

growth rates for each axes or stress metrics when transplanted to a novel location. Non-natal fragments did however, show higher predation than natal fragments (generalized linear mixed effects model, family: binomial, $z = 2.12$, $p = 0.033$). Using multiple linear regressions we observed a positive linear relationship between vertical ($\beta = 0.121$, $t(263) = 2.15$, $p = 0.02$) and horizontal ($\beta = 0.204$, $t(263) = 3.01$, $p < 0.01$) growth axes with temperature but not for perpendicular growth rates. Overall, these results suggest site adaptation does not limit the acroporid hybrid's ability to acclimate to non-natal locations. Furthermore, we also observed similar growth rate trends within optimal temperature ranges as seen with the parental species. This study provides baseline physiological data for the acroporid hybrid and supports the incorporation of *A. prolifera* in a controlled manner with current and future coral restoration efforts to re-establish *Acropora* populations throughout the Caribbean.

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The acclimatization of the Caribbean fused staghorn coral *Acropora prolifera* to non-natal locations

By
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CONTRIBUTION OF AUTHORS

Colin Howe is the lead author who organized and participated in every aspect of the manuscript except the genetic analysis.

Dr. Tyler Smith provided support with the experimental design, ecological concepts, logistical support, reviewing the manuscript and providing feedback throughout the entire manuscript.

Dr. Dan Holstein assisted in interpretation of the results and provided feedback on both the manuscript and statistical analysis component of the experimental design.

Dr. Nicole Fogarty allowed the use of her lab to help analyze coral tissue samples for genetic analysis and also provided feedback on the manuscript.

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The acclimatization of the Caribbean fused staghorn coral *Acropora prolifera* to non-natal locations

Chapter 1: Introduction

Two *Acropora* species, *A. cervicornis* and *A. palmata* (Lamarck 1816), have persisted within Caribbean coral reef ecosystems for millions of years (Budd et al., 1994; Gladfelter et al., 1978). Rapid growth rates and complex branching morphology allowed these species to form large thickets in shallow reef ecosystems, providing vital habitat for marine fishes and invertebrates (Bruckner, 2003; Tunnicliffe, 1981), and coastal shoreline protection (Bruckner, 2003; Gladfelter et al., 1978). In recent years, Caribbean *Acropora* species have been severely impacted by compounding stressors, such as hurricanes (Woodley et al., 1981), bleaching events (Highsmith, 1980; Muller et al., 2008), cold fronts (Precht & Miller, 2007; Schopmeyer et al., 2012), and most significantly, outbreaks of white band and rapid tissue loss disease (Aronson & Precht, 2001; Rothenberger et al., 2008). The cumulative effects of these stressors have resulted in a population decline of 80-98% in both *Acropora* species (Aronson & Precht, 2001; Bruckner, 2003; Miller et al., 2002). Bak et al., (1983) suggested that white band disease had a drastic effect on these species due to limited genetic diversity from high asexual reproduction. Both species were listed as “threatened” under the Endangered Species Act (Hogarth 2006) and listed as “critically endangered” by the International Union for Conservation of Nature (IUCN) in 2008 (Aronson et al., 2008a; Aronson et al., 2008b). Moreover, the natural recovery of these species is limited by low, variable rates of sexual reproduction and post-settlement larval survivorship (Bruckner, 2012; Dudgeon et al., 2010; Quinn & Kojis, 2005).

Chapter 2: Acclimatization of *Acropora prolifera*

2.1 Introduction

After the significant population decline of *A. cervicornis* and *A. palmata*, there is evidence for an increased abundance of a third acroporid taxon called, fused staghorn coral (*A. prolifera*), in the Caribbean and the Florida Keys (Aguillar-Perera & Hernandez-Landa, 2017; Fogarty 2012; Fogarty et al., 2012; Japaud et al., 2014; Wheaton et al., 2010). This acroporid taxon is a naturally occurring hybrid between *A. cervicornis* and *A. palmata* (van Oppen, 2000; Vollmer & Palumbi, 2002; Willis et al., 2006). Several populations of *A. prolifera* contain high genetic diversity (Fogarty, 2010), and in certain locations have matched or surpassed the population sizes of its parent species (Fogarty, 2012; Japaud et al., 2014; Wheaton et al., 2010). In direct opposition to the hypothesis that hybrids have reduced viability from incompatibilities between two species (Haldane, 1922; Dobzhansky, 1937), in the case of *A. prolifera*, a recent study has shown evidence of equal or higher viability when compared its parental species (Fogarty, 2012). Moreover, molecular analysis revealed *A. prolifera* at low levels, can reproduce with the parental species through backcrossing, facilitating introgression or gene flow from *A. palmata* into *A. cervicornis* (Fogarty et al. 2012; van Oppen, 2000; Vollmer & Palumbi, 2002). Recent evidence shows that not only can *A. prolifera* survive in the wild equally to its parental species, but it is also reproductively viable. The natural occurrence of viable hybridization and gene flow within the Caribbean *Acropora* taxa may provide significant evolutionary contributions to the threaten *Acropora* genus through the formation of novel genetic traits (Baums 2008; Richard & Hobbs, 2015; Seehausen, 2004; Willis et al. 2006).

2.2 Novel genetic traits

Initial evidence suggests *A. prolifera* represent an important reservoir of novel genetic information which may benefit the resilience of the Caribbean *Acropora* genus (Baums, 2008; Richard & Hobb, 2015; Willis et. al., 2006). This evidence also identifies *A. prolifera* as a useful tool in reef enhancement and coral restoration programs (Bowden-Kerby, 2014; Baums, 2008; NMFS, 2016). Propagating reefs communities with high interspecific and intraspecific diversity will increase the resilience of targeted reefs to present day environmental and ecological stressors (Duruy & Lirman, 2017). It is important, however, to address potential risks associated with high rates of hybridization where the hybrid coral backcrosses with the parental species (Edmunds, 2007; Rhymer & Simberloff, 1996). The genetic distinction between species could be dampened if backcrossing rates are high, leading to genetic swamping (Edmunds, 2007; Rhymer & Simberloff, 1996). Additionally, if selective pressure is weak on deleterious traits that can arise from hybridization between species, and backcrossing rates are high with the hybrid, this could lead to reduced viability of the parental species (Baums, 2008; Edmunds, 2007). Both threats however, are constrained by low backcrossing rates after the *Acropora* population decline (Baums et. al., 2013; NMFS, 2016; Johnson et al., 2011). Backcrossing rates also vary between species based pre-zygotic barriers for both *A. cervicornis* and *A. palmata* eggs (Fogarty et al., 2012; Vollmer & Palumbi, 2002). In choice and no-choice trials, both *A. cervicornis* and *A. palmata* eggs can be fertilized by heterospecific sperm (Fogarty et al., 2012). *A. cervicornis* (Fogarty et al., 2012) and *A. prolifera* sperm (Fogarty, Baums, unpublished data) can fertilize *A. palmata* eggs however, this occurs at much lower frequencies and it takes higher sperm concentration to do so. Moreover, the current data is inconclusive on the ecological viability of

acroporid hybrid genetic traits (Baums, 2008; NMFS, 2016). Determining this hybrid's role as a viable provider of novel genetic information, warrants ecological research to identify if these novel genotypes contain traits that will benefit or undermine its survival or subsequently how it will influence the Caribbean *Acropora* genus.

The viability and resilience of coral species in modern environmental conditions are dependent on a combination of intrinsic (genotypic) traits towards adaptability and acclimatization (Bliss 2015; Edmunds et al., 2014; Fogarty, 2012) and extrinsic traits associated with resilience in changing environmental and ecological stressors (Fogarty, 2012). For example, adaptation is a response that occurs genetically over multiple generations as a response to a recurring or consistent environmental pressure (Nelson et al., 2007). Persistent genotypes within a population subjected to reoccurring environmental pressures, contain adaptive traits that allow coral to survive locally (Bowden-Kerby, 2008; Bowden-Kerby & Carne, 2012; Seebacher & Franklin, 2012). Populations of *A. cervicornis* colonies, established in shallow forereef locations that experience consistently high wave energy contain genotypes that are adapted to the environmental conditions of that area (Bowden-Kerby 2008; Bowden-Kerby & Carne, 2012). Additionally, the physiology of genotypes adapted to specific locations may benefit or undermine survival in novel environments (Baums, 2008). Acclimatization describes the ability of an organism to adjust to changes in the environment over a single generational time scale, allowing it to maintain performance across a range of environmental conditions (Jones and Berkelmans 2010). Thus, one way to test these novel hybrid genetic traits, is to understand if site adaptation limits the ability of *A. prolifera* to acclimate to novel locations. Comparing the capacity for novel genotypes to support and maintain health, despite changes to their

environment can help describe the resiliency of this acroporid hybrid and identify if novel genetic traits will support its persistence.

2.3 Experimental rationale

The primary objective of this study is to use health metrics established for *A. cervicornis* and *A. palmata* to identify if site adaptation limits *A. prolifera* ability to acclimate to novel locations across multiple genotypes. Health metrics including growth rates, mortality, and susceptibility to disease, predation and temperature stress have been used to assess the ecological response of the parental species (Baums et al., 2003; Fogarty 2012; Forrester et al., 2013; Lirman et al., 2014; Muller et al., 2008). Given that first generation hybrids (F1) contain half of its genetic material from each parental species (van Oppen, 2000; Vollmer & Palumbi, 2002), we expect *A. prolifera* to exhibit similar ecological responses. Growth rate is a direct metric for health influenced by both extrinsic and intrinsic factors such as environment, genotype, symbiotic clade, and physiology (Lirman et al., 2014). For *Acropora* species, linear extension can vary between distinct genotypes by an order of magnitude (Lirman et al., 2014). Some *A. cervicornis* genotypes are capable of significantly faster growth rates compared to others (O'Donnell et al., 2016; Griffin et al., 2012; Lirman et al., 2010; Lirman et al., 2014) and growth rates overall can differ across thermal ranges (Lohr & Patterson, 2017; Gladfelter et al., 1978). Because of the variability seen between *Acropora* genotypes, it is important to compare multiple genotypes within this hybrid coral. Thermal conditions directly impact growth rates for scleractinians corals (Edmunds, 2005; Tanzil et al., 2013; Pratchett et al., 2015). Growth rates follow a linear response where gradual increases in temperature may support growth; however, this relationship starts to break down once above or below optimal conditions (Deutsch et al., 2008). Early growth

rate comparisons for *A. palmata* and *A. prolifera* show increased growth rates in the summer and fall months (Gladfelter et al., 1978). Growth rates for *A. prolifera* where the maximum annual water temperature was 29.5°C had a mean linear extension of 8.1 ± 3.2 (cm). Conversely, during minimum annual water temperatures (26°C) *A. prolifera* had a mean linear extension growth rate of 5.92 ± 2.2 (cm) (Gladfelter et al., 1978). The maximum optimal temperature reported for *Acropora* corals is between 28-30°C (Shinn, 1966). However, thermal conditions outside of optimal temperature ranges can lead to reduced growth rates for *A. cervicornis* (Lohr & Patterson et al., 2017). With minimal reports comparing *A. prolifera* growth rates and temperature across multiple genotypes, the secondary objective of this study is to compare the linear relationship between *A. prolifera* growth rates and changes in temperature.

Thermal conditions above optimal ranges can also stress corals and lead to increased susceptibility to diseases (Brandt & McManus, 2009; Muller et al. 2008 Patterson et al., 2002). During the 2005 bleaching event, populations of *A. palmata* suffered wide spread bleaching in St. John, USVI where temperature peaked between 30-31°C. There was a significant prevalence of disease among bleached corals compared to non-bleached corals (Muller et al., 2008). In addition to thermal stress, predation from corallivorous *Coralliophila abbreviata* and *Hermodice carunculata* can serve as a vector for disease and subsequent predation stress can increase disease susceptibility (Baums et al., 2003; Knowlton, 1992; Miller et al., 2014; William & Miller, 2005). In response, coral colonies will reallocate energy from growth or reproduction to deter predators or regenerate lost tissue (Baums et al., 2003). Moreover, in already reduced populations of *Acropora* corals, predation pressure is thought to be concentrated on remaining

colonies and can limit the success of initial fragments (Rotjan & Lewis, 2008; Williams & Miller, 2012; 2014).

The intermediate morphology of *A. prolifera* between the parental species has been taken into consideration in response to environmental and ecological conditions (Bowden-Kerby, 2008; Brewer, 2013; Fogarty, 2012; Rogers 1983). The most common morphology of *A. prolifera* exhibits more cylindrical branches similar to *A. cervicornis* (ARBT, 2005) however, other observed morphologies include tightly fused branches (Fogarty, 2012) or a “bushy appearance” (Bowden-Kerby, 2008) (Figure 1). The more cylindrical branching morphology is thought to reduce sedimentation effects at depth (Brewer, 2013; Rogers, 1983). Whereas, the bushy fused branch morphology is thought to be more resistant to strong current and wave energy (Bowden-Kerby, 2008; Fogarty, 2012). *Acropora* coral branches grow apically from the base of the colony (Kiel et al., 2012), which also serve as an important component for asexual reproduction (Bruckner, 2003; Kiel et al., 2012; Mercado et al., 2016). Thus, growth of new apical tips which form new branches has been used to determine colony productivity for *A. cervicornis* (Kiel et al., 2012; Mercado et al., 2016). Anecdotally, *A. prolifera* produce a significant number of apical tips per colony possibly as a result of this intermediate morphology. Because of this hybrid’s unique branching morphology, our third objective was to observe variation in apical tip production between distinct locations and within distinct genotypes. Overall ecological research on *A. cervicornis* and *A. palmata* shows growth rates and stress indicators are a direct metric for health which vary across genotypes. With genetic information from both species, we assume *A. prolifera* will have similar responses, thus allowing us to use previously established health metrics to analyze hybrid viability and resilience.

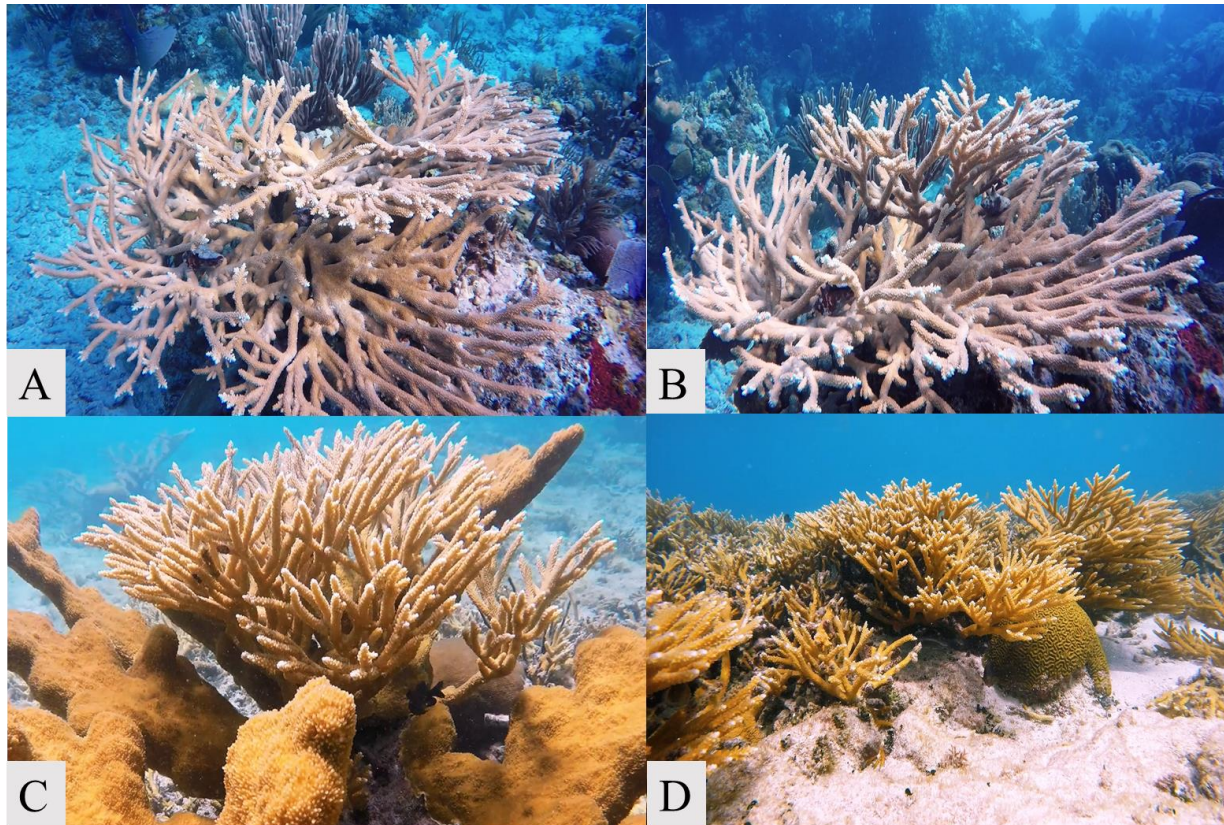


Figure 1. Distinct morphologies of *A. prolifera* observed in St. Thomas, USVI. Images (A & B) shows an *A. prolifera* colony with an open cylindrical branching profile, extending radially at 8m in depth. Image (C) shows an *A. prolifera* colony with a “Bushy” morphology at 2m in depth. Image (D) shows a thick of *A. prolifera* colonies occupying shallow water at less than 2m depth.

2.4 Experimental Design

Common garden experiments including reciprocal transplants have been used to test the resilience of *A. cervicornis* and *A. palmata* between distinct geographical locations (Bliss, 2015; Forrester et al., 2013) fore and backreef sites (Bowden-Kerby, 2008), and across *Acropora* taxa zones (Brewer, 2013; Fogarty, 2012). Reciprocal transplants involve redistributing individuals between source populations and comparing health metrics between transplanted individuals and native individuals over time. To effectively compare the acclimatization through reciprocal transplants, each donor location must contain unique characteristics, such as temperature,

current, and water quality (Bliss, 2015; Forrester et al., 2013). In conjunction with reciprocal transplant, using a reaction norms analysis can describe the phenotypic plasticity of species across genotypes and environmental conditions. Multiple genotypes are plotted each as a single horizontal line with dependent variable (e.g., location) across the x-axis and an independent variable (e.g., growth) across the y-axis (Figure 2). Using both methodologies can help identify whether differences in health metrics from each population are caused by changes to their environment, genotypic variation or an interaction between genotype and the environment.

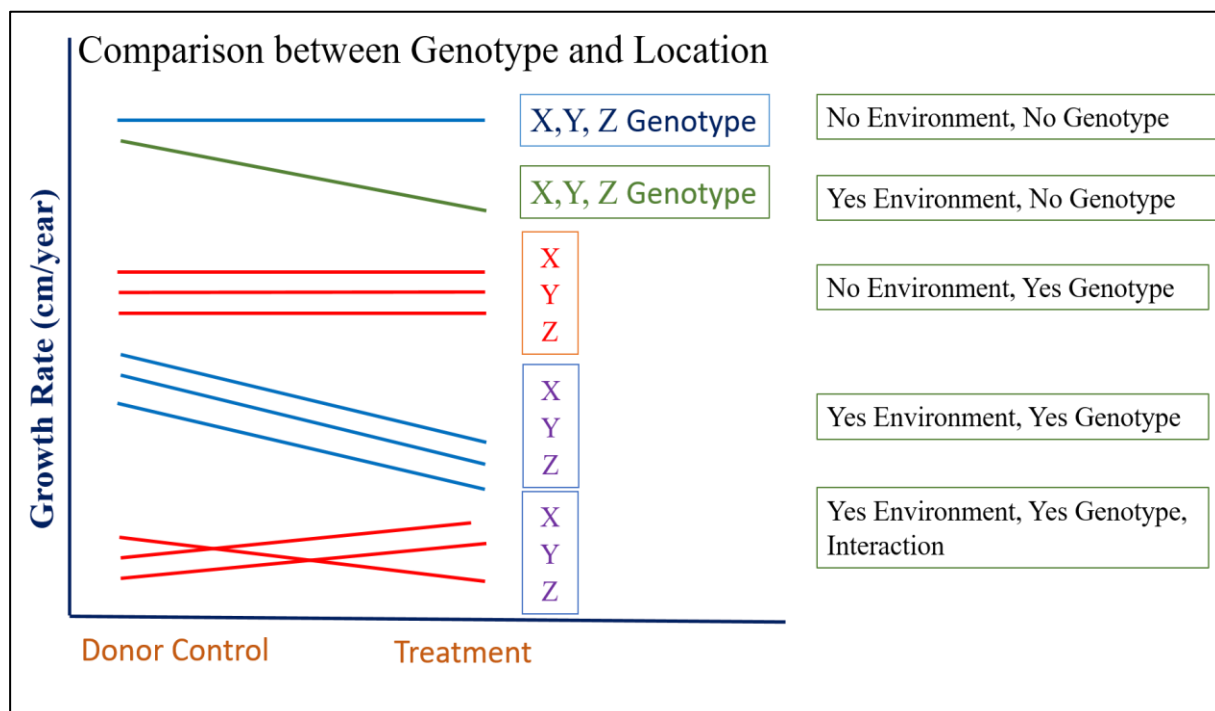


Figure 2. Reaction Norms: All possible outcomes from a reaction norm plot monitoring multiple genotypes. X,Y,Z represent three distinct genotypes. yes and no signifies if there is an effect of environment or genotype. Lastly, interaction represents an interaction effect between environment and genotype. (Examples of this figure were found at, www.biomed/brown.edu).

Restoration efforts following the Caribbean *Acropora* die-off are incentivized to use common garden experiments, stressing the importance of identifying locations where propagated coral fragments will have higher chance of survival (Baums, 2008; Bliss, 2015; Bowden-Kerby, 2008; Forrester et al., 2013). Using aforementioned methods can help develop a framework for coral restoration groups to identify viable genotypes and match these genotypes to targeted reefs for coral propagation (Baums, 2008; Forrester et al., 2013; Seebacher & Franklin 2012).

Therefore, this study also aimed to gather restoration relevant on the viability and resilience of *A. prolifera* across multiple genotypes. Most of the literature on *A. prolifera* primarily focuses on genetics, (Baums, 2008; Fogarty, 2010; Miller & van Oppen, 2003; Palumbi et al., 2012; van Oppen, 2000, Vollmer & Palumbi, 2002;), evolutionary considerations (NMFS, 2016; Willis et al., 2006; Richard & Hobbs, 2015), and reproductive characteristics (Fogarty 2010, Fogarty et al., 2012). There are limited reports on *A. prolifera* physiological response to transplantation stress, growth rates, genotypic variations, optimal thermal conditions, or susceptibility to stressor like predation, bleaching, or disease. We assume due to site adaptation, that control fragments (natal) will show higher growth rates and less signs of stress compared to the transplanted fragments (non-natal). We also assume that growth rate overall will have a positive relationship with increased temperature. There is anecdotal evidence that each source population selected for this study experiences varying levels of water current and surge conditions. Therefore, we assume there will be higher new apical tip growth rates for fragments adapted to stronger swell and surge conditions compared to fragments adapted to the calmer location.

2.5 Hypothesis

Experiment One: Comparing growth rates across genotype and between locations

H₀ Natal fragments will have significantly higher growth rates compared to non-natal fragments of *A. prolifera*.

H₀₁ Natal fragments will not have significantly different growth rates compared to non-natal fragments of *A. prolifera*.

Variables: Vertical, horizontal, and perpendicular growth rates

Experiment Two: Comparing new apical tip growth rates across genotype and between locations

H₂ There will be significantly different new apical tip growth rates between source populations of *A. prolifera*.

H₀₂ There will be no significantly different new apical tip growth rates between source populations of *A. prolifera*.

Variables: Apical tip growth rates

Experiment Three: Comparing growth rates with temperature

H₃ There will be a positive linear relationship between temperature and growth rates.

H₀₃ There will not be a positive linear relationship between temperature and growth rates.

Variables: Vertical, horizontal, and perpendicular growth rates and temperature

Experiment Four: Comparing stressors across genotype and between locations

H₄ Natal fragments will have significantly lower signs of stress indicators compared to non-natal fragments of *A. prolifera*.

H₀₄ Natal fragments will not have significantly lower signs of stressors compared to non-natal fragments of *A. prolifera*.

Variables: Percent mortality, bleaching, disease, and predation

Chapter 3: Materials and Methods

3.1 Study Sites

Inner Brass (hereafter Brass) and Flat Cay (hereafter Flat) are two geographically distinct offshore islands that were chosen for the common garden experiment (Figure 3). Brass is an offshore island on the north side of St. Thomas exposed to the Atlantic Ocean and Flat is an offshore island on the south side of St. Thomas exposed to the Caribbean Sea. To test the acclimatization of the sampled populations, we targeted locations with different environmental (water quality and current, temperature) and ecological (mortality, predation, thermal stress, disease) conditions (Rothenberger et al. 2008; Smith et al. 2008). The site selection criteria for both locations included pre-existing naturally colonies of each *Acropora* taxa, low macroalgae, windward orientation, and adequate depth. At the Flat site we know from a previous study that sedimentation rates, water clarity, and flow changes at depth (Brewer, 2013). Therefore, we controlled for depth in both sampling and out-planting (1.5 m-1.7 m).

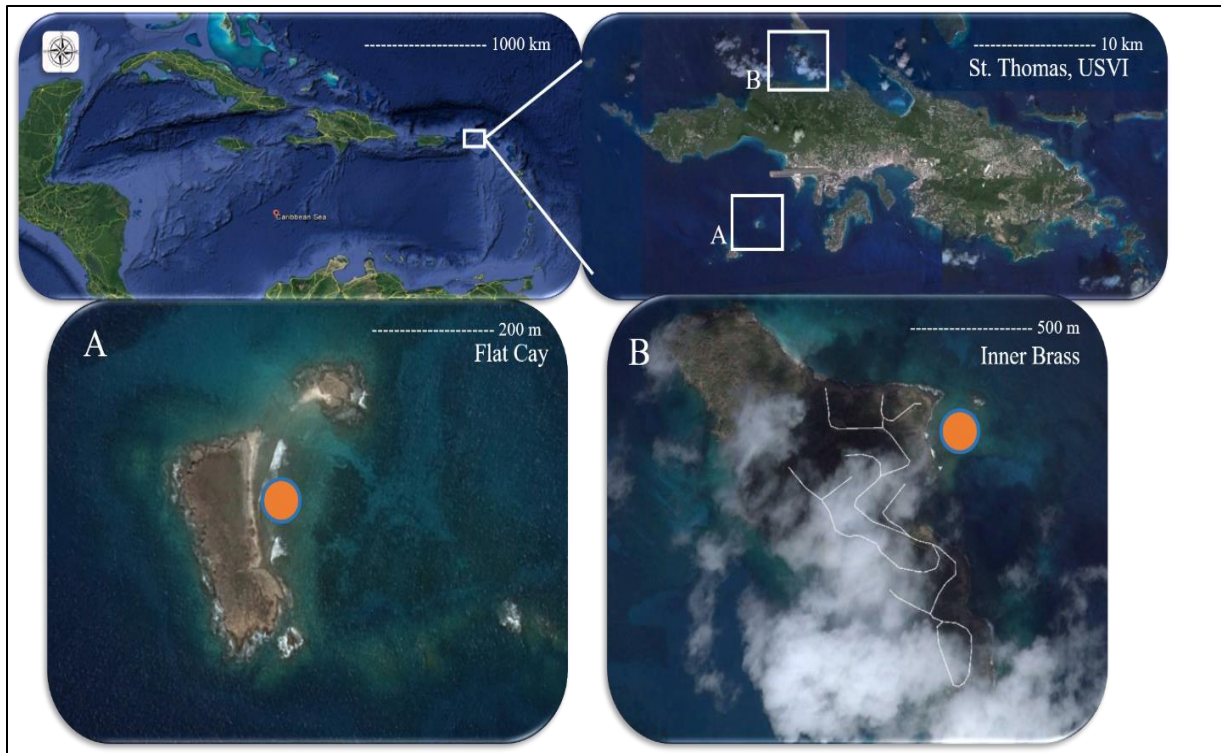


Figure 3. Study site and region for the common garden experiment. Flat is located on the south side and Brass is located on the north side of St. Thomas, USVI. Flat Cay (A) and (B) Inner Brass. The circle indicates the location where outplant plots were placed.

3.2 Reciprocal transplant

A reciprocal transplant experiment was conducted between Flat and Brass (Figure 4). First generation hybrids between *A. cervicornis* and *A. palmata* (F1) and backcrossing generations have been found in the field (van Oppen et al 2000, Vollmer and Palumbi 2002, Fogarty et al 2012), however, no evidence has been found in the field towards offspring between two hybrid corals (F2 generation). Within the scope of this study we were unable to identify which generation, fragments of *A. prolifera* belonged to. We assumed hybrid colonies incorporated in this study are F1 hybrids or backcrosses based on lack of evidence towards the presence of F2 hybrids in the wild. The genotypic identity of each donor colony was unknown prior to sampling; therefore, to maximize the collection of distinct genotypes, eight colonies at

least 10 m apart were sampled from each population. Each donor colony was visually assessed for signs of predation, disease, and thermal stress prior to sampling to ensure fragments were taken from equally viable colonies. From each donor colony, 10 fragments were collected. Due to the complex fused branching morphology, each fragment was collected between 5-8cm in size and ranged between 1-3 apical tips. Fragmentation started at Flat where a total of 80 fragments representing eight colonies were collected (Flat: $n_{\text{colony}} = 8$, $n_{\text{frag}} = 10$, $N_{\text{frag}} = 80$) and randomly and evenly distributed into two groups within each colony. A tag was attached to each individual fragment, which identified the donor colony, natal location, and treatment group (1-5, control, 6-10 transplant) (Figure 5). After each fragment from Flat was tagged they were staged at the Flat outplant plot in mesh plastic crates. The same day, 80 Brass fragments representing 8 donor colonies (Brass: $n_{\text{colony}} = 8$, $n_{\text{frag}} = 10$, $N_{\text{frag}} = 80$) were tagged and staged at the Brass outplant plots. Due to strong wind and current we waited two days before outplanting fragments at either location. Starting at Flat, we collected the treatment corals, placed them in buckets filled with seawater, headed to Brass by boat, and outplanted them with the control fragments from Brass. We followed the same steps at Brass and outplanted the Brass treatment fragments with Flat control fragments. There were two outplant plots at each location. Each out-plant plot was cleared of macroalgae and excess sediments with a wire brush prior to outplanting. Within each plot a total of 40 fragments consisting of transplanted and control fragments were haphazardly out-planted in a (5 x 8 fragment), (1 x 2 m) plot directly on the substrate and attached with epoxy putty (Allfix) (Figure 6).

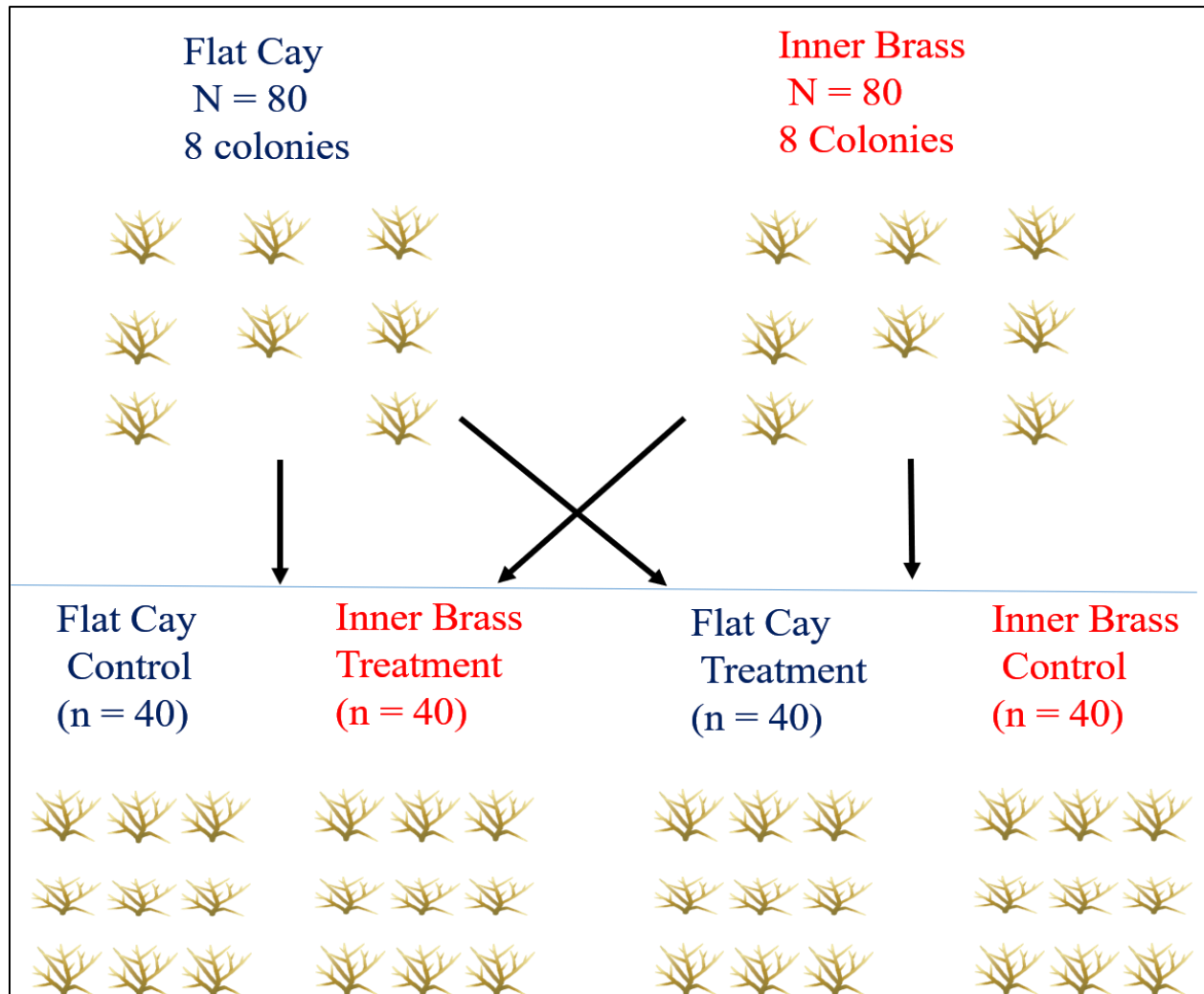


Figure 4. Diagram for reciprocal transplants. The diagram shows the source population, number of donor colonies and number of fragment taken from each population. The fragment collected from each site were evenly split between control and treatment groups. Adapted from Bliss, 2015.

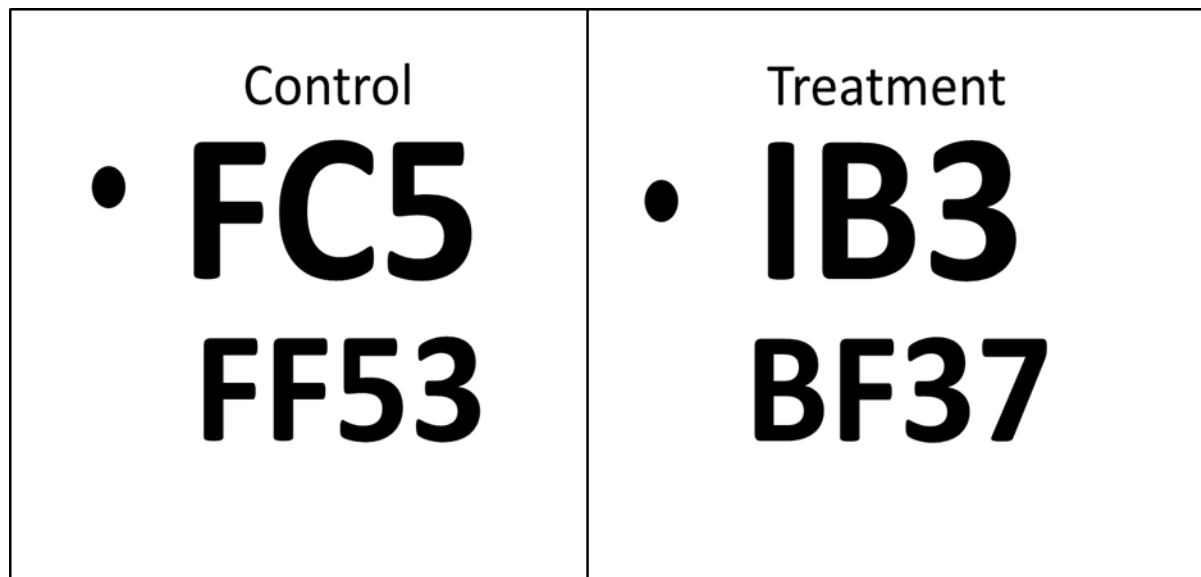


Figure 5. Image of tags attached to each fragment. FC & IB represent natal location. The single digit number represent the donor colony one of eight. FF and BF represent natal location and the first number represent which donor colony the fragment belongs to. The last number represent one of the ten fragments collected from each donor colony. 1-5 were selected as controls and 6-10 were selected for transplants.

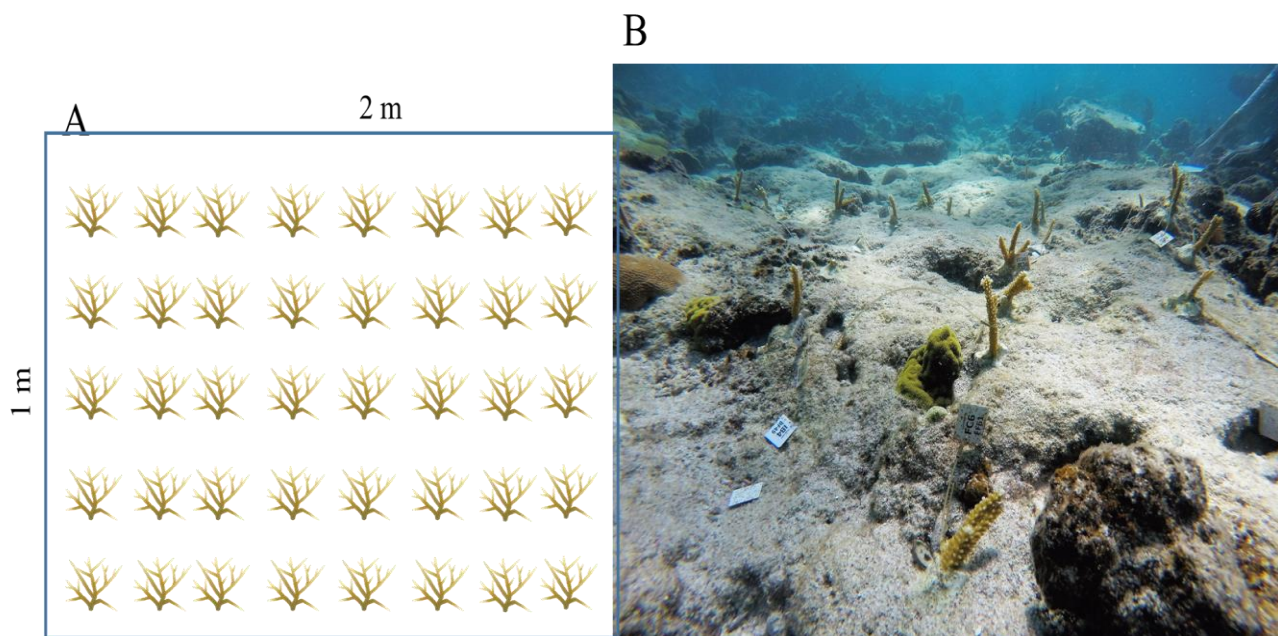


Figure 6. (A) Diagram of the plot size and number of fragments within each outplant plot ($n = 40$). (B) Photo of outplanted plot at Flat Cay (February, 2016). At each location there were two outplant plots containing a haphazard selection of treatment and control fragments.

3.3 Genotype

To determine genotypes, tissue samples from each donor colony were collected and sent to the Fogarty Laboratory at Nova Southeastern University for analysis following protocols in Fogarty (2010). Using microsatellites developed by Baums et al. (2005) for genotyping the hybrid, five loci (166, 181,182,187,207) were amplified using PCR and compared use gel electrophoresis. Peaks were also analyzed using GeneMapper.

3.4 Growth Rates

Each fragment was measured immediately after outplanting. In order to detect any morphological differences between location and genotype, we measured growth along three separate axes. Using a flexible ruler, the total vertical growth (height) was measured from the base of living tissue to the highest apical tip. Total horizontal growth (length) for each fragment was measured from the horizontal extent of the branches. Total perpendicular growth (width) was measured perpendicular to length at the base of each fragment (Figure 7). Each growth metric was monitored over nine months between December, 2016 and August, 2017. Data collection was attempted each month, however logistical issue prevented data collection in April, June, and July of 2017. Growth rates (cm/month), were calculated using total growth (cm) divided by total number of days for the entire study, times 30 $((H_2 - H_1)/T) * 30$. Monitoring growth rates between data collection (month), use the same equation however instead of T = total number of day throughout the study, T = days between data collections.

Because of *A. prolifera* unique branching morphology, we attempted to observe any differences between location and across genotypes for new apical tip growth rates. At the start (December 2016) and end (August 2017) of the experiment the number of apical tips were

counted (Figure 8). New apical tip (At) growth rate was reported as new apical tips per month, where the final number of tips were subtracted from the initial number of apical tips divided by the total number of days times 30 $((At_2 - At_1)/T) * 30$.

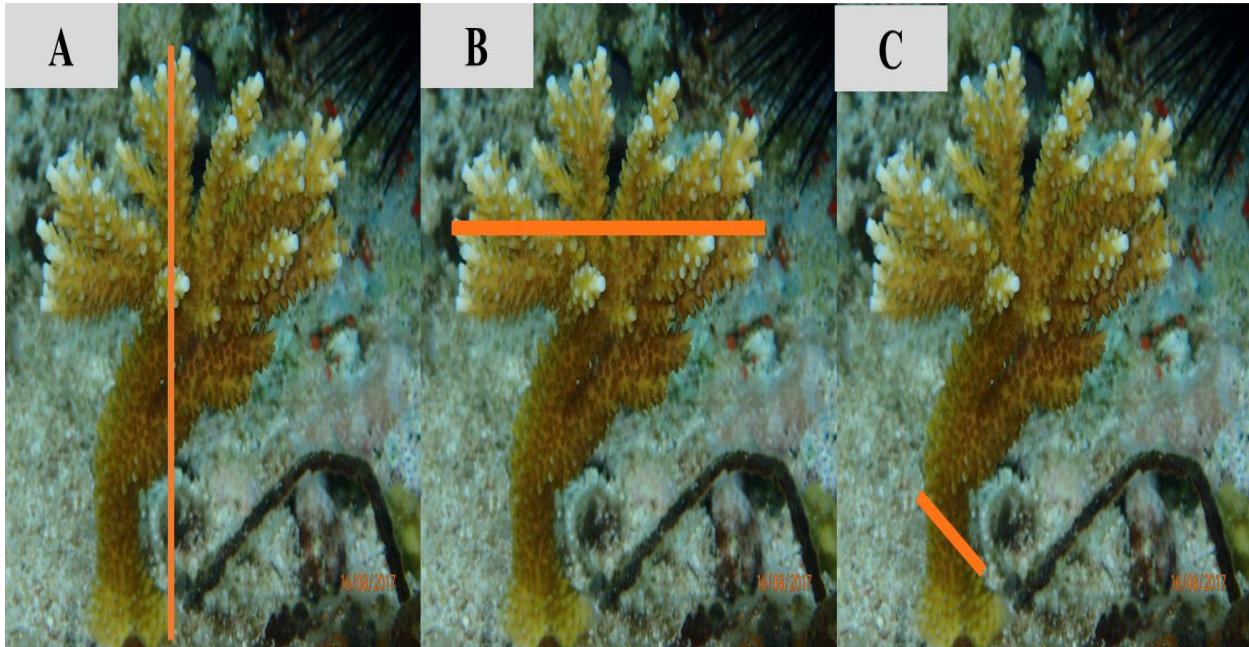


Figure 7. Image growth metrics. Growth rates across three linear axes collected from each fragment. (A) Vertical growth, (B) Horizontal growth, (C) Perpendicular growth.

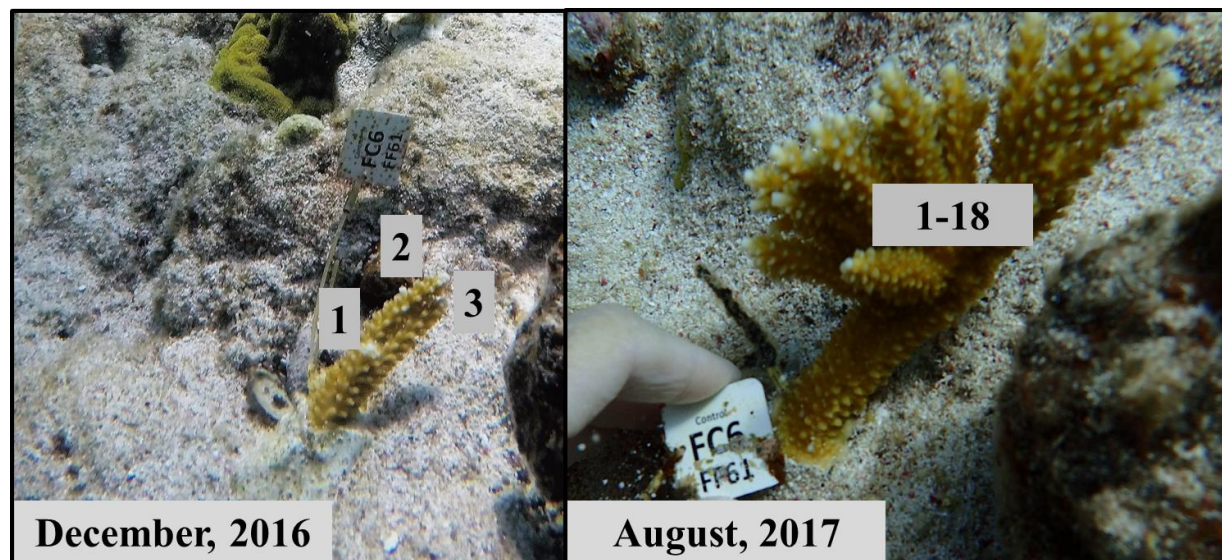


Figure 8. Images of the Flat control fragment (FF61) at the start and end of the experiment. Number of apical tips were counted at the start of the experiment and at the end to identify new apical tip growth rates.

3.5 Environmental Factors

Less than one month after the initial outplanting was completed, a follow up survey was conducted at each site to monitor any acute mortality or dislodged fragments after strong swells and surge impacted the north side of St. Thomas in November and December 2016. The Flat site was untouched mostly likely protected by the island itself. However, both Brass outplant plots sustained substantial damage which resulted in many fragments becoming dislodged or missing and most of the fragments were severely broken or dead. (Figure 9). The remaining fragments that survived showed signs of stress and paling. Because *A. prolifera* belong to an endangered genus, the remaining fragment were transported to an offshore *in situ* coral nursery. Although a significant setback this provides striking evidence that the north side experiences strong swell and current condition. Anecdotally, this is a common phenomenon along the northern coast of St. Thomas, especially during the winter months. This suggest that pre-existing populations at Brass

are adapted to these conditions. Moving forward, the reciprocal transplant design shifted to a common garden experiment without the use of reaction norms. Subsequently, this study focused on observing Flat outplant plots, to compare differences between non-natal (Brass) and natal (Flat) genotypes.



Figure 9. Images from Brass location where strong swell and current damaged both outplant plots. Many fragments were missing, dead or severely damaged.

To monitor temperature conditions, temperature loggers (Hobo WaterTemp Pro v2, Onset Computer Corporation, Bourne, MA) were placed at Flat Cay in January, 2017, in proximity to outplanted fragments to collect continuous temperature conditions every 15 minutes. For each fragment presence/absence data for mortality, disease, bleaching, and predation (hereafter, stressors) were recorded during each data collection.

3.6 Statistical Analysis

All statistical analyses were completed in R-studio (R Core Team, 2016). Growth rates for each axes, and new apical tips were compared between natal and non-natal genotypes using linear mixed effects model with location as a main effect and genotype as a random nested effect (within site). The linear relationship between growth rates (cm/month) within data collection (months) and temperature was calculated using multiple linear regressions. Additional linear mixed effect models were also used to compare growth rates between months. Growth rates and month were factored as main effects and genotype was factored as a random nested effect (within site). Presence/absence of stressors were compared using a generalized linear mixed effects model with stressor as a main effect and genotype as a random nested effect.

Chapter 4: Results

4.1 Genetic Analysis

This study identified six genotypes out of 16 colonies sampled, with three genotypes from each location (Table1). Fragments from one of the eight Brass donor colony were damaged at Flat during the outplant phase of the experiment and was excluded from this study. The Flat donor colonies (FC) 4,6,7,9,11, and 12, were one genotype, labeled FC01. Donor colony 5, and 8 were each a unique genotype labeled FC02 and FC03 respectively. The Brass donor colonies (IB) 1,3,4, and 5 were one genotype, labeled IB01. Donor colonies 4 and 8 were one genotype labeled IB02. Donor colony 10, was the third genotype labeled IB03. The subsequent results compared three genotypes comprised of eight Flat colonies and three genotypes comprised of seven Brass colonies.

Table 1: Genotype Analysis of *A. prolifera* donor colonies

Microsatellites		166		181		187			182		207	
Donor	Genet	Allele		Allele		Allele			Allele		Allele	
		1	2	1	2	1	2	3	1	2	1	2
FC 4	A	138	141	155	158	103	109	112	141	162	153	171
FC 5	B	141	168	155	173	106	109	109	141	180	153	171
FC6	A	138	141	155	158	103	109	112	141	162	153	171
FC 7	A	138	141	155	158	103	109	112	141	162	153	171
FC 8	C	138	141	155	161	103	109	112	141	168	162	165
FC 9	A	138	141	155	158	103	109	112	141	162	153	171
FC 11	A	138	141	155	158	103	109	112	141	162	153	171
FC12	A	138	141	155	158	103	109	112	141	162	153	171
IB 1	D	138	138	155	173	103	109	112	141	156	147	174
IB 3	D	138	138	155	173	103	109	112	141	156	147	174
IB 4	D	138	138	155	173	103	109	112	141	156	147	174
IB 5	D	138	138	155	173	103	109	112	141	156	147	174
IB 8	E	141	141	155	158	103	109	118	141	156	147	174
IB 9	E	141	141	155	158	103	109	118	141	156	147	174
IB 10	F	138	138	155	158	103	109	112	162	168	153	183

4.2 Growth rates and temperature

Growth analysis included fragments that survived the entire sample period. Fragments that were broken and left with less than 3cm of live tissue were excluded. Growth rate averages (cm/year) were calculated from nine months of actual growth. (Table 2).

Table 2: Growth rates for *A. prolifera*

Site	n	Vertical Growth		Horizontal Growth		Perpendicular Growth		Apical Tip Growth	
		(cm/year)	Total (cm)	(cm/year)	Total (cm)	(cm/year)	Total (cm)	(cm/year)	Total (apical tips)
FC	28	4.46 ± 0.57	3.13 ± 0.40	6.53 ± 0.93	4.58 ± 0.66	3.80 ± 0.53	2.66 ± 0.37	13.49 ± 2.01	9.46 ± 1.41
IB	26	5.36 ± 0.59	3.76 ± 0.41	6.65 ± 0.75	4.67 ± 0.52	3.94 ± 0.65	2.77 ± 0.45	15.46 ± 1.39	10.85 ± 0.98

At Flat, the average temperature across the study (January and August, 2017) ranged from a monthly minimum mean of 26.5 ± 0.28 °C SE and a monthly maximum mean of 29.37 ± 0.27 °C (Figure 10). August had the highest average temperature (29.37 ± 0.27 °C), however, the highest temperature recorded was in July, 2017 (30.48°C). The lowest average temperature occurred in January 2017 (26.5 ± 0.28 °C). The lowest recorded temperature was recorded in March (25.59°C). The largest change in average temperature occurred between May to June with a temperature increase of 0.81 °C.

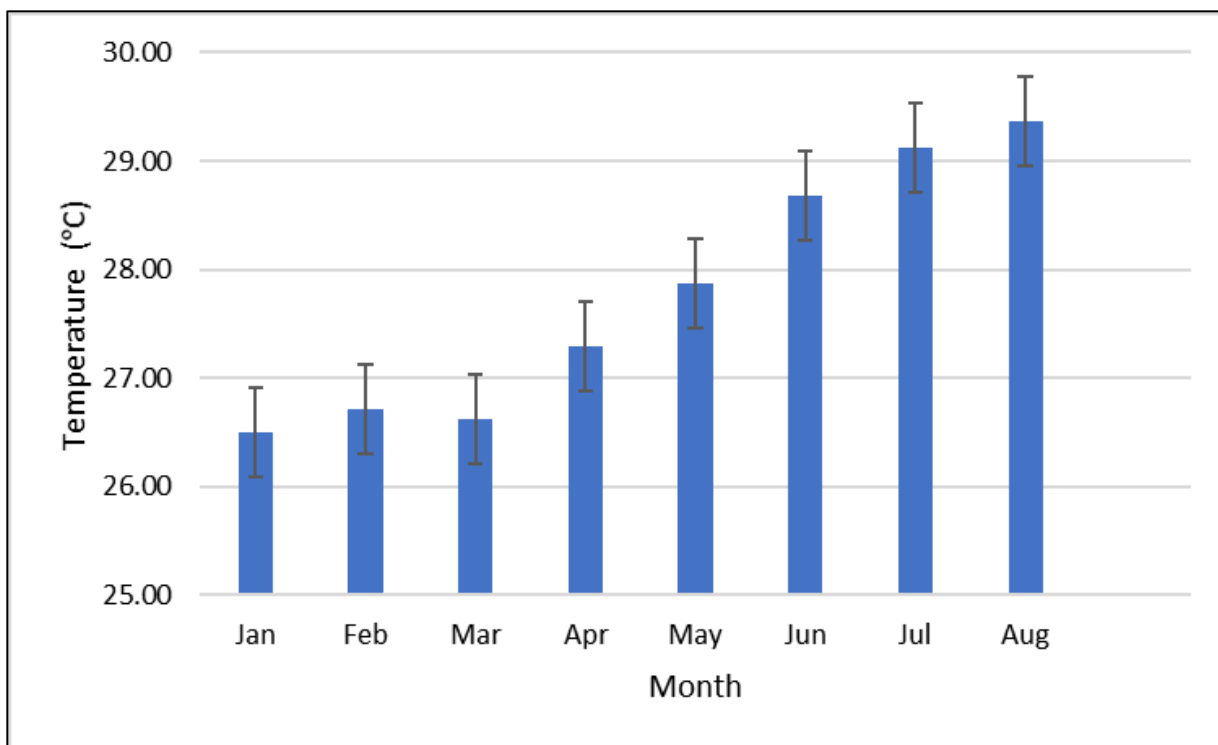


Figure 10. Average temperature. Conditions at Flat Cay site for each month. Value represent average between two hobo loggers placed in proximity to out-plant location for each month. MEAN (\pm SE) value represent average temperature over the nine-month study.

The average vertical growth rate for natal fragments (FC) was 0.37 ± 0.05 cm/mo ($n = 28$). The average vertical growth rate for non-natal fragments (IB) was 0.44 ± 0.05 cm/mo ($n = 26$). There was no significant difference in vertical growth rates between natal and non-natal fragments with genotype factored as a random nested effect (linear mixed effects model, $t = .560$, $p = 0.443$) (Figure 11). The initial mean height, for each fragment was 5.83 ± 1.7 cm (MEAN \pm SE) across all genotypes.

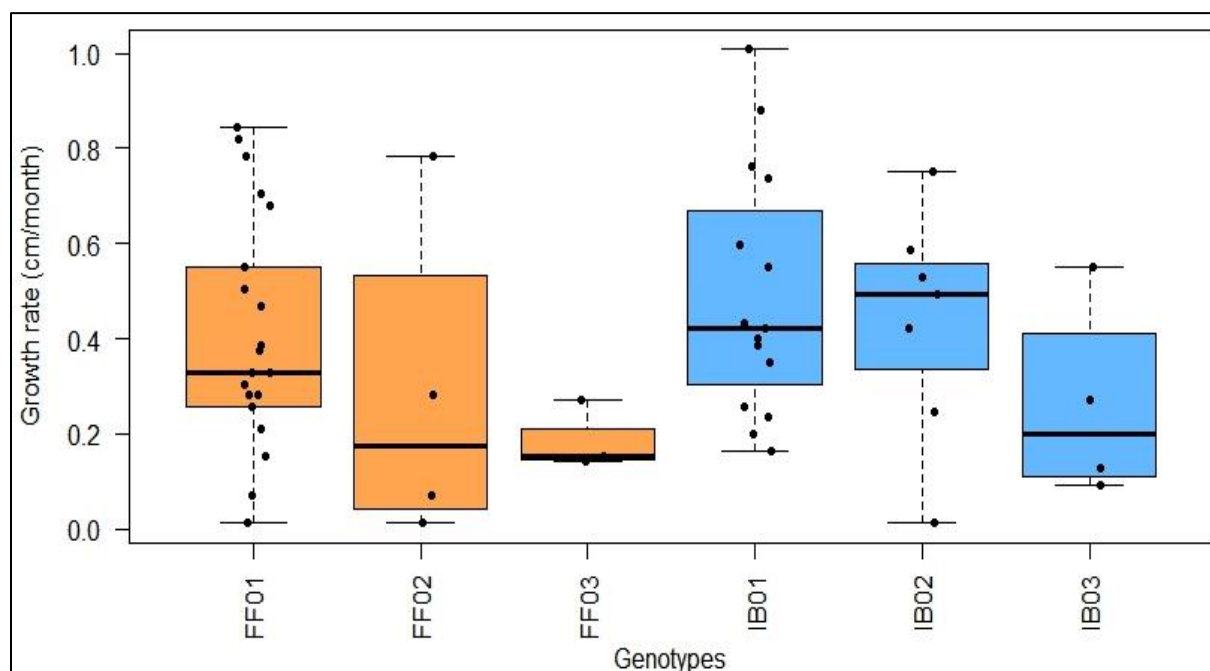


Figure 11. Average vertical growth rates (cm/month) for natal genotypes (FF) in orange and non-natal fragments (IB) in blue. There was no significant difference in growth rates (vertical) between natal and non-natal fragments (Linear mixed effects model, $p = 0.443$). Size of the box represent dispersion in the data across quartiles. Area above the line represent upper quartile, below the line represents the lower quartile and the line represents the median. Error bars indicate variation outside of quartile.

The average horizontal growth rate for natal fragments (FC) was 0.54 ± 0.07 cm/mo ($n = 28$). The average horizontal growth rate for non-natal fragments (IB) was 0.55 ± 0.06 cm/mo ($n = 26$). There was no significant difference in horizontal growth rate between natal and non-natal fragments with genotype factored as a random nested effect (linear mixed effects model, $t = 0.62$, $p = 0.951$) (Figure 12). The initial mean length for all fragments were 1.82 ± 1.01 cm (MEAN \pm SE) across all genotypes.

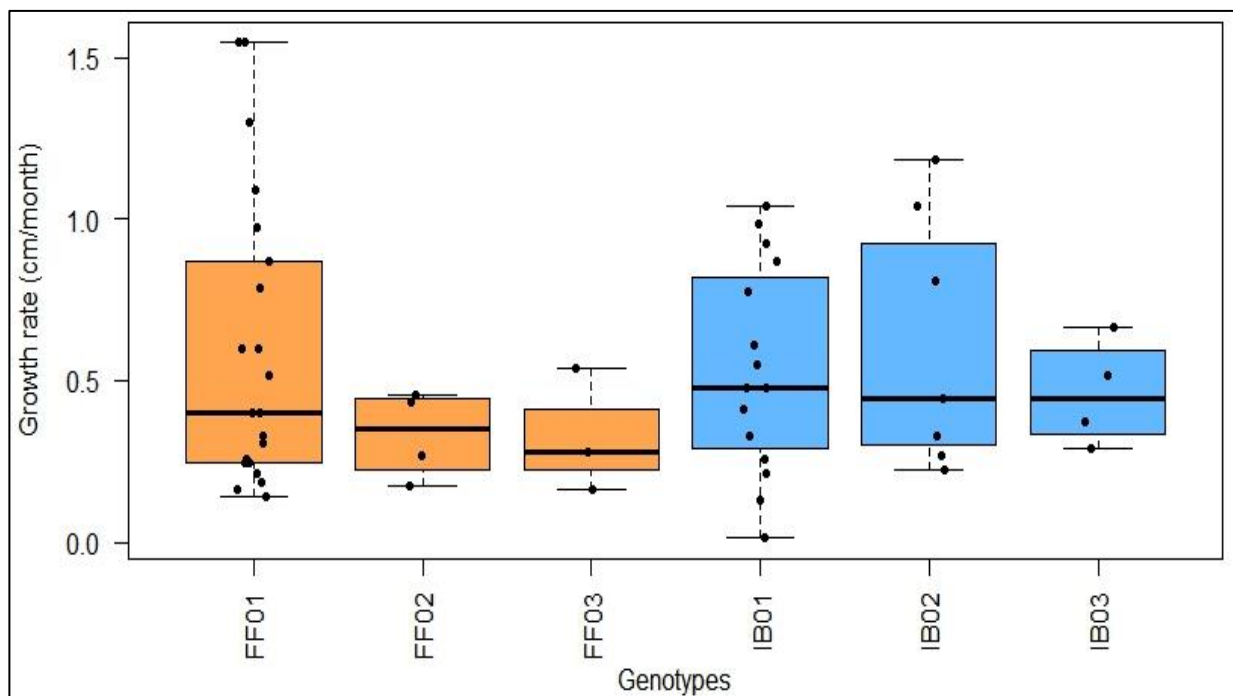


Figure 12. Average horizontal growth rates (cm/month) for natal genotypes (FF) in orange and non-natal fragments (IB) in blue. There was no significant difference in growth rate (length) between natal and non-natal fragments (linear mixed effects model, $p = 0.951$). Size of the box represent dispersion in the data across quartiles. Area above the line represent upper quartile, below the line represent lower quartiles and the line represent the median. Error bars indicate variation outside of quartile.

The average perpendicular growth rate for natal fragments (FC) was 0.31 ± 0.04 cm/mo ($n = 28$). The average perpendicular growth rate for non-natal fragments (IB) was 0.32 ± 0.05 cm/mo ($n = 26$). There was no significant difference in perpendicular growth rate between natal and non-natal fragments with genotype factored as a random nested effect (linear mixed effects model, $t = 0.601$, $p = 0.589$) (Figure 13). The initial mean width for fragments were 1.24 ± 0.4 cm (MEAN \pm SE) across all genotypes.

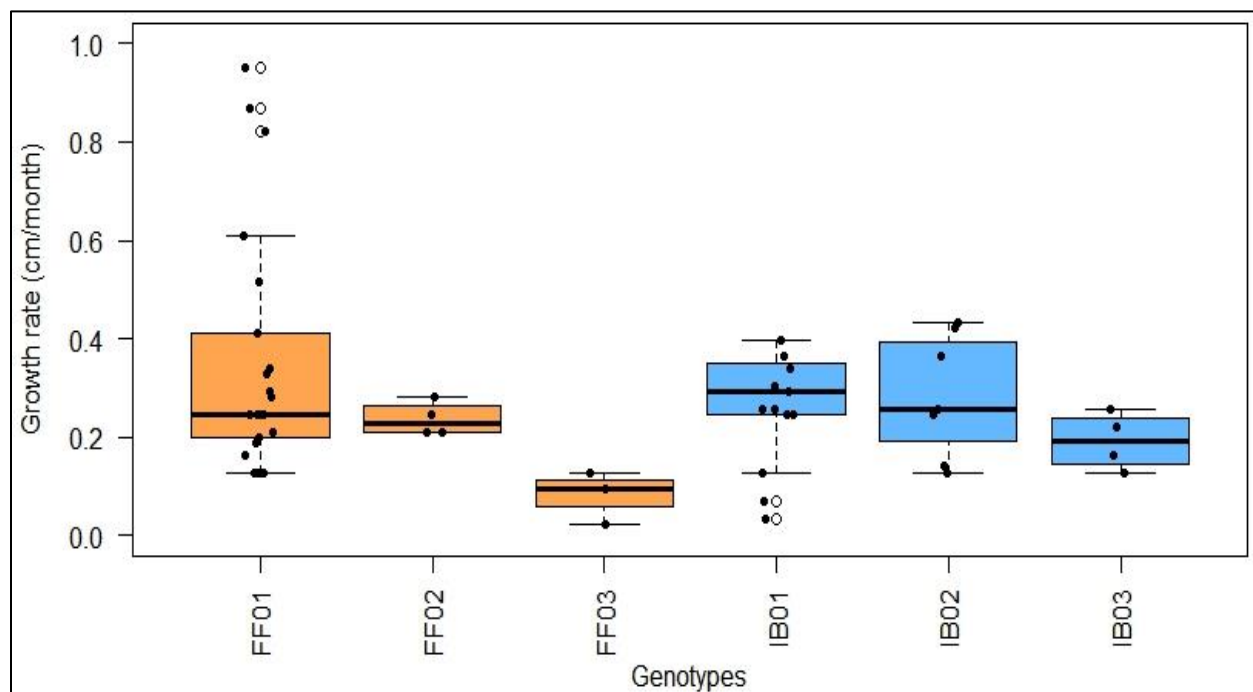


Figure 13. Average perpendicular growth rates (cm/month) for natal genotypes (FF) in orange and non-natal fragments (IB) in blue. There was no significant difference in growth rate (width) between natal and non-natal fragments (linear mixed effects model, $p = 0.589$). Size of the box represent dispersion in the data across quartiles. Area above the line represent upper quartile, below the line represent lower quartiles and the line represent the median. Error bars indicate variation outside of quartile.

The growth rate for new apical tips for natal fragments (FC) was 1.10 ± 0.17 apical tips/mo (n =28). New apical tip growth rate for non-natal fragments (IB) was $(1.3 \pm 0.12, (n = 26)$. There was no significant difference in new apical tip growth rate between natal and non-natal fragments with genotype factored as a random nested effect (linear mixed effects model, $t = 1.194, p = 0.238$) (Figure 14). The initial number of apical tips for all fragments was 1.72 ± 0.1 cm (MEAN \pm SE) across all genotypes.

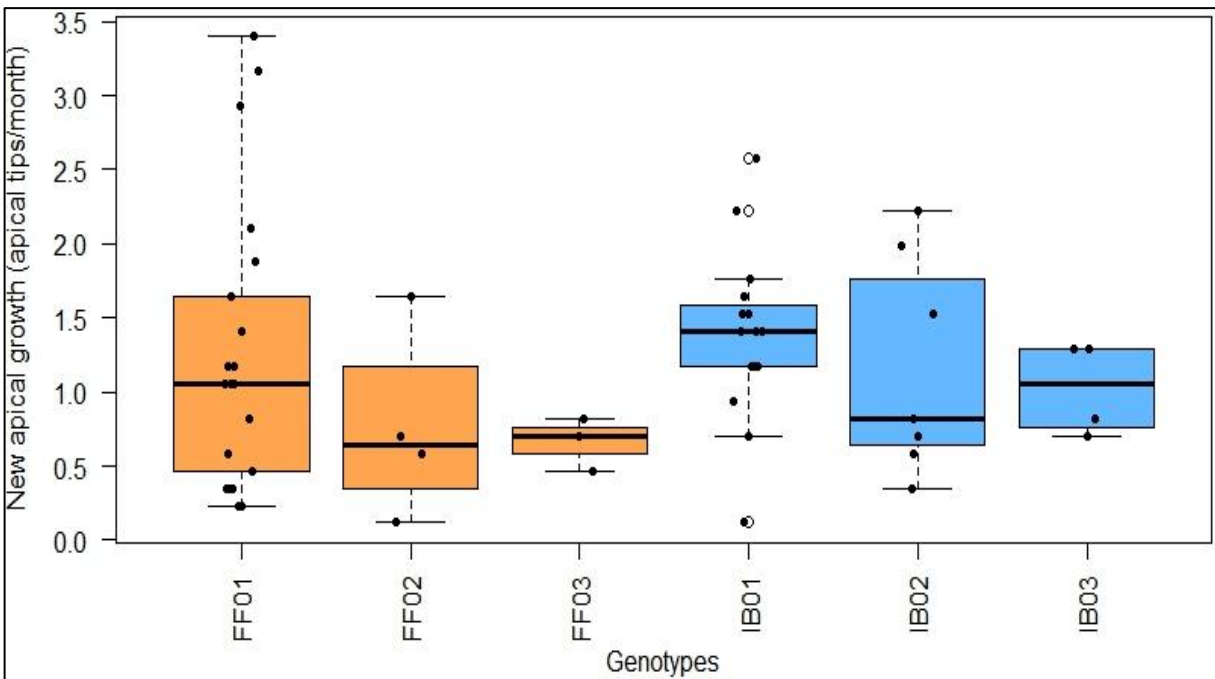


Figure14. Average growth of new apical tips (apical tips/month) for natal genotypes (FF) in orange and transplanted fragments (IB) in blue. There was no significant difference in growth rate (new apical tips) between natal and transplanted fragments (linear mixed effects model, $p = 0.238$). Box represent data distribution within quartiles. Size of the box represent dispersion in the data across quartiles. Area above the line represent upper quartile, below the line represent lower quartiles and the line represent the median. Error bars indicate variation outside of quartile.

With no interaction or effect from location or genotype, we found there was a positive linear relationship between temperature and vertical growth rates (regression analysis $\beta = 0.121$, $t(263) = 2.15$, $p = 0.02$) and horizontal growth rates (regression analysis $\beta = 0.204$, $t(263) = 3.01$, $p < 0.01$) throughout the study. (Figure 15,16). There was no significant linear relationship between temperature and perpendicular growth rates (regression analysis $\beta = 0.07$, $t(263) = 1.42$, $p = 0.16$) (Figure 17). For growth rates (within month) across each axis, there was no interaction or effect from location or month. For growth rates within month (for each axis), month and growth rate were factored as a main effects and genotype was factored as a random nested effect. Vertical growth rates showed significantly lower growth rates in January (linear mixed effects model, $t = -2.63$, $p < 0.01$) and in May (linear mixed effects model, $t = 2.20$, $p = 0.04$). Horizontal growth rates with month and growth rate factored as a main effects and genotype factored as a random nested effect, also resulted in significantly lower growth rates in January (linear mixed effects model, $t = -5.53$, $p < 0.01$) and in May (linear mixed effects model, $t = -4.41$, $p < 0.01$). There were no significant differences between monthly perpendicular growth rates (linear mixed effects model, $t = 0.543$, $p = 0.61$).

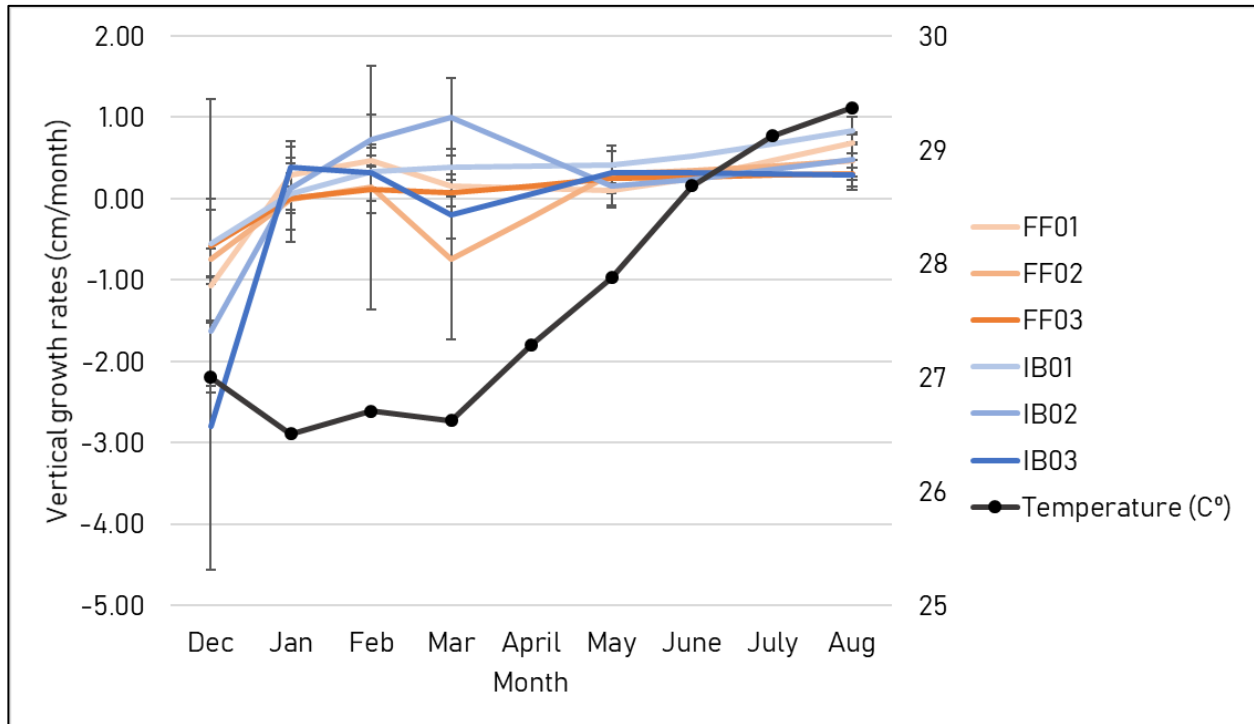


Figure15. Average vertical growth rates for each genotype at each data collection month (MEAN \pm SE) and temperature. December temperature average was collected from NOAA satellite sea surface temperature. The remaining temperature averages for each month were collected *in situ*. (regression analysis $\beta = 0.121$, $t(263) = 2.15$, $p = 0.02$).

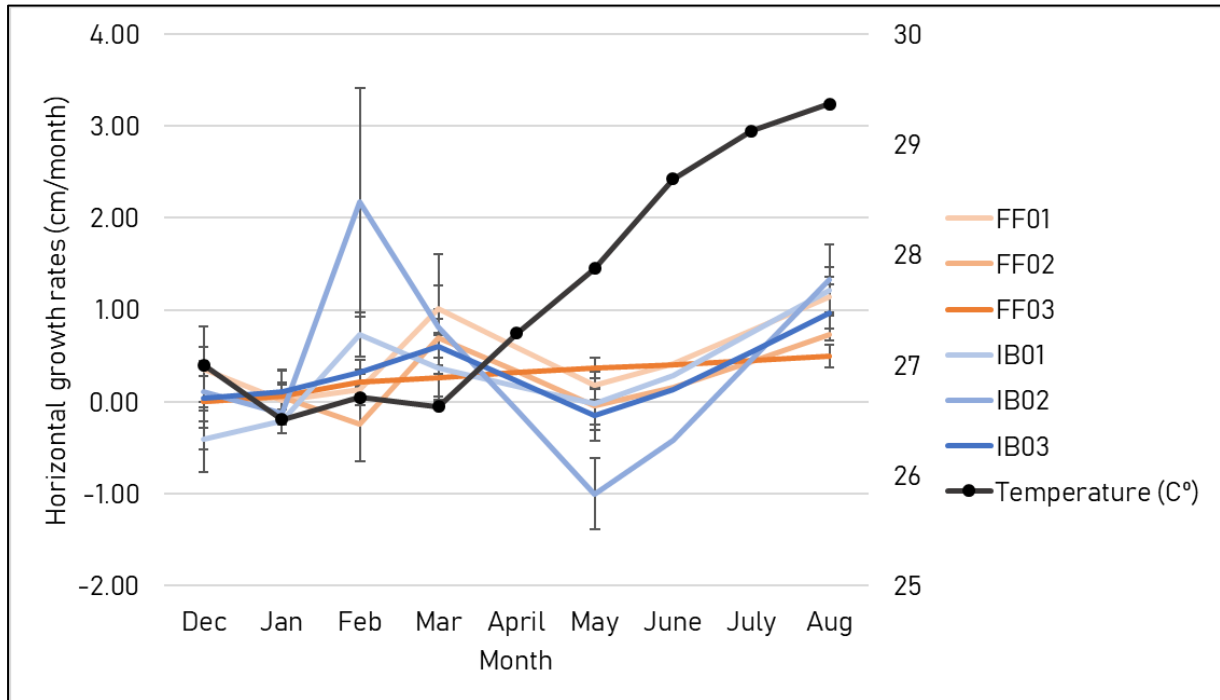


Figure16. Average horizontal growth rates for each genotype at each data collection month (MEAN \pm SE) and temperature. December temperature average was collected from NOAA satellite sea surface temperature. The remaining temperature averages for each month were collected *in situ*. (regression analysis $\beta = 0.204$, $t(263) = 3.01$, $p = 0.01$).

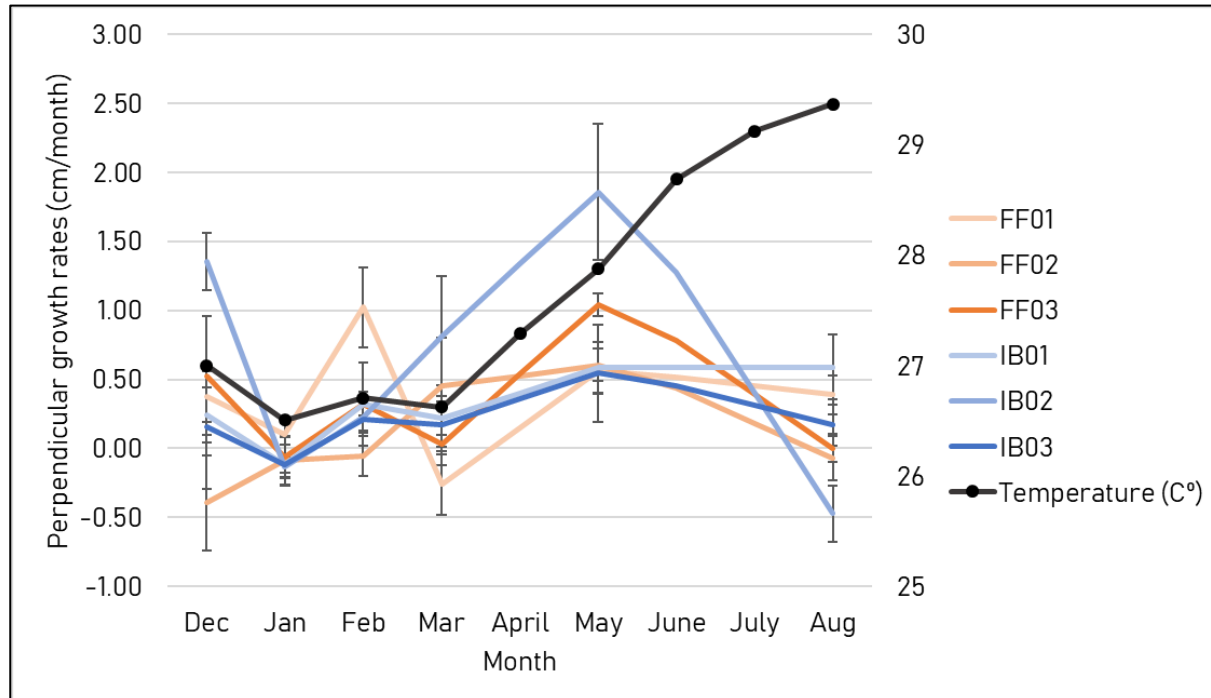


Figure17. Average perpendicular growth rates for each genotype at each data collection month (MEAN \pm SE) and temperature. December temperature average was collected from NOAA satellite sea surface temperature. The remaining temperature averages for each month were collected *in situ*. (regression analysis $\beta = 0.07$, $t(263) = 1.42$, $p = 0.16$).

4.3 Signs of stress

Percent mortality was compared across non-natal and natal genotypes and between locations. There was no significant difference in percent mortality between natal and non-natal fragments with genotype factored as a random nested effect (Generalized linear mixed effects model, family: binomial; $z = 0.066$, $p = 0.947$). Flat genotype mortality ranged between 20-40% while Brass genotype mortality ranged between 11 - 32% (Figure 18).

Percent bleaching was compared across non-natal and natal genotypes and between locations. There was no significant difference in percent bleaching between natal and non-natal fragments with genotype factored as a random nested effect (Generalized linear mixed effects

model, family: binomial, $z = 0.043$ $p = 0.96$). Bleaching across flat genotypes ranged between 0-40% while bleaching for Brass genotypes ranged between 0 - 20% (Figure 18).

Percent predation was compared across non-natal and natal genotypes and between locations. There was significantly higher percentage of predation on non-natal fragments compared to natal fragments with genotype factored as a random nested effect (Generalized linear mixed effects model, family: binomial, $z = 2.12$, $p = 0.033$). Two non-natal genotypes showed significant higher signs of predation compared to the third which show no signs of predation. Of the three natal genotypes, FC01 was the only natal genotype with signs of predation (3%), while Brass genotype percent predation ranged between 0 - 24% (Figure 18).

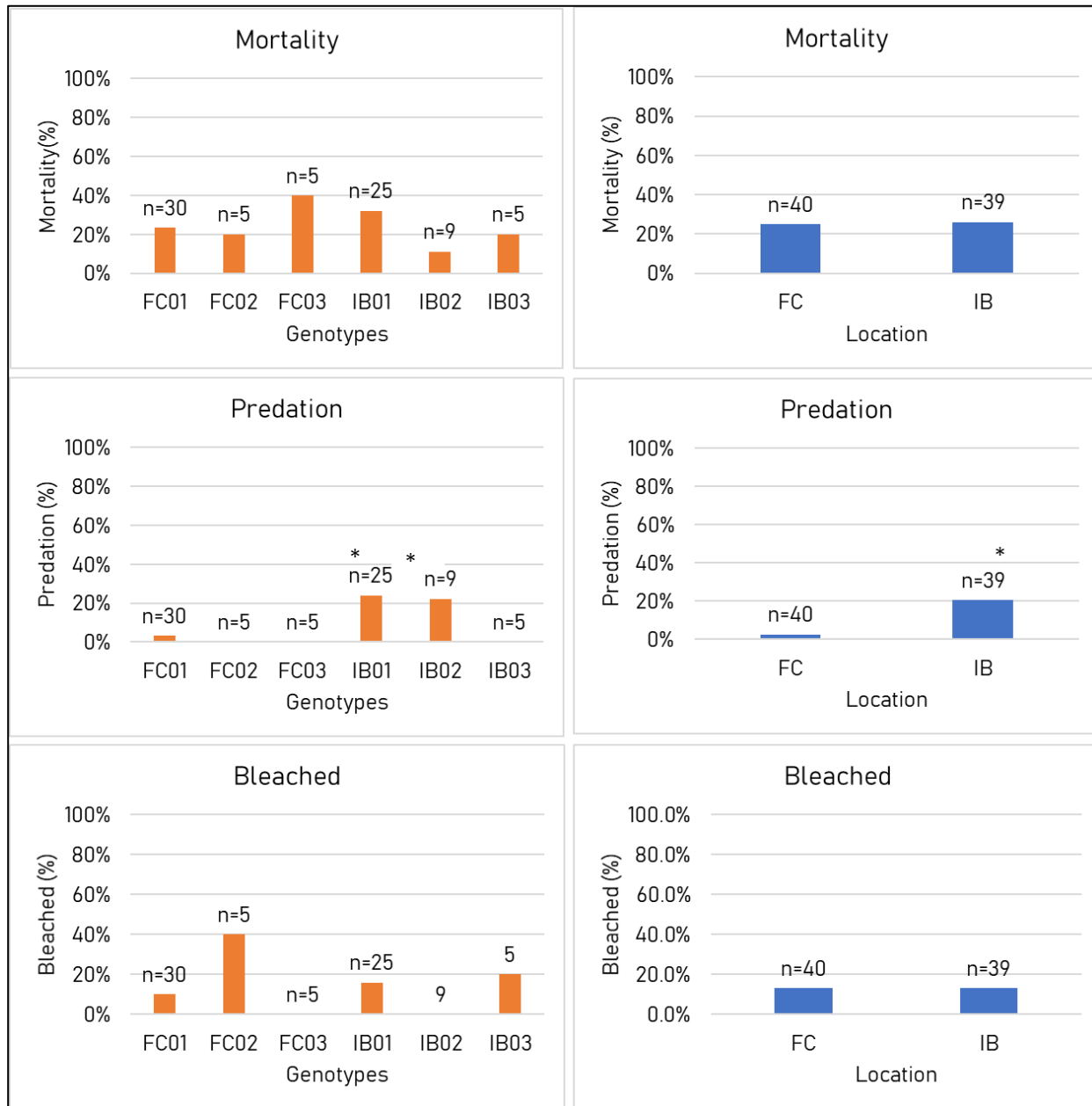


Figure 18: Prevalence of mortality, predation, and bleaching between genotype and location. Natal and non-natal genotypes in orange, total natal and non-natal fragments in blue. Predation was the only significantly different across genotype and location ($p = 0.033$).

Chapter 5: Discussion

5.1 Growth rates

Considering the compounding stressors that reduced *Acropora* populations throughout the Caribbean, there is an urgent need to understand the evolutionary process that creates and preserves coral resilience (Richard & Hobb, 2015; Willis et al., 2006). This evolutionary process includes generating novel viable genetic information through sexual reproduction and hybridization (Richard & Hobb, 2015; Willis et al., 2006). To describe the viability and resilience of novel hybrid genotypes we analyzed the intrinsic and extrinsic response to changing environmental conditions. From the first experiment we saw no significant differences when comparing growth rates from multiple axes across genotypes and between source populations. Overall, these results show that non-natal fragments of *A. prolifera* can be transplanted to novel locations within the USVI without negative impacts to their health compared to the native population. Although there was slight variability in growth rates across genotypes, and between locations, Brass genotypes showed no reduction in any growth axes compared to Flat genotypes. Without the northern Brass site, it is difficult to determine if the growth rates for Brass genotypes at Flat would differ in the natal range. It is likely that Brass fragments contains adaptive traits associated with consistent swell and surge conditions. Observations from a full reciprocal study could identify if the Brass growth metrics in non-natal locations are similar to or distinct to growth rates in natal locations. Although we could not determine if site adaptation benefited Brass fragments in non-natal locations, our results show that site adaptation does not limit distinct *A. prolifera* genotypes fragments to acclimate to non-natal locations.

Apical tips are highly productive regions of the *Acropora* colony (Kiel et al., 2012; Miller et al., 2014) and serve as an important component for asexual reproduction (Bruckner, 2003; Lirman et al., 2014; Mercado et al., 2016). Furthermore, the number of apical tips and their respective growth rates is another metric of colony productivity (Mercado et al., 2016). From our second experiment, we observed no significant differences in new apical tip growth rates across genotypes and between locations. Although new apical tip production across genotypes varied, overall, new apical tip production rates were high. Initial fragments produced an average of ten new apical tips within just nine months (Table 2). Each apical tip if fragmented again, will grow into a new clonal colony, thus increasing the likelihood of asexual reproduction and rapid local colonization.

The morphology of each fragment is influenced by the number of apical tips and their associated growth rates. Within the scope of the study, we did not attempt to measure each linear extension for each new branch. Instead we utilized growth rates across multiple axes to capture any morphological differences between natal and non-natal genotypes. Growth rates for each axis between location and genotypes was not significant however, our data shows there was more total growth (cm) along the vertical and horizontal axes compared to perpendicular axis at the base of the colony (Table 2). Interestingly, from our third experiment we also saw as temperature increases, vertical and horizontal growth rates significantly increased but perpendicular growth rates did not. Temperature is an important factor in metabolic rates for many organism (e.g., Angilletta, 2009; Pörtner, 2002). For scleractinians corals, temperature can affect calcification rates, thus temperature can directly influence growth (Edmunds, 2005; Tanzil et al., 2013). Our results mirror early reports on higher *Acropora* growth rates in optimal thermal

conditions during the summer months (Gladfelter et al., 1978; Shinn, 1966). Our data in terms of growth confirms that *A. prolifera* responds similarly to the parental species in optimal thermal conditions. It is important to mention that while growth rates do have a positive relationship with temperature, overall growth rates and health of *Acropora* species are dependent on a combination of ecological and environmental conditions. Water quality and flow, sedimentation and light all influence coral growth rates (Allemand et al. 2011; Larsen & Webb, 2009; O'Donnell et al., 2016; Smith et al. 2008). Since all fragments were observed in the same location, with outplant plots less than a meter apart, we can assume that environmental conditions affected both groups equally. Conditions outside optimal thermal ranges can limit growth rates for corals (Shinn, 1966; Tanzil et al., 2013). The lowest average monthly temperature was in January (26.5 ± 0.028 °C) which corresponded with significantly lower growth rates for vertical and horizontal growth. Lower metabolic rates in cooler temperatures could explain why we saw lower growth rates. However, it is also possible less light exposure during shorter days in the spring could cause lower growth rates. Growth rates for both vertical and horizontal growth also decreased in May with an average mean temperature of 27.88 ± 0.01 °C. This reduction in growth within optimal thermal conditions could not be ecologically explained. Most likely this reduction in growth was caused by human error between different samplers. Overall, newly fragmented branches of *A. prolifera* produce more growth across the vertical and horizontal axes compared to the base of the colony and growth rates increase as temperature reaches the upper limits of optimal thermal conditions.

5.2 Stress prevalence

There was no significant difference in mortality between natal and non-natal fragments across genotypes and between locations despite Brass fragments experiencing more transplantation stress compared to Flat control fragment. Flat fragments were manually fragmented but never left the water to be transported. It is possible that stress from removing Brass fragments from the water, transportation by boat and the placing them in novel locations would negatively influence health metrics compared to natal fragments. However, we were unable to detect any differences in health due to transplantation stress. The one noticeable exception of high mortality was in regard to the north site, Brass. Outplanting at the northern site took place during strong swell and surge, compounded by difficult working conditions, ultimately hindering fragment survival. Flat in comparison, experienced less surge and swell conditions and no fragments were dislodged or missing days after the strong swell and surge season. From anecdotal observation both locations experience moderate swell and wave conditions throughout most of the year; however, during the winter months, Brass experience stronger water current conditions. For coral restoration efforts, site selection criteria requires pre-existing populations of *Acropora* colonies, adequate depth, low signs of algae and corallivores, and low to moderate water flow (Johnson et al. 2011). Within these site criteria, Brass served as an ideal location for the outplanting however, the timing for the reciprocal transplant was not optimal. In the future, it is important to incorporate local knowledge within site selection criteria to avoid issues like seasonal variation in swell and surge events.

The significant decline of the *Acropora* species due to compounding stressors has arrived at a depensatory threshold such that predation has now become a significant limitation on

the natural recovery of the species (Rotjan & Lewis, 2008; Williams et al. 2014; Williams & Miller, 2012). Predation was the only sign of stress that resulted in significant differences between natal and non-natal fragments. Brass corals showed significantly higher signs of predation compared to Flat fragments. Two Brass genotypes showed significantly more predation compared to the third which showed no signs of predation. Flat fragments show low signs of predation with only 3% of one genotype showing signs of predation from *C. abbreviata*. Variable genetic traits towards predation could explain why we saw significantly higher signs of predation on two genotypes and not the third. It is possible Flat fragments developed stronger defenses to predators they are accustomed with. Examples of coral defense against corallivores include nematocysts, morphology and second metabolites that deter predators (Glynn & Krupp, 1986; Gochfeld, 2004; Keesing, 1990; McIlwain & Johnes 1997). Interestingly, the intermediate branching morphology for *A. prolifera* is also thought to limit predation rates compared to the parental species (Fogarty, 2012). However, with no detectable differences across the growth metrics, it is difficult to determine if that was a factor in this study. Without the full reciprocal transplant, it is difficult to determine why more predation was observed on non-natal fragment compared to natal fragments. It is possible that Brass genotypes do not experience as much predation in their natal range and thus, do not develop strong defenses against predation. The introduction of novel fragments could have attracted predators. Studies show corallivores can use olfactory cues in the water column to locate prey items (Lindsay, 2009; Wolf, 2012). Moreover, *C. abbreviata* show preference towards acroporid corals (Baums et al. 2003). Similar examples in the Pacific ecosystems show corallivores prefer the *Acropora* genus due to obtaining higher protein/energy content (Keesing, 1990; Wolf et al., 2014). Although rates of predation on non-

natal fragments were significantly higher, this still did not limit growth compared to natal fragments. *H. carunculata* and *C. abbreviata* are known to be vectors for acroporid disease (Williams & Miller, 2005; Sussman, et al., 2003); however, no signs of disease were found throughout the study. Disease prevalence has been shown to increase in the later summer months in warmer conditions (Patterson et al., 2002; Muller et al., 2008). Our sampling ended in August, 2017 just as water temperatures started to peak. The following month, hurricane Irma a category 5 hurricane decimated shallow water coral reefs throughout the Puerto Rico and Virgin Islands region. Thus, we could not include additional observations after nine months. Limited sampling time could explain why we saw no signs of disease or limited signs of bleaching between natal and non-natal fragments in the summer months. However, low occurrence of bleaching for *A. prolifera* in parts of Belize and Curacao, even in shallow water conditions suggest the hybrid can tolerate high UV irradiance and temperature conditions (Fogarty, 2012). Overall, our results from growth metrics and stressors, suggest that *A. prolifera* is a shallow water generalist who can persist in non-natal locations.

5.3 Coral Restoration

This experimental design and subsequent results directly relates to an ongoing discussion regarding the role *A. prolifera* can play in current coral restoration efforts throughout the Caribbean. Our results address the debate on hybrid viability in terms of site adaptation and acclimatization. Comparable health metrics to natal fragments provide evidence that coral restoration programs can successfully transplant *A. prolifera* fragments to non-natal locations. The overall goal of coral restoration is a multifaceted approach to establishing self-sustaining populations of coral species (Bowden-Kerby, 2014; Carne et al. 2016; Griffin et al. 2012;

Johnson et al. 2011; NMFS, 2016; Richard and Hobb, 2015; Young et al. 2012). By housing, rearing and propagating distinct species and genotypes, restoration groups can promote natural recovery by closing the gap between reproductive colonies and propagate multiple genotypes in targeted locations (Drury & Lirman, 2017). The experimental design of this study incorporated coral restoration research methodologies in several ways, in order to provide preliminary baseline data which is comparable to current and future coral restoration studies. First, clearing macroalgae from the outplant site and securing fragments with epoxy allows small *Acropora* fragment to establish a firm foothold and increases the likelihood of survival compared to loose naturally fragments branches (Williams & Miller, 2010). In addition, no plastics or metallic material was left at the outplant site and the epoxy will soon be overgrown by a veneer of live coral tissue. Secondly, this study followed site selection criteria, choosing areas with existing populations of *Acropora* corals, adequate depth, moderate flow, and low macroalgae.

Thirdly, we measured indicators of health throughout a common garden experiment to gauge how different genotypes are influenced by site adaptation and transplantation stress. Analyzing health metrics across multiple genotypes of *A. prolifera* provides initial baseline data on the genotypic viability and resilience for this hybrid. Several coral restoration recovery management plans emphasize propagating multiple genotypes in various locations to both increase resilience and increase natural propagation through sexual reproduction (Bowden-Kerby, 2014; Bruckner, 2003; Baums 2008; Edwards, 2010; Johnson et al. 2011). In this capacity, our data supports this acroporid hybrid's assumed role of being a viable reservoir of novel genetic information that could assist the rapid adaptation of the entire acroporid population. Thus, this study adds to growing support of propagating *A. prolifera* in a controlled

manner due to its viability in current environmental conditions and as an additional reproductive body which may increase the persistence of novel genotypes (Baums, 2008; Bowden-Kerby, 2014; NMFS, 2016). In light of gene swamping and inbreeding/outbreeding threats, we suggest that if coral restoration programs incorporate *A. prolifera*, they do so only under controlled experiments. Restoration objectives must consider closing the gap between reproductively isolated colonies to increase sexual reproduction within species and incorporate *A. prolifera* at lower abundances to facilitate low level introgression in targeted sites. For example, in Puerto Rico natural *A. prolifera* populations are believed to introgress with *A. cervicornis* populations, assisting with increased genetic population structure in localized areas (NMFS, 2016; Vollmer & Palumbi, 2007). Overall, incorporating *A. prolifera* in a controlled manner, may facilitate increased genetic diversity within outplant sites. The controlled propagation of genotypically diverse fragments of each *Acropora* taxa may allow for the creation of distinct genotypes and resilient acroporid reefs.

5.4 Future considerations

Molecular research has jumped ahead of ecological studies conducted on *A. prolifera* thanks to the advancement of molecular technologies. Future studies should focus on locating and analyzing F2 and F3 generation hybrids to identify if later generations maintain viability and resiliency similar to F1 hybrids. This will bolster the push for coral restoration programs utilizing *A. prolifera*. Additionally, as science teases apart coral response to disease, sub-optimal temperature, and low water quality conditions, future studies should continue to analyze how this hybrid responds to changing conditions and if it utilizes novel ways to survive. Coral species are known to create optimal habitat which supports not only fish and invertebrates but also a

community of microbiota within secreted mucus surrounding the coral tissue (Rohwer et al., 2002; Rohwer et al., 2001) and within their tissues and skeleton (Rosenberg et al., 2007).

Analyzing and comparing the relationship between associated microbiome and symbiodinium of *A. prolifera*, may provide insight on how these hybrids regulate themselves, mediate disease and survive in shallow strong light and UV irradiance conditions. Overall as we continue to see a natural increase of this hybrid coral, it is important we understand the trajectory of this novel hybrid in Caribbean coral reef ecosystems, potentially steer this population in ways that benefit the reef but most importantly, develop methods and understanding for when another naturally occurring coral hybrid begins to emerge.

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