12-10-2021

Optimizing the Time to Transfer Sexually Produced Corals of Porites Astreoides, Agaricia Agaricites, and Montastraea Cavernosa to an Offshore Nursery

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Thesis of
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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

December 2021

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By

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Abstract

As reefs continue to decline globally and become unable to recover on their own, restoration becomes essential to abate reef degradation and boost reef recovery until the main sources of the degradation are addressed. Sexual propagation is an important restoration technique that still requires optimization. One of the major knowledge gaps is determining the optimal time to transfer newly-settled sexually-produced corals from an aquarium to an offshore nursery without compromising their survival and growth. This study transferred settlers from *Porites astreoides, Agaricia agaricites,* and *Montastraea cavernosa* to an offshore nursery at approximately one week, five weeks, and nine weeks post-settlement, with a fourth group always remaining in the aquarium as a control, and found that settlers from all three species could be transferred offshore around 8-12 weeks post-settlement without compromising their survival and growth. At this time, corals were at a stage of development that may have offered many advantages that aided in their survival and growth, such as a fully established community of Symbiodinaceae, grown to a more competitive size, and had hit some developmental milestones. The novel method in which the tiles with the corals were attached to the nursery trees, i.e., the "kebabs", likely also played a role in their survival. The cost-benefit analysis performed, showed that the longer the corals remained *ex situ* the more they costed to rear for restoration. Moving corals offshore prior to the 8-12 weeks post-settlement timepoint is possible, and reduces the costs associated with rearing mass amounts of corals but has tradeoffs in survival and growth. Determining the optimal time at which to transfer corals offshore helps restoration practitioners deploy large batches of newly settled corals to an offshore nursery at an age that no longer compromises their survival and growth and may help the settlers to acclimate to local ocean conditions (e.g., acquire beneficial symbionts) from a very early age, potentially making them better suited to their environment.

Keywords: coral restoration, sexual propagation, grow-out, outplanting, cost-benefit analysis

Introduction

Coral reefs are one of the most diverse ecosystems in the world, estimated to impact nearly one-quarter of all marine species (Knowlton et al., 2010). However, coral reefs have been steadily declining for at least the past five decades due to a variety of global and local stressors, such as ocean warming, pollution, and overfishing, especially of herbivores (Pandolfi et al., 2003; Bellwood et al., 2004; Jackson et al., 2014). These stressors diminish the habitats of the corals, and the water quality around them, ultimately causing the corals to bleach and/or die (Hughes et al., 2003; Zaneveld et. al., 2016; Morrison et al., 2019). As coral colonies die, the remaining adult colonies become geographically distanced from one another and this separation serves as a barrier to sexual reproduction as it reduces the probability that viable gametes from individual colonies will meet and fertilize (Levitan & Petersen, 1995; Schmidt-Roach et al., 2020). Additionally, if the remaining adult corals are in a prolonged state of stress, they will preferentially allocate their energy towards survival instead of reproduction (Rodrigues & Grottoli, 2007). If so, this will reduce the production of gametes, and further reduce the chances of successful fertilization. As this happens, the Allee effect begins to emerge where the fitness of the species decreases due to the reduction in the number of offspring produced (Gascoigne & Lipcius, 2004). Without producing enough offspring to replace both the corals lost to anthropogenic stressors and natural causes, the reefs will continue to degrade (Richmond et al., 2018; Riegl et al., 2009; Richmond, 1997).

Due to the chronic nature of the stressors, many coral reefs have become unable to recover naturally (Goreau & Hilbertz, 2005) and are in need of restoration (Harriott & Fisk, 1989). While full recovery is not possible until the direct causes of the decline are addressed, coral restoration can boost reef recovery by increasing coral cover and genetic diversity (Goreau & Hilbertz, 2005; Rinkevich, 2005). Restoration can take advantage of the ability of corals to reproduce both asexually and sexually. Traditionally, restoration techniques have relied on asexual coral propagation where fragments are taken from existing healthy adult corals and then transferred to nurseries for grow-out or transplanted directly to the restoration site (Rinkevich, 1995; Guest et al., 2014; Lirman & Schopmeyer, 2016;). While fragmentation and transplantation can quickly increase coral biomass at a site, it is not a robust restoration technique, due to being limited by the amount of donor adult colonies and not contributing to increasing the genetic diversity; this is

especially true when local colonies are used as the donors, given that the fragments have the same genotypes as the colonies from which they were cut (Iwao et al., 2014; National Academies of Sciences, Engineering, and Medicine, 2019). More recently, sexual propagation has been introduced as a necessary and valuable technique for active restoration. Sexual propagation entails collecting coral gametes— whether in the field or from corals in aquaria— fertilizing the gametes, and rearing the larvae to competency (Rinkevich, 2005; Omori & Iwao, 2014). Once the larvae are competent, they can either be brought out to the reef and released in hopes that they will naturally recruit to the area (Nonaka et al., 2003; Omori & Iwao, 2014; dela Cruz & Harrison, 2017) or be settled onto tiles and grown *ex situ* until the settlers reach an age or size suitable to either be transferred to an offshore coral nursery or outplanted directly to the reef (Rinkevich, 2005; Guest et al., 2014; Omori & Iwao, 2014; Edwards et al., 2015). Sexual propagation is becoming a favored method since it does not require fragmentation of existing adult colonies, it produces large numbers of genetically diverse offspring, and the resulting higher genetic diversity from the addition of these corals can increase the resistance and persistence of the ecosystem (Guest et al., 2014; Iwao et al., 2014; Isbell et al., 2015; Baums et al., 2019).

Sexual propagation of corals *ex situ* has many advantages, but is expensive, laborious, as well as space and time-consuming (Edwards & Gomez, 2007; Edwards et al., 2010; Henry et al., 2019), and thus requires optimization. There have been considerable technical advances in coral husbandry and fertilization biology, from determining optimal sperm concentrations to increase fertilization success (Oliver & Babcock, 1992), to rearing and inducing larvae to settle *ex situ* (Marhaver et al., 2015; Chamberland et al., 2017), and to growing multiple species of adult corals in aquaria (Borneman & Lowrie, 2001; O'Neil, 2015). The most recent breakthrough in coral husbandry has been the creation of an aquarium setup that induces gonad maturation and synchronous spawning of corals *ex situ*, by mimicking natural annual and daily temperature, photoperiod, insolation, and lunar cycles (Craggs et al., 2017). Presently, one of the major limitations to sexual propagation is the ability to successfully rear high quantities of coral settlers quickly, inexpensively, and without requiring too much space and labor. These costs could be reduced if the sexually produced corals were transferred to offshore nurseries when their survival and growth were no longer compromised, compared to if they had remained *ex situ*; however, this optimal time of transfer remains to be determined. In addition, there is a risk— not just an

expense— to rearing corals *ex situ* as it is always possible that something can go wrong with a tank, be it equipment failure or something biological like a ciliate outbreak, that can cause all the corals in a system to be lost. Furthermore, the longer coral settlers are retained in an artificial environment, the more likely that traits are selected for that environment, which may not suit them well when they are transferred to their natural habitat (Baums et al., 2019). Moving newly settled corals offshore as early as possible without compromising their survival and growth would not only reduce the costs, labor, and space associated with raising them, but it could also safeguard some of the progeny by being able to rear the corals in multiple locations (i.e., *in situ* and *ex situ*) so that not all are lost if there is a misfortune like a strong storm or equipment failure.

Across sexual propagation studies, there is a wide array of post-settlement time points at which sexually produced larvae and coral settlers have been transferred to offshore locations. In some studies, competent larvae were released at offshore reefs or *in situ* settlement structures (Edwards et al., 2015; dela Cruz & Harrison, 2017; dela Cruz & Harrison, 2020). In other studies, the newly settled corals were transferred once they had deposited skeleton (Guest et al., 2014; Boch & Morse, 2012), when they were 3 weeks old (Chamberland et al., 2017), 6 months old (Villanueva et al., 2012), or 10 months old (Nakamura et al., 2011). The optimal size or age at which to transfer sexually produced coral settlers has yet to be empirically determined. Theoretically, this should be when survival and growth rates of corals transferred *in situ* are comparable to those that remained *ex situ* to offset the costs of remaining in *ex situ* husbandry care. There are advantages and disadvantages to outplanting both larger and/or older corals vs. smaller and/or younger corals. Older/larger corals may be less susceptible to predation and space competition but may have lower survival rates when outplanted because the biotic and abiotic conditions at the reef are different from the *ex situ* conditions in which they had been raised (dela Cruz, 2019; Boch & Morse, 2012). Younger/smaller corals that are outplanted to the reef while still developing may become better adapted by acquiring local, beneficial symbionts (algae and bacteria) (Baums, 2008). Smaller corals, however, are usually more susceptible to predation, competition, and/or overgrowth by algae, and injury from herbivores like snails, sea urchins, and grazing fish (Sato, 1985; Doropoulos et al., 2012; Suzuki et al., 2018; dela Cruz, 2019). Determining the optimal size and age for the transfer of settlers to offshore nurseries is essential for the success of mass-scale restoration using sexual propagation.

The first four months post-settlement is known to be a time when new, sexually produced corals face the highest rates of mortality (Raymundo & Maypa, 2004; Forsman et al., 2015; Conlan et al., 2017). If offshore nurseries could be used for the grow-out of newly settled sexually produced corals during this initial four month period without compromising survival and growth rates, it would reduce costs, labor, and space associated with rearing sexually produced corals *ex situ*. To determine the optimal time at which to transfer *ex situ* sexually propagated corals to offshore nurseries, this study compares survival and growth of coral settlers from three species transferred from an aquarium to an offshore nursery at three different time points post-settlement. Specifically, recruits of three species— *Porites astreoides, Agaricia agaricites,* and *Montastraea cavernosa*— were transferred offshore at approximately 1 week post-settlement, 5 weeks post-settlement, and 9 weeks post-settlement, and at 13 weeks post-settlement timepoint were collected and their survival and size were compared to settlers which remained in the *ex situ* aquarium for the full 13 weeks post-settlement. Survival and growth data collected at the end of the 13 week post-settlement period was used to recommend the optimal time to transfer sexually produced corals from land-based to offshore nurseries to reef managers. However, the time at which to transfer corals offshore for optimal survival and growth may not necessarily align with optimal production operations of a facility, therefore a cost benefit analysis was also made to compare the costs necessary to raise these settlers to each timepoint tested. These results are essential to reduce the amount of space, time, and labor required for sexual propagation, and therefore will help contribute to upscaling restoration efforts.

Methods

Study Species

The coral species used in this experiment were chosen because they are commonly found along the Florida Reef Tract and represent a variety of different stress tolerances and reproductive strategies (Chiappone & Sullivan, 1996; Ginsburg et al., 2001; Somerfield et al., 2008). *Porites astreoides* and *Agaricia agaricites* are considered hardy or weedy species, denoting they are not as affected by changes in environmental conditions as other corals (Green et al., 2008; Walton et al., 2018; Jones et al. 2020). Additionally, *P. astreoides* and *A. agaricites* are brooding species, meaning they have internal fertilization and release already competent

larvae (Thornhill et al., 2006; Fourney & Figueiredo 2017; Fulmore, 2019). *Montastraea cavernosa* is an important reef-building stony coral (Porter et al., 2001; Horta-Puga & Carriquiry, 2008; Jones et al., 2020) that is also susceptible to the stony coral tissue loss disease (Porter et al., 2001; Walton et al. 2018), both of which make it a species of interest for restoration (Florida Keys National Marine Sanctuary, 2011). *Montastraea cavernosa* are gonochoric broadcast spawners, meaning each individual colony is either male or female,releasing sperm or eggs into the water column, respectively (Richmond & Hunter, 1990; Szmant 1991).

Porites astreoides release larvae in the months of April and May with maximal larval releases a few days before and after the new moon (McGuire, 1998). One week before the April 2020 new moon, adult colonies of *P. astreoides* were collected by SCUBA divers via hammer and chisel from a hard bottom coral community in Broward County, Florida. *Agaricia agaricites* typically release larvae in the spring months, with a peak around May, and have maximal larval releases starting zero to seven days before the full moon (Van Moorsel, 1983; McMahon, 2018; Fulmore, 2019). Adult colonies of *A. agaricites* were collected by divers via hammer and chisel five days before the full moon in May of 2020, from a nearshore, artificial reef constructed from ecojacks in Broward County, Florida. Once at the surface, the *P. astreoides* and *A. agaricites* were wrapped in bubble wrap, placed in coolers, and brought back to the Oceanographic Center at Nova Southeastern University (NSU) where colonies were temporarily housed in an outdoor recirculating 1500 L tank for roughly two weeks. At 1600 (EST) each day during the *P. astreoides* and *A. agaricites* respective expected larval release windows, adult colonies were placed in the larval collection system described in Anderson (2018) following the same collection methods.

Adult *M. cavernosa* colonies were collected by SCUBA divers via hammer and chisel from a hard bottom coral community in Broward County, Florida in August of 2019. They were transported to the Oceanographic Center at NSU and housed from the point of collection through the duration of this experiment in a 1136 L indoor recirculating aquarium that was set up as an induction system as described in Craggs et al. (2017). *Montastraea cavernosa* have been observed to spawn the week after the full moon in August and/or September, with spawning starting as early as 15 minutes after sunset (Szmant, 1991). When these colonies spawned, eggs and sperm were collected and mixed in bowls for fertilization. The resulting larvae were held in

recirculating 95 L conical tanks with 53 μm mesh filters connected to a 341 L sump with a protein skimmer until the larvae reached competency.

All adult corals were target fed an 1 L slurry containing 1 tsp Polyp Lab ® Reef-Roids, 1 tsp Reef Nutrition ® Oyster Feast, 1 tsp Reef Nutrition ® Real Oceanic Eggs, 1 tsp of Brightwell Aquatics CoralAmino, and live rotifers that had been enriched with Rotigrow Plus® algae approximately one hour before being fed to the corals. Corals were fed 6 days a week.

Larval settlement

Six weeks before each expected spawning window, 3.2 x 3.2 cm ceramic tiles (Oceans Wonders®) were prepared for this experiment by writing a number on one side with a permanent marker and drilling a hole in one corner of the tile using a Bosch 1/8 in. Carbide Tipped Drill Bit. The tiles were then put into a colander and submerged in a recirculating tank at NSU housing adult corals, to be conditioned. This allows bacterial films to grow on the surface of the tiles which serve as a positive settlement cue for stony coral larvae (Webster et al., 2004).

Once larvae were competent, they were moved into settlement baskets. The settlement baskets were plastic rectangular (29.8 cm x 21.0 cm x 13.3 cm) bins with two circular 10 cm wide holes cut out along each long side of the basket which were covered by 105 μm mesh to allow water exchange. Right before adding in the competent larvae, the settlement baskets were lined with overlapping conditioned settlement tiles to allow larvae to be able to swim to the underside of the tile and to prevent any anoxic areas (Figure 1). The baskets were suspended via PVC pipes so that the bottom half of the basket with the mesh covered holes were in the water of an indoor recirculating raceway. To further promote settlement, finely ground crustose coralline algae (CCA), a known settlement cue for coral larvae (Webster et al., 2004), was sprinkled over the tiles. Because *P. astreoides* and *A. agaricites* release competent larvae a few hours before and during sunrise, a Hydra Twenty Six HD light was affixed to the scaffolding over the baskets and set to turn on and off at natural sunrise and sunset times, respectively, at a photosynthetically active radiation (PAR) of 5 μmol photons $m^{-2}s^{-1}$. No light was turned on over the baskets containing *M. cavernosa* larvae.

Every day after larvae were introduced into the settlement baskets, three tiles were gently removed, placed into a bowl of saltwater, and examined under the microscope to determine if settlement had occurred. Once it was observed that multiple tiles had metamorphosed settlers (i.e., when larvae had attached to the tile and metamorphosed from a planula to a flat, round polyp, Figure 2), each tile was removed, examined under the microscope, and a map of the location of the settlers was drawn for each tile to be able to track each individual settler (Figure 3). New tiles were added into the settlement baskets until all remaining larvae either settled or died. After mapping, the tiles were placed on eggcrate racks in the recirculating indoor aquarium.

Figure 1. Larval baskets with 2 holes cut out and covered in mesh on each long side containing layered settlement tiles

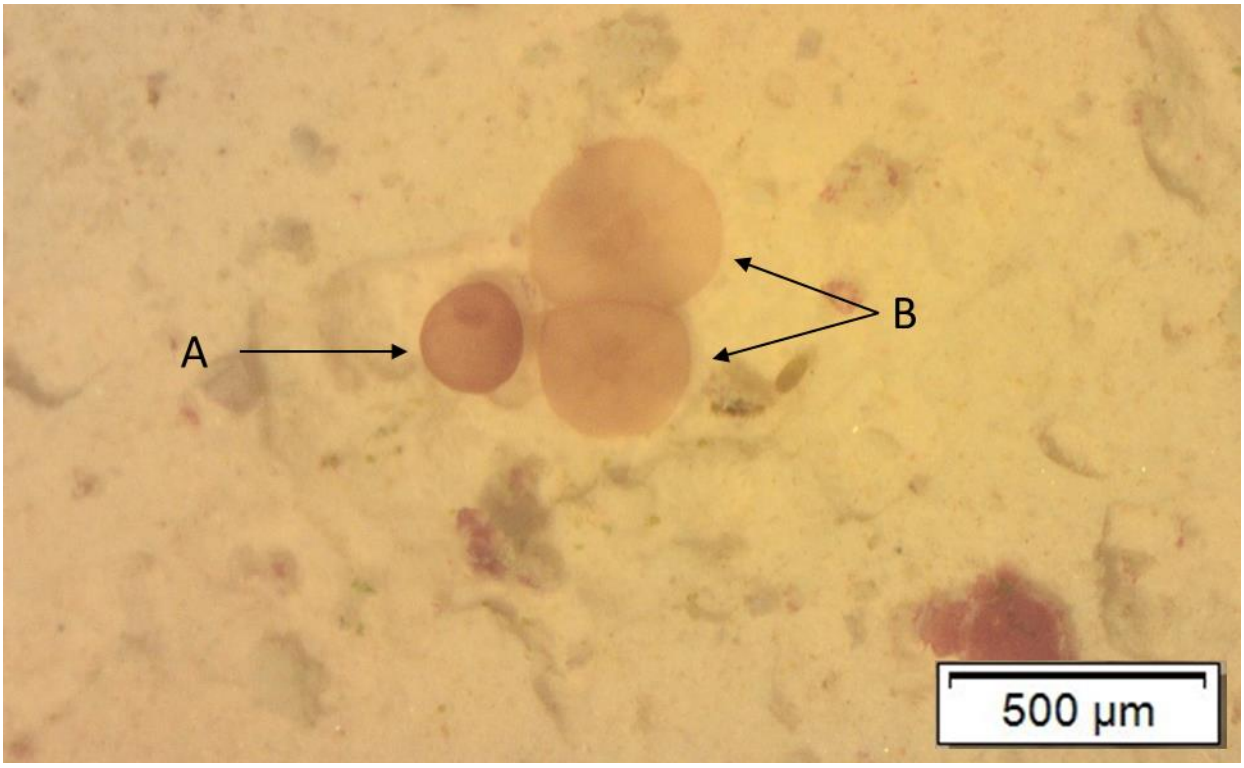

Figure 2. (A) A coral larva in the middle of metamorphosis that is still round and not well attached onto the substrate. (B) coral settlers that have completed metamorphosis and are flat and securely attached onto the substrate

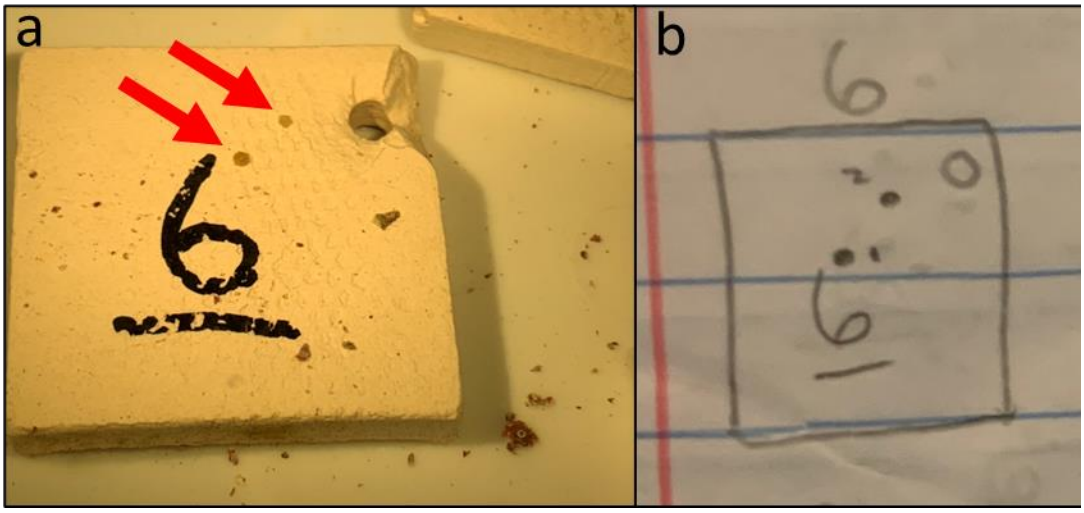

Figure 3. (a) Tile 6 with two visible settlers in the upper right-hand corner (pointed at by the two red arrows). (b) Map drawing of tile 6 with position and number of each settler marked.

Experimental treatments

To test how early a coral settler can be transferred to an offshore nursery without compromising their survival and growth, four experimental treatment groups were devised. In the first treatment, tiles with coral settlers were transferred to the offshore coral nursery via SCUBA divers approximately one week after settlement and hung on a coral tree. In the second treatment, coral settlers were reared in the indoor recirculating tank for approximately five weeks before being transferred to the offshore nursery. In the third treatment, coral settlers were reared in the indoor recirculating tank for approximately nine weeks before being transferred to the offshore nursery. The fourth treatment served as a control where tiles with coral settlers were reared in the aquarium for the approximate 13 week duration of the experiment. The actual timepoints at which each treatment for each species was transferred sometimes varied by 1-2 weeks due to logistics, weather, and the Covid19 global pandemic (Table 1). Since the *P. astreoides* released larvae over multiple days, settlement occurred from April 18, 2020 through April 26, 2020. April 22, 2020 is the median settlement day and was used as the settlement day for both the approximate transfer day and for the cost benefit analysis. Therefore, the experiment lasted 12 weeks for *P. astreoides,* and Treatment 1 will thereafter be referred to as 1 week post-settlement, Treatment 2 as 4 weeks post-settlement, and Treatment 3 as 8 weeks post-settlement. Since *A. agaricites* released larvae over multiple days, settlement occurred from May 8, 2020 through May 18, 2020. May 13, 2020 is the median settlement day and was used as the settlement day for both the approximate transfer day and for the cost benefit analysis. Therefore, the experiment lasted 13 weeks for *A. agaricites*, and Treatment 1 will thereafter be referred to as 1 week post-settlement, Treatment 2 as 5 weeks post-settlement, and Treatment 3 as 9 weeks post-settlement.

Table 1. Timeline for when the first three treatments of each species was transferred offshore with the fourth treatment always remaining in the aquarium. Yellow boxes represent coral settlers are in the aquarium while black boxes represent the corals being in the offshore nursery.

Porites astreoides	Settlement Complete April 22, 2020	1 week post-settlement May 2, 2020	4 weeks post-settlement May 22, 2020	8 weeks post-settlement June 19, 2020	12 weeks post-settlement July 16, 2020
Treatment 1					
Treatment 2					
Treatment 3					
Treatment 4					

Agaricia agaricites	All Settlement Complete May 13, 2020	1 week post-settlement May 22, 2020	5 weeks post-settlement June 19, 2020	9 weeks post-settlement July 16, 2020	13 weeks post-settlement Aug. 14, 2020
Treatment 1					
Treatment 2					
Treatment 3					
Treatment 4					

= Offshore nursery

= Aquarium

Montastraea cavernosa	Settlement Complete Aug. 21, 2020	3 weeks post-settlement Sept 11, 2020	7 weeks post-settlement Oct. 12, 2020	12 weeks post-settlement Nov. 13, 2020	15.5 weeks post-settlement Dec 8, 2020
Treatment 1					
Treatment 2					
Treatment 3					
Treatment 4					

The NSU offshore nursery is located in a large sand patch 9 m deep and 700 m from the shoreline in Broward County, Florida. The nursery trees are 1.5 m long and are suspended 0.3 m from the bottom which allows corals to be suspended in the water column between 0.3 and 2.4 m. The nursery is equipped with temperature loggers which recorded temperatures every hour from May 1, 2020, through June 26, 2020, and every two hours thereafter.

The indoor recirculating aquarium for this experiment consisted of two connected 454 L raceways and a common 341 L sump. Each raceway had one Finnex TH Deluxe Titanium heater while the sump contained one Finnex TH Deluxe Titanium heater, one drop-in Aqua Logic chiller, one ASM G-3 Protein Skimmer, two SMART UV Sterilizers (Pentair EU25-U), one phosphate reactor (PhosBan Reactor 550), one calcium reactor with a secondary chamber, 5 pieces of live rock, and a 45.7 cm x 30.5 cm perforated container filled with bioballs. The system was manually set to mimic a truncated annual temperature cycle (23.9°C in February to 28.3°C in September) based on data gathered by SECREMP from the southeast Florida Reef Tract from 2007-2018 (excluding bleaching years). Once settlement was complete, settlers were placed

under Hydra Twenty Six HD lights set to a PAR of 10 µmol photons $m^{-2}s^{-1}$. Subsequent increases in PAR over the settlers followed curves and recommendations described in McMahon (2018) and Kreh (2019). While the coral settlers were in the recirculating tank, they were target fed a 1 L slurry containing 0.5 tsp Polyp Lab ® Reef-Roids, 1 tsp Reef Nutrition ® Oyster Feast, 1 tsp of Brightwell Aquatics CoralAmino, and live rotifers that had been enriched with Rotigrow Plus® algae approximately one hour before being fed to the corals. The corals were fed this food six days a week. Right before feeding, the flow to the tank was turned off and remained off for one-hour post-feeding. Additionally, tiles with corals on them were hand-cleaned typically starting around the third week post-settlement due to algae beginning to grow. The tiles were then continued to be hand-cleaned approximately every other week due to algal growth rates.

For each species, each tile was recorded and randomly assigned a number 1-4, representing the four treatments. Larvae/gametes released over multiple days were separated into groups to make sure that each treatment not only had similar numbers of settlers, but also had relatively similar numbers of larvae from different release dates.

For this experiment, two coral nursery trees were constructed similar to those described in Nedimyer et al. (2011). These trees consisted of a 1.5-m-long PVC trunk which had ten 1.22 m long branches (with holes running down the length of the branches) through the trunk of the tree. The trees were screwed into the sandy bottom substrate at the offshore nursery belonging to Nova Southeastern University. The trees were evaluated monthly to determine if the trunk and branches needed to be hand cleaned, which was never necessary during the duration of this experiment. The nursery has a maximum depth of 9.14 m and buoys were attached to the tops of the trees to suspend them 0.91 m above the seafloor. To hang the tiles from treatments 1-3 on the trees, the tiles were strung up into kebabs (Figure 4). The kebabs were made by cutting a piece of 90.7 kg weighted monofilament, crimping a metal crimp on one end, sliding a piece of Parker Parflex (0.6 cm diameter) airline hosing cut to about 1.5 cm long onto the monofilament, then sliding a tile onto the monofilament, followed by another piece of airline hose, then another tile and so on until there were five or six tiles on the monofilament. The last tile was followed by another piece of airline hose and then a metal crimp was crimped next to it to hold everything in place. A tag with the identification of the kebab was zip tied onto one of the end crimps. The tiles were only constructed into kebabs the afternoon before they were transported to the nursery.

Otherwise, they remained on racks in the aquarium where they were cared for in a traditional aquaculture manner (i.e. were placed in a horizontal orientation to be parallel to the artificial lights, and thus could be removed from the tank for hand-cleaning, and easily hand-fed). Once the kebabs were constructed, they were zip tied to PVC rods that laid across the raceway to suspend the kebabs in water overnight without damaging any of the settlers. Before being strung into the kebabs, each tile was checked under the microscope and compared to the original map to assess survival up to that timepoint to know whether mortality of a settler occurred before or after deployment to the offshore nursery. The next morning, Tupperware® plastic food storage containers were filled with saltwater and four to five kebabs were placed in a single container and the lid was closed over the monofilament to hold the kebabs in place as much as possible (Figure 5a). A rubber band that was 30 cm in diameter connected to a one-pound dive weight, was wrapped around the container to help with transport in the water (Figure 5b and 5c). The containers were placed into 19 L buckets which were filled with saltwater for the boat ride from NSU to the offshore nursery. Once in the nursery, a diver attached the kebabs to the tree by sticking one end of the monofilament through a crimp, then sticking the monofilament though a hole on a branch, then back through the crimp, and crimping it. The same was done with the other end of the monofilament three or four holes down from the original (Figure 4). Kebabs were haphazardly hung on different branches on the tree. To remove the kebabs at the end of the experiment, a diver cut both loops to free the kebabs from the tree, placed them into Tupperware® plastic food storage containers, put the containers in 19 L buckets filled with saltwater for the boat ride to NSU.

At approximately 13 weeks post-settlement for each species-specific experiment, all kebabs in the offshore nursery were cut from the trees and brought back to the Marine Larval Ecology and Recruitment Lab at NSU where they were placed in a 75.7 L container equipped with two Danner air pump bubblers with air stones attached, two small SunSun Submersible Water Pump, and a heater set to 24.4°C. All tiles in each treatment were examined under the microscope using the maps made after initial settlement to check for survival. Any coral that was deemed alive, defined has having a mouth surrounded by some visible tissue, was photographed with an Olympus LC20 digital camera attached to an Olympus SZ61 dissecting microscope. CellSens was used to measure the live tissue area in these pictures to determine final size of the surviving settlers amongst all four treatments.

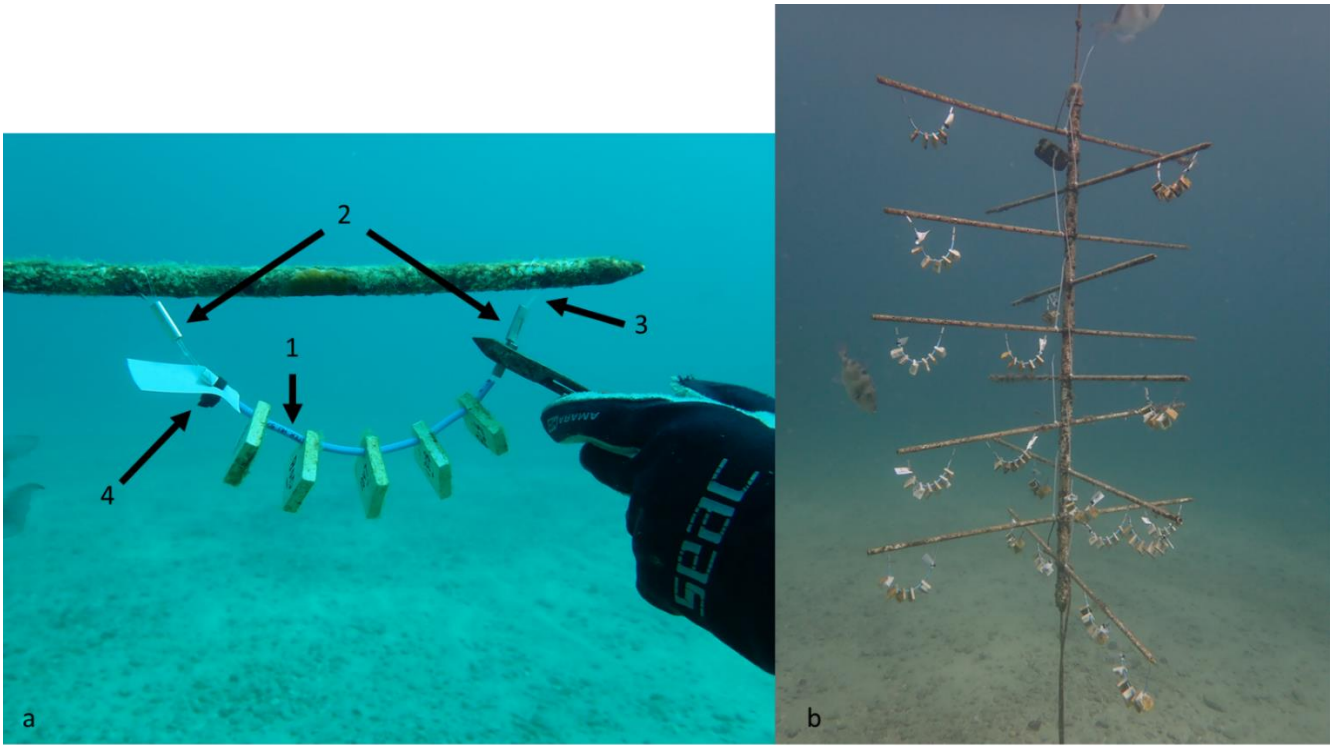

Figure 4. (a) Close up image of an individual kebab (1) air hose spacers (blue pieces between the tiles) (2) metal crimps (3) monofilament (4) waterproof paper tag zip tied to the kebab. (b) Multiple kebabs hanging on a nursery tree

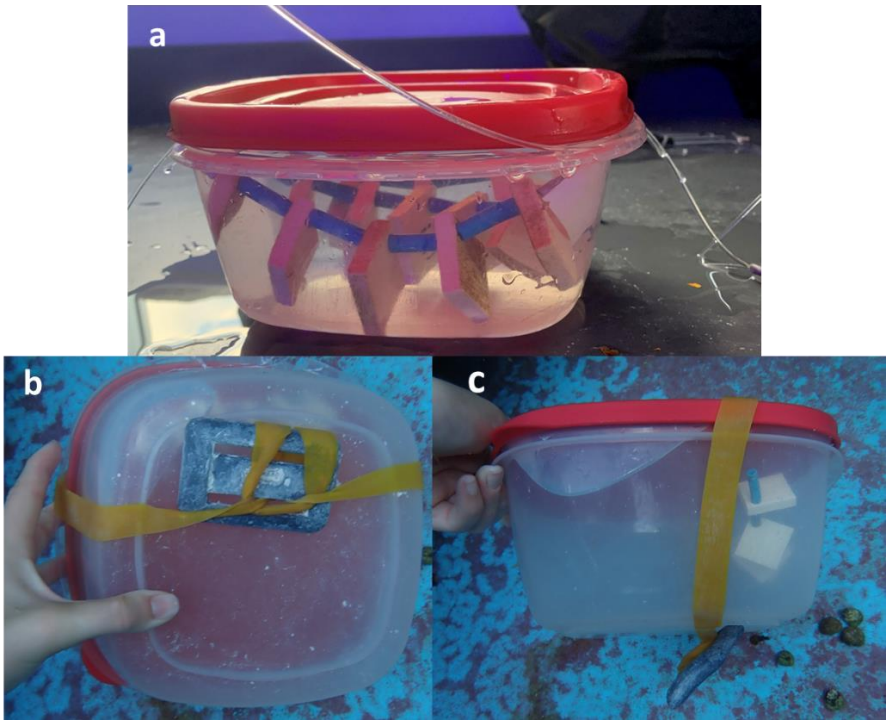

Figure 5. (a) Kebabs in Tupperware® plastic food storage containers for transport. (b) and (c) Tupperware with a 30 cm rubber band with dive weight wrapped around the Tupperware to help with transport and utility in the offshore nursery.

Cost-Benefit Analysis

A cost-benefit analysis was created following the guide of Edwards et al. (2010). This cost-benefit analysis included only the operational costs of caring for the settlers while they were in the aquarium, the consumptive supplies needed to make the kebabs, the cost of labor for each day the corals were cared for, the costs of boat and SCUBA tank rentals, and the labor for transferring the corals to the offshore nursery, as well as the cost of monthly offshore nursery maintenance trips. The cost benefit did not include any *ex situ* or *in situ* infrastructure costs— such as the costs to build the aquarium or the nursery trees— or the costs of any supplies/infrastructure that could continue to be reused such as eggcrate racks, the Tupperware® containers, crimpers, etc., nor electricity and freshwater costs. The costs of goods and supplies factored into the cost benefit analysis were listed as what it costed the Marine Larval Ecology and Recruitment Lab to purchase them. The boat and SCUBA tank rentals were consistent of the rates offered by NSU to its students and employees. The cost of labor was based on the hourly salary paid by the Marine Larval Ecology and Recruitment Lab to its Graduate Research

Assistant I employees. Because one cannot control how many larvae settle on a tile, the treatments did not start with the same number of settlers. As result, to compare treatments for each species, the cost per surviving coral had to be estimated using a standardization. Specifically, the average number of settlers in all four treatments of a species was calculated. Next, the total cost for an individual treatment of that species was calculated and divided by the average number of initial corals multiplied by the percent survival of that treatment. i.e. Cost per surviving coral in a treatment = (Total cost of a treatment/(Average number of corals in all 4 treatments ×(Survival proportion at the end of the experiment for the specific treatment))).

Data Analysis

To compare the final survival between treatments, I used a one-way ANOVA, or a Kruskal-Wallis test if the data did not meet the parametric assumptions. Since the number of settlers per tiles varied amongst the tiles, survival was analyzed as proportion of survival by tile.

To compare the growth between treatments, the surface area of the corals at the end of the experiment was compared between treatments using a one-way ANOVA, or a Kruskal-Wallis test if the data did not meet the parametric assumptions.

These tests were run in R using RStudio version 3.6.1.

Results

Porites astreoides

The time at which the coral settlers were moved to the offshore nursery had a significant effect on their final survival ($\chi^2 = 12.1$, df =3, $p = 7.04 \times 10^{-3}$, Figure 6a). Corals transferred offshore 1 week-post settlement had a final survival of 58.7%. Most of the mortality occurred when these corals were offshore (37.6%) while only 3.7% died while they were in the aquarium. Of the corals that made it out to the field, 61.0% survived. Corals transferred offshore 4 weeks post-settlement had a final survival of 56.9%. Most of the mortality occurred when theses corals were offshore (34.1%) while only 8.9% died while they were in the aquarium. Of the corals that made it out to the field, 62.5% survived. Corals transferred offshore 8 weeks post-settlement had a final survival of 70.0%. A little over half of this mortality occurred when the corals were in the

field (16.2%) while 13.8% died while they were in the aquarium. Of the corals that made it out to the field, 81.3% survived. The corals that remained in the aquarium for the 12 weeks of the experiment had a final survival of 73.5%. The final survival of corals transferred offshore at 1 week-post settlement and the ones transferred 8 weeks post-settlement did not significantly differ from any of the other treatments (p=1, p=1, p=0.18, respectively for corals moved offshore at 1 week vs 4 weeks, 1 week vs. 8 weeks, and 1 week vs. aquarium only treatments; and p=0.25, p=1, respectively for corals moved offshore at 8 weeks vs. 4 weeks and 8 weeks vs. aquarium only treatments). However, the survival of the corals that remained in the aquarium throughout the experiment (12 weeks) was only significantly different from the survival of the corals transferred offshore at 4 weeks post-settlement ($p=6.15 \times 10^{-3}$) (Figure 6a).

The time at which settlers were moved to the offshore nursery had a significant effect on their growth and surface area at the end of the experiment ($\chi^2 = 27.6$, df = 3, $p = 4.31 \times 10^{-6}$, Figure 6b). On average, the corals that remained in the aquarium for the duration of the experiment exhibited the largest surface area (7.48 ± 0.48 mm^2, average ± SE), being significantly larger than the corals transferred offshore at 1 and 4 weeks post-settlement (5.22 ± 0.53 mm^2, $p=1.49 \times 10^{-3}$ and 4.99 ± 0.67 mm^2 , $p= 4 \times 10^{-6}$), respectively. However, the surface area of the aquarium only corals were not significantly greater than the corals transferred offshore 7 weeks post-settlement (5.73 ± 0.43 mm^2, p=0.067). The final surface area of the corals transferred offshore 1 week-post-settlement was not significantly different from the ones transferred offshore 4 weeks post-settlement (p=1), nor the ones transferred at 8 weeks post-settlement (p=0.99). The corals transferred 8 weeks post-settlement had a surface area significantly larger than the ones transferred offshore four weeks prior (p= 0.046) (Figure 6b).

The longer the *P. astreoides* corals remained in the aquarium, the greater the cost per surviving coral was (Table 2). Specifically, the costs to raise *P. astreoides* settlers at the land-based nursery for 10, 30, and 58 days plus the cost of transfer, and offshore nursery maintenance (for applicable treatments) was $46.81, $67.29, and $79.67 per surviving coral, respectively. The costs to raise *P. astreoides* settlers at the land-based nursery for 86 days was $99.96 per surviving coral.

Table 2. Survival, Growth, and cost per coral results for the four treatments over 12 weeks of *P. astreoides.* N/A refers to not applicable.

Porites astreoides				
	Transferred 1 week post-settlement	**Transferred 4 weeks post-settlement**	**Transferred 8 weeks post-settlement**	**Aquarium only**
Total number of corals at the start of experiment	109	123	130	113
Number of corals transferred to nursery	105	112	112	N/A
Percent Survival in the aquarium	96.3%	91.1%	86.2%	73.5%
Number of corals alive at the end of experiment	64	70	91	83
Percent survival in offshore nursery	61.0%	62.5%	81.3%	N/A
Percent final survival	58.7%	56.9%	70.0%	73.5%
Average Final Size (± SE) (mm^2)	5.22 ± 0.53	4.99 ± 0.67	5.73 ± 0.43	7.48 ± 0.48
Cost per Surviving Coral (USD)	$46.81	$67.29	$79.67	$99.96

Agaricia agaricites

The time at which settlers were moved to the offshore nursery had a significant effect on the final survival of the corals (χ^2 (3) = 18.756, p= 3.07×10^{-4}, Figure 6c). Corals transferred offshore 1 week post-settlement had a final survival of 69.6%. Most of the mortality occurred when these corals were in the field (29.0%) while 1.4% died while they were in the aquarium. Of the corals that made it out to the field, 70.6% survived. Corals transferred 5 weeks post-settlement had a final survival of 71.4%. All of the mortality occurred when these corals were in the field as none of the corals died while they were in the aquarium. Corals transferred 9 weeks post-settlement had a final survival of 92.5%. A little over half of this mortality occurred when the corals were in the field (4.5%) while 3.0% died while they were in the aquarium. Of the corals that made it out to the field, 95.4% survived. The corals that remained in the aquarium for the full 13 weeks of the experiment had a final survival of 89.38%. The post hoc analysis showed that none of the treatments were significantly different from each other in terms of final survival (Figure 6c).

The time at which settlers were moved to the offshore nursery had a significant effect on their growth and surface area at the end of the experiment (χ^2 (3) = 77.131, $p < 2.2 \times 10^{-16}$, Figure 6d). On average, the corals that remained in the aquarium for the duration of the experiment exhibited the largest surface area (57.88 ± 4.04 mm^2), being significantly larger than the corals transferred offshore at 1 and 5 weeks post-settlement (10.10 ± 1.30 $mm^2$and 17.95 ± 2.03 mm^2, respectively; p=0 and $p = 1 \times 10^{-6}$, respectively). However, the surface area of the aquarium only corals were not significantly greater than the corals transferred offshore 9 weeks post-settlement (44.89 ± 3.98 mm^2, p=1). The final surface area of the corals transferred offshore 1 week-post settlement was not significantly different from the corals transferred offshore 5 weeks post-settlement (p= 0.47), but they were significantly smaller than the corals transferred offshore 9 weeks post-settlement (p=0) (Figure 6d).

The longer the *A. agaricites* corals remained in the aquarium, the greater the cost per surviving coral was (Table 3). Specifically, the costs to raise *A. agaricites* settlers at the land-based nursery for 9, 37, and 64 days plus the cost of transfer, and offshore nursery maintenance (for applicable treatments) was $59.94, $96.91, and $103.11 per surviving coral, respectively. The costs to raise *A. agaricites* settlers at the land-based nursery for 89 days was $133.39 per surviving coral.

Table 3. Survival, Growth, and cost per coral results for the four treatments over 13 weeks of *A. agaricites.* N/A refers to not applicable.

Agaricia agaricites				
	Transferred 1 week post-settlement	**Transferred 5 weeks post-settlement**	**Transferred 9 weeks post-settlement**	**Aquarium only**
Total number of corals at the start of experiment	69	56	67	113
Number of corals transferred to nursery	68	56	65	N/A
Percent survival in aquarium	98.6%	100%	97%	89.4%
Number of corals alive at the end of experiment	48	40	62	101
Percent survival in offshore nursery	70.6%	71.4%	95.4%	N/A
Percent final survival	69.6%	71.4%	92.5%	89.4%
Average Final Size (± SE) (mm^2)	10.1 ± 1.30	18.0 ± 2.03	44.9 ± 3.98	57.9 ± 4.04
Cost per Surviving Coral (USD)	$59.94	$96.91	$103.11	$133.39

Montastraea cavernosa

The time at which settlers were moved to the offshore nursery had a significant effect on the final survival of the corals ($\chi^2 = 53.857$, df=3, $p= 1.20 \times 10^{-11}$, Figure 6e). Corals transferred offshore 3 weeks post-settlement had a final survival of 11.7%. Most of the mortality occurred when the corals were in the field (77.7%) while only 10.7% died while they were in the aquarium. Of the corals that made it out to the field, 13.0% survived. Corals transferred 7 weeks post-settlement had a final survival of 55.9%. Most of the mortality occurred when the corals were in the field (33.3%); only 10.8% died while they were in the aquarium. Of the corals that made it out to the field, 62.6% survived. Corals transferred offshore 12 weeks post-settlement had a final survival of 71.7%. Contrarily to what happened with the other two species, most of this mortality occurred when the corals were in the aquarium (20.4%) while only 8.0% died in the field. Of the corals that made it out to the field, 90.0% survived. The corals that remained in the aquarium for the full 15.5 weeks of the experiment had a final survival of 76.53%. The final survival of corals transferred offshore 3 weeks post-settlement was significantly lower than all of

the other treatments ($p= 2.94 \times 10^{-4}$, p=0, p=0, 3 weeks vs. 7 weeks, 12 weeks, and aquarium only, respectively). The survival of the corals transferred offshore at 7 and 9 weeks post-settlement and the corals that always remained in the aquarium were not significantly different from one another (p= 0.47, p= 0.10, p=1, respectively for 7 weeks vs. 9 weeks, 7 weeks vs. aquarium only, 9 weeks vs. aquarium only) (Figure 6e).

The time at which settlers were moved to the offshore nursery had a significant effect on their surface area at the end of the experiment ($\chi^2= 26.891$, df=3, $p= 6.21 \times 10^{-6}$, Figure 6f). On average, the corals that were transferred offshore 12 weeks post-settlement exhibited the largest surface area (0.75 ± 0.05 mm^2) and were significantly larger than the corals transferred offshore at 3 and 7 weeks post-settlement as well as the corals that always remained in the aquarium (0.31 ± 0.07 mm^2, $p= 1.48 \times 10^{-3}$; 0.45 ± 0.04 mm^2, $p=1.61 \times 10^{-3}$; and 0.50 ± 0.05 mm^2 $p=2.89 \times 10^{-4}$, respectively). The size of corals transferred offshore at 3 and 7 weeks post-settlement and the corals that always remained in the aquarium for the duration of the experiment were not significantly different from one another (p=0.67, p=0.73, p=1, respectively for 3 weeks vs. 7 weeks, 3 weeks vs. aquarium only, and 7 weeks vs. aquarium only) (Figure 6f).

The costs to raise *M. cavernosa* settlers at the land-based nursery for 21, 52, and 84 days plus the cost of transfer, and offshore nursery maintenance (for applicable treatments) was $358.29, $115.31, and $123.20 per surviving coral, respectively. The costs to raise *M. cavernosa* settlers at the land-based nursery for 110 days was $139.14 per surviving coral (Table 4).

Table 4. Survival, Growth, and cost per coral results over 15.5 weeks for the four treatments of *M. cavernosa.* N/A refers to not applicable.

Montastraea cavernosa				
	Transferred 3 weeks post-settlement	**Transferred 7 weeks post-settlement**	**Transferred 12 weeks post-settlement**	**Aquarium only**
Total number of corals at the start of experiment	103	102	113	98
Number of corals transferred to nursery	92	91	90	N/A
Percent survival in aquarium	89.3%	89.2%	79.6%	76.5%
Number of corals alive at the end of experiment	12	57	81	75
Percent survival in offshore nursery	13.0%	62.6%	90.0%	N/A
Percent final survival	11.7%	55.9%	71.7%	76.5%
Average Final Size (± SE) (mm^2)	0.31 ± 0.07	0.45 ± 0.04	0.75 ± 0.05	0.50 ± 0.05
Cost per Surviving Coral (USD)	$358.29	$115.31	$123.20	$139.14

Optimal Transfer Time

There was not a significant difference in survival between the four *P. astreoides* treatments, however for final size, the treatment with the highest median final size was the aquarium only treatment, but it was not significantly different only from the treatment that was transferred offshore 8-weeks post-settlement. Thus, this timepoint serves as a good cutoff point when determining the best transfer time for growth. Therefore, using both the survival and growth results, the best, conservative time to move *P. astreoides* settlers to an offshore nursery is around the 8-week post-settlement timepoint. There were no significant differences in survival between the four *A. agaricites* treatments. However, for final size, the treatment with the highest median final size was the aquarium only treatment, but it was not significantly different only from the treatment that was transferred offshore 9-weeks post-settlement. Thus, this transfer timepoint was good to maximize growth. Therefore, using both the survival and growth results, the best, conservative time to move *A. agaricites* settlers to an offshore nursery is around 9-weeks post-settlement. For *M. cavernosa* the only treatment that had a significantly lower average survival

were the corals transferred offshore 3-weeks post-settlement. For final size, the corals with the highest median final size were those transferred offshore 12-weeks post-settlement. Therefore, using both the survival and growth results, the best, conservative time to move *M. cavernosa* settlers to an offshore nursery is around the 12-week post settlement timepoint. It was also observed, for all species tested, that the percent final survival of the corals increased the longer they remained in the aquarium before being transferred offshore.

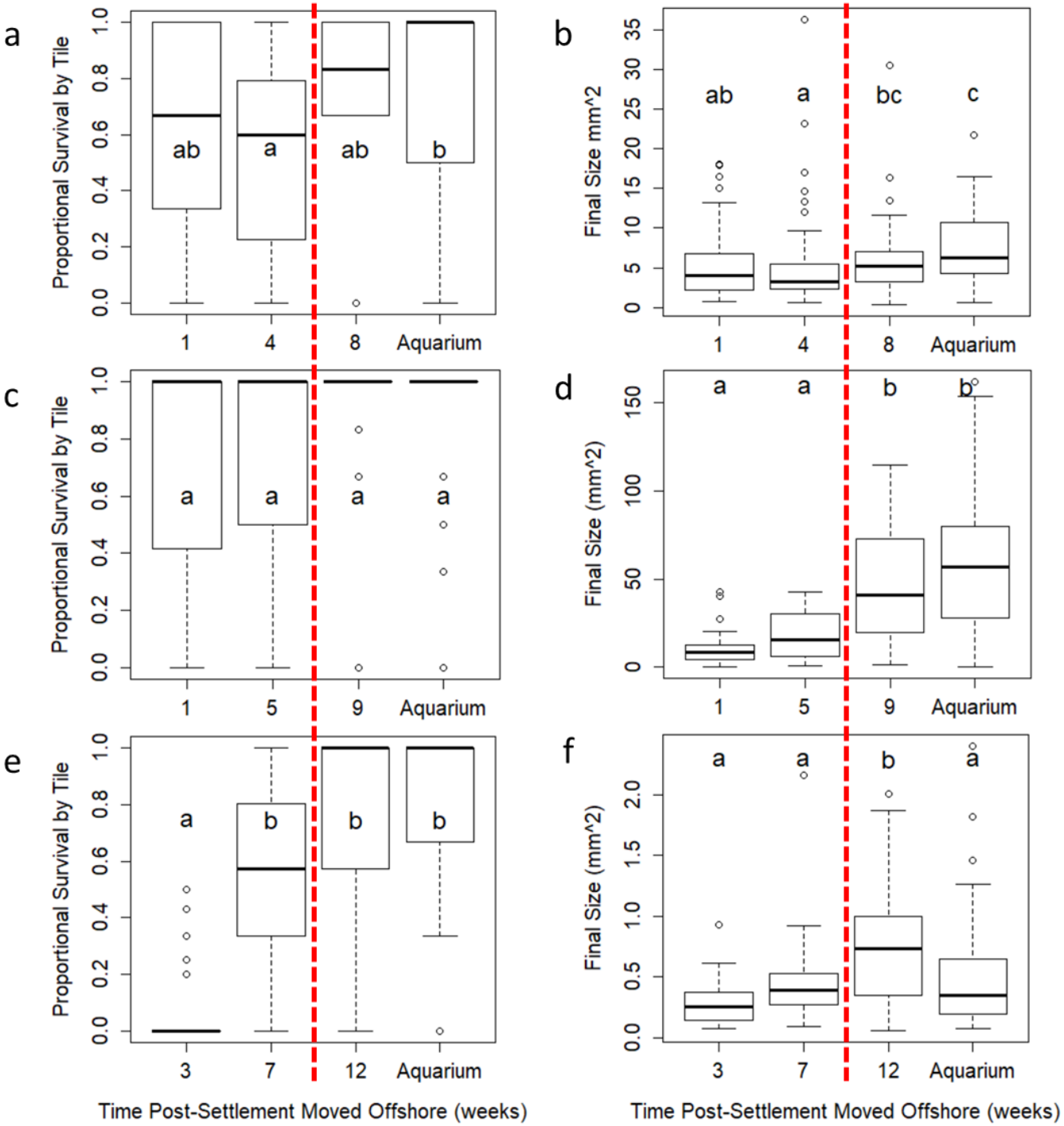

Figure 6. Proportional survival by tile and final size of *P. astreoides*, *A. agaricites*, and *M. cavernosa* at the end of their respective experiments. The vertical red dashed lines on (a)-(f) represent the time at which transferring the corals to an offshore nursery did not compromise their survival and growth which occurred around the 8-12 weeks post-settlement timepoint. The thick horizontal black lines on the boxplots represent the median observations. (a) Proportional survival by tile of *P. astreoides* in the four treatments at the end of the 12 week experiment. (b) Final growth (surface area, mm^2) of *P. astreoides* in the four treatments at the end of the 12 week experiment. (c) Proportional survival by tile of *A. agaricites* in the four treatments at the end of

the 13 week experiment. (d) Final growth of *A. agaricites* in the four treatments at the end of the 13 week experiment. (e) Proportional survival by tile of *M. cavernosa* in the four treatments at the end of the 15.5 week experiment. (f) Final growth of *P. astreoides* in the four treatments at the end of the 15.5 week experiment. Similar letters indicate that there was not a significant difference between treatments whereas different letters indicate there was a significant difference between treatments.

Discussion

This study suggested that the optimal time to transfer newly settled, sexually-produced corals of *P. astreoides, A. agaricites,* and *M. cavernosa* from a land-based aquarium to an offshore nursery is 8-12 weeks post-settlement (Figure 6). At this time, corals were at a stage of development that aided their survival. Eight to twelve week old coral settlers likely had both a high density and fully established symbiotic community of Symbiodinaceae, well developed tentacles for heterotrophic feeding and defense, grown to a size that made them less vulnerable to competition for space, and had potentially accumulated sufficient energy reserves (from being fed a rich diet for 7-11 weeks) to help endure the stress of the transition to the offshore nursery.

The establishment of a dense consortium of Symbiodinaceae is one potential reason for the higher success of settlers transferred offshore 8-12 weeks post-settlement. When corals are transferred to an offshore nursery, they are exposed to the natural light spectrum and photosynthetically active radiation (PAR) levels (averaging 240 µmol photons.m^{-2} s^{-2} at midday on offshore reefs in this region; Sofonia & Anthony, 2008; Fourney & Figueiredo, 2017) which can be a harsh difference from the light spectrum and lower PAR exposure in the indoor aquarium. While *P. astreoide* and *A. agaricites* were given some Symbiodinaceae via vertical transmission (Richmond & Hunter 1990; Sharp et al., 2012), the initial symbiont density may not have been sufficient to guarantee high survival and growth post-transfer from the aquarium to the offshore nursery (Figure 7). According to past studies, newly settled corals maximize survival and growth when reared at low PAR values, around 10 µmol photons m^{-2} s^{-1}, for the first few weeks, and higher PAR values thereafter (McMahon, 2018; Kreh, 2019). Both McMahon (2018) and Kreh (2019) suggested the high densities of Symbiodiniaceae, concomitant with developed tentacles, as the likely reason to this shift in desired light levels occurring at 8-12 weeks. Symbiodiniaceae can provide anywhere from 78% to 97% of the carbon needed by a coral (Falkowski et al. 1984; Muscatine, 1990; Sutton & Hoegh-Guldberg, 1990). Being able to rely

on Symbiodiniaceae for a large portion of their carbon and energy needs, and not having to rely solely and/or heavily on heterotrophic feeding, was most likely an advantage for these 8-12 week old corals, as corals typically rely more heavily on autotrophy to meet their nutritional needs (Falkowski et al., 1984; Muscatine, 1990; Sutton & Hoegh-Guldberg, 1990; Teece et al., 2011). Additionally, Symbiodiniaceae are known to produce mycosporine-like amino acids (MAAs), which act like a sunscreen and can provide protection from ultraviolet radiation (UV) to the coral (Dunlap, & Chalker, 1986; Dunlap et al., 1998; Banaszak et al., 2000). Since the corals transferred offshore 8-12 weeks post-settlement had a dense assemblage of Symbiodiniaceae, they were most likely able to produce MAAs which likely helped protect them from UV. In addition to this UV protection, there is evidence that some species of Symbiodiniaceae can produce saturated betaine lipids which can offer a degree of protection against bleaching from elevated temperatures (Roach et al. 2021).

The developed feeding tentacles of the 8-12-week post-settled corals most likely also played a role in their higher survival and growth. Corals are not only autotrophs, but are also avid carnivores and will eat most (size appropriate) organisms that come in close contact with them (Yonge, 1930; Goreau et al. 1971; Porter, 1976). While the corals of this study were reared in the aquarium, they were fed a rich diet six days a week for 7-11 weeks before being transferred offshore. The food included DHA-enriched live rotifers to elicit a heterotrophic feeding response, as well as dissolved sources of nutrition like ground oysters and amino acids for the passive reception of nutrients without active feeding (Goreau et al. 1971; Conlan et al. 2017). When autotrophic and heterotrophic feeding are used in tandem, energy obtained from heterotrophic feeding is used to increase skeleton and tissue growth (Treignier et al., 2008). This likely occurred with the corals in the aquarium, especially those that stayed for 7-11 weeks post-settlement, which could have aided their later survival in the offshore nursery. Having tentacles for heterotrophic feeding most likely also supported the survival of the corals because the waste byproducts from this mode of feeding is used by the Symbiodiniacea (Muller-Parker & D'Elia, 1996). While many of the corals had Symbiodiniaceae early on, their survival and growth may have also been higher at 8-12 weeks post-settlement due to their well-developed tentacles being able to fully support heterotrophic feeding which produced more/sufficient metabolic waste products for their Symbiodiniaceae to consume. Additionally, once these corals had been transferred to the offshore nursery, the corals were likely able to continue using their tentacles to

catch zooplankton to supplement their carbon needs not provided by their Symbiodiniaceae, further aiding their survival and growth post-transfer.

The corals transferred from the aquarium to offshore nursery 8-12 weeks post-settlement were larger and much more developed than their counterparts transferred at earlier timepoints (Figures 7 & 8), potentially offering competitive advantages. Coral mortality is typically high at earlier stages of development but is known to exponentially decrease as corals grow (Raymundo & Maypa, 2004; Forsman et al., 2015; Conlan et al., 2017). Despite the fact that each species attained different sizes at 8-12 weeks post-settlement, it is possible that at this timepoint the corals had reached (or were getting close to reaching) their own species-specific "size-escape threshold," i.e. where were large enough to substantially reduce the risk of predation and increase their ability to withstand natural stressors (Paine, 1976; Doropoulos et al., 2012; dela Cruz & Harrison, 2020). At this stage, the corals most likely had fully developed sweeper tentacles and mesenterial filaments, which are used by corals as a means of protection of themselves and defense of their territory (Lang & Chornesky,1990; Kass-Simon & Scappaticci, 2002). This process was observed in *A. agaricites* at 3 weeks post-settlement, where settlers in the aquarium were observed creating "halos" around themselves keeping the surrounding algae at bay (Figure 9).

There was a marked difference in the survival of first sets of corals transferred offshore between *P. astreoides* and *A. agaricia* (I week post-settlement), versus *M. cavernosa* (3 weeks post-settlement), which may be due to their symbiotic and aposymbiotic nature at the time of settlement, respectively. *Porites astreoides* and *A. agaricites* are given Symbiodiniaceae and bacteria through vertical transmission from their parents (Richmond & Hunter 1990; Sharp et al., 2012), whereas corals from broadcast spawning species must acquire these through horizontal transmission from their surroundings (Richmond & Hunter, 1990). The early acquisition of all of the constituents of a holobiont (i.e. bacteria, viruses, Symbiodiniaceae, etc.), which provide essential nutrients, passage of trace metals, vitamins, cofactors, and more, to the developing coral (Webster and Thomas, 2016; Bourne et al., 2016; Webster & Reusch, 2017) may have contributed to the high survival of the earliest offshore transfers of *P. astreoides* and *A. agaricites* settlers, compared to the high mortality of the earliest offshore transfers of *M. cavernosa* settlers. It can take up to two weeks for a newly-settled polyp to acquire

Symbiodinaceae (Babcock & Hayward, 1986), so it is likely that the *M. cavernosa* settlers transferred to the offshore nursery 3 weeks post-settlement did not have a high enough density of these constituents. It could have also been due to the much smaller size of the *M. cavernosa* 3 weeks post-settlement compared to the larger sized of the *P. astreoides, A. agaricia* at 1 week post-settlement. Another reason for the high mortality of the *M. cavernosa* settlers transferred offshore 3 weeks post-settlement may have been the warmer temperatures of the water at the time of transfer offshore and shortly afterward. Due to the natural timing of larval release and spawning of the *P. astreoides, A. agaricia,* and *M. cavernosa*, respectively, the settlers of each species had to be transferred to the offshore nursery in different months. The 3 weeks post-settled *M. cavernosa* settlers were transferred to the offshore nursery at the beginning of a 34 consecutive day period where temperatures in the nursery were at or above 29.4°C, the thermal bleaching threshold for the Caribbean (Tošić & Navas-Camacho, 2012; Bayraktarov et al., 2013; Foo & Asner, 2020), including two days where the temperature exceeded 30.4°C. This may have contributed to the higher mortality of the earliest transfers of *M. cavernosa* settlers relative to *P. astreoides* and *A. agaricia* settlers transferred to the offshore nursery at 1-week post settlement, who did not experience a temperature greater than or equal to 29.4°C until 54 and 34 days post-transfer, respectively.

For all species, most tiles placed in the offshore nursery were eventually colonized by barnacles and algae. Based on the map drawings that were made post-settlement, barnacles often settled right on top of a coral settler. It is likely that corals and barnacles have the same settlement cues, such as presence of microbial biofilms (Dobretsov & Rittschof, 2020). Algae were also observed partially or completely covering some settlers of all species in all treatments, including the aquarium only treatment. Competition for space was likely accounted for a large source of mortality of coral settlers.

The time of transfer offshore that optimizes survival and growth may not necessarily correspond to the optimal budgetary or production logistics of a facility. From a strictly biological standpoint, the results of this study show that the earliest that corals can be transferred to an offshore nursery, without compromising their survival and growth, is around 8-12 weeks post-settlement. However, culturing corals *ex situ* is expensive and laborious, and facilities may be limited in their ability to afford raising mass amounts of corals for long periods of time. For the specific aquarium system used in this experiment, it costed $101.39 per day to cover the

food, maintenance, supplies, and labor required for rearing corals. Whereas for the offshore nursery used in this experiment, the cost was $24.95 per day due to monthly nursery check-ins and associated cost of labor. Thus, the longer corals remain *ex situ*, the more they will cost. While the cost per surviving coral seems high in this experiment, the aquarium used was only being used at roughly one-quarter of its full capacity and thus the cost per surviving coral was high. The aquarium used can hold roughly 2,000 tiles, and therefore a minimum of 2,000 corals. If the aquarium had 2,000 corals, then it would cost 0.05 cents per coral per day. Likewise, if the offshore nursery had 2,000 corals, then it would cost about 0.01 cent per coral per day. Therefore, transferring corals to offshore nurseries earlier can ease the burden on budgets, infrastructure, and resources; however, it comes with trade-offs that each restoration practitioner must take into account when considering their specific goals and capabilities. For example, in this study, transferring *A. agaricites* settlers offshore at their "biologically optimal" 9 weeks post-settlement timepoint (overall survival of 92.5%, average final size 44.9 mm^2) costed $103.11 per surviving coral, while if transferred 1 week post-settlement their overall survival decreased to 69.6% and average final size to 10.1 mm^2 (77.5% smaller), but the cost per coral was substantially cheaper at only $59.95 per surviving coral (41.86% reduction). The difference between the biological and budgetary optimum is however much less stark for *M. cavernosa.* Transferring *M. cavernosa* settlers offshore at their "biological optimal" 12 weeks post-settlement (overall survival 71.7%, average final size 0.75 mm^2) costed $123.20 per surviving coral, while transferring them 7 weeks post-settlement decreased overall survival to 55.9% (22.0% decrease) and decreased average final size to 0.45 mm^2 (40.0% reduction) while it only reduced the cost per surviving coral by 6.40% to $115.31 per coral. Since survivorship of *M. cavernosa* was so low in the treatment moved offshore 3 weeks post-settlement, this timepoint could not be considered a biological or budgetary optimum (costs increased by 190.8% and average final size decreased by 38%, compared to those moved offshore 12 weeks post-settlement).

The biological and budgetary optimal times to transfer corals reared *ex situ* to *in situ* nurseries will vary between locations, as the costs of facilities and labor, and quality of the *in situ* environment (water quality, PAR, abundance or lack of food and predators, etc.) are bound to differ. Additionally, the geographical origin of the parental colonies used may influence results and should be considered. Locally derived parental colonies (as the ones used in this study) are

more likely to produce locally-adapted offspring by passing on mutations to their progeny acquired during their lifetimes (Vasquez-Kuntz et al., 2020). Therefore, restoration and husbandry practitioners need to tailor the transfer of coral settlers to offshore environments to their abilities, available resources, and goals, while anticipating trade-offs.

For coral populations to recover, global and local stressors undoubtedly need to be mitigated. Active restoration can, however, accelerate this recovery and introduce new (potentially stress-tolerant) genotypes in the populations (Goreau & Hilbertz, 2005; Rinkevich, 2005) in the meantime. For sexual propagation to be successful it is imperative that the outplanted corals survive, and that the scale of restoration matches or exceeds the currently observed loss. For that, coral culturing techniques need to be optimized and the costs of rearing corals *ex situ* need to be severely decreased. The finding of this study that sexually produced coral settlers may only need to be cared for in aquaria for 8-12 weeks post-settlement before being transferred offshore provides a way to reduce the costs, labor, and time associated with raising massive amounts of sexually produced corals for restoration. This result is important twofold. First, it reduces costs of *ex situ* rearing while maintaining good survival for large batches of newly settled corals and frees up space in the nursery for the next batch of corals. Second, an earlier deployment offshore may also allow the settlers to acclimate to local ocean conditions (e.g., acquire locally beneficial symbionts) from a very early age, potentially making them better suited to their environment and less vulnerable to disease, ocean warming, and other stressors (Reshef et al., 2006; Palumbi et al., 2014; Kopac & Klassen, 2016; Webster & Reusch, 2017). In terms of new, optimized techniques, the "kebab" structure (Figure 4) used in this study to grow the coral settlers in the offshore nursery, is a novel design that addresses many constraints to the culture of newly settled corals *in situ*. In this design, tiles were strung up in a vertical orientation so that there was enough separation between the tiles for the corals to still have access to light, nutrients, and flow, and sediment and detritus accumulation was reduced, which is commonly a large source of mortality for small and young corals via smothering (Sato, 1985; Birkeland 1977; Fourney and Figueiredo 2017). The small separation between the tiles in the kebabs makes it hard for fish to get in between the tiles helping to reduce death from predation and accidental grazer injury– which is another large source of mortality for small and young corals (Sato, 1985; Doropoulos 2012; dela Cruz & Harrison, 2020). The manner in which the kebabs were attached to the nursery tree prevented the kebabs from getting tangled or wrapped around the branches further

helping to prevent any damage to corals on the tiles. It is very likely that these structures added to the survival and growth success seen in this study. However, it is possible that these structures will only be beneficial for the first few months of grow-out, as the tiles/corals will need to be transferred to an area accessible to herbivores once the corals are at a size suitable of not being damaged or killed by accidental grazing, to help prevent algae overgrowth. Finding the optimal time at which to move *ex situ* reared corals offshore and developing a new design to culture newly settled corals offshore will hopefully contribute to upscaling restoration efforts, increasing the potential for it to be carried out at ecologically relevant scales.

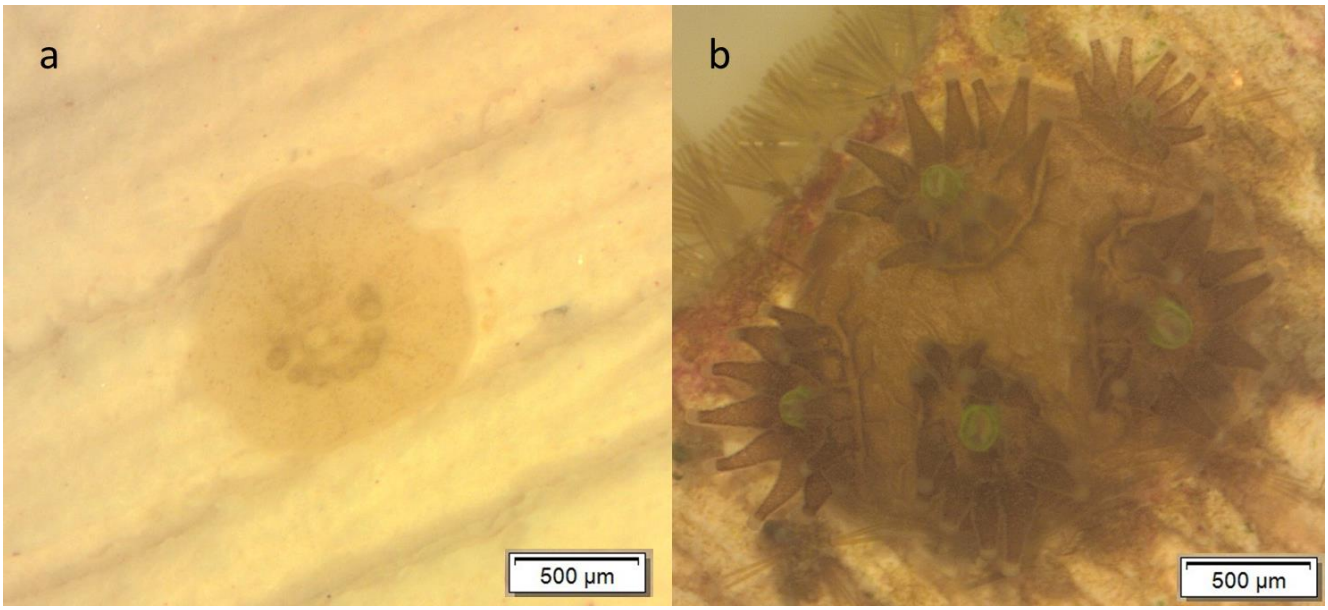

Figure 7. Photographs depicting the difference in development and Symbiodinaceae density between (a) a *P. astreoides* settler at 6 days post-settlement and a (b) *P. astreoides* settler at 6.5 weeks post-settlement. Note it is not the same settler in both photographs.

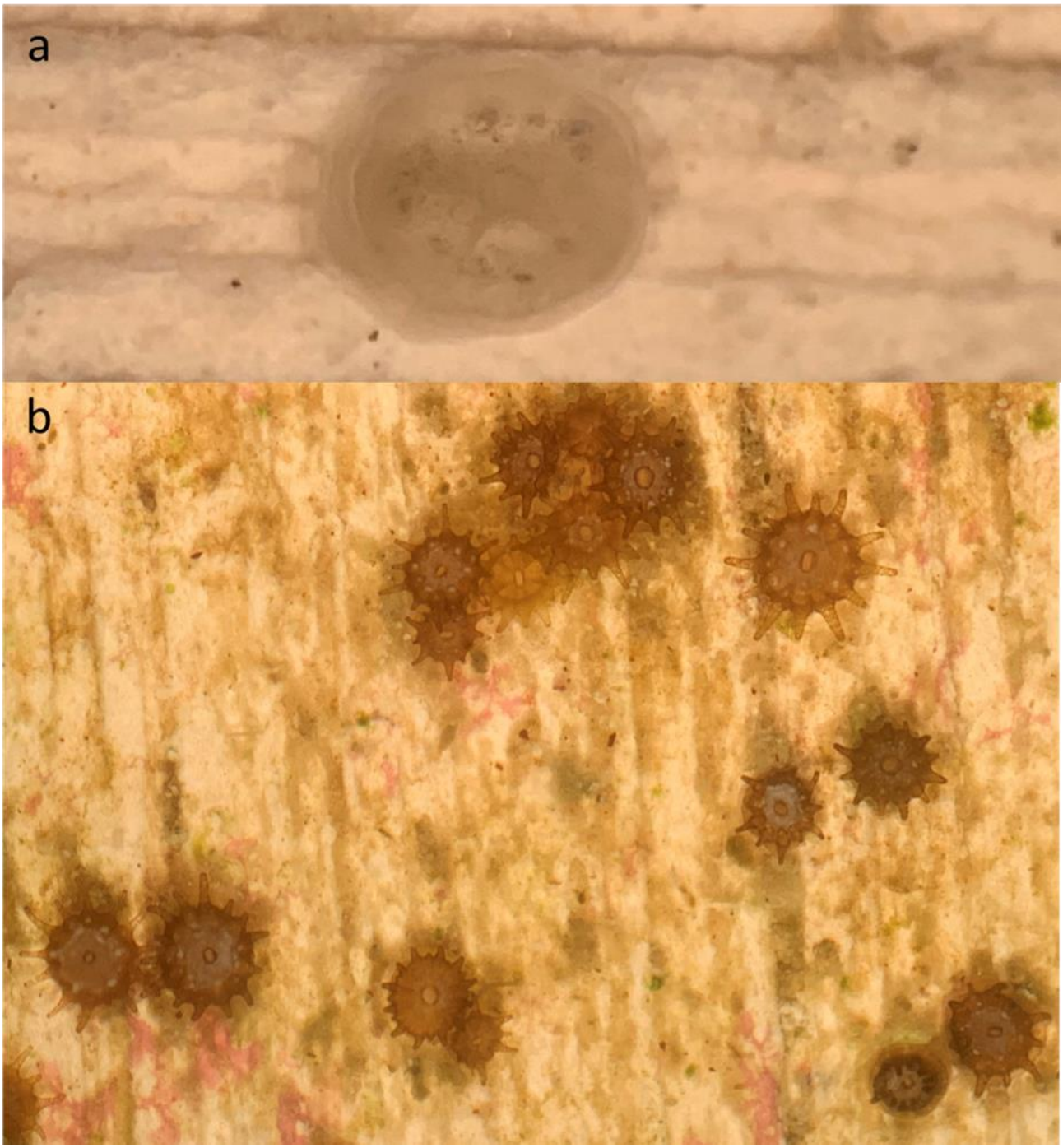

Figure 8. Photographs depicting the difference in development between (a) an *M. cavernosa* settler at 2 weeks post fertilization and (b) *M. cavernosa* settlers at 9 weeks post fertilization. Note the magnification is not the same between the two pictures

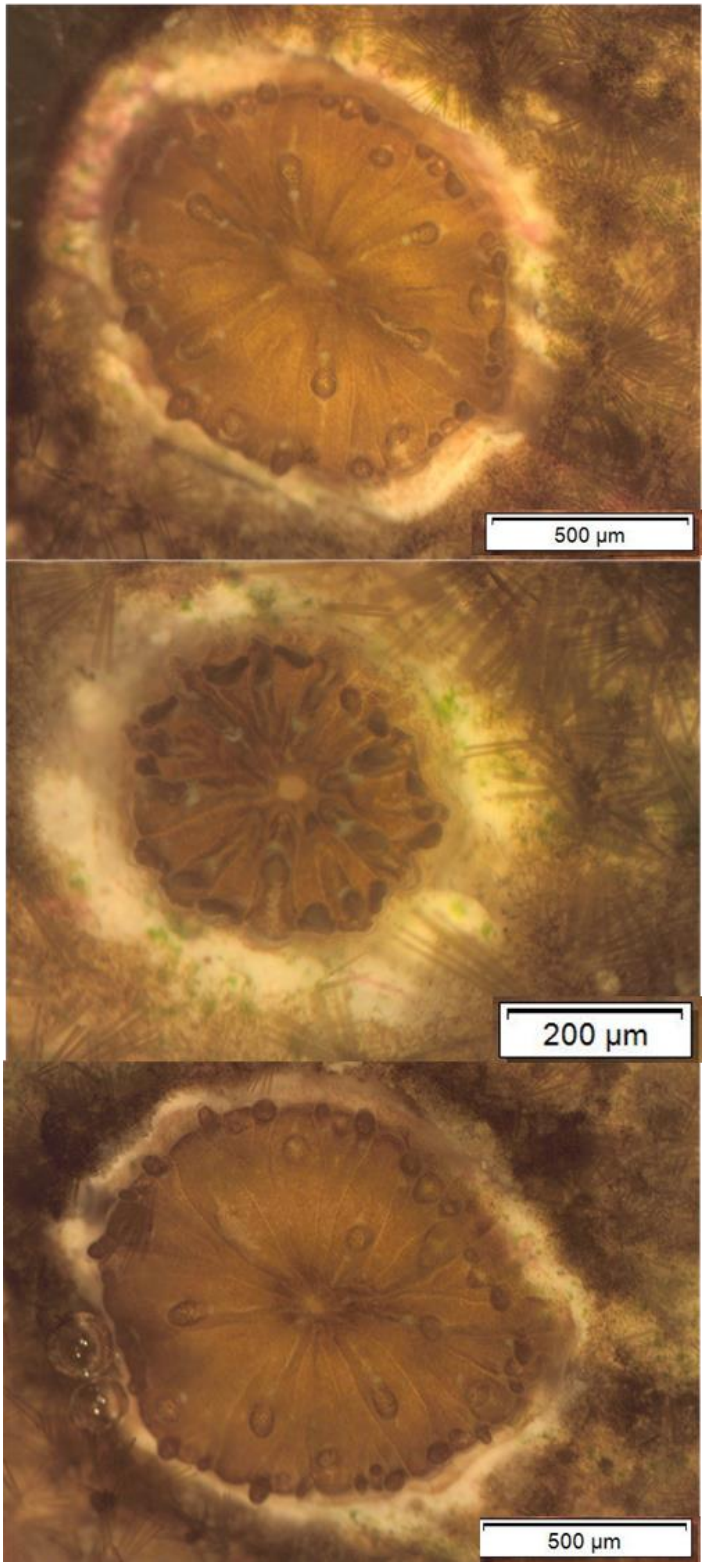

Figure 9. Three different *A. agaricites* at 3 weeks post-settlement creating halos around themselves to keep the algae at bay. Note the magnification is not the same between the three pictures.

Acknowledgements

Temperature logs in the offshore nursery were provided by the Coral Reef Restoration, Assessment & Monitoring Laboratory at NSU. Adult colonies of *M. cavernosa* were collected under Special Activity License SAL-17-1902-SRP. Adult colonies of *P. astreoides* and *A. agaricites* were collected under Special Activity License SAL-20-2238A-SCRP which also authorized the transfer of the coral settlers of *M. cavernosa, P. astreoides* and *A. agaricites* to the offshore nursery.

Thank you to Florida Fish and Wildlife Conservation Commission for granting these permits and Florida Department of Environmental Protection for providing funding to the Marine Larval Ecology and Recruitment Lab at NSU for the husbandry of the *M. cavernosa* broodstock. Thank you to the Lerner-Gray Memorial Fund of the American Museum of Natural History for helping to fund this project. Thank you to the Southern Florida Chapter of The Explorers Club, Inc. for helping to fund this project. Thank you to Dr. Dave Gilliam for allowing the installation of trees in the Broward nursery for this project and to the researchers in the Coral Reef Restoration, Assessment & Monitoring Laboratory at NSU for allowing me to occasionally tag along on dive days and for keeping an extra eye on my trees. Thank you to my lab members, especially Murphy McDonald, Morgan Short, and Ashlee Steinberg for all of your help and support throughout this experiment! Thank you to my family for all of your support during this experiment! Thank you to my whole committee, Drs. Dave Gilliam, Margaret Miller, Diego Lirman, and Joana Figueiredo for your edits and support. I want to especially thank my PI, Dr. Joana Figueiredo, for all the help and guidance you provided to me during this experiment and the writing process!

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