. The line is the line of best fit and the points are observations.

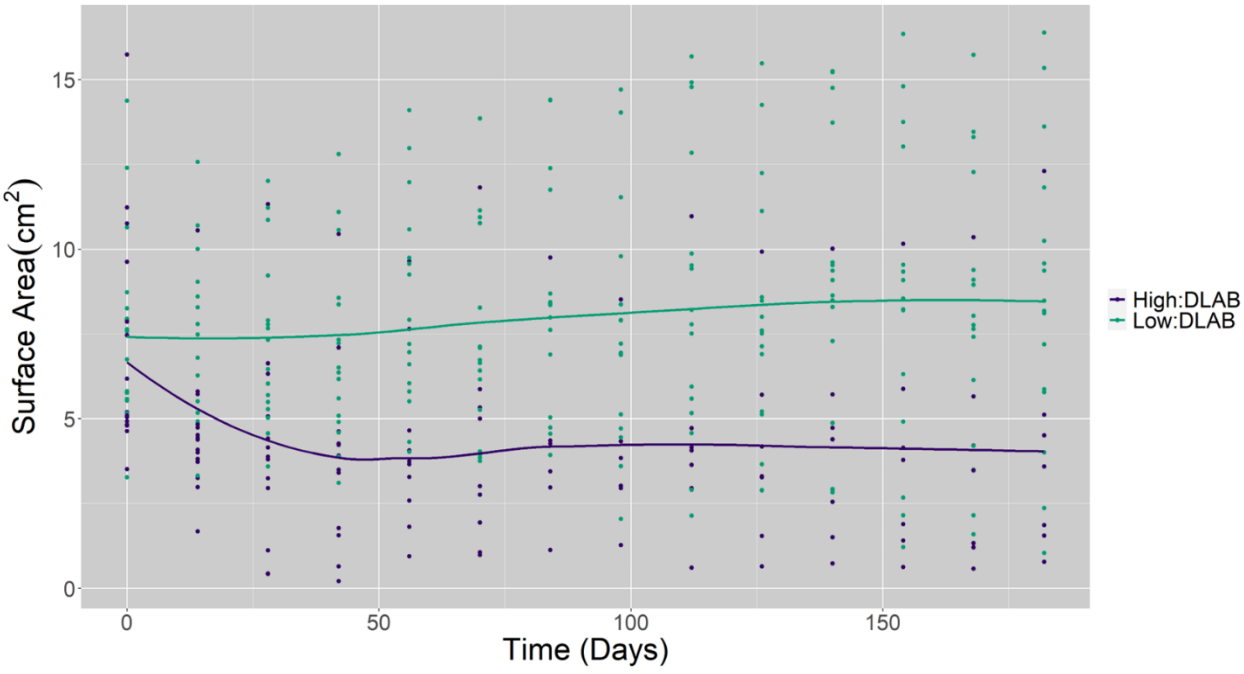


Figure 9. Surface Area of D. labyrinthiformis over time by Water Flow Rate. The line is the line of best fit and the points are observations.

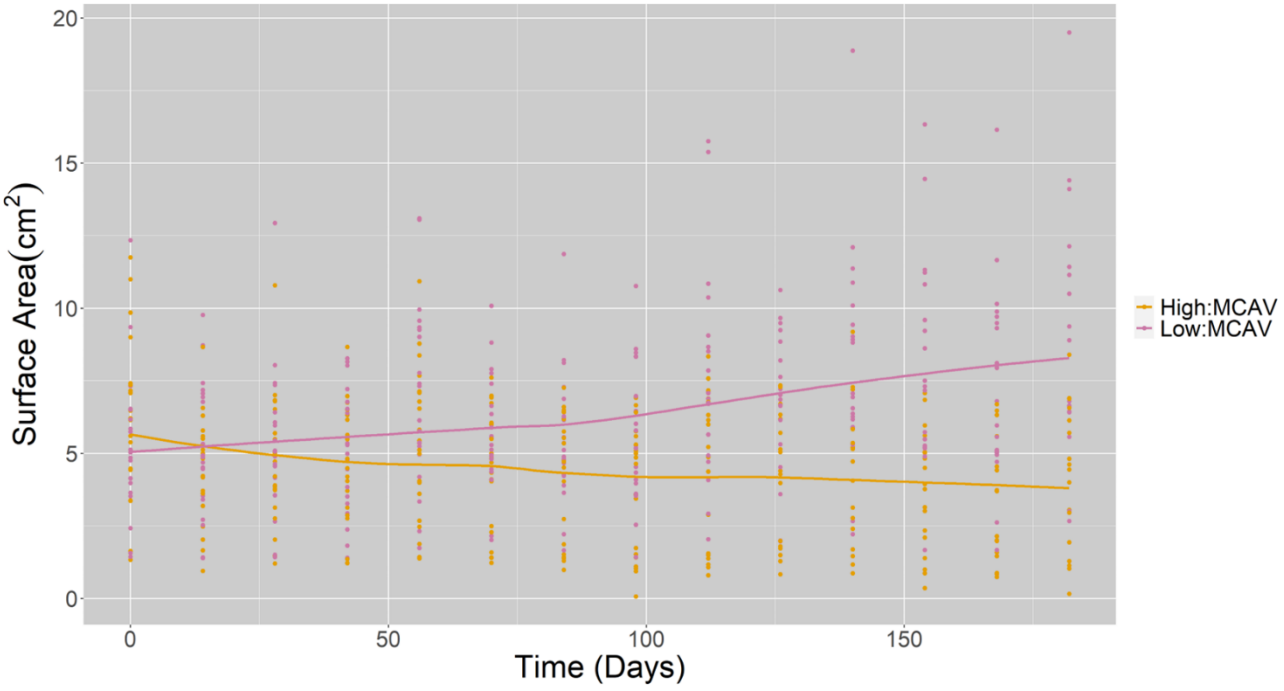


Figure 10. Surface area of M. cavernosa over time by Water Flow Rate. The line is the line of best fit and the points are observations.

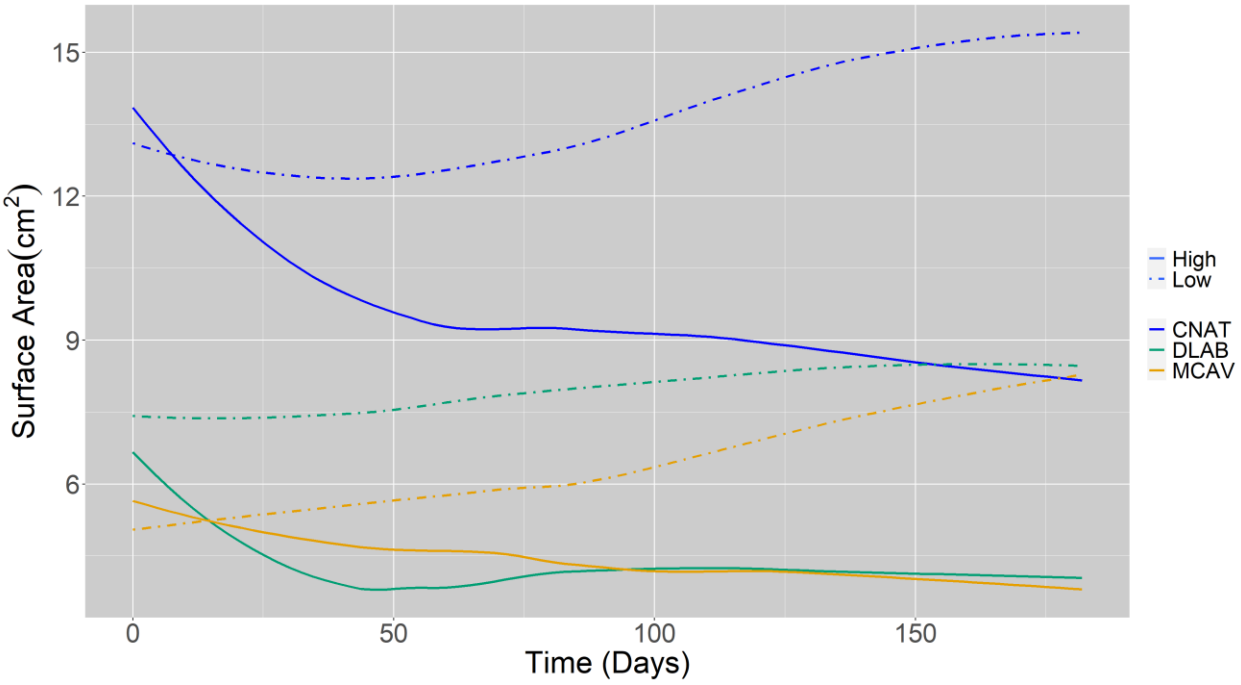


Figure 11. Surface area over time by coral species (CNAT=C. natans, MCAV=M. cavernosa DLAB= D. labyrinthiformis) and Water Flow Rate, High being solid and Low dashed. The lines are lines of best fit.

Table 1. All coral species in Low Water Flow over Time

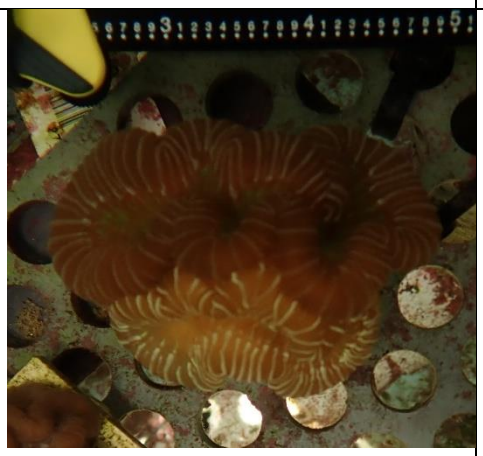
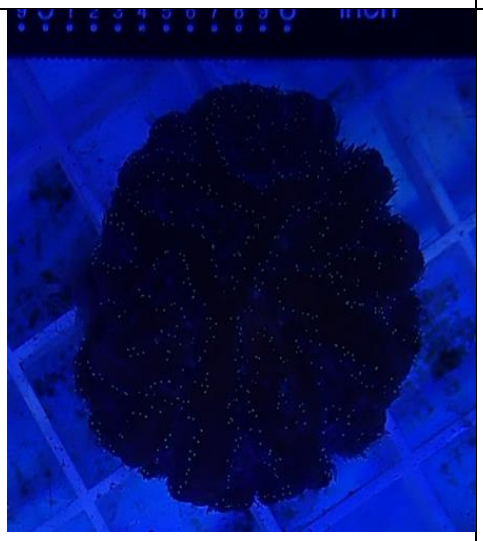
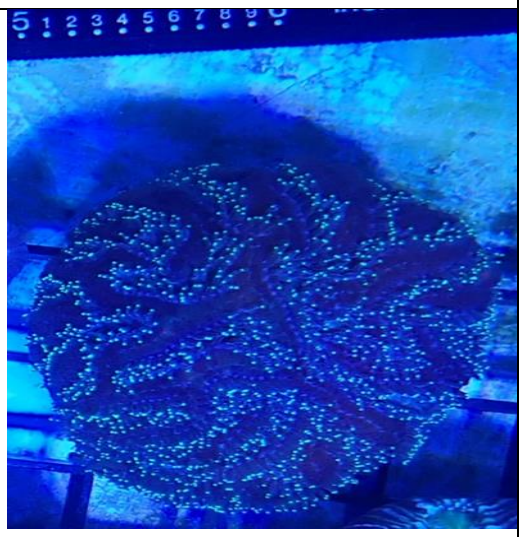
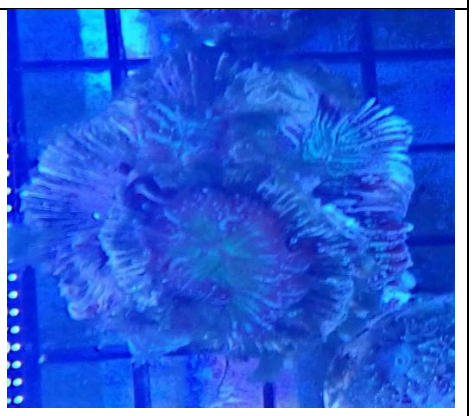
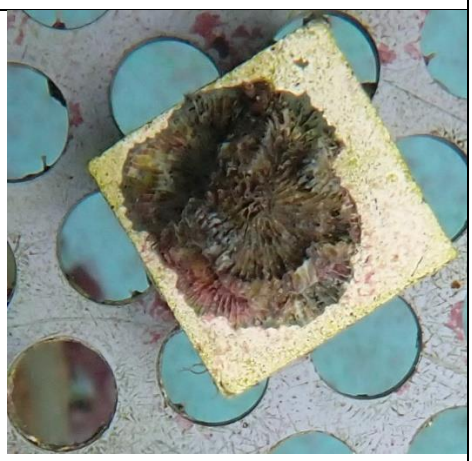
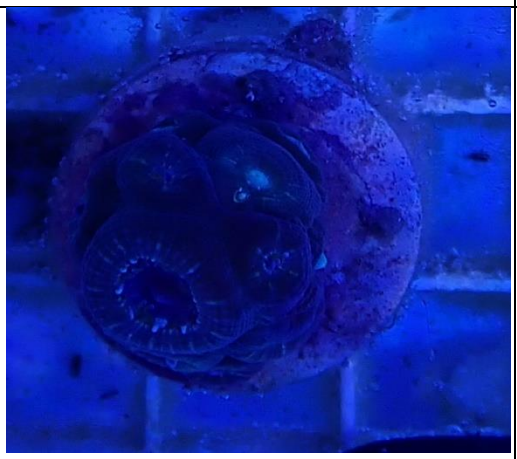
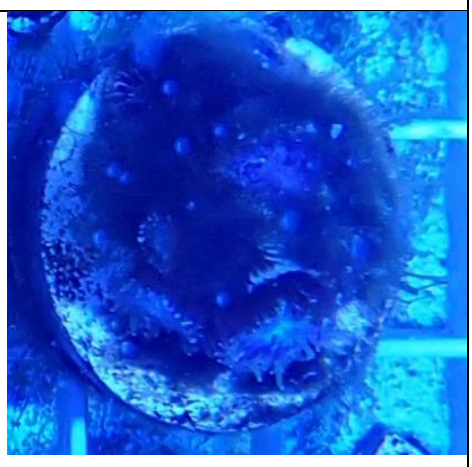
Time	Day 0	Day 182
Low Flow ***C.natans***		
Low flow ***D. labyrinhiformis***		
Low Flow ***M. cavernosa***		

Table 2 All coral species in High Flow treatments over Time

Time	**Day 0**	**Day 182**
High Flow *C. natans*		
High Flow *D. labyrinthiformis*		
High Flow *M. cavernosa*		

Discussion

Colpophyllia natans, Diploria labyrinthiformis, and *Montastraea cavernosa* juveniles had increased survival and growth when raised in a low water flow (0.1 ± 0.1m/s) compared to a high water flow rate (0.4 ±0.1m/s). Survival and growth differed between species with *D. labyrinthiformis* having the lowest survival in high flow and *M. cavernosa* having the highest average growth rate. The tank location (indoor vs. outdoor with artificial vs. natural light) and assigned tank had no effect on growth or survival, suggesting either practice as viable options.

The difference in survival between corals in high and the low water flow stems from the physical injury that the increased flow caused and its consequences. By first retracting their polyps constantly, the corals lost substantial surface area for photosynthesis and were unable to effectively capture prey, leading to reduced energy for recovery and growth. While some water flow is necessary to bring prey items to the coral (Sebens et al., 1998), the high water flow rate irritated, and then inured them. These injured areas can act as entry points for disease and infection (Page & Willis, 2007). In a study on *Orbicella faveolata* and black band disease, it was found that when exposed to infectious bacteria, fragments that had active or recent injuries were infected 100% of the time while uninjured fragments of the same coral were not (Aeby & Santavy, 2006). Other widespread coral diseases, such as skeletal eroding band, also have much higher colonization rates on coral injuries (Paige & Willis, 2007).

The flow induced injuries were also rapidly colonized by algae which may have further impeded survival and growth. Algae mitigation is already one of the most time-consuming tasks of coral aquaculture, thus an increase in the amount required to manually remove algae is not best practice. Even if the tissue loss halts and the coral survives, the algae can still cause abrasions in the coral tissue, shade of the coral, potentially release allotropic chemicals and metabolites that attract corallivores, affect the microbial community of the coral and act as vectors for disease (Venera-Ponton et al., 2011 ,Sweet et al., 2013). Algae also have the ability to act as a safe harbor and transmitter of diseases, thus are a serious concern for the long-term health of corals reared in captivity. In a study on *Acropora muricata* exhibiting signs of white syndrome and *O. faveolata* with yellow band disease, samples of surrounding algal colonies revealed that both algae composition and the microbial communities differed significantly between the healthy and unhealthy corals, and that several of the species of algae present

harbored both potential infectious bacteria for both diseases and ciliates that can act as disease vectors (Sweet et al., 2013). After two weeks of exposure to *Halimeda opuntia*, a common Caribbean macroalgae, 55% of adult colonies of *O. faveolata* were infected with white plague type II and none of the healthy, algae free corals developed the infection (Nugues et al., 2004). Even when coral and algae are not in direct contact, the coral can still suffer, e.g. *Pocillopora verrucosa* coral separated from the green alga *Dictyosphaeria cavernosa* by a 0.02µm mesh still exhibited 100% mortality within 2 days from bacterial infection; however, coral fragments that were treated with the antibiotic ampicillin had a survival rate of 100% (Smith et al., 2006). All three studies demonstrate the importance of manual algal removal and algal growth prevention. Competition with algae can also lead to reduced tissue thickness and zooxanthellae concentration within the corals. Competition with mixed turf algae leads *O. faveolata* to lose zooxanthellae and chlorophyll α density and loss of tissue area and volume (Quan-Young & Espinoza-Avalos, 2006). In summary, induced injuries and subsequent algal colonization, demonstrating that this elevated flow rate was detrimental to the survival of the coral juveniles.

Growth was faster under low water flow. The corals that were under the high water flow survived although, were still injured. Recovering from injury likely diverted energy away from growth; in contrast, corals in the low water flow treatment could direct energy towards growth. Many corals can change their energy allocation to adapt to environmental stressors or conditions for growth, recovery, or reproduction (Ward, 1995, Rinkevich, 1996). Without this energy drain, the low flow corals grew considerably over the course of the experiment, some nearly doubling in size (Figures 8-11). Some amount of water flow is always required to have healthy growth. Without adequate flow, disease and bleaching events can be exacerbated by lack of oxygen exchange as it often a limiting factor (Finelli et al., 2005; Nelson & Altieri, 2019). Water flow also brings in nutrients from off the reefs and food for the corals to use (Leichter et al., 2003). However, a low water flow rate (0.1m/s) seems to be more beneficial to the culture of juvenile corals. The average monthly growth rate for *C. natans, D. labyrinthiformis* and *M. cavernosa* was 0.3944 cm^2, 0.1684 cm^2, and 0.5888 cm^2 respectively. However, the observed growth rates differ from what has been observed in the field. A study of *C. natans*, *D. labyrinthiformis* and *M. cavernosa* among other species found that between 6 sites off the coast of northern Jamaica between 2000 and 2008 that the average radial growth rate over the course of a year for these species was 6.34 ± 3.1667 mm for *C. natans*, 4.3267 ±1.5267 mm for *D. labyrinthiformis* and

6.45 ±1.3833 mm for *M. cavernosa* (Crabbe, 2009). In order to more accurately compare these rates to my results, I assumed outward growth would be a circular pattern, then extrapolated the surface area increase from the radial increase per year by converting millimeters to centimeters, squaring the radii then multiplying by pi. This generates monthly surface area growth rates of 0.052615 ±0.01313 cm^2 for *C. natans*, 0.024505 ±0.00305 cm^2 for *D. labyrinthiformis* and 0.054458 ±0.002505cm^2 for *M. cavernosa*. This is only an approximation and is likely not the true rate but is still useful for comparison. These rates are significantly slower than what was observed in this experiment. However, the only the starting size of the *C. natans* was similar to this experiment, with the other two species starting at larger sizes in the Crabbe study. Smaller coral individuals tend to have a faster relative growth rate due to their smaller size and this may explain the difference. Another study on coral recruits settled in artificial substrate and outplanted showed a growth rate for *C. natans* recruits of 1.7 mm in diameter per month or 0.022698 cm^2 every month with the same previous mathematical assumptions (Van Moorsel, 1988). Again, the starting sizes are significantly different as is the age as these corals were recruits and up to under 2 years old and those used in my experiment were 2 years or older. Similar studies were conducted on *D. labyrinthiformis* and found growth rates of 4.68, 3.18 2.98 and 3.5 mm/year radially (Logan et al.,1994). This is still much slower than the observed rate in my experiment. This large gap may be due to the more stable conditions in aquaria and the increase quantity and quality of food, the lack of predation, disease and other stressors, leaving more energy for growth or may simply demonstrate how growth rates vary over a corals life span naturally, regardless of conditions. In either case, corals in properly maintained *ex situ* nurseries seem to grow faster.

The effect of water flow on survival and growth varied between coral species, likely due to their different morphologies and natural conditions (habitats) they are adapted to. *Diploria labyrinthiformis* is the least fleshy of the three species studied, which seemed to make them more susceptible to fast waterflow. This species was more frequently injured and would quickly lose more tissue coverage due to its thinness, leading to a higher mortality. Differences in growth between species in the low flow treatment may also be due to morphology. Surface area of the juvenile was used as the growth metric and *Colpophyllia natans* naturally has large fleshy polyps compared to the other species. This may have skewed the data to show more growth as it is easier to grow tissue than it is skeleton. *D. labyrinthiformis* had the slowest growth and it has the

most skeleton to tissue ratio. This may be just how these species naturally grow and increase their skeleton over time. However, in this study, the coral experienced chronic, constant, and unidirectional flow. This would seldom, if ever occur naturally on a reef. The natural tides at least twice a day would cause the general direction of the flow to change as well as its speed. Weather conditions, temperature, the shape of the reef and other factors would cause the rate of the water flow to change. It has been shown that the natural cycle of high and low flow due to tides can have benefits in mitigation photoinhibition during high temperature events (Smith & Birkeland, 2007). I chose these constant rates due to limitations of space and available equipment but the effects of fluctuating, multi directional flow is an area of study that should be pursued more thoroughly to find the true optimal conditions for coral aquaculture. It may be that surging up to the high rate water flow rates is fine for those short time windows of peak flow during tides or storms as long as it returns to a lower rate, but further study is required.

Differences in survival and growth between species under different water flows could possibly also reflect the habitat (location of the reef and its hydrodynamics) they are adapted to. Each treatment rate used in the study was based on water flow rates found on different parts of the reef structure. Reef crests or fore reefs at 3m depth have an average water flow of 0.4 ± 0.1m/s, which was used for the high flow rate treatment. The low flow rate of 0.1 ± 0.1 m/s, mimicked the deeper (9m) reef slope or back reef zone (Adey & Steneck 2003, Johansen, 2014). The fact that these species occupy different niches within the reef may explain why they settle, grow, and survive where they do. In the Florida Reef Tract, *Acropora palmata* are typically found on the reef crest while the patch reefs are dominated by *A. cervicornis* and *M. annularis. Colpophyllia natans* is commonly found on mid channel and offshore patch reefs, *D. labyrinthiformis* is most common on mid channel and inshore/offshore patch reefs and *M. cavernosa* is most common in the ridge complex of reefs and in the mid channel reefs (Graus & Macintyre, 1989, Burman et al., 2012). These patch reef locations experience the same lower flow rate as chosen of 0.1 ±0.1 m/s (Jones, 1964). However, these areas never experience constant flow rates. Naturally the water flow conditions fluctuate due to tides, weather, temperature, and other factors, limiting how much can be inferred about natural distribution due to water flow from this experiment. Further studies involving fluctuations in water flow and transplantation onto parts of the reef with high and low water flow, such as crests, back and fore reef slopes, would be required to definitely state that the water flow is a leading cause.

The most surprising result of this experiment was that the light source type had no effect on the survival and growth rates. Both coral indoors and outdoors were exposed to roughly the same Photosynthetically Active Radiation (PAR), ~150- 250 µMol/m^2s, the only difference was the spectra of artificial light (LEDs) versus natural sunlight. This may mean that the light spectrum programed and produced by the LEDs is now accurate enough to imitate natural sunlight at reef depth very closely to the point where they are essentially the same. However, those in the outdoor systems received the spectrum of the surface waters, as they were only a few centimeters below the surface rather than meters, where these coral species naturally occur. This may mean that at least at this stage of their life cycle that PAR is more important than spectrum, provided it is close enough to natural conditions. This may simply be a result of improving technology that has closed the gap with what nature produces. However, there have been many other studies on other species and the effects of artificial versus natural lighting sources with different results. One study on *A. cervicornis* compared LEDs and natural light and found that coral had higher calcification rates under LEDs than natural sunlight, but lower photosynthetic efficiency (Slagel et al., 2021). Several studies found that different light intensities and spectrums greatly affect growth rates over time, but could be species specific (Schlacher et al., 2007, Schutter et al., 2008). As the technology improves, it may simply become a choice of what is available and what is more cost effective when deciding what light source to use when aquaculturing these species. However, more in depth studies looking at growth, photosynthetic efficiency, skeletal structure, species specific needs, and other parameters are needed.

To effectively restore corals reefs, both physically and genetically, coral sexual propagation must be optimized and tailored to the individual species of interest. By doing so, corals can be produced more reliably, more cost effectively and in the larger numbers required. In this study, by experimenting with the effects of light source type (indoor vs. outdoor) and water flow rate on three key reef building coral species, I have demonstrated that there is room for improvement in current aquaculture methods. In specific regard to the three species of coral recruits used, *Montastraea cavernosa, Diploria labyrinthiformis* and *Colpophyllia natans,* I conclude that there is no benefit in adding additional water flow above the rate of 0.1± 0.1m/s. In fact, water flow above this rate is detrimental to the health, survival, and growth of the coral recruit. I also recommend that for these species, as long as the light spectra and irradiance mimic the area the species are native to, there is no significant advantage between using natural sunlight

through a shade cloth and artificial lights produced by LEDs. The decision to rear corals indoors or outdoors can instead depend on the cost of indoor vs. outdoors equipment (and the frequency these need to be replaced) and suitability or the nursey location.

References

Adey, W. H., & Steneck, R. S. (2003). Highly productive eastern caribbean reefs: Synergistic effects of biological, chemical, physical, and geological factors. *NOAA Symp.Ser.for Undersea Research, 3,* , 167–187. https://doi.org/10.1007/springerreference_205799

Aeby, G. S., & Santavy, D. L. (2006). Factors affecting susceptibility of the coral Montastraea faveolata to black-band disease. *Marine Ecology Progress Series*, *318*, 103–110. https://doi.org/10.3354/meps318103

Blackall, L. L., Wilson, B., & van Oppen, M. J. (2015). Coral-the world's most diverse symbiotic ecosystem. *Molecular Ecology*, *24*(21), 5330–5347. https://doi.org/10.1111/mec.13400

Boström-Einarsson, L., Babcock, R. C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S. C., Hancock, B., Harrison, P., Hein, M., Shaver, E., Smith, A., Suggett, D., Stewart-Sinclair, P. J., Vardi, T., & McLeod, I. M. (2020). Coral restoration – a systematic review of current methods, successes, failures and future directions. *PLOS ONE*, *15*(1). https://doi.org/10.1371/journal.pone.0226631

Bowden-Kerby, A. (2001). Low-tech coral reef restoration methods modeled after natural fragmentation processes. *Bulletin of Marine Science*, *69*(2), 915–931. Retrieved May 6, 2022, from https://www.ingentaconnect.com/content/umrsmas/bullmar/2001/00000069/00000002/art00052.

Brander, L., & Beukering, P. van. (2013, January). *The total economic value of U.S. coral reefs: A review of the literature*. NOAA Institutional Repository. Retrieved April 28, 2022, from https://repository.library.noaa.gov/view/noaa/8951

Burman, S. G., Aronson, R. B., & van Woesik, R. (2012). Biotic homogenization of coral assemblages along the Florida Reef Tract. *Marine Ecology Progress Series*, *467*, 89–96. https://doi.org/10.3354/meps09950

Chindapol, N., Kaandorp, J. A., Cronemberger, C., Mass, T., & Genin, A. (2013). Modelling growth and form of the scleractinian coral *Pocillopora verrucosa* and the influence of hydrodynamics. *PLoS Computational Biology*, *9*(1). https://doi.org/10.1371/journal.pcbi.1002849

Comeau, S., Edmunds, P. J., Lantz, C. A., & Carpenter, R. C. (2014). Water flow modulates the response of coral reef communities to ocean acidification. *Scientific Reports*, *4*(1). https://doi.org/10.1038/srep06681

Crabbe, M. J. C. (2009). Scleractinian coral population size structures and growth rates indicate coral resilience on the fringing reefs of North Jamaica. *Marine Environmental Research*, *67*(4–5), 189–198. https://doi.org/10.1016/j.marenvres.2009.01.003

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*, *7*(24), 11066–11078. https://doi.org/10.1002/ece3.3538

Davis, K. A., Pawlak, G., & Monismith, S. G. (2021). Turbulence and coral reefs. *Annual Review of Marine Science*, *13*(1), 343–373. https://doi.org/10.1146/annurev-marine-042120-071823

Doropoulos, C., Elzinga, J., ter Hofstede, R., van Koningsveld, M., & Babcock, R. C. (2019). Optimizing industrial-scale coral reef restoration: Comparing harvesting wild coral spawn slicks and transplanting gravid adult colonies. *Restoration Ecology*, *27*(4), 758–767. https://doi.org/10.1111/rec.12918

Douglas, A. E. (2003). Coral bleaching—how and why? *Marine Pollution Bulletin*, *46*(4), 385–392. https://doi.org/10.1016/s0025-326x(03)00037-7

Estrada-Saldívar, N., Molina-Hernández, A., Pérez-Cervantes, E., Medellín-Maldonado, F., González-Barrios, F. J., & Alvarez-Filip, L. (2020). Reef-scale impacts of the stony coral tissue loss disease outbreak. *Coral Reefs*, *39*(4), 861–866. https://doi.org/10.1007/s00338-020-01949-z

Finelli, C. M., Helmuth, B. S., Pentcheff, N. D., & Wethey, D. S. (2005). Water flow influences oxygen transport and photosynthetic efficiency in corals. *Coral Reefs*, *25*(1), 47–57. https://doi.org/10.1007/s00338-005-0055-8

Fisher, R., Bessell-Browne, P., & Jones, R. (2019). Synergistic and antagonistic impacts of suspended sediments and thermal stress on corals. *Nature Communications*, *10*(1). https://doi.org/10.1038/s41467-019-10288-9

Fisher, R., O'Leary, R. A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R. E., & Caley, M. J. (2015). Species richness on coral reefs and the pursuit of convergent global estimates. *Current Biology*, *25*(4), 500–505. https://doi.org/10.1016/j.cub.2014.12.022

Fitt, W., Brown, B., Warner, M., & Dunne, R. (2001). Coral bleaching: Interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs*, *20*(1), 51–65. https://doi.org/10.1007/s003380100146

Frieler, K., Meinshausen, M., Golly, A., Mengel, M., Lebek, K., Donner, S. D., & Hoegh-Guldberg, O. (2012). Limiting global warming to 2 °C is unlikely to save most coral reefs. *Nature Climate Change*, *3*(2), 165–170. https://doi.org/10.1038/nclimate1674

Garrison, V. H., & Ward, G. (2012). Transplantation of storm-generated coral fragments to enhance Caribbean coral reefs: A successful method but not a solution. *Revista De Biología Tropical*, *60*, 59. https://doi.org/10.15517/rbt.v60i0.19845

Gattuso, Jean-Pierre, Allemand, Denis, & Frankignoulle, Michel. (1999). Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on

interactions and control by carbonate chemistry. *American Zoologist*, *39*(1), 160–183. https://doi.org/10.1093/icb/39.1.160

Graus, R. R., & Macintyre, I. G. (1989). The zonation patterns of Caribbean coral reefs as controlled by wave and light energy input, bathymetric setting and reef morphology: computer simulation experiments. *Coral Reefs*, *8*(1), 9–18. https://doi.org/10.1007/bf00304687

Guest, J. R., Heyward, A., Omori, M., Iwao, K., Morse, A., & Boch, C. (2010). Rearing coral larvae for reef rehabilitation. In A. Edwards (Ed.), *Reef rehabilitation manual: Rearing coral larvae for reef rehabilitatio*n (pp. 73–98). Coral Reef Targeted Research & Capacity Building for Management Program

Hench, J. L., & Rosman, J. H. (2013). Observations of spatial flow patterns at the coral colony scale on a shallow reef flat. *Journal of Geophysical Research: Oceans*, *118*(3), 1142–1156. https://doi.org/10.1002/jgrc.20105

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., Baird, A. H., Baum, J. K., Berumen, M. L., Bridge, T. C., Claar, D. C., Eakin, C. M., Gilmour, J. P., Graham, N. A., Harrison, H., Hobbs, J.-P. A., Hoey, A. S., Hoogenboom, M., Lowe, R. J., … Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the anthropocene. *Science*, *359*(6371), 80–83. https://doi.org/10.1126/science.aan8048

Hughes, T. P., Ayre, D., & Connell, J. H. (1992). The evolutionary ecology of corals. *Trends in Ecology & Evolution*, *7*(9), 292–295. https://doi.org/10.1016/0169-5347(92)90225-z

Johansen, J. L. (2014). Quantifying water flow within aquatic ecosystems using load cell sensors: A profile of currents experienced by coral reef organisms around Lizard Island, Great Barrier Reef, Australia. *PLoS ONE*, *9*(1). https://doi.org/10.1371/journal.pone.0083240

Jones, J. A. (1964). Ecological studies of the southeastern Florida patch reefs. part I. Diurnal and seasonal changes in the environment. *Deep Sea Research and Oceanographic Abstracts*, *11*(3), 494. https://doi.org/10.1016/0011-7471(64)90581-9

Logan, A., Yang, L., & Tomascik, T. (1994). Linear skeletal extension rates in two species of diploria from high-latitude reefs in Bermuda. Coral Reefs, 13(4), 225–230. https://doi.org/10.1007/bf00303636

Leichter, J. J., Stewart, H. L., & Miller, S. L. (2003). Episodic nutrient transport to Florida coral reefs. *Limnology and Oceanography*, *48*(4), 1394–1407. https://doi.org/10.4319/lo.2003.48.4.1394

Mass, T., Brickner, I., Hendy, E., & Genin, A. (2011). Enduring physiological and reproductive benefits of enhanced flow for a stony coral. *Limnology and Oceanography*, *56*(6), 2176–2188. https://doi.org/10.4319/lo.2011.56.6.2176

Nakamura, T., & Yamasaki, H. (2005). Requirement of water-flow for sustainable growth of pocilloporid corals during high temperature periods. *Marine Pollution Bulletin*, *50*(10), 1115–1120. https://doi.org/10.1016/j.marpolbul.2005.06.025

Nakamura, T., van Woesik, R., & Yamasaki, H. (2005). Photoinhibition of photosynthesis is reduced by water flow in the reef-building coral *Acropora digitifera*. *Marine Ecology Progress Series*, *301*, 109–118. https://doi.org/10.3354/meps301109

Nelson, H. R., & Altieri, A. H. (2019). Oxygen: The universal currency on coral reefs. *Coral Reefs*, *38*(2), 177–198. https://doi.org/10.1007/s00338-019-01765-0

Nugues, M. M., Smith, G. W., Hooidonk, R. J., Seabra, M. I., & Bak, R. P. (2004). Algal contact as a trigger for coral disease. *Ecology Letters*, *7*(10), 919–923. https://doi.org/10.1111/j.1461-0248.2004.00651.x

Page, C. A., & Willis, B. L. (2007). Epidemiology of skeletal eroding band on the Great Barrier Reef and the role of injury in the initiation of this widespread coral disease. *Coral Reefs*, *27*(2), 257–272. https://doi.org/10.1007/s00338-007-0317-8

Quan-Young, L. I., & Espinoza-Avalos, J. (2006). Reduction of zooxanthellae density, chlorophyll a concentration, and tissue thickness of the coral *Montastraea faveolata* (Scleractinia) when competing with mixed turf algae. *Limnology and Oceanography*, 51(2), 1159–1166. https://doi.org/10.4319/lo.2006.51.2.1159

Rada-Osorio, D., Gómez-Lemos, L. A., & García-Urueña, R. (2022). Early development of the threatened coral *Acropora cervicornis*. *Hydrobiologia*, *849*(11), 2477–2486.

Rinkevich, B. (1996). Do reproduction and regeneration in damaged corals compete for energy allocation? *Marine Ecology Progress Series*, 143, 297–302. https://doi.org/10.3354/meps143297 https://doi.org/10.1007/s10750-022-04838-4

Rocha, R. J. M., Pimentel, T., Serôdio, J., Rosa, R., & Calado, R. (2013). Comparative performance of light emitting plasma (LEP) and light emitting diode (LED) in ex situ aquaculture of scleractinian corals. *Aquaculture*, *402-403*, 38–45. https://doi.org/10.1016/j.aquaculture.2013.03.028

Ruiz-Moreno, D., Willis, B. L., Page, A. C., Weil, E., Cróquer, A., Vargas-Angel, B., Jordan-Garza, A. G., Jordán-Dahlgren, E., Raymundo, L., & Harvell, C. D. (2012). Global coral disease prevalence associated with sea temperature anomalies and local factors. *Diseases of Aquatic Organisms*, *100*(3), 249–261. https://doi.org/10.3354/dao02488

Schlacher, T. A., Stark, J., & Fischer, A. B. P. (2007). Evaluation of artificial light regimes and substrate types for aquaria propagation of the staghorn coral *Acropora solitaryensis*. *Aquaculture*, *269*(1-4), 278–289. https://doi.org/10.1016/j.aquaculture.2007.04.085

Schutter, M., Crocker, J., Paijmans, A., Janse, M., Osinga, R., Verreth, A. J., & Wijffels, R. H. (2010). The effect of different flow regimes on the growth and metabolic rates of the scleractinian coral *Galaxea fascicularis*. *Coral Reefs*, *29*(3), 737–748. https://doi.org/10.1007/s00338-010-0617-2

Schutter, M., Kranenbarg, S., Wijffels, R. H., Verreth, J., & Osinga, R. (2011). Modification of light utilization for skeletal growth by water flow in the scleractinian coral *Galaxea fascicularis*. *Marine Biology*, 158(4), 769–777. https://doi.org/10.1007/s00227-010-1605-3

Schutter, M., van Velthoven, B., Janse, M., Osinga, R., Janssen, M., Wijffels, R., & Verreth, J. (2008). The effect of irradiance on long-term skeletal growth and net photosynthesis in *Galaxea fascicularis* under four light conditions. *Journal of Experimental Marine Biology and Ecology*, *367*(2), 75–80. https://doi.org/10.1016/j.jembe.2008.08.014

Sebens, K. P., Helmuth, B., Carrington, E., & Agius, B. (2003). Effects of water flow on growth and energetics of the scleractinian coral *Agaricia tenuifolia* in Belize. *Coral Reefs*, *22*(1), 35–47. https://doi.org/10.1007/s00338-003-0277-6

Sebens, K. P., Grace, S. P., Helmuth, B., Maney Jr., E. J., & Miles, J. S. (1998). Water flow and prey capture by three scleractinian corals, *Madracis mirabilis , Montastrea cavernosa and Porites porites* , in a field enclosure. *Marine Biology*, *131*(2), 347–360. https://doi.org/10.1007/s002270050328

Slagel, S., Lohr, K., O'Neil, K., & Patterson, J. (2021). Growth, calcification, and photobiology of the threatened coral *Acropora cervicornis* in natural versus artificial light. *Zoo Biology*, *40*(3), 201–207. https://doi.org/10.1002/zoo.21589

Smith, J. E., Shaw, M., Edwards, R. A., Obura, D., Pantos, O., Sala, E., Sandin, S. A., Smriga, S., Hatay, M., & Rohwer, F. L. (2006). Indirect effects of algae on coral: Algae-mediated, microbe-induced coral mortality. *Ecology Letters*, *9*(7), 835–845. https://doi.org/10.1111/j.1461-0248.2006.00937.x

Smith, L. W., & Birkeland, C. (2007). Effects of intermittent flow and irradiance level on back reef porites corals at elevated seawater temperatures. *Journal of Experimental Marine Biology and Ecology*, *341*(2), 282–294. https://doi.org/10.1016/j.jembe.2006.10.053

Souter, D., Planes, S., Wicquart, J., Logan, M., Obura, D., & Staub, F. (Eds.). (2022, February 25). *The sixth status of corals of the world: 2020 report*. Global Coral Reef Monitoring Network (GCRMN). Retrieved May 5, 2022, from https://gcrmn.net/2020-report/

Spalding, M., Burke, L., Wood, S. A., Ashpole, J., Hutchison, J., & zu Ermgassen, P. (2017). Mapping the global value and distribution of coral reef tourism. *Marine Policy*, *82*, 104–113. https://doi.org/10.1016/j.marpol.2017.05.014

Spalding M.D., Ravilious C., Green E.P. (2001). *Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project*.

(Version 4.1). UNEP-WCMC, WorldFish Centre, WRI, TNC. https://doi.org/10.34892/t2wk-5t34

Stanley, G. D. (2003). The evolution of modern corals and their early history. *Earth-Science Reviews*, *60*(3-4), 195–225. https://doi.org/10.1016/s0012-8252(02)00104-6

Stat, M., Carter, D., & Hoeghguldberg, O. (2006). The evolutionary history of symbiodinium and scleractinian hosts—symbiosis, diversity, and the effect of climate change. *Perspectives in Plant Ecology, Evolution and Systematics*, *8*(1), 23–43. https://doi.org/10.1016/j.ppees.2006.04.001

Sweet, M. J., Bythell, J. C., & Nugues, M. M. (2013). Algae as reservoirs for coral pathogens. *PLoS ONE*, *8*(7). https://doi.org/10.1371/journal.pone.0069717

Van Moorsel, G. W. N. M. (1988). Early maximum growth of stony corals (Scleractinia) after settlement on artificial substrata on a Caribbean Reef. *Marine Ecology Progress Series*, *50*, 127–135. https://doi.org/10.3354/meps050127

Venera-Ponton, D. E., Diaz-Pulido, G., McCook, L. J., & Rangel-Campo, A. (2011). Macroalgae reduce growth of juvenile corals but protect them from parrotfish damage. *Marine Ecology Progress Series*, *421*, 109–115. https://doi.org/10.3354/meps08869

Ward, S. (1995). Two patterns of energy allocation for growth, reproduction and lipid storage in the scleractinian coral *Pocillopora damicornis*. *Coral Reefs*, *14*(2), 87–90. https://doi.org/10.1007/bf00303428

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*. https://doi.org/10.3389/fmars.2018.00323

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. A. (2019). Coral Reef Ecosystem Services in the anthropocene. *Functional Ecology*. https://doi.org/10.1111/1365-2435.13331