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An Investigation into the Factors Influencing Growth and Survival of Caribbean Acroporid Corals in a Floating Nursery

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By:

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

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Abstract

For decades, coral reef ecosystems have been in decline. To promote recovery, restoration efforts have been implemented for many degraded reefs across the globe. In the Caribbean, there is restoration focus on the coral genus *Acropora*. Current methods target *Acropora cervicornis* and *A. palmata*, two threatened species of branching coral that can mate to form a hybrid taxon, *A. prolifera.* By including the hybrid in restoration efforts, researchers may better understand how this taxon may promote nursery expansion and outplanting in restoration efforts. Establishing efforts in novel areas may further advance restoration methods by comparing location differences in nursery success. For this project, Nova Southeastern University in conjunction with Norwegian Cruise Lines established three coral nursery sites at Great Stirrup Cay (GSC), The Bahamas. The goal of this project was to identify parameters that optimize successful fragment growth and survival in an *in-situ* floating tree coral nursery. A successful pilot study beginning in February 2018 using *A. cervicornis* and *A. palmata* at one nursery site allowed the project to move forward with an expansion to two additional nurseries after 5 months. Fragments from *A. cervicornis, A. palmata,* and *A. prolifera* were collected from reefs around New Providence by the Perry Institute of Marine Science and transported to GSC (n=157) in June 2018. These fragments were attached to floating trees at each of three nursery sites. Fragments were differentiated by nursery site, taxa, fragment type (apical, middle, and basal), and genotype. Linear growth, percent mortality, and condition data were collected monthly for each fragment. After 13 months, site significantly affected fragment survival ($p<0.05$), while taxon and fragment type did not. Taxon, site, and fragment type are important factors affecting total linear extension. Apical *A. prolifera* fragments had the greatest growth by the end of the study period compared to all other taxa and fragment types. This study highlights the importance of careful consideration of nursery location to optimize survival. Coral taxa and fragment type should be considered when comparing growth within a nursery, especially for future use of coral fragments in outplanting. Coral restoration managers may benefit from capitalizing on fast growing hybrids for outplanting to degraded reefs and increasing the scale of nursery projects, with consideration of competition between the three acroporid species in outplanting methods.

Keywords: *Acropora cervicornis, Acropora palmata, Acropora prolifera,* hybrid, coral restoration, coral nursery

Introduction

The need for conservation and restoration of our world's natural resources have come to the forefront of research worldwide as we face a changing climate. Global issues such as deforestation, rising global temperatures, pollution, and the overuse of natural resources are serious threats to the continuation of many species (Vitousek, 1994; Malhi et al., 2008; Cinner et al., 2015). These stressors are just as prevalent in marine ecosystems as terrestrial environments (Derraik, 2002; Shahidul Islam & Tanaka, 2004; Harley et al., 2006; Hughes et al., 2017). With increased global threats, coupled with local stressors, economically important marine ecosystems are at risk of being lost.

Coral reefs are one of the world's most important natural resources. Coral reef ecosystems host a diversity of marine species, many of which are commercially important (Moberg & Folke, 1999). They are connected to many other vital habitats, including seagrass beds and mangroves, which are essential nursery grounds for numerous fish and invertebrate species (Heck et al., 2008; Holbrook et al., 2015). They protect coastlines from storm damage by acting as a barrier, dissipating up to 97% of wave energy from large tropical storms and hurricanes (Cesar et al., 2003; Ferrario et al., 2014; Storlazzi et al., 2019). Coral reef habitats also support a large tourism industry for many island nations and coastal regions (Cesar et al., 2003). Coral reefs are responsible for an estimated $29.8 billion (USD) in goods and services per year (Cesar et al., 2003), with nearly $1.8 billion (USD) in protection services to coastal infrastructure in the United States alone (Storlazzi et al., 2019).

Though coral reefs are of vital importance, they are threatened by anthropogenic sources. Nearly 27% of the world's coral reefs have been completely lost due to destructive events and stressors (Cesar et al., 2003), and it is estimated that 75% of coral reefs worldwide are threatened as a result of these anthropogenic stressors (Bellwood et al., 2004; Johnson et al., 2011). Direct anthropogenic impacts to coral reefs include physical damage from storms, ship groundings, anchor lines, and destructive fishing practices (Lirman & Fong, 1997; Hughes & Connell, 1999; Fox & Caldwell, 2006). Industrial pollution from oil spills and outfall from sewage pipes can cause harmful algal blooms, while sedimentation from dredging and other coastal construction can bury and smother reef organisms (Babcock & Smith, 2000; Woodley et al., 2000; Bellwood et al., 2004; Shahidul Islam & Tanaka, 2004). Other global stressors have also had negative impacts on coral reefs.

Rising ocean temperatures are also an effect of anthropogenic carbon loading in the atmosphere. A rise in ocean temperatures can cause coral bleaching events, a stress response during which coral symbionts, algae in the family *Symbiodinaceae* (LaJeunesse et al., 2018), are expelled from the coral tissue (Brown, 1997; Heron et al., 2016). Once the algae cells are expelled from the coral, individual coral colonies may not recover if the stress continues (Douglas, 2003; Eakin et al., 2010), and if they do recover, a colony may have reduced growth, skeletal deposition, and reproduction (Baker et al., 2008). A rise in ocean temperatures may also contribute to disease outbreaks across the globe, resulting in large scale coral mortality (Weil, 2004; Harvell et al., 2007; Eakin et al., 2010). The increase in storm intensity due to rising global sea temperatures reduces the recovery potential between storm events, wherein destruction to coral reefs by storms alone may require decades to recover (Hughes, 1994; Smith et al., 2015; Cheal et al., 2017). While disturbance to a reef is natural, the increasing frequency of disturbance events has shifted some reef communities from coral to algal dominated. Local disturbance events, including predator outbreaks, disease, overfishing, and storm damage cause these phase shifts (Hughes, 1994; Voss & Richardson, 2006; Mumby & Steneck, 2008; Edwards, 2010). Coral reefs in regions suffering from both chronic global stressors and local threats are at greater risk of a shift from a coral dominated habitat, resulting in the degradation of the coral reef community (Bellwood et al., 2004; Vollmer & Palumbi, 2006).

In the Caribbean, significant losses in scleractinian coral cover have been documented since the 1980's (Gardner et al., 2003; Eakin et al., 2010; Jackson et al., 2014). In this region, prolonged exposure to many years of stressors, such as rising ocean temperatures, sea level rise, disease, overfishing, and increased pollution, have driven declines in coral cover (Gardner et al., 2003; Weil, 2004; Mumby et al., 2007; Eakin et al., 2010; Edwards, 2010; Jackson et al., 2014). Many of these effects have compounded on another, increasing the rate of coral decline. Much of this loss in coral cover is attributed to branching acroporid corals, which contribute to shallow reef infrastructure (Bruckner, 2002; Gardner et al., 2003).

Acropora is one of the most speciose genera of corals, with approximately 180 species worldwide (Vernon, 2000). The Caribbean is home to two acroporid species, *Acropora cervicornis* and *A. palmata*, which historically were found on many reefs across the region (Aronson & Precht, 1997; McNeill et al., 1997; Bruckner, 2002; Vollmer & Palumbi, 2002; Miller & Van Oppen, 2003; Bellwood et al., 2004).*Acropora cervicornis* and *A. palmata* are

important scleractinian corals due to their extensive branching forms, which provide habitat and structure to the reef environment (Bruckner, 2002). These species provide many ecosystem services in the Caribbean, like building reef framework through carbonate deposition, providing microhabitats for fish species, and wave protection from storms(Bruckner, 2002). These corals reproduce sexually through broadcast spawning (Szmant, 1986; Vargas-Angel & Thomas, 2002), but are also capable of reproducing asexually through fragmentation (Rinkevich, 1995; Lirman & Fong, 1997; Smith & Hughes, 1999).

These two coral species are also capable of reproducing with each other, creating an F1 hybrid, *Acropora prolifera* (Vollmer & Palumbi, 2002; Kitchen et al., 2019). *Acropora prolifera* can reproduce asexually through fragmentation like the parental species. The hybrid has also been shown to reproduce sexually with the parental species, but has not been verified to reproduce sexually with itself (Vollmer & Palumbi, 2002; Fogarty, 2012). This backcrossing is important to the life history of these Caribbean corals; by backcrossing, the genetic material from one parent (e.g. *A. cervicornis*) may be taken in by the next generation of the parental species (e.g. *A. palmata*), thus increasing genetic diversity between the two parental species through the hybrid (Vollmer & Palumbi, 2002; Fogarty, 2010, 2012). In some cases, the hybrid has equal or superior fitness as the parental species in a natural setting (Fogarty, 2012; Howe, 2018; Nylander-Asplin, 2018). Hybrid survival success and backcrossing potential is of value for the continuity of these Caribbean taxa, especially considering the decline of the parental *Acropora* species.

Since the 1970's, disease and severe storm damage throughout the Caribbean have led to a significant decline of the two parental acroporid species (Jackson et al., 2014). Before the 1970's, *A. cervicornis* and *A. palmata* dominated many reef habitats, contributing up to 50% of total stony coral cover above 20 meters depth (Bellwood et al., 2004). These species have declined by 95% in some parts of the Caribbean over the last 30 years (Bruckner, 2002). Acroporid corals can form high density thickets of connected coral colonies, which make them particularly susceptible to environmental stressors (Smith & Hughes, 1999; Bruckner, 2002). While storm damage allows acroporid corals to reproduce asexually by fragmentation, damage from increased hurricane prevalence, combined with diseases such as White Band, can destroy large patches of coral (Aronson & Precht, 2001; Jackson et al., 2014). Coral disease, with the addition of disturbance events, likely caused the majority of *Acropora* declines in the region

(Bruckner, 2002). However, reduction of other reef organisms may also have contributed to coral loss. Overfishing, particularly within herbivorous reef fish, has led to a decrease in grazers on the reef (Jackson et al., 2014) which has led to an increase in macroalgae cover (Lirman, 2001). A disease event that killed large numbers of the herbivorous sea urchin, *Diadema antillarem*, also likely contributed to this shift, as macroalgae smothered newly settled coral across the Caribbean (Hughes et al., 1985; Hughes, 1994; Bellwood et al., 2004). As such, *A. cervicornis* and *A. palmata* were listed as threatened under the United States Endangered Species Act as of 2006 (National Fisheries Marine Service, 2006) and as critically endangered by the International Union for the Conservation of Nature (IUCN)'s Red List as of 2008 (Aronson et al., 2008b; Aronson et al., 2008a). To facilitate species recovery, many organizations throughout the Caribbean are working to increase *Acropora* abundance through active restoration efforts.

A restoration effort in tropical marine environments targets scleractinian corals, as they are critical to the structure of the reef (Yap et al., 1992; Rinkevich, 2005; Johnson et al., 2011; Griffin et al., 2012; Young et al., 2012). In many cases, these efforts are achieved by the creation and maintenance of coral nurseries. Nurseries provide a sheltered area for corals to grow, while regular maintenance may limit loss from disease and predation. There are a variety of recommendations on how to manage nurseries to best suit the needs of a target species (Edwards, 2010; Johnson et al., 2011; Schopmeyer et al., 2017). While various methods of growing corals *in situ* have been attempted (Herlan & Lirman, 2008; Putchim et al., 2008; Edwards, 2010; Johnson et al., 2011; Young et al., 2012; Schopmeyer et al., 2017), the 'gardening technique' proposed by Baruch Rinkevich (1995) has been adopted as a general practice for many reef restoration organizations. Based on silviculture practices, coral fragments are grown in *in situ* nurseries before being outplanted to local reefs (Rinkevich, 1995; Lirman, 2000; Zimmer, 2006). Coral fragments used within nurseries are collected from different genotypes of the target species, which allows for greater diversity in future outplanting.

Once the corals have grown to a mature size, they may be fragmented to expand the nursery and/or outplanted to degraded reefs (Harriott & Fisk, 1988; Clark & Edwards, 1995; Soong & Chen, 2003; Lirman et al., 2010; Griffin et al., 2012). Thus, success in a nursery is crucial to the success of the outplanted corals. A nursery set up varies depending on the target species, but typically involves some structure in which coral fragments are temporarily attached. This structure can be either floating in the water column or attached to the bottom. Depending on

the attachment method, the materials used range from lines, PVC trees, rebar tables and frames, or cement blocks (Johnson et al., 2011). In this way, corals can be quickly grown in a more controlled and protected environment, i.e. the nursery. Survival in a nursery varies greatly on nursery method and environmental conditions, but mortality is typically greater in the first month or two in the nursery compared to following months (Lirman et al., 2010; Griffin et al., 2012). Growth also varies by species and has been shown to be positively related to Total Linear Extension (TLE) and the number of branches in *A. cervicornis* (Lirman et al., 2014). Genetic variability has been increasingly identified as an important factor in the success of restoration for branching corals. By including different genotypes in a nursery setting, when out planting occurs, there is an improved chance of genetic diversity in sexual reproduction between outplants (Baums, 2008; Johnson et al., 2011). To increase genetic variability in nursery fragments, collection may be done from a wide regions of donor colonies, while also targeting colonies that are from areas that have adaptive potential, i.e., different environmental conditions (Baums et al., 2019). Further research is being conducted on the inclusion of sexual reproduction and increased genotypic diversity in restoration methods (Baums et al., 2019; Randall et al., 2020).

As of 2012, there are 60 active restoration projects occurring across the Caribbean (Young et al., 2012). Advances in restoration have been successful in increasing coral stock, but rarely include hybrid coral species. Hybrid species are often sterile (Ortiz-Barrientos et al., 2007), which has raised the question as to whether outplanting a hybrid may reduce the genetic diversity of coral outplant stock or cause other genetic crossing issues, as seen in forestry practices (Merkle et al., 2006; Richards & Hobbs, 2015). In *A. prolifera*, the potential for backcrossing would likely maintain or increase genetic diversity. This mechanism could prove beneficial to increasing genetic variability *Acropora* restoration efforts, particularly with an increase in environmental stressors.

For the future of coral reefs, it is important for researchers to study nursery conditions and locations to optimize coral growth and survival. There is abundant knowledge on coral nursery setup and maintenance for success; however, local variability in ocean settings, the inclusion of a hybrid taxa, and other related factors have not been studied. There is still much to be learned from establishing coral restoration projects in varied locations, especially in areas where very little has been published. By establishing nursery projects in a previously understudied area, knowledge of environmental locations that lead to successful survival and

growth may be expanded. Finally, as hybrid corals have rarely been included in restoration efforts, there is a need to understand how these corals perform from an ecological perspective to understand if they should be included in future restoration efforts.

This study investigates factors that may influence growth and survival of Caribbean acroporid coral species, including their hybrid, at three *in-situ* nurseries located in The Bahamas. Here I investigate a variety of factors and their impact on coral fragment survival and growth, including nursery site selection, fragment type, taxa, and genotype. By better understanding elements that may influence a coral fragment's performance in a nursery setting, researchers can then determine which combination of factors will lead to greater success in the expansion of nurseries and outplanting.

Methods

Study Location

This study was conducted at Great Stirrup Cay (GSC), The Bahamas, from February 2018 to July 2019. GSC is located at the northern end of the Berry Islands in the central Bahamas (Fig. 1). GSC is a private island owned by Norwegian Cruise Line® (NCL), which receives thousands of cruise ship visitors every week. Coral reefs fringe the northern side of the island, and seagrass beds and sand patches are common to the south. The deeper reefs (~15 m) on the northern side of the island are rugose spur and groove composed of large mounding corals including *Orbicella* spp. and *Montastraea* genera, gorgonians, and sponges. On the eastern side of the island, reefs flats contain branching acroporid species and smaller mounding corals, along with various species of gorgonians.

Figure 1. Map of Great Stirrup Cay nursery sites. Inset: The Berry Islands in relation to Florida and the greater Bahamas.

Study Species

Acropora cervicornis is found on shallow reefs up to 20 m depths; *A. palmata* can be found on shallow reef crests to 10 m depth in areas with high wave energy (McNeill et al., 1997; Johnson et al., 2011). Both *A. palmata* and *A. cervicornis* can grow up to ~10 cm per year (McNeill et al., 1997). *Acropora cervicornis* has long, thin branches extending from a central basal attachment, while *A. palmata* has wide, flattened branches that also extend from a central basal attachment point (Neigel & Avise, 1983) (Fig. 2). *Acropora prolifera* has an intermediate morphology between its parental species, and as such has been shown to effectively grow in both high energy and deeper habitats (Vollmer & Palumbi, 2002; Fogarty, 2012). All three taxa can naturally reproduce asexually via fragmentation, making them ideal candidates for coral restoration (Rinkevich, 1995; Herlan & Lirman, 2008; Griffin et al., 2012; Schopmeyer et al., 2017).

Figure 2. Caribbean Acropora taxa from left to right: *A. cervicornis, A. palmata,* and *A. prolifera.* Photo credit: Morgan V. Hightshoe.

Nursery Setup

Three GSC nursery sites were included in this study. Nursery locations included two southern sand flat sites (N1 and N2) and one northern reef slope site (N3) (Fig. 1; Appendix A, Table 6). Nursery sites were chosen based on depth, accessibility, and protection from human interference via direct tourist activities - all sites were in shallow water and were easily accessible by boat from the island, but far enough from shore that snorkelers and other water activities had limited impact. Three coral nursery trees© (Nedimyer et al., 2011) were placed at each nursery site. Nursery trees were made from PVC and fiberglass rods with pre-drilled holes along each rod. The trees were tagged and secured to the seabed using sand (helix) anchors (Fig.

3a) or epoxied eyebolts, depending on the substrate type (sand or hard bottom, respectively). Trees were tied to the anchors using polypropylene rope with plastic tubing through a metal shackle, such that the middle branch was at a depth of approximately three meters below the surface (Fig. 3b). Every tree contained five branches with corals attached to the middle three branches. Six corals were attached per branch using 80 lb. test monofilament approximately 10 cm apart (Fig. 3c. 3d).

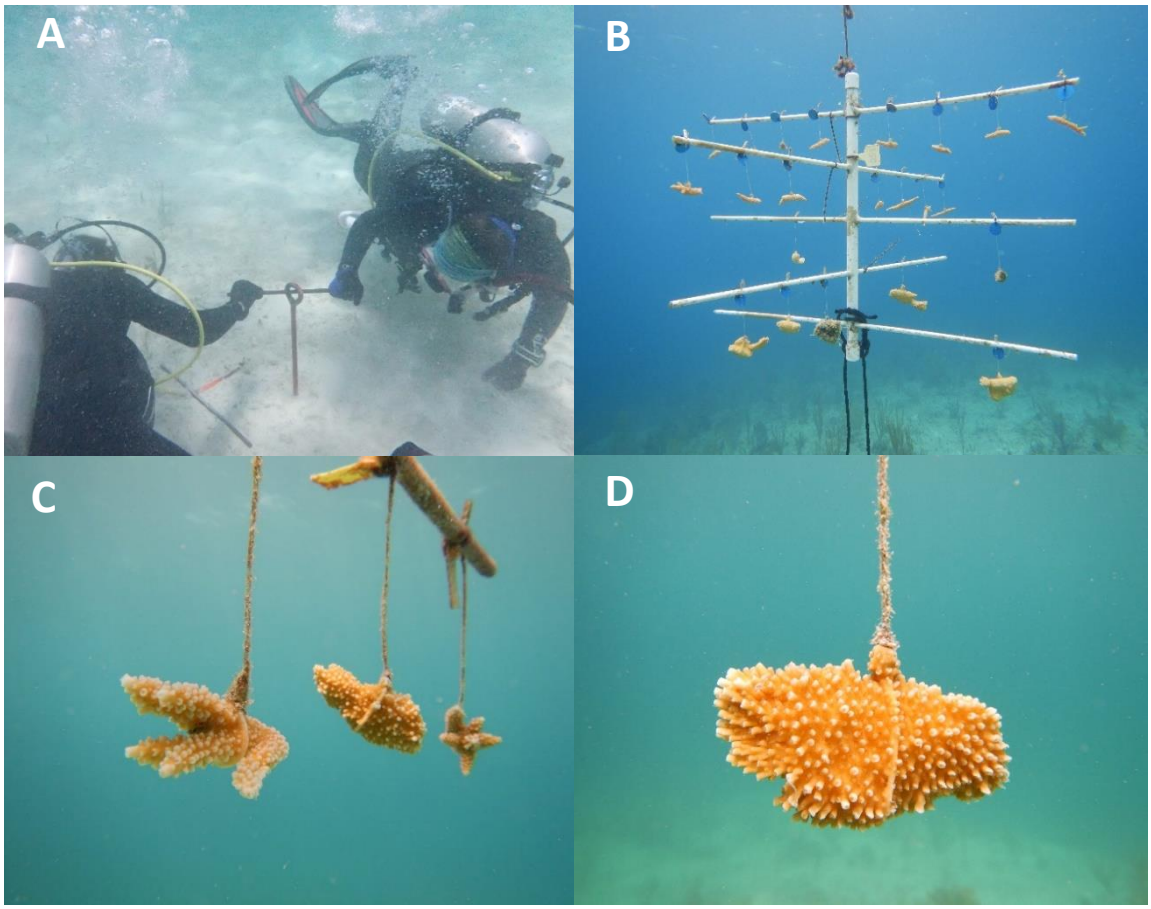

Figure 3. A) Installation of sand (helix) anchors into substrate, B) Tree setup, C) Fragment setup, containing fragments (left to right): *A. cervicornis, A. palmata,* and *A. prolifera,* and D) Monofilament attachment to fragments.

Part I: Pilot Study

A pilot study (Part I) was conducted to determine if nursery site locations in shallow water were appropriate for continued nursery success; in particular, if target taxa fragments could survive successfully in the shallow water around the island, as suitable site locations were limited. Pilot study coral fragments of *A. cervicornis* and *A. palmata* were collected throughout the greater Berry Islands in February 2018 (Fig. 4). No colonies of *A. prolifera* were found during this collection. Donor colonies were located at a depth of approximately 1.8 - 4.6 m (Appendix A, Table 5). Donor colonies were at least 10 m apart to increase confidence of genotypic uniqueness. A tissue sample was also collected for genetic analysis. Collection was conducted using a hammer and chisel or diagonal cutters. Fragments were transported to GSC in a seawater filled cooler, with the water refreshed as needed. Three 15 cm fragments were collected from each colony (n=9 *A. cervicornis* and n=23 *A. palmata*). Each 15 cm fragment was sectioned into three smaller 5 cm fragments (n=27 *A. cervicornis* and n=69 *A. palmata*) (Appendix A, Tables 7-9). The fragments were labeled as apical (A), middle (M), and basal (B) sections, as per origin on the donor branch (Fig. 5). Length and width, size/number of branches, and condition data were recorded for each smaller fragment. Fragments were randomly attached to nursery trees at site N2 with a unique tag number. After four months, it was determined that a shallow water nursery would be applicable for this area based on the survival of pilot coral fragments, and the experimental portion of the study was initiated (Part II). As the pilot study was only used for applicability of the nursery setup, these fragments were excluded from statistical analysis.

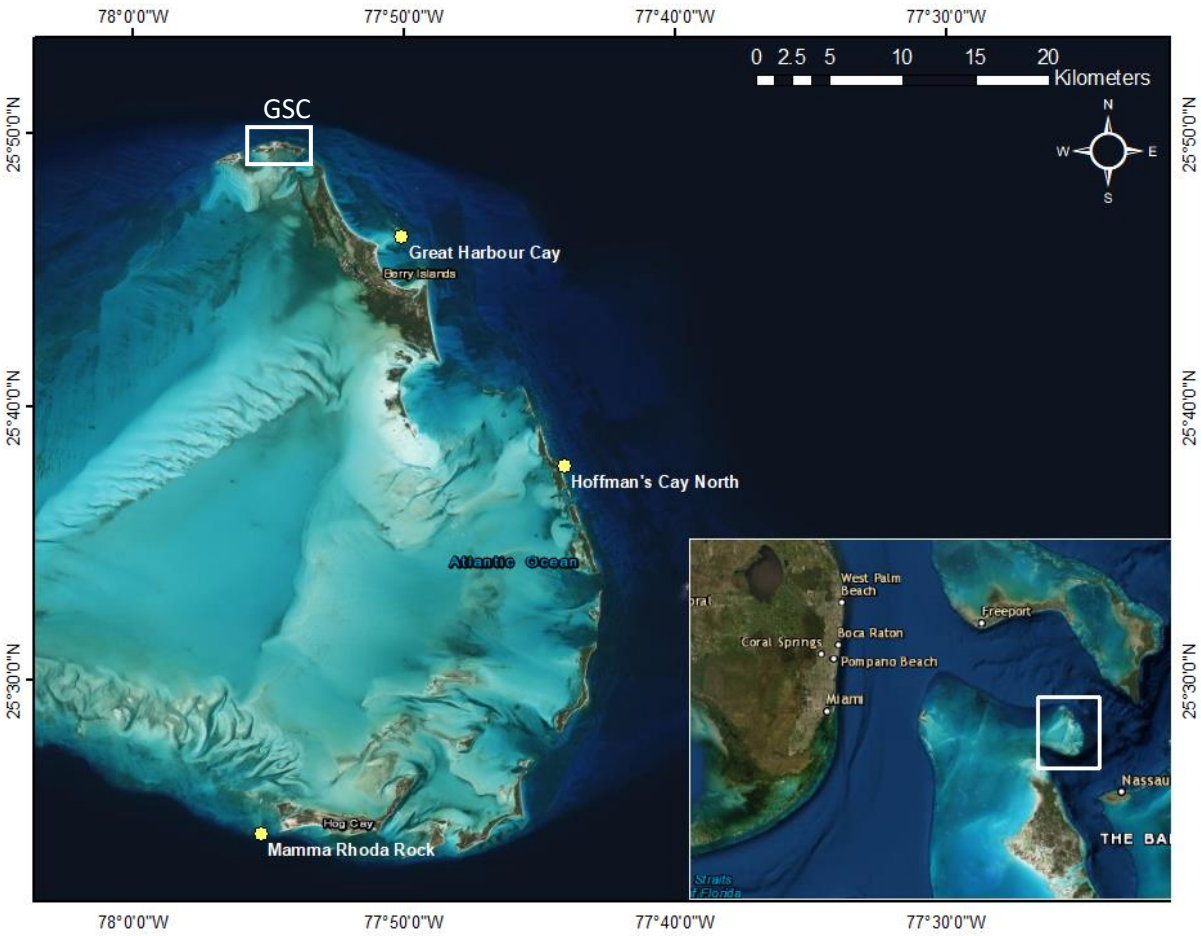

Figure 4. Map of pilot coral collection locations around the Berry Islands. Inset: The Berry Islands in relation to Florida.

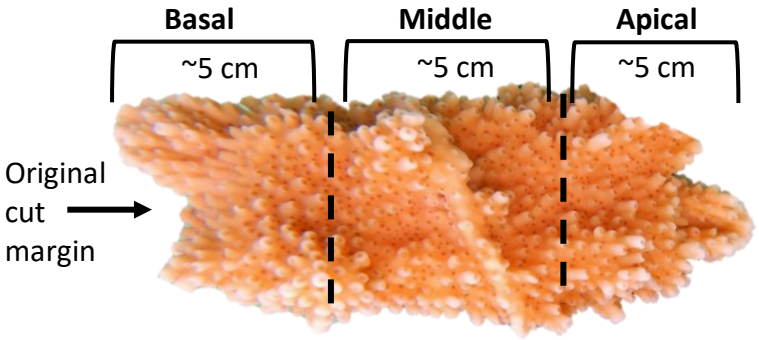

Figure 5. Fragment type was designated from the portion of the donor fragment. The first 5 cm (proximal end) were considered the apical fragment type, the next 5 cm were the middle fragments, and the interior most 5 cm of the donor fragment were the basal fragments.

Part II: Experimental Study

Acropora cervicornis, A. palmata, and *A. prolifera* fragments were collected around the reefs of New Providence, The Bahamas, in June 2018 for Part II of the study (Fig. 6). Collections were conducted by the Perry Institute of Marine Science (PIMS), a project collaborator, in the same way as the pilot coral collections. Collections were done at a different location from Part I due to lack of hybrid colonies and unique genotypes around the study sites at GSC. Fragments were collected between 0.6 – 2.7 m depth and ≥10 m apart to increase the confidence of genotypic variation (Appendix A, Table 6). A sample from the original colony fragment was collected for genetic analysis. Fragments were harvested in the same manner as Part I coral collection and transported in plastic Ziploc bags, inside of Bubble Wrap® lined coolers. Ice packs were placed in the coolers for temperature regulation. Collection targeted six unique genotypes for each taxon, with three 15 cm branches collected from each donor colony. These fragments were transported to N2 nursery site the same evening of original collection (n=19 *A. cervicornis*, n=18 *A. palmata,* n=17 *A. prolifera*).

The following day, the 15 cm donor colony fragments (n=18 per taxa) were cut into smaller sections and attached to the nursery trees (n=57 *A. cervicornis*, n=51 *A. palmata,* and n=49 *A. prolifera*) (Fig. 7; Appendix A, Tables 7-9). Fragments were sectioned in the same manner as the pilot coral fragments (apical, middle, and basal sections) and were distributed across the three trees at each site. In total, all taxa and fragment types were represented at each site in a crossed design (Fig. 7). Genotype analysis was completed after fragment deployment. By spreading genotypes across trees and across sites, the risk of losing a genotype to abiotic factors like storm damage was reduced. Each fragment was marked by a metal tag attached to the branch of the trees, above each coral. Placement on coral tree, coral fragment size, and condition data were recorded immediately. An Onset HOBO® pendant temperature logger was attached to one tree at each site, recording temperature every two hours.

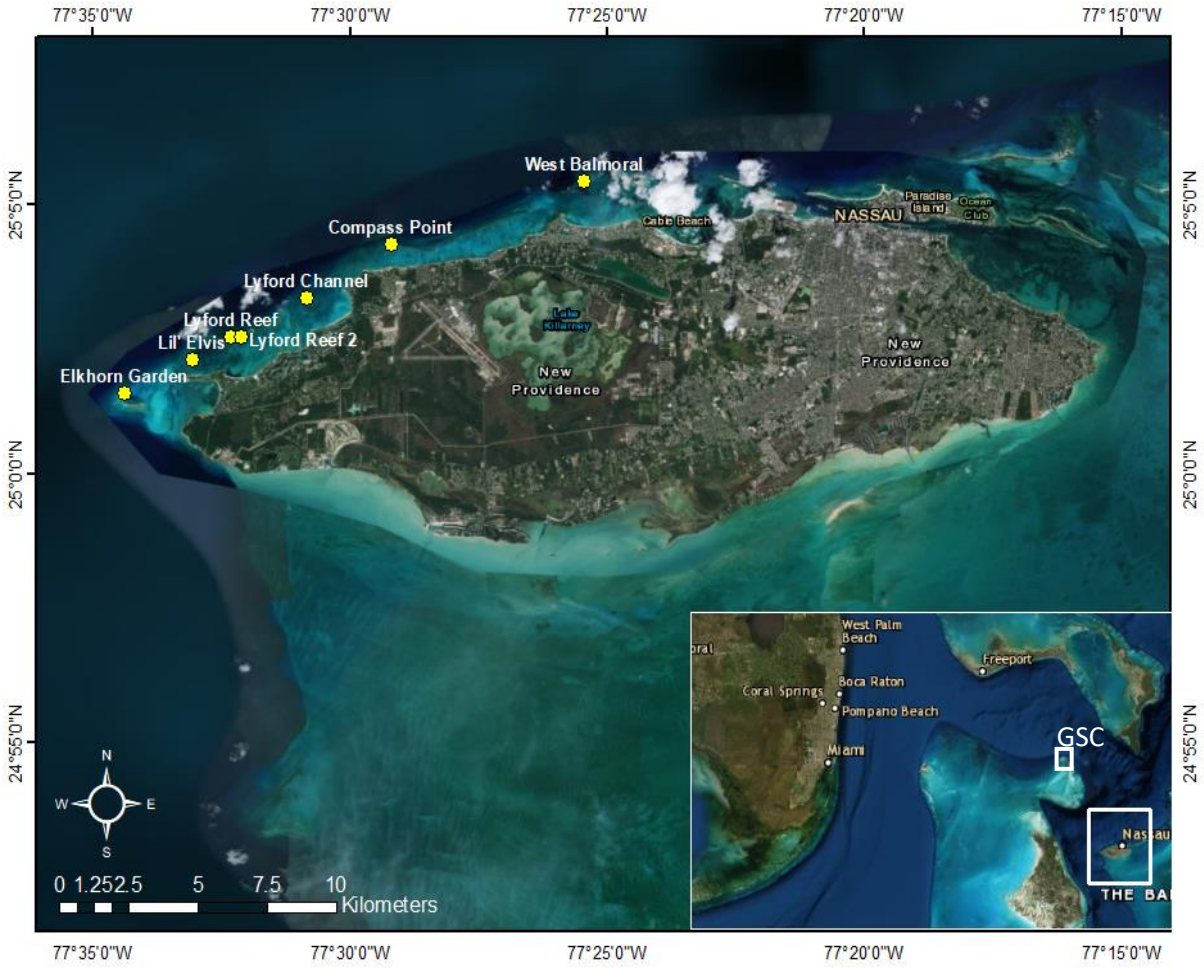

Figure 6. Map of Part II coral collection locations around New Providence. Inset: New Providence in relation to Florida and the Berry Islands with GSC highlighted.

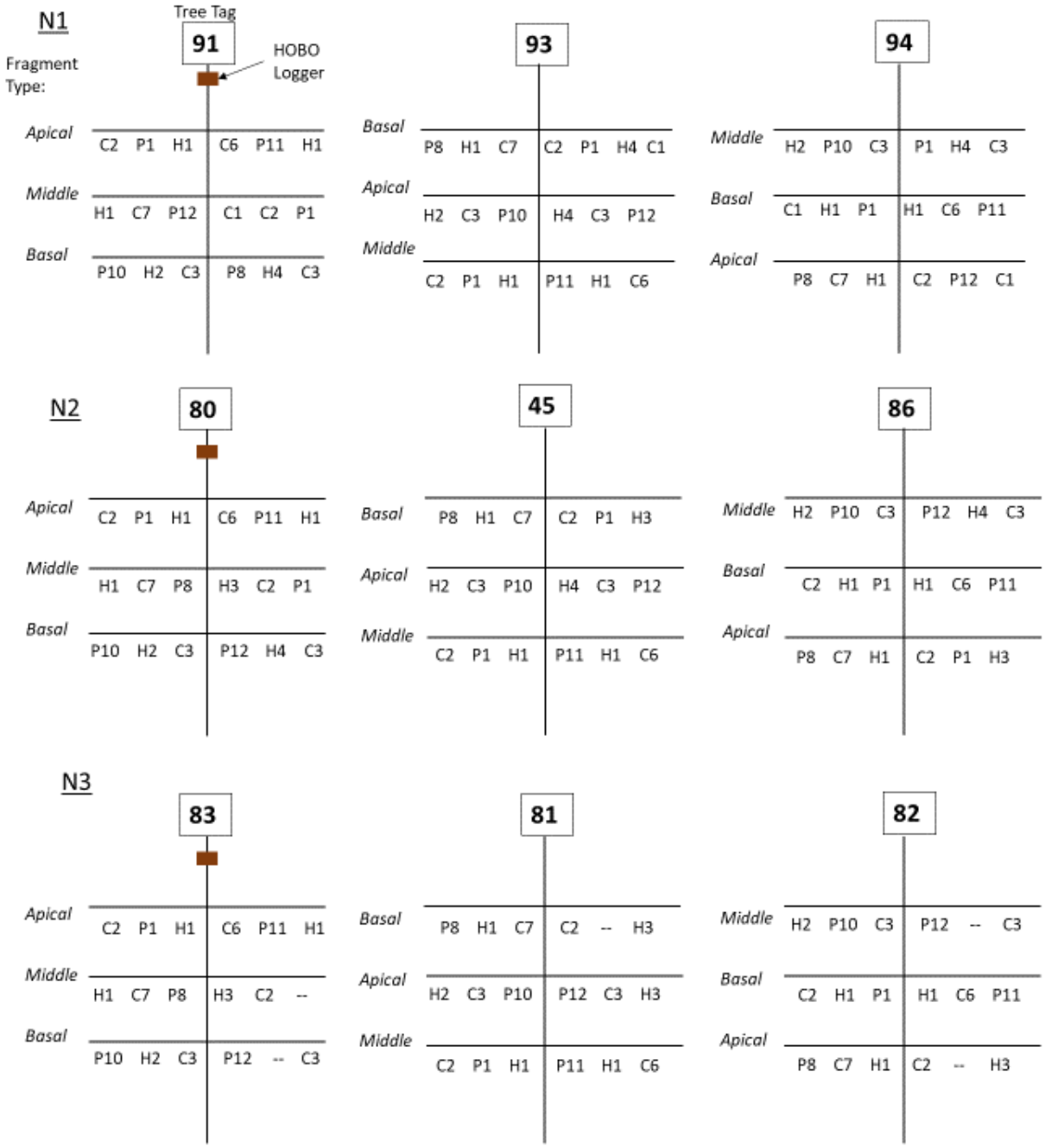

Figure 7. Nursery site setup for Part II. C1 denotes *A. cervicornis*, genotype 1, P1 denotes *A. palmata*, genotype 1, and H1 denotes *A. prolifera* (hybrid), genotype 1, etc., as confirmed by genetic analysis. Fragment types are distributed among site by tree branch. Appendix A, Tables 9-12 lists specific information regarding total fragments per taxa, genotype, fragment type, and site. Dashes denote no fragment attached.

Genetic Analysis

Genetic samples were collected from all donor colonies. A small ~1 cm sample was cut and placed in a ~1 mL centrifuge tube and filled with 96% molecular grade ethanol. DNA was extracted using magnetic bead protocol, as described in Fogarty et al., 2012. This was followed by PCR amplification using five microsatellite markers (Baums et al., 2005; Fogarty et al., 2012; Hightshoe, 2018). After fragment analysis (conducted at Florida State University), peaks for each fragment loci were analyzed using GeneMapper 5™ software. Genotypes were confirmed with matching loci using the Excel microsatellite toolkit (Park, 2001).

Nursery Maintenance and Data Collection

Nursery sites were visited monthly between June 2018 to July 2019, during which the trees were cleaned and fragment data were collected. Data included measurements of total length, total width, number of branches, branch length(s), % mortality, and condition data (disease, predation, bleaching presence/absence). Linear extension (mm) was calculated as the total sum of the fragment length along the main axis plus the length of all branches >1 cm (Fig. 8b). This was then multiplied by partial mortality estimates to get Total Linear Extension (TLE) (mm) for live coral tissue. Images were also taken of each fragment with a scale bar. TLE was measured in Image J if branch measurements could not be completed in the field (Fig. 8b; Image J Version 1.52n, 2018). Data was not collected in April 2018 and May 2019 due to logistical conflicts in scheduling.

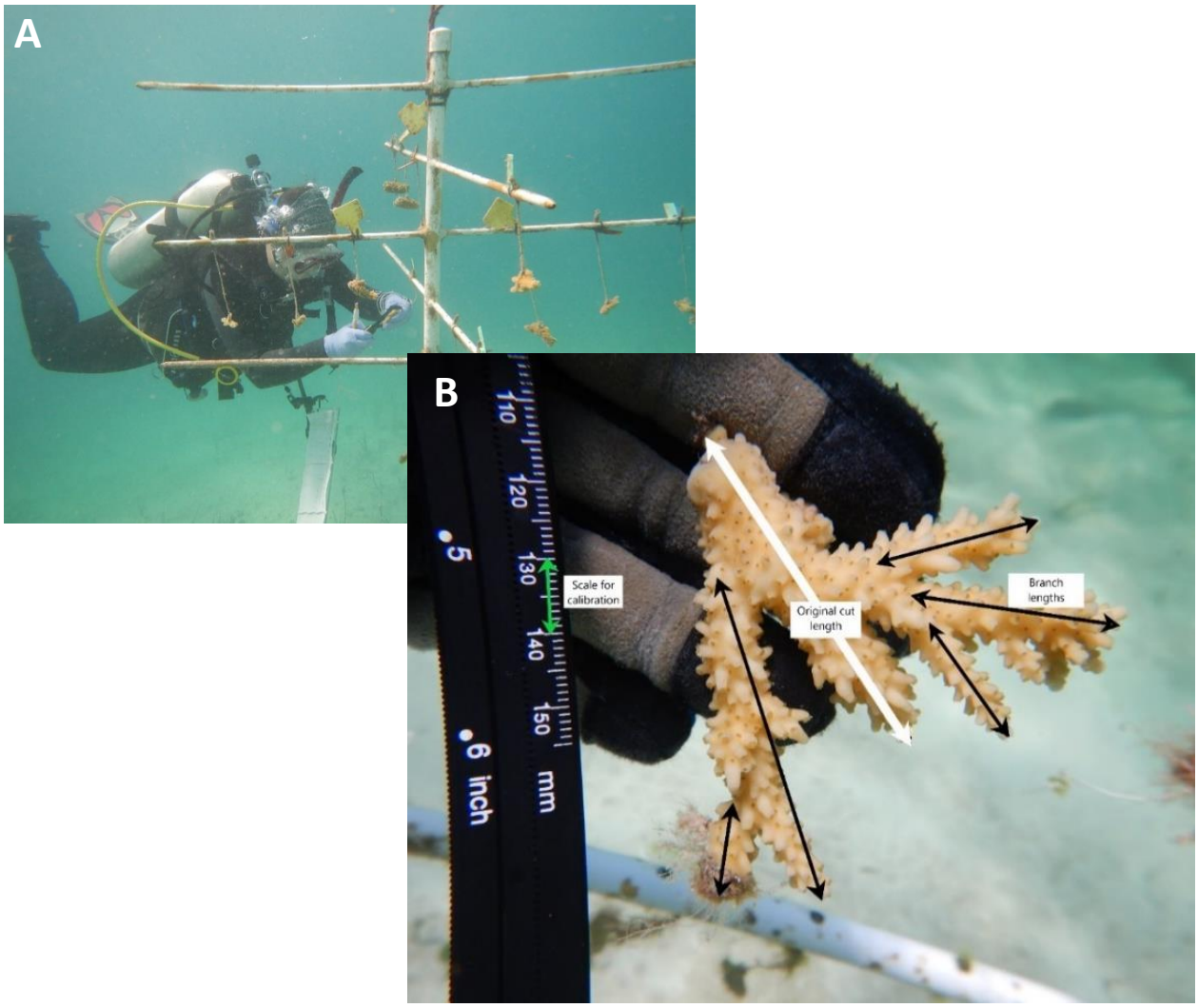

Figure 8. A) Data collection, and B) Example of TLE calculation done in the field or Image J, if applicable. Highlighted are the original cut length, branch lengths, and scale used in Image J for calibration.

Statistical Analysis

Fragment survival and TLE data were analyzed using R statistical software (R_Core_Team, 2017). The pilot study was conducted to determine applicability of shallow sites in overall nursery success and did not included all the factor levels as listed in Part II. Descriptive results will be presented using this data. A Survival Analysis (Cox model) was run on Part I fragments to test if independent variables effected total colony mortality in the nursery (Therneau & Grambsch, 2000; Therneau, 2015; Kassambara & Kosinski, 2018). Independent categorical variables included in the survival analysis were taxa, genotype, and fragment type. The dependent

variable was the survival status of the coral (Alive = 0, Dead = 1). To test differences between initial and final TLE values, a Factorial ANOVA was conducted. Partial mortality was included in TLE for the growth analysis by multiplying the total TLE by percent mortality of each fragment.

For Part II, various survival and growth plots were created through the package 'ggplot2' to examine raw data (Wickham, 2016). Partial mortality was included in TLE for the growth analysis by multiplying the total TLE by percent mortality of each fragment. A Survival Analysis (Cox model) was run on Part II fragments to test if independent variables effected total colony mortality in the nursery (Therneau & Grambsch, 2000; Therneau, 2015; Kassambara & Kosinski, 2018). Independent categorical variables included in the survival analysis were taxa, genotype, fragment type, and nursery site. The dependent variable was the survival status of the coral (Alive = 0, Dead = 1). Survival analyses were also run without the first month to test if there were differences in the factors affecting mortality due to acclimation to the nursery.

To model the response of growth as a function of the categorical variables of taxa, fragment type, and site, a Factorial ANOVA and Generalized Additive Mixed Model (GAMM) was run on the Part II coral fragment data (Eq. 1) (Wood, 2011). In the Factorial ANOVA, other factors that were not the target factor were pooled. The GAMM included potential additive and interactive effects of factors that other statistical tests may not account for. The GAMM allows for dependency between individuals; in this case, the TLE at month *n* depends on month *n*-1. Independent categorical variables included taxa, site, and fragment type. Once fragments had died, they were excluded from the remaining analysis. Important terms were identified by backwards selection (i.e., each term was sequentially dropped from the full model in turn) using Akaike's Information Criteria (AIC) scores as the selection criterion - the lowest scores indicated a better model fit. A term was considered unimportant in explaining the observed variance if the difference in the AIC scores (dAIC) was <2, marginally important if the dAIC was 2 - 4; and important if the dAIC was >4. The model included time in the nursery as a smoothed term, with the factors either all included or dropped to test effects on the dependent variable (TLE). Results from the Minimally Adequate Model (MAM), the model used for this analysis and resulting post-hoc tests, are shown in Table 1. The MAM was validated by visual examination of the model residuals verses fitted values using plot(gam model) and gam.check(gam model) functions (Appendix B, Fig.'s 20 and 21).

```
gam(TLE~s(TimeNursery)+factor(Taxa)+s(TimeNursery,by=Taxa)+factor(Site)+
factor(FragType)+s(TagNum,bs="re"),
method="ML", data=NoNA, family="Gamma")
```

(Eq. 1)

The MAM was fitted with the Gamma distribution and inverse link function, which is commonly used for positive skewed integer data. Unique tag numbers were included as a random effect to allow for the dependence between repeated measures on each fragment (Appendix B, Fig. 19). The interaction term included was time in the nursery multiplied by taxa. Model validation did not indicate any problems, based on residuals plots. Pairwise comparisons of the factor levels in the MAM were conducted by using the 'emmeans' package (Lenth, 2019). This allows for determining which levels of each factor are significantly different, i.e., if *A. prolifera* fragments differ in TLE from the parental species.

Plots for the important factors were created based on the values calculated from the MAM. The MAM fit a prediction growth curve based on the fragment data, including any partial mortality. Thus, the term 'prediction' as used here refers to the results of the smoothed curve as modeled in the MAM. For the resulting plots, the marginal effects of each defined variable are displayed in relation to TLE, with the other factors held at a reference level: i.e., background variables are held constant to see the effects of each factor on TLE. Each level of the background factor was used to see of changes were made to the prediction plots, which resulted in a similar growth pattern at all reference levels of each factor.

Genotype was excluded from the GAMM model due to low sample size of certain genotypes. When comparing TLE values of new growth for each fragment between genotypes overall, a Kruskal Wallis chi-squared test was uses. To test differences between genotypes within a taxon, a One-Way ANOVA (parametric) or Kruskal Wallis chi-squared test (non-parametric) was used. If data met parametric assumptions, a Tukey's test (Tukey HSD) could be used in post-hoc analysis and visualized using the 'multcompView' package, which assigns letters to each group to show significant differences (Graves et al., 2015).

To test differences in prevalence of conditions, a Kruskal-Wallis chi-squared test was used. Conditions examined were bleaching (Blch), paling (Pale), and algal overgrowth interactions (OGA). No other conditions (disease, predation, etc.) were reported with enough replicates to be used in analysis.

Average daily temperature was calculated in Excel using the HOBO® temperature logger data. Data was organized in Excel, imported into R, and analyzed with a Kruskal Wallis t-test to determine whether the nursery sites had significantly different temperatures over the study period (Pinheiro et al., 2017).

Table 1. Results from MAM dAIC scores for parametric and smoothed terms. dAIC describes differences when a term is dropped from the model. If a dAIC difference >4 is observed that factor is deemed to have an important effect on TLE.

Parametric Terms Summary (based on ANOVA and AIC scores)				
Term	*df*	*F*	*p-value**	*dAIC [when dropped]*
Taxa	2	11.323	1.33e-05	5.71
Site	2	3.702	0.024935	5.89
Fragment Type	2	7.823	0.000419	11.1

Smooth Terms Summary (based on ANOVA and AIC scores)				
Term	*EDF*	*Ref df*	*p-value**	*dAIC [when dropped]*
Time Nursery	5.121e+00	6.199E+00	<2e-16	6.64
Tag Number (random effect)	8.584e+01	1.090e+02	<2e-16	592.43

Results

Part I: Pilot Study - Mortality

Pilot coral total mortality was 35% the first month in the nursery, then dropped to < 4% in the following 16 months. In the final month, July 2019, total mortality increased to 5.17% (Fig. 9; Appendix A, Table 10). No factors (taxa, fragment type, genotype) had a significant effect on the survival of the pilot corals (Survival Analysis Cox model, p>0.05).

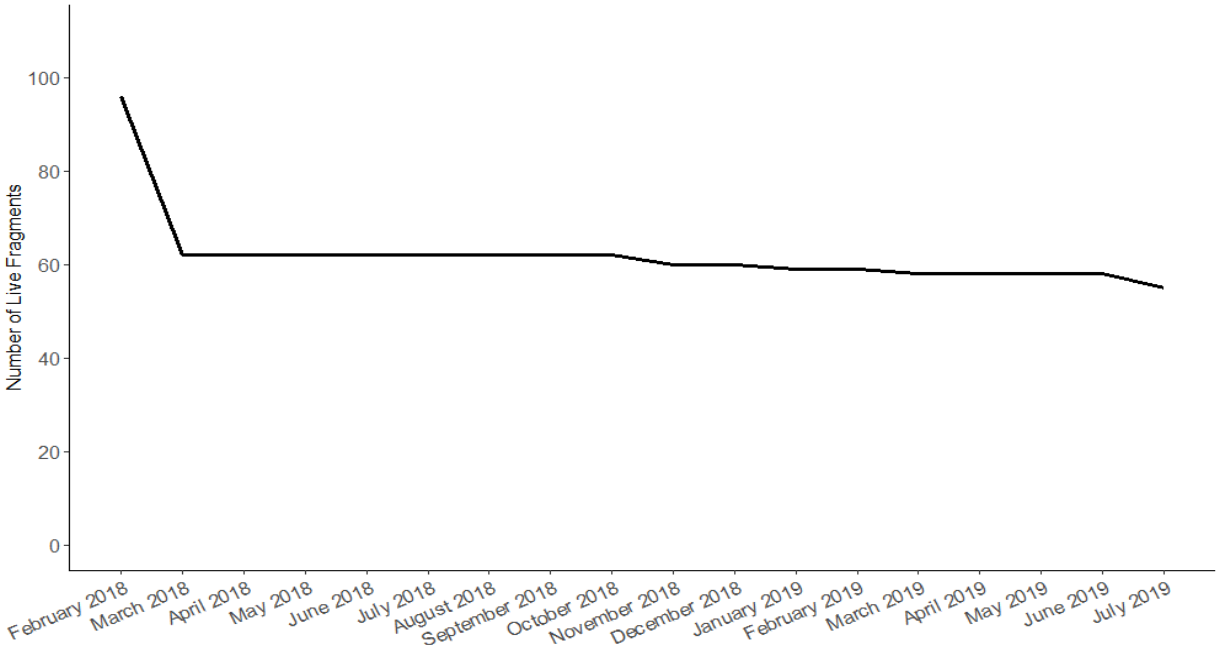

Figure 9. Overall pilot coral fragment survival over time.

Part I: Pilot Coral – Growth

Live TLE (mm) increased 10.8% by the end of the study period across all fragments, which includes TLE lost due to total mortality (Fig.10). Mean TLE gained by month 17 was greatest in *A. palmata* (29.2 mm +/- 6.6 SE) compared to *A. cervicornis* (10.7 mm +/- 5.3 SE). Middle fragments had the greatest mean new TLE (mm) (31.8 mm +/- 9.1 SE) compared to apical (17.5 mm +/- 6.9 SE) and basal fragments (22.8 mm +/- 9.9 SE). Genotype P2 (*A. palmata*) had the greatest mean new TLE (49.6 +/- 14.3 SE) compared to all other genotypes (Table 2). When comparing initial to final TLE for each fragment (Factorial ANOVA), there were no significant differences between factor groups (taxa, fragment type, and genotype) (Kruskal-Wallis test and Pairwise Wilcoxon test, p>0.05).

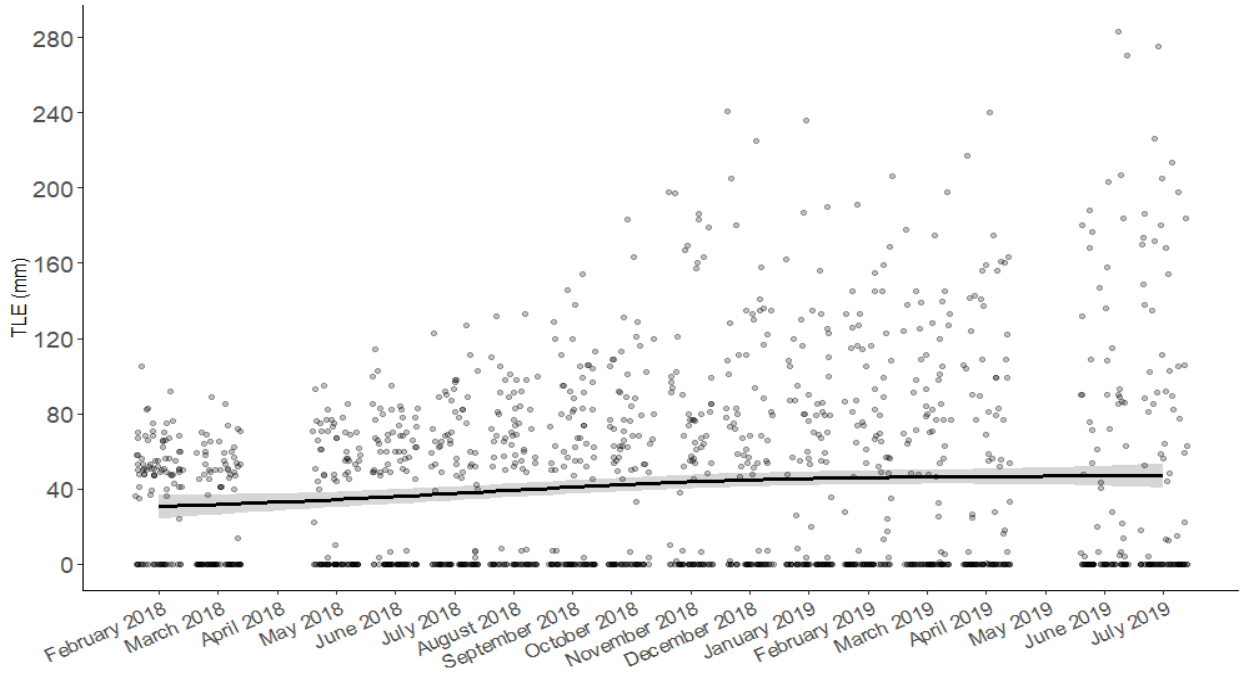

Figure 10. Overall pilot coral fragment growth (TLE) over time. Each point represents a unique fragment measurement. Line shows general growth trend, with grey area around line indicating standard error. Data was not collected in April 2018 and May 2019.

Table 2. Part I: Pilot coral descriptive statistics for TLE (mm) gained over 17 months by taxa, fragment type, and genotype, including partial mortality. Growth/decline values were calculated by ((Final TLE-Initial TLE)/Initial TLE)*100. Genotypes numbers are different than the genotypes in Part II. * numbers have sample size of ≤ 3 fragments remaining at time 17.

Taxa	Mean New TLE (mm)	Std. Error	% Growth/Decline
A. cervicornis	10.7	5.3	-12.0
A. palmata	29.2	6.6	39.9

Fragment Type	Mean New TLE (mm)	Std. Error	% Growth/Decline
Apical	17.5	6.9	-7.0
Middle	31.8	9.1	35.7
Basal	22.8	9.9	37.3

Genotype	Mean New TLE (mm)	Std. Error	% Growth/Decline
C4	1.4	9.7	-41.6
C5	15.4	6.3	1.8
P2	49.6	14.3	17.8
P3	45.7	18.8	182.6
P4*	4.4	4.4	-35.6
P5	27.7	13.7	153.0
P6*	0	11.1	-79.7
P7*	20.6	13.4	-29.1

Part II: Experimental Coral – Mortality

From an initial 157 fragments, 66 survived to the end of the study period (13 months). During the first month in the nursery (June 2018), overall total mortality was 32.5%. Monthly mortality dropped to <5% until July 2019 (32.7% mortality), the end of the study period (Appendix A, Table 10). Fragment mortality further broken down by each factor across the whole study period is given in Appendix C, Table 11. At the end of the study period, only one fragment (*A. palmata*, basal fragment) was alive at site N1. No disease was observed on any coral fragments over the course of study at all sites. Site significantly affected experimental coral fragment survival (Survival Analysis Cox model, z=-5.47, p=4.5e-08). Site N3 fragments had the greatest survival throughout the study period (Fig. 11; Appendix C, Table 11). Site was also the only significant factor when the analysis was run without the first month of mortality (Survival Analysis Cox model, z=-5.161, p=2.46e-07). This was done to account for mortality due to stress from travel or acclimation in the nursery sites in the first month. Species, fragment type, and genotype had no significant effect on experimental coral fragment survival (p>0.05) and were thus pooled in the resulting plot (Fig. 11).

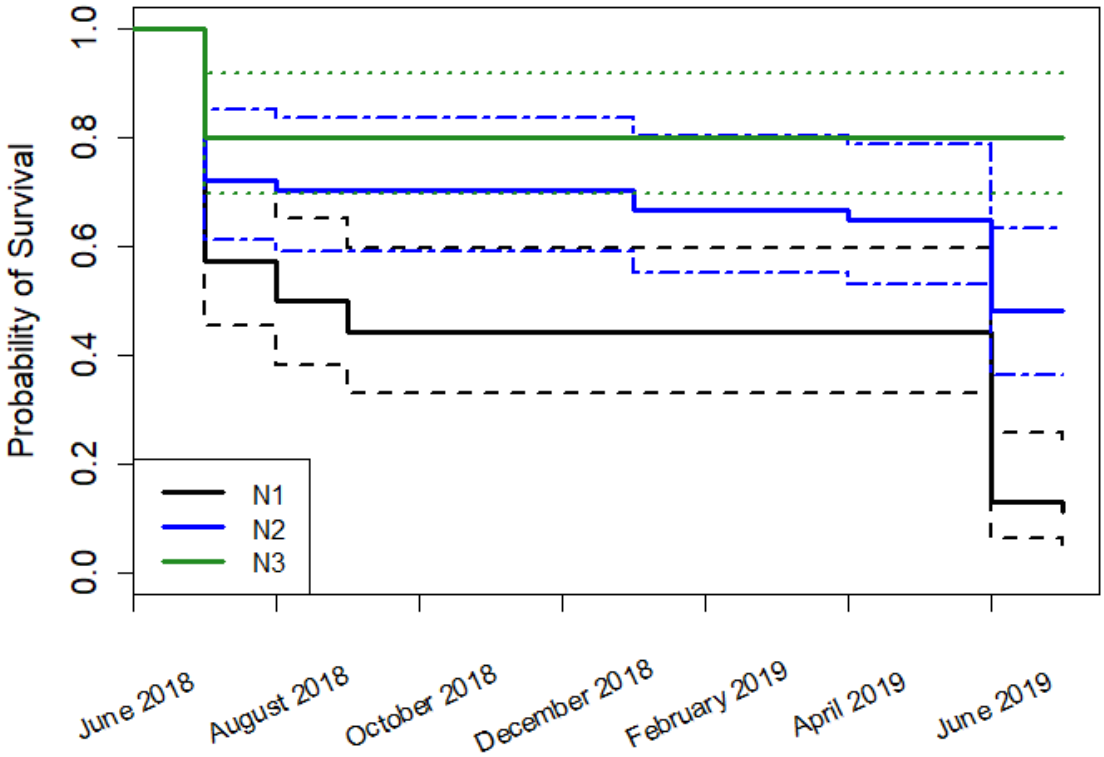

Figure 11. Survival analysis plot by site (p<0.05). Dotted lines denote confidence intervals for each site.

Part II: Experimental Coral - Growth

Overall, TLE (mm) increased by 10.2% by the end of the study period (13 months) across all fragments (Fig. 12). Mean TLE (mm) gained by month 13 was greatest in *A. prolifera* fragments (68.9 mm +/- 13.1 SE), compared to *A. palmata* (25.2 mm +/- 6.8 SE) and *A. cervicornis* (16.2 mm +/- 5.6 SE). Apical fragments had the greatest mean new TLE (47.4 mm +/- 11.7) SE compared to middle fragments (36.1 mm +/- 8.9 SE) and basal fragments (23 mm +/- 5.9 SE). Coral fragments at site N3 had the greatest increase in TLE (new TLE) (76.8 mm +/- 12.9 SE) compared to site N1 (2.9 mm +/- 2.9 SE) and site N2 (30.8 mm +/- 7.0 SE). Genotype H3 (*A. prolifera)* had the greatest mean new TLE (120.8 mm +/- 36.7 SE) (Table 3). Growth further broken down by each factor across the whole study period is described in Appendix C, Table 12. There were no significant differences in fragment sizes at initial collection (Kruskal-Wallis test, p>0.05).

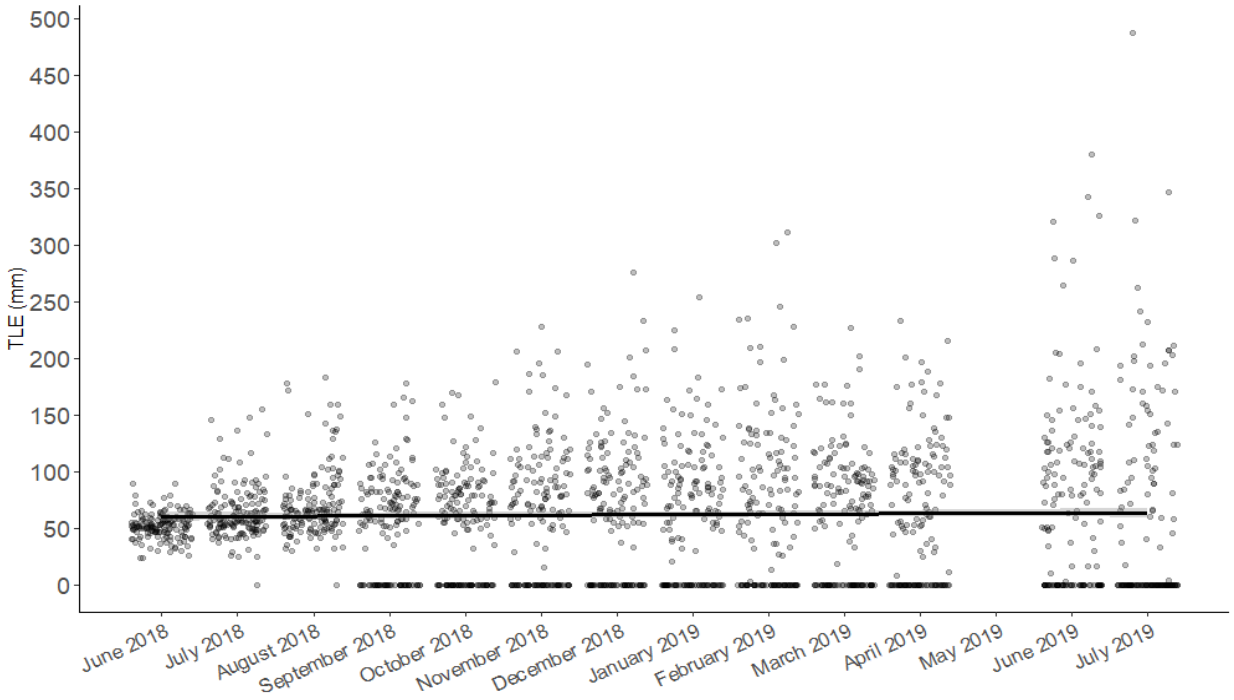

Figure 12. Overall Part II: experimental coral fragment growth (TLE) over time. Each point represents a unique fragment measurement. Line shows general growth trend, with grey area around line indicating standard error. Data was not collected in May 2019.

Table 3. Part II: Experimental coral descriptive statistics for TLE (mm) gained over 13 months by taxa, fragment type, site, and genotype, including partial mortality. Growth/decline values were calculated by ((Final TLE-Initial TLE)/Initial TLE)*100. Genotypes numbers are different than the genotypes in Part I. * numbers have sample size of < 3 fragments remaining at time 13.

Taxa	Mean New TLE (mm)	Std. Error	% Growth/Decline
A. cervicornis	16.2	5.6	-34.3
A. palmata	25.2	6.8	-13.7
A. prolifera	68.9	13.1	86.1

Fragment Type	Mean New TLE (mm)	Std. Error	% Growth/Decline
Apical	47.4	11.7	41.8
Middle	36.1	8.9	-18.7
Basal	23.0	5.9	8.0

Site	Mean New TLE (mm)	Std. Error	% Growth/Decline
N1*	2.9	2.9	-93.0
N2	30.8	7.0	10.4
N3	76.8	12.9	129.9

Genotype	Mean New TLE (mm)	Std. Error	% Growth/Decline
C1*	0.0	0	-100
C2	14.5	7.1	-34.8
C3	35.6	14.9	3.8
C6	3.7	5.1	-46.3
C7*	0	3.2	-76.6
P1	2.2	1.1	-69.4
P8	27.3	15.8	109.8
P10	79.9	23.8	-56.8
P11	6.6	45.4	-14.0
P12*	25.6	15.7	-1.8
H1	82.7	19.2	125.3
H2*	46.4	24.8	36.3
H3	120.8	36.7	215.8
H4*	0.0	0	-100

When comparing initial to final TLE for each fragment (Factorial ANOVA), there were significant differences between factor groups (chi-sq=139.3, df=106, p=0.016). *A. prolifera* had significantly higher mean growth than the parental species. All sites were significantly different from each other, where site N3 had the greatest mean growth (Paired Samples Wilcoxon test, $p>0.05$). There were no significant differences in mean TLE between fragment types (Paired Samples Wilcoxon test, $p>0.05$).

Taxa, site, and fragment type were identified as important parametric factors effecting growth (TLE) over time in the MAM (GAMM ANOVA, $p<0.05$). As a reminder, this model did not include fragments that had total mortality from the month they had died. As shown in the MAM curve predication plots, *A. prolifera* fragments had the greatest average TLE monthly across all fragment types and sites (Fig. 13a). Based on the pairwise comparison post-hoc on TLE, *A. prolifera* fragments were significantly different to *A. cervicornis* and *A. palmata* fragments ($p<0.05$), with *A. prolifera* fragments having greater mean TLE at the end of the study period (13 months). Sites N1 and N3 TLE values were significantly different to N2 ($p<0.05$), where site N2 had lower mean TLE at 13 months. Apical and basal fragments TLE values were significantly different from middle fragments ($p<0.05$), where middle fragments had lower mean TLE at 13 months (Fig. 14). Overall, *A. prolifera* fragments at sites N1 and N3 had the greatest TLE (mm) at the end of the study period (Fig. 14; Appendix D, Fig.'s 22-25).

Acropora prolifera showed greatest TLE increase from July 2018-November 2019 and April 2019-July 2019, while *A. cervicornis* and *A. palmata* had greatest average TLE increases from July 2018-January 2019 (Fig. 13a). All fragment types showed greatest TLE increases between July 2018-January 2019 and April-July 2019 (Fig. 13b). All sites had the greatest TLE increases from July 2018-January 2019 and April-July 2019, with a brief plateau in growth from January-April 2019 (Fig. 13c).

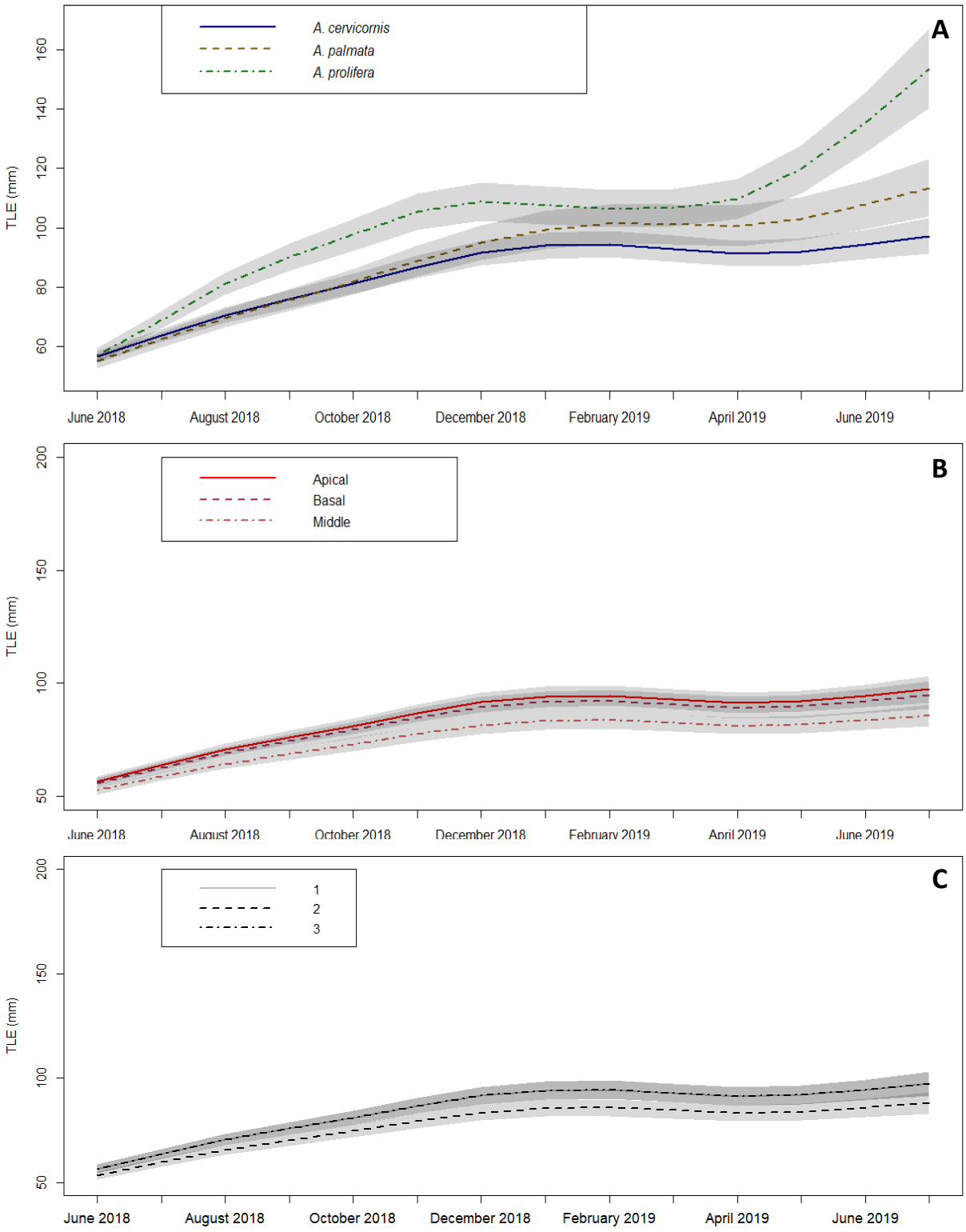

Figure 13. Growth (TLE) over time based on MAM model by A) taxa, B) fragment type, and C) site. TLE in mm is along the y-axis. Time is along the x-axis. Factor variables are given in each figure legend. Grey shaded areas denote standard error. Site N1 underlies N3 in Figure C.

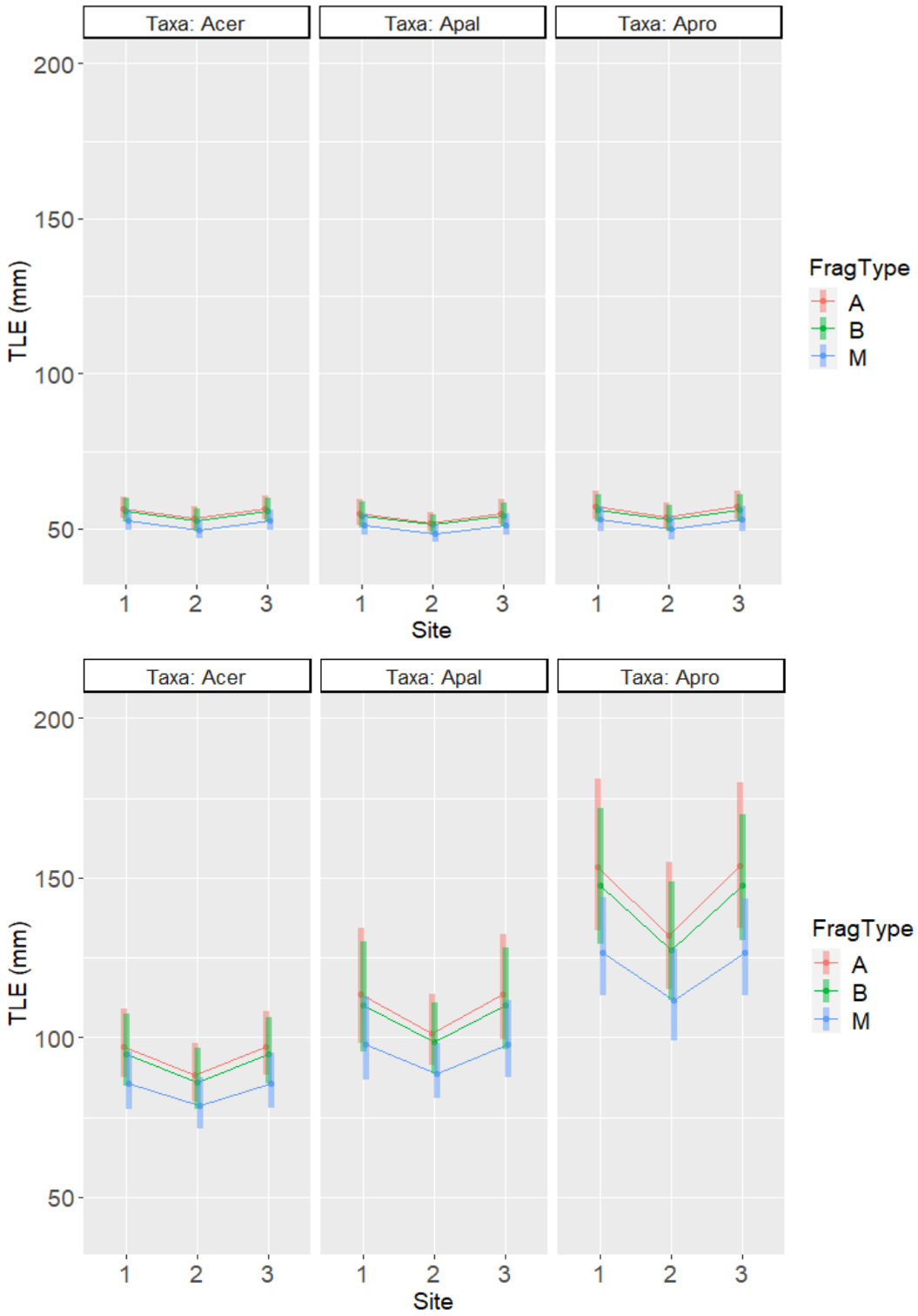

Figure 14. TLE (mm) by factor group at *top*: initial collection (time 0) (top); and *bottom*: final (time 13). Taxa is listed along the top bar of each plot. Site is listed along the x-axis. Fragment types are differentiated by color in the legend on the right. Mean TLE values at the given time point are represented by a point at each site and for each fragment type withing the taxa plots. Confidence intervals are shown with colored bars extending from each mean point.

As confirmed by genotypic analysis, there were 5 unique genotypes present for *A. cervicornis*, 5 unique genotypes for *A. palmata*, and 4 unique genotypes for *A. prolifera*. Genotype was not included in the MAM model based on low number of replicates by the end of the study period. Figure 15 shows TLE growth patterns by genotype. Overall, genotype does have a significant effect on final fragment TLE values (chi-sq=33.3,df=11,p=0.00048). Genotypes C1 and C7 were excluded from analysis due to low sample size by the end of the study period. Genotype does have a significant effect on final TLE within *A. cervicornis* genotypes (F(3,15)=4.1, p=0.026). Genotypes within *A. cervicornis* were not significantly different (Tukey HSD, p>0.05). Genotype does have a significant effect on final TLE within *A. palmata* genotypes (F(4,16)=4.2, p=0.016). Genotype P10 was significantly different from P1 and P11 (p=0.021 and p=0.049), where the sum of fragments in genotype P10 have higher final mean TLE values than P1 and P11. All other genotypes within *A. palmata* were not significantly different from each other (Tukey HSD, p>0.05). Genotype does not have a significant effect on final TLE values within *A. prolifera* genotypes alone (chi-sq=0.72, df=2, p=0.7). *A. prolifera* genotypes had the greatest TLE throughout study period, as confirmed by the results for *A. prolifera* fragments in the MAM. All fragments from genotypes C1 and H4 had died by July 2019. Genotype identification results from the genetic analysis are shown in Appendix A, Table 9.

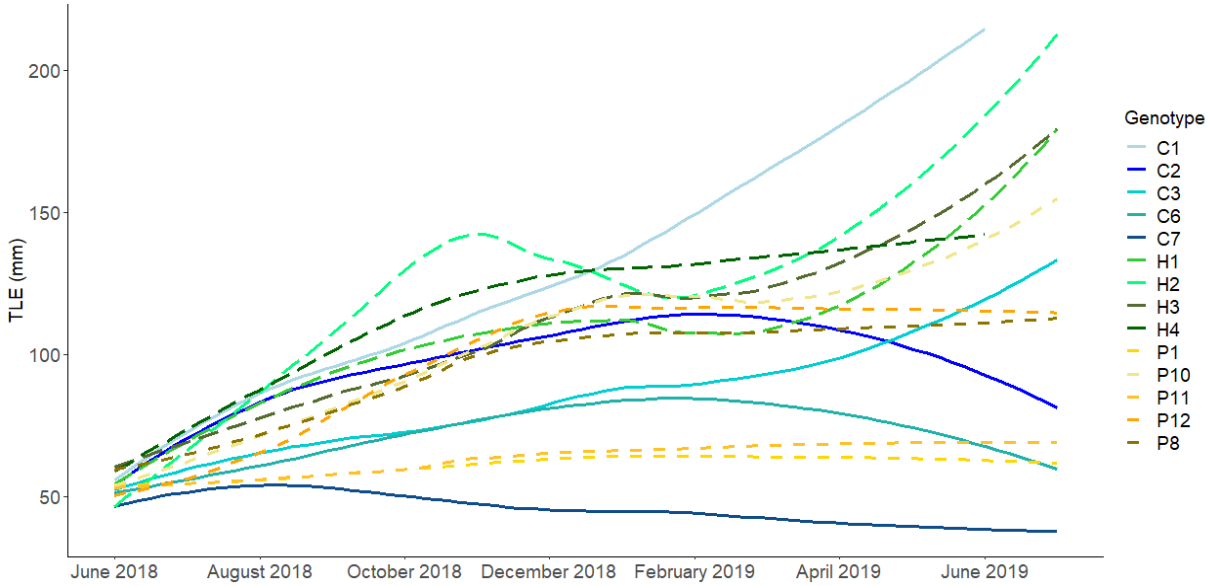

Figure 15. Growth (TLE) over time by genotype. TLE in mm is along the y-axis, while time is along the x-axis. C, P, and H denote *A. cervicornis*, *A. palmata*, and *A. prolifera*, respectively.

Condition Results

Condition prevalence does not significantly differ over time (chi-sq=6.59, df=12, 0.88). Condition type does have a significant effect on prevalence (chi-sq=40.76, df=2, p=1.408e(-9)) (Fig. 16). There was no disease observed on any coral fragments during the study period. Prevalence of bleaching was significantly different than algal overgrowth (OGA) interactions and paling, where bleaching prevalence was much lower overall. The combined effects of condition and site does have a significant effect on prevalence (chi-sq=48.82, df=8, p=6.894e(-8)) (Fig. 17). At site N1, bleaching and OGA were significantly different, where OGA prevalence was greater. At site N2, bleaching and OGA were significantly different, and bleaching and paling were significantly different. Bleaching prevalence was lower than OGA and paling at site N2. Between site N1 and N2, bleaching and OGA were significantly different, where OGA was greater. Between site N1 and N3, bleaching and OGA were significantly different, where OGA was greater. Between site N2 and N3, bleaching and OGA were significantly different, and bleaching and paling were significantly different. There were no significant differences between conditions within site N3 (Fig. 17).

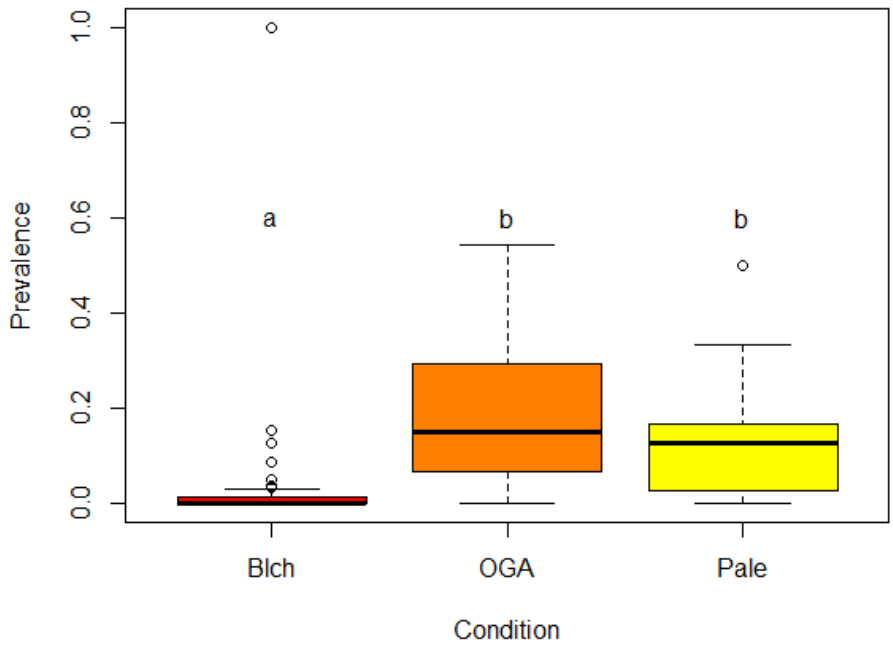

Figure 16. Overall prevalence by condition. Bleaching prevalence is significantly different (lower) than OGA and paling, as shown by the group designation letters above each box.

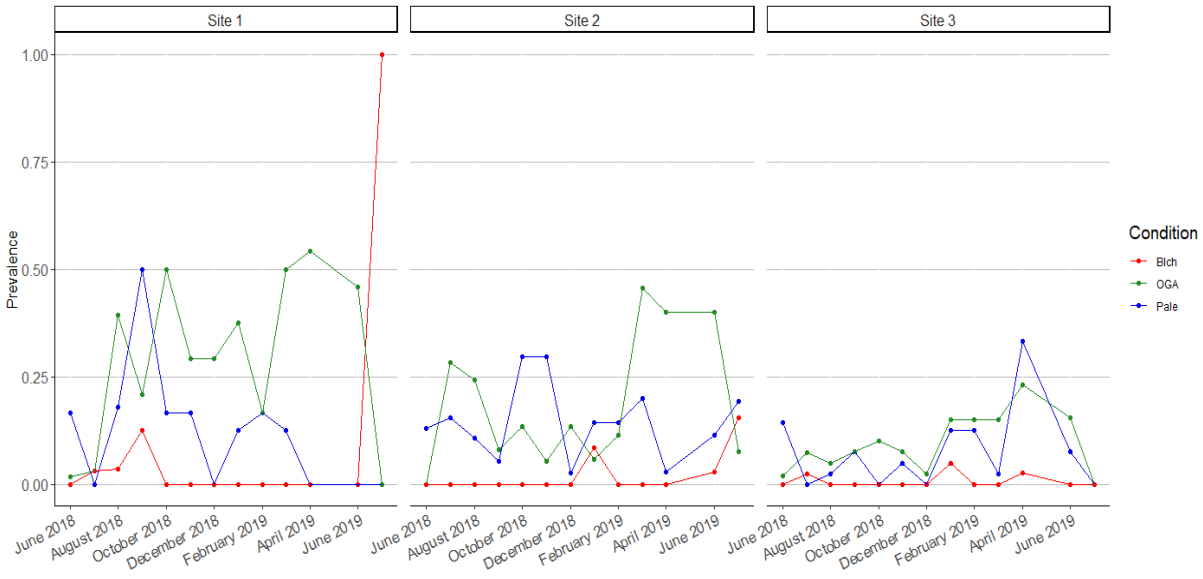

Figure 17. Prevalence of conditions by site over time. Prevalence is shown along the y-axis. Site is listed along to top x-axis, while month is listed along the bottom x-axis. Conditions are listed in legend to the right.

Temperature Results

There were over 100 days throughout the 13 month study period when the daily average temperature was ≥29.8ºC, a published bleaching threshold for The Bahamas based out of Lee Stocking Island (Manzello et al., 2007) (Fig. 18). For use in binning the temperature data, a 30ºC threshold was used; in both years (2018 and 2019), site N1 had the greatest number of days above 30ºC during the 13-month study period (101 days and 33 days, respectively (Appendix E, Fig.'s 26-28). There were 6 periods in the summer months where seven or more consecutive days were >29.8ºC, occurring in June - September of 2018 and June/July of 2019. Water temperature did not significantly differ between sites (Kruskal-Wallis test, $p>0.05$). When comparing just the summer months (June-September 2018, June-July 2019), there were no significant differences in temperature between sites in either year (One-way ANOVA/Kruskal-Wallis test, $p>0.05$).

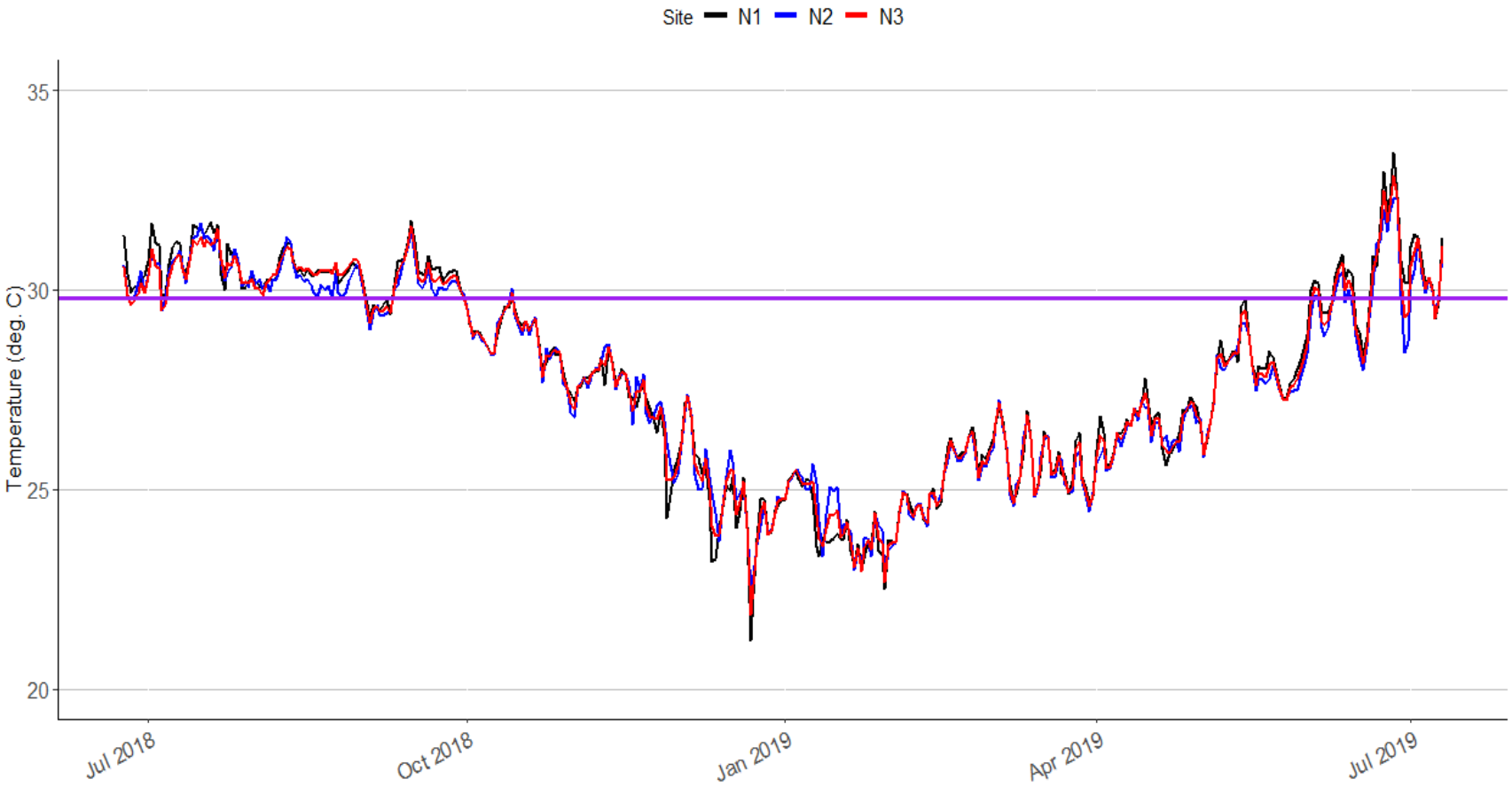

Figure 18. Mean daily temperature by site. Purple line denotes published approximate bleaching threshold at 29.8ºC (Manzello et al., 2007).

Discussion

This study has important implications for coral restoration methods, particularly concerning the hybrid taxa, *A. prolifera.* While there is some concern about using hybrid species in restoration, further research into how hybrid corals survive and grow compared to their parental counterparts would help determine if they are beneficial to the resilience of coral reefs. In this study, I offer three main findings that may be beneficial to restoration management: (1) the hybrid taxa, *A. prolifera*, performed better, in terms of growth, in a shallow water nursery setting, (2) site selection plays an important role in coral fragment survival, (3) and the proportion of different fragment types may be influencing overall growth in a coral nursery.

The hybrid exhibited greater growth over time than either parental species. *Acropora prolifera* has been shown to have similar, if not better, fitness to the parental species in a natural setting, and may be a faster growing taxon overall (Fogarty, 2012; Howe, 2018; Nylander-Asplin, 2018). This could be due to the growth form of *A. prolifera* which branches prolifically, adding linear tissue faster than its parental counterparts (Vollmer & Palumbi, 2002; Fogarty, 2012). This branching morphology may explain the differences in TLE (mm) over time, and also aligns with findings that an increase TLE is positively correlated with growth (Lirman et al., 2014).

While the hybrid's branching morphology is like the parental species, the fused branches of the hybrid taxon may serve a different ecological service. For example, the structure of *A. palmata* serves as a place for larger fish and invertebrates to live and hide; in contrast, the hybrid's fused branches are more compact and have a close structure, and as such may be more beneficial to the larval stages of fish and invertebrates. Also, there is the potential that with more investigation, the hybrid may adapt to changing climate conditions better than the parental species (Willis et al., 2006; Richards & Hobbs, 2015). As such, this taxon may contribute to expanding nursery scale or outplanting to degraded reefs sooner than the parental species as ocean conditions change. A restoration project may initially choose to outplant *A. prolifera* to secure rubble and increase overall reef structure, and then incorporate the parental species to increase genotypic diversity. There has been growing evidence that genotype plays a role in a coral's resistance to climate change (Baums, 2008; Drury et al., 2016; Drury et al., 2017; O'Donnell et al., 2017). In the future, it will be important to include genotype as a factor in scaled up investigations (Baums et al., 2019). Likewise, by including the hybrid taxa, there is potential for greater sharing of genetic material with the parental species, and possibly unique genotype crosses to be investigated.

However, there is concern that the hybrid may outcompete the parental species if included in restoration practices (Richards & Hobbs, 2015; Kovach et al., 2016). It is for this reason that there is little inclusion of the hybrid in restoration methods, particularly in outplanting. To address this concern, pilot outplanting studies could investigate the differences in growth and survival by comparing the parental species and the hybrid in a field setting. This could be done by outplanting nursery grown fragments from all taxa in the same area in separate clusters, with enough separation between taxa that there would be no concern of competition between coral taxa. A comparison between all three acroporids of outplanted corals could determine if growing in a nursery adds to hybrid fitness, i.e., if the hybrid will outcompete the parental species on a larger restoration scale. Prior research has investigated the growth of wild acroporid coral colonies, where growth rates were higher in some *A. prolifera* genotypes compared to *A. cervicornis* (Bowden-Kerby, 2008). In contrast, linear growth rates in *A. cervicornis* were higher than in *A. prolifera* in a study done by Weil et al. (2019). As in our results, Weil et al. (2019) also found increased growth for both *A. cervicornis* and *A. prolifera* during the winter and spring months. Therefore, growth of coral colonies may be highly variable depending on site location and environmental conditions. By incorporating the hybrid in different aspects of the restoration process, communication between projects regarding the hybrids' growth and survival as small fragments and outplants would increase the knowledge of how this taxon fits into the larger picture of coral restoration under changing climate conditions.

Site selection has proven to be an important factor in the success of other nurseries, with local temperature anomalies, water quality and movement, and nursery depth affecting survival (Shafir et al., 2006; Johnson et al., 2011). In this study, all trees were placed at approximately the same depth, so differences from depth alone is not likely contributing to site differences in survival and growth. Establishing nursery sites in areas with increased water flow and greater nutrient flux may allow for higher survival (Edwards, 2010). However, coral fragments at nursery sites that are more exposed to the elements may suffer greater stress from abrasion from sand movement and other overgrowth elements in the water column than at more protected locations (Bowden-Kerby, 2001; Young et al., 2012). In this study, the site with the greatest survival and growth, N3, was located on the northern side of the island, along the natural reef line and was potentially impacted by more severe weather conditions. This site may have been exposed to environmental conditions that were not present at the other two sites, as factors that

were not included in the scope of this study. The possible positive effects from a higher water flow (and probable nutrient and food availability) at site N3 may have led to increased overall survival and growth, where greater exposure to more severe weather was negligible during the study period.

Site N1 had the lowest overall fragment survival. This was likely due to a combination of reduced water flow and increased surface temperatures during the summer months, particularly in June - July 2019 where high mortality occurred. Many mature coral colonies are under great stress during the hot summer months, since temperatures may reach outside of their optimal range (Johnson et al., 2011). At site N1, the benefits from a more protected location may have conflicted with stagnant water, leading to the greatest mortality and loss of TLE. While turbid conditions may reduce the impact of irradiance on coral health (Wagner et al., 2010; van Woesik et al., 2012; Morgan et al., 2017), high sediment input and long-term turbidity can increase prevalence of disease and other stressors to corals (Pollock et al., 2014). It is also possible that hypoxia may have occurred at this site, especially during times of reduced water flow and higher water temperatures. Hypoxia has been shown to have a detrimental effect on coral health, where low oxygen environments reduced photosynthesis and bleaching was observed (Zhu et al., 2004; Haas et al., 2014).This could be a factor for future investigation at nursery sites, as it may have contributed to decreased survival and growth at site N1.

For this study, fragments that survived had similar growth at the more protected site as the exposed reef site (N1 vs. N3). This could be due to the nature of the GAMM model, as it did not include fragments after they had died (total mortality). As such, site selection for survival alone is important before considering growth. It is possible that if a fragment did survive, the protected site did contribute to overall growth. There is the possibility that these corals were receiving food and other nutrients from the nearby seagrass beds, as prior studies have shown connectivity between adjacent seagrass beds and coral reefs via fish species and particulate matter (Dorenbosch et al., 2005; Heck et al., 2008). From a management perspective, site selection criteria should consider not only depth, water temperature, and site availability, but also how hydrodynamics and nutrient flux may contribute to the success of a nursery site. Locations with the optimal depth and nutrient flux, increased water flow, adequate light attenuation, and a limited range of temperatures would likely lead to the most successful coral fragment survival and growth (Edwards, 2010; Johnson et al., 2011) . Oftentimes site selection may be limited by

logistical mobility and access, so conducting a pilot study may assist in determining optimal site selection.

Apical fragments displayed the greatest TLE (mm) increase compared to middle and basal fragments. Since these fragments were at the tips of the donor colony, they may be primary locations of growth on the original colony itself (Gladfelter et al., 1989; Rinkevich, 2000; Bowden-Kerby, 2001). This is supported by the idea that collecting from the tips of donor colonies may lead to a faster rate of growth, while also reducing impact to the donor colonies themselves (Rinkevich, 2000; Bowden-Kerby, 2001; Herlan & Lirman, 2008). Previous studies have demonstrated gradients along *A. cervicornis* branches, where carbon compound transport was allocated toward the tips of colonies (Taylor, 1977) and respiration was higher in the terminal tips of *A. palmata* colonies (Gladfelter et al., 1989). In both cases, this implies the tips of acroporid colonies are areas of increased growth, where metabolic rates may be greater compared to the rest of the colony (Taylor, 1977; Gladfelter et al., 1989). While this may explain the increased TLE in apical ends, increased stress from clipping at two locations may also explain the differences in growth between fragment types.

Middle and basal fragments had two areas of recent exposed tissue from the fragmentation process. More exposed skeleton may lead to increased disease of weakened coral fragments, if other stressors (like increased temperatures) are present (Muller & van Woesik, 2012). With open lesions, there is also the possibility for settlement of other organisms, like algae, that may affect the long-term growth of nursery fragments. In this study, initial algal settlement on the exposed coral skeleton occasionally occurred in the first month of nursery placement before the coral had an opportunity to heal. While no disease was observed on nursery fragments in this study, open or overgrown lesions may have contributed to partial mortality that lasted through months, leading to decreased growth in the middle and basal fragments compared to apical fragments. While some studies have found that pruning of colonies in a nursery leads to increased productivity after 1 year (Lirman et al., 2014), further investigation would need to be done to determine if this holds true at other nursery sites. Investigation into metabolic differences between fragment types would also help determine best collection and fragmentation process in expansion of a nursery and in later outplanting.

Future Directions and Recommendations

This study was established to control for certain factors in a floating coral tree nursery. While this setup was applicable to GSC, there are other methodologies for a coral nursery that may be more conducive to a different physical environment. A pilot study was beneficial in determining applicability of this project, and using locally sourced fragments in comparison to imported fragments from other areas may prove beneficial to a nursery success in the long term, as local fragments may be locally adapted to the environment. The inclusion of the hybrid taxa along with an increased number of genotypes would be beneficial in understanding how genetic differences may impact ongoing restoration efforts. Investigation into the hybrid's fitness and ecological role in comparison to the parental species would also be beneficial for helping managers determine if they hybrid will be included in future restoration practices. Determining accessible nursery site locations for a project and investigating water flow, light attenuation, and nutrient fluxes should be considered before establishing a permanent nursery site. Collection size of small (~5cm) fragments from a donor colony is common practice - future research could investigate metabolic differences in fragment tissue along a colony branch, and how nursery fragment sizes along that branch may influence survival and growth in a nursery. For this project, data collection continues at site N3, while site N1 was terminated and corals at site N2 were moved to site N3. Future project goals include nursery expansion, outplanting, and further investigation of factors that influence outplant success.

Conclusions

The hybrid coral utilized in this study showed fitness comparable, or better than, its parental species. Coral restoration managers may benefit from capitalizing on fast growing hybrids; therefore, *A. prolifera* should be considered as an option for restoration, with a few additional points. More research into genetic differences and competition between all three acroporid taxon in outplant methods would assist in determining if the hybrid will be successful in restoration efforts. Including the hybrid taxa and increasing the number of unique genotypes in a nursery may increase genetic diversity between all three taxa future coral outplants. As shown in this study, investigation of appropriate nursery sites before setup is crucial to the success of a project. Additional environmental factors beyond temperature and depth may have a large impact on nursery success, and if possible, should be investigated prior to establishing a permanent

nursery site. Apical tips of colonies may also prove to be a source for fast growing tissues, at least when establishing a nursery site in similar conditions to this study's design. To investigate further impacts of the hybrid outside of a nursery, pilot outplant studies may implement a design focused on comparing survival and growth of each acroporid taxa separately, before combining fragment types at an outplant site or scaling up outplanting abundance.

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Appendices

Appendix A.

Summary data tables.

Table 4. GSC nursery site GPS locations.

Nursery Sites	Latitude	Longitude
Site 1 – N1	25.8193' N	77.8995' W
Site 2 – N2	25.8203' N	77.9260' W
Site 3 – N3	25.8258' N	77.9230' W

Table 5. Part I:Pilot coral collection GPS locations and depth.

Location Name	Latitude	Longitude	Depth (m)
Mamma Rhoda Rock	25.4065' N	77.9208' W	2.1
Great Harbor Cay	25.7701' N	77.8351' W	4.6
Hoffman's Cay North	25.6306' N	77.7351' W	1.8

.

Table 6. Part II: Experimental coral collection GPS locations and depth.

Location Name	Latitude	Longitude	Depth (m)
Lyford Reef	25.0422'	77.5386'	1.2
Elkhorn Garden	25.0247'	77.5732'	2.4
West Balmoral	25.0905'	77.4241'	2.7
Compass Point	25.0711'	77.4864'	2.1
Lyford Reef 2	25.0424'	77.5352'	0.6
Lil' Elvis	25.0351'	77.5508'	2.4
Lyford Channel	25.0542'	77.5140'	0.9

Table 7. Pilot and experimental studies' initial number of coral fragments per nursery site.

Part I: Pilot Study

	A. cervicornis	*A. palmata*	*A. prolifera*	*Total # fragments*
Site - N2	27	69	n/a	96

Part II: Experimental Study

Site:	*A. cervicornis*	*A. palmata*	*A. prolifera*	*Total # fragments*
N1	21	18	18	57
N2	18	18	15	51
N3	18	15	16	49
Total	57	51	49	157

Table 8. Pilot and experimental studies' initial number of coral fragments per fragment type.

Part I: Pilot Study

	Apical	*Middle*	*Basal*	*Total # fragments*
Site - N2	32	32	32	96

Part II: Experimental Study

Site:	*Apical*	*Middle*	*Basal*	*Total # fragments*
N1	18	18	18	54
N2	18	18	18	54
N3	17	16	16	49
Total	53	52	52	157

Table 9. Pilot and experimental studies' initial number of coral fragments per genotype.

Part I: Pilot Corals

A. cervicornis		*A. palmata*	
Genotype	Initial # fragments	*Genotype*	Initial # fragments
C1	9	P2	24
C2	18	P3	9
Total	27	P4	9
		P5	9
		P6	9
		P7	9
		Total	69

Part II: Experimental Corals

A. cervicornis		*A. palmata*		*A. prolifera*	
Genotype	Initial # fragments	*Genotype*	Initial # fragments	*Genotype*	Initial # fragments
C1	3	P1	15	H1	27
C2	18	P8	9	H2	9
C3	18	P10	9	H3	6
C6	9	P11	9	H4	7
C7	9	P12	9		
Total	57	**Total**	51	**Total**	49

Table 10. Pilot and experimental study number of live fragments per month with overall percent mortality.

Part I: Pilot Study		
Month	Number of Live Fragments	Percent Mortality
Feb-18	96	0.0%
Mar-18	62	35.4%
May-18	62	0.0%
Jun-18	62	0.0%
Jul-18	62	0.0%
Aug-18	62	0.0%
Sep-18	62	0.0%
Oct-18	62	0.0%
Nov-18	60	3.2%
Dec-18	60	0.0%
Jan-19	59	1.7%
Feb-19	59	0.0%
Mar-19	58	1.7%
Apr-19	58	0.0%
Jun-19	58	0.0%
Jul-19	55	5.2%

Part II: Experimental Study		
Month	Number of Live Fragments	Percent Mortality
Jun-18	157	0.0%
Jul-18	106	32.5%
Aug-18	106	0.0%
Sep-18	101	4.7%
Oct-18	101	0.0%
Nov-18	101	0.0%
Dec-18	101	0.0%
Jan-19	99	2.0%
Feb-19	99	0.0%
Mar-19	99	0.0%
Apr-19	98	1.0%
Jun-19	98	0.0%
Jul-19	66	32.7%

Appendix B.

MAM based on GAMM methods:
gam(TLE~s(TimeNursery)+factor(Taxa)+s(TimeNursery,by=Taxa)+factor(Site)+factor(Frag

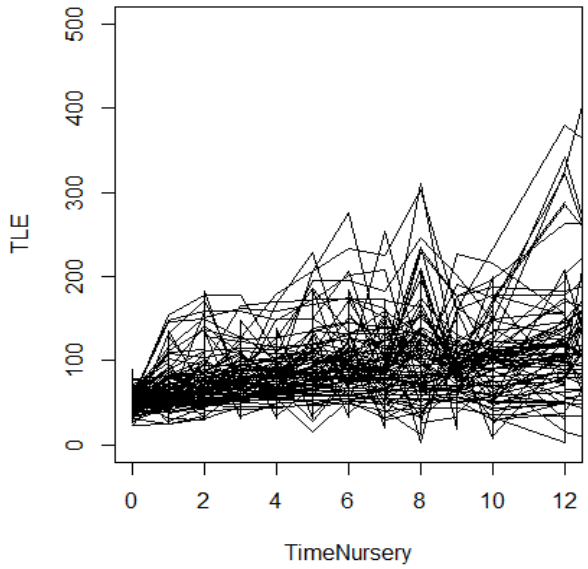

Figure 19. Raw data for unique fragment TLE over time in the nursery, with lines connecting data points over time for each individual fragment.

Type)+s(TagNum,bs="re"),method="ML", data=NoNA,family="Gamma")

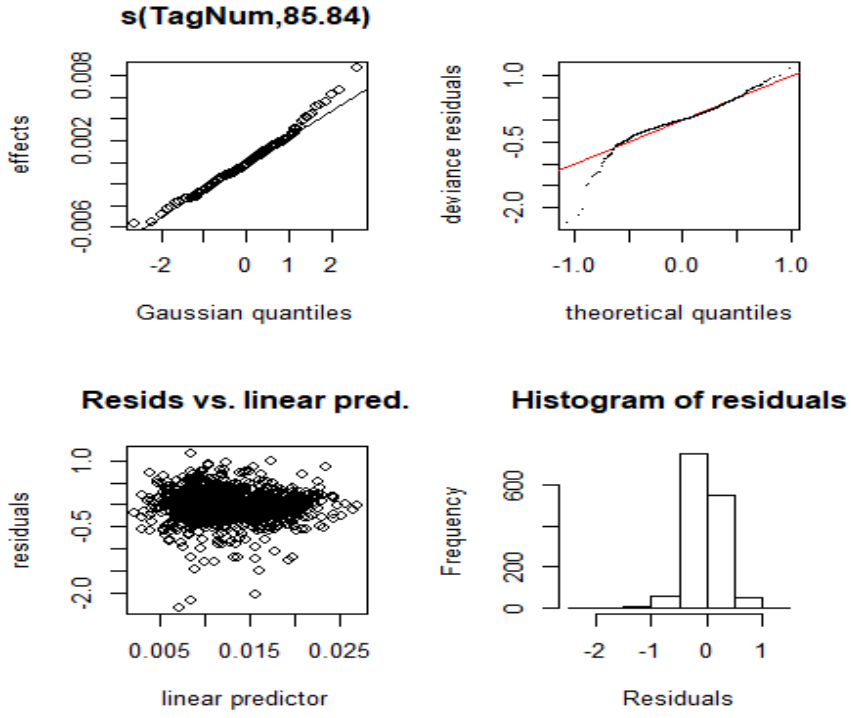

Figure 20. Gam check residuals of GAMM model.

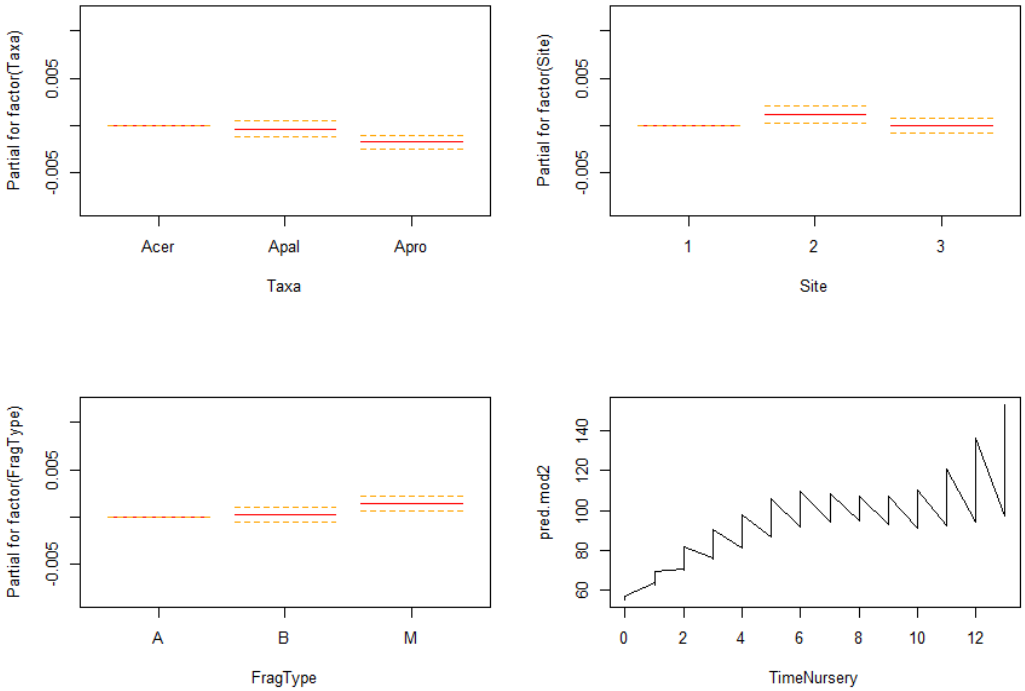

Figure 21. Term plot of GAM model including the effects of statistically important factors. Family used in model is calculated on the inverse. Line plot includes effects of categorical factors (unevenness).

Appendix C.

Survival and growth summary tables by factor.

Table 11. Part II: Experimental study initial and final (0 and 13 months) fragment numbers and percent mortality by each factor group.

:

Taxa	Site	Fragment Type	Initial # Fragments	Final # Fragments	% Mortality
A. cervicornis	N1	Apical	7	0	100%
		Middle	7	0	100%
		Basal	7	0	100%
	N2	Apical	6	3	50%
		Middle	6	2	66.7%
		Basal	6	1	83.3%
	N3	Apical	6	5	16.7%
		Middle	6	4	33.3%
		Basal	6	4	33.3%
A. palmata	N1	Apical	6	0	100%
		Middle	6	0	100%
		Basal	6	1	83.3%
	N2	Apical	6	4	33.3%
		Middle	6	2	66.7%
		Basal	6	2	66.7%
	N3	Apical	5	5	0%
		Middle	5	4	20%
		Basal	5	3	40%
A. prolifera	N1	Apical	5	0	100%
		Middle	5	0	100%
		Basal	5	0	100%
	N2	Apical	6	4	33.3%
		Middle	6	4	33.3%
		Basal	6	4	33.3%
	N3	Apical	6	6	0%
		Middle	5	4	20%
		Basal	5	4	20%
		Total	157	66	

Table 12. Part II: Experimental study initial and final (0 and 13 months) TLE and percent growth/decline values for each factor group.

Taxa	Site	Fragment Type	Initial Sum Live TLE (mm)	Final Sum Live TLE (mm)	% Growth/ Decline
A. cervicornis	N1	Apical	388	0	-100%
		Middle	380	0	-100%
		Basal	370	0	-100%
	N2	Apical	298	208.9	-30.9%
		Middle	275	192.64	-40%
		Basal	286	89.6	-68.7%
	N3	Apical	283	570.93	201.7%
		Middle	300	480	160%
		Basal	315	361.34	114.7%
A. palmata	N1	Apical	306	0	-100%
		Middle	366	0	-100%
		Basal	357.6	206.91	-42.1%
	N2	Apical	309	304.62	-1.4%
		Middle	356.8	173.1	-51.5%
		Basal	315.8	211.44	-33.1%
	N3	Apical	234	546.9	233.7%
		Middle	277.5	633.76	228.4%
		Basal	242	309.33	127.8%
A. prolifera	N1	Apical	262.5	0	-100%
		Middle	236.8	0	-100%
		Basal	277.7	0	-100%
	N2	Apical	314	748	238.2%
		Middle	253	621	245.5%
		Basal	340	485	142.7%
	N3	Apical	335	1492	445.4%
		Middle	274	835	304.7%
		Basal	273	594	217.6%
Total			8225.7	9064.47	

Appendix D.

Additional plots from post-hoc pairwise comparison test on MAM.

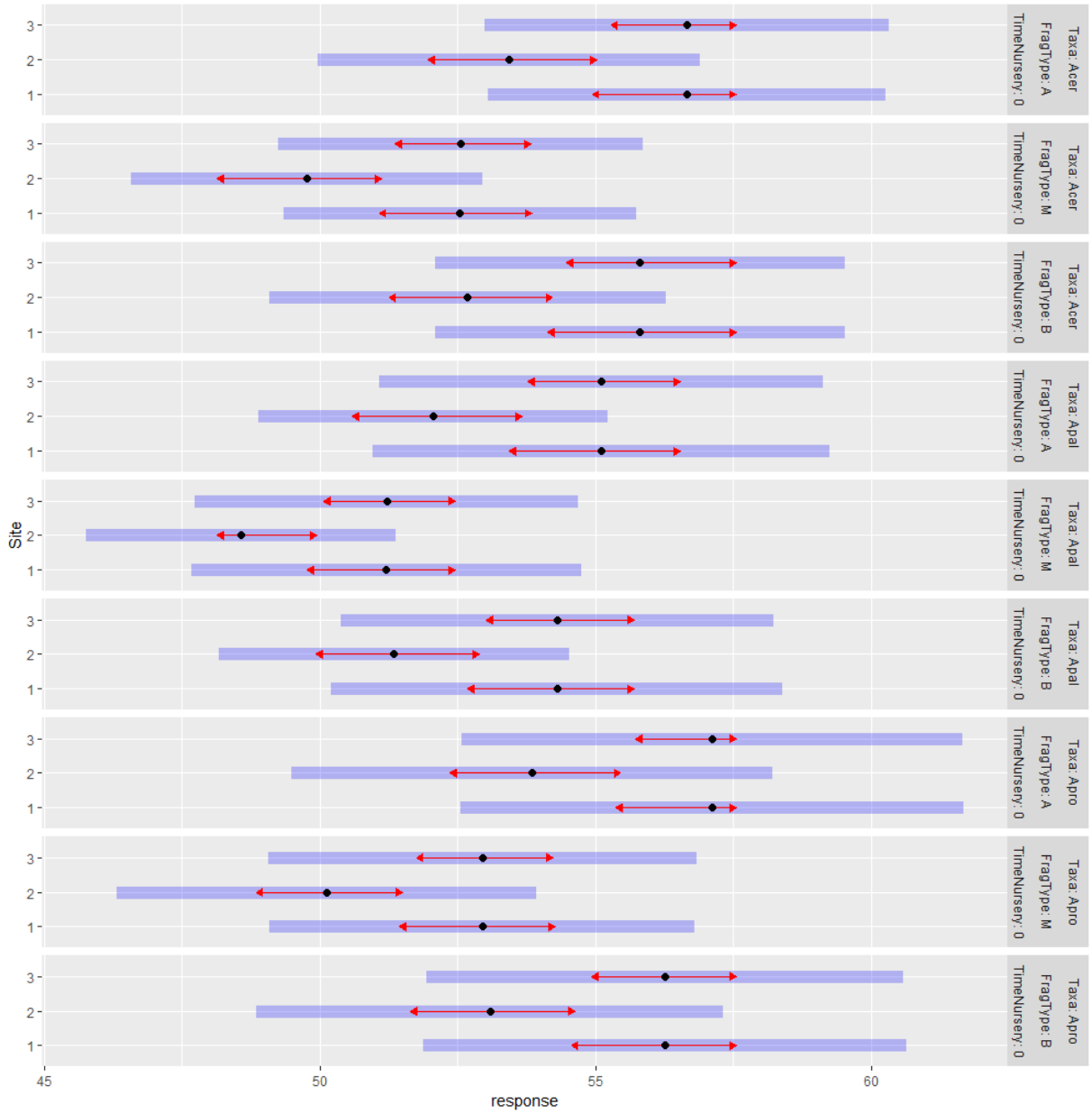

Figure 22. Post-hoc results in June 2018 (initial nursery placement). Response variable is live TLE (mm). Site is labeled along the left axis, with taxa and fragment type labeled along the right axis. The blue bars designate confidence intervals, and red arrows are comparisons between confidence intervals. Red arrows with no overlap show significant differences between factor levels.

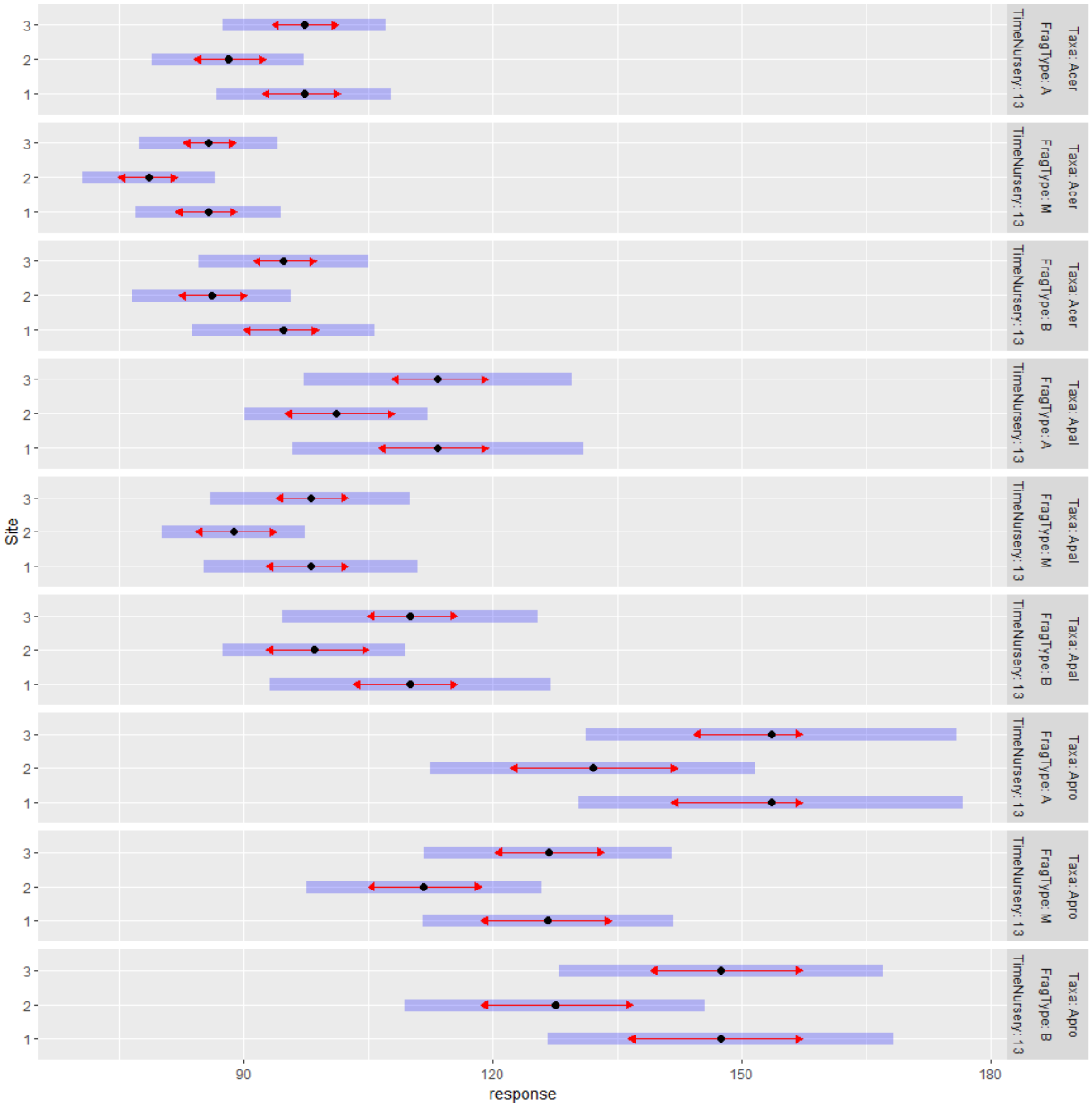

Figure 23. Post-hoc results in July 2019 (end of experiment). Response variable is live TLE (mm). Site is labeled along the left axis, with taxa and fragment type labeled along the right axis. The blue bars designate confidence intervals, and red arrows are comparisons between confidence intervals. Red arrows with no overlap show significant differences between factor levels.

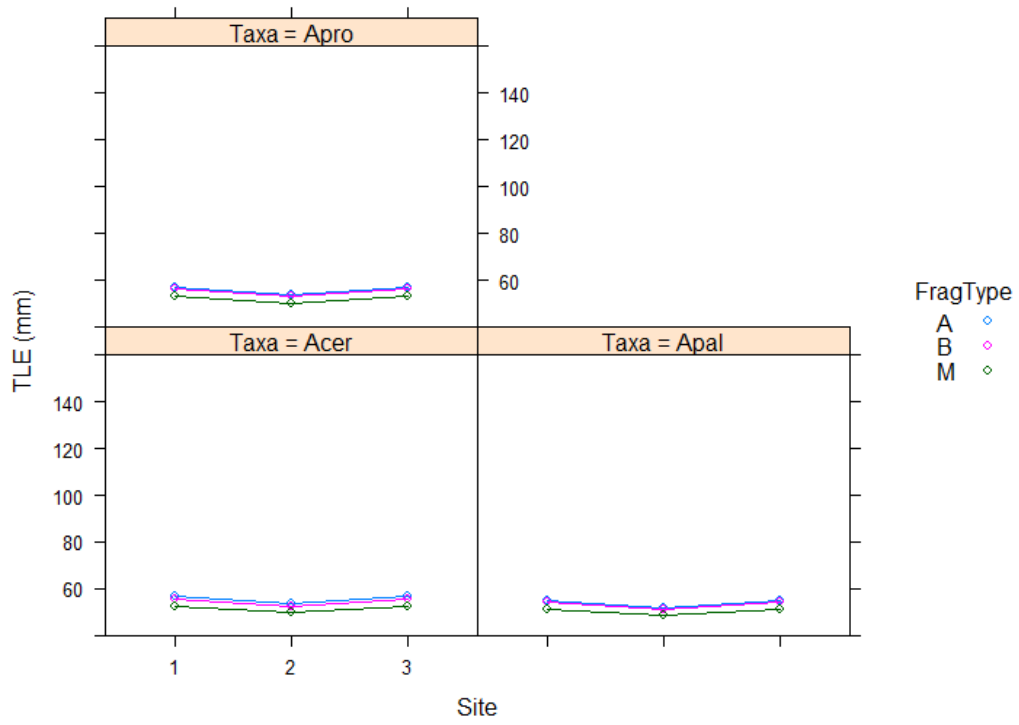

Figure 24. TLE (mm) of part II (experimental) fragments at time 0 (initial nursery placement) by taxa, site, and fragment type.

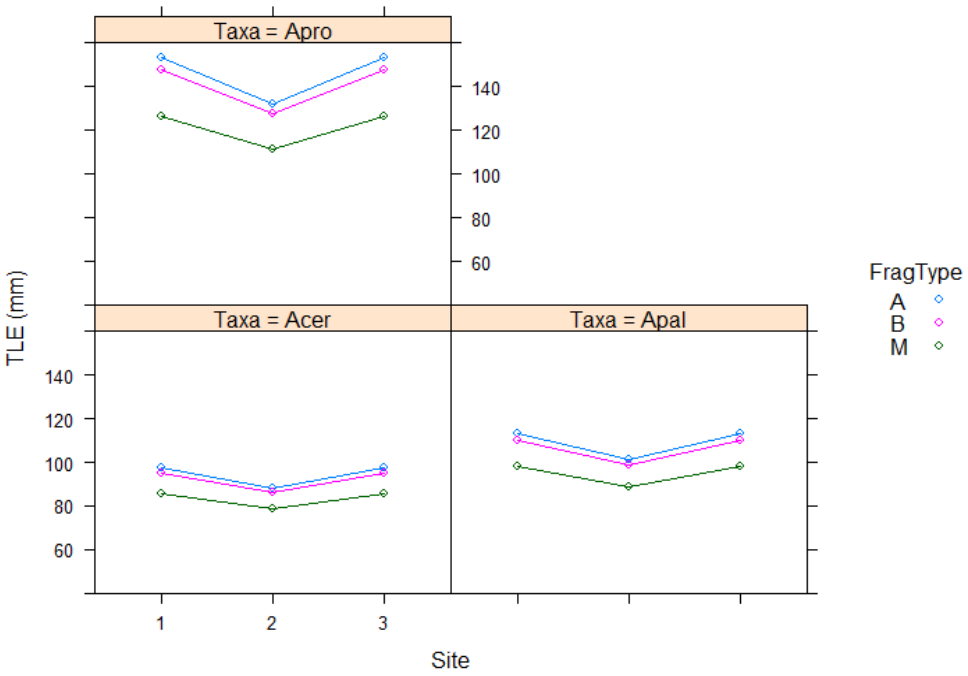

Figure 25. TLE (mm) of part II (experimental) fragments at time 13 (end of study) by taxa, site, and fragment type.

Appendix E.

Temperature binned data

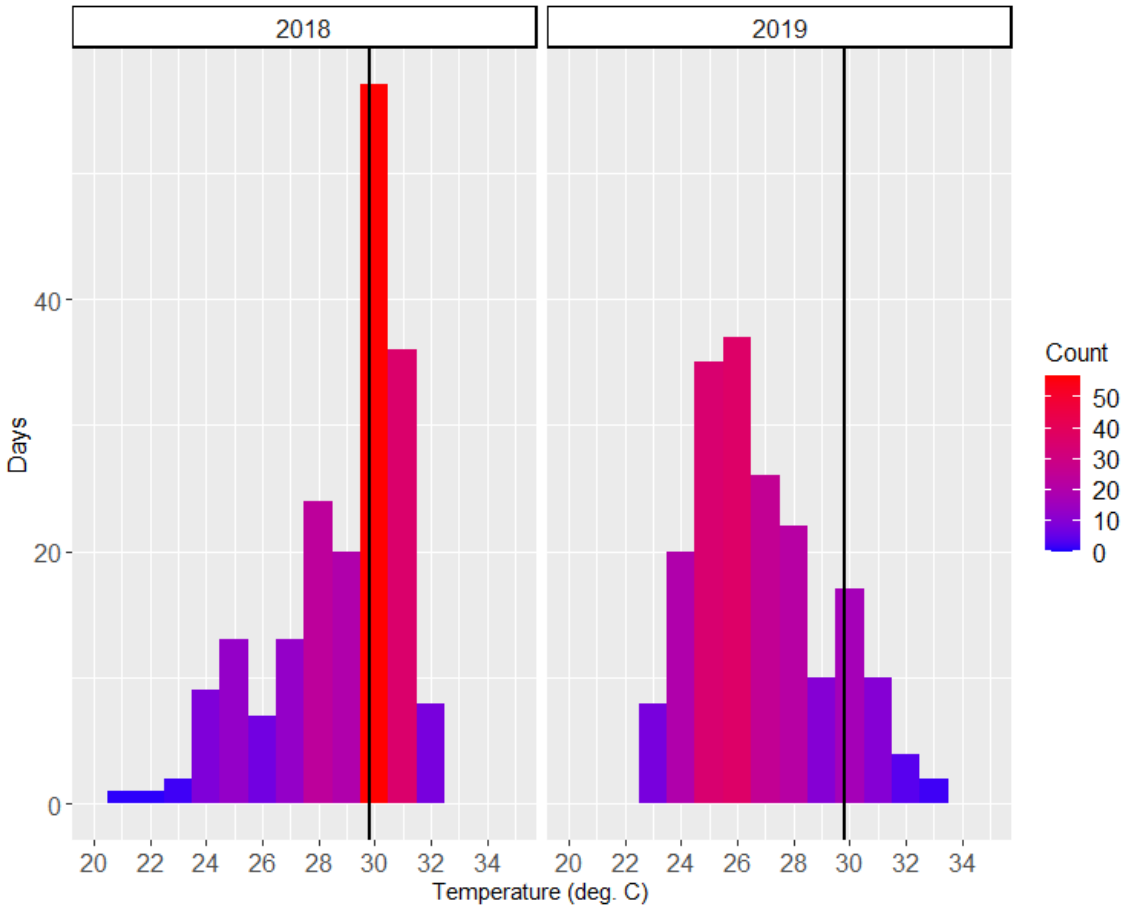

Figure 26. Frequency of days during 13-month study period at site N1 by temperature. Count of days is given by bar height. Red color indicates greater number of days at the temperature given along the x-axis; blue indicates fewer days at the given temperature. Black line indicates approximate bleaching threshold at 29.8ºC as described by Manzello et al. (2007).

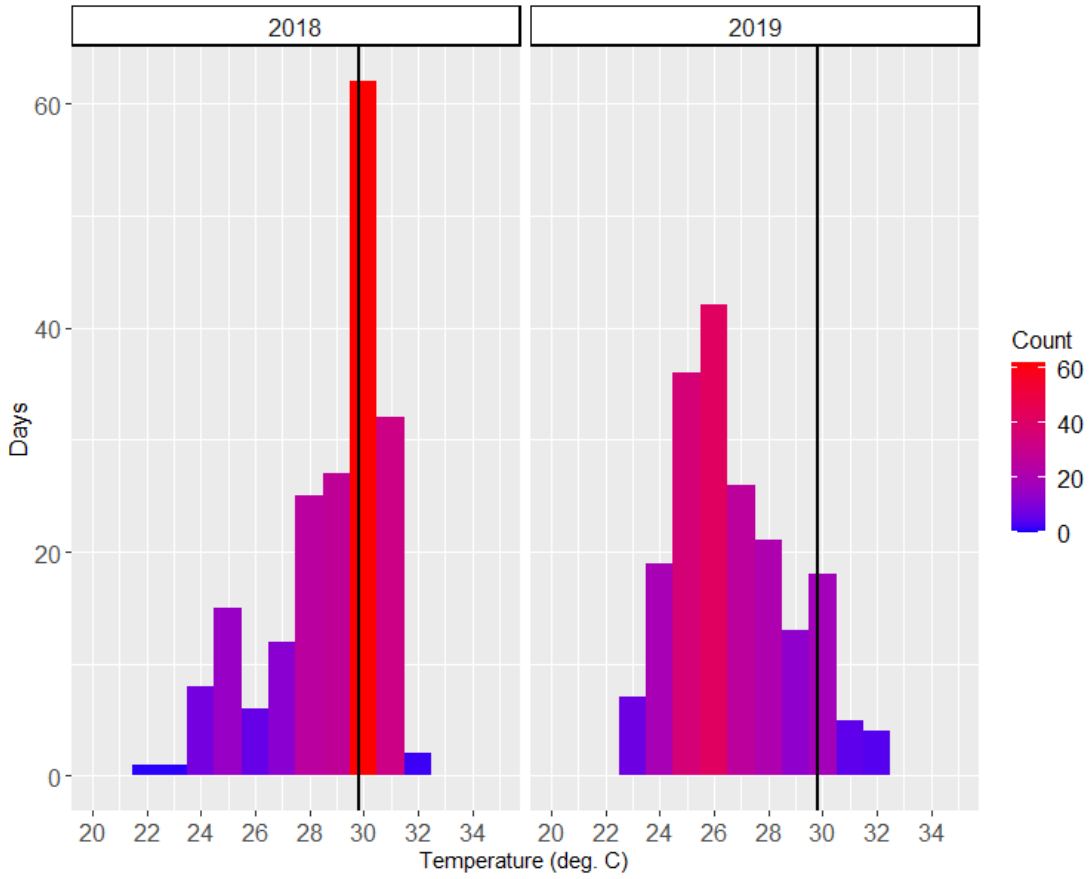

Figure 27. Frequency of days during 13-month study period at site N2 by temperature. Count of days is given by bar height. Red color indicates greater number of days at the temperature given along the x-axis; blue indicates fewer days at the given temperature. Black line indicates approximate bleaching threshold at 29.8ºC as described by Manzello et al. (2007).

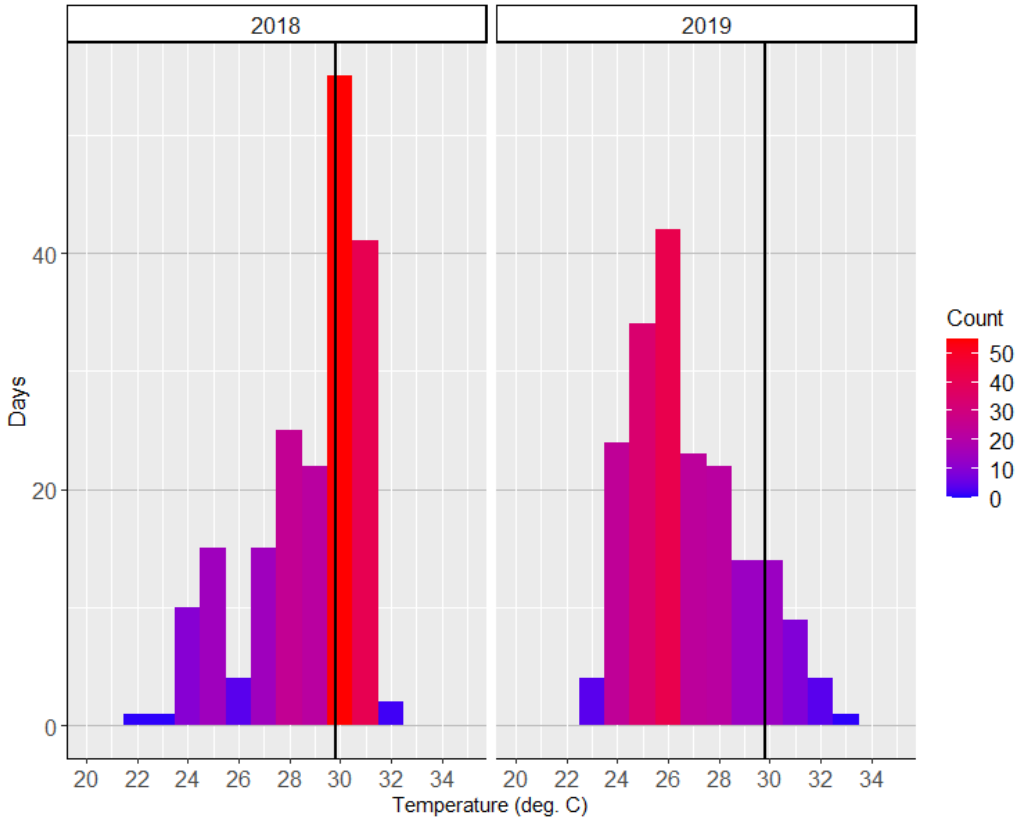

Figure 28. Frequency of days during 13-month study period at site N3 by temperature. Count of days is given by bar height. Red color indicates greater number of days at the temperature given along the x-axis; blue indicates fewer days at the given temperature. Black line indicates approximate bleaching threshold at 29.8ºC as described by Manzello et al. (2007).