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Continuous Effort Required to Maintain Populations of Outplanted *Acropora cervicornis* in the Florida Reef Tract, USA

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by

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Table of Contents

List of Tables

List of Figures

Abstract

The degradation of coral reefs due to natural and anthropogenic stressors has resulted in the expansion of coral restoration projects worldwide. In the Caribbean region, most restoration efforts focus on outplanting *Acropora cervicornis*, once a dominant branching coral, now found predominantly in spatially isolated populations. Thousands of *A. cervicornis* colonies are propagated within nurseries and outplanted onto degraded reefs every year. However, monitoring the long-term growth and survival of outplanted corals has been limited by financial, physical, and temporal constraints. In the current study, we assessed the long-term success of *A. cervicornis* restoration by determining the relationship between current populations and restoration effort. We surveyed coral demographics at 11 reefs 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 outplant. In addition to restoration effort, we investigated how past and present ecological factors of benthic cover and coral community composition affected restoration success. We found there was a negative relationship between the amount of live tissue and time since last restoration effort, suggesting that long-term survival of outplants was low. These results indicate that continuous restoration effort, likely on at least an annual basis, would be required to create lasting effects and promote success of restoration for *A. cervicornis* in the region. We also found a positive relationship between the amount of live tissue and pre-restoration coral density, indicating that areas that supported dense populations of corals may be more likely to experience restoration success. Since coral restoration will likely continue

to be an intensively used practice to mitigate coral loss, this study provides valuable information on the long-term fate of outplants and guidance for future restoration efforts.

Chapter One: 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 their 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 events (Baker et al. 2008; Hughes et al. 2018), while local stressors such as poor water quality (De'ath & Fabricius 2010), sedimentation (Miller et al. 2016), disease (Ruiz-Moreno et al. 2012), major storms, and overfishing (Hughes et al. 2007) have contributed to further degradation. To mitigate coral declines, restoration has become an increasingly popular practice (Rinkevich 2005). However, coral restoration is still in its infancy and the success of these programs is often not well understood, especially at time frames that exceed two years after outplanting. Thus, there is a need to determine long-term success and factors that may contribute to it to guide ongoing and future restoration efforts.

One goal of coral restoration is to mitigate or reverse the degraded state of a reef by enhancing coral populations. This is important, as the health and resiliency of coral reef ecosystems depend on ecological factors such as richness and diversity of the coral community (McClanahan et al. 2002; Baskett et al. 2014). Loss of reef-building corals allows for the colonization of fast growing and weedy species of stony coral, macroalgae, and octocorals (McManus & Polsenberg 2004; Ruzicka et al. 2013). Resultant shifts in the benthic community structure to non-reef building corals or non-scleractinian taxa make long-term recovery difficult (Hughes et al. 2010; Graham et al. 2013). Active coral restoration serves to immediately replenish the reef with coral colonies and adds potential for long-term benefits to reef communities through enhanced richness, diversity, and habitat structure. However, this does require that restoration efforts are long-lasting and produce populations that are able to sustain themselves despite disturbances and without continuous input. To do so, practitioners must overcome the global and local stressors on present-day reefs, where conditions no longer provide a thriving environment for many species of coral. This includes making decisions about which corals are best for restoration and how to distribute effort on reefs to result in successful restoration.

Large-scale coral restoration has occurred for over a decade, but whether these programs were successful is rarely evaluated past the initial two years after outplanting (reviewed by Bostrom-Einarsson et al. 2020). This limitation is likely due to specific requirements of grant-funded projects and the logistic impracticality of continuous monitoring. On this relatively short time scale, survival and growth rates of outplanted coral may reach benchmarks considered to reflect restoration success (Schopmeyer et al. 2017). These studies have found that short-term success is influenced by factors such as colony size at outplanting (van Woesik et al. 2021), outplant density (Ladd et al. 2016), season (Young et al. 2012), and site selection (Goergen & Gilliam 2018). Of the few studies that have monitored outplanted populations for more than two years, most have found decreased survival through time (Garrison & Ward 2012; Ware et al. 2020) with predicted survivorship less than 10% after seven years (Ware et al. 2020). Although long-term success may be possible (Carne et al. 2016), it is rarely documented, highlighting the need to focus on restoration outcomes beyond immediate post-outplant study.

In the broader Caribbean region, *Acropora cervicornis* (staghorn coral) has been the most used and studied species for restoration (Young et al. 2012). This species, along with *A. palamta* once dominated on shallow forereefs, with *A. palmata* dominating the shallow reef crest, and *A. cervicornis* dominating the surrounding deeper areas (Cramer et al. 2020). They are among the fastest growing corals, able to increase in size as much as 7 cm per year (Gladfelter et al. 1978), and have a branching morphology that creates 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 is beneficial to practitioners because colonies can be easily fragmented and suspended in *in-situ* nurseries, often using the branches to anchor the colonies to a structure that floats midway through the water column. This aids the propagation process by increasing the growth rate of colonies as it allows for them to grow in all directions (Johnson et al. 2011). Despite the qualities that make *A. cervicornis* an ideal restoration species, they are susceptible to both disease outbreaks and hurricanes, which have been responsible for the majority of acroporid decline (Aronson & Precht 2001; Speare et al. 2019). Thus, to survive long-term, outplanted colonies must overcome similar challenges as their predecessors.

To understand the long-term success of *A. cervicornis* restoration, we estimated total linear extension (TLE) of live tissue, as this method best captures the total amount of coral for branching species (Johnson et al. 2011). We then addressed the following questions: (1) What is the relationship between the TLE of restored *A. cervicornis* and outplanting effort after 8 years of restoration? (2) Is the TLE of restored *A. cervicornis* related to past or present ecological factors including past coral community composition or present abundance of two primary spatial competitors, macroalgae and octocorals? We focused on 11 sites in the upper Florida Keys, a region that has received substantial restoration efforts. We found that current live tissue within sites was strongly correlated with recent outplanting effort. In addition, efforts focused on reefs that once supported high densities of coral can positively influence the success of *A. cervicornis* restoration.

Chapter Two: Methods

Study Area

We conducted this study in the upper Florida Keys, USA, which has been an area of large-scale *A. cervicornis* restoration effort. This region contains large forereefs, which have received restoration at one or more locations within a reef. For this study, we refer to the specific location where we observed the outcome of restoration as a "site." To select sites for this study, we combined information on the location and number of *A. cervicornis* colonies outplanted in the region from 2012–2020 with data collected by three long-term monitoring projects from 2001–2011: (1) Coral Reef Evaluation and Monitoring Project (CREMP;Florida Fish and Wildlife Conservation Commission-Fish and Wildlife Research Institute 2021), (2) Disturbance Response Monitoring program (DRM; FRRP 2020), and (3) Abundance, Distribution, and Condition of *Acropora* Corals, Other Benthic Coral Reef Organisms, and Marine Debris (SCREAM; Center for Marine Science; University of North Carolina at Wilmington 2012). We selected 11 sites, each on a different forereef, where all effort was carried out with the same methods, but varied in the amount applied and which had nearby (within 1,500 m) coral demographic data from the decade prior to restoration (Figure 1). These sites were composed of spur-and-groove or ledge formations, ranging in depth from 3–10 meters. For this study, we defined effort in three ways: (1) total number of corals outplanted on the site from 2012–2020, (2) total years of outplanting on the site (i.e., the number of years outplanting occurred between 2012–2020), and (3) time in years since the last outplanting effort. From 2012–2020, effort by practitioners ranged from 200–7,080 outplants per site and a total of 21,089 outplants across all sites and all years. The total years of outplanting varied from 1–9, and time since last outplant ranged from 1–5 years (Table 1).

In situ Demographics

In October 2020, we conducted demographic surveys at each site using a random sampling design. We oriented all surveys in a manner that maximized overlap with reef. We delineated the survey area with four parallel 30 m transects, separated by 10 m between each. For each 30 m transect, we completed 1 x 10 m belt transects from the 0–10 m 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 spatial balance of survey types, we alternated the locations of each belt transect within the 30 m transects. Ultimately, we surveyed 80 m^2 at each site for *A. cervicornis* and 40 m^2 for all coral species (Figure 2).

We recorded the maximum height, diameter, and percent mortality of adult (≥4 cm) coral colonies. Maximum height was measured parallel to the axis of growth, from the lowest point of skeletal growth to the highest. Maximum diameter was measured as the widest area of skeletal growth of the outward-facing surface of a colony. We differentiated between old and recent mortality to determine the cause(s) of recent tissue death. Old mortality was defined by the absence of corallite structure and the cause of death could not be determined. Recent mortailty was defined by white skeleton with 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 total linear extension (TLE) for each colony observed (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_{live}) by first calculating ellipsoid volume (EV):

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

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_{total}):

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

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_{live} using the following equation:

$$TLE_{live} = TLE_{total}\left(1 - \left(\frac{\%\ Old\ Mortality + \%\ Recent\ Mortality}{100}\right)\right) \quad \text{(Equation 3)}$$

Ecological Factors

Demographic information for our specific study sites was not available prior to restoration, thus we calculated site values as an average of all available transects from the decade prior to the start of major restoration (2001-2011) for the entire reef in which the site was located. The maximum distance between a site and pre-restoration data used was 1,500 m. We calculated pre-restoration coral density, richness, evenness, and Shannon's diversity index for each site using data from CREMP (2011), DRM (2005–2011), and SCREAM (2001–2002, 2005-2006, 2009) (Table 2). At minimum, each program collected adult (≥4 cm) coral demographic information for a specific survey area 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 percent cover of major benthic groups to provide further information on benthic composition and discerned if a relationship existed between spatial competitors and TLE_{live} of outplants. We took benthic photos every 0.5 m along 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 3,200 per site. We identified points as *A. cervicornis*, scleractinian coral other than *A. cervicornis*, *Millepora* spp., macroalgae, octocorals, sponge, zoanthid, cyanobacteria, and bare substratum. We classified unidentifiable points as unknown and included these in total 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 focused on macroalgae and octocoral cover, since each are fast growing spatial competitors in the shallow forereef environment (Ruzicka et al. 2013; van Woesik et al. 2018). In additon, we also took into account the combined total of all spatial competitors (all groups except bare substrate and *A. cerviornis*).

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-restoration ecological factors (coral density, richness, evenness, and Shannon's diversity), and present ecological factors (individual terms of macroalgae and octocoral cover, combined macroalgae and octocoral cover, all spatial competitors combined, and available substrate). Each model contained the random effect of site to account for pseudoreplication of transects within-site. We assumed that all colonies were approximately the same size at outplanting, thus we expected a proportional increase in TLE_{live} to the total number of outplants reported for each site. We therefore included an offset for the total number of outplants.

Prior to model selection, we assessed collinearity among predictors to ensure 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 ecological factors. We found two cases of high collinearity among predictors. The first was between total years of outplanting and time since last outplant. We retained time since last outplant to understand long-term success of restoration (i.e., survival and growth of colonies) rather than the role of total years (i.e., frequency of outplanting), since we were mainly interested in whether outplanted populations had become self-sustaining. The second was between pre-outplant calculations of coral richness, evenness, and Shannon's diversity. We chose to keep Shannon's diversity since this metric incorporates both richness and evenness. We excluded the other highly correlated terms prior to model selection.

Model selection was caried out in two stages. First, we tested the suitability of three types of error distributions and five types of glmms 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). Ultimately, 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, QQ residual plots, and residual vs. 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, (3) pre-restoration Shannon's diversity. We used *ggplot2* (Wickham 2013) for visualizing effects. We conducted all data analyses using the *R* Statistical Environment (R Core Team 2020).

Chapter Three: Results

The live tissue of outplants at restored sites was related to both effort and ecological factors. TLE_{live} was generally highest at sites that had received outplants within two years of our observations and lowest for sites with four or more years since last effort (Table 3). Accordingly, time since last outplant was found to be negatively related to TLE_{live} (coef (se) = −0.58 (0.2), $z = -2.8$, $p < 0.01$) (Figure 3). Four of the 11 sites lacked any remaining outplants, despite a thorough search in and around belt transects. TLE_{live} was generally low for the seven sites with remaining outplants (mean (se) = 14.5 cm/m^2 (3.8), min–max = 2.7–28.4 cm/m^2). Of the 519 observed outplants, 139 (26%) experienced recent mortality, most often caused by predation and disease. Among the 139 colonies which experienced recent mortality, 52% was due to predation and 39% was due to disease.

The relationship between TLE_{live} and ecological factors varied depending on the data used. There was no relationship between TLE_{live} and the present-day cover of either macroalgae ($p = 0.6$) or octocorals ($p = 0.30$), so both terms were dropped from the final model. There was also no relationship with combined macroalgae and octocoral, all spatial competitors combined, or available substrate. The overall cover and density of coral was low across all sites. For all non-*A. cervicornis* species of coral, we observed a mean cover of 0.8% (se = 0.2, min–max = 0.3–1.8) and density of 2.2 colonies/m^2 (se = 0.4, min–max = 0.8–4.3). For *A. cervicornis*, we observed a mean cover of 1.5% (se = 0.5, min–max = 0–3.8) (Table 4) and density of 0.6 colonies/m^2 (se = 0.2, min–max = 0–1.5). TLE_{live} was not related to pre-restoration Shannon's diversity (coef (se)

$= -0.71$ (0.8), $z = -0.8$, $p = 0.40$) and positively related to pre-restoration density (coef (se) = 0.55 (0.2), $z = 2.6$ $p < 0.01$) (Figure 3).

Chapter Four: Discussion

Our results provided evidence that *A. cervicornis* restoration at the 11 study sites in the upper Florida Keys has not yet produced self-sustaining populations. The negative relationship between the amount of live tissue and time since last restoration effort suggests that long-term survival of outplants was low. Thus, continuous restoration effort, likely on at least an annual basis, would be required to maintain restoration of *A. cervicornis* at these sites. In addition, the density of scleractinian corals present on reefs, regardless of species, can aid in the decision-making process regarding where restoration may be most successful.

We found that TLE_{live} values were highest for sites that received outplants within two years of our observations. However, sites that had not received outplants for four or more years had either low TLE_{live} or no remaining outplants. Based on the need of new and recent effort to positively influence TLE_{live}, restoration of these sites would not be considered successful. Ultimately, to have successful restoration outplants need to survive long enough to grow and reach a point in which they repopulate naturally, especially through sexual reproduction, and without further assistance from practitioners (SER 2004). Success such as this has nearly been achieved in few instances. For example, restoration within a protected area in Belize resulted in *A. cervicornis* populations that expanded in size and were reproductively active after five years (Carne et al. 2016). Additionally, efforts to restore an area damaged by a ship grounding in Puerto Rico created a self-sustaining thicket over eight years (Griffin et al. 2015). However, studies achieving these levels of success and duration are limited (Bostrom-Einarsson et al. 2020), and even in these examples, outplanting was carried out over multiple years. Other long-term studies have documented low survival after two years (Garrison & Ward 2012; Ware et al. 2020), and even short-term studies can reveal decreased survivorship through time (Drury et al. 2017; van Woesik et al. 2021). In any case, the persistence of acute and chronic disturbances such as bleaching, disease, and major storms continue to cause mortality of outplanted *A. cervicornis*.

Nearly a third of the colonies we observed displayed recent mortality, largely attributed to predation and disease. Predation has often been a problem for restoration, especially immediately after outplanting, as 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 natural, outplanted, and nursery populations of acroporids (Miller et al. 2014a; Weil et al. 2020). In addition to these individual-scale stressors, large-scale disturbance can have important negative effects on outplanted colony survival. In the FRT, two major disturbances occurred between 2012 and 2020. First, the 2014-2017 El Niño event caused extreme thermal stress, leading to greater bleaching and disease susceptibility in those years (Hoogenboom et al. 2017; Drury et al. 2017; Muller et al. 2018). Additionally, category 4 Hurricane Irma made landfall in the Florida Keys in 2017, and caused loss of outplants through breakage and increased sedimentation (Lohr et al. 2020). This hurricane was likely responsible for the lack of outplants found at four of the sites in this study, which were no longer targeted for restoration afterwards. Although outplants may go years without experiencing such large-scale disturbances, monitoring on temporal scales that do not capture these can result in misleading conclusions about long-term success.

Location of outplanting effort is likely an important consideration for future restoration in the context of these disturbances which will continue to occur. Recent mapping suggested that backreef, deeper forereef, and patch reef habitats supported the majority of 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{Done, 1982 #76}; D'Antonio et al. 2016; van Woesik et al. 2020). In contrast, outplanted *A. cervicornis* in the shallow forereef locations will be exposed to higher levels of light and wave energy that cause bleaching and damage from disturbances (Safuan et al. 2020; Stainbank et al. 2020). Although we did not directly address site selection as a part of this study, sites with the highest values of TLE_{live} were those that were within the deeper sections of the forereef. Restoration was also greater at these sites after the passing of Hurricane Irma, giving some indication that practitioners may have taken the poor survival at exposed reefs into consideration after 2017, avoiding sites and habitats in which all outplants were lost following this event and where *A. cervicornis* has a better chance for long-term survival.

We found that reefs that supported high coral densities in the past may be better suited to continue to host *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 health status of the reef and probable outplant success (English et al. 1997). Coral diversity is also an important feature used to select target locations for restoration as it may be an indication of resiliency to allow for a greater chance for species persistence after disturbance (Graham et al. 2011; Baskett et al. 2014). We found that Shannon's diversity was marginally significant from a statistical standpoint, but the weak relationship with TLE_{live} suggests a lack of ecological significance. Likewise, macroalgae and octocoral cover were not related to the observed TLE_{live} of outplants, despite their dominance across all sites. Although they are strong spatial competitors on modern reefs (Bruno et al. 2009; Ruzicka et al.

2013), their effect on *A. cervicornis* is possibly diluted due their ubiquitous distribution among sites. However, their overwhelming presence is still important as it further reiterates the poor state of reefs, and the need for restoration.

The feasibility and ethics surrounding restoration of *A. cervicornis* remains important for discussion while environmental conditions remain poor and disturbances hinder long-term survival of the species. The techniques used to propagate and outplant large amounts of coral have now been well established and proved to be successful short-term, but strategies for achieving widespread population enhancement to the point of self-sustaining populations is lacking and needs refinement. Based on this study, we recommend that restoration practitioners focus on choosing sites based on habitat characteristics that prove to be conducive to long-term survival by providing refuge from stressors. We also suggest that once sites that support long-term success are realized, practitioners redirect their efforts to these areas specifically, and outplant at a few specific reefs rather than spreading effort across many reefs.

Although continuous efforts were required to maintain populations in the current study, coral restoration will likely continue to expand in effort in the coming years. In 2020, an initiative was launched to restore seven reefs throughout each region of the FRT with the goal to outplant over 60,000 *A. cervicornis* colonies at these sites in the next two decades (Mission Iconic Reefs; NOAA Fisheries 2019), which is threefold the number used at sites in this study. This ambitious project will cost up to $4M USD and require multi-partner cooperation to propagate, outplant, and monitor corals on these spatial and temporal scales. This initiative also looks to address issues outside of coral outplanting alone, such as planned visits to remove predators from the area and efforts to increase the presence of important herbivores. Transitioning towards incorporating these kinds of community and ecosystem scale dynamics is important for growing our knowledge on what effort is needed for success. Ultimately, these projects will need to develop ways to produce populations that not only survive and grow for 1-2 years, but that become self-sustained without continuous new efforts (SER 2004). Our study was unable to conclude that there is long-term success of *A. cervicornis* restoration in the upper Florida Keys, but points to the importance of continuing to carry out quantitative research that will build the knowledge to achieve restoration success.

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Tables and Figures

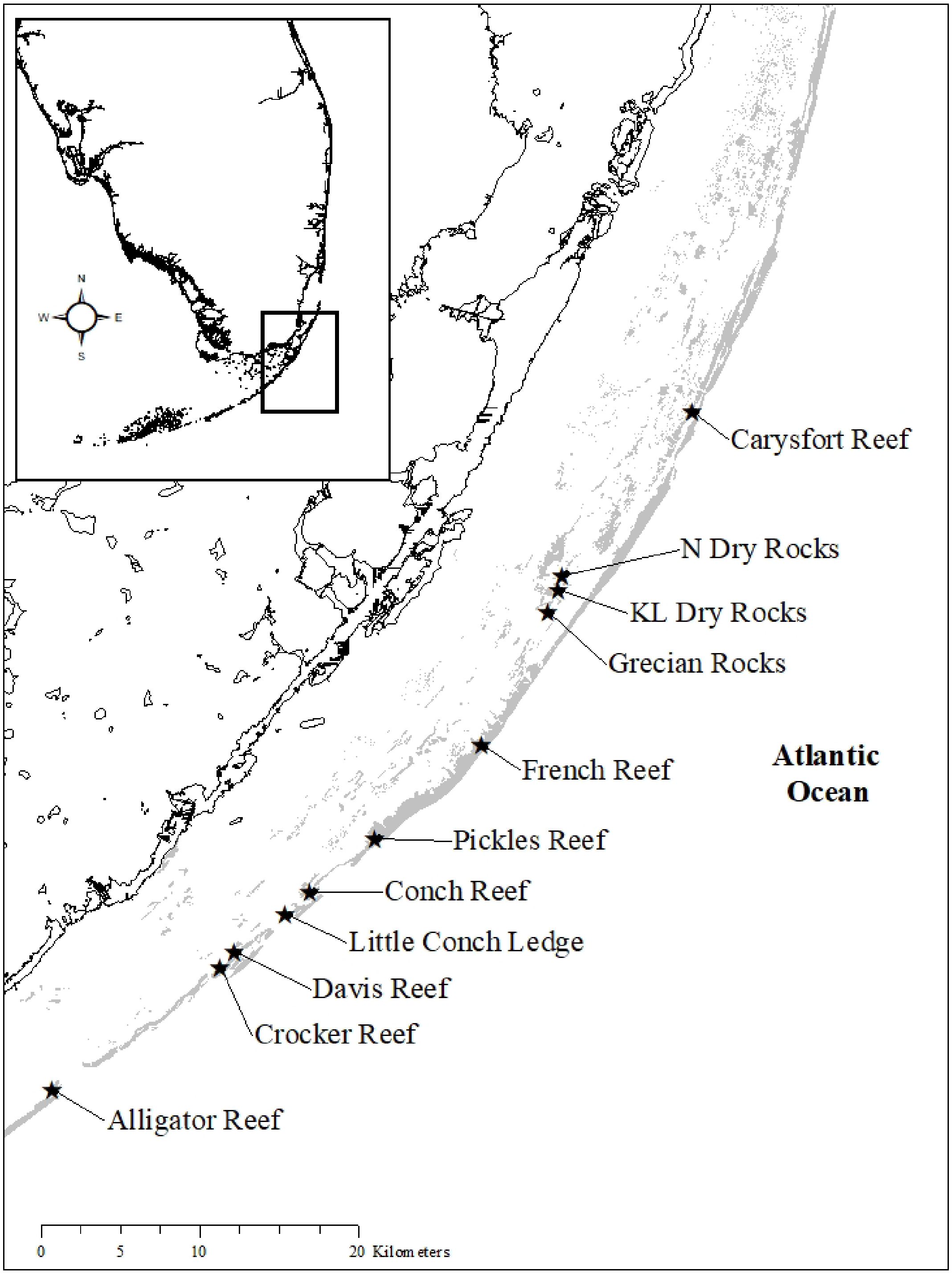

Figure 1. Map of study sites. All sites are located on forereefs in the upper Florida Keys and served as targets for coral restoration effort.

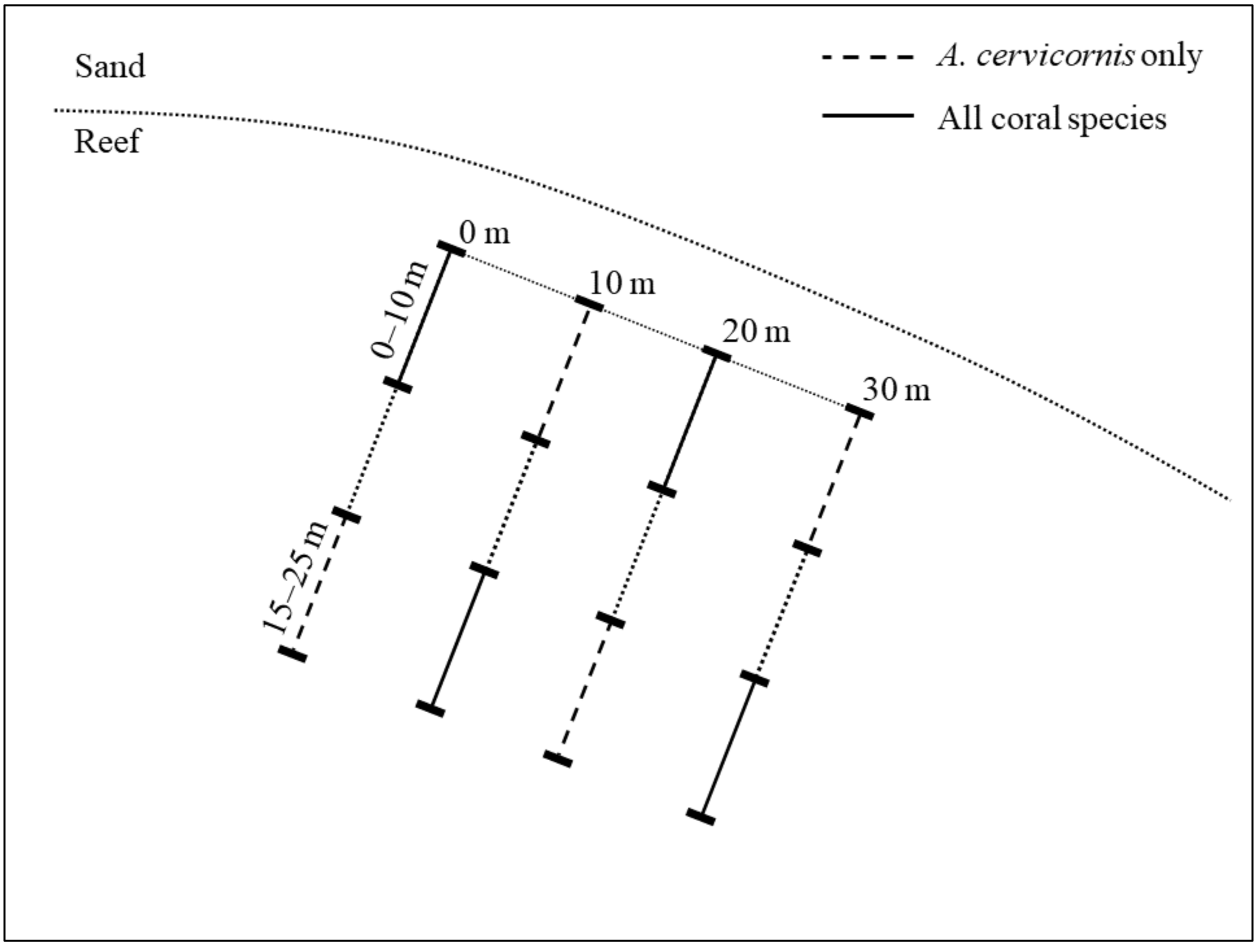

Figure 2. Transect distribution of 1 x 10 m belt transects. Solid lines represent surveys of *A. cervicornis* only and dashed lines represent demographics for all stony coral species present. Survey type locations were alternated within the 30 m transects. Ultimately, 80 m^2 at each site was surveyed for *A. cervicornis* and 40 m^2 for all coral species.

Table 1. The total number of outplants, total years of outplanting, and 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_{live}).

Site	Reported No. of Outplants	Total years of outplanting	Years since outplant	Observed No. of Outplants	Total TLE_{live}
Conch Reef	2,600	6	0	120	2,273
North Dry Rocks	2,777	3	1	120	2,004
Pickles Reef	7,080	9	0	108	1,615
Grecian Rocks	1,536	1	1	67	842
Carysfort Reef	3,148	4	1	55	777
French Reef	200	1	4	31	411
Davis Reef	1,002	3	4	18	216
Little Conch Ledge	1,482	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

Table 2. Description of project, project site, and years for surveys included in calculation of pre-restoration metrics of densityrichness, evenness, and Shannon's diversity.

Project	Project Site Name	Year	Study Site
DRM	C1012	2006	Alligator Reef
DRM	D1095	2007	Alligator Reef
DRM	I1429	2010	Alligator Reef
SCREAM	t45	2009	Alligator Reef
SCREAM	t46	2009	Alligator Reef
SCREAM	4811477	2001	Carysfort Reef
SCREAM	4821478	2005	Carysfort Reef
CREMP	Carysfort Shallow	2011	Carysfort Reef
DRM	D4046	2007	Carysfort Reef
DRM	F1114	2009	Carysfort Reef
DRM	J2723	2011	Carysfort Reef
SCREAM	t38	2009	Carysfort Reef
SCREAM	3341353	2001	Conch Reef
SCREAM	3341353	2005	Conch Reef
CREMP	Conch Shallow	2011	Conch Reef
DRM	I1406	2010	Conch Reef
SCREAM	t22	2009	Conch Reef
SCREAM	3071318	2005	Crocker Reef
SCREAM	3081317	2001	Crocker Reef

SCREAM	3081318	2001	Crocker Reef
DRM	F1126	2009	Crocker Reef
DRM	F2116	2009	Crocker Reef
DRM	I4066	2010	Crocker Reef
SCREAM	3151328	2001	Davis Reef
SCREAM	3161328	2001	Davis Reef
SCREAM	3781407	2002	French Reef
SCREAM	3801409	2005	French Reef
SCREAM	t17	2009	French Reef
SCREAM	t41	2009	French Reef
SCREAM	t42	2009	French Reef
CREMP	Grecian Rocks	2011	Grecian Rocks
DRM	I1397	2010	Grecian Rocks
SCREAM	t14	2009	Grecian Rocks
SCREAM	t15	2009	Grecian Rocks
SCREAM	4281433	2005	Key Largo Dry Rocks
DRM	E1111	2008	Key Largo Dry Rocks
SCREAM	t12	2009	Key Largo Dry Rocks
SCREAM	t13	2009	Key Largo Dry Rocks
SCREAM	t23	2009	Little Conch
SCREAM	4311435	2005	North Dry Rocks
SCREAM	3501373	2001	Pickles Reef
SCREAM	3521375	2001	Pickles Reef
SCREAM	3541377	2005	Pickles Reef
DRM	A1121	2005	Pickles Reef
DRM	A1122	2005	Pickles Reef
DRM	E1123	2008	Pickles Reef
DRM	F1095	2009	Pickles Reef
DRM	F1096	2009	Pickles Reef
SCREAM	t32	2009	Pickles Reef

Table 3. Past and present density, richness, evenness, and Shannon's diversity for the 11 study sites. Past values are calculated using all available pre-restoration survey data for a reef and are used as a single value to represent each site. Values for 2020 are calculated using the four all species transect surveys (including *A. cervicornis*). See Table 1 for further details on pre-restoration data.

Site	Time period	No. of surveys	Richness	Evenness	Shannon's diversity	Density (corals/m^2)
Conch Reef	2001-2011	5	12.8 ± 6.1	0.82 ± 0.04	1.95 ± 0.38	1.31 ± 0.23
	2020	4	3.5 ± 0.65	0.67 ± 0.09	0.99 ± 0.2	3.45 ± 0.85
N Dry Rocks	2001-2011	1	10 ± NA	0.75 ± NA	1.8 ± NA	4.3 ± NA
	2020	4	5.75 ± 0.63	0.66 ± 0.07	1.24 ± 0.08	0.78 ± 0.18
Pickles Reef	2001-2011	9	5.11 ± 0.51	0.64 ± 0.05	1.17 ± 0.12	1.57 ± 0.28
	2020	4	6 ± 0.82	0.7 ± 0.02	1.34 ± 0.09	4.25 ± 1.02
Grecian Rocks	2001-2011	4	16.5 ± 7.01	0.67 ± 0.12	1.9 ± 0.57	4.7 ± 0.69
	2020	4	5.5 ± 0.5	0.64 ± 0.07	1.2 ± 0.18	2.38 ± 0.32
Carysfort Reef	2001-2011	7	11.14 ± 4.38	0.66 ± 0.06	1.56 ± 0.33	3.12 ± 0.65
	2020	4	6.5 ± 0.96	0.74 ± 0.01	1.47 ± 0.09	3.28 ± 0.65
French Reef	2001-2011	5	9.2 ± 0.97	0.65 ± 0.06	1.49 ± 0.13	4.53 ± 0.92
	2020	4	4.75 ± 0.48	0.64 ± 0.04	1.1 ± 0.06	2.4 ± 0.3
Davis Reef	2001-2011	2	7 ± 2	0.78 ± 0.07	1.61 ± 0.34	1.02 ± 0.03
	2020	4	6.75 ± 0.85	0.71 ± 0.03	1.44 ± 0.12	4.47 ± 0.94
Little Conch	2001-2011	1	8 ± NA	0.76 ± NA	1.66 ± NA	3.85 ± NA
	2020	4	5.5 ± 0.5	0.81 ± 0.03	1.51 ± 0.11	1.2 ± 0.11
Alligator Reef	2001-2011	5	6 ± 0.77	0.71 ± 0.04	1.38 ± 0.16	1.56 ± 0.52
	2020	4	4.75 ± 0.75	0.73 ± 0.05	1.28 ± 0.18	2.25 ± 1.35
Crocker Reef	2001-2011	6	7.83 ± 1.19	0.81 ± 0.01	1.72 ± 0.11	1.77 ± 0.54
	2020	4	3.75 ± 0.75	0.65 ± 0.1	1.02 ± 0.24	4.12 ± 0.66
KL Dry Rocks	2001-2011	4	7.25 ± 0.48	0.59 ± 0.09	1.24 ± 0.2	4.72 ± 1.13
	2020	4	8 ± 0.41	0.73 ± 0.02	1.61 ± 0.07	1.27 ± 0.18

Table 4. Percent cover of major benthic groups. Values are mean ± SE (n=8 for each site, n=88 for overall values).

Site	Bare substrate	Macroalgae	Octocoral	Sponge	Cyanobacteria	*A. cervicornis*	Zoanthid	Crustose coralline algae	Other corals
Conch Reef	54.03 ± 2.94	36.88 ± 2.48	4.69 ± 0.66	0.56 ± 0.13	0.12 ± 0.07	1.41 ± 0.72	0.47 ± 0.24	1.03 ± 0.35	0.12 ± 0.07
North Dry Rocks	60.05 ± 5.01	19.16 ± 3.68	10.14 ± 0.89	2.69 ± 0.39	1.95 ± 0.55	2.76 ± 0.42	0.47 ± 0.19	0.66 ± 0.28	0.63 ± 0.17
Pickles Reef	61.92 ± 2.16	21.54 ± 2.42	7.02 ± 0.91	1.03 ± 0.34	0.40 ± 0.34	3.35 ± 1.05	1.79 ± 0.85	0.92 ± 0.31	1.07 ± 0.30
Grecian Rocks	46.75 ± 4.48	14.56 ± 1.54	28.47 ± 4.12	1.00 ± 0.21	2.09 ± 0.74	1.41 ± 0.73	1.25 ± 0.44	0.19 ± 0.06	1.78 ± 0.55
Carysfort Reef	52.84 ± 2.65	26.78 ± 2.39	8.78 ± 0.74	0.72 ± 0.26	6.56 ± 2.13	1.34 ± 0.71	0.03 ± 0.03	0.69 ± 0.19	0.94 ± 0.27
French Reef	55.44 ± 3.66	32.00 ± 3.73	7.00 ± 0.78	0.97 ± 0.21	0.16 ± 0.07	0.28 ± 0.28	0.03 ± 0.03	2.41 ± 0.92	0.69 ± 0.21
Davis Reef	52.75 ± 4.99	34.83 ± 4.24	6.52 ± 0.61	0.94 ± 0.21	0.84 ± 0.54	0	1.31 ± 0.52	1.04 ± 0.27	0.35 ± 0.11
Little Conch Ledge	60.84 ± 2.36	25.49 ± 2.67	8.77 ± 0.62	1.16 ± 0.32	0.16 ± 0.07	0	0.88 ± 0.29	1.57 ± 0.40	0.09 ± 0.07
Alligator Reef	56.91 ± 2.08	26.81 ± 3.14	11.09 ± 0.98	1.66 ± 0.76	0.53 ± 0.17	0	1.53 ± 0.48	0.5 ± 0.23	0.28 ± 0.1
Crocker Reef	69.88 ± 3.21	17.06 ± 2.47	8.34 ± 0.7	1.03 ± 0.40	0.09 ± 0.07	0	2.00 ± 0.59	0.09 ± 0.07	0.19 ± 0.04
KL Dry Rocks	62.18 ± 2.13	9.85 ± 1.13	14.45 ± 1.41	9.56 ± 1.05	0.03 ± 0.03	0	0.56 ± 0.29	0.79 ± 0.26	1.32 ± 0.20
Overall	57.6 ± 1.16	24.09 ± 1.19	10.48 ± 0.79	1.94 ± 0.30	1.18 ± 0.29	0.96 ± 0.19	0.94 ± 0.14	0.9 ± 0.13	0.68 ± 0.09

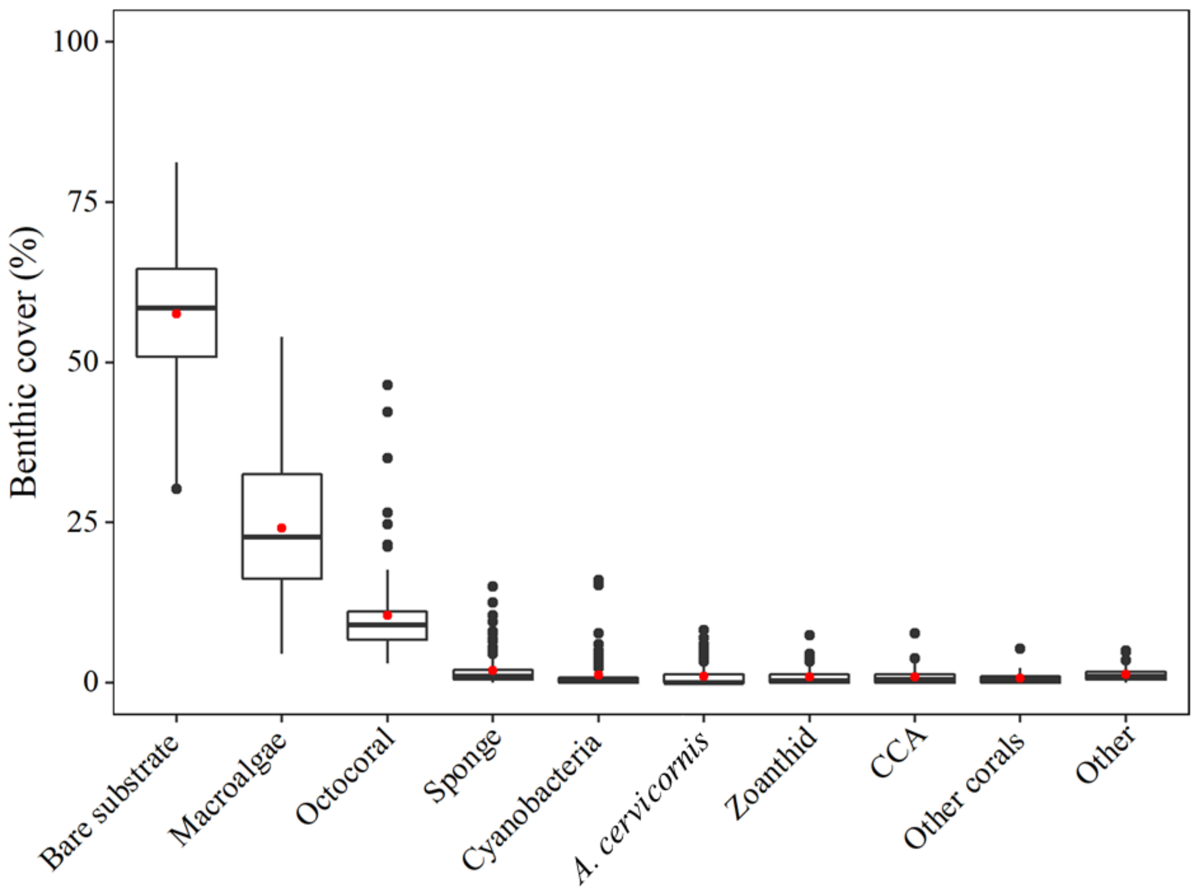

Figure 3. Overall percent benthic cover of major benthic fauna across study sites. Lower and upper box boundaries represent the 25th and 75th percentiles, respectively. The line inside the box is the median. The lower and upper error lines represent the 10th and 90th percentiles, respectively. Filled circles are data falling outside 10th and 90th percentiles. The red circle indicates the mean.

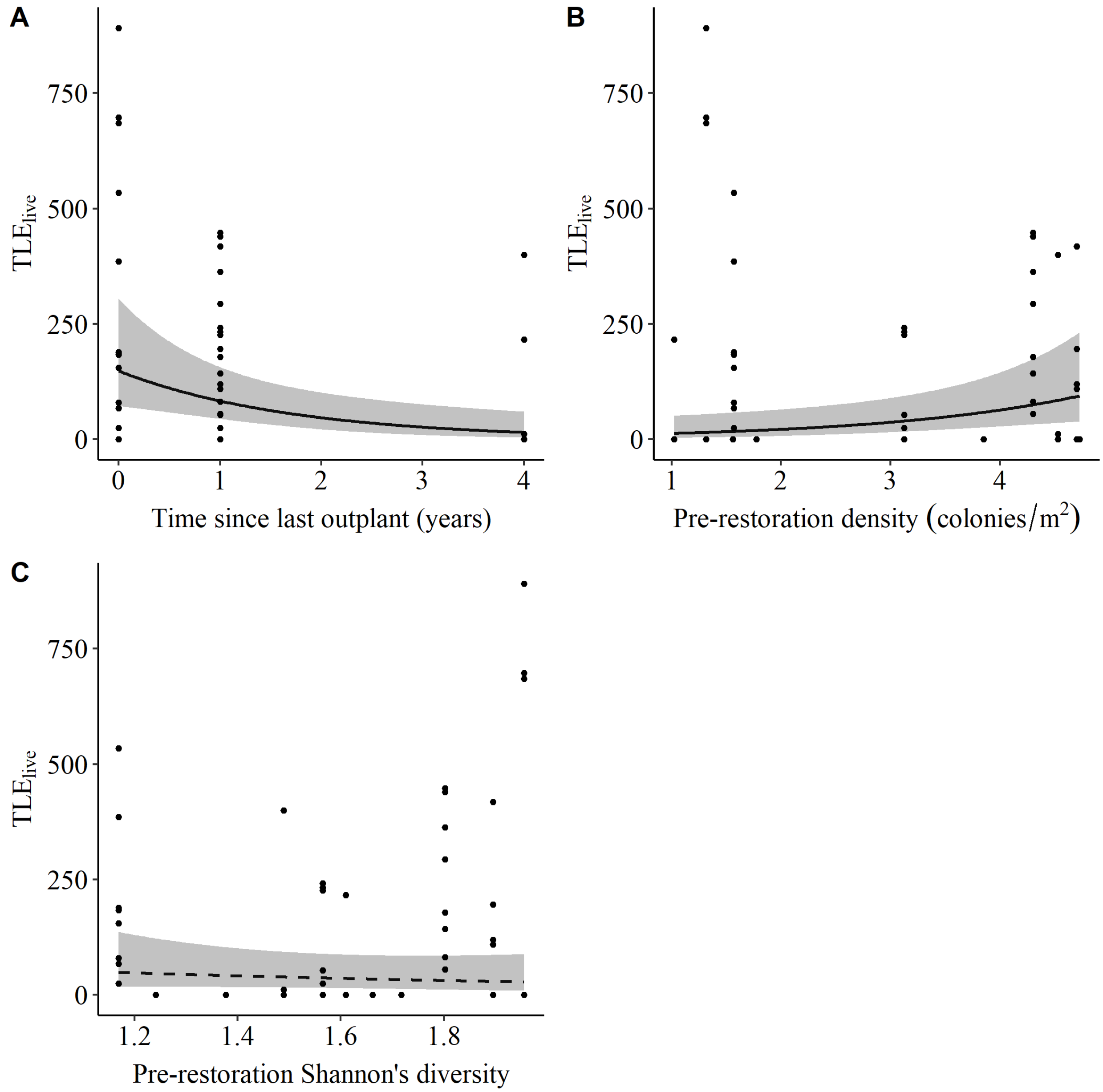

Figure 4 Relationships between TLE_{live} and the predictors (**A**) Time since last outplant (−0.58 (0.2), z = −2.8, p = 0.01), (**B**) pre-restoration density (0.55 (0.2), z = 2.6 p = 0.01), and (**C**) pre-restoration Shannon's diversity (−0.71 (0.8), z = −0.8, p = 0.40). Points represent the raw 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. Interval represents 95% confidence intervals.