Effects of herbivory by the urchin *Diadema antillarum* on early restoration success of the coral *Acropora cervicornis* in the central Caribbean

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A B S T R A C T

In an era of coral reef decline, coral restoration is receiving increasing attention, with many recent developments in culture and transplant techniques. However, how the ecological processes operating on coral reefs influence the success of restoration efforts remains largely unexplored, particularly during the first months after out-planting which are considered crucial for colony survival. Herbivory is a key process well-known to maintain a coral-dominated state, and in the Caribbean Sea, the long-spine urchin *Diadema antillarum* is thought to aid coral success by removing algae from seafloor substrate that might otherwise outcompete coral outplants. In this study, we conducted a three-month manipulative experiment in southeastern Dominican Republic to test the effect of *Diadema antillarum* density on percent living tissue and growth rate of outplanted fragments of the critically endangered coral species *Acropora cervicornis*. Increasing herbivore density had no significant effect on coral survival or growth but did increase the percent of living tissue when urchin abundance was 3× ambient levels. The greatest growth and survival outcomes were instead related to the initial size of the outplanted coral and were reduced through predation by the fireworm *Hermodice carunculata*. Our results highlight the potential importance of considering ecological processes like herbivory and predation to maximize the success of ecological restoration.

1. Introduction

The Caribbean region has experienced rapid phase shifts from coral to algae-dominated reefs over the past half century (de Bakker et al., 2016, 2017; Gardner et al., 2003; Hughes et al., 2010). The combination of decades of overfishing, global warming, poor water quality brought on by nutrient pollution and increased sedimentation, and emerging diseases have all brought about significant changes in the structure and function of reefs across the Caribbean (de Bakker et al., 2017; Eakin et al., 2010). Many populations of large reef building species have declined and/or been locally extirpated, leading to significant loss of structural complexity (Alvarez-Filip et al., 2009). This 'reef-flattening' can have far-reaching implications for the ecosystem and human well-being by reducing the abundance and diversity of associated animals, removing benefits associated with nutrient transfer, shoreline protection, defense from hurricanes and erosion (Reguero et al., 2018, 2019), and decreasing tourism and fisheries production (Alvarez-Filip et al., 2009; Newman et al., 2015).

The decline suffered by foundational coral species (i.e., reef-builders) has hastened the transition from coral to algal-dominated benthic assemblages throughout the Caribbean (Alvarez-Filip et al., 2009). Two species in particular, *Acropora palmata* (Lamarck, 1816) and *Acropora cervicornis* (Lamarck, 1816), were once some of the main reef-forming corals. However, the populations of these corals have suffered a drastic reduction (between 80 and 98%) over the last decades (Cramer et al., 2020) and in many cases have failed to recover (Croquer et al., 2016). One of the main causes of mortality associated with this reduction is white band disease, which reduced the live cover of Caribbean Acroporids by 95% throughout the region (Aronson and Precht, 2001). Even when some individuals are naturally resistant to this disease, the

percent cover is still exceptionally low (approximately 6%, Vollmer and Kline, 2008). These two species were therefore deemed "critically endangered" by the International Union for Conservation of Nature in 2008 and subsequently entered in the CITES list (Appendix II) (Japaud et al., 2015).

The rapid decline of coral reefs globally has prompted scientists and practitioners to increase and scale-up efforts to restore these valuable and iconic systems (Duarte et al., 2020; Foo and Asner, 2019; Hughes et al., 2017). A growing recognition that corals are unlikely to recover without human intervention (Lapointe et al., 2019; Morrison et al., 2019; Mumby et al., 2007; Muñiz-Castillo et al., 2019) has led to the development of rapid, feasible and cost-effective restoration techniques to aid the survival of coral populations (Boström-Einarsson et al., 2020). The hermatypic coral *Acropora cervicornis,* in particular, has been shown to be an ideal species for restoration programs: it is relatively easy to culture; it grows rapidly (between 6.5 and 11.7 cm/year); it can be easily genotyped so it is possible to increase genetic diversity; outplanting is often successful for this species in a range of reef habitats; and, due to its branching pattern, it can rapidly add high structural complexity to the reef (Agudo-Adriani et al., 2016; Laydoo, 1996; O'Donnell et al., 2017).

Current coral restoration strategies are classified into three categories: (1) asexual propagation (i.e., coral gardening, microfragmentation, and transplantation), (2) sexual propagation (e.g., assisted fertilization, larval enhancement, and recruit seeding) and (3) substrate enhancement method (e.g., artificial reefs, substrate stabilization, electric substrate enhancement and algal removal) (Boström-Einarsson et al., 2020). Attempts to reverse declining trends and/or to recover Acroporids in the Caribbean have focused on developing culture techniques allowing the rapid growth of fragments to restore reef sections and/or populations and the maintenance of nurseries to keep corals free from predation, disease, and overgrowing competitors, as well as ensuring genetic diversity (Bayraktarov et al., 2020). To date, however, coral restoration efforts have achieved varying degrees of success, limited by the high cost and small footprint of most efforts (Bayraktarov et al., 2016, 2020; Boström-Einarsson et al., 2020; Duarte et al., 2020). Across all techniques, coral restoration achieves a 60.9% success rate, largely driven by coral gardening (with more than 50% survival rates) over other techniques (Bayraktarov et al., 2019). Even accounting for these numbers, some of the scientific literature could be biased towards publishing successes rather than failures (Bayraktarov et al., 2016).

Despite their vital and well-known importance in maintaining natural systems, ecological processes are one of the most overlooked factors in coral restoration scientific studies, with only 19% of restoration studies between 1987 and 2017 incorporating any aspect of processes such as herbivory or predation (Ladd et al., 2018). Additional ecological context that could improve best practices, reduce costs, and lead to greater chances of success and upscaling of efforts would be highly valued (Foo and Asner, 2019; Young et al., 2012), especially in the early stages of restoration efforts when post-outplant survivorship remains variable, a characteristic common among fast-growing coral species (Edwards and Clark, 1999; Yap et al., 1992).

Predation, for example, has been shown to be important in determining growth rates and survivorship of *Acropora cervicornis* outplants. The corallivorous snail *Coralliophila abbreviata* (Lamark, 1816) is well-known to prey upon a variety of corals (Baums et al., 2003) and also functions as a vector and reservoir for transmission of the white band disease pathogen for *A. cervicornis* (Gignoux-Wolfsohn et al., 2012). The fireworm *Hermodice carunculata* (Pallas, 1766) is a common predator of *A. cervicornis*, capable of removing a significant amount of coral tissue and leaving behind a very characteristic and easy to identify white tip devoid of tissue (Miller et al., 2014).

In contrast, little is known about the role of herbivory in promoting coral restoration. Overgrowth by competitors such as various sponges and algae has also been shown to reduce survivorship of *A. cervicornis*, both in nurseries and when they are outplanted (Hayes, 1990; McCook

et al., 2001; Miller, 2001; Nugues et al., 2004; Smith et al., 2006; Sussman et al., 2003; Witman, 1988). Previous studies have shown that both herbivorous fish biomass and diversity can promote natural coral cover and recruitment in the Caribbean by removing these organisms from the substrate and promoting juvenile recruitment and growth (Burkepile and Hay, 2010; Lefcheck et al., 2019). Thus, it stands to reason that enhanced herbivory in the field could lead to greater survival of outplants, although this idea has yet to be tested in the field (Ladd et al., 2018).

The long-spined urchin *Diadema antillarum* (Philippi, 1845) was once one of the most abundant herbivores in the Caribbean until it suffered a massive mortality event caused by an unknown pathogen between 1983 and 1984, reducing its populations by 94–99% in many locations (Lessios et al., 1984). This mortality event is usually marked as the key transition point to an algal-dominated state in the Caribbean (de Ruyter van Steveninck, 1987; de Ruyter van Steveninck and Bak, 1986; Hughes, 1994). The status of *D. antillarum* is uncertain, with some studies reporting a recovery of local populations while others report low or no recovery (Chiappone et al., 2002; Edmunds and Carpenter, 2001; Lessios, 2005). In cases where this herbivore shows signs of recovery, it is usually accompanied by improvements in the recruitment and survival of certain coral species, as well as a decrease in the coverage of macroalgae (Coyer et al., 1993; Edmunds and Carpenter, 2001; Idjadi et al., 2010; Lirman, 2001; Maciá et al., 2007; Myhre and Acevedo-Gutiérrez, 2007; Sammarco, 1982). These results suggest that targeting locations with higher abundances of urchins or co-restoring this species could improve overall coral restoration efforts.

In this study, we conducted a 90-day experiment to test the idea that herbivory can promote the early stages of coral restoration by manipulating the density of *Diadema antillarum* in caged and uncaged plots of *Acropora cervicornis* outplants. We hypothesized that an increase in the density of *D. antillarum* would reduce competitors such as macroalgae, turfs and other macrophytes on the benthos and thereby increase growth rates and enhance the probability of survivorship for coral outplants.

2. Methods

2.1. Study site

The experiment was conducted in a patch reef (5–6 m depth), located within the Southeastern Reefs Marine Sanctuary, in the Dominican Republic (68°51′ W; 18°22′ N). The reef is about 1 km off a populated coastline with high levels of coastal development and tourism pressure. The site is composed of hard substrate colonized by scattered scleractinian coral colonies accounting for 10–15% live coral cover with an estimated average of 1–1.2 individuals of *D. antillarum* per square meter. Methods for estimation of *D. antillarum* density and size are described below.

2.1.1. Diadema antillarum survey

To estimate the natural densities of *D. antillarum* and complement previous information on benthic community structure at our study site, we conducted a visual survey on October 25, 2019 at 9 AM. For this survey, three 10 m-long by 1 m-wide belt transects were randomly deployed parallel to the coastline at three haphazardly selected sites (total $N = 9$) between 6 and 8 m depth. We recorded all *D. antillarum* individuals within our belt transects and measured their test diameter using a caliper. From these estimates, we determined the number and size of urchins necessary to include within each treatment.

2.2. Experimental design

Three experimental sites were haphazardly selected on the reef of study. At each of the three sites, fifteen 4-m² (2 × 2 m) plots were deployed for a total of forty-five plots in the experiment. We randomly assigned $n = 8$ individual fragments of *A. cervicornis* to each plot,

outplanting 360 fragments in total (8 fragments × 45 plots). Thirty-six out of the forty-five plots were caged using hexagonal (4 × 2.5 cm), galvanized, and flexible mesh tied up to four rebars on each corner with cable ties. Cages were 30 cm in height with no ceiling. The upper part of the walls were tilted 90° towards the center to avoid urchin escape. Three divers nailed the cages into the substrate manually, making sure that all cage walls were attached to the bottom with no holes and/or spaces.

Caged treatments consisted of: (a) 2-fold natural urchin density within cages (8 urchins/4m^2); (b) 3-fold natural urchin density within cages (12 urchins/4m^2); (c) total exclusion of urchins; and (d) a procedural control consisting of partially opened cages that allowed access by urchins. The remaining nine plots were uncaged (ambient control), which allowed the access of urchins at their natural density (4/4m^2). After cage deployment and treatment assignment, three divers collected and placed *D. antillarum* individuals (average test diameter = 6.9 ± 2.3 cm) inside the cages to establish the experimental treatments. During the experiment, all cages were visited weekly to check cage integrity and replace missing urchins to maintain the experimental densities.

Additionally, since sediments have been shown to have a series of direct and indirect detrimental effects for corals, affecting water quality, increasing respiration rates, mucus production, survival and the overall energy budget of corals (Riegl and Branch, 1995; Rogers, 1990), sedimentation rates were assessed. Three cylindrical PVC and fiberglass sediment traps were attached on the outside of each experimental unit and covered at the top with the same mesh used in the containment cages. The height of the sediment traps was 20 cm, and their diameter was 11 cm, giving an area of 95 cm^2. All treatments and sediment traps were surveyed monthly from December 2019 to February 2020. A schematic of the experimental design is provided in Fig. S1.

2.2.1. Acropora cervicornis outplants

A. cervicornis fragments were collected from the Dominican Foundation for Marine Studies (FUNDEMAR) coral nurseries in Bayahibe, where at least 32 *A. cervicornis* genotypes have been identified (Calle-Triviño et al., 2020). Fragments were clipped, placed in containers, and outplanted onto our study site, coinciding with FUNDEMAR's outplanting season since it is considered a less stressful time for coral outplants due to fewer active storms and lower temperature stress compared to the rest of the year. To minimize stress during transfer, all fragments were rapidly transported from the donor site to the experimental plots in ~20 min. Fragments ranging from 7 to 139 cm with a mean size of 51.9 ± 23.7 cm were outplanted by fixing them onto the substrate, mainly in a horizontal position, with 3 points of the fragment touching the substrate, using Apoxie marine cement sculpt®.

2.2.2. Monitoring of experimental plots

Each plot was evaluated at 0, 30, 60, and 90 days after treatment establishment to survey coral fragment and benthic community state and to recover sediment traps. For this, each fragment was individually photographed perpendicular to the substrate, keeping a standardized distance of 50 cm. We later analyzed the images using Image J (Rueden et al., 2017) for initial size, percent of living tissue, survivorship, and predation activity, determining the identity of the predator based on the characteristics of the markings: *D. antillarum* predation marks were characterized by erosion on denuded skeletons (Bak and van Eys, 1975) whereas *H. carunculata* predation was characterized by bright white tips with no erosion on it (Miller et al., 2014). Additionally, at least four random branches per colony were identified and followed to calculate apical growth rate.

To estimate changes in benthic composition associated with the experimental plots, we randomly photographed two 1 m^2 subsections of each plot from a height of approximately 2 m in each month of the experiment. We then used the online software CoralNet (Lozada-misa et al., 2017) to estimate cover of major benthic functional groups (e.g., turf algae, fleshy macroalgae, live coral, etc.) underneath 25 random

points. We divided the number of points in each category by 25 and averaged across the two photos to calculate the mean percent cover of each category per m^2.

Finally, each set of sediment from traps were collected and returned to the lab where they were washed with fresh water and dried using a stove Quinci lab 10–140 Incubator for 2 days at 62 °C. Once completely dry, they were weighed to the nearest mg using a precision balance.

2.3. Statistical analysis

To examine associations between benthic features in our photoquadrats in the experimental treatments, we conducted canonical correspondence analysis (CCA) based on Chi-square distance using the function `cca` in the *vegan* package (Oksanen, 2011). To test for the effects of our treatments and covariates, we constructed generalized linear mixed effects models for growth rate, survival, and percent living tissue (100*[length of living tissue/(length of living + dead tissue)]) of each coral outplant. Growth rate was log$_{10}$-transformed and modelled as a function of the following fixed effects: treatment (5 levels), the percent of living tissue, the initial size of the outplant, the mean sedimentation rate per plot, the sampling date (30, 60 or 90 days), the number of predation marks by fireworms (*Hermodice carunculata*), and predation by urchins (*Diadema antillarum*). We further fit a varying-intercept random effect of site. The growth rate model was fit using the *nlme* package (Pinheiro et al., 2020). Survival and percent living tissue was modelled using a quasi-binomial distribution (due to the variance being much smaller than the mean) and the same fixed and random structure as for the growth model (minus the percent of living tissue as a predictor) using the `glmmPQL` function in the *MASS* package (Venables and Ripley, 2002).

Assumptions of both models were assessed visually, and collinearity assessed using variance inflation factors. Model pseudo-R^2 values were calculated for fixed effects only (marginal) and fixed and random effects (conditional) using the *piecewiseSEM* package (Lefcheck, 2016). Finally, we applied Tukey post-hoc contrasts to identify which treatments were significantly different from one another in terms of percent living tissue using the `cld` function in the *multcomp* package (Hothorn et al., 2008). All analyses were conducted in R version 4.0.3 (R Core Team, 2020). All codes and data to reproduce the analysis are provided in the Supplementary Materials.

3. Results

The canonical correspondence analysis identified a higher cover of macroalgae and coralline crustose algae in our exclusion treatments and a reduced cover of turf algae with sediment in the 2×- and 3×-urchin density treatments (Fig. 1, Fig. S2). Turf algae with sediment cover seem to have been replaced by sediment without turf algae. This result indicates that urchin herbivory reduced algal cover in our experimental plots as expected.

In all, 87.1% of our fragments survived over the course of the experiment. Coral survivorship was unaffected by our experimental treatments but significantly increased by initial outplant size and reduced over time (Fig. 2, Table 1). Similarly, growth rate was unaffected by our experimental treatments but responded strongly to initial size and time (Fig. 3, Table 2). Additionally, greater evidence of predation by the fireworm *H. carunculata* was associated with lower growth rates (Fig. 3D). Furthermore, we observed and recorded minimal evidence of *D. antillarum* predation upon the coral outplants, however, there was not a statistical effect of the number of these marks on either of these responses (Tables 1, 2).

We did, however, recover a significant effect of our experimental treatments on the percent of living coral tissue (Fig. 4, Table 3). Based on Tukey post-hoc comparisons of means, the 3×-density treatment had 1.45× higher percent living tissue than the ambient treatment, and 1.5× higher than the experimental control (Fig. 4A). The post-hoc tests
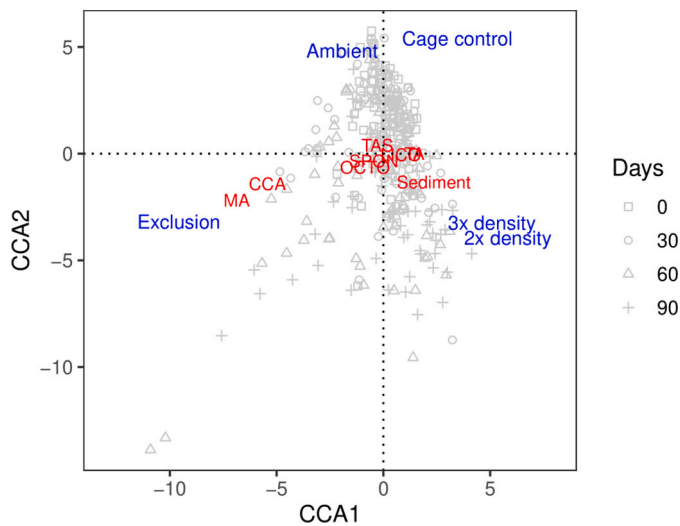
Fig. 1. Canonical correspondence analysis relating benthic composition (major categories in red) in each plot and time period (grey dots) to the experimental treatments (in blue). Abbreviations for benthic categories: MA = macroalgae, CCA = crustose coralline algae, OCTO = octocorals, SPON = sponges, TA = turf algae, TAS = turf algae with sediment, LICO = live coral, Sediment = sediment. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

revealed no difference between our procedural control and ambient control. As with survival and growth, the percent of living coral tissue was enhanced by initial size and declined through time (Fig. 4B, C). Additionally, higher sedimentation increased growth rate and percent living tissue (Fig. S3). In all, the fixed effects alone (marginal R^2) explained 39.2, 5.8 and 2.7% of the total deviance in growth rate, survival and living tissue, respectively, and the fixed and random effects together (conditional R^2) explained 41.1, 7 and 5.5%.

4. Discussion

Our study of the role of ecological processes on coral restoration revealed both positive (i.e., *Diadema antillarum* herbivory) and negative effects (i.e., predation by fireworms) on the amount of living tissue, growth and survivorship of *Acropora cervicornis* outplants. The lack of statistical differences between ambient and procedural controls further

suggests that the positive effect of herbivory on percent living tissue was due to a higher density of urchins. While fish herbivory may have also affected the transplants due to the open-cage design, we note that this effect should be similar for all plots. Furthermore, we would have expected parrotfish to mask the actual effect of urchin herbivory on living tissue if our site would have had healthy populations of large herbivore fish such as *Scarus* spp., *Sparisoma viride* (Bonnaterre, 1788) and/or large schools of surgeon fish. However, recent inventory shows that large herbivores are scarce in Bayahibe and nearby areas (Cortés-Useche et al., 2018). This might be a consequence of overfishing which as been acknowledged as a serious problem and a major driver of coral reef decline in the Dominican Republic (Wielgus et al., 2010). Our results therefore suggest that co-occurring ecological processes delivered by urchins and fireworms can significantly influence the success of coral restoration in the Caribbean.

Modelling of outplant survival revealed no significant effect of our experimental treatments (Table 1), which can in part be explained due to the overall high survivorship observed (87.1%). Thus, we propose percent living tissue as a potentially more accurate response to our treatments, and indeed it is only for this variable that we see a positive response to the 3× urchin density (Fig. 4A). In these plots, the cover of macroalgae like the brown alga *Dictyota* sp. was reduced, while they became increasingly dominant in our urchin exclusion plots (Fig. 1, Fig. S2). Moreover, the benthos in our study area was naturally occupied with an extensive cover of turf algae (TA) and turf algae with sediment (TAS), which can negatively affect neighboring corals (Vermeij et al., 2010). In treatments with increased densities of *D. antillarum*, turf algae was also reduced (Fig. 1, Fig. S2). These results suggest that while *D. antillarum* is usually described as a macroalgae grazer (Myhre and

Table 1
Analysis of deviance from a generalized linear mixed effect model of the proportion of survivorship of the outplants. Asterisks denote levels of statistical significance (* = p<0.05; ** = p<0.01; *** = p< 0.001)

Predictor	χ^2	d.f.	*P*-value
Turf cover	1.22	1	0.269
Treatment	0.761	4	0.944
Initial Size	8.956	1	0.003**
Sedimentation	0.42	1	0.517
Time	10.931	2	0.004**
Predation (*D. antillarum*)	0.085	1	0.77
Predation (*H. carunculata*)	2.28	1	0.131

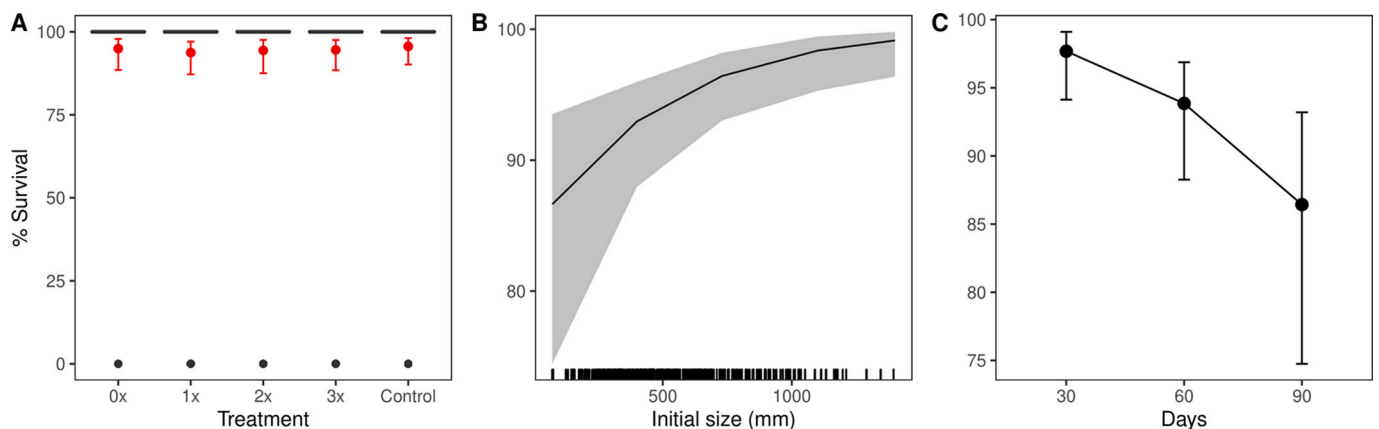Abbreviations; d.f = degrees of freedom; χ^2 = Chi-square.

Fig. 2. Model predictions of coral outplant survival (% transplants remaining) as a function of: (A) experimental treatment (total exclusion or 0× density, ambient or 1× urchin density = 4/m², 2× ambient density = 8/m², 3× ambient density = 12/m², and a cage control). Red points are marginal means +/− 95% confidence intervals estimated from a generalized linear mixed effects model (GLMM), accounting for other covariates in the model; (B) initial size of the transplant (in mm) where a rug plot along the x-axis denotes the distribution of raw values, and the line and shaded regions reflects fitted values from the GLMM +/− 95% confidence intervals; and (C) the days since coral outplanting where points are estimated means from the GLMM +/− 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
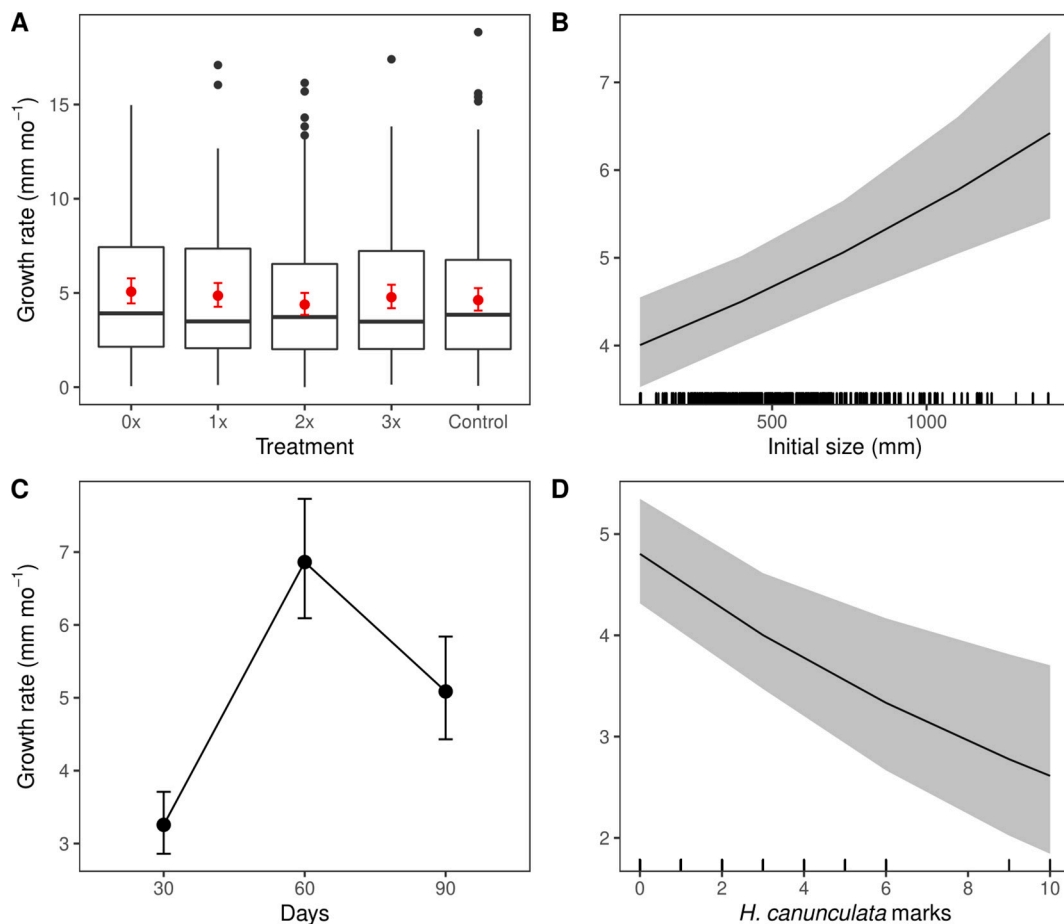
Fig. 3. Model predictions of coral outplant growth rate (in mm per month) as a function of: (A) experimental treatment; (B) initial size of the transplant; (C) the days since coral outplanting; and (D) the number of marks by the fireworm *H. cananculata* where the rug plot along the x-axis denotes the distribution of raw values, and the line and shaded regions reflects fitted values from the GLMM +/− 95% confidence intervals. Interpretations are the same as in Fig. 2.

Table 2

Analysis of deviance from a generalized linear mixed effect model of log_{10}-transformed coral growth rate. Asterisks denote levels of statistical significance (* = p<0.05; ** = p<0.01; *** = p< 0.001)

Predictor	χ^2	d.f.	*P*-value
Turf cover	0.249	1	0.618
Treatment	6.609	4	0.158
% Living Tissue	31.117	1	<0.001***
Initial Size	22.672	1	<0.001***
Sedimentation	5.522	1	0.019*
Time	190.589	2	<0.001***
Predation (*D. antillarum*)	1.399	1	0.2368
Predation (*H. carunculata*)	12.331	1	<0.001***

Acevedo-Gutiérrez, 2007; Sammarco, 1980), it can also consume TA and TAS if other preferred sources of food are not available. Both pathways reduce potential algal competition with the newly introduced corals, which are already dealing with considerable outplanting stress (Hernández-Delgado et al., 2014). Minimizing sources of stress is an important step for success, as the balance between tissue growth and mortality determines colony survival (Weil et al., 2020).

One recommendation that arises from our results is that parallel restoration of urchins could provide additional co-benefits for *A. cervicornis* restoration. The abundance of urchins in our high-density treatment (3 urchins/m²) is still well below the estimated historical densities of *D. antillarum* in the Caribbean (e.g., 7.9/m², Kissling et al., 2014). This has prompted several efforts to restore this urchin *ex situ* (Chandler et al., 2017; Feehan et al., 2016; Sharp et al., 2018). Indeed,

NOAA's recent plan to enhance corals in the Florida Keys National Marine Sanctuary includes the release of three-quarters of a million urchins (as well as the herbivorous king crab) over three phases to reduce algal growth and achieve densities similar to those observed in our surveys (NOAA, 2020). However, we advise some caution in this approach, as *D. antillarum* can also feed on adult corals or reduce the success of newly-settled larval recruits, and therefore hinder coral survivorship (Bak and van Eys, 1975). In fact, we observed *D. antillarum* consuming coral outplants in our treatments; however, these wounds healed quickly and did not seem to pose a long-term threat for them. We also did not recover a significant effect of the number of *D. antillarum* marks on any of our responses in our statistical models (Tables 1–3) but further research is necessary to study these effects on other coral species.

Another recommendation is related to a larger initial size of the outplants, which was positively and significantly related to growth rates, survivorship, and the amount of living tissue that they were able to maintain and produce over the course of the experiment (Figs. 2B, 3B, 4B). Other studies corroborate that a larger initial size of *A. cervicornis* outplants could improve their initial chances of survival, and in later stages, it can promote their sexual reproduction capacity (Goergen and Gilliam, 2018; Soong and Chen, 2003). Establishing a cost-benefit relationship between the amount of tissue to be transplanted and the resulting productivity is a particularly important objective from a restoration point of view, and our study adds to the growing literature suggesting that achieving this optimization can lead to more effective and feasible restoration (Bayraktarov et al., 2020; Boström-Einarsson et al., 2020; Foo and Asner, 2019).

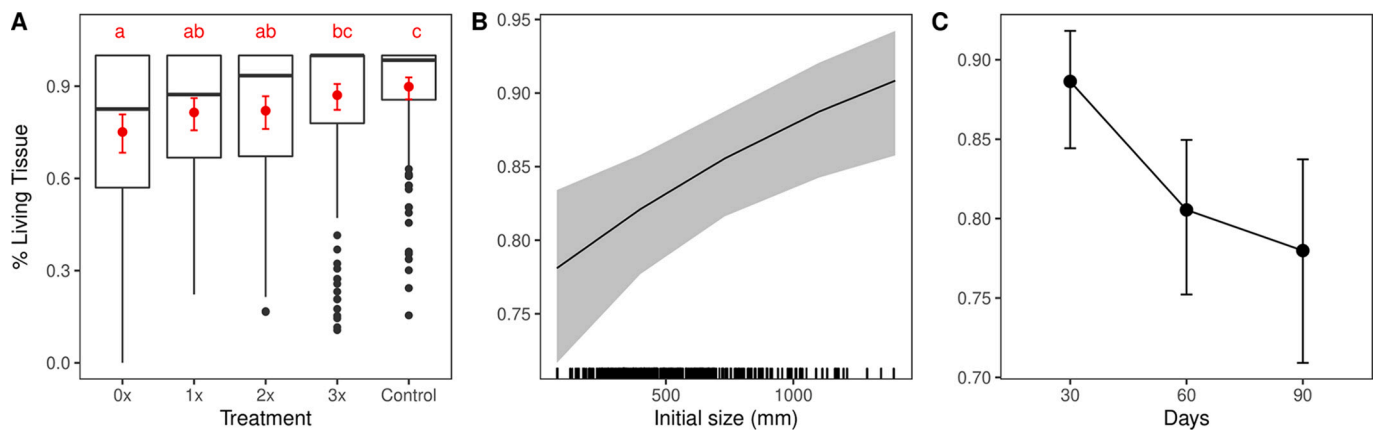In contrast, *H. carunculata* predation had a significant negative effect

Fig. 4. Model predictions of the precent of living coral tissue as a function of: (A) experimental treatment, where letters denote significant differences among experiment treatments from a post-hoc Tukey test.; (B) initial size of the transplant; and (C) the days since coral outplanting. Interpretations are the same as in Fig. 2.

Table 3

Analysis of deviance from a generalized linear mixed effect model of the proportion of living coral tissue. Asterisks denote levels of statistical significance (* = p<0.05; ** = p<0.01; *** = p< 0.001)

Predictor	χ^2	d.f.	P-value
Turf cover	0.001	1	0.979
Treatment	36.699	4	<0.001***
Initial Size	10.101	1	0.002**
Sedimentation	8.163	1	0.004**
Time	12.805	2	0.002**
Predation (*D. antillarum*)	0.879	1	0.349
Predation (*H. carunculata*)	0.166	1	0.684

on growth ($P < 0.001$) (Fig. 3D). Increasing fireworm predation may be responsible for the decline in living tissue of the transplanted colonies over time, although our models statistically control for this effect when predicting the effects of our treatments, suggesting that predation is a pervasive underlying threat to restoration success. One potential solution that has been proposed could be removing the predated tips to facilitate their recovery (Miller et al., 2014) and physically removing fireworms when possible. However, if restoration efforts continue scaling up, this method could become impractical. Selection of sites with high densities of fireworm predators, such as white grunts (*Haemulon plumierii,* Lacepède, 1801) or sand tilefish (*Malacanthus plumieri,* Bloch, 1786), as well as other corallivore predators (i.e. *Thais deltoidea,* Lamarck, 1822), may help minimize predation on coral outplants, acting as potential biological controls (Delgado and Sharp, 2020; Ladd et al., 2018; Ladd and Shantz, 2016). The role that such trophic cascades might play in controlling corallivores and increasing the success of coral restoration deserves further exploration and is an exciting frontier for the field.

Outplant stress may explain why we found no effects of our experimental treatments on coral growth (Fig. 3A), which averaged about 5 mm per month and is within the range expected for *A. cervicornis* (Weil et al., 2020). The large growth differences observed between the 3 months of study, especially at the peak of growth in the second month, suggest that after an initial recovery period of approximately 4 weeks (Fig. 3C), the outplanted colonies made a high investment in their growth. This trend is consistent with the observations of Lirman et al. (2010), who reported growth peaks in transplanted fragments of *A. cervicornis* between 3 and 6 weeks after transplantation, and somewhat similar to the observations of Castanaro and Lasker (2003) for the Caribbean octocoral *Pseudopterogorgia elisabethae* (Bayer, 1961).

During the three-month duration of our study, the sedimentation rate recorded in the three areas chosen was increasing, going from an average of approximately 6000 g/4 m^2 in the first month to an average

of more than 15,000 g/4m^2 in the third, probably an effect of the rainy season and the subsequent sediments released by the nearby Chavon river. Despite this, we found a minimal but positive effect of sedimentation on the living tissue maintained by the outplants ($P = 0.004$), as well as on the growth rates ($P = 0.019$) (Fig. S3). Although sedimentation rates are one of the main causes of the loss of coral cover in Dominican reefs (Torres et al., 2001), the branched form of *A. cervicornis* makes this species more resistant to sedimentation by decreasing the surface where sediment particles can be deposited (Rogers, 1983). The positive effect was therefore most likely due to a spurious correlation with some unmeasured variable that was associated with both the high sedimentation rates, growth rates, and increased living tissue—for example, increased nutrient delivery with riverine discharge or declining seasonal temperatures—although this relationship deserves further exploration.

5. Conclusions

In summary, while there is not one single solution for a successful coral transplant operation, we provide three recommendations to keep in mind when investing time and money into the initial restoration phase of *A. cervicornis*:

(1) utilize as large an outplant of *A. cervicornis* as is possible (up to 139 cm of linear tissue, the largest size used in our experiment);
(2) select sites with low populations of the fireworm *H. carunculata* (or high abundance of fireworm predators) to limit loss of coral tissue due to direct predation;
(3) depending on achievable densities, co-restore the urchin *D. antillarum* with *A. cervicornis* to reduce benthic algae and ameliorate stress on the outplants during the critical early months of their introduction.

Because many sites still only have natural abundances of *D. antillarum* below 3 individuals/m^2, we do not specifically recommend targeting sites where urchins are present to maximize restoration success. We recognize, however, that the benefits of urchin grazing at low densities may manifest over longer periods than our study, so we do not necessarily discourage people from outplanting in sites with presence of *D. antillarum*. We also suggest that future studies analyze the genotype of the donor colony to determine whether any of the effects here could be modulated by the underlying genetics of the transplants. In conclusion, there is still much to research and learn to optimize the restoration of *A. cervicornis*, but through an integration of classic community and restoration ecology, we may increase our chances of restoring this key reef-builder to the Caribbean.

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Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2021.151541.

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