



## RESEARCH ARTICLE

# Restoration success limited by poor long-term survival after 9 years of *Acropora cervicornis* outplanting in the upper Florida Keys, United States

Tiffany S. Boisvert<sup>1,2</sup> , Rob R. Ruzicka<sup>1</sup>, Stephanie A. Schopmeyer<sup>1</sup>, Christopher D. Stallings<sup>2,3</sup> 

The degradation of coral reefs has resulted in the expansion of coral reef restoration projects worldwide. In the tropical western Atlantic, most restoration efforts focus on outplanting *Acropora cervicornis*, once a dominant reef-building branching coral, now found predominantly in spatially isolated populations. Hundreds of thousands of *A. cervicornis* colonies are outplanted onto degraded reefs every year; however, long-term growth and survival data of outplanted corals is limited. In this study, we assessed the long-term restoration of *A. cervicornis* by determining the relationship between surviving outplant populations and restoration effort. We surveyed coral populations at 11 sites in the upper Florida Keys that represented a gradient of restoration effort, defined by the total number of outplants, number of outplanting years, and time since last outplanting. We found a negative relationship between the amount of *A. cervicornis* live tissue and time since last outplanting, suggesting that outplants are not surviving longer than 2 years. In addition to restoration effort, we investigated how past and present benthic community metrics such as coral density and diversity may influence long-term outplant survival. We found a positive relationship between the amount of live *A. cervicornis* tissue and pre-restoration coral density, suggesting that areas that previously supported dense populations of corals may facilitate restoration success. Ultimately, this study finds that restored *A. cervicornis* populations decline over time, and continued outplanting effort is needed for the persistence of the species in certain areas. This study also highlights the need for more long-term monitoring to inform adaptive management and restoration strategies.

**Key words:** acroporid, coral population enhancement, coral outplanting, coral transplantation, long-term monitoring, restoration success

## Implications for Practice

- In the upper Florida Keys, nursery-raised *Acropora cervicornis* outplanted from 2012 to 2020 did not result in long-term survival of populations.
- Due to frequent and intense disturbances, focusing restoration biennially at fewer sites known to have success is likely more pragmatic than focusing across a greater number of sites on 1- to 2-year time frames.
- We suggest that long-term monitoring of coral reef restoration efforts should be emphasized to better understand factors associated with success.

## Introduction

Over the last half century, natural and anthropogenic drivers have caused major global declines in coral population sizes and changes in the composition of reef communities (Hoegh-Guldberg et al. 2007; Lough et al. 2018). Climate change has led to higher water temperatures, which have increased the frequency and severity of bleaching, disease outbreaks, and major storms (Baker et al. 2008; Ruiz-Moreno et al. 2012; Hughes et al. 2018), while local stressors such as poor water quality (De'ath & Fabricius 2010), increased turbidity from coastal construction, dredging operations (Miller et al. 2016), and

overfishing (Hughes et al. 2007) have contributed to further degradation. To mitigate coral declines, coral propagation and restoration have become increasingly popular practices (Rinkevich 2005; Young et al. 2012; Boström-Einarsson et al. 2020). However, the application of restoration design and techniques is still in its infancy, and the long-term success of restoration programs is often not well understood, especially at time frames that exceed 2 years after outplanting (Hein et al. 2017). Based on literature reviews of past coral

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<sup>1</sup>Florida Fish and Wildlife Conservation Commission, Fish & Wildlife Research Institute, 100 8th Avenue SE, Saint Petersburg, FL 33701, U.S.A.

<sup>2</sup>University of South Florida College of Marine Science, 140 7th Ave South, Saint Petersburg, FL 33701, U.S.A.

<sup>3</sup>Address correspondence to C. D. Stallings, email [stallings@usf.edu](mailto:stallings@usf.edu)

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reef restoration efforts, the mean duration of monitoring was less than 2 years, which may be sufficient for evaluating transplantation techniques, but not appropriate for evaluating their contribution to population enhancement or re-establishing coral communities (Hein et al. 2017; Boström-Einarsson et al. 2020). Thus, there is a need to evaluate the long-term (e.g. ≥5 years) success of coral reef restoration efforts and identify factors that may contribute to survival.

A major goal of coral reef restoration is to mitigate or reverse degraded reefs by enhancing reef-building coral populations. As reef-building corals are lost, space is opened for the colonization of fast-growing and weedy species of stony coral, macroalgae, and octocorals (McManus & Polsenberg 2004; Ruzicka et al. 2013; Bell et al. 2021). Once these organisms become dominant, recruitment for most coral species is inhibited, leading to the formation of non-scleractinia alternative stable states (Dudgeon et al. 2010; Harper et al. 2023). Overall, the result of these shifts is a degraded reef with decreased coral species richness and diversity, which are closely linked to the health and resiliency of reefs, and in turn linked to many ecosystem functions and services (Graham et al. 2013). Active coral reef restoration serves to immediately replenish the reef with reef-building coral colonies and adds potential for long-term benefits to reef communities through increased coral cover, enhanced richness and diversity, and improved habitat structure. By improving coral cover, restoration ultimately could have the capacity to improve local resilience (Shaver et al. 2022) and ensure the sustainability of the ecosystem services that reefs provide (e.g. fisheries, tourism, and coastal protection). However, this assumes that restoration efforts will produce coral populations that survive long term, become sexually reproductive, and can become self-sustaining, despite continued losses that stem from natural disturbances and persisting anthropogenic stressors (SER 2004). Therefore, restoration must be performed at a frequency and scale that overcomes present-day disruptions from global and local stressors that have already significantly reduced reef condition and quality. This includes collecting information about where restoration might be most successful based on the past and current state of the reef and making decisions about how to effectively distribute outplanting effort on reefs in sufficient abundance to achieve optimal long-term success.

In the broader tropical western Atlantic (TWA) region, staghorn coral (*Acropora cervicornis*) and elkhorn coral (*A. palmata*) have been the most frequently used species for restoration (Young et al. 2012; van Woesik et al. 2020). Both species were once the principal reef builders of TWA shallow forereefs, with *A. palmata* occupying the shallow reef crest, and *A. cervicornis* being abundant in the surrounding deeper reef zones and back reef (Cramer et al. 2020). Currently, these species are both listed as threatened under the Endangered Species Act (NMFS et al. 2014) and critically endangered on the World Conservation Union red list (World Conservation Union 2022), warranting the need for population enhancement and restoration. *A. cervicornis* is among the fastest growing corals, with mean linear growth up to 7 cm per year (Gladfelter et al. 1978; Tunnicliffe 1983) and a branching

morphology that can create dense thickets that provide structural complexity known to promote high biodiversity on coral reefs (Miller et al. 2002; Alvarez-Filip et al. 2009). The branching structure of *A. cervicornis* is beneficial to practitioners because colonies can be easily propagated via asexual fragmentation in situ nurseries, which results in increased growth in all directions (Johnson et al. 2011). Despite the qualities that make *A. cervicornis* an ideal restoration species, acroporids are highly susceptible to disease outbreaks, thermal stress, and hurricanes, all of which have been responsible for their decline (Aronson & Precht 2001; Precht & Miller 2007).

Large-scale coral outplanting of *A. cervicornis* has occurred for over two decades in the TWA, with practitioners outplanting hundreds of thousands of corals each year (Boström-Einarsson et al. 2020), but whether these activities have translated into successful restoration has rarely been evaluated. Most post-outplant monitoring does not extend beyond 2 years due to grant restricted timelines and the high cost of performing long-term in situ assessments. Permitting obligations generally establish a 1- to 2-year requirement to assess post-outplant survival (Boström-Einarsson et al. 2020; Hein et al. 2020) but often focus on the short-term health and condition of the outplants. Although survival and growth rates of outplanted coral on this time scale may reach benchmarks considered to reflect initial outplanting success (Schopmeyer et al. 2017), evaluation of the long-term benefits to reef function and service are limited and do not consider whether the outplants have the potential to contribute to natural recovery (Johnson et al. 2011; Carne & Baums 2016). Of the few studies that have evaluated outplant performance beyond 2 years, most have found decreased survival through time and low retention of colonies (Garrison & Ward 2012; Forrester et al. 2014; Ware et al. 2020) with survivorship dropping to less than 10% after 7 years (Ware et al. 2020). Even though higher long-term outplant survival has been observed on reefs less degraded than those in Florida (e.g. Belize) (Carne et al. 2016), these examples are rare, highlighting the importance of understanding restoration outcomes beyond those immediately following outplanting and factors that may contribute to long-term survival.

To better understand if *A. cervicornis* outplanting efforts have provided long-term restoration benefits in Florida, we evaluated the relationship between current *A. cervicornis* population status and outplanting effort at 11 sites in the upper Florida Keys over 9 years. We used criteria from previous studies and literature reviews to define long-term restoration success as the survival of the outplants for at least 5 years after outplanting (Hein et al. 2017; Boström-Einarsson et al. 2020). The 11 sites represented a gradient of restoration effort, which varied in the total number of outplants received, the number of years over which outplanting occurred, and the amount of time since last outplanting. In addition to the outplanting effort, we investigated how past and present benthic community metrics such as pre-outplanting coral density or diversity and the contemporary abundance of competing reef taxa affected restoration success. We used coral demographic surveys to estimate the total linear extension (TLE) of live tissue

(cm) on restored *A. cervicornis* to specifically address the following questions: (1) What is the relationship between the  $TLE_{live}$  of restored *A. cervicornis*, outplanting effort, and restoration success?; and (2) was the  $TLE_{live}$  of restored *A. cervicornis* related to pre-outplant coral cover, density, diversity, or present-day abundance of spatial competitors such as macroalgae and octocorals?

## Methods

### Site Selection

We conducted this study in the upper Florida Keys, United States, a region that has been the recipient of large-scale *Acropora cervicornis* outplanting efforts. Sites chosen for this study were selected

using State of Florida permit information that quantified the number of *A. cervicornis* colonies outplanted between 2012 and 2020. The 11 study sites were shallow spur-and-groove reefs that ranged in depth from 3 to 10 m. Outplanting was conducted by a single practitioner, which minimized the introduction of differences in outplanting techniques and the restoration objectives of different practitioners. We defined restoration effort in three ways: (1) total number of corals outplanted on the site from 2012 to 2020, (2) total years of outplanting on the site (i.e. the number of years outplanting occurred between 2012 and 2020), and (3) time (in years) since the last outplanting effort, all of which varied across sites (Fig. 1). From 2012 to 2020, effort ranged between 200 and 7080 outplants per site, and cumulatively, a total of 21,089 corals were outplanted across all sites aggregated for all years. The total years of

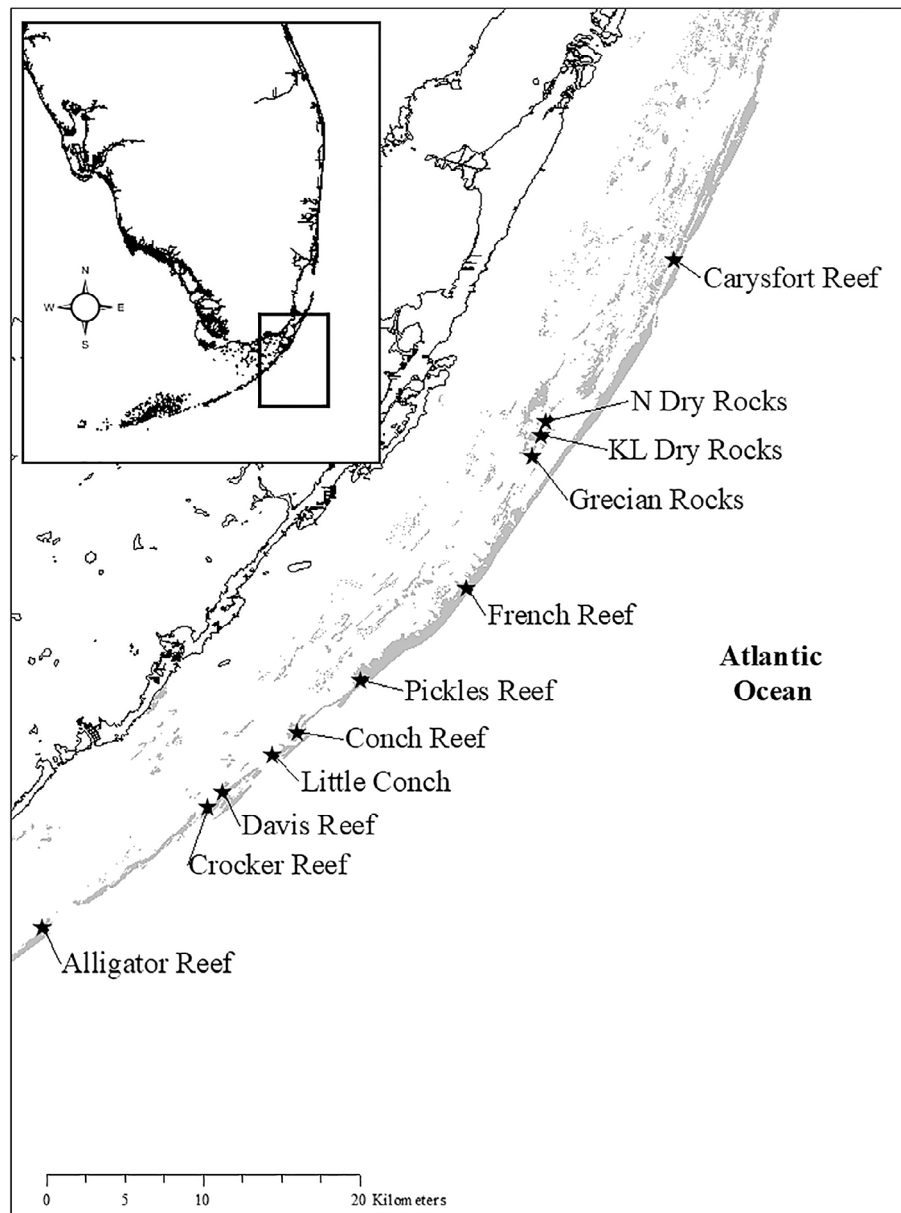


Figure 1. Map of study sites. All sites are located on forereefs in the upper Florida Keys and served as targets for coral reef restoration effort between 2012 and 2020.

**Table 1.** The total number of outplants, total years of outplanting effort, time since last outplant, and the total number of observed outplant colonies in October 2020 with respective calculations of total linear extension of live tissue (TLE<sub>live</sub>).

| Site               | Reported no. of outplants | Total years of outplanting | Years since outplant | Observed no. of outplants | Total TLE <sub>live</sub> |
|--------------------|---------------------------|----------------------------|----------------------|---------------------------|---------------------------|
| Conch Reef         | 2600                      | 6                          | 0                    | 120                       | 2273                      |
| North Dry Rocks    | 2777                      | 3                          | 1                    | 120                       | 2004                      |
| Pickles Reef       | 7080                      | 9                          | 0                    | 108                       | 1615                      |
| Grecian Rocks      | 1536                      | 1                          | 1                    | 67                        | 842                       |
| Carysfort Reef     | 3148                      | 4                          | 1                    | 55                        | 777                       |
| French Reef        | 200                       | 1                          | 4                    | 31                        | 411                       |
| Davis Reef         | 1002                      | 3                          | 4                    | 18                        | 216                       |
| Little Conch Ledge | 1482                      | 2                          | 4                    | 0                         | 0                         |
| Alligator Reef     | 506                       | 1                          | 4                    | 0                         | 0                         |
| Crocker Reef       | 410                       | 1                          | 4                    | 0                         | 0                         |
| KL Dry Rocks       | 348                       | 3                          | 4                    | 0                         | 0                         |

outplanting varied from one to nine, and time since the last outplant ranged from 1 to 5 years (Table 1).

### Coral Population Demographics

In October 2020, we conducted demographic surveys at each site. We conducted all surveys using SCUBA and used the site coordinates within permit reports to locate outplants. Because coordinates are often used to denote large reef areas where outplants are located, we initially performed a roving diver survey to visually assess the presence of outplants and identified the area with the highest density of outplants. After this location was determined, all surveys were oriented in a manner that maximized overlap with the reef and avoided sand while including the area with the highest outplant density. If no outplants could be located during the roving diver survey, we surveyed the suitable reef area nearest the provided coordinates. We delineated the survey area with four parallel 25 m transects, separated by 10 m between each. For each 25 m transect, we completed 1 × 10 m belt transects between the 0–10 and 15–25 m distances. This resulted in eight belt transects surveyed per site. We divided effort equally between two types of demographic surveys: (1) all stony coral species present and (2) *A. cervicornis* only. To maintain the spatial balance of survey types, we alternated the locations of each type of belt transect within the 25 m transects (Fig. S1). In all, we surveyed 80 m<sup>2</sup> at each site for *A. cervicornis* and 40 m<sup>2</sup> for all coral species (Fig. S1). Although some wild *A. cervicornis* colonies may have been present at a site, all colonies within the transects were determined to be outplants based on the site being designated for outplanting by practitioners, the aggregation of colonies into “clusters” (a common outplanting technique used by restoration practitioners to encourage fusion of outplants of similar genotypes), the observance of epoxy at the bases of the colonies, and the presence of identification tags.

We recorded the maximum height, diameter, and percent mortality of adult (≥4 cm) coral colonies. We measured maximum height parallel to the axis of growth, from the lowest point of skeletal growth to the highest, and maximum diameter as the widest area of skeletal growth of the outward-facing

surface of a colony. We defined old mortality by the absence of corallite structure and the cause of death could not be determined. In contrast, we defined recent mortality by the presence of white skeletal tissue with an intact or slightly eroded corallite structure. In the case of recent mortality, we recorded the cause of death under the general categories of disease, predation, overgrowth or interaction with other biota, physical damage, and unknown.

### TLE of Live *A. cervicornis* Tissue

We calculated the amount of live *A. cervicornis* tissue by estimating TLE (cm) using the maximum height and diameter for each colony observed within the belt transects (Johnson et al. 2011). In its simplest form, TLE is the sum of all branch lengths within an entire colony. Therefore, this unit can incorporate colony morphology and represent the amount of coral tissue present. We estimated the TLE of live tissue (TLE<sub>live</sub>) by first calculating ellipsoid volume (EV):

$$EV = \frac{4}{3}\pi \times \frac{a}{2} \times \left(\frac{b}{2}\right)^2 \quad (1)$$

where  $a$  = maximum colony height, and  $b$  = maximum colony diameter. We then used the product from Equation (1) to estimate TLE of the entire colony (TLE<sub>total</sub>):

$$TLE_{total} = 10 \left[ \frac{\log_{10}(EV) - 0.201}{1.586} \right] \quad (2)$$

where the constants were from the predictive regression relationship derived by Kiel et al. (2012) specifically for *A. cervicornis*. Finally, because colony dimensions were inclusive of the entire colony skeleton, regardless of mortality, we accounted for our estimates of percent mortality (sum of old and recent mortality) to calculate TLE<sub>live</sub> using the following equation:

$$TLE_{live} = TLE_{total} \left( 1 - \left( \frac{\%old\ mortality + \%recent\ mortality}{100} \right) \right) \quad (3)$$



## Benthic Community Metrics

To evaluate how long-term restoration success might have been influenced by wild coral diversity and abundance at a site, we incorporated prior benthic community composition data in our analyses. All study sites had nearby (within 1500 m) pre-outplant coral demographic information available from the decade prior to restoration (2001–2011) from various long-term monitoring programs (Table S1). Because the pre-outplant information did not directly overlap with the specific location of our transects, we calculated site values as an average of all nearby transect data available. We calculated pre-restoration coral density, richness, evenness, and Shannon's diversity index for each site using data from three long-term monitoring programs between 2001 and 2011: (1) Coral Reef Evaluation and Monitoring Project (CREMP; FFWCC-FWRI 2021), (2) Disturbance Response Monitoring Program (DRM; FRP), and (3) Abundance, Distribution, and Condition of *Acropora* Corals, Other Benthic Coral Reef Organisms, and Marine Debris (SCREAM; CMS, UNCW 2012). Data from the following years were extracted for each program: CREMP (2011), DRM (2005–2011), and SCREAM (2001–2002, 2005–2006, 2009) (Tables S1 & S2). At minimum, each program collected adult ( $\geq 4$  cm) coral demographic information for a specific survey area at each site using belt transects that allowed for compatible calculations of values. All values were calculated with the *vegan* package (Oksanen et al. 2020) in R (R Core Team 2020).

In addition, we calculated the present-day percent cover for several benthic groups recognized as known spatial competitors with *A. cervicornis* to determine if their abundance was related to the  $TLE_{live}$  of outplants. We took benthic photos every 0.5 m along the eight transects, resulting in a total of 20 images per transect, and 160 images per site. We analyzed images using PointCount99 (Dustan et al. 1999) using 20 randomly placed points per image, totaling 400 points per transect, and 3200 per site. We identified points as *A. cervicornis*, scleractinian coral other than *A. cervicornis*, *Millepora* spp., macroalgae, octocorals, sponge, zoanthid, cyanobacteria, and substrate. We classified unidentifiable points as "unknown" and included them in the percent cover calculations. We then calculated cover by dividing the number of points identified in each category by the total number of points for each transect. We calculated macroalgae, zoanthids, sponges, and octocoral cover as each are fast-growing spatial competitors in the shallow forereef environment capable of inflicting mortality on corals (Lirman 2001; Ruzicka et al. 2013; van Woesik et al. 2018). In addition, we took into account the combined total of all spatial competitors (all groups except bare substrate and *A. cervicornis*) which may affect outplant success.

## Data Analysis

We used generalized liner mixed models (glmm) to examine  $TLE_{live}$  (response) as a function of the fixed effects of effort (total years of outplanting and time since last outplant), pre-outplanting benthic community metrics (coral density, richness, evenness, and Shannon's diversity), and present-day benthic community metrics (individual terms of macroalgae

and octocoral cover, combined macroalgae and octocoral cover, all spatial competitors combined, non-*A. cervicornis* coral cover, and available substrate) (Table S3). A random effect of "site" was added to each model to account for multiple transects within-site. We assumed that all colonies were approximately the same size at outplanting; thus we expected a proportional increase in  $TLE_{live}$  relative to the total number of outplants observed at each site. We therefore included an offset for the total number of outplants.

Prior to model selection, we assessed collinearity among predictors to ensure the reliability of parameter estimates and avoid misidentification of important predictors (Dormann et al. 2013). In the case of high collinearity ( $>0.7$ ; Dormann et al. 2013), we chose to keep predictors that best answered our study questions regarding effort and benthic community metrics. We found two cases of high collinearity among predictors. The first was between total years of outplanting and the time since last outplant. We retained time since last outplant to understand the long-term success of restoration (i.e. survival and growth of colonies) rather than the role of total years (i.e. frequency of outplanting), because we were mainly interested in whether outplanted populations were surviving through time. The second was between pre-outplant calculations of coral richness, evenness, and Shannon's diversity. We chose to keep Shannon's diversity as this metric incorporates both richness and evenness. We excluded the other highly correlated terms prior to model selection.

Model selection was carried out in two stages. First, we tested the suitability of three types of error distributions and five types of glmm using the package *glmmTMB* (Brooks et al. 2017). Overall, two types of zero-inflated (nbinom1 and nbinom2), two types of negative binomial (nbiom1 and nbiom2), and a single hurdle model (truncated\_nbinom1) were compared with Akaike Information Criterion (AIC) corrected for small sample size (AICc). The negative binomial (nbinom1) had the best fit for the data and was used throughout. Second, we assessed the significance of each predictor term in a backward stepwise manner, in which all terms were used in the initial model and were sequentially removed based on AIC. Contending models were further assessed for goodness of fit through dispersion test, quantile-quantile residual plots, and residual versus predicted plots using the *DHARMa* package (Hartig 2021). The most parsimonious model included three fixed effects: (1) time since last outplant, (2) pre-restoration coral density, and (3) pre-restoration Shannon's diversity. We used *ggplot2* (Wickham 2013) for visualizing effects and conducted all data analyses using the R Statistical Environment (R Core Team 2020).

## Results

$TLE_{live}$  was highest at sites that had received outplants within 2 years of our study and lowest for sites with 4 or more years since the last outplanting effort (Table 1). Accordingly, time since the last outplant was found to be negatively related to  $TLE_{live}$  (coefficient [SE] =  $-0.58$  [0.2],  $z = -2.8$ ,  $p < 0.01$ ) (Fig. 2). We observed no living *Acropora cervicornis* outplants at 4 of the 11 sites, despite a thorough search during both the preliminary roving diver surveys and the belt transects.  $TLE_{live}$

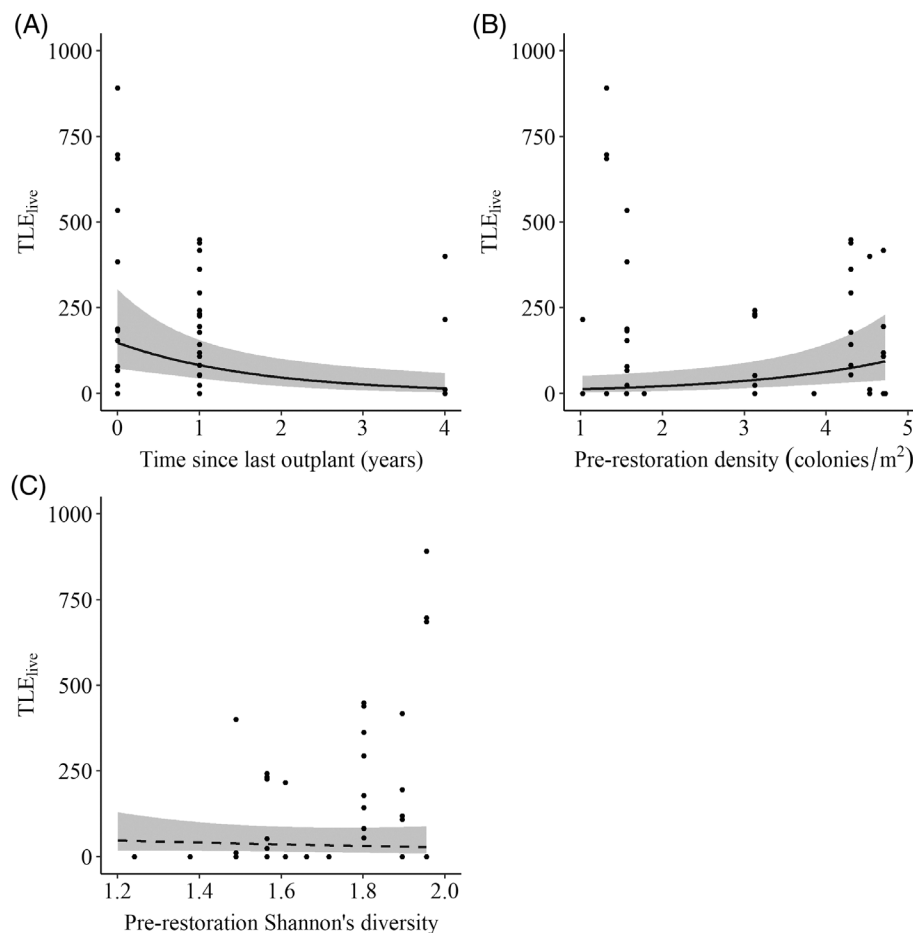


Figure 2. Relationships between  $TLE_{live}$  (coefficient [SE]) and model predictors. (A) Time since last outplant ( $-0.58$  [0.2],  $z = -2.8$ ,  $p < 0.01$ ), (B) pre-restoration density ( $0.55$  [0.2],  $z = 2.6$ ,  $p = 0.01$ ), and (C) pre-restoration Shannon's diversity ( $-0.71$  [0.8],  $z = -0.8$ ,  $p = 0.40$ ). Points represent the raw data for each of the 88 transects, where one point may represent multiple transects of the same value, and the line represents the predicted values from the final model. Intervals represent 95% CIs.

at the seven sites with surviving outplants averaged  $14.5 \text{ cm}^2/\text{m}^2$  ( $SE = 3.8$ , min–max =  $2.7$ – $28.4 \text{ cm}^2/\text{m}^2$ ). A total of 519 outplants were observed within our transects across the seven sites. Of these 519 outplants, 139 (26%) had recent mortality associated with evidence of predation and disease. Among the 139 colonies with recent mortality, 52% of colonies displayed evidence of predation, while 39% showed signs of disease.

The  $TLE_{live}$  of restored *A. cervicornis* was also related to one of the pre-outplant ecological factors but was not related to any present-day benthic community metrics.  $TLE_{live}$  was positively correlated with pre-restoration coral density (coefficient [SE] =  $0.55$  [0.2],  $z = 2.6$ ,  $p = 0.01$ , colonies/m<sup>2</sup>) (Fig. 2) but was not significantly correlated with pre-restoration Shannon's diversity ( $p = 0.4$ ). There was no significant relationship between  $TLE_{live}$  and the present-day cover of either macroalgae ( $p = 0.9$ ), octocorals ( $p = 0.9$ ), macroalgae and octocorals combined ( $p = 0.9$ ), all spatial competitors combined ( $p = 0.8$ ), non-*A. cervicornis* coral cover ( $p = 0.4$ ), or available substrate ( $p = 0.9$ ), so all terms were excluded from the final model.

In terms of achieving long-term benefits, the overall mean cover and density of coral were low across all sites but were highest at those with *A. cervicornis* outplants present. At the six sites in which *A. cervicornis* cover was detectable, *A. cervicornis* cover was 1.76% ( $SE = 0.46$ , min–max =  $0.3$ – $3.35$ ), which was nearly two times the non-*A. cervicornis* cover of 0.9% ( $SE = 0.2$ , min–max =  $0.13$ – $1.78$ ). *A. cervicornis* density was  $2.22 \text{ colonies/m}^2$  ( $SE = 0.4$ , min–max =  $1.1$ – $3.63$ ) at these six sites. Although non-*A. cervicornis* species of coral cover (0.7%,  $SE = 0.5$ , min–max =  $0$ – $1.8$ ) (Table S2) and density ( $2.2 \text{ colonies/m}^2$ ,  $SE = 0.4$ , min–max =  $0.8$ – $4.3$ ) were low across all sites, they were lowest at the four sites without measurable *A. cervicornis* cover (0.44%,  $SE = 0.2$ , min–max =  $0.1$ – $1.3$  and  $2.0 \text{ colonies/m}^2$ ,  $SE = 0.6$ , min–max =  $0.8$ – $4.3$ ) (Table S4).

## Discussion

This study provides evidence that *Acropora cervicornis* outplanting at the 11 study sites over 9 years in the upper Florida Keys has not translated into long-term species enhancement or

broad restoration success. Four of the 11 sites had no detectable *A. cervicornis*, indicating variability in outplant survival, similar to the findings of Banister and van Woesik (2021), and that site conditions, the number of outplants, or the frequency of outplanting did not contribute to the long-term survival of outplants at some sites in the upper Florida Keys. Although *A. cervicornis* cover was higher than the wild coral cover at four sites, each of these sites had received outplants within the last 2 years. In addition, the observed negative relationship between the amount of live tissue and time since the last outplanting effort suggests that the long-term survival (>5 years) of outplants was minimal across all sites, and thus, continued outplanting would be required to maintain an *A. cervicornis* population in the upper Florida Keys. Our results also documented a positive relationship between live tissue and pre-restoration coral density indicating that sites with higher scleractinian density in the past can aid in the decision-making process regarding where restoration may be better focused.

In our study,  $TLE_{live}$  values were highest for sites that received outplants within 2 years while sites that had not received outplants for 4 or more years had the lowest  $TLE_{live}$  or no surviving outplants. These findings show that outplants were unable to survive long term and are unlikely to repopulate on their own. To have successful *A. cervicornis* restoration, outplants need to survive and grow to a point that they reproduce naturally through sexual reproduction and withstand disturbances such that they no longer require population enhancement from practitioners (SER 2004). Unfortunately, this level of success has been achieved in only a few restoration projects. For example, restoration in a protected area of Belize resulted in *A. cervicornis* populations that expanded in size and were reproductively active after 5 years (Carne et al. 2016) and efforts to restore an area damaged by a ship grounding in Puerto Rico created a self-sustaining thicket over 8 years (Griffin et al. 2015a). However, these examples of successful long-term restoration each received sustained effort with outplanting being carried out continuously over multiple years and at higher frequencies than those in this study. In addition, it is possible that reefs in these areas may be less degraded (e.g., have much greater pre-restoration coral density than those in this study) allowing for a higher chance of success. Although we recognize that our study design likely led to some outplants being undetected at our sites, roving diver surveys confirmed that the four sites in this study without recent replenishment of outplants had a complete absence of *A. cervicornis* after a combined 2398 colonies were outplanted. If outplants were unable to persist at these four sites, it is possible that populations at the other seven restoration sites in this study may not persist unless outplanting efforts continue.

Multiple short-term studies have demonstrated high rates of mortality within 2 years of outplanting (Drury et al. 2017; Ladd et al. 2019; van Woesik et al. 2021) and long-term studies have documented an increasing rate of mortality through time (Garrison & Ward 2012; Ware et al. 2020). Among the surviving outplants observed in this study, nearly a third of them displayed recent mortality, largely attributed to predation or disease. Predation has often hampered early outplanting success

because the newly introduced tissue is preferentially targeted by corallivores (Miller et al. 2014b; Cano et al. 2021). Similarly, diseases have been a pervasive problem for wild, nursery-reared, and outplanted populations of acroporids (Miller et al. 2014a; Weil et al. 2020). In addition to these colony-level causes of mortality, large-scale disturbances can have negative effects on outplanted populations. Along Florida's Coral Reef, two major disturbances occurred between 2012 and 2020. First, the 2014–2015 El Niño caused extreme thermal stress, leading to greater bleaching and disease susceptibility in those years (Drury et al. 2017; Hoogenboom et al. 2017; Muller et al. 2018). Additionally, Hurricane Irma, one of the most powerful storms to directly strike the Florida Keys in the last 50 years, made landfall in September of 2017 and caused a widespread loss of outplants by means of displacement, breakage, scouring, and sedimentation (Lohr et al. 2020). Due to the proximity of the sites to one another, it is possible that Hurricane Irma was responsible for the few or lack of outplants found at four of the sites in this study, which were no longer targeted for restoration after the storm. Although outplants may go years without enduring a major disturbance, monitoring at time frames that do not capture the effects of these events can result in misleading conclusions about long-term success (Goergen et al. 2019).

Given the susceptibility of *A. cervicornis* to abiotic stressors, the location of outplanting within reefs is also an important consideration to minimize disturbance and promote successful restoration (Shaver et al. 2020). Recent mapping in the Florida Keys suggested that backreef, deeper forereef, and patch reef habitats can support natural and outplanted *A. cervicornis* populations (Miller et al. 2008; van Woesik et al. 2020). These habitats have low to moderate wave energy, moderate to high water flow, moderate to high turbidity, and low irradiance, all conditions favorable for *A. cervicornis* (Done 1982; D'Antonio et al. 2016; van Woesik et al. 2020). In contrast, outplanted *A. cervicornis* in the shallow forereef locations are exposed to higher levels of light and wave energy that cause bleaching and damage from storm-driven surge (Safuan et al. 2020; Stainbank et al. 2020; van Woesik et al. 2021). Although within-site placement of the outplants was not directly addressed as a part of this study, sites with the highest values of  $TLE_{live}$  were those with outplants situated within sections of the forereef that were deeper than the reef crest or within hardbottom surrounding the spur formations. Outplanting effort was also greater at these within-reef locations after the passing of Hurricane Irma, suggesting that after 2017, the within-reef placement of outplants may have been adjusted due to the poor survival of *A. cervicornis* in shallow forereef areas that were exposed to greater surge and irradiance. Specifically, for upper Florida Keys future restoration efforts, outplanting should avoid locations like the reef crest at shallow forereefs and more importantly consider other habitat types or locations other than shallow forereefs which will provide *A. cervicornis* with better conditions for long-term survival.

Additionally, we found that reefs that supported high coral densities in the past may be better suited for the long-term survival of *A. cervicornis* outplants. Existing coral cover has long

been considered an important factor for selecting reefs for restoration (Ladd et al. 2018; Ogden-Fung et al. 2020), as it may reflect a positive baseline status of the reef and probable outplant success (English et al. 1997). Coral diversity is also an important feature used to select restoration locations as it may indicate resiliency which promotes species persistence after disturbance (Graham et al. 2011; Baskett et al. 2014). However, Shannon's diversity was not related to  $TLE_{live}$ , thus coral diversity was not a good predictor of *A. cervicornis* restoration success compared to coral density in the upper Florida Keys. Likewise, macroalgae and octocoral cover were not related to the observed  $TLE_{live}$  of outplants, despite their high abundance across all sites. Although macroalgae and octocorals are strong spatial competitors on modern reefs (Bruno et al. 2009; Ruzicka et al. 2013), their effect on *A. cervicornis* long-term survival is possibly diluted due to their ubiquitous distribution and high abundance among sites in this study. However, their overwhelming presence is still relevant, as it further reiterates the declining state of reefs, and the need for coral restoration. Even a combination of all spatial competitors was not related to the observed  $TLE_{live}$  of outplants, pointing to other factors such as predation and disease as key influencers of survival. Although our models focused on biotic factors, we recognize that there are many other abiotic factors (e.g. temperature, irradiance, and water quality) that affect the survival of outplants that were not included as part of this study and should be monitored to identify other potential sources of mortality to optimize long-term survival. Additionally, incorporating resilience principles (e.g. project planning and design, coral selection, site selection, and broader ecosystem context; Shaver et al. 2022) and ecological processes (e.g. herbivory, competition, predation, and nutrient cycling; Ladd et al. 2018) into the design and implementation of coral reef restoration should be applied by practitioners to encourage long-term survival.

Currently, because environmental conditions remain poor and both acute and chronic stressors continue to hinder the long-term survival of the species, the feasibility and ethics of *A. cervicornis* restoration are important topics for discussion. Multiple advancements have improved early outplanting success, including size at outplanting (van Woesik et al. 2021), outplant density (Griffin et al. 2015b; Ladd et al. 2016), or the time of outplanting (Young et al. 2012) but strategies for achieving long-term survival and widespread population enhancement need improvement. Based on this study, we recommend that restoration practitioners focus site selection based on habitat characteristics that prove to be conducive to long-term survival by providing refuge from stressors. In addition, environmental variables such as salinity, temperature, irradiance, fetch, chlorophyll-a concentrations, and total nitrogen concentrations provide favorable conditions for the survival of outplanted *A. cervicornis* congeners (Banister et al. 2024). These factors and corresponding site selection can be species-specific. For example, this study shows higher persistence of *A. cervicornis* at sites with higher pre-outplant scleractinian coral percent cover and density from the decade prior to restoration. We also suggest that when sites that support long-term success are identified, practitioners redirect their efforts to these areas specifically,

focusing higher effort at select reefs, rather than spreading low effort across many reefs.

*A. cervicornis* restoration is likely to expand at additional locations in the coming years to attempt to recover historical levels of its spatial abundance. In 2020, an initiative was launched to restore seven iconic reefs in the Florida Keys over the next two decades, including Carysfort Reef used in this study (Mission Iconic Reefs; NOAA Fisheries 2019). One of the goals of this initiative is to outplant over 60,000 *A. cervicornis* colonies at these seven reefs, which is threefold the number of colonies that were outplanted over 9 years to the sites evaluated in this study. This ambitious project is estimated to cost up to \$4 M USD and require multi-partner cooperation to propagate, outplant, and monitor the survival of the corals. This initiative also looks to improve the efficacy of coral outplanting through site maintenance, such as planned visits to remove corallivorous predators from the area and efforts to increase the presence of important herbivores. Transitioning toward incorporating community and ecosystem-scale dynamics is important for addressing knowledge gaps on what effort is needed to improve the long-term survival of outplanted *A. cervicornis*, as well as other coral species populations. Eventually, these projects will need to develop ways to produce and maintain populations that survive long term without continuous outplanting and site maintenance.

Our study was unable to conclude that recent outplanting efforts have achieved long-term restoration success of *A. cervicornis* at sites in the upper Florida Keys. Our study did identify important considerations that the coral restoration community should consider when developing a strategic approach, such as integrating recurring outplanting efforts with carefully selected sites. Additionally, these efforts will need to be monitored over long-term time scales so that practitioners can make informed decisions about where efforts should be better focused. For reefs in the upper Florida Keys, it is important to consider that successful restoration of *A. cervicornis*, described as creating self-sustaining populations that survive, grow, and reproduce on their own, may never be achieved. However, this does not mean that restoration efforts are not needed. Instead, restoration can continue to augment these populations, allowing for the persistence of the species on Florida's Coral Reefs.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Distribution of  $1 \times 10$  m belt transects.

**Table S1.** Description of monitoring project, project site, and years for surveys included in calculation of pre-restoration metrics of density, richness, evenness, and Shannon's diversity.

**Table S2.** Past and present density, richness, evenness, and Shannon's diversity for the 11 study sites.

**Table S3.** Parameters of the glmm.

**Table S4.** Percent cover of major benthic groups at *A. cervicornis* outplant sites surveyed during this study.

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