



Optimizing the productivity of a coral nursery focused on staghorn coral *Acropora cervicornis*

Kathryn E. Lohr^{1,5,*}, Sonia Bejarano¹, Diego Lirman², Stephanie Schopmeyer²,
Carrie Manfrino^{3,4}

¹Central Caribbean Marine Institute, Little Cayman Research Centre, North Coast Road, Little Cayman, KY3-2501, Cayman Islands

²Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy, Miami, FL 33149, USA

³Central Caribbean Marine Institute, PO Box 1461, Princeton, NJ 08540, USA

⁴School of Environmental and Sustainability Sciences, Kean University, 1000 Morris Ave, Union, NJ 07083, USA

⁵Present address: The University of Florida/IFAS, School of Forest Resources and Conservation, The Florida Aquarium Center for Conservation, 529 Elsberry Rd., Apollo Beach, FL 33572, USA

ABSTRACT: The rapid decline of the staghorn coral *Acropora cervicornis* throughout the Caribbean prompted the development of coral gardening as a management strategy to restore wild stocks. Given that coral gardening relies on propagating corals collected from wild donor colonies, it is imperative to optimize growth within a nursery to reduce dependence on wild collections. This study determined the maximum amount of coral that may be clipped from a colony during propagation without causing mortality or decreased growth. We applied 3 experimental treatments to 12 nursery-reared staghorn corals, in which 25, 50, or 75% of the colony's total biomass was removed and fragmented to create additional, smaller fragments. Four additional colonies served as unfragmented controls. Treatment had no effect on colony productivity, defined as the ratio of new tissue growth to initial colony size, over 87 d. Similarly, treatment had no effect on the rate at which colonies developed new branches. Results indicate that 75% of the biomass of staghorn colonies may be removed without affecting their growth. We anticipate that our observations will have practical applications for maximizing propagation of staghorn coral within nurseries throughout the wider Caribbean while minimizing the impact of this management measure on remnant wild populations.

KEY WORDS: Staghorn coral · Restoration · Coral gardening · Coral nursery · Fragmentation · Propagation · Caribbean

INTRODUCTION

Coral reef ecosystems worldwide have undergone considerable changes resulting from a complex synergy between natural and anthropogenic disturbances (Done 1992, Hughes 1994). Throughout the Caribbean, mortality of reef-building corals followed by the gradual collapse of their skeletal structures has contributed to major ecosystem phase shifts over the last 4 decades (Gardner et al. 2003, Alvarez-Filip et al. 2009). Not only have these shifts been associ-

ated with important losses of biodiversity in benthic communities, but they have also resulted in seemingly locked states of macroalgal dominance (Mumby et al. 2007) and contributed to a region-wide decline in fish fauna (Paddack et al. 2009). Both coral mortality and loss of habitat structure pose serious threats to coastal livelihoods that depend on the goods and services sustained by coral reefs, such as shoreline protection and artisanal fisheries (Bythell & Sheppard 1993, Rogers & Beets 2001, Nagelkerken & Nagelkerken 2004).

*Corresponding author: kelohr@ufl.edu

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The staghorn coral *Acropora cervicornis*, once a dominant species on a variety of reef habitats throughout the Caribbean (Knowlton et al. 1981, Tunnicliffe 1983, Jackson et al. 2001), suffered widespread mortality following devastating hurricanes between the 1960s and 1980s (Woodley et al. 1981, Aronson & Precht 2001). In the 1980s, the remaining populations were almost entirely terminated by white band disease (Bythell & Sheppard 1993, Aronson & Precht 2001). With the paucity of *A. cervicornis* and its congener *A. palmata* persisting over the last 4 decades, Caribbean reefs have sustained an important gap in their portfolio of benthic functional groups (Bellwood et al. 2004). Few other Caribbean coral species provide the amount of structural 3-dimensionality characteristic of acroporids in shallow high-energy environments (Sheppard et al. 2005, Alvarez-Filip et al. 2009, M. K. Johnson et al. 2011). Therefore, it is unlikely that other reef-building species can substitute their role as barriers against shoreline erosion, and sources of fish and macroinvertebrate refugia. As a means of recognizing the severity of this ecosystem loss, both species were listed as threatened under the US Endangered Species Act (NMFS 2006).

Although patchy and localized recovery of acroporids has been observed recently (Lidz & Zawada 2013), consistent regional-scale natural recovery of viable populations seems unlikely mainly due to the species' low rates of larval recruitment (Kojis & Quinn 2001). Coral reef restoration has therefore been adopted as a management strategy with the immediate goal of replacing dead colonies in devastated areas to speed up natural population recovery (Kojis & Quinn 2001, Epstein et al. 2003). Coral gardening, one of the most common and versatile coral restoration techniques, involves an initial propagation stage in which small portions of wild coral colonies (referred to as donors) are collected and subdivided in smaller fragments. These fragments are then reared on artificial structures within an *in situ* nursery until they are large enough to be transplanted back to natural reef habitats (Rinkevich 1995, 2000). *A. cervicornis* is an ideal candidate for nursery rearing because artificial propagation techniques mimic the species' natural asexual fragmentation that is typically induced by storms (Bowden-Kerby 2001). Consequently, nurseries of varying scope and size focused on *A. cervicornis* have been established in a number of locations in the Caribbean (Herlan & Lirman 2009, M. E. Johnson et al. 2011, Young et al. 2012). In 2012, an *A. cervicornis* nursery was

installed on Little Cayman Island in the Cayman Islands with the goal of analyzing and refining a variety of coral propagation techniques and restoring coral populations on local reefs.

Although relatively cost effective compared to other restoration techniques, rearing corals in nurseries can be costly and labor intensive. Moreover, given the generalized scarceness of wild adult *A. cervicornis* colonies, an imperative objective of nursery initiatives is to maximize nursery productivity whilst collecting the minimum amount of donor tissue (e.g. Herlan & Lirman 2009). Given the increased popularity of *A. cervicornis* nurseries and the relative ease with which one can be initiated, it is important to investigate the methodological steps that will optimize their performance and yield. A set of best practices for coral gardening with respect to *A. cervicornis* has been developed, including strategies to minimize impacts on wild donor colonies, improve survivorship of donated branches, and enhance survivorship of transplanted colonies (Lirman et al. 2010, M. E. Johnson et al. 2011). Despite this extensive work, no studies have systematically determined the maximum amount of tissue that can be clipped from a colony during fragmentation without harming it. Investigating this would therefore be a valuable addition to existing nursery guidelines. Such findings have the potential to improve the effectiveness of restoration efforts throughout the Caribbean.

Here we used a small-scale monospecific nursery located on Little Cayman Island as an opportunity to determine what proportion of coral tissue can be clipped off to propagate nursery-reared *A. cervicornis* without harming donor colonies. We specifically tested whether the percent of the donor colony that is fragmented had an effect on its growth rate in terms of the amount of new growth and the rate of acquisition of new branches. We anticipate that the information presented here will be useful to scientists and conservation practitioners seeking to optimize the artificial propagation of *A. cervicornis* and may ultimately increase outputs of coral restoration efforts.

MATERIALS AND METHODS

Study area

This study was conducted in 2013 during the initial propagation stage of the monospecific *Acropora cervicornis* nursery maintained by the Central Caribbean Marine Institute and the Cayman Islands De-

partment of Environment on Little Cayman Island in the Cayman Islands. The nursery is located 400 m off the north coast of the island within the Bloody Bay Marine Park (19.699° N, 80.060° W) on a wide area of flat carbonate pavement in the shallow portion of the forereef (~6.5 m). It was first populated in September 2012 with 58 fragments collected from 4 adult colonies located at geographically distinct locations within 2 sites off the southeast coast of the island. For the purpose of this study, the 4 adult colonies were assumed to be dissimilar genotypes. Fragments were suspended in mid-water by attaching them to 3 line nursery structures, consisting of 3-strand polypropylene line (~10 m in length) suspended by a polystyrene fishing float, and have since grown steadily without the incidence of coral disease or corallivore predation. The propagation stage of the nursery began in March 2013 when 16 first-generation colonies ranging in size from 31 to 103 cm (mean \pm SE = 48.19 \pm 4.74) were selected for further fragmentation.

To determine what level of fragmentation could maximize the productivity of the nursery without affecting growth rate of the donor colony, 3 fragmentation treatments were selected and 4 replicate first-generation colonies were assigned to each treatment. Fig. 1 provides a schematic of the experimental

design. To account for the potential variability in growth rate among the 4 genotypes, 1 colony of each genotype was assigned to each treatment. First-generation colonies were fragmented such that 25, 50, and 75% of their total size was clipped to generate new (second-generation) fragments. Four first-generation colonies were left intact and served as experimental controls. During this propagation stage, between 1 and 9 second-generation fragments of approximately 5 cm in length were obtained from each first-generation parent colony depending on the size of the parent colony and the treatment assigned. A total of 48 second-generation fragments were generated.

Control and experimental second-generation fragments were haphazardly distributed on a suspended PVC tree (Nedimyer et al. 2011) within the nursery to avoid spatial clustering of colonies of the same genotype or treatment. For the purpose of this study, we focused on monitoring the growth rate of first-generation fragments by inspecting these initially in March 2013, and 35, 70, and 83 d later. During inspections, each colony's total number of branches equaling at least 1.5 cm in length was counted, and its total linear extension to the nearest cm was measured *in situ* using rulers (e.g. M. E. Johnson et al. 2011).

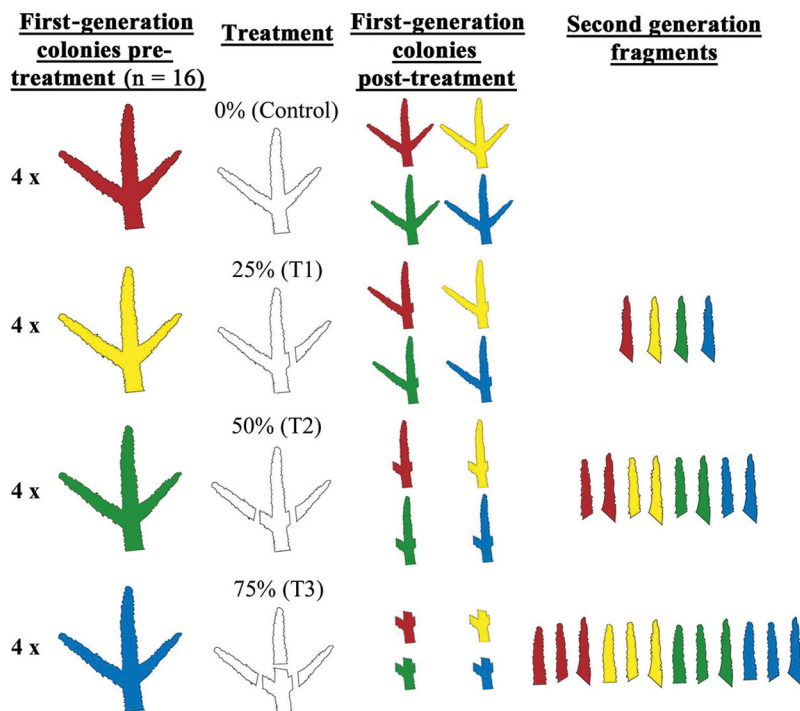


Fig. 1. Experimental design used during this study, illustrating the fragmentation treatments and the level of replication per treatment. Colors represent different genotypes of staghorn coral *Acropora cervicornis*. Four first-generation colonies from each genotype were fragmented during the experiment

Data analysis

The normalized increase in size (p) was calculated for each colony using the expression:

$$p = \frac{x_f - x_i}{x_i} \quad (1)$$

where x_f corresponds to the size of the fragment at a given time point, and x_i is the size of the fragment at the beginning of the study.

To identify the fragmentation treatment(s) that optimize growth of nursery-reared *A. cervicornis* during propagation, 2 statistical models were fitted. First, a linear mixed-effects model allowing for repeated observations on the same fragment to be correlated was fitted using the function `lme` of the R package 'nlme: linear and nonlinear mixed effects models' (Pinheiro et al. 2014). To allow for temporal correlation among the model residuals, a first-order autoregressive

correlation structure (corAR1) was applied to the deepest level (on each individual time series) (Zuur et al. 2009). The adequacy of this model was verified by plotting the standardized residuals against (1) the fitted values to check for homogeneity and (2) each explanatory variable to check for violations of independence (Zuur et al. 2007).

Second, a generalized estimation equation allowing for repeated measures and assuming a Poisson error structure was fitted to predict the total number of new branches as a function of fragmentation treatment (i.e. fixed factor). This model was fitted using the function `geeglm` of the `geepack` R package (Højsgaard et al. 2006). The model was examined for overdispersion by verifying that the scale parameter ϕ was not significantly different from that assumed in a Poisson distribution (i.e. 1) (Crawley 2007). ϕ was calculated by squaring the Pearson residuals, adding them up, and dividing the sum by $n - r$, where n was the number of observations and r the number of regression parameters in the model (Zuur et al. 2007). The adequacy of the model was tested by plotting the Pearson residuals against (1) the fitted values to check for homogeneity and (2) each explanatory variable to check for violations of independence (Zuur et al. 2007).

RESULTS

No partial or whole-colony mortality affected fragmented first-generation colonies or resulting fragments in any of the treatment groups. One of the colonies assigned to the control treatment group detached from the PVC structure and was lost between 0 and 35 d and was not included in analyses. The growth rate of fragmented first-generation colonies and resulting fragments ranged between 0.01 and 0.06 cm branch⁻¹ d⁻¹ (mean \pm SE = 0.035 \pm 0.002). Average annual growth per branch was 12.92 \pm 0.54 cm. There was no significant effect of the experimental treatments on growth of fragmented first-generation colonies, defined as the proportion of new growth normalized by initial fragment size, over time ($p = 0.934$, Fig. 2a). There was also no significant effect of the experimental treatments on growth of resulting second-generation fragments ($p = 0.864$). Fragmented first-generation donor colonies acquired between 0 and 0.16 branches d⁻¹ (mean = 0.04 \pm 0.01), and experimental treatments had no significant effect on the rate of acquisition of new branches for these colonies ($p = 0.976$, Fig. 2b). Data on mean growth and branching per genotype is provided in Table A1 in the Appendix.

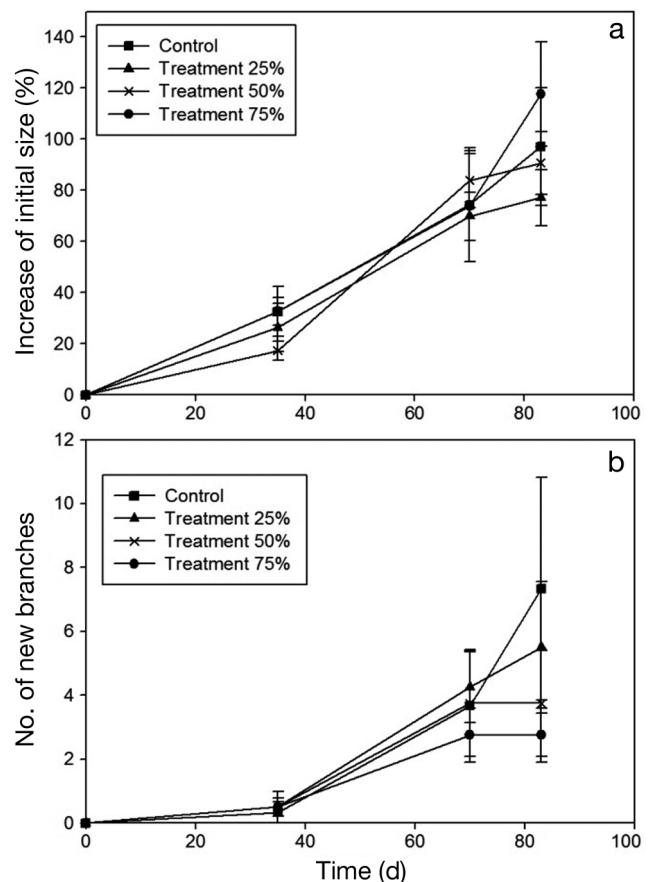


Fig. 2. (a) Proportion of new growth of first-generation donor colonies of staghorn coral *Acropora cervicornis* standardized by initial size (expressed as a percentage) over time. There was no statistically significant effect of experimental treatment on productivity of first-generation donor colonies over time ($p = 0.934$). (b) Number of new branches acquired over time by treatment. There was no statistically significant effect of experimental treatment on the rate of new branch acquisition ($p = 0.976$). Error bars represent \pm SE

Propagating a first-generation nursery colony of a mean size of 48.19 \pm 4.74 cm is expected to produce between 2.25 \pm 0.95 and 6.25 \pm 1.03 new 5 cm fragments yr⁻¹ depending on the chosen level of fragmentation (Table 1). When new growth of both fragmented donors and resulting second-generation fragments was combined, the combined amount of new growth increased with the level of fragmentation (Fig. 3).

DISCUSSION

Rearing coral colonies in a nursery is a relatively simple and increasingly common method for restoring populations of *Acropora cervicornis* on Carib-

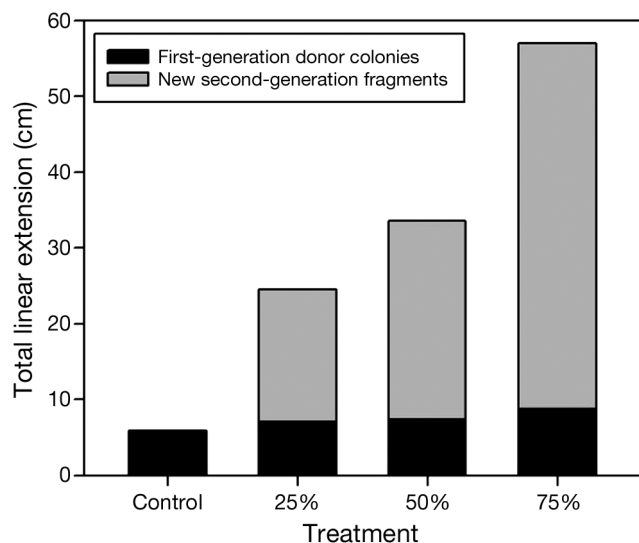


Fig. 3. Total amount of new growth of staghorn coral *Acropora cervicornis* donor colonies and resulting second-generation fragments after the conclusion of the study (83 d) by treatment, standardized by initial size

Table 1. Mean productivity (\pm SE) of the staghorn coral *Acropora cervicornis* nursery per year calculated by combining the growth rates of donors and second-generation fragments, and accounting for the mean number (\pm SE) of 5 cm second-generation fragments produced by treatment

| Fragmentation (%) | Productivity (cm yr ⁻¹) | No. of second-generation fragments |
|-------------------|-------------------------------------|------------------------------------|
| 0 | 4.17 \pm 1.01 | 0 |
| 25 | 12.65 \pm 3.89 | 2.25 \pm 0.95 |
| 50 | 17.42 \pm 2.82 | 3.75 \pm 0.48 |
| 75 | 31.87 \pm 8.04 | 6.25 \pm 1.03 |

bean reefs (Bowden-Kerby 2001, Herlan & Lirman 2009). The urgent need to minimize reliance on collections from scarce wild colonies demands measures to maximize the intrinsic productivity of nurseries. This study established that up to 75% of a donor coral can be clipped to create new fragments without negatively affecting the donor's survivorship, growth, or rate of branch acquisition after 83 d. During this study, fragmenting 75% of the tissue of a first-generation colony resulted in an 8-fold increase in overall nursery productivity when the growth of the fragmented first-generation colony and its resulting second-generation colonies are considered together. No fragmentation threshold beyond which first- and second-generation colonies are likely to suffer mortality or decreased growth was detected in this study, indicating that

this value lies beyond 75%. However, these results should be carefully interpreted given the limited temporal scope of the study.

Our results indicated no difference in the rate of addition of new branches among experimental treatments. Due to the relatively short duration of this experiment (i.e. 3 mo) our study may have failed to capture differences in the rate of branch acquisition, which may emerge over longer temporal scales. A longer study (e.g. 12 mo) is recommended to determine whether a higher percent of fragmentation results in a faster rate of addition of new branches. If this is the case, the considerations of space availability for propagation approaches using 75% fragmentation must be regarded as conservative.

A further caveat to consider when interpreting the lack of a treatment effect in our study is the number of samples in the context of statistical power. Given that our experiment was conducted on a small-scale nursery, and aimed to minimize the amount of tissue collected from wild colonies, a small number of samples per treatment was used ($n = 4$). Such small sample sizes may have precluded the capacity of the statistical tests aimed at detecting treatment effects, particularly when effects were weak and variability was large. Standard deviation (SD) increased with time for both growth (from 0.15 to 0.33) and branching rates (from 0.64 to 3.85). A power analysis indicated that with our sample size, differences in growth among treatments had to be ≥ 0.35 cm branch⁻¹ d⁻¹ at the beginning of the study and ≥ 0.78 cm branch⁻¹ d⁻¹ at the end of our experiment in order to be detected as significant with 0.80 probability. Similarly, for significant differences in branching rate to be detected, these would have had to be ≥ 1.5 branches d⁻¹ at the beginning of the study and ≥ 9.2 branches d⁻¹ at the end of the experiment. The magnitude of the observed inter-treatment differences also increased over time, but remained below these thresholds for both growth rate ($\Delta = 0.45$ cm branch⁻¹ d⁻¹) and branching rate ($\Delta = 0.17$ –4.6 branches d⁻¹). This indicates that our study would have benefited from larger sample sizes ($n = 12$) to maximize the chances of detecting treatment effects. Larger sample sizes will be possible in larger nurseries, or at a future stage when the Little Cayman nursery is larger and more developed.

Mortality was not observed among fragmented first-generation colonies or resulting fragments during the course of this study. This is consistent with other *A. cervicornis* nurseries in the Caribbean region, which typically exhibit high survivorship

(i.e. >70%) during the first year after propagation (Young et al. 2012). Growth of branches monitored in this study was consistent with published measurements for *A. cervicornis* (Tunncliffe 1983). High water quality in Little Cayman and a lack of environmental disturbance during the course of the study likely contributed to the lack of mortality and positive growth trend observed among the nursery population.

Ward (1995) found that fragmentation has the potential to increase susceptibility of fragmented donors and resulting fragments to stressors such as storms and disease outbreaks. For this reason, we recommend avoiding fragmentation during peak hurricane season (i.e. June to November), when storms have a higher probability of directly damaging corals and leading to spikes in disease prevalence (Knowlton et al. 1981, Brandt et al. 2013, Miller et al. 2014).

Despite the lack of observed mortality or decreased growth and branching, fragmentation has been found to have long-term impacts on fecundity in some coral species (Smith & Hughes 1999, Lirman 2000, Okubo et al. 2007). Temporary loss of fecundity is thought to be a result of corals shifting resources from reproduction to repair and growth following fragmentation (Szmant 1986, Lirman 2000, Okubo et al. 2007). In *A. palmata*, naturally fragmented colonies and resulting fragments did not produce gametes until 4 yr after fragmentation (Lirman 2000). Further studies are required to determine the effect of fragmentation on fecundity in *A. cervicornis*. Until more information on fecundity following fragmentation is available for *A. cervicornis*, it may be prudent to avoid fragmenting nursery colonies immediately prior to outplanting to minimize any potential recovery time.

Determining the optimal level of fragmentation during propagation must involve careful analysis of the availability of space in the nursery, the cost involved in ensuring all structures remain clean and functional, and local restoration goals. Fragmenting large portions of first-generation colonies would obviously produce the largest number of new corals but would require the largest amount of space and may exceed the number of transplants required locally. The results presented here may serve as guidelines to extrapolate short-term productivity of small-scale nurseries over different time scales, thus enabling restoration managers to adjust nursery productivity to meet specific conservation goals. Nursery expansion or frequency of transplantation events can therefore be planned to suit both nursery space avail-

ability and feasible numbers of transplants required in local reefs.

Genetic diversity should also be carefully considered during fragmentation. This study did not allow us to test the effect of genotype on productivity due to low replication within treatments. However, differences in genotype have been shown to impact growth rate and survivorship (Bowden-Kerby 2008, Griffin et al. 2012, Lirman et al. 2014). Therefore, individual growth rates of genotypes should be monitored in order to detect genotypic differences, and fast-growing genotypes should be fragmented less frequently or fragmented to produce fewer new colonies. This type of strategy will prevent genetic imbalances within nurseries. It is important to maintain genetically diverse populations within nurseries to avoid adverse conditions during transplantation such as founder effects or genetic swamping (Baums 2008).

A maximum fragmentation approach may be ideal for expanding a small-scale nursery provided there is adequate space availability. It is important to note that the results presented here are only applicable to propagation within a coral nursery, and a 75% fragmentation strategy is likely not optimal for removal of tissue from a wild donor colony given risks to fecundity and increased susceptibility to storm damage and disease. Our study can be used to plan nursery development and expansion, thus facilitating restoration and conservation efforts for *A. cervicornis* throughout the Caribbean region. In addition to species-specific considerations, these findings could be relevant for other branching coral species with similar growth rates and asexual reproduction strategies, but may not be appropriate for species less adapted to natural fragmentation.

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Appendix. Table A1. Mean \pm SE growth rate (measured as cm new growth standardized by initial size) and branching rate (mean number of new branches) per genotype (A–D) of staghorn coral *Acropora cervicornis* at different survey times

| Genotype | 35 d | 70 d | 83 d |
|-----------------------|-----------------|-----------------|-----------------|
| Growth rate | | | |
| A | 0.19 \pm 0.05 | 0.59 \pm 0.09 | 0.72 \pm 0.09 |
| B | 0.31 \pm 0.13 | 0.89 \pm 0.17 | 1.19 \pm 0.03 |
| C | 0.21 \pm 0.06 | 0.56 \pm 0.14 | 1.16 \pm 0.04 |
| D | 0.27 \pm 0.01 | 0.95 \pm 0.20 | 1.06 \pm 0.30 |
| Branching rate | | | |
| A | 0.00 \pm 0.00 | 1.33 \pm 0.33 | 3.75 \pm 2.43 |
| B | 0.75 \pm 0.48 | 3.00 \pm 1.08 | 5.33 \pm 1.76 |
| C | 0.33 \pm 0.33 | 5.67 \pm 1.33 | 7.67 \pm 2.91 |
| D | 0.50 \pm 0.50 | 3.33 \pm 1.67 | 3.33 \pm 1.67 |

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