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Coral Castles: Protecting Polyps from Parrotfish Predation

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NOVA SOUTHEASTERN UNIVERSITY

HALMOS COLLEGE OF ARTS AND SCIENCES

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Abstract

Florida's coral reefs are in a state of near-constant degradation concomitant with ever-increasing coastal development and associated anthropogenic impacts. Government agencies, non-profits, and concerned citizens have spent significant time and resources combating these negative impacts. One primary method of mitigating damage to coral reefs is to transplant corals onto degraded reefs using corals that have been grown in nurseries. While many challenges of reef restoration have been overcome, parrotfish predation on freshly transplanted corals persists as a significant issue. Parrotfish are recognized as an essential species on healthy reefs but can also hinder reef restoration efforts by biting young, newly transplanted corals. This project endeavored to reduce the labor and costs of transplant operations by reducing the impacts of predation on transplanted corals. To minimize predation on newly transplanted coral fragments, this project utilized a protective structure that coral fragments are attached to before transplant.

Three novel prototype parrotfish exclusion devices were tested *in-situ*; these prototypes deemed "Coral Castles," have a barrier of biodegradable polyhydroxyalkanoate (PHA) tubes integrated with a concrete base. Two separate fragment transplanting trials, one using *Porites astreoides* and one using *Orbicella faveolata*, were monitored for several months. The Coral Castle prototypes were found to significantly reduce the number of bites incurred by transplanted corals as well as significantly reduce dislodgment, improving survivorship. The *in-situ* biodegradation rate of PHA, described as mass loss, is quantified in a separate experiment. The end goal was to produce an easily secured tile that does not obstruct coral growth, require maintenance, or allow parrotfish to easily predate upon the coral.

Keywords: restoration, predation, coral, PHA, exclusion device, parrotfish, biodegradation

Acknowledgments

There is no possible way that I could have conducted this research without the help and support of my fellow colleagues. I extend my most sincere thanks (in no particular order) to Dr. Brian Walker and the members of the GIS and Spatial Ecology lab; Sasha Wheeler, Alexandra Wagner, Hunter Noren, Reagan Sharkey, Samantha Buckley, Allie Kozachuk, Amanda Zummo, and Zachary Graff. I also wish to extend the same sentiments to Dr. David Gilliam and the members of the Coral Reef Restoration, Assessment & Monitoring lab; Shane Wever, Marina Garmendia, Dr. Nick Jones, John Alfirevich, and Sarah Leinbach. All these folks took on more work than I could have ever hoped to ask for by scouting for appropriate test sites, transplanting all the corals used in these experiments, and committing to months of monitoring thereafter. These predation trials could not have happened without their tremendous efforts.

I would also like to thank Dr. Abigail Renegar and Dr. Kirk Dotson for their prolonged commitment to this project since it started in 2021. This project has gone through many twists and turns before coming into its final form. I could not have done it without their guidance, patience, and dedication. Dr. Renegar also deserves a special thank you for helping me get back on track when I felt lost or needed to be reminded of what it was that I was doing when things were chaotic. While these experiments ultimately did not utilize the training and the predation trials were modified to become *in-situ* experiments, I would like to thank Dr. David Kerstetter for his guidance in completing the training to obtain IACUC permitting for an *ex-situ* coral predation trial. It is my hope that I will be able to utilize the training to obtain experimental permits in the future to further explore parrotfish predation.

I would be remiss to not also thank Catherine Bilodeau, Maeve Clarke, and Ellen Skelton, who assisted me with taking specimen photos prior to their deployment and collecting biodegradation samples when I was away. I also need to thank my fellow onshore nursery staff members, Austin Blakeslee and Amanda Travers, who cared for the corals used in these experiments, prior to the *in-situ* testing, when I could not be there to tend them myself.

Lastly, I would like to express gratitude to two companies, WinCup Inc. and Humidi.co, for providing me with samples of their PHA products from which I constructed numerous prototypes of exclusion devices. These PHA samples were also used in the biodegradation trial.

Preface

The predator exclusion devices tested in this thesis, “Coral Castles,” are protected intellectual property of Dr. Kirk Dotson and are patent pending.

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Introduction

Around the globe, coral reefs face ever-increasing challenges as climate change and human development continue to change the climate and ecology of Earth (Bellwood et al., 2004; Hughes et al., 2003; Mumby et al., 2006; Wagner et al., 2010). Repeated bleaching events, pollution, and disease outbreaks have greatly degraded coral reefs by reducing coral coverage and overall biodiversity (Aeby et al., 2019; Graham & Nash, 2012; Kramer, 2003; Vermeij et al., 2010). These compounding factors have hampered coral reefs from recovering on a global scale despite efforts to counteract coral loss. In particular, the decline of Florida's coral reefs has been documented as far back as the 1960s as multiple bleaching events, multiple diseases, syndromes, and continued coastal development have reduced coral coverage (Rasher & Hay, 2010; Walton et al., 2018; Williams et al. 2021). Decades-long damage has been perpetuated by increased frequency of bleaching events, and poor water quality associated with sedimentation and a myriad of non-point source pollutants, such as fertilizers, plastics, and chemicals (Wagner et al., 2010). However, the most notable recent catastrophe to strike the Florida Reef Tract is Stony Coral Tissue Loss Disease (SCTLD).

This disease has caused significant damage since it first emerged on the reefs of Miami-Dade County in 2014 (Precht et al., 2016; Walton et al., 2018). Even large colonies only survive for as long as 4 months without interventions such as antibiotics and firebreak techniques (Aeby et al., 2019; Shilling et al., 2021). In untreated cases, a lesion of dying tissue with a paling or discolored margin will spread across the infected colony, with occasional lesions forming in separate parts of the coral (Aeby et al., 2019). Unlike other prior diseases and syndromes, SCTLD directly targets many species of corals, such as those listed in Table 1, that are essential to constructing and reinforcing the foundations of the Florida Reef Tract (Jones et al., 1994). While there is currently no identified pathogen that causes SCTLD, it does appear to be the most contagious when an infected colony is within 1.5-3 m of a healthy colony (Williams et al., 2021). It can be spread through direct contact with infected tissue and mucus as well as through seawater. This allows the disease to readily spread in areas of higher coral coverage. There is also a notable spread over distances (>100 km), which appears to happen in waves (Muller et al., 2020; Williams et al. 2021). This is especially alarming given the high lethality of SCTLD. Some reefs have lost as much as 30% of live colony density, resulting in a 60% reduction in live tissue coverage (Walton et al., 2018). The disease has been so devastating that government officials mobilized teams of

biologists & aquarists in 2019 to collect SCTLD-naïve corals into *ex-situ* gene-banks to secure the genetic diversity needed for future restoration projects.

Table 1. Corals regarded as susceptible to Stony Coral Tissue Loss Disease complied by the U.S. National Oceanic and Atmospheric Administration. * denotes a species listed in the U.S. Endangered Species Act (NOAA 2020).

Species name	Common name
Agaricia agaricites	Lettuce coral
Agaricia fragilis	Fragile saucer coral
Colpophyllia natans	Boulder brain coral
Dendrogyra cylindrus *	Pillar coral
Dichocoenia stokesii	Elliptical star coral
Diploria labyrinthiformis	Grooved brain coral
Eusmilia fastigiata	Smooth flower coral
Meandrina meandrites	Maze coral
Montastraea cavernosa	Great star coral
Madracis auretenra	Ten-ray star coral
*Mycetophyllia spp.**	Cactus coral
Orbicella annularis *	Lobed star coral
Orbicella faveolata *	Mountainous star coral
Orbicella franksi *	Boulder star coral
Porites astreoides	Mustard hill coral
Porites porites	Clubtip finger coral
Pseudodiploria strigosa	Symmetrical brain coral
Pseudodiploria clivosa	Knobby brain coral
Siderastrea radians	Lesser starlet coral
Siderastrea siderea	Massive starlet coral
Solenastrea bournoni	Smooth star coral
Stephanocoenia intersepta	Blushing star coral

Enhancing restoration of species which have been severely impacted by SCTLD on the Florida Reef Tract, including at least five endangered species which are denoted in Table 1, has become a priority for many restoration projects. Thanks to the efforts of the Florida Reef Tract Rescue, coordinated by Florida Fish and Wildlife Commission, there is a diverse genetic pool to draw from to produce the next generation of corals. On-shore nurseries which hold corals of opportunity, or corals which have been collected due to construction projects, are also a promising source from which to propagate corals for restoration. Improvements in coral propagation techniques such as induced captive spawning and subsequent larval settlement, micro fragmentation, and advancements in captive coral nutrition, have greatly augmented the ability to

produce large numbers of corals. However, these corals need to be transplanted from nurseries to the reefs by divers and then survive long enough to spawn to make a meaningful contribution to wild coral populations and overall reef recovery.

Restoring reefs is a costly, laborious, and time-intensive endeavor. Producing coral is meticulous work with many opportunities for Murphy's law to intervene, so when enough corals are produced to contribute to restoration it is paramount that the corals are treated with care as they are transplanted at their destination. Even when corals are grown and transplanted with care there is still the hurdle of transplant predation to overcome (Koval et al, 2020; Rivas et al., 2021; Unsworth et al., 2020). While it is expected for coral colonies in Florida to be predated upon by a variety of corallivores, such as sea snails in the *Coralliophila* genus and butterflyfishes, in the genus *Chaetodon*, there is unexpectedly high predation damages from the Stoplight parrotfish, *Sparisoma viride* (Rempel et al., 2020; Rotjan & Lewis, 2005; Rotjan & Lewis, 2006; Rotjan & Lewis, 2009, Rivas et al., 2021; Sanchez et al., 2004).

The biomass of herbivorous fishes on some reefs is comprised of as much as 80% parrotfish, which are essential for combating macroalgae and the dominate herbivore since the population collapse of *Diadema antillarum*, the long-spined sea urchin. Macroalgae can stifle a coral colony's growth and fecundity by means of allelopathy and outcompete corals for space on the reef (Miller & Hay, 1998; Rasher & Hay, 2010; Vermeji et al., 2010). Algae covered reefs also provide less viable settlement space for larval corals, decreasing coral recruitment on the reef (Steneck, 2014). Additionally, consistent grazing by parrotfishes promotes the growth of crustose coralline algae which acts as a settlement cue for many species of coral; this is vital, especially in areas where water quality is subpar and macroalgae are more prolific due to enhanced nutrient availability. Parrotfish utilize their strong beaks, comprised of fused teeth, to bite into the substrate. This allows them to feed upon both endolithic algae within the reef as well as the macroalgae growing on the surface of the substrate. This feeding modality can be divided into two primary categories, excavating and scraping. Excavators, such as *S. viride*, can bite deeply into the substrate, removing algae and endolithic organisms. Conversely, scrapers take a notably wider and more shallow bite on the surface of the substrate, thus primarily removing only the very surface of the substrate.

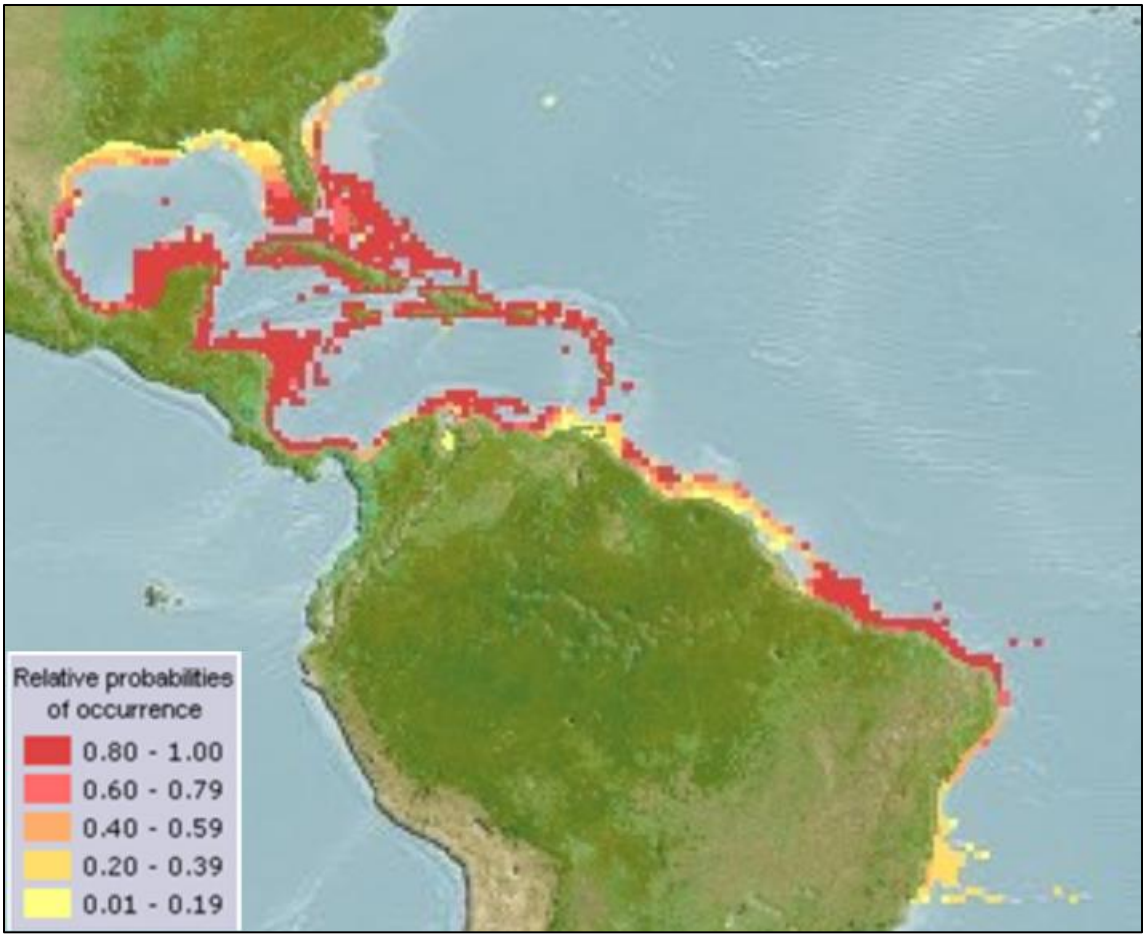

Figure 1. The native range of *Sparisoma viride*. Dark red areas denote high probabilities of occurrence, decreasing as the color transitions to bright yellow. This parrotfish is well spread beyond the bounds of the Caribbean, having widespread implications for transplant activities. Map generated using AquaMaps (2019).

While parrotfishes are a vital part of a healthy reef ecosystem, they also cause their fair share of damage. While primarily acting as an herbivore, *S. viride* also consumes a noteworthy amount of live coral tissue, especially when corals have well-developed gonads that are rich in nitrogen and lipids, leading to a reduction in fecundity during spawning season (Rotjan & Lewis, 2009). When feeding upon live corals there are two primary modes of feeding: 1) “Spot biting” (Figure 2A), is when the fish feeds upon the surface of the coral intermittently, taking small bites which are scattered over the surface of the colony, and 2) “focused biting” (Figure 2B) when the parrotfish takes multiple bites directly next to and atop one another. This type of feeding removes a swath of tissue from the colony.

Healthy coral can recover almost completely in as little as 65 days from these predation events if the damage is less than ~1.25cm^2 (Rempel et al., 2020). After this size threshold is surpassed, healing rates decline abruptly until the size of the predation wound reaches ~8.2cm^2, whereafter the healing is negligible, often only healing the edges of the wound within the same 65-day time frame (Rempel et al., 2020). This predation can become overwhelming for the colony and damage from predation can result in whole colony mortality with damaged tissues serving as a potential entry point for disease, necrosis, and algal infestation (Koval et al., 2020; Kramer, 2003). This predation becomes especially problematic for small, transplanted colonies and coral fragments that lack significant tissue area to mitigate the damage, and which parrotfish preferentially feed upon. Additionally, the aggression and force with which the parrotfish bite can dislodge newly transplanted corals which ultimately leads to their premature demise because the coral can easily fall into areas ill-suited for their survival. In some cases, as much as 94% of transplanted colonies have been documented as incurring notable parrotfish predation within two weeks of transplant (Brownlee, 2010). With transplant activities not only encompassing restoration but also environmental mitigation activities, such as removing corals from perceived threats such as construction or dredging activities, there are considerable opportunities for parrotfish predation to result in diminished success of transplant efforts. While many methods have been trialed with varying degrees of success, a "silver bullet" is yet to be found (Harrell & Lirman, 2023; Koval et al., 2020; Rivas et al., 2021; The Florida Aquarium, 2022; Unsworth et al., 2020).

Cages and spikes, which encase the colony, are well documented to deter parrotfish from biting on transplants (Rivas et al., 2021). However, they require notable dive-time to deploy and once the structures are removed, parrotfish seemingly recognize the coral as a "new" transplant and will begin to preferentially feed upon it (Rivas et al., 2021). Additionally, cages require cleaning to remove biofouling which reduces waterflow over the coral and blocks sunlight. In a similar methodology, Patrick's Parrotfish Protectors, a teepee-like structure made from bamboo skewers, was tried by The Florida Aquarium in order to obstruct parrotfish predation attempts (The Florida Aquarium 2022). While both cheap and biodegradable, protection provided by the structure resulted in notable predation rates and total dislodgment but improved in comparison to the controls with no protection (The Florida Aquarium, 2022).

Another attempt at resolving excessive predation on outplants, with greater success, has been embedding corals in concrete as they are planted onto the substrate. This has been shown to provide a significant level of protection from predation but amplifies complication from sediments (Koval et al., 2020). The coral is nearly flush with the substrate, meaning sediments can easily accumulate on the tissue. This causes mortality over time if the sediment is not removed by the current or by other means. Taking the time to sculpt the cement around the coral also requires more working time per outplant, thus divers cannot outplant as many corals per dive as they might otherwise be able to if the outplanting procedure were more streamlined.

Attempts to change the corals' palatability for parrotfish have also been tested. Feeding corals a dried powder made from *Dictyota*, a common macroalgae on the reefs of southeastern Florida, prior to outplanting was found to reduce predation on *Pseudodiploria sp.* and *O. faveolata* for one month (Harrell & Lirman, 2023). However, this result was dependent upon feeding coral the *Dictyota* powder for 2 months prior to outplanting. This poses an issue for corals that need to be relocated immediately, such as in areas where there are no holding facilities, or when the sheer number of corals that need to be planted is too great for them to be held onshore for an extended period. This solution, while promising for these two species, creates a bottleneck for restoration efforts by requiring significant onshore infrastructure, skilled staff, and a pipeline to create the volume of specialized feed required to inoculate the corals over the course of 2 months, all of which will increase the cost of each outplant.

With the pressures of pending coastal construction, dredging, and extreme weather events, the need for a solution is greater now than ever. However, inspiration struck after seeing a robust stainless-steel structure that successfully excluded parrotfish so the investigators could evaluate changes to the benthic reef habitat in the absence of large parrotfish (Steneck, 2014). The device, while effective in its purpose, seemed overly robust, costly, and difficult to deploy en masse. Various iterations of designs for parrotfish exclusion devices soon followed and materials research lead to an ideal solution, a concrete tile with integrated PHA predator exclusion structures, the Coral Castle.

Material engineering and biochemistry has created an overlooked solution to creating a strong yet biodegradable parrotfish exclusion device. The biopolymer polyhydroxyalkanoate (PHA) is a biodegradable plastic that is produced by bacteria. Polyhydroxyalkanoates (PHAs) are naturally produced by bacteria and archaea through the fermentation of carbon substrates (a food

source, typically canola oil) within the cell (Moeller & Matyjaszewski, 2012). The material is light, approximately 1.25g/cm^3 depending on the manufacturer, and is fairly strong (Vandi et al., 2018). PHA manufacturing has become increasingly cost-effective and efficient in recent years, and coupled with improvements in manufacturing processes and international interest in "green materials," has led to a spur in PHAs products manufacturing (Paula-Eliasa et al., 2021); McAdam et al., 2020). The most common products being produced from PHAs are primarily focused on replacing single-use items which have been produced almost entirely using traditional petroleum-derived plastics.

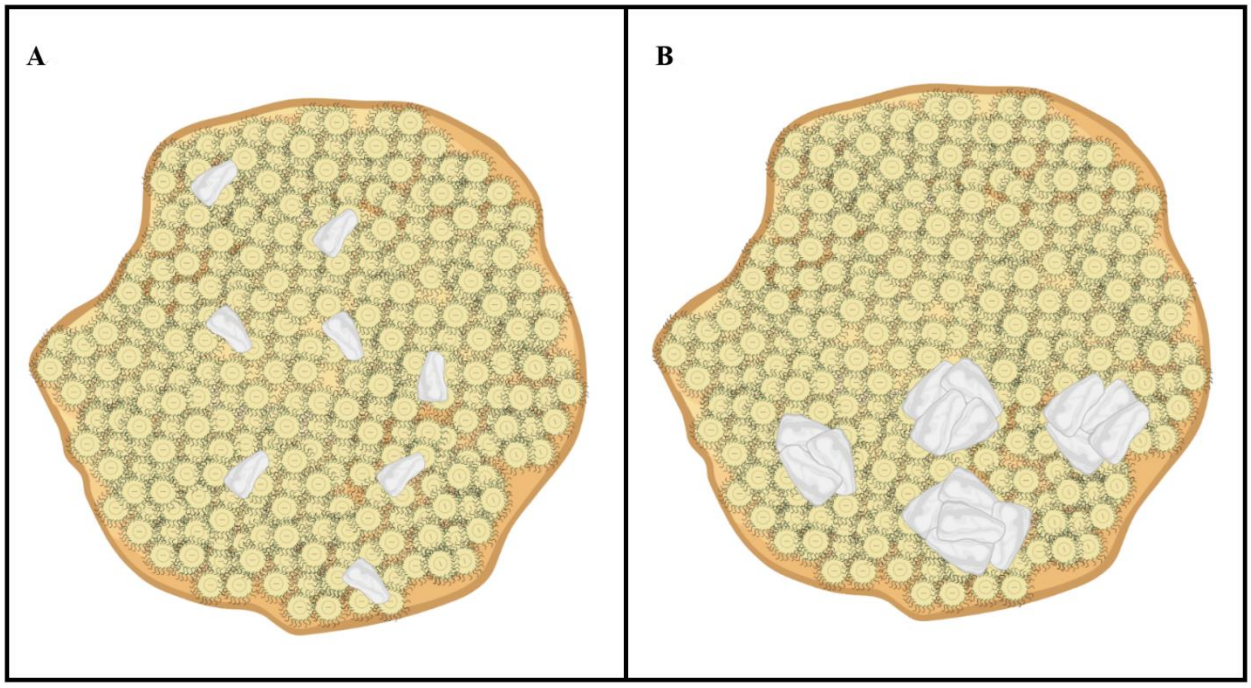

Figure 2. Variations in parrotfish feeding styles when feeding upon live coral. A) "Spot biting" is the scattered and seemingly random pattern of bites across the whole colony. B) "Focused biting" causes a single large scar which occurs when bites overlap with one another. Figure produced using Biorender.com

Polyhydroxyalkanoate is completely biodegradable in nearly all types of common environments, including marine (Doi et al., 1992; Kusaka et al., 1999). The decomposition of PHA is primarily dependent on the group of enzymes known as PHA depolymerases (dPHA) which is produced by a myriad of archaea, bacterium and fungi that utilize PHA as an energy and carbon source (Paula-Eliasa et al., 2021; Gebauer & Jendrossek 2006; Jendrossek & Handrick 2002). There are two pathways by which PHA degrades; anaerobically, such as when PHA is buried in sediments or anoxic waters, which produces carbon dioxide and methane. Whereas aerobic

biodegradation, occurring above ground and in oxygenated environments with adequate water flow, produces carbon dioxide and water (Urmeneta et al., 1995).

Both biodegradation processes depend on up microorganisms colonizing upon the surface of the PHA structure and producing dPHA enzymes to erode the surface. Rates of erosion vary with species of colonizing microorganisms, environmental conditions, and material density. (Jendrossek & Handrick, 2002) Another driving factor for the overall biodegradation rate of PHA structures is the surface area-to-mass ratio. Objects that have a greater surface area-to-mass ratio tend to degrade more quickly (Dilkes-Hoffman et al., 2019). This is strong linkage between the biodegradation rate and the sure area-to-mass ratio is because the biodegradation of PHA is primarily surface erosion as opposed to bulk erosion. Surface erosion is degradation which is contained to the surface of an object, whereas bulk erosion also results in degradation from within (Von Burkersoda et al., 2002).

Given the strength, biodegradability, and biocompatibility of PHA, it seems an like an ideal candidate for use in creating a time, and cost, effective solution to parrotfish predation on coral transplants. The "Coral Castle" addresses the bottleneck that parrotfish predation poses to restoration. This device uses a concrete foundation to hold PHA tubes in place around a coral, which is mounted in the center of the device (Figure 3). The PHA tubes are spaced to allow sufficient waterflow over the coral to prevent sedimentation but placed close enough together that a parrotfish will be unlikely to attempt to feed on the coral at the center, as if it were protected by a cage or spikes. However, unlike a cage, the protective structure should not need to be cleaned after deployment and will biodegrade on its own, eliminating the need for divers to do any follow-up maintenance. Additionally, the concrete foundation of the device should allow for quick and efficient out planting by divers since the only *in-situ* preparation needed is to quickly brush the substrate clean before laying down cement or another adhesive.

Objectives

PHA degradation

Despite an increase in biopolymer utilization and manufacturing, there is little to no data regarding how long it takes PHA products to degrade in the coastal waters of southern Florida. Therefore, a primary objective of this experiment is to generate data to help estimate the biodegradation rate of polyhydroxyalkanoate in the marine environment of Southeast Florida.

Prototype trials

Developing a predator exclusion device, such as the prototype shown in Figure 3, that shares the positive attributes of both a fully encompassing cage and mounting the coral flush with the reef to protect the margins would be extremely useful for increasing transplant survival rates. The primary goals of a new prototype parrotfish exclusion device should focus on providing sufficient protection from direct bites from parrotfish, reducing the rate of transplant dislodgment, thus improving overall survivorship. The design should also be conscientious of complications from sedimentation and risk of obstructive biofouling. Furthermore, it would be extremely advantageous if the divers did not have to spend significant time setting up the device *in-situ* or spend time retrieving it after predation effects subside.

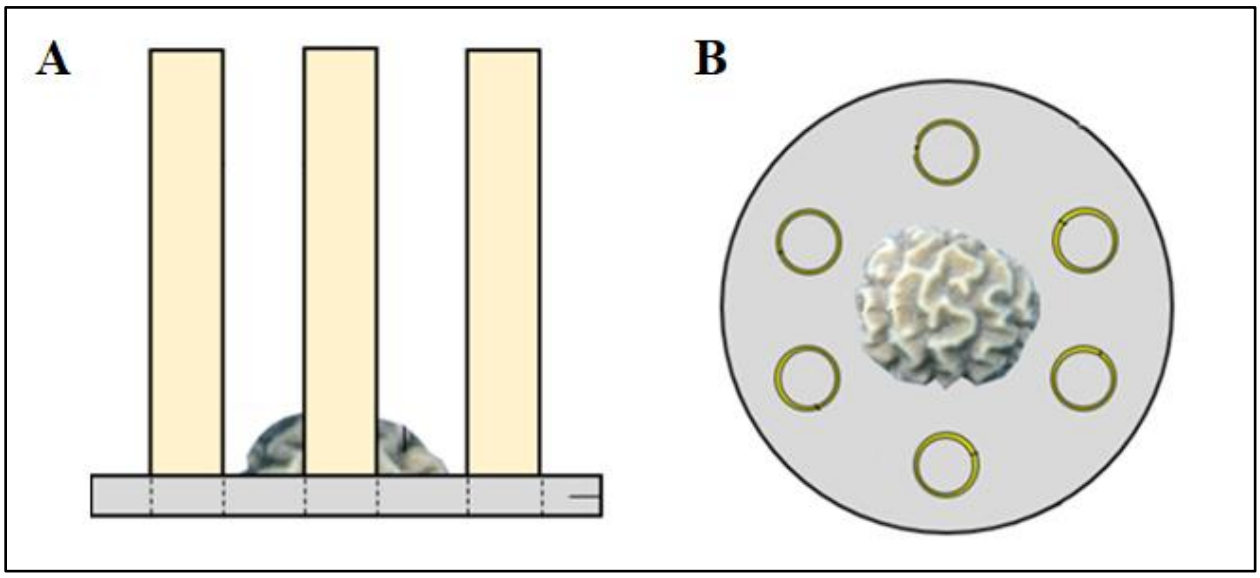

Figure 3. A) A side view of a coral fragment protected within a Coral Castle utilizing PHA tubes manufactured by Humidi. B) A top view, scale diagram of a Coral Castle. The yellow rings denote the placement of PHA tubes which are embedded into the concrete foundation. Coral Castle designs are variable and are currently patent pending. Figure prepared by Dr. Kirk Dotson.

Methods and Materials

PHA degradation

The degradation rate in the marine environment of the three types/sizes of PHA structures used to construct the Coral Castles was examined by measuring mass loss over time. A total of 1200 PHA samples were placed in three weighted mesh laundry bags; Bag A contained 400 11.4 x 1.9 cm tubes and Bag B contained 400 9.6 x 1.9 cm tubes, each with a 1 mm wall thickness, produced by Humidi Co.; and Bag C contained 400 16.035 x 0.7 cm drinking straws produced by

Phade. Each bag was secured using paracord to the same cleat of the docks in the boat basin of the NSU Guy Harvey Oceanographic Center in Dania Beach, Florida, on the eastern side of Port Everglades. Prior to deployment on February 13th of 2023, all PHA samples were labeled using a permanent marker, and the individual mass of all samples were measured using an Ohaus Adventurer AX324 analytical balance.

Once weekly, for 20 weeks, the bags were retrieved from the bottom, and 20 randomly selected PHA tubes were removed from each bag. The bags were then redeployed. The collected tubes were rinsed with RO water and scrubbed gently with a toothbrush to clear away debris (such as sediments and biofouling), then left to dry in a fume hood with negative ventilation for 48 hours at approximately 25 °C. Once fully dried, the PHA tubes were individually reweighed to determine mass loss, where mass loss (grams) = initial mass (grams) – final mass (grams). Once selected, tubes were not replaced.

Prototype trials

The effectiveness of the novel parrotfish exclusion device was tested in two separate *in situ* trials (one trial with *Orbicella faveolata* and one trial with *Porites astreoides*). Each trial tested four tile types: control tiles and Coral Castle prototypes A, B, and C.

The control tiles were cement disks constructed with Titan America LLC. Portland-Limestone Cement Type 1L cast in a 12.7 cm diameter, 0.9 cm thick, circular silicone mold. Coral Castle prototypes A, B, and C were made in the same manner but also included the PHA structures used to deter parrotfish. Types A and B used the same 11.4 x 1.9 cm and 9.6 x 1.9 cm tubes, respectively, as in the biodegradation experiment. Type C used the 16.035 x 0.7 cm Phade straws, which were shortened to the same height as Type B (9.6 cm). Wall-to-wall spacing, the open space between the PHA structures, of all prototypes was ~4 cm.

Once the cast tiles dried for 48 hrs., a drill with a 1/4” masonry bit was used to form a hole near the perimeter of the tile to attach an ID tag with a zip tie. Tiles were prepared in the same manner for both *in situ* trials, apart from a small ceramic peg which was integrated into the bottom on the tiles that were used in the *Orbicella faveolata* trial. This additional component was requested by the dive team to ensure that the tile could be secured on their designated outplant site.

Fragments used in each of the prototype trials were cut from corals which were collected as “corals of opportunity” and held in the NSU Onshore Coral Nursery at the Guy Harvey Oceanographic Center. Corals held onshore are fed three times weekly using Reef Blizzard and

Coral Amino, both produced by Brightwell Aquatics. All fragments were cut using a Gryphon AquaSaw XL C40-CR Custom 42 with the accompanying 42" Gryphon Diamond bandsaw blade. Cutting was done using saltwater from each coral's respective holding system mixed with Lugol's Iodine, manufactured by Brightwell Aquatics, at a concentration of 0.5 ml/L. The saw was flushed clean and new saltwater/iodine mix was poured into the saw every 10 minutes or when cutting a different colony, whichever came first. Once fragments were cut, they were gently rinsed with water from their respective holding system before being placed into the holding system.

Once all the corals for trial were cut, they were affixed to their Coral Castle using Reef Glue Gel (Ocean Wonders). Each Coral Castle, with its fragment, was then photographed and returned to the onshore nursery to heal before transplant.

Orbicella faveolata

Fragments of *O. faveolata* (n=40) were cut on February 22nd, 2023 from a single colony (collected from the inner reef of Dania Beach, Florida as authorized under license SAL-20-1727-SCRP) held in the onshore coral nursery. The fragments were randomly assigned to a tile type test group with 10 fragments per tile type.

Seven days later a team of divers planted all 30 Coral Castle prototypes and 10 control tiles in a randomized, 8 x 5 grid with approximately 0.5 m spacing between transplants. The Coral Castles were secured to the reef structure by creating a 1" deep, 3/8" diameter pilot hole into the rock using a Nemo Underwater Drill-50M. The Coral Castle's integrated stem was then coated with 2-part marine epoxy and inserted into the pilot hole. The Coral Castle, alongside a scalebar, was then photographed using an Olympus TG-5 underwater camera.

The outplants were assessed after 24 hours (03/02/2023), 7 days (03/08/2023), 28 days (03/29/2023), 59 days (04/26/2023), 98 days (06/07/2023), and 118 days (06/27/2023). Top-down photos including a scalebar were taken by divers. Divers also noted if there was any damage to the Coral Castle or if there was excessive algae growth on the PHA structures that could smother the coral but did not clean the Coral Castle.

Figure 4. Divers distributing Coral Castles around the test site at the beginning of the *Porites astreoides* predation trial. Photo taken by, and used with permission from, Shane Wever.

Porites astreoides

On May 9th, 2023, 120 fragments of *Porites astreoides* were cut from 3 colonies (collected from the Osborne Tire Reef as authorized by license SAL-22-2482-R) that were held in the onshore coral nursery. The fragments were randomly assigned to a tile type test group, with 30 fragments per tile type.

On May 16th, 7 days later, a team of divers planted all 90 Coral Castle prototypes and 30 control tiles into 3 separate randomized radial grids, all on the same dive site. The spacing between transplants was approximately 1 m. The Coral Castles were secured to the reef structure by cleaning a section of reef with a wire brush and adhering the bottom of the tile with Titan Portland Limestone Cement Type I/II. The Coral Castle, alongside a scalebar, was then photographed using an Olympus TG-5 underwater camera.

The outplants were assessed after 24 hours (05/17/2023), 9 days (05/25/2023), 29 days (06/14/2023), 71 days (07/20/2023), and 94 days (08/14/2023). Top-down photos including a scalebar were taken by divers. Divers also noted if there was any damage to the Coral Castle or if there was excessive algae growth on the PHA structures that could smother the coral but did not clean the Coral Castle.

Data Analysis

PHA degradation

Non-linear regression was used to describe the observed degradation rate of the PHA samples. There were no comparisons made amongst the different groups as the goal was simply to describe the degradation rate of the different PHA tubes. While the experiment was intended to run for 20 weeks with all three types of PHA tubes, the short Humidi tube exposure was limited to 16 weeks because some samples were lost; the mesh bag which contained those tubes was found to have a large hole.

Prototype trials

Incurred bites & tissue area

For both transplant trials, a restricted maximum likelihood (REML) model was used to compare both the number of bites each test group incurred during the duration of the experiment as well as to compare their beginning and ending tissue area. When comparing the number of incurred bites of each group, the REML model was used in conjunction with a Geisser-Greenhouse epsilon (ε) correction to compensate for a loss of sphericity. The REML model comparing tissue area did not need this correction because the concept of sphericity does not apply to data sets with only two levels. Post hoc analysis (Tukey's multiple comparisons test, $\alpha=0.05$) was used to examine specific differences between test groups where appropriate. No transformations were used on these datasets and the two transplanting trials were analyzed separately in their entirety.

Survivorship

Overall survival of *P. astreoides* fragments was analyzed using the Kaplan-Meier method with a log-rank Mantel-Cox test ($\alpha=0.05$) to compare the survival curves. For the purposes of the *P. astreoides* analysis, the dislodgment of a coral fragment from the center of the Coral Castle was treated as a death. Overall survival of *O. faveolata* fragments could not be analyzed using the Kaplan-Meier method, as the only deaths that occurred during the predation trial were a result of widespread sedimentation. With 100% survival and 5 censored replicates, there was no

conceivable difference in predation related survivorship between the control and experimental groups for this species.

Results

PHA degradation

Biodegradation of the Phade straws was slower than anticipated, but still notable over the 20-week exposure (Figure 5A). Quadratic regression of mass loss over time was expressed as $Y(\text{grams}) = 0.8148+(-0.006338*X)+(-0.0003365*X^2)$ with an $R^2 = 0.918$. Given the starting mass of 0.873 ± 0.02 g, it was estimated that it would take approximately 62 weeks to fully biodegrade with an average daily mass loss of 0.002 grams.

Biodegradation of both Humidi tube types were also slower than anticipated, but still notable over the 20-week exposure (Figures 5B and 5C). Quadratic regression of mass loss over time for short tubes was expressed as $Y(\text{grams}) = 7.907 + (0.03283*X) + (-0.007034*X^2)$ with an $R^2 = 0.961$. Given the starting mass of 7.918 ± 0.02 g, it was estimated that it would take approximately 126 weeks to fully biodegrade with an average daily mass loss of 0.009 grams. Biodegradation of the long tubes was expressed as $Y(\text{grams})=7.907+(.03283*X)+(-.007034*X^2)$ with an $R^2 = 0.9849$. Given the starting mass of 8.468 ± 0.02 g, it was estimated that it would take approximately 81 weeks to fully biodegrade with an average daily mass loss of 0.015 grams.

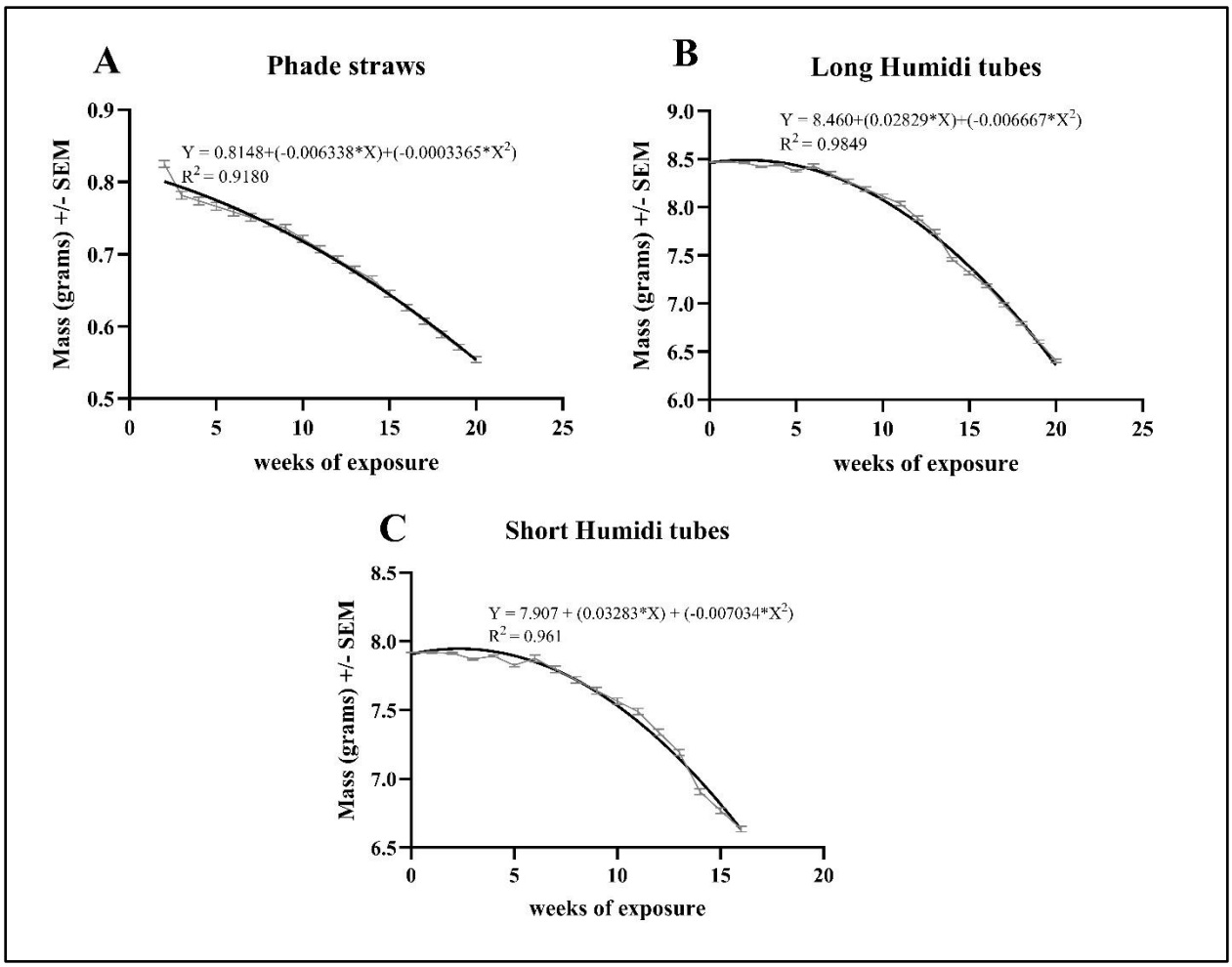

Figure 5. A) Mass loss of Phade straws over 20 weeks of exposure. B) Mass of long Humidi tubes over 20 weeks of exposure. C) Mass loss of short Humidi tubes over 16 weeks of exposure. Note that any increase of mass represented by the regression line is an artifact of line fitment, no increase of mass was seen at any point during the biodegradation trial.

Prototype trials

Incurred bites

Predation on the *O. faveolata* transplants was less intense than expected. The 6 total bites in this trial were observed on 40% of the control tiles. No bites occurred on any corals after the first 28 days (Figure 6A). An REML mixed-effects model (α=0.05, ε=0.1845) showed a significant increase in total bites over time (p=0.0491, $F_{(1.108,\ 37.84)}$ =3.993), a highly significant difference in the number of total bites between treatment groups (p=0.0021, $F_{(3,\ 36)}$ =5.976), and a highly significant difference in the number of incurred total bites over time according the coral's treatment group (p= <0.0001, $F_{(18,\ 205)}$=4.051). Post hoc analysis (Tukey's multiple comparisons test,

α=0.05) was unable to resolve specific differences amongst treatment groups despite all the bites in the experiment occurring on controls.

Observed predation on the *P. astreoides* was far greater than the *O. faveolata* fragments, with test tiles accruing 83 bites over 94 days, of which 78 bites were on control tiles, 1 bite occurred on a Type B tile, and 4 bites were on Type C tiles (Figure 6B). The greatest number of bites overall happened between days 9 and 29, where 36 new bites were noted, 33 on controls and 3 on Type C. An REML mixed-effects model (α=0.05, ε =0.3688) showed a highly significant increase in total bites over time (p=<0.0001, $F_{(1.844, 208.8)}$ =59.12), a highly significant difference in the number of bites between treatment groups (p=<0.0001, $F_{(3, 116)}$ =71.09), and a highly significant difference in the number of incurred bites over time according the coral's treatment group (p= <0.0001, $F_{(15, 566)}$=51.14). By day 94, 97% of all controls had incurred at least one bite. Comparatively, low percentages of corals protected by Type A (0%), Type B (3%), and Type C (17%) tiles had bites.

Post hoc analysis (Tukey's multiple comparisons test, α=0.05) found significant differences between treatment groups of *P. astreoides* fragments 9 days after transplant, where both Type A and Type B Coral Castle prototypes had significantly fewer average bites per fragment than the control group (p=0.0264 for both Type A and B). At 9 days post transplant, the Type C Coral Castles did not significantly differ from any other treatment group. However, by 29 days post-transplant all prototypes had incurred significantly less bites than the control group (p=<0.0001 for all), but still did not significantly differ from each other. By day 94, all prototypes still had significantly less bites than the control group (p=<0.0001) and did not significantly differ from one another. The 95% confidence intervals of this post hoc analysis can be seen in Appendix C.

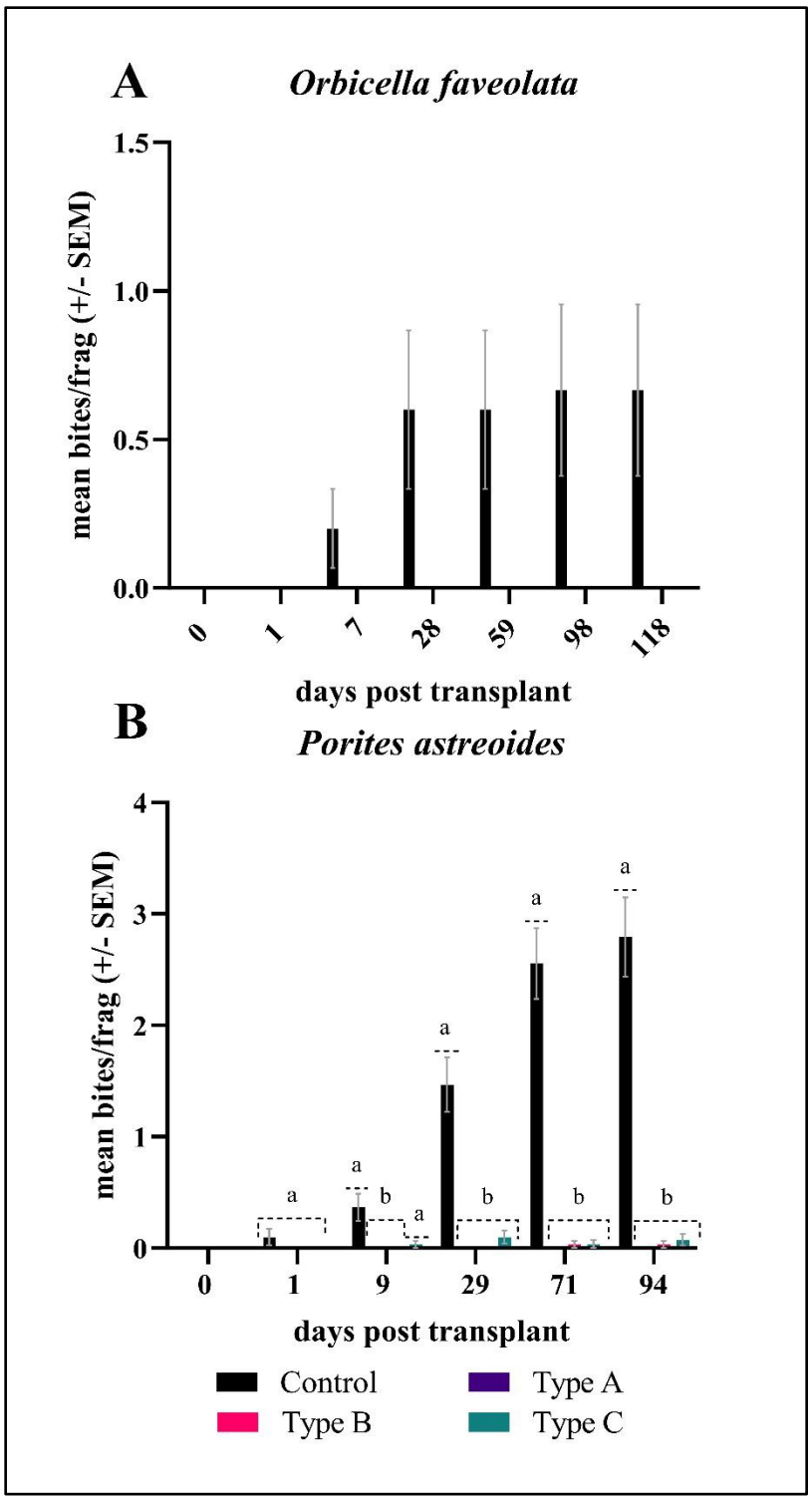

Figure 6. A) Bites on *O. faveolata* fragments (mean ± SE) for each tile type during the monitoring period. Note that the number of replicates was reduced between 04/26/2023 and 06/07/2023, which increased the mean despite the experimental group not accumulating any new bites. B) Bites on *P. astreoides* fragments (mean ± SE) for each tile type during the monitoring period.

Tissue area

Mean tissue area of *O. faveolata* fragments were compared using an REML mixed-model (α=0.05, ε =n/a, with assumed sphericity). Corals on all tile types had notable growth 118 days after transplant (Table 2 and Figure 7A); a highly significant increase in tissue area was observed for all corals over time (p=<0.0001, $F_{(1, 31)}$ =42.59), with no significant difference in the tissue area among treatments groups (p=0.1552, $F_{(3, 36)}$ =1.852), and no significant difference in the tissue area over time according the coral's treatment group (p= <0.1005, $F_{(3, 31)}$=2.265).

Table 2. *Orbicella faveolata* and *Porites astreoides* fragment tissue area on each tile type.

Orbicella faveolata	Initial area (cm^2)	% change	Final area (cm^2)	Mean growth (cm^2)/day
Control	8.01 ± 0.38	+ 21.2%	9.71 ± 0.50	+ 0.014
Type A	8.43 ± 0.35	+ 27%	10.70 ± 0.53	+ 0.019
Type B	7.82 ± 0.40	+ 37.4%	10.75 ± 0.47	+ 0.025
Type C	7.22 ± 0.27	+ 39.7%	10.08 ± 0.43	+ 0.024
Porites astreoides				
Control	9.40 ± 0.48	+ 28%	12.02 ± 3.42	+ 0.028
Type A	9.23 ± 0.43	+ 30%	11.31 ± 3.35	+ 0.022
Type B	8.97 ± 0.42	+ 22%	10.92 ± 2.74	+ 0.021
Type C	8.55 ± 0.44	+ 29%	11.05 ± 2.42	+ 0.027

Mean tissue area of *P. astreoides* fragments was also compared using an REML mixed-model (α=0.05, ε =n/a, with assumed sphericity). Corals on all tile types had notable growth 94 days post-transplant (Table 2 and Figure 7B), with a highly significant increase in tissue area for all corals over time (p=<0.0001, $F_{(1, 31)}$ =42.59), no significant difference in the tissue area among treatments (p=0.1552, $F_{(3, 36)}$ =1.852), and no significant difference in tissue area over time according to the coral's treatment group (p= 0.1005, $F_{(3, 31)}$=2.265).

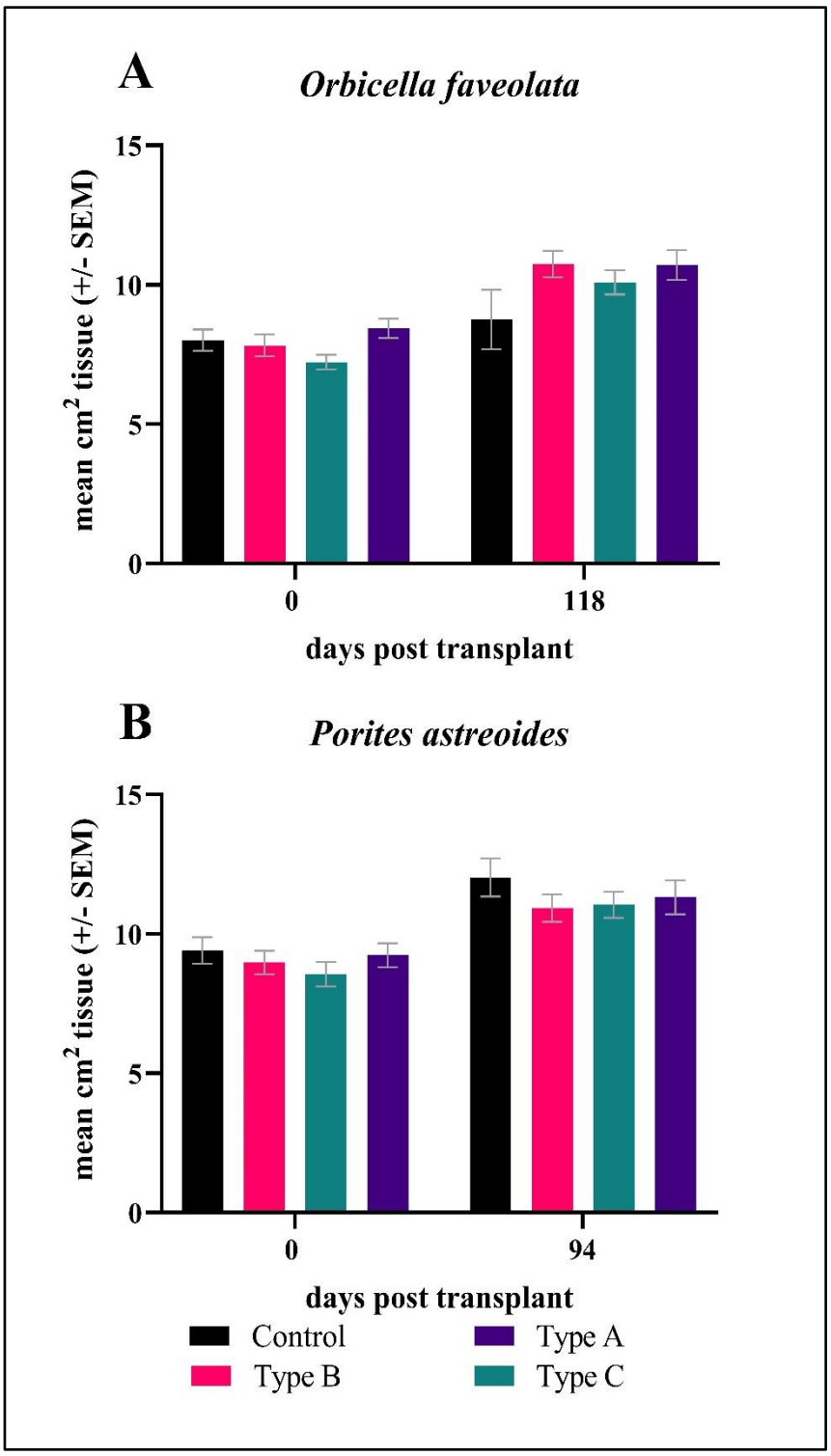

Figure 7. A) *Orbicella faveolata* fragment tissue surface area (mean ± SE) at the beginning and end of the monitoring period, and B) *Porites astreoides* fragment tissue surface area (mean ± SE) at the beginning and end of the monitoring period.

Survivorship

A Kaplan-Meier survival curve for *Porites astreoides* is shown in Figure 8; the survival curves were significantly different between tile types (χ^2= 9.648, df=3, p=0.0218, log-rank Mantel-Cox test). Corals on control tiles were the most likely to die due to predation, followed by the corals on Type C tiles. Corals on Type A and B tiles were the least likely to die from predation (0%). Over the course of the 94-day monitoring period, 5 corals (17%) on control tiles and 3 corals (10%) on Type C tiles were lost to predation. The survival analysis for the *O. faveolata* predation trial was ultimately unnecessary, as no coral mortality occurred due to factors encapsulated by the experiment.

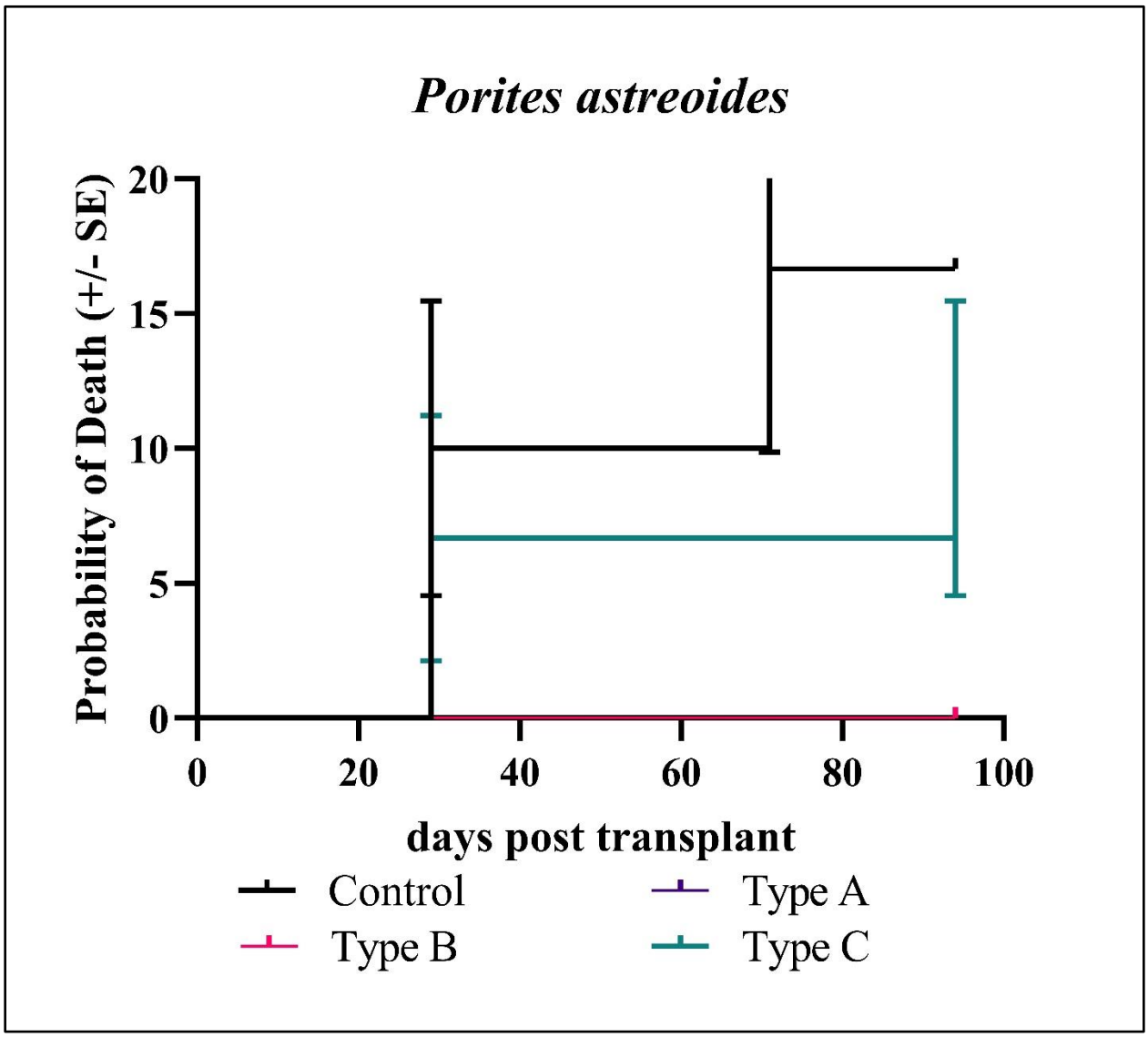

Figure 8. A Kaplan-Meier survival curve displaying survival of all *Porites astreoides* fragments in each tile type test group.

One event of note occurred during the *O. faveolata* predation trial. On April 12th, 2023, Fort Lauderdale received approximately 63.5 cm of rain in a single day. This caused historic flooding in the area and vastly overwhelmed the local area's stormwater infrastructure. This, coupled with rough sea conditions, led to widespread sedimentation of the experimental site. While one of the goals of the predation trial was to quantify sedimentation if it had occurred as a result of the Coral Castles and controls, the sedimentation that led to the complete loss of 5 corals (1 control, 1 Type B, and 3 Type C) was not considered to be part of the experimental results because the sediments which smothered the corals was also smothering a widespread area around the coral and the reef area in general, including some of the low-profile benthic features of the experimental site.

Discussion

PHA degradation

Degradation of PHA samples in this biodegradation trial were notably slower than what was expected in comparison to other studies using PHA films and small discs (Cho et al., 2021; Sridewi et al., 2006; Volova et al., 2010; Voinova et al., 2008). Although the shape of the degradation curve is similar to other trials done in tropical mangrove habitats (Sridewi et al., 2006), the very light and thin PHA straws, which have been shown to degrade in marine aquaria within 10 weeks, did not degrade completely (Phade Products, 2021). A meta-study compiled from 14 other experiments found that the general marine biodegradation rate is an average of 0.04-0.09 mg $day^{-1}cm^{-2}$ (Dilkes-Hoffman et al., 2019). Given the surface area of the PHA straws, the degradation rate calculated by Dilkes-Hoffman would result in complete disintegration of the straw in 24-54 weeks as opposed to the 64 weeks estimated by this study. This rudimentary estimation of the total biodegradation times of the Phade straw, using the degradation rates from Dilkes-Hoffman, does not account for the change in the surface area of the straw over time; the surface becomes increasingly coarse as it degrades thus increasing the surface area. Knowing the surface area will increase over time with a concomitant increase in the overall rate of biodegradation, it can be hypothesized that the straws could decompose at a rate more similar to the timeline seen in the prototype deployments, decomposed and broken up by ~9 weeks.

It is possible that fouling on the mesh bags stifled water flow, resulting in slower biodegradation rate of the PHA. It is also a possibility that the samples were too crowded in the mesh bag, again restricting water flow and thus curtailing necessary bacterial formation, resulting

in reduced biodegradation. A more probable explanation is the availability of microbes to degrade the PHA. Organisms that produce dPHA, the enzyme used to breakdown PHA, can be generally categorized into two groups; those that produce dPHA while they are growing and those that produce the enzyme only when nutrient-limited (Basnett et al., 2017). Given the general water quality of the intercoastal canal and of Port Everglades, it is unlikely that the microbes here are nutrient-limited. The Atlantic Intracoastal Canal (a large canal which begins in Portsmouth, Virginia and terminates at Government Cut in Miami, Florida) and the other smaller waterways which riddle the Fort Lauderdale area are well known for carrying contaminants from stormwater runoff, industrial waste, and seepage from aging septic systems scattered along the winding canals of the area (Kearney, 2023). Bacterial contamination is often found in concentrations that are well in excess of what is considered to be safe levels for recreational use of the waterways; sometimes measuring as much as 100x the safety threshold due to the availability of ambient nutrients (Kearney, 2023). Therefore, it is conceivable that the microorganisms colonizing the PHA samples in this experiment had limited need to produce dPHA, resulting in slowed biodegradation rates. The likelihood of occurrence of these different types of PHA-digesting organisms is unknown.

This poor water quality contrasts greatly with the more oligotrophic conditions of the reef sites where the Coral Castle prototype trails were conducted. The PHA structures of the Coral Castles had visibly more degradation than the samples in the dedicated biodegradation trial. The PHA straws in the Type C prototypes in the *O. faveolata* trial were completely degraded after 98 days, and the straws used in the *P. astreoides* trial were crumbling and partly disintegrated by 94 days. These observations align with other experiments and observational data regarding PHA degradation, and support the notion that nutrient limitation may be key factor for the timely biodegradation of PHA (Dilkes-Hoffman et al., 2019; Phade Products, 2021).

Practical data regarding the biodegradation timeline of PHA consumer products is becoming increasingly important as the phasing out of single-use plastic products garner more and more attention from both consumers and policy makers. Just as there are many different types of plastics that are currently used in disposable consumer goods today, it is likely that their eco-friendly replacements will be made from more than one material. Overall, PHA is a prominent biopolymer that offers to be a cost-effective and eco-friendly alternative to the most popular plastics used in today's straws, packaging, and more. Additionally, PHAs have been shown to have exceedingly low toxicity, high biocompatibility, and are even be suitable for in vivo usage (Paula-

Eliasa et al., 2021). As a biopolymer that supersedes its plastic-replacement relatives, such as polylactic acid (PLA) in terms of marine biodegradability, opportunities abound to incorporate PHA into disposable products that frequently end up in the water (Catarci-Carteny & Blust, 2021; Greene, 2012). Consideration should be taken to review what other applications PHA could be used for in place of traditional plastics. One such novel use would be using the material for predator exclusion devices for coral transplants, as shown in the experimental trials described in this study.

To generate meaningful localized data, more biodegradation experiments will need to be conducted which encompass inland, intercoastal, and nearshore waters of Southeastern Florida. Water chemistry and bacterial loads are highly variable throughout the region and could have tremendous impact on the degradation rates of PHA. An experiment encapsulating weekly water chemistry, such as DOC, DO, temperature, pH, and a nutrient profile accompanying the biodegradation of PHA in different parts of the waterways around the greater Fort Lauderdale area and nearshore reefs would serve as a valuable frame of reference of biodegradation rates in the local area that regulators and policy makers could use to make informed, data-backed decisions. Identifying microbes colonizing PHA samples would also provide further insight into how PHA can be expected to degrade in the marine environment of southeastern Florida.

Prototype trials

The *O. faveolata* predation trial was very successful, with only 6 individual bites on control corals during the first month of the experiment, and no new bites at any point in the following 3 months. In comparison, corals protected by prototype Coral Castles incurred no bites over the duration of the entire trial. Additionally, protection provided by the prototypes did not interfere with the growth of the fragments; all 3 prototypes showed no significant difference in growth in comparison to the controls, nor from each other, by the end of the 118-day monitoring period.

Greater predation during the *P. astreoides* predation trials yielded higher resolution, albeit similar, insights to the effects of the Coral Castle prototypes than the *O. faveolata* trial. By 94 days post-transplant, all prototype tile designs provided protection which significantly reduced parrotfish bites on the coral fragments and thus significantly improved survivorship. However, it is of note that fragments on the Type C tiles had the most bites of the 3 prototype tile types, and all the bites incurred by corals on Type C tiles resulted in complete dislodgment, and thusly death, of the coral. It is possible that the thin PHA straws used in the Type C tiles are not strong enough to deter the largest or the most determined parrotfish. It is also conceivable that fish which have

attempted to feed on the protected coral multiple times learn that the straws can be forced out of the way given enough effort and the fragment dislodgment observed could be explained by these higher intensity feeding efforts. Lastly, in congruence with the *O. faveolata* trial, growth of the corals in all groups were not significantly different from another at the end of the 94-day observation period.

While Coral Castles were highly effective in reducing bites and mortality, other methods have also been effective in reducing parrotfish predation and improving coral transplant survival. Koval et al. (2020) embedded coral transplants in concrete in a way that the sides of the transplants were no longer exposed to potential predators, preventing dislodgment from the reef and also reducing the total predation upon them. However, because the coral was countersunk into the concrete, this allowed sediment to accumulate on the coral tissues (Koval et al., 2020). This can lead to potential mortality in areas that have high sediment transport or areas where sedimentation is high after periods of rough weather or intense currents.

Other attempts at reducing parrotfish predation on coral transplants have been less successful than Coral Castles and concrete embedding. Feeding *Dictyota* powder to corals had significant short-term effects for *O. faveolata* and *Pseudodiploria*, resulting in less than 2% mortality within the first 24 hours of transplant and 18% mortality at the one-month survey time. The effects of this treatment on other species were significantly less successful and did not provide sufficient protection for the coral transplants. Similarly, bathing the corals for 3 hours 24 – 48 hours prior to transplant significantly reduced predation and mortality on the fragments for the first 24 hours after transplant. However, that protection did not last, and all of the out plants were lost by the one-week survey time due to predation (Harrell & Lirman, 2023). One other significant disadvantage with this is that corals must be held and fed specialized food for 2 months. This increases the costs of restoration efforts and limits the volume of corals that can be prepped for restoration because it takes specialized facilities and teams to care for these organisms.

Another attempt at protecting coral transplants in an organic fashion was attempted by Rivas et al. (2021). In this experiment *Acropora cervicornis* was used as a deterrent to parrotfish, by transplanting corals between 25 - 50 cm away from an *A. cervicornis* colony. Mortality varied between 64% and 92%, increasing as distance from the guardian staghorn coral increased (Rivas et al., 2021). While this experiment did show that proximity to *A. cervicornis* colonies can provide protection, the mortality rate was still high and was dependent upon the presence of already

endangered *A. cervicornis* colonies. Additionally, this method is not suitable for restoration areas that are in deeper water where staghorn coral would not typically grow. These deeper portions of the reef tract are becoming increasingly important areas for restoration of massive corals.

Three methodologies to reduce parrotfish predation, more similar to this study, were also tested by Rivas et al. (2021). Metal cages were placed around coral transplants which completely isolated the coral from potential parrotfish predation. This experiment resulted in a 100% survival rate after four weeks, but survival decreased to 22% one week after the cages were removed. An open topped cage was also trialed, but resulted in 64% mortality after 4 weeks, and increased to 97% mortality one week after removing the structure (Rivas et al., 2021). Surrounding corals with metal spikes was also trialed, resulting in 19% mortality over the course of the first four weeks. However, as seen with the other structures, mortality increased to 72% only a week after the spikes were removed (Rivas et al., 2021).

An unpublished study by The Florida Aquarium used a tent made of bamboo skewers, with some success. Overall, while the bamboo is biodegradable, the skewers do not provide sufficient protection, with 42% of corals incurring predation and 26% becoming dislodged in the early parts of the experiment. At this time, it is unclear if the bamboo structure is falling apart or if it is being dismantled by would-be predators (The Florida Aquarium, 2022).

Overall, the success of the above methodologies are lacking in comparison to the results of the Coral Castle prototype trials, either due to high overall mortality, cost of materials, extra labor to remove the protective structures, or a combination therein. Most notably, predation does not suddenly increase after the loss of the protective barrier, which is a reoccurring issue of other tested methodologies. Coral Castles offer a novel solution to the long-standing issue of coral transplant predation by parrotfish.

Conclusions

Through utilizing PHA, Coral Castles show great promise in protecting transplanted corals that would otherwise suffer from parrotfish predation pressure. This predator exclusion device provides noteworthy protection with mortality rates between 0 and 10% for all prototypes tested. In comparison to other attempted methods, and most importantly, there has been no observed increase in predation after the PHA structure has disintegrated away from the tile. This contrasts greatly to the cage and spike methods where survivorship was initially greatly improved, but once the protection was removed the corals were heavily predated upon and the survival-benefits of

their initial protection was completely lost. Protecting corals from parrotfish using Coral Castles have the potential to greatly reduce transplant predation-associated mortality when attempting to restore populations of massive coral species.

Further refinement of the design will reduce the necessary volume of material needed to provide adequate protection for corals and reduce manufacturing costs, making the device more affordable when needed en masse, where a few cents per transplant could represent a significant savings. Continuing research will focus on optimizing the design, seeking to reduce incurred predation as close to zero as possible while still targeting the decomposition timeframe of no more than 6-8 months, ensuring that transplanted corals can escape the window of heightened predation. Future experiments focusing on protecting newly settled corals from incidental mortality, caused by grazing invertebrates and small fishes, will be used to further validate the effectiveness of the Coral Castle design and determine if the design is not only suitable for fragments and small colonies, but for newly settled coral larvae as well.

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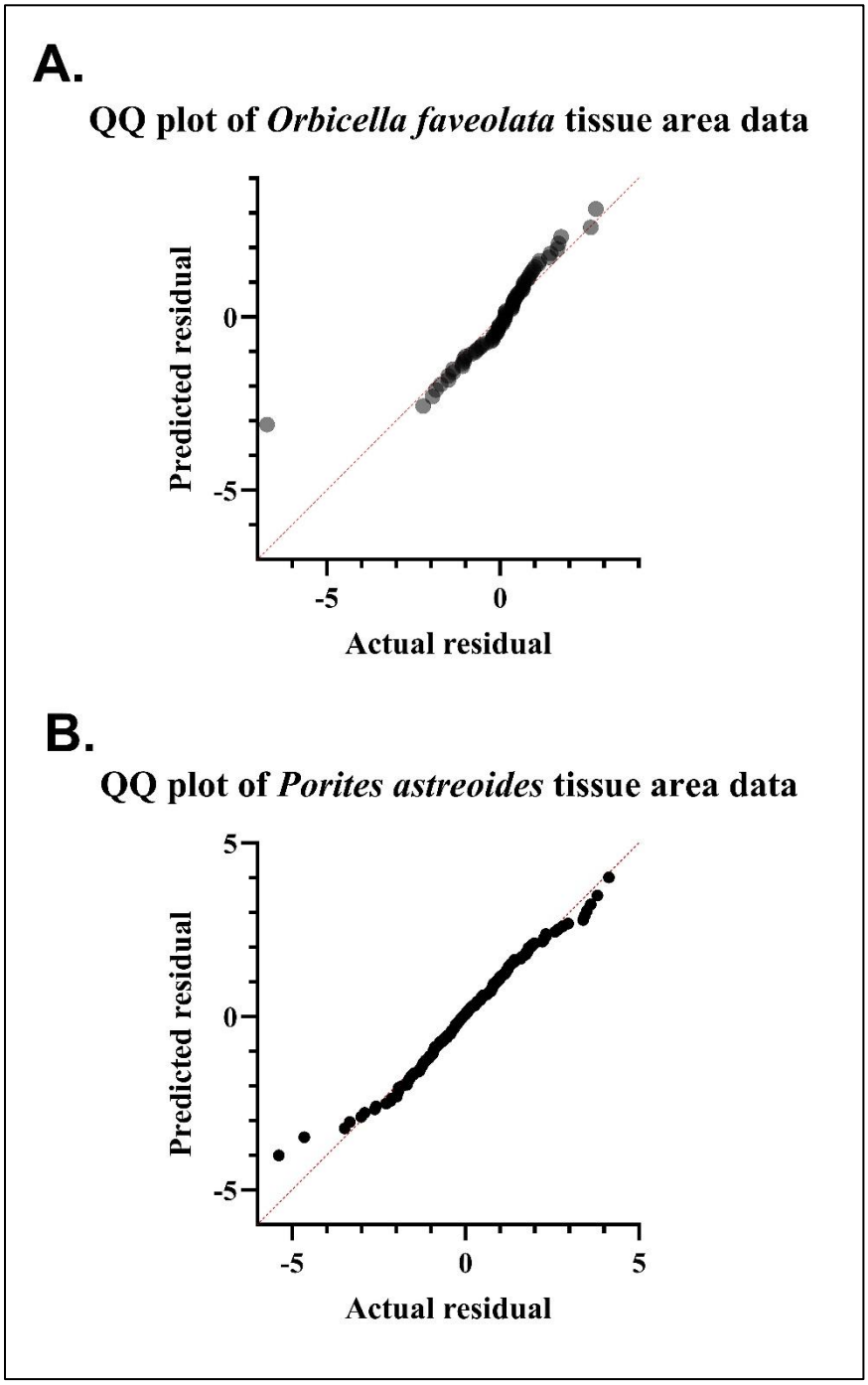
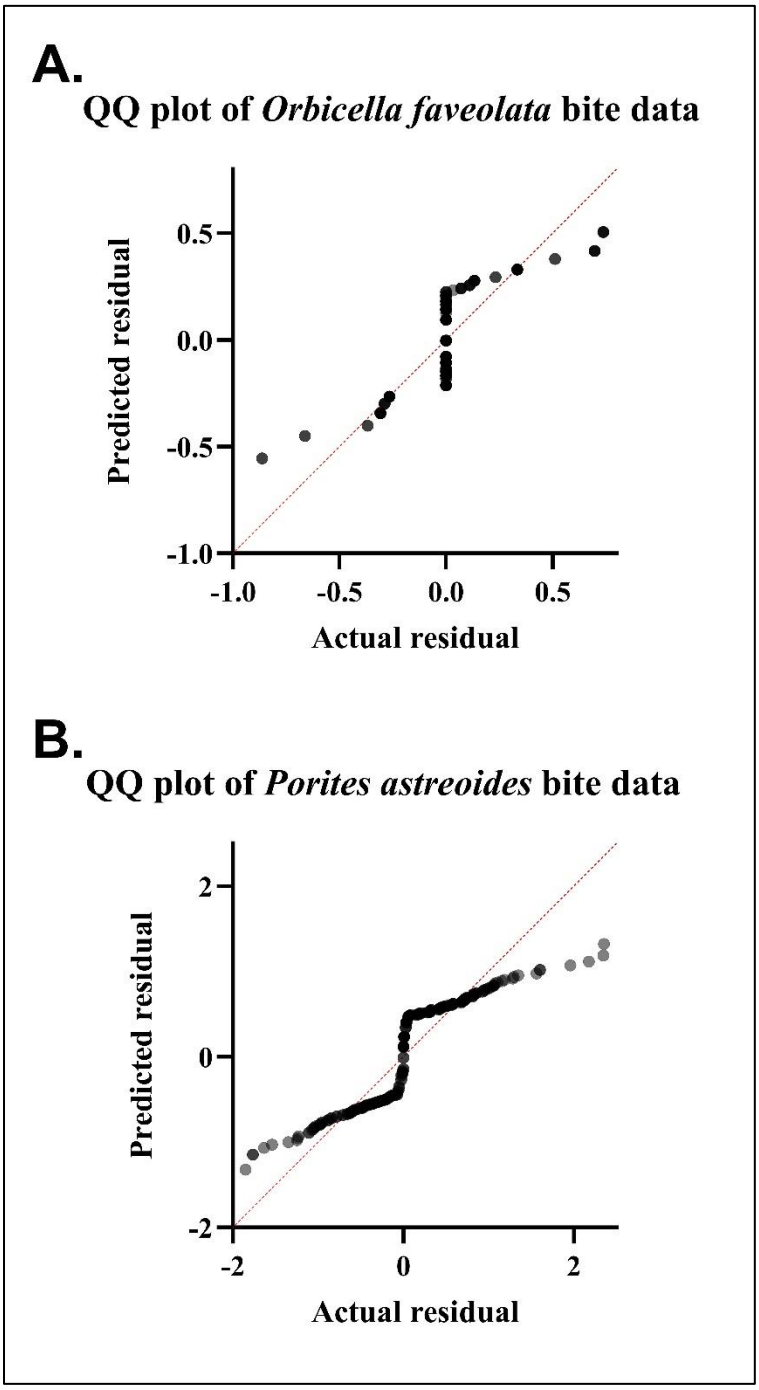
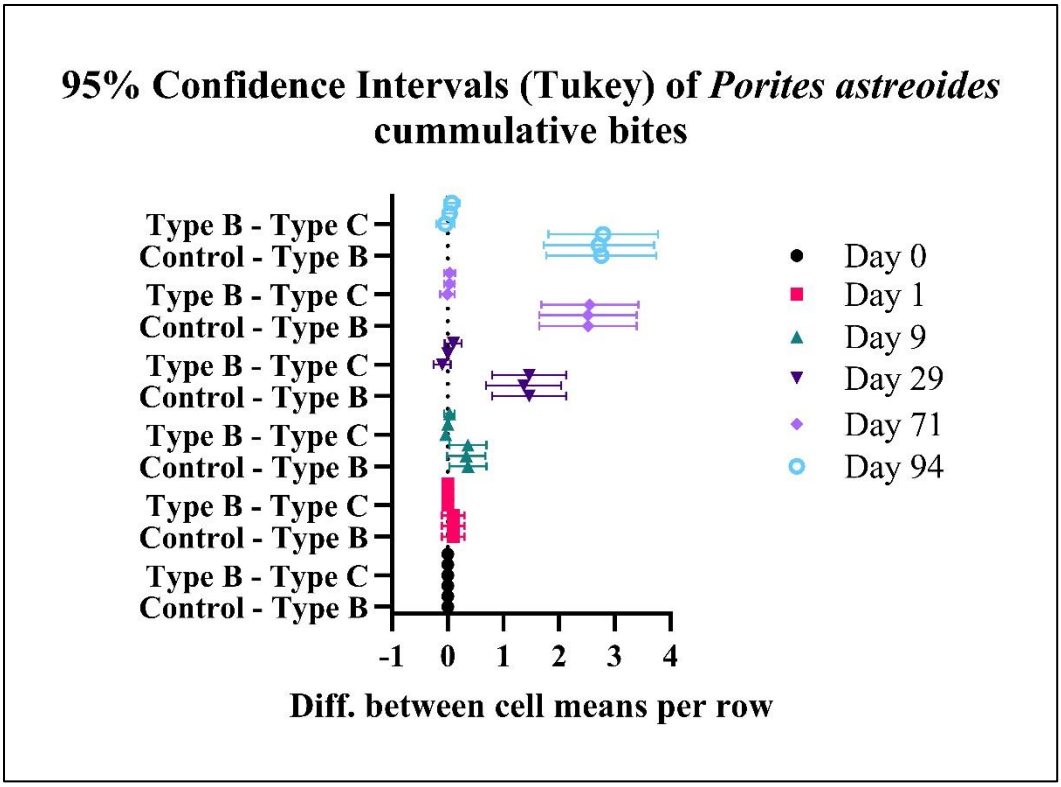
Appendices



Appendix A. A) QQ Plot of *Orbicella faveolata* tissue area data. B) QQ Plot of *Porites astreoides* tissue area data.



Appendix B. A) QQ plot of *Orbicella faveolata* bite data. B) QQ plot of *Porites astreoides* bite data.



Appendix C. 95% confidence intervals for post-hoc analysis of *Porites astreoides* bite data.