



# Should Hybrids Be Used in Coral Nurseries? A Case Study Comparing Caribbean *Acropora* spp. and Their Hybrid in the Bahamas

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For decades, coral reef ecosystems have been in decline due to environmental stressors such as rising sea temperatures, increased disease prevalence, and other local anthropogenic sources. Considering this decline, coral restoration efforts in the Caribbean have been implemented to promote reef recovery with a focus on the coral genus *Acropora*. Current methods target the threatened species *Acropora cervicornis* and *A. palmata*, but little is known about the restoration potential of their hybrid taxon, *A. prolifera*. Using interspecific hybrids with higher fitness than one or both parental species has gained traction as a novel restoration technique. For this study, three *in situ* coral tree nurseries were established around Great Stirrup Cay, The Bahamas, to compare the growth and survival among acroporid taxa. Three 150 mm fragments from six putative genotypes of each acroporid taxa were collected from reefs around New Providence, The Bahamas, and transported to Great Stirrup Cay in June 2018. One fragment from each genotype was transported to each nursery site, cut into three sections (apical, middle, and basal), and suspended from PVC coral trees. Fragment survival was collected monthly for 13 months, and Total Linear Extension (TLE) values were calculated for each fragment monthly for 12 months. Nursery site significantly affected fragment survival, while taxon and fragment section did not. Total fragment mortality was 29.3% in the first month but ranged from 0 to 5% for the rest of the study period until July 2019 (32.7% of remaining fragments died primarily at N1). Overall, *A. prolifera* growth was significantly greater than the parental species. Taxon, nursery site, and fragment section were identified as important factors affecting TLE. Apical *A. prolifera* fragment sections at site N3 had the greatest average linear growth at 12 months and had the greatest average growth rate per month. This study highlights the rapid growth rate of hybrid corals and suggests that fragment sections have equivalent survival and growth. Consequently, these results suggest that restoration managers may capitalize on fast growing hybrids for outplanting to degraded reefs and to increase the scale of nursery projects.

**Keywords:** *Acropora*, hybrid, coral restoration, coral nursery, Caribbean

## INTRODUCTION

In the face of climate change and other environmental threats, conservation and restoration of the world's natural resources are now at the forefront of scientific research (Harris et al., 2006; Heller and Zavaleta, 2009; Jackson and Hobbs, 2009). Global issues such as deforestation, rising global temperatures, pollution, and the overuse of natural resources are serious threats to marine ecosystems and terrestrial environments (Vitousek, 1994; Derraik, 2002; Shahidul Islam and Tanaka, 2004; Harley et al., 2006; Malhi et al., 2008; Cinner et al., 2015; Hughes et al., 2017b). As such, finding ways of protecting these environments are critical to the continuity of the global biome.

Coral reefs are one of the world's most important and threatened marine ecosystems (Sebens, 1994; Maragos et al., 1996; Reaka-Kudla, 1997; Hughes et al., 2017a). They host a diversity of ecologically and commercially important marine species (Moberg and Folke, 1999), are essential nursery grounds for numerous fish and invertebrate species (Heck et al., 2008; Holbrook et al., 2015), protect coastlines from storm damage (Cesar et al., 2003; Ferrario et al., 2014; Storlazzi et al., 2019), and support an extensive tourism industry for many island nations and coastal regions (Cesar et al., 2003). Unfortunately, nearly 27% of the world's coral reefs have been lost due to destructive events and stressors (Cesar et al., 2003). Local anthropogenic threats (e.g., physical damage, overfishing, pollution, sedimentation), and larger global stressors (e.g., temperature increases, increased disease prevalence and storm damage, ocean acidification), are drivers of coral decline (Lirman and Fong, 1997; Hughes and Connell, 1999; Babcock and Smith, 2000; Woodley et al., 2000; Bellwood et al., 2004; Shahidul Islam and Tanaka, 2004; Fox and Caldwell, 2006; Voss and Richardson, 2006; Pandolfi et al., 2011; Smith et al., 2015; Cheal et al., 2017; Hughes et al., 2017b; Hughes et al., 2018). Increased sea temperatures can cause coral bleaching, a stress response during which colony pigmentation may be lost and often the microalgae symbionts found in coral tissue are expelled (Brown, 1997; Baker et al., 2008; Heron et al., 2016), which can lead to colony death if the stress is prolonged (Douglas, 2003; Eakin et al., 2010). Increasing ocean temperatures have also been linked to increases in disease outbreaks, resulting in large-scale coral mortality (Weil, 2004; Harvell et al., 2007; Muller et al., 2007; Eakin et al., 2010). Disturbance to a reef is natural but continued impacts of chronic stressors has changed coral reef community composition from one benthic group to another (Hughes et al., 1985; Hughes, 1994; Lirman, 2001; Bellwood et al., 2004; Knowlton and Jackson, 2008; Jackson et al., 2014; Jones et al., 2020).

In the Caribbean, the increase of such stressors and their compounding effects has led to significant losses in scleractinian coral cover since the late 1970s (Gardner et al., 2003; Eakin et al., 2010; Jackson et al., 2014). Much of this loss is attributed to the severe decline (up to 95%) of the Caribbean acroporid corals, *Acropora cervicornis* and *A. palmata* (Aronson and Precht, 2001; Bruckner, 2002). Prior to the 1970s, *A. cervicornis* and *A. palmata* were the major contributors to many reef habitats across the Caribbean (Aronson and Precht, 1997; McNeill et al., 1997; Bruckner, 2002; Gardner et al., 2003;

Miller and van Oppen, 2003; Bellwood et al., 2004), contributing up to 50% of total stony coral cover above ~20 m depth (Bellwood et al., 2004). These species provide many ecosystem services, including vital habitats for fish and invertebrates, reef structure through carbonate deposition, and coastal wave protection from storms (Bruckner, 2002). Acroporids primarily rely on asexual reproduction through fragmentation (Rinkevich, 1995; Lirman and Fong, 1997; Smith and Hughes, 1999), but also reproduce sexually through hermaphroditic broadcast spawning (Szmant, 1986; Vargas-Angel and Thomas, 2002; Fogarty et al., 2012). The two parental species are also capable of reproducing with each other to produce an F1 hybrid, *Acropora prolifera* (van Oppen et al., 2000; Vollmer and Palumbi, 2002; Kitchen et al., 2019). Like the parental species, *A. prolifera* can reproduce asexually through fragmentation, and the molecular signatures suggest they reproduce sexually with the parental species (Vollmer and Palumbi, 2002; Kitchen et al., 2019; Kitchen et al., 2021). In recent decades, *A. cervicornis* and *A. palmata* have declined in abundance primarily from disease, but also bleaching, storm damage, and predation (Aronson and Precht, 2001; Bruckner, 2002; Jackson et al., 2014). In response to their decline, *A. cervicornis* and *A. palmata* were listed as threatened under the United States Endangered Species Act as of 2006 (National Marine Fisheries 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., 2008a,b). In recent years, hybrid abundance has increased at some sites in the Caribbean, despite losses in the parental species (Fogarty, 2010, 2012; Japaud et al., 2014; Nylander-Asplin et al., 2021).

To facilitate recovery of *A. cervicornis* and *A. palmata*, many organizations through the Caribbean are working to increase *Acropora* abundance and genetic diversity (Johnson et al., 2011; Young et al., 2012; Baums et al., 2019; Boström-Einarsson et al., 2020). In many cases, these efforts are achieved by the creation and maintenance of coral nurseries, which provides a sheltered area for corals to grow away from the reef and predators. This 'gardening technique' proposed by Rinkevich (1995) has been adopted as a general practice for many reef restoration organizations. Based on silviculture practices, coral fragments are collected from different genotypes of the target species, grown in *in situ* nurseries, and outplanted to local reefs (Rinkevich, 1995; Lirman et al., 2010; Lirman, 2000; Zimmer, 2006). This method of coral gardening has been widely adapted across the globe for large-scale restoration efforts.

Caribbean *Acropora* restoration research has led to improvements in propagation techniques, as well as the recovery of localized populations of the parental species (Ware et al., 2020), but there is limited information and use of the hybrid in restoration. While the parental species have been in decline, the hybrid has persisted on many reefs in the Caribbean with equal or increased abundance, better survival, and equal or less susceptibility to disease and other environmental pressures (Fogarty, 2012; Irwin et al., 2017; Howe, 2018; Nylander-Asplin et al., 2021; Weil et al., 2020). Furthermore, research on the early life stages of *Acropora* species in the Pacific suggests hybrid larvae had equal or greater fitness compared to the parental species (Chan et al., 2018, 2019b). Although hybrids are often

thought to be sterile (Ortiz-Barrientos et al., 2007), *A. prolifera* can successfully reproduce with both *A. cervicornis* (Kitchen et al., 2019) and *A. palmata* via backcrossing (van Oppen et al., 2000; Vollmer and Palumbi, 2002; Kitchen et al., 2019). Backcrossing is noted among many marine organisms (Arnold and Fogarty, 2009) and provides an avenue for the genetic material from one parent to be exchanged between congeners, that may have led to reticulate evolution (Veron, 1995; Willis et al., 2006). Backcrossing may enhance the adaptive potential of the threatened parental species in a changing environment by providing increased genetic diversity (Willis et al., 2006), or at the very least, acroporid hybrids may provide needed infrastructure to shallow reefs while the parental species continue to decline.

To identify the potential of using hybrids in restoration, this study investigates factors (nursery site, taxa, fragment section, and genotype) that may influence growth and survival of the threatened Caribbean acroporid coral species and their naturally occurring hybrid at three *in situ* nurseries in The Bahamas.

## MATERIALS AND METHODS

### Study Location

This study was conducted at Great Stirrup Cay (GSC) (25.824 N, -77.91 W), The Bahamas, from June 2018 to July 2019. Great Stirrup Cay is located at the northern end of the Berry Islands in the central Bahamas (Figure 1). Great Stirrup Cay 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 flats are common to the south. The deeper fringing reefs (~15 m) on the northern side of the island are composed of large mounding corals including *Orbicella* spp. and *Montastraea cavernosa*, gorgonians, and sponges. On the eastern side of the island, reefs flats contain scattered acroporid colonies and smaller mounding corals, along with various species of gorgonians.

### Study Species

*Acropora cervicornis* is typically found on shallow reefs down to 20 m depths; *A. palmata* is usually found on shallow reef crests to 10 m depths in areas with high wave energy (McNeill et al., 1997; Johnson et al., 2011). *Acropora palmata* can grow up to ~10 cm per year (McNeill et al., 1997; Bak et al., 2009), while *A. cervicornis* has been recorded growing much faster, depending on location and genotype (Gladfelter et al., 1978; Lirman et al., 2014; Schopmeyer et al., 2017). *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 and Avise, 1983). *Acropora prolifera* is described as having a “bushy” or “palmate” morphology that is intermediate between the parental species and originally attributed, at least in part, to the maternal species (Vollmer and Palumbi, 2002). Recent molecular evidence from hybrid samples across a broader geographic range suggests egg donor is not predictive of hybrid morphology (Kitchen et al., 2021). Hybrids are often found at shallow depths (<2 m) with moderate to high wave energy, but occasionally can be found in

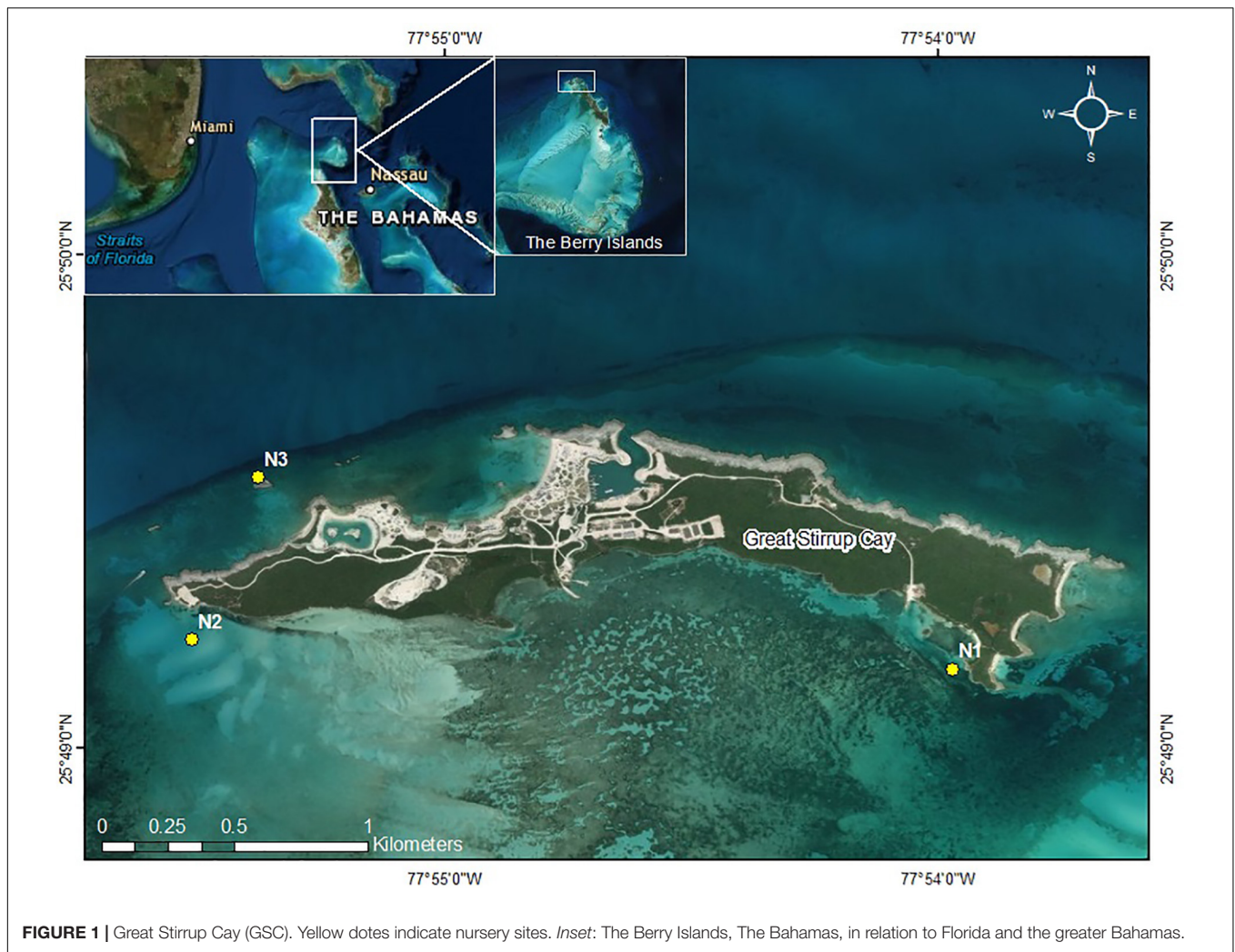
deeper, calmer environments (Fogarty, 2012). All three taxa can naturally reproduce asexually via fragmentation, making them ideal candidates for coral restoration (Rinkevich, 1995; Herlan and Lirman, 2008; Griffin et al., 2012; Schopmeyer et al., 2017).

### Nursery Sites

Three replicate nursery sites were established at GSC. Nursery locations included two southern sand flat sites (N1 and N2) and one northern reef slope site (N3) with depths ranging from 2.5 to 3.5 m (Figure 1). Site N1 was located near adjacent seagrass beds, while site N2 was established in sand near a boat channel on the western side of the island. Site N3 was the most exposed nursery site in terms of wave action and seasonal wind patterns. Sites were chosen based on depth, accessibility, storm protection, and isolation from human impact. Nursery sites were not placed on the east end of the island near wild *A. cervicornis* and *A. palmata* colonies due to limited accessibility from high wave energy and shallow depths. Turbidity was dependent of time of year, with site N1 observationally having greater turbidity than sites N2 and N3 but better protection from wave action due to seasonal weather patterns and storms. Three coral nursery trees® (Nedimyer et al., 2011) were placed 5 m apart in a line 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 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. Every tree contained five branches with corals attached to the middle three branches. Each branch was spaced 15 cm apart and installed perpendicular to the one above to avoid abrasion and shading effects between coral fragments. Six corals were attached per branch approximately 10 cm apart using 80 lb. test (0.89 mm) monofilament.

### Coral Collection

*Acropora cervicornis*, *A. palmata*, and *A. prolifera* fragments were collected from the reefs around New Providence, The Bahamas, in June 2018 using a hammer and chisel or diagonal cutters. Fragments were collected from colonies between 1 and 3 m depth and ≥10 m apart to increase the confidence of genotypic variation. Collection targeted six putative genotypes for each taxon; a small tissue sample was collected to confirm clonal identity. Three 150 mm branches (fragments) were collected from each donor colony ( $n = 19$  *A. cervicornis*,  $n = 18$  *A. palmata*,  $n = 18$  *A. prolifera*). An extra branch from a separate colony was collected for *A. cervicornis* due to greater availability and the potential loss of other fragments due to stress of transport. *Acropora palmata* and *A. prolifera* were not as widely available, and so only the minimum number of branches were collected. The three branches from each colony were placed in heavy duty plastic zipper bags filled with seawater and transported inside of Bubble Wrap® lined coolers. Ice packs were placed in the coolers for temperature regulation and were flown to GSC. Upon arrival the water was changed and the fragments were transported to nursery site N2. The following day, one 150 mm fragment



**FIGURE 1** | Great Stirrup Cay (GSC). Yellow dots indicate nursery sites. *Inset*: The Berry Islands, The Bahamas, in relation to Florida and the greater Bahamas.

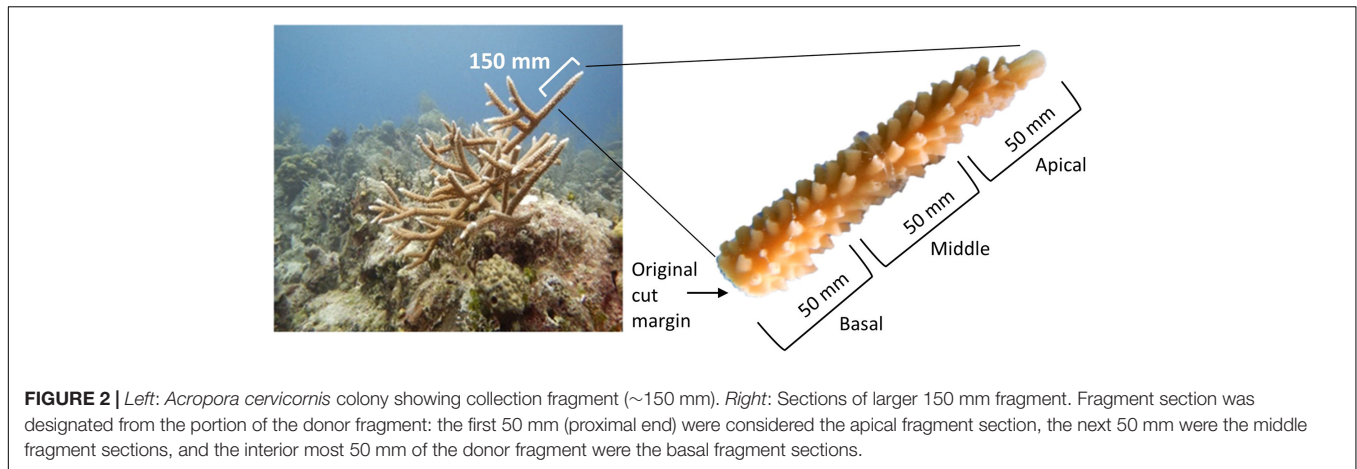
from each genotype was transported to each nursery site and cut into three smaller 50 mm sections ( $n = 57$  *A. cervicornis*,  $n = 51$  *A. palmata*, and  $n = 49$  *A. prolifera*). The sections were labeled as apical, middle, and basal, as per origin on the donor branch (**Figure 2**) and were distributed across the three trees at each site (**Figure 3**). Five *A. prolifera* and three *A. palmata* fragments were not included in the nursery due to poor visual condition after transport, and three extra *A. cervicornis* sections were included from initial collection. Note, this created a slightly uneven sampling design. All taxa, putative genotypes, and fragment sections were replicated at each site in a crossed design (see **Supplementary Figure 2**). However, later genetic analysis revealed some of the putative genotypes were clone mates and therefore contained more fragments. Tree location, coral section size (length, width, and size/number of branches), and condition data were recorded immediately. Each section was marked by a metal tag attached to the branch of the trees above each coral. An Onset HOBO pendant temperature/light logger was attached to one tree at each site and recorded temperature data every 2 h to capture daily fluctuations and maximize the length of deployment based on available memory.

## Data Collection

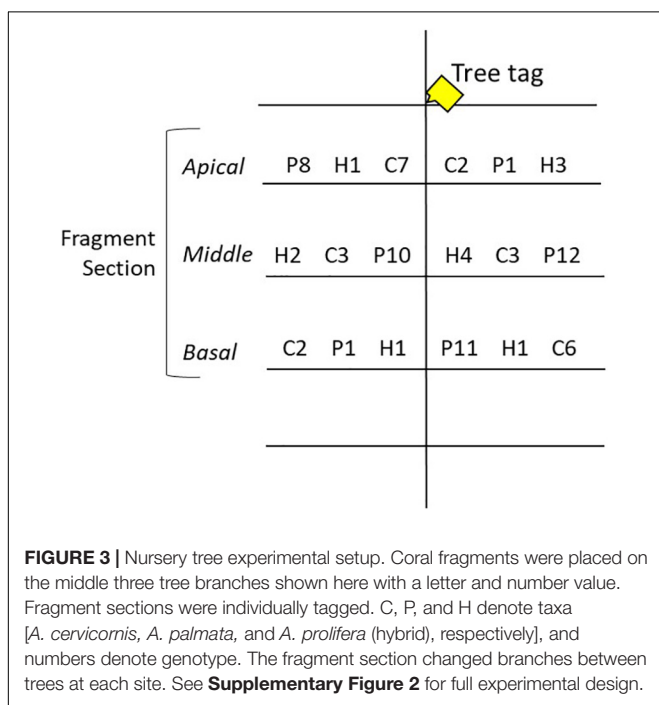
Nursery sites were visited monthly between June 2018 and July 2019, during which the trees were cleaned and data were collected. Data included total length, total width, number of branches > 10 mm, branch length(s), % mortality, and condition data (presence/absence of disease, predation, bleaching). Size measurements were taken with calipers to the mm. Images were also taken of each fragment with a scale bar. Linear extension was measured in ImageJ if branch measurements could not be completed in the field (ImageJ Version 1.52n, 2018).

## Genetic Analysis

Genetic samples were collected from all donor colonies. A small ~10 mm 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 (Fogarty et al., 2012 modified from Baums et al., 2005). After fragment analysis (conducted at Florida State University), peaks for each fragment loci were analyzed using



**FIGURE 2** | Left: *Acropora cervicornis* colony showing collection fragment (~150 mm). Right: Sections of larger 150 mm fragment. Fragment section was designated from the portion of the donor fragment: the first 50 mm (proximal end) were considered the apical fragment section, the next 50 mm were the middle fragment sections, and the interior most 50 mm of the donor fragment were the basal fragment sections.



**FIGURE 3** | Nursery tree experimental setup. Coral fragments were placed on the middle three tree branches shown here with a letter and number value. Fragment sections were individually tagged. C, P, and H denote taxa [*A. cervicornis*, *A. palmata*, and *A. prolifera* (hybrid), respectively], and numbers denote genotype. The fragment section changed branches between trees at each site. See **Supplementary Figure 2** for full experimental design.

analysis including all months, a survival analysis was run without the first month to test if there were differences in the factors affecting mortality due to collection, transport, and acclimation to the nursery.

For all growth analyses, data was analyzed up to 12 months, due to the loss of most fragments at site N1 at 13 months. For all fragments, linear extension (mm) was calculated as the total length measurement along the main axis plus the length of all branches >10 mm. This was then multiplied by partial survivorship (%) estimates to get Total Linear Extension (TLE) (mm) of live coral tissue. A Kendall’s tau correlation was done to examine if the number of branches correlated to an increase in TLE. To test differences between changes in linear growth for surviving fragments (Growth = final-initial TLE) at 12 months, a Kruskal Wallis rank sum test was conducted, followed by a *post hoc* pairwise comparison using the Wilcoxon Rank sum test. An ANOVA was also conducted followed by a Tukey’s HSD *post hoc* test to confirm factor differences.

To model the response of growth over time as a function of the independent categorical variables of taxa, fragment section, and nursery site, a Generalized Additive Mixed Model (GAMM) was run on the TLE data (Wood, 2011). Genotype, temperature, and light intensity were excluded from the models due to low sample size or the addition of a confounding factor to the model. Once fragments had died, they were excluded from dataset at the time in which they had died. Important terms were identified by backward selection (i.e., each term was sequentially dropped from the full model in turn) using Akaike’s Information Criteria (AIC) scores. The final GAMM was then termed the Minimally Adequate Model (MAM) and was used for resulting analysis and *post hoc* tests. The MAM was validated by visual examination of the model residuals versus fitted values using plot(gam model) and gam.check(gam model) functions. Model validation did not indicate any problems based on residual plots. Pairwise comparisons on factor levels were then conducted using the “emmeans” package (Lenth, 2019).

As *A. palmata* has a more planar structure compared to *A. cervicornis* and *A. prolifera*, an analysis was conducted to compare average growth rate per month. For each surviving *A. palmata* fragment at 12 months, the total length\*width

GeneMapper 5™ software. Unique and clonal genotypes were identified using the Excel microsatellite toolkit (Park, 2001). To identify descriptive information (stutter peaks, null alleles, large allele dropout), fragment loci were run through Micro-checker Version 2.2.3 (van Oosterhout et al., 2003).

### Statistical Analysis

Fragment survival and TLE data were analyzed using R statistical software (R Core Team, 2017). Various survival and growth plots were created through the package ‘ggplot2’ to examine raw data (Wickham, 2016). A Survival Analysis (Cox model) was run to test if the independent variables of taxa, genotype, fragment section, and nursery site affected total colony mortality in the nursery (Therneau and Grambsch, 2000; Therneau, 2015; Kassambara and Kosinski, 2018). In addition to a survival

measurements were multiplied by two and then by partial survivorship (%) estimates to determine live fragment tissue sizes used in the growth rate equation. Width measurements were taken at the widest central point of the fragment, not including branch extensions. Photographic analysis of initial versus final width was completed for a subset of surviving *A. palmata* fragments ( $n = 12$ , minimum of 3 fragments from each site) to determine if width changed significantly during the full 13-month experimental period. Further description of the growth rate analysis and width comparison can be found in the **Supplementary Materials**.

When comparing values of new linear growth (mm/12 mo) for each fragment between genotypes, a Kruskal Wallis chi-squared test was used. 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) was used in *post hoc* analysis and visualized using the "multcompView" package (Graves et al., 2015).

To test differences in prevalence of conditions, a Kruskal-Wallis chi-squared test and Pearson's chi-squared test were used and data was visualized using the "pgirmess" (Giraudoux, 2018) and "vcd" (Zeileis et al., 2007) packages in R Studio. Conditions examined were bleaching (Blch), paling (Pale), and algal overgrowth interactions (OGA). No other conditions (disease/predation) were reported with enough replicates to be used in analysis.

Average daily temperature and average daily light intensity was calculated in Excel using the HOBO® temperature logger data. Loggers were deployed in March 2018, November 2018, and March 2019. While the study period did not include March 2018, this data was included in the light intensity analysis to increase the sample size and document site variability. Daily temperature data was calculated across the whole study period (June 2018–July 2019). Light intensity was measured in lux (lumen/ft<sup>2</sup>). Photosynthetically active radiation (PAR) is typically used for light measurements, but to convert from lux to PAR a calibration curve and equation must be generated for each individual logger using a PAR meter (Long et al., 2012), which was not available for comparison. Light intensity was recorded throughout the study period, but due to biofouling of the sensor only the first week of light data after logger deployment was used in statistical analysis. Data was organized in Excel, imported into R, and analyzed with a Kruskal Wallis *t*-test and resulting *post hoc* analyses to determine whether the nursery sites had significantly different temperatures over the study period.

## RESULTS

### Survival and Mortality

Of the initial 157 fragments, 66 (42%) survived to the end of the study period (13 months). Of those fragments surviving at 13 months, 28.8% were *A. cervicornis* fragments, 31.5% were *A. palmata* fragments, and 39.7% were *A. prolifera* fragments. During the first month in the nursery (June 2018), overall total mortality was 29.3% (mortality being defined by fragments with

no living tissue, not partial tissue loss). After the first month, monthly mortality ranged from 0 to 5% to July 2019. In July 2019, 32 fragments died, equating to 32.7% of the overall remaining fragments. Mortality was greatest at site N1, where only one fragment (*A. palmata*, basal fragment) was alive by the end of the study period. Site significantly affected coral fragment survival (Survival Analysis Cox model,  $z = -5.47$ ,  $p = 4.5e-08$ ), with site N3 fragments showing the greatest survival throughout the study period (**Figure 4**). No other factors had a significant effect on survival. Site was also the only significant factor in the survival analysis when the first month was excluded (to account for any mortality due to transport stress) (Survival Analysis Cox model,  $z = -5.161$ ,  $p = 2.46e-07$ ).

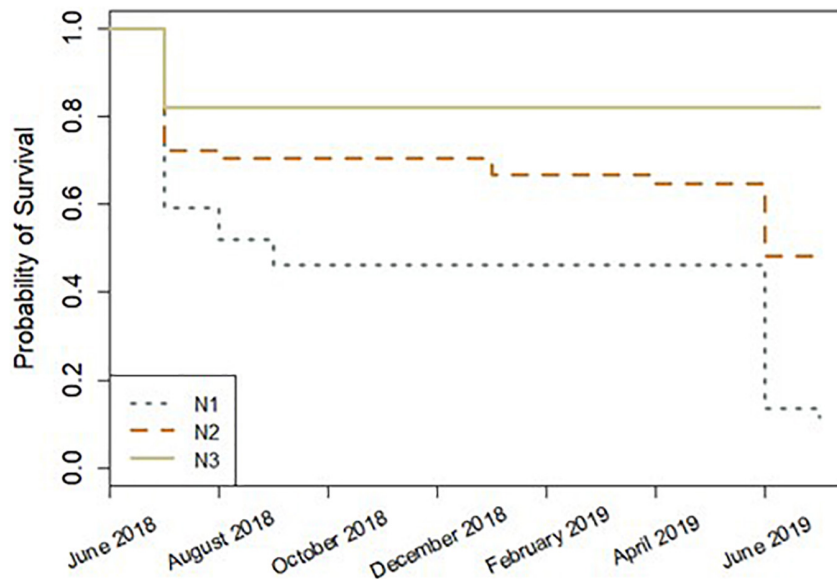
## Growth

### Descriptive Statistics and Linear Growth Analysis

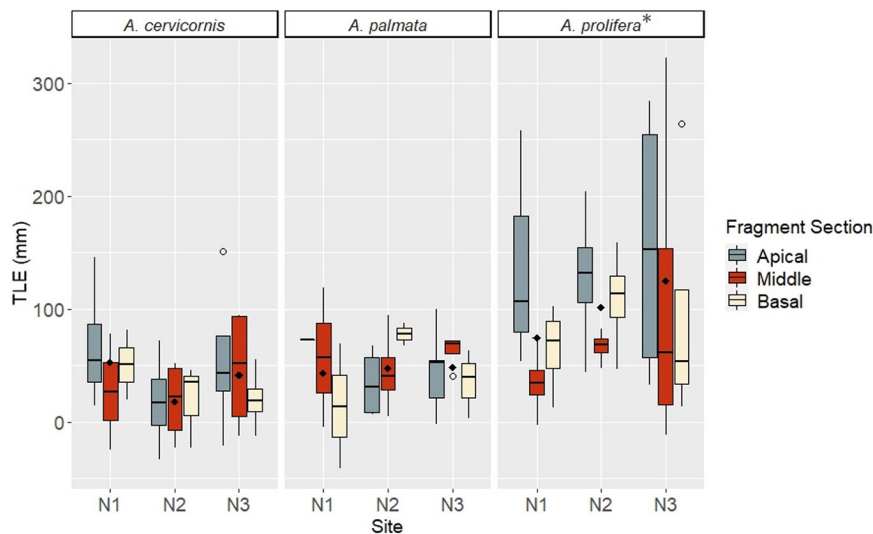
Over 12 months, total TLE (mm) increased by 15.8%. There were no significant differences in the sizes of the ~50 mm sections at initial nursery setup (Kruskal-Wallis test,  $p > 0.05$ ). For surviving corals, linear growth (final – initial fragment TLE) and the final number of branches were significantly positively correlated [Kendall's tau correlation,  $z(97) = 7.4452$ ,  $p = 9.678e^{-14}$ ]. The equation that best describes the relationship is: Growth (TLE) =  $29.83 + (13.16 * \text{number of branches})$ , where the number of branches changes depending on the individual fragment.

Factors included in the growth analysis based on TLE were taxa, site, and fragment section. When comparing growth (final – initial TLE) for surviving fragments, mean linear growth values did not significantly differ among factor groups (Kruskal Wallis rank sum test,  $p > 0.05$ ). However, a *post hoc* comparison indicated *A. prolifera* had significantly greater average growth (102.5 mm/12 mo  $\pm$  14.4 SE), than *A. cervicornis* (35.6 mm/12 mo  $\pm$  7.9 SE) and *A. palmata* (47.4 mm/12 mo  $\pm$  7.2 SE) (Paired Samples Wilcoxon rank sum test,  $p < 0.05$ ) (**Figure 5**). Apical fragments had the greatest average growth (78 mm/12 mo  $\pm$  4.2 SE), although not significantly different (Paired Samples Wilcoxon rank sum test,  $p > 0.05$ ) compared to middle fragments (53.3 mm/12 mo  $\pm$  4.0 SE) and basal fragments (57.6 mm/12 mo  $\pm$  3.6 SE). Site N3 showed greater average growth of fragments (74.1 mm/12 mo  $\pm$  4.2 SE) compared to N1 (60.9 mm/12 mo  $\pm$  3.0 SE) and N2 (55.2 mm/12 mo  $\pm$  4.8 SE), although sites were not significantly different from each other (Paired Samples Wilcoxon rank sum test  $p < 0.05$ ) (**Figure 5**). An ANOVA between factor groups suggested a significant effect of taxa on linear growth (Analysis of Variance: Taxa –  $df = 2$ ,  $F = 10.344$ ,  $p = 0.000114$ ). Apical *A. prolifera* fragments at site N3 had the greatest mean growth based on TLE after 12 months (**Figure 5**).

For the growth rate analysis, apical *A. prolifera* fragments at site N3 had the greatest average growth rate per month (10.47%) compared to all other factor combinations, and *A. prolifera* average growth rate per month was significantly greater than the parental species (Paired Samples Wilcoxon rank sum test,  $p < 0.05$ ). *Acropora palmata* width measurements found no significant difference between initial and final mean widths (Parametric two-sample *t*-test,  $t = 0.154$ ,  $df = 21.9$ ,



**FIGURE 4 |** Survival analysis plot by site for 13 months (June 2018–July 2019). Lower survival probability values indicate lower survival, and higher survival probability values indicate greater survival.



**FIGURE 5 |** Growth (TLE) by taxa, fragment section, and site at 12 months. Taxa are listed along the top bar of each plot. Site is listed along the x-axis within each taxa group. Fragment sections are differentiated by color in the legend on the right. Open circles indicate outliers; filled diamonds indicate mean values for the site. A \* indicates significance.

$p = 0.879$ ). Mean change in width was 3.02 mm and ranged from 0.4 to 9.17 mm, with 90% between 0.4 and 4.58 mm. The **Supplementary Materials** contain further results of the growth rate and width analyses.

### GAMM Analysis

Taxa, site, and fragment section were identified as important factors influencing growth over time (change in TLE, or  $\text{mm}/\text{mo}^{-1}$ ) in the MAM (GAMM ANOVA,  $p < 0.05$ ). The MAM included potential additive and interactive effects of

factors that other statistical tests may not account for. To allow for dependency between individual fragments over time, initial size of each fragment was included in the TLE values across all time points.

*Acropora prolifera* fragments had significantly greater mean TLE values at 12 months compared to *A. cervicornis* and *A. palmata* fragments based on the MAM *post hoc* pairwise comparison ( $p < 0.05$ ). *Acropora prolifera* fragments also had the greatest average monthly linear growth across all fragment sections and sites (**Figure 6A**). Based on the MAM, apical

and basal fragment TLE values at 12 months were significantly greater than middle fragments ( $p < 0.05$ ) (Figure 6B). The MAM indicated apical *A. prolifera* fragments at site N1 had the greatest TLE (mm) at 12 months (June 2019), before most fragments at N1 died the next month (July 2019). However, 12-month TLE values between sites were not significantly different ( $p > 0.05$ ) (Figure 6C).

## Genotype

Genetic analysis confirmed there were five unique *A. cervicornis* and *A. palmata* genotypes, and 4 unique *A. prolifera* genotypes. Micro-checker found no evidence of scoring errors due to stutter peaks, large allele dropout, or null alleles across the five loci for each of the three taxa. Genotype did not have a significant effect on survival (Survival Analysis Cox model,  $p > 0.05$ ). When analyzing the different genotypes of each taxon individually, genotype had a significant effect on linear growth values between taxa (Kruskal Wallis rank sum test,  $\chi^2 = 33.3$ ,  $df = 11$ ,  $p = 0.00048$ ). Genotypes within *A. cervicornis* were not significantly different from each other (Tukey HSD,  $p > 0.05$ ). Within *A. palmata*, the mean linear growth after 12 months in genotype P10 was significantly greater than P1 and P11 ( $p = 0.021$  and  $p = 0.049$ , respectively). All other genotypes within *A. palmata* were not significantly different from each other (Tukey HSD,  $p > 0.05$ ). Genotype did not have a significant effect on linear growth values within *A. prolifera* genotypes ( $\chi^2 = 0.72$ ,  $df = 2$ ,  $p > 0.05$ ).

## Conditions

Disease was not observed during the study period. Condition prevalence did not significantly differ over time ( $\chi^2 = 3.1137$ ,  $df = 11$ ,  $p > 0.05$ ). Condition type significantly affected prevalence ( $\chi^2 = 22.28$ ,  $df = 2$ ,  $p = 1.453e^{-5}$ ). Prevalence of bleaching was significantly lower than algal overgrowth interactions (OGA) and paling (Multiple comparison test,  $p < 0.05$ ). There was a significant association between condition and taxa ( $\chi^2 = 16.818$ ,  $df = 4$ ,  $p = 0.002097$ ). Prevalence of OGA was less than expected in *A. palmata*, and prevalence of paling was more than expected in *A. palmata*; all other combinations of taxa and conditions occurred as expected. There was not a significant association between site and condition ( $\chi^2 = 5.4002$ ,  $df = 4$ ,  $p = 0.2486$ ), i.e., all combinations of condition and site occurred as expected.

## Temperature and Light Results

During the study period, water temperatures ranged from 21.2°C to 33.5°C across all sites. Water temperatures at N1 ranged from 21.2°C to 33.5°C, at site N2 from 22.5°C to 32.3°C, and at N3 from 21.8°C to 32.9°C. Water temperature did not significantly differ between sites (Kruskal-Wallis test,  $p > 0.05$ ), although site N1 had the greatest number of days (134) above a published bleaching threshold (29.8°C, Manzello et al., 2007) compared to sites N2 and N3 (123 and 126 days, respectively). Summer months (June–September 2018, June–July 2019) were compared specifically to determine if there were significant temperature differences in times of potentially greater heat stress. In the summer months, water temperatures ranged from 29.01°C to

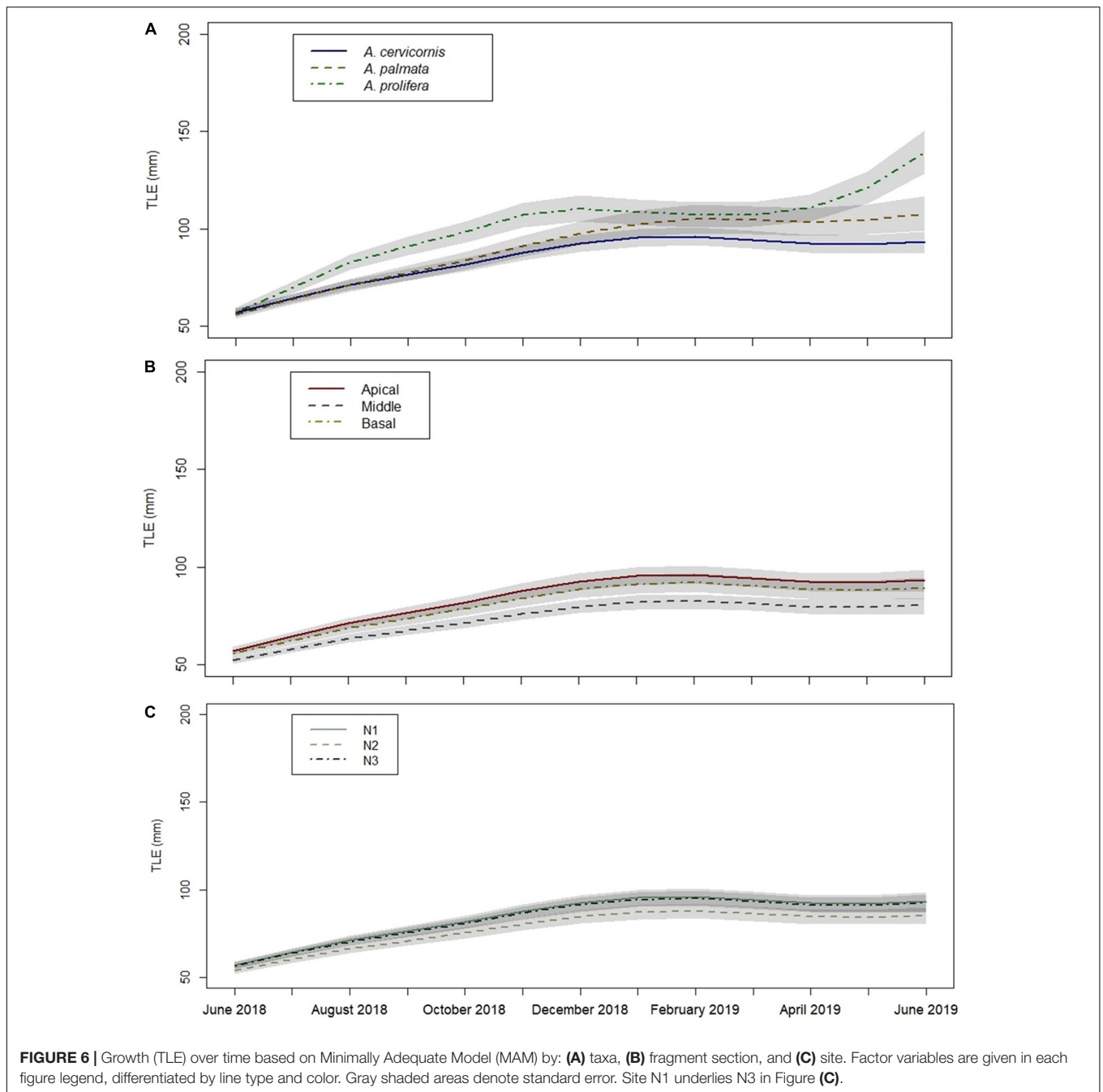
31.72°C in 2018 and from 27.98°C to 33.45°C in 2019. When comparing just the summer months, there were no significant differences in mean temperatures between sites in 2018 and 2019 (One-way ANOVA/Kruskal-Wallis test,  $p > 0.05$ ). There were six periods in the summer months where seven or more consecutive days were  $> 29.8^\circ\text{C}$ . Temperature stress based on Degree Heating Weeks (DHW) was calculated, which considers the number of days the sea surface temperature is  $\geq 1^\circ\text{C}$  above the approximate mean summer maximum temperature over a 12-week period (Wellington et al., 2001; Liu et al., 2006; Kayanne, 2017). For this study one DHW is equal to seven days  $\geq 30.8^\circ\text{C}$ . At all sites in July 2018 there were 8 to 9 consecutive days above this threshold, corresponding to 1 DHW. At sites N2 and N3 in June 2019, 7 consecutive days were above the threshold, also corresponding to 1 DHW. In July 2019, all but one coral fragment had died at site N1, likely attributed to bleaching.

Daily light intensity was variable between sites, although the variability was not consistent across logger deployments. At one week after initial logger deployment (March 2018), daily average light intensity ranged from 438.65 to 1434.47 lumen/ft<sup>2</sup> across all sites but was not significantly different between sites (Kruskal-Wallis,  $p > 0.05$ ). In November 2018, daily average light intensity ranged from 145.83 to 459.75 lumen/ft<sup>2</sup> across all sites one week post-deployment and was significantly greater at site N2 than N1 and N3 (Kruskal-Wallis rank sum test,  $\chi^2 = 9.719$ ,  $df = 2$ ,  $p = 0.00775$ ; Paired Samples Wilcoxon rank sum test,  $p < 0.05$ ). Sites N1 and N3 did not significantly differ from each other after the second logger deployment (Paired Samples Wilcoxon rank sum test,  $p > 0.05$ ). At one week after the third logger deployment (March 2019), daily average light intensity ranged from 387.5 to 8987.47 lumen/ft<sup>2</sup> across all sites. Daily average light intensity one week after the third deployment was significantly different between sites (Kruskal-Wallis rank sum test,  $\chi^2 = 12.445$ ,  $df = 2$ ,  $p = 0.00198$ ), where light intensity was significantly greater at site N3 than sites N1 and N2, and light intensity at site N1 was significantly lower than N2 (Paired Samples Wilcoxon rank sum test,  $p < 0.05$ ). Site N1 had lower light intensity than N2 and N3 in March 2018 and 2019 and had lower intensity than site N2 in November of 2018.

## DISCUSSION

This study is the first to examine differences in survivorship and growth between the parental and hybrid taxa of Caribbean acroporid corals in a nursery setting, along with differences among fragment sections and nursery locations. While there are reservations about using hybrids in coral restoration due to genetic swamping concerns, the benefits of including fast-growing hybrid coral to quickly increase reef structure likely outweighs the potential long-term drawbacks. This study identified three main findings that will be beneficial to restoration management: (1) the hybrid taxon, *A. prolifera*, demonstrated greater growth in a shallow water nursery setting than the parental species, (2) using non-apical fragments did not compromise survival or growth, and (3) nursery site selection plays an important role in coral fragment survival.





There is growing evidence to suggest the *A. prolifera* hybrid has similar, if not higher, fitness than the parental species and may be a faster growing taxon overall (Gladfelter et al., 1978; Fogarty, 2012; Howe, 2018; Weil et al., 2020; Nylander-Asplin et al., 2021). This study provides further evidence that *A. prolifera* grows faster than the parental species. Our results found that the number of branches correlates with increased TLE over time, which is consistent with Lirman et al. (2014) and may explain why the prolifically branching hybrid had greater growth. As seen in other studies (Gladfelter et al., 1978; Crossland, 1981; Scheufen et al., 2017), growth of all taxa

fluctuated seasonally and was greater in warmer months than in the cooler winter/spring months. Prior research has investigated the growth of wild acroporid coral colonies, where growth rates were higher in certain *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 Puerto Rico (Weil et al., 2020), suggesting colony growth may be highly dependent on site location, environmental conditions, and genotype. With its rapid growth and prolific branching morphology, the hybrid is likely to reach outplanting goals by quickly increasing coral biomass and reef structure, albeit the

fused branches of the hybrid taxon may provide a different ecological service than the parental species. 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 may be more beneficial to the smaller fish and invertebrates.

Wild hybrid colonies have been found in greater abundance and in better health than their parental counterparts at some Caribbean sites (Fogarty, 2012; Hernández-Fernández et al., 2019; Nylander-Asplin et al., 2021). In surveys across the Caribbean, hybrid disease prevalence was equivalent to *A. palmata* and less than *A. cervicornis* (Fogarty, 2012). Despite hybrids often inhabiting shallower habitats (~1 m) than the parental species, hybrids had comparable prevalence of paling or bleaching, which was low overall at surveyed sites (Fogarty, 2012). These characteristics, combined with the equal survivorship and rapid growth seen in our study, make the hybrid an ideal candidate to scale-up restoration. Addition of the hybrid could increase reef structure while also increasing the probability of genetic diversity within taxa (Willis et al., 2006; Richards and Hobbs, 2015; Nylander-Asplin et al., 2021). Hybrids could provide shallow water habitat with limited bleaching and paling, fast growth, and potentially less susceptibility to disease compared to one or both parental species, as our work and previous research indicates.

There is concern that the hybrid may outcompete the parental species or reduce genetic diversity if included in restoration practices, as seen in other research in forestry practices (Merkle et al., 2006; Richards and Hobbs, 2015; Kovach et al., 2016). However, concerns about genetic swamping of the parental species on evolutionary scales must not outweigh the immediate ecological need for shallow coral reefs, particularly when the state of coral reefs is dire. Genetics also play an important role in a coral's resistance to climate change and disease (Baums, 2008; Vollmer and Kline, 2008; Drury et al., 2016, 2017; O'Donnell et al., 2017; Baums et al., 2019; Chan et al., 2018, 2019a,b). With the inclusion of the hybrid, there is potential for greater sharing of genetic material across the three acroporid taxa via backcrossing, which may improve the adaptive potential of coral populations (Baums et al., 2019). Chan et al. (2019a) details a decision tree to address if/when a hybrid should be used in conservation efforts overall. To specifically address *A. prolifera* concerns, pilot studies could investigate differences in growth and survival of nursery grown coral by outplanting fragments in the same area in separate clusters, with enough separation between colonies to reduce competition between coral taxa. While there is overlap in habitat range among Caribbean acroporid taxa (Fogarty, 2012), further separation by habitat type/depth could help address competition concerns. This could include outplanting *A. prolifera* to shallow back reef areas, *A. palmata* along reef crests, and *A. cervicornis* to deeper reef slopes.

Apical fragments displayed the greatest TLE increase compared to middle and basal fragments, with the apical hybrid fragments having the greatest growth overall. Because these fragments were at the tips of the donor colony and contained the apical polyp, they were the primary location of growth on the original colony (Gladfelter et al., 1989; Rinkevich, 2000;

Bowden-Kerby, 2001). This supports 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 (Rinkevich, 2000; Bowden-Kerby, 2001; Herlan and 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). The results of these studies indicate that 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). In this study, there were no significant differences in linear growth by fragment section, which could be accounted for by branching on both cut margins of the middle and basal sections. Some studies have found that pruning of larger colonies of branching corals in a nursery leads to increased productivity after one year (Lirman et al., 2014), and similar exposure in massive corals by microfragmentation has led to a greater increase in tissue compared to singular colony (Page et al., 2018). In contrast, excessive pruning may lead to an increased risk of disease/overgrowth or reduce reproductive capability in the long-term (Epstein et al., 2001; Muller and van Woessik, 2012). Here, middle and basal fragments had two areas of recent exposed tissue from initial fragmentation, which can lead to increased risk of disease and other deleterious stress responses (Muller and van Woessik, 2012). Lesion colonization by opportunistic settlers, like algae, may affect the long-term growth of nursery fragments. In this study, initial algal settlement on the exposed coral skeleton was observed across all sites 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, leading to differences in growth between fragment sections. Further investigation of metabolic and chemical differences within a colony are needed to understand the role fragment section may play in nursery expansion and outplanting.

Site selection has proven to be an important factor in the success of coral nurseries, with temperature, water quality, and depth affecting survival (Shafir et al., 2006; Johnson et al., 2011; Young et al., 2012). The high mortality observed during the first month was likely due to transportation and acclimation stress. Transportation stress is difficult to avoid but can be reduced by multiple water changes and temperature control, if available. Storm and severe weather conditions may increase the risk of impact on nursery sites (Bowden-Kerby, 2001; Young et al., 2012), though previous research indicates that establishing nursery sites in areas with increased water flow may allow for higher survival (Edwards, 2010). Here, the site with the greatest survival and average growth, N3, was located on the unprotected northern side of the island. While site N1 fragment growth did not significantly differ from the other sites, it did have the lowest overall survival. Although we were unable to measure hydrodynamics at the study sites, we did observe stagnant conditions at site N1, likely contributing to the bleaching and subsequent mortality at this site in July 2019. Survival at site N2 was lower than N3 but

greater than N1, possibly due to increased water flow from the channel near this nursery location. Temperature and depth were consistent across all sites; therefore, it is likely that other environmental conditions, while not directly measured in this study, influenced survival and growth. Research by Nakamura and van Woesik (2001) demonstrated that branches in *Acropora digitifera* survived better in increased water flow conditions, even when exposed to higher water temperatures. Similarly, natural colonies and outplants of *A. cervicornis* had greater survival and abundance in areas with moderate to high water flow (D'Antonio et al., 2016; van Woesik et al., 2020). In this study, the negative impacts of stagnant water and increased water temperatures at all sites during the summer months likely outweighed the benefits of a more protected location. As suggested by Schopmeyer et al. (2017), survivorship < 80% over 12 months after collection may be due to poor nursery locations or genotypic differences. While Schopmeyer et al. (2017) compared *A. cervicornis* fragments, the same benchmarks could be applied for all taxa used in this study, and as such it is likely that site differences contributed to the less-than-ideal survival.

The light intensity data recorded after the third deployment (March 2019) shows differences between sites, with site N1 having the lowest intensity. Site N1 was located nearest to seagrass beds but in fine sediment compared to the other two nursery locations. It was the site that observationally had the greatest turbidity across the study period, which aligns with the low lux (lumens/ft<sup>2</sup>) values from the light logger data. However, it is difficult to extrapolate this information further into the summer months. PAR is a useful metric to determine the ideal light intensity for photosynthesizing organisms, such as coral symbionts. Unfortunately, the lux data collected in this study requires direct calibration with a PAR meter, which was not available for comparison. As such, the light intensity data was used only as a secondary indicator of environmental conditions after temperature in this study. Turbid conditions may reduce the impact of irradiance on coral health (Wagner et al., 2010; van Woesik et al., 2012; Morgan et al., 2017; Sully and van Woesik, 2020; van Woesik et al., 2020). Other research has shown connectivity between adjacent seagrass beds and coral reefs via fish species and particulate matter (Dorenbosch et al., 2005; Heck et al., 2008), which could lead to increased food/nutrient supply (and therefore growth) for nursery fragments. However, high sediment input and long-term turbidity can increase prevalence of disease and other stressors to corals, likely impacting long-term growth and survival (Pollock et al., 2014; Ng et al., 2016).

Overall, growth is only a secondary measure of success if nursery fragments do not survive. As such, site selection based on survival alone should be a priority before considering growth. Site selection criteria should consider depth, water temperature, site accessibility, hydrodynamics, and nutrient flux in the area, which could be evaluated using smaller pilot studies. Locations with optimal depth, moderate water flow, adequate light attenuation, and a limited range of temperatures will likely lead to the most successful coral fragment survival and growth (Edwards, 2010; Johnson et al., 2011).

## CONCLUSION

The hybrid coral utilized in this study showed greater fitness than the parental species. Coral restoration managers should consider the fast-growing hybrid *A. prolifera* as an option for restoration. The hybrid survives as well as and grows faster than the parental species, and as such is a potential option to increase shallow reef infrastructure through restoration. Including the hybrid taxa and increasing the number of unique parental genotypes in a nursery will increase genetic diversity among all three taxa in future restoration activities. As shown in this study, evaluating appropriate nursery sites before setup is crucial to project success. Although apical tips of colonies prove to be a source for fast growing tissue, further research is needed to confirm there are no tradeoffs between growth and survival. Finally, our study took place over the course of one year at a remote island in the Bahamas. Incorporating the hybrid in different aspects of active restoration at sites throughout the Caribbean or at larger scales would help determine how this taxon fits into the larger picture of coral restoration.

## DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available due to authorization required by the program sponsor. Upon approval, data will be provided by the corresponding author. Requests to access the datasets should be directed to CV, cassie.vanwynen@gmail.com.

## AUTHOR CONTRIBUTIONS

CV, MH, and NF designed the study. CD obtained permitting for the project. CV, MH, NF, and CD scouted and set up nursery sites. CV, MH, and CD collected corals for the nurseries. MH and CV were responsible for project logistics, data collection, and nursery maintenance, with assistance from NF and DG, and conducted genetic processing and analysis. NF and DG were responsible for project budgeting. CV organized and analyzed the data and wrote the manuscript drafts. CV, MH, NF, and DG contributed to interpretation of results. All authors contributed to final draft edits before submission.

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participate in the data analysis, interpretation, or in the writing of this manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.669966/full#supplementary-material>

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- Supplementary Figure 1** | Coral collection locations around New Providence, shown by the yellow points. *Inset*: New Providence (in box) in relation to Florida and the Berry Islands.
- Supplementary Figure 2** | Nursery site experimental setup. Coral fragments were placed on the middle three tree branches shown here with a letter and number value. Fragment sections were individually tagged. C, P, and H denote taxa (*A. cervicornis*, *A. palmata*, and *A. prolifera* (hybrid), respectively), and numbers denote genotype. Not all putative genotypes were unique, and so some genotypes had a higher number of fragments after analysis. The fragment section changed branches between trees at each site. Dashes denote no fragment attached.
- Supplementary Figure 3** | Growth (TLE) over time by genotype. TLE (mm) is along the y-axis, and time is along the x-axis. C, P, and H denote *A. cervicornis*, *A. palmata*, and *A. prolifera* (hybrid), respectively.
- Supplementary Figure 4** | Frequency analysis of conditions present across the study period by taxa. Conditions are listed along the top x-axis, with taxon listed along the y-axis. Algal overgrowth, bleaching, and paling are denoted by OGA, Blich, and Pale, respectively. Blue boxes indicate that the condition occurred more than expected for a specific taxon, while red indicates the condition occurred less than expected. Gray boxes indicate that a condition occurred as expected for that taxon.
- Supplementary Figure 5** | Mean daily temperature by site from June 2018 to July 2019. Purple line denotes published approximate bleaching threshold at 29.8°C (Manzello et al., 2007). Sites are differentiated by color, shown in the legend.
- Supplementary Table 1** | Linear growth (TLE) at 12 months by genotype. C, P, and H denote *A. cervicornis*, *A. palmata*, and *A. prolifera* (hybrid), respectively. Genotype with \* indicates only 3 fragments left at 12 months.
- Supplementary Table 2** | Monthly temperature ranges (°C) from June 2018 to July 2019.
- Supplementary Table 3** | GPS coordinates for nursery locations.
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