

Restoring Blue Coral in a Blue World: Responses of
Heliopora coerulea to Transplantation Between Two
Contrasting Environments

By

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Guam reefs experienced significant climate change-related mortality from 2013 to 2017, triggering a concerted effort to develop a pro-active restoration strategy. Initial efforts focus on reef flats, which are less impacted by Crown-of-Thorns Sea star outbreaks than forereefs. However, shallow reef flats vary greatly in water flow, sedimentation, temperature, light, and herbivory. One species with potential for improving habitat complexity in widely differing environments is the heat-tolerant stony octocoral, *Heliopora coerulea*. This species displays two complex morphologies across a wide habitat range and can spatially dominate, which suggest potential use in restoration. Differential performance of the two morphologies were examined in contrasting environments to determine if one or both are a candidate for restoration in degraded reef flats on Guam. This question is addressed via a reciprocal transplantation experiment between a non-degraded site, Piti Marine Preserve, and a degraded site, Agat Cemetery, where both morphologies are found. Environmental monitoring established statistically different light, temperature, pH, *Enterococcus*, and suspended sediment regimes between sites. Piti is characterized by high water quality and moderate temperatures and low *Enterococcus* concentrations; Agat is turbid, with more variable temperature and *Enterococcus* levels beyond EPA acceptable limits. Fragments of both morphologies from both sites were reciprocally transplanted in December 2020 with growth and survival monitoring through August 2021. Simultaneously, a third set of fragments from the same source colonies were cultured in an ocean nursery to determine if *H. coerulea* benefits from nursery grow-out prior to outplanting. Results showed that final volumetric growth of branching fragments growing in direct outplant sites was significantly higher than those of the ocean nursery. Final volumetric growth of plating fragments was significantly higher in the non-degraded site than those growing in either the degraded site *or* the ocean nursery. Final basal growth of both morphologies was not significantly different across all outplant sites. The recommendation from this study is the direct transplantation of *H. coerulea* fragments to suitable substrate. Site selection should focus on the plating morphology outplanted to non-degraded sites and the branching morphology to either degraded or non-degraded sites. From this study, *H. coerulea* is an ideal candidate for coral restoration on Guam.

Keywords: *coral restoration, coral nursery, reciprocal transplantation*

Table of Contents

Abstract	2
Introduction	5
<i>Global and Local Impacts on Coral Reefs</i>	5
<i>Coral Restoration and Techniques</i>	6
<i>Coral Outplant Success</i>	9
<i><u>Heliopora coerulea</u> and its Characteristics</i>	11
Objectives	14
Hypotheses	14
Materials and Methods	15
<i>Selecting Reciprocal Transplant Sites – Description</i>	15
<i>Asexually Propagating <u>H. coerulea</u> Morphologies via Fragmentation</i>	15
<i>Establishing Plots and Outplanting</i>	16
<i>Monitoring Survival and Growth of Asexual Fragments in Contrasting Environments</i>	17
<i>Reciprocal Transplant Sites – Environmental Monitoring</i>	17
<i>Determining Distribution and Local Abundance of <u>H. coerulea</u> morphologies</i>	18
<i>Analysis</i>	19
Results	22
<i>Differential Growth Responses</i>	22
<i>Reciprocal Transplant Site Environmental Data</i>	28
<i>Distribution and Abundance of <u>H. coerulea</u> Morphologies</i>	30
Discussion	33
<i>Transplant Survival and Growth</i>	33
<i>Nursery Culture Implications</i>	34
<i>Source Colony Effect</i>	35
<i>Reciprocal Site Environmental Differences</i>	35
<i>Distribution and Abundance</i>	36
Implications for Restoration	38
Literature Cited	39

TABLES

Table 119
Table 2.....24
Table 3.....30

FIGURES

Figure 1 A,B.....8
Figure 2 A,B.....12
Figure 3.....13
Figure 4.....19
Figure 5.....16
Figure 6.....23
Figure 7.....26
Figure 827
Figure 927
Figure 10.....28
Figure 11 A-E.....29
Figure 1231
Figure 13 A-H32

SUPPLEMENTAL TABLES

Supp. Table 1.....47
Supp. Table 2.....48
Supp. Table 3.....48
Supp. Table 4.....49

INTRODUCTION

Global and Local Environmental Impacts on Coral Reefs

Tropical and subtropical countries in the Pacific region rely on coral reefs for the ecosystem goods and services they provide (Laurans et al. 2013). These goods and services include recreational diving and snorkeling, coastal protection, and fisheries. Despite multiple valuable services, coral reefs in the Pacific and globally face several anthropogenic threats including non-sustainable fishing practices, sedimentation, pollution, non-sustainable tourism practices, and climate change, which greatly impact coral reef biodiversity, ecosystem function, and overall ecosystem health (Cesar 2000). Smith et al. (2016) present trends in coral cover throughout the Pacific that while variability is high between countries, data show many signs of reef decline, especially around population centers. The authors concluded the main drivers of reef decline in the Pacific are large-scale coral bleaching, storm damage, Crown-of-Thorns Sea star outbreaks, and local anthropogenic stressors.

On Guam there is significant coral reef, water quality, and fisheries monitoring and research activity by numerous institutions, including the University of Guam Marine Laboratory (UOGML), the National Oceanic and Atmospheric Administration (NOAA), the Guam Division of Aquatic and Wildlife Resources (DAWR), the Guam Environmental Protection Agency (EPA), the National Parks Service (NPS), and the US Fish and Wildlife Service (USFWS). The long-term monitoring data on Guam's reefs reveal declines in coral health and cover across the last 60 years (Burdick et al. 2008, NOAA 2014). In the 1960s, coral cover was estimated at 50% on the fore-reef slopes and a decline to less than 25% cover was observed by the 1990s (Goldberg et al. 2008). A significant reason for this decline was Crown-of-thorns Starfish (COTS) predation on hard corals. From 1967 to 1969, Chesher (1969) reported over 90% coral mortality from COTS predation across a large portion of the west coast of Guam with subsequent recovery over time (Jones et al. 1976). Burdick et al. (2008) conducted surveys across 17 sites on Guam in 2006. The authors found high COTS

numbers ranging from approximately 100 to over 1,600 individuals in six of the 17 sites, with resulting high coral mortality. In 2016 coral cover was assessed on Guam through field surveys of the reef slope at 20 shallow (5 m) and 18 deep (12 m) sites (Maynard et al. 2017). This study found coral cover was 25% on average in the shallow survey areas and 19% in the deep areas. Further, Guam reefs suffered significant mortality from repeated climate change-related events from 2013 to 2017. Raymundo et al. (2019) reported a loss of roughly 30% of live coral cover from bleaching, disease, and subaerial exposure from extreme tides by 2017. In addition, the authors found there were significant species-specific differences in responses to bleaching, with some of the most complex reef-building morphologies suffering the greatest reduction. From observed trends, Guam's coral reefs are exhibiting an accelerated coral cover loss over time with little recovery.

Resilience in a complex ecosystem such as a coral reef is measured as the capacity for the ecosystem, after single or multiple disturbances, to return to a stable state, or equilibrium, without shifting to a different stable state (Hughes et al. 2005). With the death of reef building corals due to disturbance, a reef area can become occupied by non-reef-building organisms, such as macroalgae or zoanthids, characterizing a process known as phase shift (Adam et al. 2020). Studies are showing that high coral reef resilience once seen globally are on the decline due to ocean warming, ocean acidification, and anthropogenic impacts (Pandolfi and Jackson 2006; Anthony et al. 2011). As Guam braces for predicted further alteration in reef structure and function due to climate change, finding ways of increasing reef resilience to climate change is paramount (Weijerman et al. 2015).

Coral Restoration and Techniques

A management tool that can be used to enhance coral reef recovery and contribute to resilience is active coral transplantation, where juveniles or colony fragments from a healthy

reef are introduced to augment or restore populations at sites with suitable water and substrate conditions for coral establishment and growth (Yap et al., 1998). Restoration via transplantation may be warranted at sites that are not recovering naturally, possibly due to low natural recruitment rates or low resilience of existing species. Kendall and Poti (2015) modeled connectivity between Marianas islands and found recruitment limitation on Guam. The authors found Guam's reefs to be largely self-seeding, reliant on local populations for recruitment. If there are low population numbers of a species, transplantation of coral fragments can reduce the reliance on reproductive success of wild colonies on source reefs and eventually increase the size of the spawning population (Soong and Chen 2003; Epstein, Bak, and Rinkevich 2003) so active planting of healthy reef building corals will lead to a higher chance for successful reefs.

A method commonly used to increase coral stock for transplantation is asexual fragmentation. Asexually fragmenting colonies from healthy wild populations and rearing in either *in situ* or *ex situ* nurseries prior to outplanting has become a common practice in the reef restoration field (Omori 2005; Levy et al. 2010; Young et al. 2012; Rinkevich 2019). This method is one variation of the 'coral gardening' concept which involves cutting or chiseling a fragment, or nubbin, of coral from a parent colony, attaching it to a suitable substrate, and providing a refuge environment - or nursery - during a grow-out phase. Following the grow-out phase the fragment is outplanted and monitored (Rinkevich 2021). A coral nursery allows the juveniles to increase in size while being protected, monitored, and maintained. Smaller fragments tend to have higher mortality rate than larger fragments when outplanting (Forrester et al. 2013). Thus, while harvesting smaller fragments from source colonies for outplanting reduces damage to them, a nursery grow-out phase can then increase survival of such fragments in preparation to outplanting. Conversely, use of larger fragments may preclude the need for a protected grow-out phase but impacts to source colonies are greater (Epstein, et al.

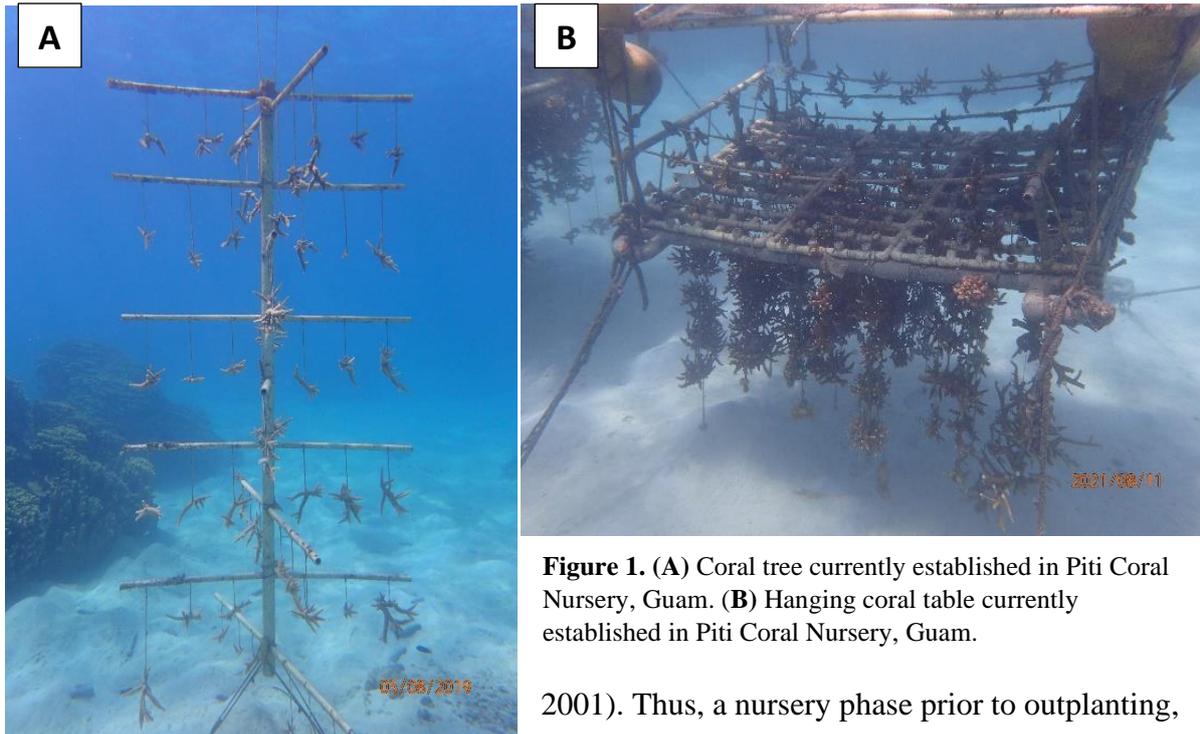


Figure 1. (A) Coral tree currently established in Piti Coral Nursery, Guam. (B) Hanging coral table currently established in Piti Coral Nursery, Guam.

2001). Thus, a nursery phase prior to outplanting, rather than direct transplantation, has proved to increase coral growth and survivability and may be preferable to direct transplantation (de la Cruz et al. 2015; Afiq-Rosli et al. 2017).

Several coral propagation methods are utilized among coral nurseries globally, for example utilizing a mid-water floating structure to hang corals for increasing coral growth rates (Lirman and Schopmeyer 2016). On Guam, there are two established coral nurseries, Piti Coral Nursery, located in Piti Bomb Holes Marine Preserve, and Merizo Coral Nursery, located in Cocos Lagoon. Both are currently in place for culturing and propagating of *Acropora* species found on Guam using multiple structures (Raymundo et al. 2022). Both nurseries have established coral trees (Figure 1A) and Piti Nursery has hanging coral tables (Figure 1B) and permanent low-relief metal frames. A coral tree is built with a PVC central column, or trunk, with PVC or fiberglass branches perpendicular to each other and spaced along the central column (Nedimyer et al. 2011). Corals are attached to the branches using monofilament that is passed through drilled holes. A hanging coral table uses a PVC frame that is suspended within the water column using anchors and buoys. Multiple corals are attached on a single line and hung underneath the PVC frame to optimize space. Once the

corals have reached optimal size, they are pruned, and the fragments are outplanted to the selected reef site. A fragment of the original wild-sourced colony is maintained in the nursery to reduce continued wild colony collection and is important for the sustainability of the nursery-reared corals.

Coral Outplant Success

After outplanting, outplant success can be measured over time as survival, growth, and fecundity of coral fragments in the outplanting site. Increased survival and growth of fragments is equated with higher outplanting success. Outplanting success can be variable due to outplants experiencing high mortality from a variety of biotic and abiotic stressors (Ladd et al. 2018; Muehllehner et al. 2016). Foo and Asner's (2020) findings indicate that the maximum temperature experienced during outplanting was a strong predictor of coral survival, giving perspective to the role of thermal limits, seasonal fluctuations, and water depth when choosing outplanting sites. Pausch et al. (2018) found significant differences in survival and bleaching susceptibility of genotyped corals that underwent thermal stress. The differential responses of genotyped individuals within a species population can lead to thermally resistant genotypes being more favorable for use in coral restoration. Fish predation on outplanted fragments of species of massive corals in Southern Florida was a major predictor of outplant survivorship and success (Page et al. 2018; Koval et al. 2020). Page et al. (2018) recommended larger fragments while Koval et al. (2020) recommended changing outplant methods to decrease likelihood of predation stress. Monitoring of initial and long-term responses of outplanted species to a myriad of stressors can better determine coral outplant success.

Choosing the right site to outplant is critical to coral restoration as a management tool because outplanting of corals is one of the more costly and time-consuming steps for coral

restoration (Hein et al. 2018). When choosing sites for outplanting, Ladd et al. (2018) found many restoration programs consider ideal outplanting sites have the following characteristics: herbivore presence, available substrate, and little to no benthic competitors. But not all outplanting sites are going to contain ideal conditions. Some outplant sites with the above characteristics can be classified as non-degraded outplant sites while a site with low herbivory presence or human-impacted are a degraded site. The success of restoration efforts depends partly on whether characteristics of source sites impact coral performance after transplantation (Shearer et al. 2009). If a species shows low success in a degraded site with environmentally different characteristics from the source site, that species may have to be limited to outplant sites with a similar environment to the source site. Many coral restoration projects around the world are centered on outplanting corals to degraded sites and must consider source site selection as well as outplant site selection to maximize outplanting success of target restoration species (Tsang et al. 2020).

One way to determine coral's reaction to transplantation is to reciprocally transplant between sites. Reciprocal transplantation is the process by which corals are collected from two source sites, exchanged between the two sites and outplanted. This process can be used to identify if there are population or environmental influences on the growth and survival of transplanted corals (Rinkevich 2005). Studying coral responses to reciprocal transplantation has implications in the coral restoration field; once reef sites' effect on coral is better understood, informed decisions on source and outplant site selection for different coral species and populations can be made. In Raymundo (2001) the author concluded the differences in environmental quality between transplant sites affected coral transplant performance the most. Other studies showing coral transplantation into sub-optimal conditions indicate success of coral establishment in these sites is often low (Birkeland et al. 1979; Forrester et al. 2013). It

is important for restoration practices to consider source and outplant site conditions to increase coral survivorship and growth.

***Heliopora coerulea* and its Characteristics**

Worldwide, about 86 coral species and hundreds of thousands of colonies are successfully farmed in different types of nurseries using the ‘coral gardening’ concept, and several novel transplantation methodologies have been developed (Rinkevich 2014). Coral restoration activities utilizing a coral nursery grow-out phase prior to outplanting is a growing field on Guam and many agencies are working together to establish a coral restoration framework to further outplanting activities on degraded reef areas. Currently there are eight *Acropora* species in culture in two ocean nurseries on Guam. The Guam Reef Resilience Strategy (Hoot 2019) is a recent initiative which states the need for expanding the number of species in culture and including others of local ecological importance to increase ecological function and resilience in Guam’s coral reefs. More species are needed to replace lost reef function and one such species with potential for improving habitat complexity is the bleaching-resistant stony octocoral, *Heliopora coerulea*.

Octocorals (Octocorallia) are the most diverse Subclass in the Phylum Cnidaria and can be found in various marine environments, including shallow tropical reefs, deep seamounts, and submarine canyons (McFadden et al. 2010). *Heliopora coerulea* (blue coral) Pallas 1776, is unique among the Sub-class Octocorallia because of its crystalline aragonite skeleton onto which iron salts precipitate to create blue pigmentation (Hill 1960). Colonies are found across the Indo-Pacific in a wide range of reef habitats and exhibits bleaching resistance and resilience during thermal stress events (Harii et al. 2014; Richards et al. 2018; Guzman et al. 2019). Atrigenio et al. (2020) showed this species has an increased competitive advantage in warmer waters compared to scleractinian corals and Guzman et al. (2019) documented

increased growth rates in seawater temperatures up to at least 31 °C, providing further evidence that *H. coerulea* may become increasingly important reef-builders under ongoing ocean warming. In addition, habitat degradation, harvesting for jewelry, and the tourism trade in other geographic locations have led to its listing as vulnerable by the IUCN Red List of Threatened Species (Obura et al. 2008) and in Appendix II of the Convention on International Trade of Endangered Species (<https://www.cites.org/eng/app/index.php>). Guam does not allow poaching of this coral species.

Two growth forms of this coral exist throughout the Pacific Ocean both in the Indian Ocean and western Pacific ranging from the Guam to the Kuroshio Current region (Japan and Taiwan) south to northwestern Australia (Taninaka et al. 2021). As seen in Figure 2, A is a branching morphology while B is a vertical plating morphology; both are present on Guam. Until Taninaka et al. (2021), it was unknown whether *H. coerulea* were insipient species or a single species with morphological differences. This study has identified the *H. coerulea* population on Guam as a genetically isolated subclade highlighting the localized genetic structure of this species on Guam (Figure 3). However, there is still uncertainty regarding genetic structure of the two morphologies on Guam. But the structure of the *H. coerulea* population may be explained by the reproductive strategy of this species.

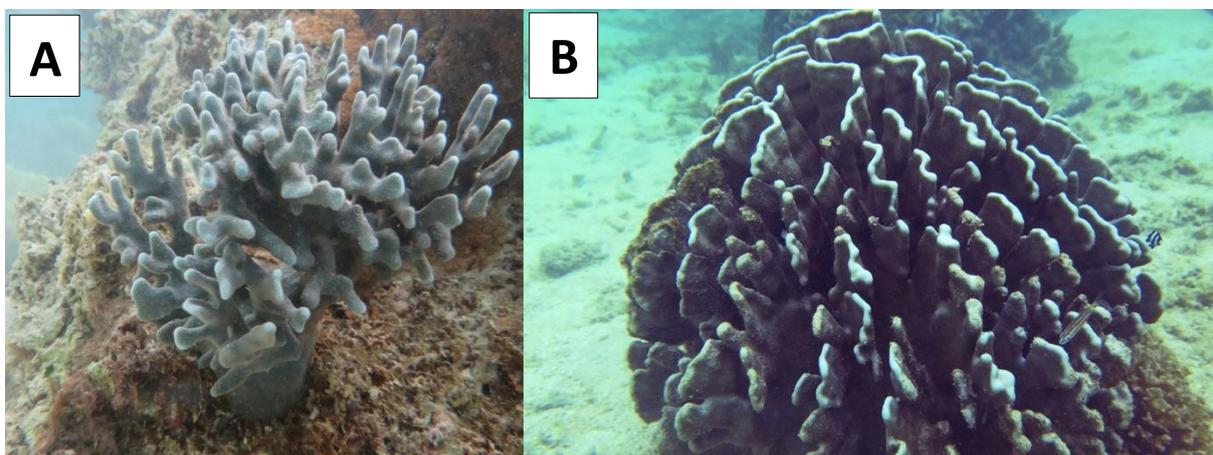


Figure 2. Distinct complex morphologies of *Heliopora coerulea* present on Guam. (A) Branching form; (B) Plating form. Photos: L. Raymundo

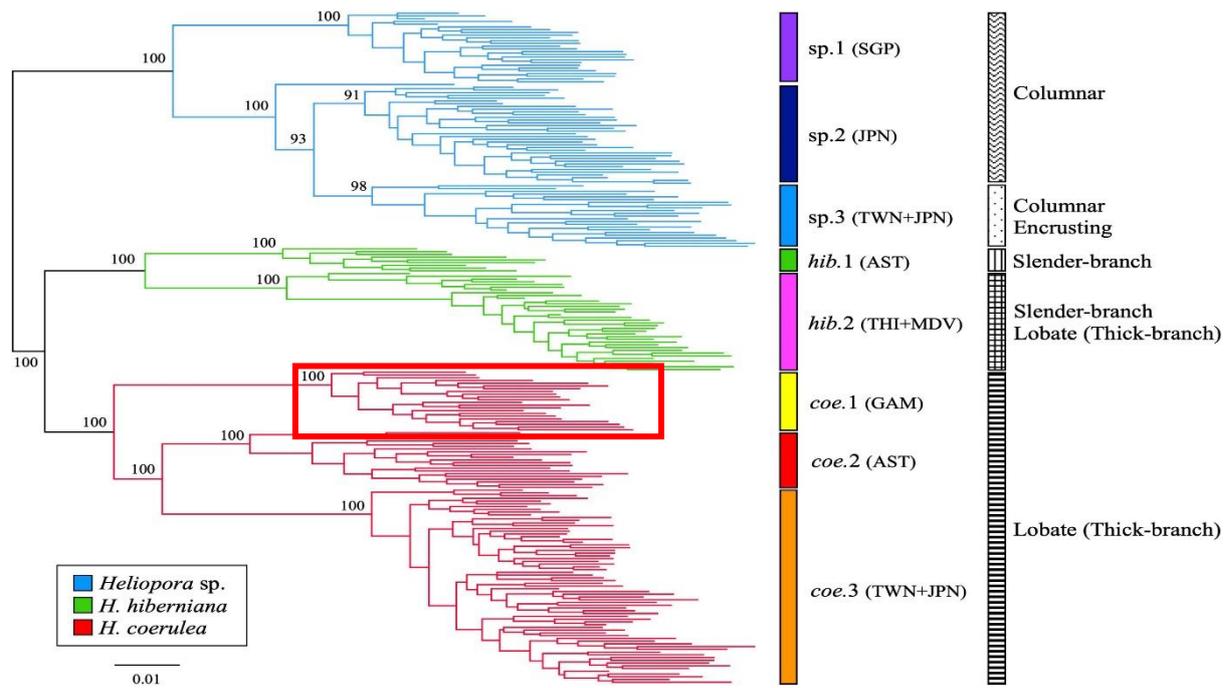


Figure 3. Red box indicates the genetically isolated subclade of *H. coerulea* on Guam (taken from Taninaka et al. 2021)

Scleractinian and octocorallian corals have two distinct modes of sexual reproduction: spawning and brooding. Within both modes, a species can also have hermaphroditic and gonochoric reproductive strategies. Spawning species release sperm and eggs into the water column which leads to external fertilization, development, and settlement over the course of several days (Harrison and Wallace 1990, Richmond and Hunter 1990). Usually, larvae are positively buoyant and disperse outside the natal reef by wind-driven surface currents (Willis and Oliver 1990). For gonochoric brooding species, such as *H. coerulea*, reproductively mature male colonies release sperm into the water column which are taken in by the female colonies and eggs are fertilized internally (Babcock 1990). Once the azooxanthellate larva is fully developed, it is released from the surface of the female colonies (Babcock 1990, Harii and Kayanne 2003). Brooded larvae are more negatively buoyant and ready to settle more quickly than spawned larvae, which suggests a likelihood that brooded larvae will settle on their natal reef (Harrison and Wallace 1990). This also suggests that introducing transplanted colonies to areas with a smaller population of adult colonies will result in higher reproductive success and recruitment due to a higher probability of successful fertilization and would be

more likely to allow establishment of new populations in areas where larvae are unlikely to recruit, due to distance or current patterns.

Blue coral exhibits complex, habitat-forming morphologies and can spatially dominate a reef community, which identifies it as a significant non-scleractinian reef builder (Zann and Bolton 1985). Due to its relative resistance to thermal stress and high skeletal density that may make colonies less vulnerable to damage (Courtney et al. 2021), *H. coerulea* may become an increasingly important reef builder under ongoing climate change. Colonies of this species can grow typically up to 100 cm in diameter (<https://www.sealifebase.ca/summary/Heliopora-coerulea.html>), but colonies have been recorded in surveys for this study up to 400 cm diameter. The size potential and their complex structure can replace lost topographic complexity and, thus, habitat. Additionally, *Heliopora* corals are likely dispersal limited and tend to form dense aggregations (Harri et al. 2002), suggesting they may be an underappreciated genus for restoration using stress-tolerant species on degraded reefs. These attributes suggest that it has potential for restoring shallow habitat quality in Guam in areas particularly impacted by recent bleaching mortality.

OBJECTIVES

The overarching goal of this study is to test whether the two growth forms, branching and plating, of *Heliopora coerulea* are candidates for culture and restoration on Guam given the variability in site quality among potential restoration sites. There is one objective:

O₁: To determine the distribution and abundance of the two growth forms of *Heliopora coerulea* on the nearshore reefs of Guam.

HYPOTHESES

H₀₁: Survival and/or growth of fragments of the two morphologies will not differ when growing in a degraded vs. a not-degraded site.

H_{A1}: Survival and/or growth of fragments of the two morphologies will differ when growing in a degraded vs. a not-degraded site.

H_{O2}: Survival and/or growth of fragments of the two morphologies will not differ when transplanted within their source reef as opposed to their reciprocal reef.

H_{A2}: Survival and/or growth of fragments of the two morphologies will differ when transplanted within their source reef as opposed to their reciprocal reef.

H_{O3}: Survival and/or growth in the two morphologies will not differ between directly-transplanted vs. nursery-reared fragments.

H_{A3}: Survival and/or growth in the two morphologies will differ between directly-transplanted vs. nursery-reared fragments.

MATERIALS AND METHODS

Selecting Reciprocal Transplant Sites

Two presumed contrasting environments were chosen to test the two *H. coerulea* morphologies range of responses to direct transplantation. The transplant sites for this project were Piti Bomb Holes Marine Preserve and Agat Cemetery (Figure 4 circled sites). These sites were two of the twenty sites surveyed for the *H. coerulea* distribution and abundance on Guam (see below). After completing the survey, the relative abundance of both morphologies and differing environmental conditions indicated these two sites would provide significantly contrasting environments. Piti Marine Preserve has clearer water, moderate to high water flow, and high coral cover. Agat Cemetery has higher turbidity and lower water flow and coral cover. Piti Coral Nursery, within Piti Marine Preserve, was used to determine the necessity for a nursery grow-out phase versus directly transplanted to reef sites.

Asexually Propagating *H. coerulea* Morphologies via Fragmentation

Fragments were collected from n=20 wild-sourced colonies of each morphology from Agat Cemetery and Piti Bomb Holes Marine Preserve (40 total) for fragmentation. Selected colonies were at least 10 m apart to minimize collection of clonal colonies. Less than 10% of each colony was carefully removed with a hammer and chisel, to minimize stress to source

colonies (Epstein, Bak, and Rinkevich 2001). Fragments were immediately transported to the University of Guam Marine Laboratory in fresh seawater and allowed to recover in a holding tank with flowing seawater and shade. After ~7 days, 13 fragments approximately 5 x 2 cm were cut from each of the 40 collected *H. coerulea* (520 in total) using a Gryphon[®] diamond wet saw. Twelve fragments from each colony were attached to labeled tiles using Loctite[®] superglue (cyanoacrylate) and allowed to recover in lab tanks until new tissue appeared along the cut edges. One fragment from each source colony was deposited in the UOG Biorepository by freezing at -80°C for future genetic sampling (not included in this thesis).

Establishing Plots and Outplanting

In the direct transplant sites, a flat pavement area large enough to outplant four 1 m² plots was found chosen. A random number generator was used to randomize placement of clonal fragments in established plots within the nursery and the direct transplant sites. During outplanting the plots were measured out and the pavement was scrubbed using steel brushes to

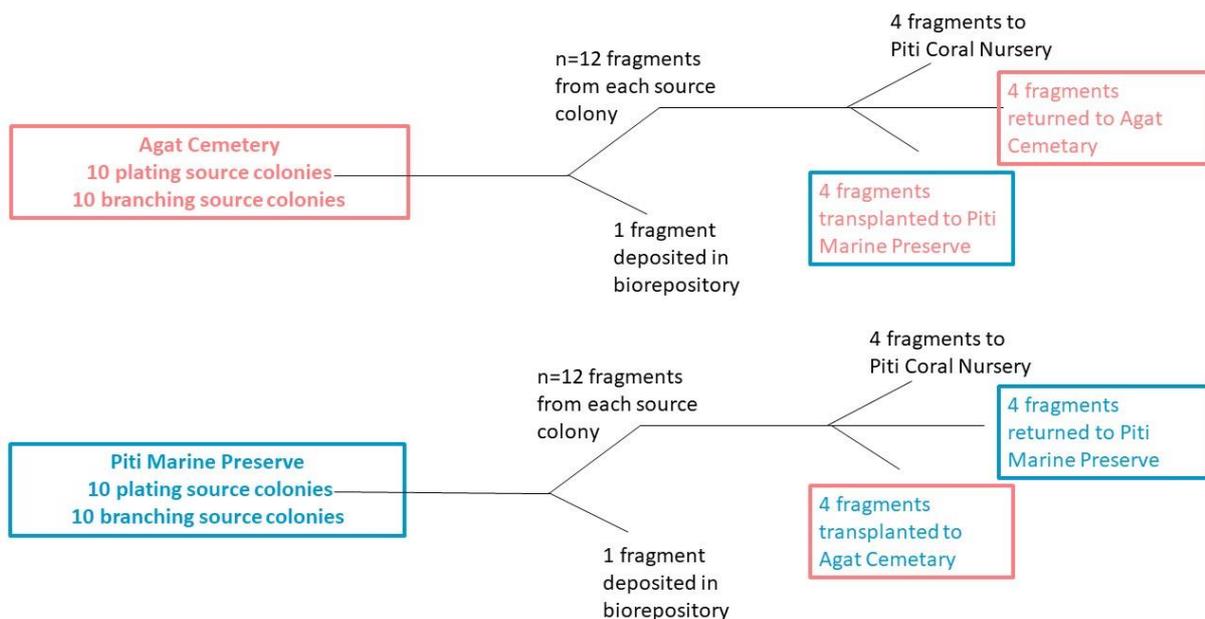


Figure 5. Reciprocal transplant experimental design.

remove algae and debris. Tiles directly transplanted to Piti and Agat Cemetery were affixed to CaCO₃ pavement using an in-house cement mix (containing sand, Plaster of Paris, and Portland Cement) for a total of 160 fragments deployed at each outplant site (Figure 5). Tiles outplanted to Piti Nursery were affixed with plastic zip ties on white egg crate styrene lighting panels attached to a PVC frame on top of a mid-water coral table. This allowed for even spacing and stabilization of fragments within four PVC plots on the coral table.

Monitoring Survival and Growth of Asexual Fragments in Contrasting Environments

Fragments were monitored for nine months (December 2020 – August 2021), and tiles were cleaned and maintained throughout the study. Any fragment that had disconnected from its tile in the interim was re-glued with Splash Zone® 2-part marine epoxy. Survival was assessed, and growth measured bi-weekly using a combination of photos taken directly above fragments and use of calipers to measure fragment height *in-situ*. Between survey ten (4/7/2021) and eleven (5/5/2021), there was a month gap due to inclement weather. Two metrics of growth were tracked: *Basal surface area*, defined as horizontal growth of the fragment directly to substrate; and *Estimated fragment surface area*, defined as growth of the fragment above the substrate. All images taken for fragment and basal surface area of the *H. coerulea* fragments were analyzed using ImageJ® image analysis software. Adult source colonies were also monitored monthly by taking photos of fragment removal areas on the colony to assess the time it takes new tissue to cover the exposed coral skeleton and recover from fragmentation.

Reciprocal Transplant Sites Environmental Monitoring

Environmental parameters were monitored at both sites to quantify site differences during the study period. Each site had an Onset HOBO Pendant® temperature/light logger and HOBO water level logger (Bourne, Massachusetts) deployed through the duration of the experiment. A handheld YSI 6-Series Multiparameter Water Quality Sonde (Yellow Springs, Ohio) was used to measure pH *in-situ* during biweekly site visits. *Enterococcus* levels were established using secondary public-access data collected from Guam Environmental Protection Agency (<https://nwis.waterdata.usgs.gov/gu/nwis/qwdata?introduction>; Accessed 09/2021). Suspended sediment levels were determined post-hoc by collecting water samples once in the dry season (December 2021) and wet season (April 2022). Post-hoc sampling was necessary due to YSI turbidity logger failure during the study period. The collector waded 10-15 m from shore and collected three 1-li samples 0.5m below the surface. The samples were processed by filtering the water through 47mm circle microfiber filters previously dried to constant dry weight. The filters were dried a second time for 5 d and weighed using a Mettler® balance. to determine average weight of suspended solids in both sites. Finally, to determine the amount of suspended solids in the samples, the initial dry weight of the filter paper was subtracted from the final dry weight. To characterize the benthic community at both sites, six ten-meter transects were laid perpendicular to shore at each transplant site and surveyed using LIT (line-intercept transect) method. Categories for benthic cover included: fleshy macroalgae, live hard coral, dead coral, pavement, sand, and soft coral.

The *Enterococcus*, pH, temperature, and light levels monitored and the rain gauge data from Mount Chachao Rain Gauge near Piti Marine Preserve and Almagosa Rain Gauge near Agat Cemetery (USGS Current conditions for Guam) indicated a transition from the dry to the wet season between April and May 2021. Environmental data were then analyzed using these two seasons: the dry season (December 2020-April 2021) and the wet season (May 2021-

August 2021). Piti Nursery was not separately monitored due to its proximity to, and similarity with, the Piti Marine Preserve transplant site.

Characterizing Distribution and Local Abundance of *H. coerulea* Morphologies

Heliopora coerulea inhabit shallow reef flats and were previously thought to be scattered in patches on Guam. Prior observations from reef surveys of Guam's Long Term Monitoring Project led to choosing these 20 survey sites. For this aspect of the study, *reef flats* are defined as shallow (1-5m) reef areas shoreward side to the reef crest. Depth is shallow, and water temperature more variable. *Fore-reefs* are defined as a mid-depth (7-10 m) reef area seaward of the reef crest. The topography becomes more vertical, with subsurface terraces or slopes that face the open ocean. Timed (~50 min) swim surveys with two snorkelers or divers were conducted on 15 reef flats and 5 fore-reef sites (Figure 4). The surveys recorded all colonies encountered during the swim, maximum colony diameter and the relative abundance of the two growth morphologies. Survey area at each site was calculated using Google Earth Pro®, by measuring the internal area of a polygon within each site where the survey was conducted. Overall density and density of both morphologies were calculated within each site based on survey area estimations. Colony maximum diameters

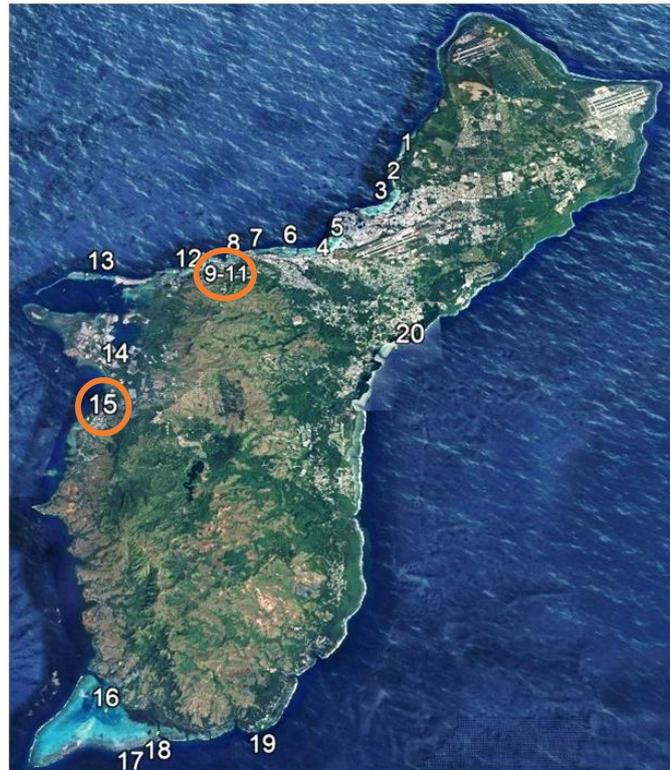


Figure 4. Map of Guam showing survey sites to assess the current distribution and abundance of *H. coerulea* on Guam reef flats and lagoon. Fore-reef sites marked with an asterisk. 1=Tanguisson; 2*=Gun Beach; 3=Tumon Bay; 4*=Alupang Island; 5=Easy Agana Bay; 6=West Agana Bay; 7=Adelup reef flat; 8*=Asan Cut; 9-11=Piti Bomb Holes Marine Preserve; 12=Tepungan reef flat; 13=Luminao; 14= Dodi Beach; 15=Agat Cemetery; 16=Cocos Lagoon; 17*=Babi Island; 18=Achang reef flat; 19=Inarajan; 20*=Pago Bay.

were binned into previously established colony size classes (Raymundo and Kerr 2015) (Table 1). These surveys informed the selection of reciprocal transplant sites and will be utilized when evaluating future outplanting sites.

Table 1. Coral colony size class determined from Raymundo and Kerr (2015).

Size Class	Max. Diam. Range (cm)
1	1-10
2	11-30
3	31-60
4	61-100
5	101-200
6	201-600

Analysis

Once image analysis was complete, individual fragment volume was calculated by multiplying fragment surface area and height. Fragment percent growth over the study period was calculated by comparing fragment volume from sequential surveys (F_{SV}) to fragment volume from the initial survey (F_{IV}) (Forrester et al. 2013):

$$\% \text{ Volumetric Growth} = ((F_{SV} - F_{IV}) / F_{IV}) * 100 + 100$$

All fragments were normalized to start at 100% volume to account for any subsequent partial mortality or loss of volume due to breakage or fragmentation. This method was necessary due to initial fragment size variation.

To calculate percent basal growth over the study period, an initial basal surface area measurement was taken at the first survey by adding initial fragment surface area (F_{ISA}) to initial visible basal surface area (F_{IBA}). Initial fragment surface area (F_{ISA}) was added to successive basal surface area (F_{SBA}) measurements for the remaining surveys to find total basal surface area at each survey (F_{TBA}) (Neil et al. 2021). This method was used to normalize data due to some fragments lacking visible basal growth upon the start of data collection. Percent growth over time would be highly skewed on fragments with no initial basal surface area without adding initial fragment surface area into the formula at each timepoint as a

baseline for all fragments throughout the study. Basal percent growth over the study period was found by comparing basal surface area from sequential surveys to initial survey (Forrester et al. 2013).

$$\% \text{Basal Growth} = ((F_{\text{TBA}} - F_{\text{IBA}}) / F_{\text{IBA}}) * 100 + 100$$

All fragments started at 100% basal surface area to account for differences in initial size and determine increased or decreased basal growth over time.

Actual volumetric measurement of fragments over time was not possible in this study due to fragments being permanently affixed to substrate with no destructive sampling. Use of inferred fragment volume from above calculations is thus an estimate of actual fragment volume variability within the inferred volumetric ellipse, so comparisons between both morphologies were not feasible. Any fragments lost during the study period were removed from subsequent analysis.

Thus, within each outplant site four designated fragment groups were created: Agat-sourced branching fragments (Agat branching), Agat-sourced plating fragments (Agat plating), Piti-sourced branching fragments (Piti branching), and Piti-sourced plating fragments (Piti plating). Effect of source reef and outplant site on growth on both morphologies was tested by running two-way ANOVAs, using source reef and outplant site as predictors, also testing for an interaction between source reef and outplant site. Post-hoc Tukey HSD tests were run when significance was found, to determine the direction of the difference. A Repeated-Measures ANOVA was used to determine if there were specific source colonies driving growth trends within the Piti and Agat fragment groups at each outplant site. Any source colonies that were statistical outliers in 8 or more surveys were identified and were removed from the data to determine if these source colonies were driving the overall volumetric and basal growth trendline.

Analyses were conducted on the environmental data by running a two-way ANOVA, using site and season as predictors, also testing for an interaction between site and season, and if significant, a post-hoc Tukey HSD test determined if a particular environmental parameter significantly differed between seasons or between sites (Supp. Table 1).

Distribution and abundance data were analyzed using a binomial test determine if the proportion of each morphology abundance differed between morphologies within the two reef zones. Colony density per morphology and total density of all colonies per site were calculated using abundance counts and total area surveyed at each site. Density was standardized across sites to a count per 400 m² (Table 2). Eight sites (five reef flat and three fore-reef) with a total colony density of $\geq 5/400\text{m}^2$ were further analyzed using a two-sample Kolmogorov-Smirnov test for morphology size class distribution trends within the reef flat and fore-reef.

RESULTS

Differential Growth Responses

At the study's conclusion, both Piti and the Nursery sites had a 100% fragment survival rate and Agat had a 99.075% fragment survival rate. No fragments were lost in Piti or the Nursery and in Agat Cemetery, four fragments were lost during storm swell (two Piti-sourced plating, one Piti-sourced branching, and one Agat-sourced plating fragment).

Basal growth over the study period was variable across outplant sites. From initial outplanting to the start of the fourth month of growth, survey 1 to 8, all groups showed an increase in basal growth, but fragments outplanted to Agat had the fastest observed initial increase in basal growth. From the fourth month to the end of the study, survey 9 to 19, basal

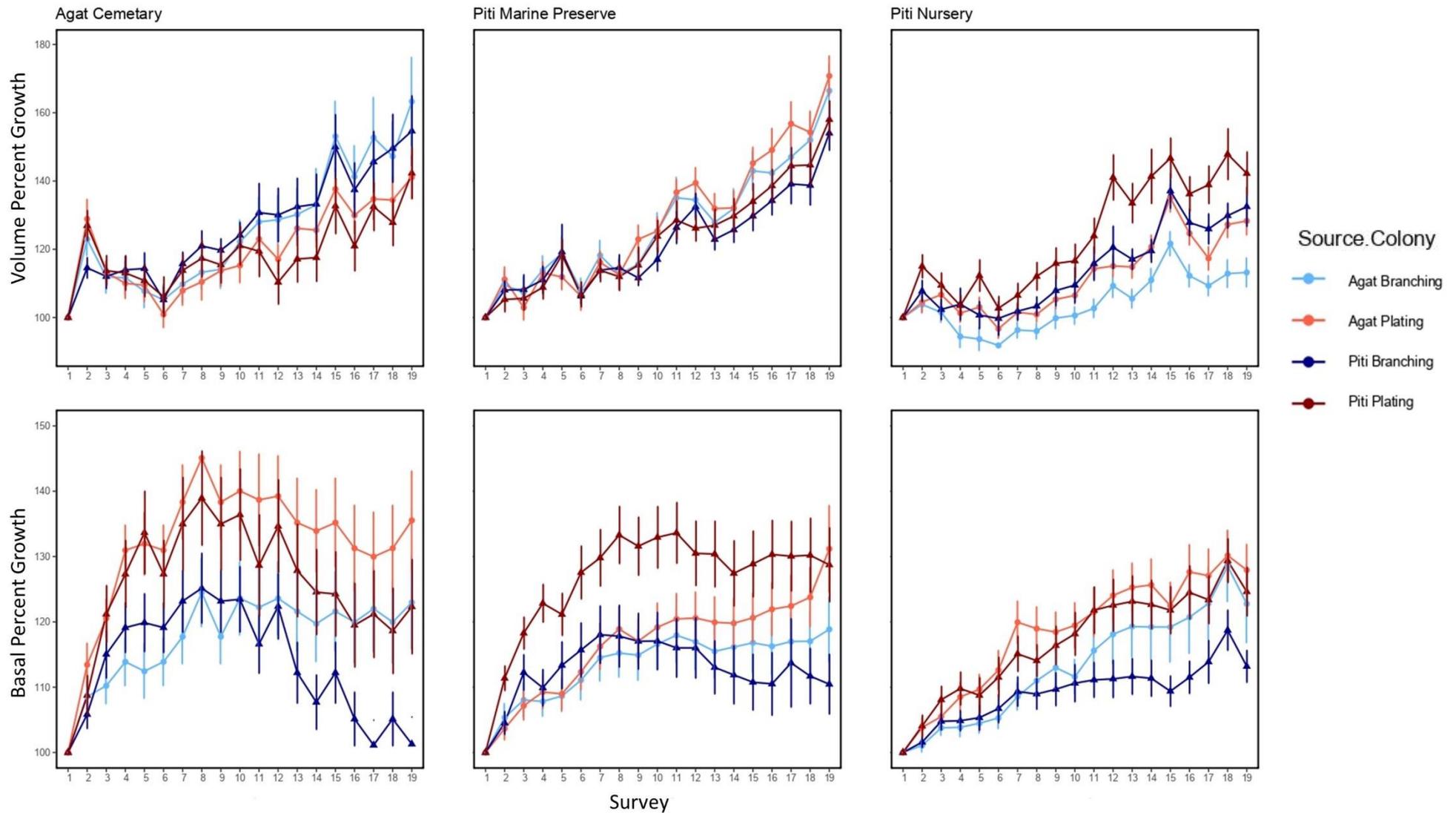


Figure 6. Volume (first row) and basal (second row) percent growth over the course of the study period (mean \pm SE of % change in growth). Surveys were conducted at two-week intervals with Survey 1 on 12/2/2020 and Survey 19 on 8/25/2021.

Table 2. ANOVA table that tested outplant site and source reef effects on fragment growth of both morphologies at the final survey. Significant results bolded. Significance codes: 0 ‘****’ 0.001 ‘***’ 0.01 ‘**’

Branching Morphology				
Volume	Two-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Outplant Site	F=13.096	p=4.06e^{-6***}	Piti Nursery < Agat	p=0.000591
			Piti Nursery < Piti	p=0.00031
Source Reef	F=0.08	p=0.931	NS	NS
Outplant Site: Source Reef	F=2.177	p=0.116	NS	NS
Basal				
Outplant Site	F=0.755	p=0.471	NS	NS
Source Reef	F=10.565	p=0.00132**	Piti < Agat	p=0.0013218
Outplant Site: Source Reef	F=1.182	p=0.30835	NS	NS
Plating Morphology				
Volume	Two-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Outplant Site	F=13.042	p=4.26e^{-6***}	Piti < Agat	p=0.0005714
			Piti Nursery < Piti	p=0.0000064
Source Reef	F=0.026	p=0.872	NS	NS
Outplant Site: Source Reef	F=2.479	p=0.086	NS	NS
Basal				
Outplant Site	F=0.191	p=0.827	NS	NS
Source Reef	F=1.768	p=0.185	NS	NS
Outplant Site: Source Reef	F=0.553	p=0.576	NS	NS

growth was relatively neutral or slightly decreasing across all outplant sites. In Agat, the Agat plating had the highest net percent basal increase, and the Piti branching had the biggest decrease in net percent basal growth by the end of the study (Figure 6). By the end of the study, the Agat branching fragments showed significantly more basal growth than Piti branching at a mean of 21% to 8% increase in basal surface area respectively (Table 2).

Throughout the study period, all fragment groups outplanted to Agat and Piti showed positive volumetric growth while fragments outplanted into the Nursery had a generally decreasing volumetric growth until three months of growth in the nursery, survey six (Figure 6). While all groups had an increase in volume by month one, almost all fragment groups showed a decrease in volume by the end of the first month, the 3rd survey. Decreased volumetric growth was also observed across all outplant sites between survey 5 and 6 (beginning of February 2021), but all groups recovered by survey 7. From the 5th to the 9th month of growth, survey 11 to 19, both source reef and morphology groups showed differentially influenced volumetric growth in each site. This trend could be explained by the transition from the dry to the wet season after survey 11.

The overall final percent volumetric growth of branching fragments outplanted to the Nursery (23% increase) was significantly lower from those in Agat (59% increase) and Piti (60% increase) (Table 2). The overall final percent volumetric growth of plating fragments outplanted to Piti (64% increase) were significantly higher from fragments in Agat (41% increase) and the Nursery (35% increase) (Table 2). The significant differences in volumetric growth observed in for both morphologies are driven by the Agat-sourced fragments (Table 2, Suppl. Table 1). The Agat-branching final percent volumetric growth showed significant differences between outplant sites with the Nursery (13% increase) showing significantly lower final growth compared to Agat (63% increase) and Piti (66% increase) (Figure 10, Supp. Table 1). Agat-plating final percent volumetric growth showed significantly more

growth in Piti (71% increase) compared to fragments outplanted to Agat (41% increase) and the Nursery (28% increase) (Supp. Table 1).

Fragments of the four source/morphology groups differed in final net volumetric and basal growth based on outplanting to their source or reciprocal transplant site. Agat-plating fragments grew significantly more in their reciprocal site, Piti (71% increase), than in their source reef (41% increase) (Fig. 7). And while the Piti-plating final volumetric growth between sites was not significant, Figure 7 shows Piti-plating grew more in Piti (58% increase) compared to Agat (42% increase). All four source/morphology groups demonstrated higher final basal growth in their source site compared to their reciprocal site, though these differences were not significant (Figure 7, Supp. Table 1).

By the end of the survey, nineteen of the twenty source colonies in Agat Cemetery and all source colonies in Piti Marine Preserve had resheeted over the initial fragmentation wound and completely recovered from fragment collection. No negative health or visual

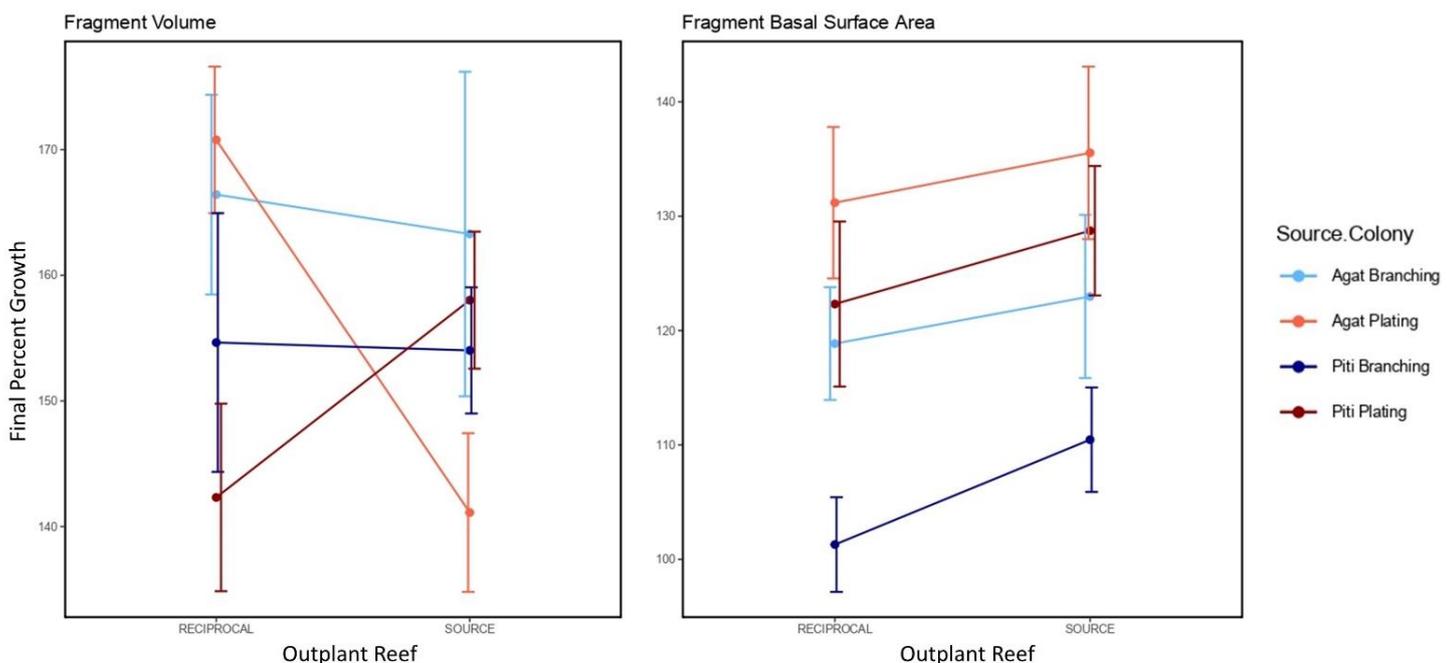


Figure 7. Final percent volumetric (left) and basal (right) percent growth of fragments at (mean \pm SE of % change in growth) dependent on outplant to source versus reciprocal reef.

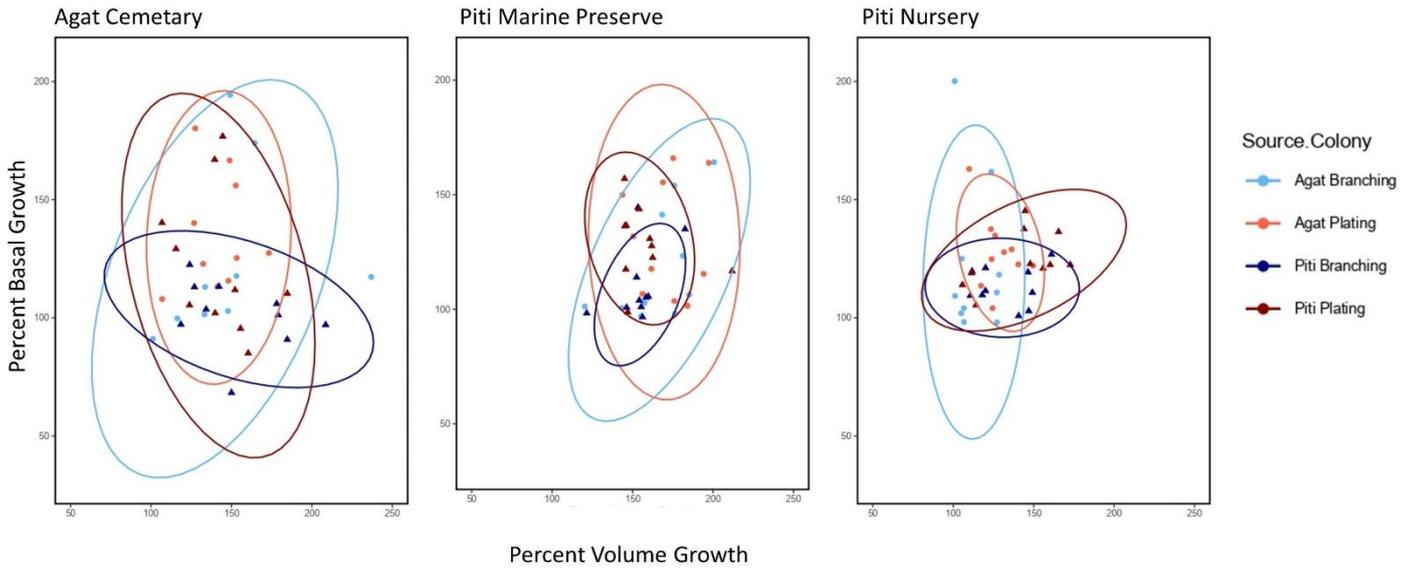


Figure 8. Final percent volumetric growth (X) and final percent basal growth (Y) for the two transplant sites and the nursery. Ellipses represent the variation of final basal and volume growth within the source/morphology groups.

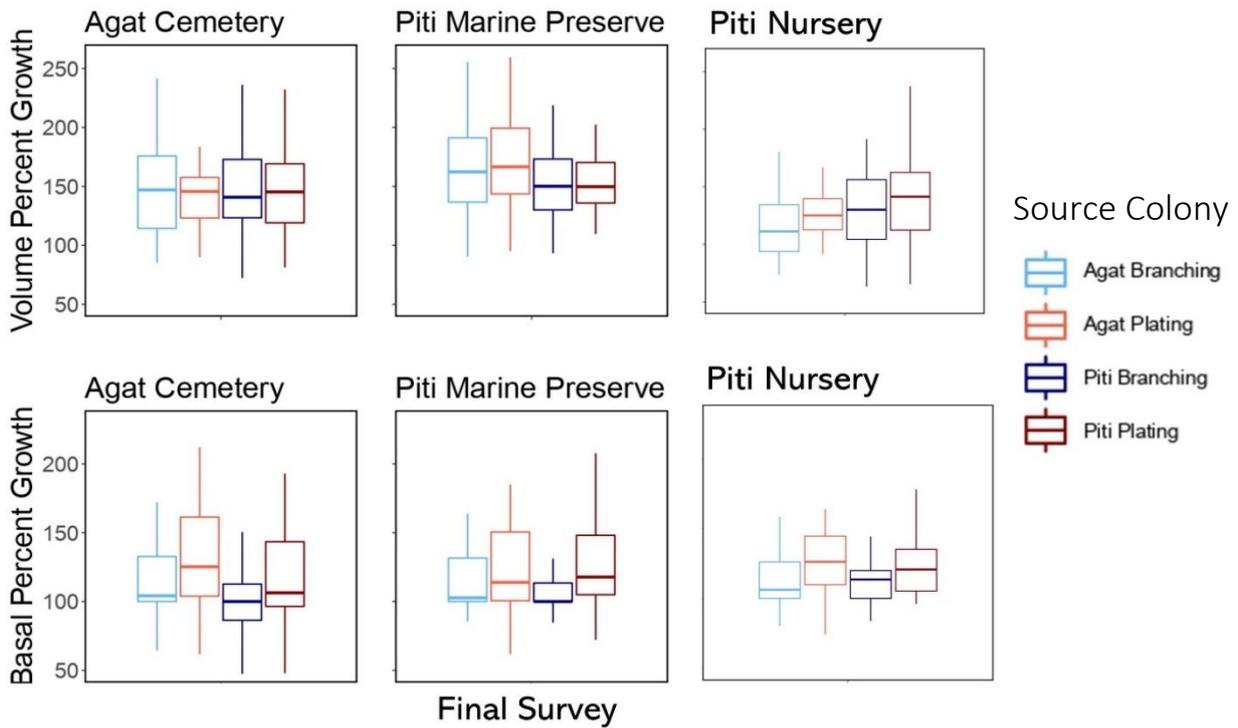


Figure 9. Final percent fragment volumetric growth and final percent basal growth for the two transplant sites and the nursery.

impacts were observed on any source colony from either source site by the end of data collection. Source colony percent growth variation across all groups within all outplant sites was significantly different at the different time points in the study (Supp. Table 2). This variability in source colony and fragment final percent growth is characterized in Figure 8 and 9 respectively, showcasing the difference in final basal and volumetric growth within each group. Supplemental Table 3 shows the significant outliers found at each outplant site throughout the study. Removing the outliers from the analysis determined that these source colony outliers did not drive the growth trend in their groups; growth trends between source-morphology groups did not change.

Reciprocal Transplant Site Environmental Data

The trends across all environmental parameters in Figures 10 and 11 exhibit the differing environmental makeup Piti and Agat have *within* and *between* seasons. Benthic cover data indicated a high percent of pavement, rubble, and sand in Piti while Agat was predominately rubble and sand (Figure 10). Fleshy macroalgae was present only in Agat

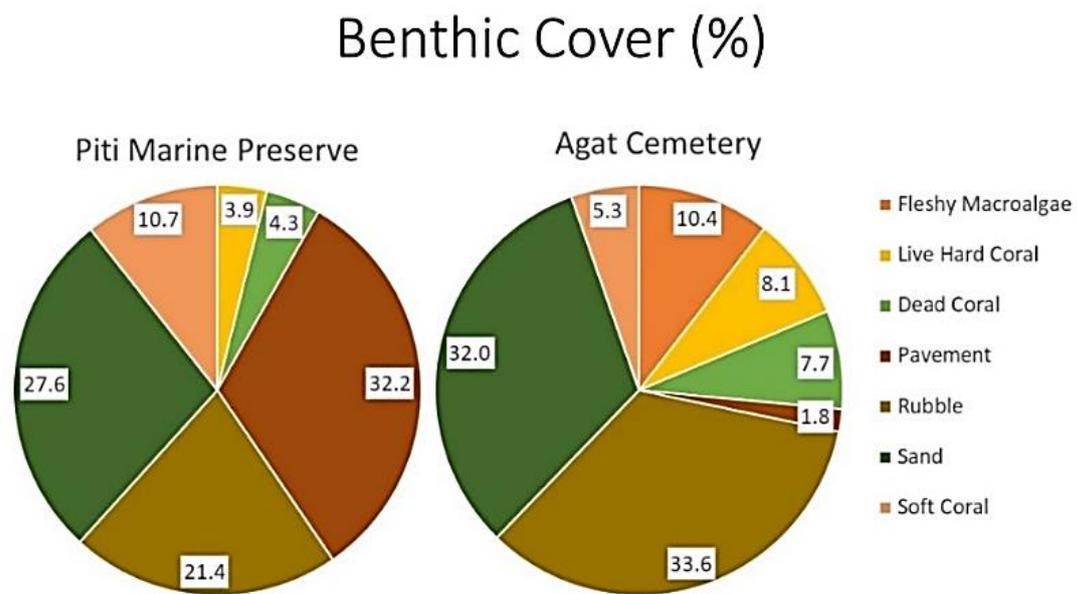


Figure 10. Percent benthic cover at both transplant sites averaged from 6 10-meter transects using LIT (line-intercept transect) method.

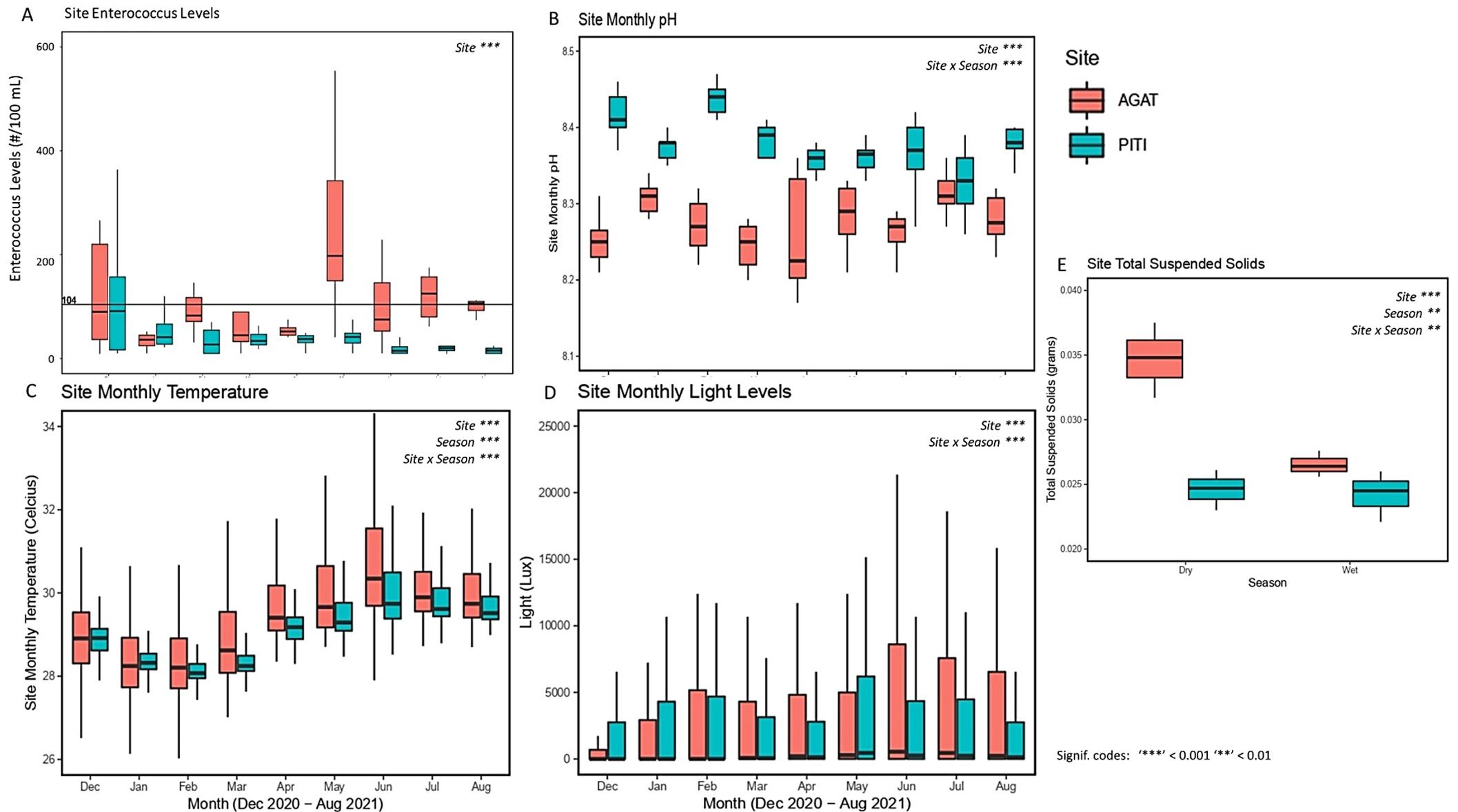


Figure 11. Transplant site environmental data from Guam EPA (A), YSI 6-series multi-parameter water quality sonde (B), HOBO Pendant temperature/light logger (C,D), and 1 liter water samples taken at both sites during the dry and wet seasons (E). In Figure 11A, the horizontal line seen on this graph represents the acceptable limit count of *Enterococcus* in a water sample; samples that show concentrations above acceptable EPA standards - 104 enterococci per 100 ml - are declared polluted (National Water Quality Monitoring Council).

during the surveys (Figure 10). *Within* the dry season pH, temperature, light, and suspended sediment were all found to be significantly different between Piti and Agat (Figure 11 B-E, Supp. Table 4). From the graphs, Agat had lower pH, higher suspended sediment levels, and more variable temperature and light levels compared to Piti in the dry season. From the *Within* the wet season, during the second half of the study, *Enterococcus*, pH, temperature, and light were significantly different between Piti and Agat (Figure 11 A-D, Supp. Table 4). The graphs show Agat had lower pH, higher *Enterococcus* levels, and more variable temperature and light levels compared to Piti in the wet season. *Between* seasons Agat exhibited significant differences in all environmental parameters, except *Enterococcus*, while Piti only exhibited significantly different shifts in temperature and light (Supp. Table 1).

Distribution and Abundance of *H. coerulea* Morphologies

Across all sites surveyed, the branching morphology was more abundant than the plating morphology (BINOMIAL; $n=614$ to $n=540$ colonies respectively; $p=0.0316$). I observed no colonies in five sites, in the central-west area of Guam. Only two sites had colonies

Table 3. Table of abundance survey results. Highlighted rows indicate a site that had a total density of over 5 corals per 400 m² meter area.

Site #	Site Name	Site Type	BR Density (400 M ²)	PL Density (400 M ²)	Total Density (400 M ²)
1	TANGUISSON	REEF FLAT	0.00	0.00	0.00
2	GUN BEACH	FORE-REEF	2.70	0.00	2.70
3	TUMON	REEF FLAT	0.00	0.00	0.00
4	ALUPANG ISLAND	FORE-REEF	8.74	16.60	25.35
5	EAST AGANA	REEF FLAT	0.76	0.67	1.43
6	WEST AGANA	REEF FLAT	0.00	0.00	0.00
7	ADELUP	REEF FLAT	0.00	0.00	0.00
8	ASAN CUT	FORE-REEF	10.42	1.12	11.54
9	ASAN-PITI	REEF FLAT	3.29	2.05	5.34
10	PITI	REEF FLAT	0.74	0.96	1.69
11	PITI FAR	REEF FLAT	7.45	8.80	16.24
12	TEPUNGAN FLAT	REEF FLAT	0.00	0.00	0.00
13	LUMINAO	REEF FLAT	0.39	0.28	0.67
14	DODI BEACH	REEF FLAT	2.42	7.11	9.52
15	AGAT	REEF FLAT	1.14	0.70	1.85
16	COCOS	REEF FLAT	0.08	0.48	0.56
17	BABI ISLAND	FORE-REEF	10.65	1.43	12.08
18	ACHANG CHANNEL	REEF FLAT	1.87	3.21	5.08
19	INARAJAN	REEF FLAT	6.94	6.48	13.42
20	PAGO BAY	FORE-REEF	0.34	0.00	0.34

with branching morphology and no plating morphology (Site 2, 20). A significant difference was found in morphological abundance on fore-reef sites; the branching morphology was dominant over the plating morphology (BINOMIAL; $n=325$ to $n=177$ colonies respectively; $p=3.89e^{-11}$). Within reef flat sites, the plating morphology was more abundant than the branching morphology (BINOMIAL; $n=363$ to $n=289$ colonies respectively; $p=0.004216$).

The size class trends

seen within the five reef flat sites show a right-skewed, bell-shaped curve for plating vs. branching morphologies, with the maximum abundance in size class 4 (Fig. 12). The branching morphology had maximum abundance in size class 3. The size class distribution per morphology was not statistically different (K-S TEST; $n=246$ branching to $n=321$ plating colonies respectively; $p=0.8928$). Within the three fore-reef sites, the branching morphology

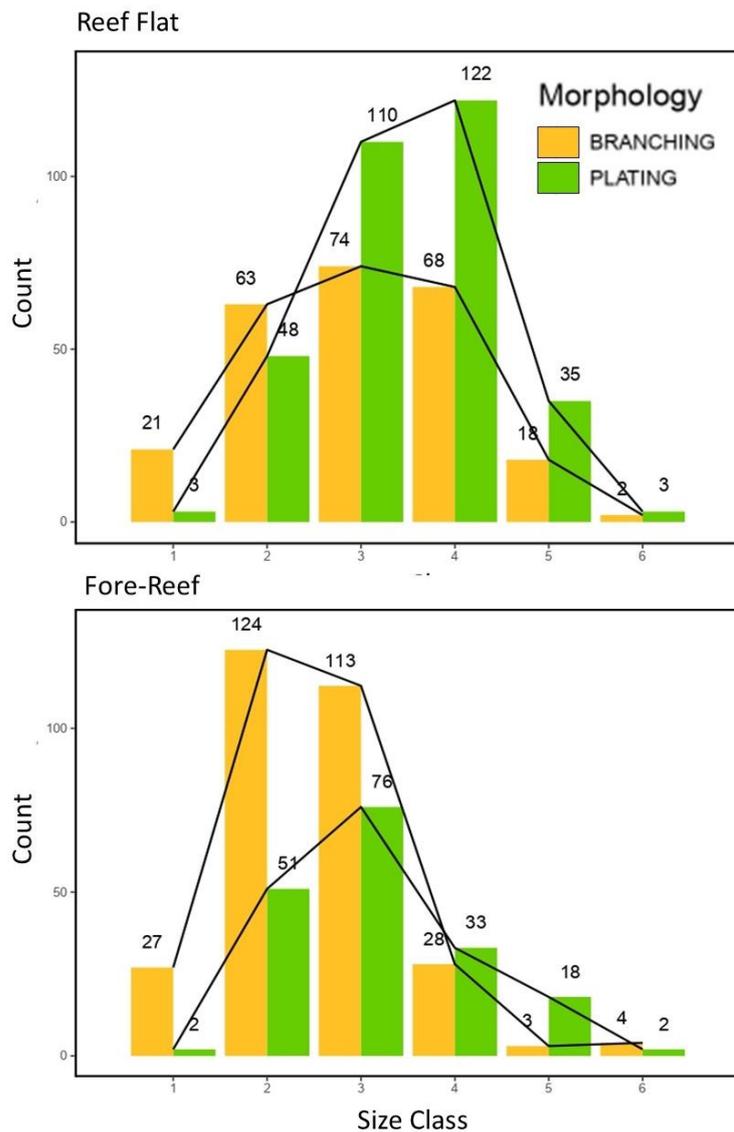


Figure 12. Counts of colonies of both morphologies within each size class (refer to Table 1) across 5 reef flat and 3 fore-reef sites with total density of 5 and above (see Table 2).

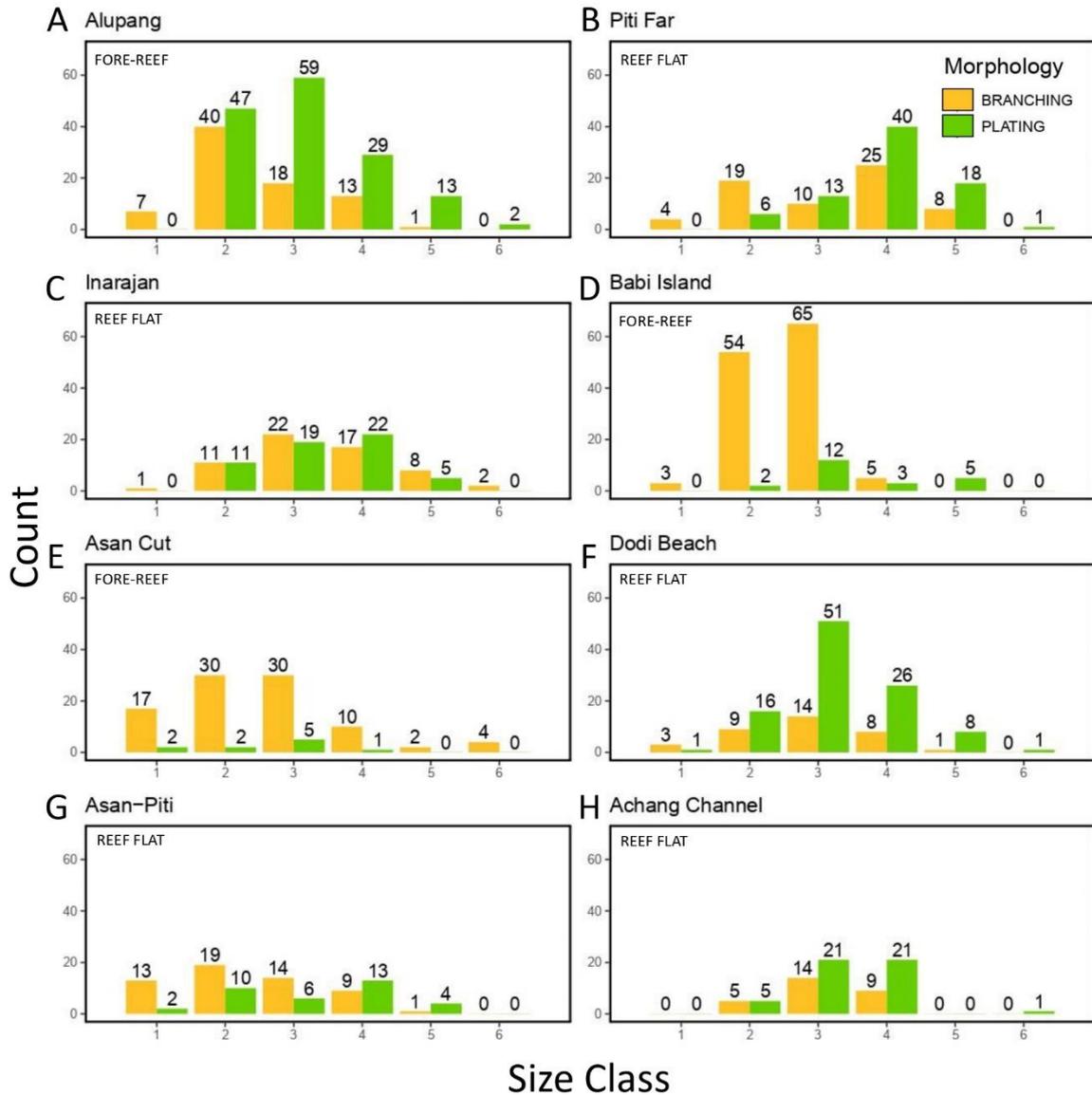


Figure 13. (A-H) Counts of colonies of both morphologies within each size class (refer to Table 1) across 8 sites with total density of 5 and above. Graph A (Alupang) has the highest total density descending to graph H (Achang Channel) with the lowest total density

showed a left-skewed, bell-shaped curve when compared to the plating morphology, with maximum abundance in size class 2. The plating morphology had maximum abundance in size class 3. The size class distribution was not statistically different between morphologies (K-S TEST; $n=299$ branching to $n=182$ plating colonies respectively; $p=0.8928$). The reef flat sites trended towards a higher abundance of larger plating colonies as opposed to the fore-reef sites, with a higher abundance of smaller branching colonies. All three fore-reef sites followed the trend of a higher abundance of smaller branching colonies while Alupang also

had a co-existing large population of plating colonies that were not seen at Babi Island and Asan Cut (Figure 13. A,D,E). There was no apparent trend in the reef flat sites, however when the sites are combined, a trend forms towards a higher abundance of larger plating colonies seen in Figure 12.

DISCUSSION

Transplant Survival and Growth

Across all outplant sites, *H. coerulea* transplants showed net positive volumetric and basal growth for all four source-morphology groups. Algal overgrowth or sand burial of fragments was not seen at any sites. A few fragments with exposed skeleton when initially outplanted did not fully re-sheet, concluding that this species would benefit from minimal exposed skeleton when attached to suitable substrate during future outplanting activities (Koval et al. 2020). No disease, predation, or unknown partial mortality was observed on any fragment during the course of the study. At the end of April 2021 (5 months post-transplant), there was a storm that could have affected the continued volumetric growth of the source/morphology groups from some fragment detachment from tiles and acute environmental stresses. Basal growth was unaffected by the weather conditions, but it did show trends towards an initial increase in growth after outplanting and subsequently slower growth three months post-transplant. Commonly, coral fragment will first put down tissue and skeleton onto the substrate to secure themselves to the reef (Guest et al. 2011; Coppari et al. 2019) prior to upward growth. For this species in particular, the basal growth in the first three months after initial outplanting was much higher than that during the rest of the study (Figure 6). This suggests that across outplant sites, the fragments were energetically focusing

on increasing basal area first before putting energy into volumetric growth (Villanueva et al. 2012).

Across outplant sites, the differences in final volumetric growth seen in both morphologies was driven by Agat-sourced fragments (Table 2, Supp. Table 2). Agat branching fragments grew significantly more in the two direct transplant sites compared to those in the Nursery, while the Agat plating fragments grew more in Piti compared to the other two sites. Piti-sourced fragments were not significantly affected by outplant to a degraded or non-degraded reef site. This suggests strategies when planning for future outplant sites for *H. coerulea*. Out of all the source-morphology groups, plating fragments sourced from a degraded site like Agat could grow volumetrically more in a non-degraded site, such as Piti.

Nursery Culture Implications

Monitored environmental parameters did not indicate differences in Piti Nursery compared to the other sites suggesting that environmental parameters were not responsible for the growth differences in the nursery. Across outplant sites, Piti Nursery fragments generally had lower volumetric growth compared to both direct transplant sites. While it is unclear what was driving this response, I speculate that it could be due to differences in water movement. The fragments in the nursery were growing on a mid-water floating table which moved slightly with water currents, unlike the fragments that were cemented down in the direct-transplant sites. That gentle water motion could have resulted in the fragments being exposed to less flow overall, which might have influenced growth rates. The tables moving with the water is possibly providing less current “stress” on the fragments as they were growing. Boch and Morse (2012) found fragment growth was significantly higher in sites

with higher seawater flow. Forrester et al. (2019) examined the direct transplantation method versus nursery grown coral fragments of *Acropora cervicornis* and found that between the two, direct transplantation was a more time- and cost-effective method for similar growth and survival results. Overall, due to the significantly lower volumetric growth in the Nursery, this indicates that this coral grows more through direct transplantation rather than implementing a short nursery grow-out phase. However, while fragments did grow slower in the nursery, the survival rate matched the direct outplanted fragments. I recommend that a nursery setting would be beneficial for decreased harvesting of wild source colonies or to protect specific genetic stock or breeding colonies.

Source Colony Effect

In this study, although final volumetric and basal growth between source colonies was variable within sites, no source colony determined as an outlier was observed at more than one outplant site and there were no source colony driven growth trends within sites (Supp. Table 4). This suggests that there will not be increased outplant success of fragments sourced from Piti or Agat based on source colony (Baums et al. 2019). Growth differences between fragments and source colonies are to be expected and phenotypic plasticity will play a role between morphologies and between sites to an extent (Lohr et al. 2020; Conetta 2021) but for this study, source colony selection is not a significant influence on growth and survival of *H. coerulea* fragments at these three sites.

Reciprocal Site Environmental Differences

Agat Cemetery and Piti Marine Preserve environments were significantly different in assessed attributes across the study period. Agat exhibited significant differences in all

environmental parameters *between* seasons, except *Enterococcus*, suggesting highly variable environmental conditions and water quality. And while *Enterococcus* was not significantly different across the study, Agat was declared polluted by Guam EPA six of the nine months surveyed. The seasonal differences in Agat were most likely driven by land runoff and water movement within the site. The Agat coast has dense residential development moving far inland. During the dry season, lower water movement leads to a more turbid, low light, low pH environment. In contrast, the wave action from increased storm events in the wet season may act as a flushing mechanism, creating a more stable light, pH, and temperature environment (Fifer et al. 2021). Piti has a main road running along the coastline but has high vegetation cover on the landward side of the road with no residential areas and few buildings set back from the road. Piti showed significant seasonal shifts only in temperature and light from the dry to the wet season, which may be due to expected variable thermal and light conditions on reef flats due to shallow water depths and shifts in tides (Raymundo et al. 2019). These differences suggest classifying Agat as a degraded site and Piti as a non-degraded site.

Distribution and Abundance

Little was previously known about the distribution and abundance of *H. coerulea* on Guam and my surveys increased the database on differential abundance of the two known morphologies at different sites. Observed clustering of colonies within sites can be explained by this coral's reproductive strategy and larval dispersal limitation caused by its negative buoyancy (Harii and Kayanne 2003). Low *H. coerulea* density at some sites could also be explained by tidal currents and physical barriers limiting larval movement (Thompson et al.

2018). These factors could be why some survey sites with similar environmental conditions had high abundance while others had no colonies in a comparable survey area.

When comparing *H. coerulea* size class, morphology, and distribution between the reef flats and fore-reefs, the fore-reef sites showed higher abundance of smaller branching colonies as opposed to the reef flat sites, which trended towards a higher abundance of larger plating colonies. Wave energy on the fore-reefs is higher due to exposure to open ocean currents. This wave stress could favor smaller branching colonies with less vertical surface area resistance against water motion, as opposed to the large surface area of a flat, kite-like plating colony (Madin et al. 2014; Cresswell et al. 2020). In the reef flat sites, there is lower wave energy which could lead to the higher abundance of larger plating colonies. The high variability of morphologic and size distribution on Guam's reef flats and fore-reefs suggests future studies are necessary to better understand the morphology-based differences in nutrient intake, environmental disturbance capacity, and larval dispersal and density.

The eight sites with the highest density were not concentrated along a geographic area of Guam, suggesting that the population of *H. coerulea* on Guam has the potential to be present in other fore-reef and reef flat environments not surveyed. The number of corals falling within size class four (61-100 cm) and above display the reef habitat potential of this species. Any shifts to altered reef states that are dominated by non-reef building species could threaten the ecosystem services and biological function of coral reefs (Hughes et al. 2010; Adam et al. 2020). Maintaining the three-dimensional structure and habitat on reefs is important (Graham et al. 2015). Colonies of this species provide this habitat. At some sites, colonies were recorded up to 400 cm in diameter suggesting old, stable colonies that have survived the recent large-scale mortality events affecting reef-building scleractinian species (Raymundo et al. 2019). In some reef systems, it has been shown octocoral abundance is increasing with scleractinian decline after severe bleaching events (Lenz et al. 2015).

IMPLICATIONS FOR RESTORATION

There was no fragment mortality and low partial mortality during the study period, though four fragments were lost due to dislodgement from the substrate. There was no significant difference in overall growth between Agat, a degraded site, and Piti, a non-degraded site. The lowest growth rates, in the coral nursery, suggest a recommendation that the preferred method of outplanting for this species is direct transplantation of fragments onto suitable substrate (Forrester et al. 2019).

Using tiles as a stable base is a popular method in coral restoration (Forsman et al. 2015; Page et al. 2018; Suggett et al. 2018) and was used in this study to secure fragments onto natural reef substrate. Future recommendations would be to collect fragments from wild or nursery-based source colonies and directly connect coral fragments to substrate. Tiles were used successfully in this study, but direct transplantation will eliminate transportation stress of fragments into a lab setting and remove introduction of tiles to the outplant site.

Tsang et al. (2020) found source site selection as well as outplant site selection are important to maximize outplanting success of target species. Raymundo (2001) concluded differences in environmental quality between transplant sites affected fragment growth the most. On Guam, site selection for future outplanting efforts of *H. coerulea* should focus on the plating morphology outplanted to non-degraded sites and the branching morphology to either degraded or non-degraded sites to increase outplant success.

In conclusion, due to the reproductive strategy and challenging larval dispersal of this species (Harii and Kayanne 2003), human involved outplanting of this species into a myriad of sites will be advantageous by expanding *H. coerulea* habitat range to allow for greater potential for natural fertilization and larval success. Due to the findings of this study, *Heliopora coerulea* would be an ideal candidate for coral restoration activities on Guam.

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SUPPLEMENTAL TABLES

Supp. Table 1. ANOVA table that tested outplant site effects on fragment growth of all groups across outplant sites at the final survey. Significant results bolded. Significance codes: 0 ‘****’ 0.001 ‘***’ 0.01 ‘**’ 0.05 ‘*’ 0.1 ‘.’ 1

Agat Branching				
Volume	One-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Outplant Site	F=10.78	p=5.04e⁻⁵****	Piti Nursery<Agat	p=0.0004806
			Piti Nursery<Piti	P=0.000195
Basal				
Outplant Site	F=0.146	p=0.864		
Piti Branching				
Volume	One-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Outplant Site	F=2.9	p=0.059.		
Basal				
Outplant Site	F=3.009	p=0.0532.		
Agat Plating				
Volume	One-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Outplant Site	F=15.78	p=8.58e⁻⁷****	Piti Nursery<Piti	p=0.0000008
			Agat<Piti	p=0.000619
Basal				
Outplant Site	F=0.354	p=0.702		
Piti Plating				
Volume	One-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Outplant Site	F=1.981	p=0.142		
Basal				
Outplant Site	F=0.392	p=0.677		

Supp. Table 2. Repeated measures ANOVA table that tested source colony effects on fragment growth trends of all groups across the survey period. Significant results bolded. Significance codes: 0 ‘****’ 0.001 ‘***’ 0.01 ‘**’ 0.05 ‘.’ 0.1 ‘.’ 1

Agat				
Repeated Measures ANOVA	Volume		Basal	
Agat plating	F=9.427	p=2.26e^{-17*}	F=10.524	p=4.42e^{-16*}
Piti plating	F=5.296	p=1.57e^{-9*}	F=4.116	p=4.72e^{-7*}
Agat branching	F=10.768	p=1.25e^{-19*}	F=2.753	p=0.000375*
Piti branching	F=9.992	p=2.44e^{-18*}	F=8.694	p=4.42e^{-16*}
Piti				
Repeated Measures ANOVA	Volume		Basal	
Agat plating	F=29.023	p=1.71e^{-41*}	F=9.825	p=4.67e^{-18*}
Piti plating	F=19.508	p=9.81e^{-32*}	F=15.625	p=7.68e^{-27*}
Agat branching	F=31.902	p=5.5e^{-44*}	F=4.54	p=5.57e^{-8*}
Piti branching	F=20.195	p=1.55e^{-32*}	F=3.868	p=1.6e^{-6*}
Nursery				
Repeated Measures ANOVA	Volume		Basal	
Agat plating	F=28.262	p=8.39e^{-41*}	F=15.933	p=2.97e^{-27*}
Piti plating	F=22.598	p=3.33e^{-35*}	F=18.904	p=5.14e^{-31*}
Agat branching	F=13.012	p=3.9e^{-23*}	F=3.335	p=2.2e^{-5*}
Piti branching	F=21.549	p=4.61e^{-34*}	F=7.948	p=1.01e^{-14*}

Supp. Table 3. Repeated measures ANOVA table comparing significant source colony outlier effect on volumetric and basal growth trends results. Significant results bolded. Significance codes: 0 ‘****’ 0.001 ‘***’ 0.01 ‘**’ 0.05 ‘.’ 0.1 ‘.’ 1

Site	Outlier Source Colony	Outlier in (Volume/ Basal)	ANOVA with outlier		ANOVA with outlier removed	
Agat	AB5	Volume	F=10.768	p=1.25e^{-19*}	F=14.547	p=3.68e^{-24*}
Agat	AB2	Basal	F=2.753	p=0.000375*	F=2.056	p=0.01.
Agat	PB7	Basal	F=8.694	p=4.42e^{-16*}	F=7.078	p=1.18e^{-12*}
Agat	PB9	Basal	F=8.694	p=4.42e^{-16*}	F=7.229	p=6.28e^{-13*}
Nursery	PB10	Volume	F=21.549	p=4.61e^{-34*}	F=31.387	p=6.96e^{-41*}
Nursery	AB2	Basal	F=4.54	p=5.57e^{-8*}	F=1.995	p=0.013*
Nursery	AB6	Basal	F=4.54	p=5.57e^{-8*}	F=2.789	p=0.000351

Supp. Table 4. ANOVA table that tested outplant site and seasonal significance on environmental data. Significant results bolded. Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘.’ 1

<i>Enterococcus</i>	Two-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Site	F=11.72	p=0.000795***	Wet: Piti-Agat	p=0.0029881
Season	F=0.336	p=0.563299		
Site:Season	F=2.787	p=0.09714		
pH	Two-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Site	F=92.83	p=<2e⁻¹⁶***	Agat: Wet-Dry	p=0.01134
Season	F=0.777	p=0.37866	Dry: Piti-Agat	p=0
Site:Season	F=9.914	p=0.00175**	Wet: Piti-Agat	p=0.00128
Temperature	Two-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Site	F=487.38	p=<2e⁻¹⁶***	Piti: Wet-Dry	p=0
Season	F=6615.61	p=<2e⁻¹⁶***	Agat: Wet-Dry	p=0
Site:Season	F=56.28	p=6.69e⁻¹⁴***	Dry: Piti-Agat	p=0
			Wet: Piti-Agat	p=0
Light	Two-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Site	F=0.195	p=0.659	Piti: Wet-Dry	p=0
Season	F=487.664	p=<2e⁻¹⁶***	Agat: Wet-Dry	p=0
Site:Season	F=153.189	p=<2e⁻¹⁶***	Dry: Piti-Agat	p=0
			Wet: Piti-Agat	p=0
Suspended Sediment	Two-Way ANOVA	Significance	Post Hoc comparison	Tukey HSD
Site	F=29.35	p=0.000633***	Agat: Wet-Dry	p=0.00448
Season	F=13.9	p=0.0058**	Dry: Piti-Agat	p=0.00114
Site:Season	F=11.41	p=0.0096**		