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RESEARCH ARTICLE

Multi-year evaluation of rearing techniques for three sexually propagated Caribbean corals in a restoration setting

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In response to declining coral populations worldwide, conservation groups are increasingly applying restoration strategies to bolster abundance and diversity, including sexual propagation of corals. Collection and fertilization of coral gametes as well as larval rearing and settlement have been successful. However, post-settlement stages remain a bottleneck (80–100% mortality), which makes this technique costly to implement at scale. To address this challenge, we compared the survival and colony size of three sexually propagated Caribbean coral species, *Diploria labyrinthiformis*, *Pseudodiploria strigosa*, and *Orbicella faveolata*, reared at three levels of investment: direct outplant to reef, in situ field nursery rearing, and ex situ aquaculture facility rearing. As part of coral sexual propagation work in St. Croix, United States Virgin Islands, recruits were reared for 1 year before being outplanted to reef plots and were monitored annually for three subsequent years. The cost-effectiveness of each rearing strategy was calculated at each monitoring time point via coral seeding unit yield and cost per seeding unit. Although survival was low at 4 years (0–1.8%), corals reared in the in situ nursery displayed significantly higher survival and therefore lower cost per seeding unit than the other two investment strategies. These results highlight the benefits of an in situ nursery stage to increase long-term juvenile survival and cost-effectiveness. The return on investment of corals reared in the in situ nursery suggests that outplanting sexually propagated corals may be a viable restoration strategy; however, the low proportion of corals surviving at 4 years highlights current limitations when outplanting on degraded reefs.

Key words: coral reefs, cost analysis, *Diploria labyrinthiformis*, in situ coral nursery, *Pseudodiploria strigosa*, sexual reproduction

Implications for Practice

- In situ nursery rearing for at least 1 year confers colony size benefits and increased survival of sexually propagated brain corals.
- Current algae-dominated reefs limit assisted scleractinian coral recruitment success due to hypothesized benthic competition and microbial, physical, and chemical antagonism.
- Multi-year fate-tracking and cost analyses are both region- and program-specific and are imperative for conducting effective restoration projects.

Introduction

Coral reefs are in stark decline worldwide due to an array of natural and anthropogenic stressors, compounded by increasingly severe disturbances related to human-derived climate change (Hughes 1994; Hughes et al. 2003; Hoegh-Guldberg et al. 2017). These stressors have synergistically shifted coral reefs toward an altered steady state of algae dominance (Jackson et al. 2014), characterized by increased microbialization and altered reef water chemistry, which further promote algal growth and scleractinian coral decline (McDole et al. 2012; Haas et al. 2016; Nelson et al. 2023). Current models estimate that 70–90% of coral reefs will be lost by 2050 if average global temperatures continue to warm by 1.5°C (Hoegh-Guldberg et al. 2019; Intergovernmental Panel on Climate Change 2023). Given that coral reefs are among the most biodiverse ecosystems and provide valuable ecosystem services by supporting fisheries, tourism, and shoreline protection (Gattuso et al. 2014; Burke & Spalding 2022), efforts to

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enhance reefs through active coral restoration have grown over recent decades (reviewed in Boström-Einarsson et al. 2020).

When approaching reef restoration, it is important to consider how coral populations naturally recover following episodic disturbances through variable reproductive strategies, that is, via adult colony regeneration and larval recruitment (Linares et al. 2011; Doropoulos et al. 2015). Colony regeneration, or asexual propagation, whereby fragments from wild donor colonies are repeatedly fragmented and grown out in nurseries, has been utilized as a restoration technique for over 40 years (Bowden-Kerby 2001; Young et al. 2012). While straightforward to implement and successful on small scales, this approach relies on existing coral biomass and does not foster novel genetic diversity, thought to be a key factor in promoting population resilience under changing environmental conditions (Reusch et al. 2005; Baums 2008; Baums et al. 2013). An alternative technique that addresses these demographic and genetic limitations is sexual propagation, which harnesses the production of millions of gametes by broadcast spawning corals to mass fertilize and produce coral propagules ex situ (reviewed in Randall et al. 2020).

Broadcast spawning corals are dominant reef-builders in the Caribbean and are key to reef persistence via mass larval supply (Szmant 1986). Following mass spawning and fertilization, successful recruitment to the population is dependent on the availability of competent larvae, successful settlement, and survival through early juvenile stages (Babcock & Mundy 1996; Arnold & Steneck 2011). In the Caribbean, this influx of new individuals to sustain coral populations has declined substantially in recent decades (Hughes & Tanner 2000; Vermeij et al. 2011), impaired by stressors such as increased algal cover (Arnold et al. 2010), heat stress (Randall & Szmant 2009), and lower fertilization rates due to reduced connectivity (Baums et al. 2019) and synchronicity (Shlesinger & Loya 2019) among metapopulations. In the face of natural recruitment failure, sexual propagation provides a promising approach to generating millions of diverse coral propagules for seeding reefs. Many advances in gamete collection, fertilization, and larval culture methods have been made over the past two decades (Banaszak et al. 2023); however, low recruit survival combined with the cost of sexual coral propagation impedes its application as an effective restoration method on ecologically meaningful scales.

Given that coral recruit mortality is high when outplanted to reefs shortly after settlement, a key question is whether a period of nursery rearing can increase recruit survival and thus optimize cost-effectiveness. Several studies in the Pacific have demonstrated survival and growth benefits conferred by in situ nursery rearing for sexually propagated acroporids (e.g., Guest et al. 2014; Ligson et al. 2020; Humanes et al. 2021) and massive species (Guest et al. 2023), whereas a dearth of information exists surrounding the long-term return on investment of nursery rearing in the Caribbean (Chamberland et al. 2015; Henry et al. 2021). Therefore, we aimed to determine if juvenile survival of three Caribbean coral species can be increased by investing in an intermediate nursery rearing stage for the first year post-settlement and whether this intermediate increases cost-effectiveness.

Here we examine the effect of three levels of rearing investment (low, medium, and high) on survival and colony size of Grooved brain coral (*Diploria labyrinthiformis*; Linnaeus 1758), Symmetrical brain coral (*Pseudodiploria strigosa*; Dana 1846), and Mountainous star coral (*Orbicella faveolata*; Ellis and Solander 1786). The species chosen are current or recommended targets for sexual restoration efforts (Baums et al. 2019), contribute to reef structure, and have suffered major declines in the United States Virgin Islands (USVI) in the past two decades (Miller et al. 2009; Grove 2023). These species represent a range of proficiency in natural recruitment, with *Orbicella* spp. exhibiting severely low natural recruitment (Hughes & Tanner 2000), while recruitment of brain coral species such as *P. strigosa* remains robust (Baums et al. 2019). Sexually propagated coral recruits were settled onto seeding units (SUs) and either directly outplanted onto the reef (low investment, high mortality risk), reared for 1 year in an in situ field nursery (FN) (medium investment and potential reduction in risk), or reared for 1 year in an ex situ aquaculture facility (AF) (high investment, low risk of predation, competition, and disease). After 1 year, all surviving corals were outplanted to the reef, and survival and maximum diameter (mm) of outplanted corals were measured annually for the subsequent 3 years. A cost evaluation of each investment strategy was completed based on cost per seeding unit retaining a minimum of one coral.

Methods

Study Site

This study was conducted at The Nature Conservancy's (TNC) Coral Innovation Hub in St. Croix, USVI. The in situ nursery and outplant reef site are located at Channel Rock (Lat/Long: 17.77°N, 64.59°W), a patch reef at approximately 7.5 m depth located within the protected East End Marine Park. Channel Rock receives low exposure to anthropogenic impact due to its location outside of St. Croix's northeastern barrier reef complex, neighboring a low population density shoreline, but has been impacted by the emergence of stony coral tissue loss disease (Brandt et al. 2021), bleaching (Miller et al. 2009), and the recent invasion of *Ramicrusta* species (Edmunds et al. 2019).

Gamete Collection, Larval Rearing, and Settlement

Gametes were collected by SCUBA divers during a succession of spawning events in 2020 on coral reefs in two bays on the north side of the island, Cane Bay (Lat–Long: 17.77°N, 64.81°W) and Tamarind Reef (17.76°N, 64.67°W) (Table S1; Fig. S1). Weighted nylon mesh nets attached to plastic funnels and 50 mL polypropylene vials were deployed over spawning coral colonies, concentrating positively buoyant egg-sperm bundles into vials for collection and transport (Hagedorn et al. 2021). Within 2 hours of spawning, gametes were cross-fertilized in 100-µm filtered ozone-sterilized seawater (FSSW). Fertilized embryos were distributed into 1 L polycarbonate fat separators and rinsed with FSSW to remove excess sperm.

Fertilization for all three species was observed to be between 85 and 95%. Embryos were dispersed at an approximate density of 1 larva/mL into 110 L containers immersed in flow-through raceway tank systems, with raceways maintained at approximately 28°C (Fig. 1C). Partial water changes (approximately 75%) were conducted daily at first and then every other day to reduce microbial load and maintain a stable pH in the rearing environment throughout development (Vermeij 2006; Hagedorn et al. 2021).

Prior to spawning, SUs (Fig. S2) were conditioned for 1 month at the St. Croix Yacht Club dock (*D. labyrinthiformis*, 17.76 N, −64.60 W) or at TNC's Cane Bay nursery (*P. strigosa* and *O. faveolata*, 17.77°N, 64.81°W) to develop a natural biofilm and crustose coralline algae (Fig. S1). Ceramic SUs were designed by SECORE International, Inc. in 2020, were approximately 120 cm^2 in surface area (Fig. S2), and have previously been found viable as coral SUs (Randall et al. 2023). Thirty conditioned SUs were introduced to a 110 L larval culture bin for each species upon observing larvae swimming in the water column (2–4 days post-fertilization). Conditioned SUs introduced to *D. labyrinthiformis* for settlement were not cleaned, which resulted in poor water quality in larval cultures and notable benthic competition to settled recruits (shading). For this reason, SUs used for *P. strigosa* and *O. faveolata* settlement were scrubbed of macro-fouling organisms prior to larval introduction. Once settlement was observed, freshly isolated Symbiodiniaceae from adult conspecifics were introduced to cultures to inoculate recruits with symbionts (Supplement S1). Following observed symbiont uptake, settled recruits were scored and mapped on each SU using a stereo microscope. Due to the manner in which SUs were affixed to reef substrate, all sides except the bottom surface were scored. Once scored, SUs with ≥1 settled recruit were moved to a flow-through raceway for temporary holding until transfer to rearing treatments.

Rearing Investment Treatment Setup

Three weeks after fertilization (6 weeks for *O. faveolata*), SUs were assigned to one of three rearing investment treatments: direct outplant to reef plots (DO), in situ FN, or ex situ AF (Figs. 1 & 2). The 30 SUs for each species were re-scored. SUs with no settlers were removed from the experiment. The remaining SUs (27 for *D. labyrinthiformis*, 27 for *P. strigosa*, and 21 for *O. faveolata*) were ordered by settler density and then randomly assigned to one of the three treatments, ensuring there were no significant differobbences in initial settler count between treatments (analysis of variance $p > 0.05$). SUs assigned to DO were deployed over a 50-m^2 area at Channel Rock reef, with at least 1 m separation between SUs (Fig. 1A). Plot depths ranged from 6 to 8 m for *D. labyrinthiformis* and *O. faveolata* and 4–6 m for *P. strigosa*. Macroalgae were scrubbed from the reef substrate, and SUs were attached to benthos by masonry nail and cable tie (Figs. 1A & S2b). DO received no further maintenance and was solely revisited for monitoring. SUs assigned to FN were attached by cable tie to a polyvinyl chloride and plastic mesh nursery table at 7.5 m depth with the table top approximately 1 m above sand (Fig. 1B). Tables were cleaned by SCUBA divers every 1–2 months to remove fleshy macroalgae and cyanobacteria. SUs assigned to AF were maintained in a 650-L outdoor closed system flow-through raceway tank with a whole system exchange rate of 15,000 gal per hour (Fig. 1C). Seawater was ozone sterilized prior to entering the system and was continuously filtered through a 200 µm filter. The raceway received natural sunlight filtered through 95% UV ray-blocking shade cloth. The following seawater parameters were maintained as precisely as possible: temperature: 28°C, pH: 7.8–8.3, salinity: 33–35 ppt, dissolved oxygen: 6–12 ppm, oxidation reduction potential (ORP): 370–390 mV. The raceway was cleaned biweekly, and SUs were cleaned monthly under a stereoscope

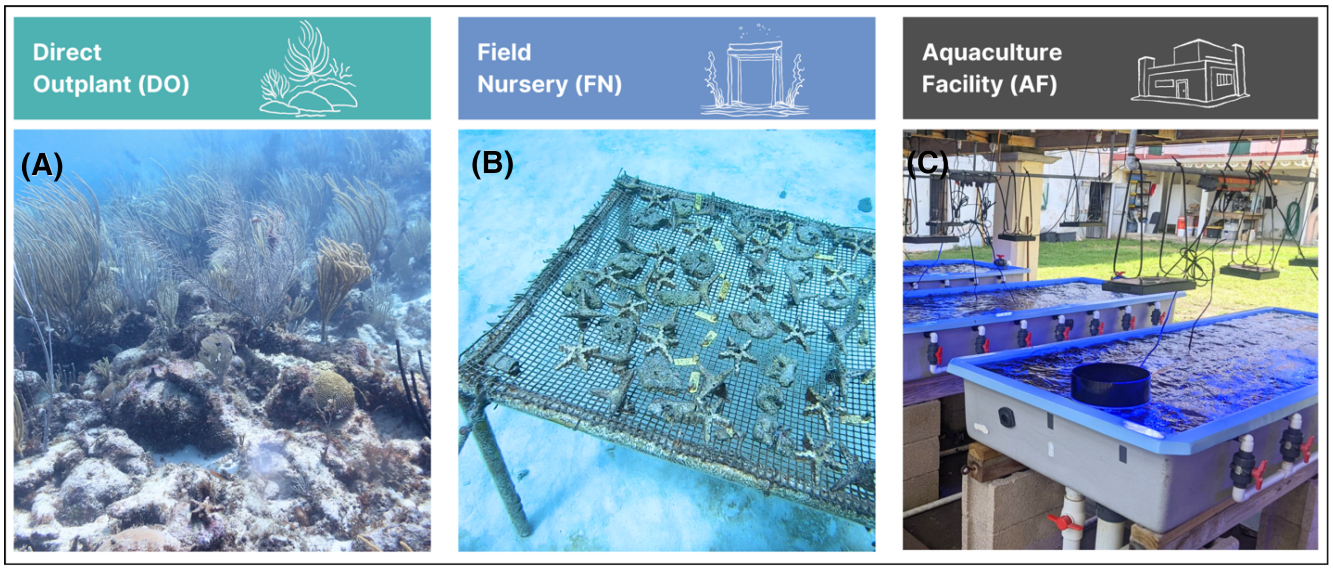


Figure 1. Coral recruit rearing investment treatments. (A) Direct outplant to reef (DO, low investment), (B) in situ field nursery table (FN, medium investment), (C) ex situ aquaculture facility (AF, high investment).

with fine paintbrushes and syringe needles until December 2020 when herbivores (*Clibanarius tricolor*, *Paguristes cadenati*, and *Astraea* spp.) were introduced. Large pieces of fleshy macroalgae were removed by hand as needed. Coral recruits were not fed throughout the duration of treatment. A HOBO UA-002-64 pendant temperature and light data logger was deployed at each rearing treatment (Fig. S3).

Outplanting and Monitoring

After 1 year of rearing, SUs in the AF and FN treatments harboring ≥1 surviving juvenile were outplanted to Channel Rock reef in proximity (<30 cm) to directly outplanted SUs (Fig. 2). Each original outplant plot then had one SU from each investment treatment ($n = 3$ per plot). Survival was scored by divers on SCUBA at 6, 12, 24, 36, and 48 months (±3 months depending on species) using blue light underwater flashlights (Nightsea FL-1 LED), with an additional survival monitoring time point added following the 2023 thermal stress event (16.8°C degree heating weeks; NOAA Coral Reef Watch null) (Fig. 2). Maximum colony diameter (mm) of juvenile corals was measured to the nearest 0.1 mm using Vernier calipers at 12, 24, 36, and 48 month time points (±3 months) (Figs. 2 & 3). Two touching polyps were considered a chimera when a distinct skeletal line was present and were counted and measured individually.

Statistical Analyses

Statistical tests were performed in R (v2023.03.0 + 386 Rstudio, Inc.; https://github.com/enixon96/SPIkids) and conducted at a significance level of $\alpha = 0.05$. To test for differences in juvenile coral survival, investment treatments were compared using a Kaplan–Meiers survival analysis (Kaplan & Meier 1958) followed by a Log-Rank post hoc pairwise comparison. Differences in individual coral size, proxied by maximum colony diameter (mm), were compared between treatments at each time point using Welch's t test followed by a Games–Howell post hoc (Games & Howell 1976). Due to discrepancies in survival scoring, if a SU received a higher score than in the previous time point, it was standardized to the lowest of the two scores. Therefore, n values for survival and colony size may differ slightly, and reported survival is conservative. SU yield, defined as the proportion of SUs in a treatment retaining at least one coral recruit, was compared at 12, 24, 36, and 48 months via a Fisher exact test with the Freeman–Halton extension followed by a pairwise Fisher exact test post hoc comparison (Freeman & Halton 1951). SUs that were absent or not located at a time point were removed prior to analysis.

Cost Analysis

SU yield is a metric commonly used by restoration practitioners to quantify sexual coral restoration success and associated financial costs (e.g. Chamberland et al. 2015; Randall et al. 2023). We defined SU yield as the proportion of SUs within the restoration site that harbored at least one living coral. Retention (i.e. whether a SU remained secured to the reef plot) was not considered a metric in SU yield calculations because it is independent of rearing technique.

Restoration costs were calculated using the methods outlined in Edwards (2010) and used in other coral restoration cost-efficiency studies (e.g., Chamberland et al. 2015). Costs were

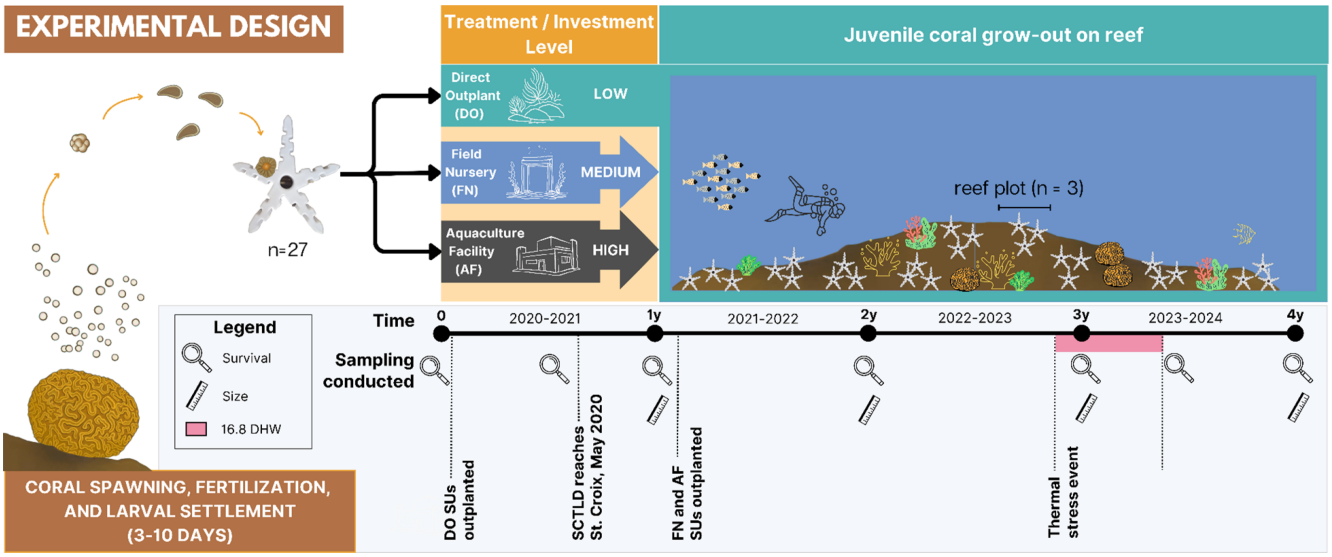


Figure 2. Experimental design of coral recruit rearing investment treatments, outplanting, and subsequent monitoring. Coral larvae were settled onto conditioned SUs, which were scored and distributed into three rearing treatments: direct outplant (DO), in situ field nursery (FN), and ex situ aquaculture facility (AF) ($n = 9$ SUs per treatment). SUs were scored for survival at 6 months and for the subsequent 3 years. Following 1 year of rearing, corals were outplanted to DO plots ($n = 3$ per outplant plot, 1 × SU per treatment) at Channel Rock reef. Noteworthy stress events, that is, the appearance of stony coral tissue loss disease (SCTLD) on St. Croix and the 16.8°C degree heating weeks 2023 thermal stress event, have been added to the timeline for reference.

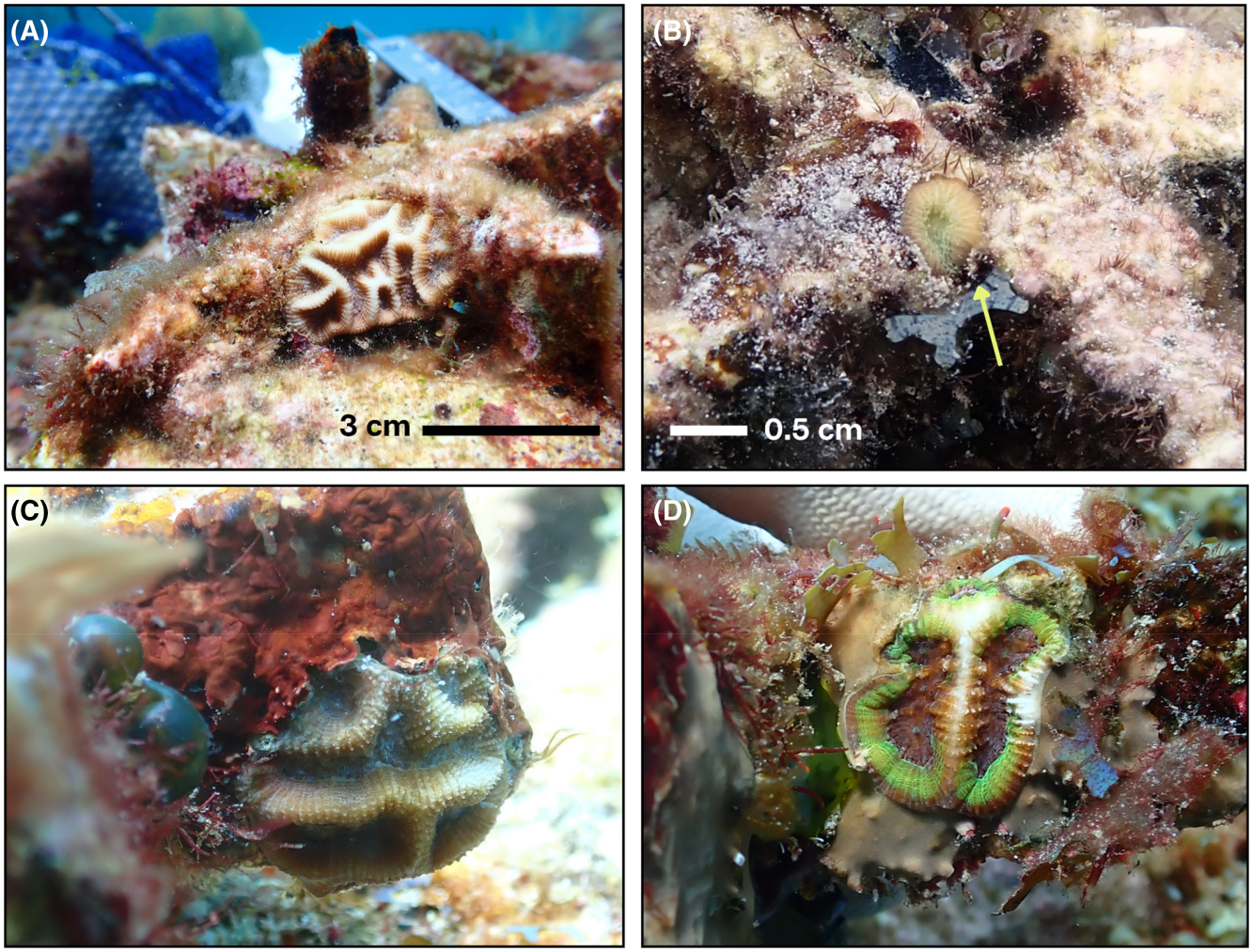


Figure 3. Photos depicting 3- and 4-year-old juvenile corals. (A) Juvenile *Pseudodiploria strigosa*, (B) juvenile *Diploria labyrinthiformis*, (C) *Ramicrusta* encroaching on juvenile *P. strigosa*, (D) *Millepora* encroaching on juvenile *P. strigosa*.

divided into six stages (preparation, gamete collection, hatchery, rearing, outplanting, and monitoring) and seven cost categories (equipment, consumables, labor, dive gear, SCUBA tanks, boat use, and other). The following tasks were included in each cost category: (1) preparation—creation of a local spawning calendar, one spawning site survey, conditioning, and manual scrubbing of SUs; (2) gamete collection—three nights of spawning observation and/or gamete collection dives; (3) hatchery—one night of gamete fertilization, 1 week of larval rearing, 1 month of recruit rearing; (4) rearing—nursery setup and transfer to nursery (FN only), nursery or aquaria maintenance, and SU care; (5) outplanting—transfer to outplant site; deployment of SUs to reef; and (6) monitoring—initial scoring of 27 SUs in the laboratory; annual survival scoring of 27 SUs and measurement of surviving juveniles (Table S2).

Costs to establish the AF were not included in the cost analysis because this was a one-time expense, and the analysis was based on running costs. Running costs of the AF included utilities, operational costs (e.g. maintenance, repair, and replacement of system parts), consumables for maintenance and monitoring of water tables, and labor. The installation costs for the in situ nursery were included since nursery structures are not considered permanent and typically need to be replaced after three to 5 years of use. Maintenance costs included dive gear, SCUBA tanks, and boat upkeep, as well as marina fees, insurance, and fuel for boat use. Equipment, including dive gear, was estimated to have a lifespan of 3–5 years, and SCUBA tanks and boats were estimated to have a lifespan of 10 years. Per-use costs were calculated by dividing the purchase price by years of use and the number of uses per year. Labor was divided into two categories (subject matter expert and local practitioner), and hourly wages were based on median wages for equivalent categories within TNC.

Costs were calculated assuming 4000 SUs based on the capacity of the AF. SU yield was modeled by applying the percent yield of the SUs monitored in the experiment to 4000 SUs. Cost per SU was calculated at 1-, 2-, 3-, and 4-year time points by dividing the total restoration cost by SU yield.

Results

Coral Recruit Survival

Mean settlement of *Diploria labyrinthiformis* was 37.81 (SD = 18.96) recruits per SU with a range of 8–79 recruits per SU, and an approximate settlement rate of 3.4%. In total, 368 recruits were assigned to DO, 336 to FN, and 317 to AF. Early mortality was high (63–69% at 6 months) across all treatments (Fig. 4A). Survival continued to decline across all treatments throughout the study; however, corals initially reared in FN displayed significantly higher survivorship compared to AF or DO, while AF and DO did not significantly differ in survival (*K-M*: $\chi^2 = 23.1$, $p < 0.01$; FN vs. AF, FN vs. DO $p = 0.04$, AF vs. DO $p = 0.86$). At 1 year, the FN treatment (19.6% survival; $n = 66$ corals) conferred two times and six times higher survival than DO (9.5% survival; $n = 35$ corals) and AF (3.2% survival; $n = 10$ corals), respectively (Fig. 4A). This trend continued through the 24 and 36 months time points with FN survival two times and eight times higher than in DO and AF, respectively (Fig. 4A). By 48 months, survival dropped to 1.8% ($n = 6$ corals) for FN, 0.54% ($n = 2$ corals) for DO, and 0% for AF (Fig. 4A).

Mean settlement of *Pseudodiploria strigosa* recruits was 69.44 (SD = 38.1) recruits per SU and ranged from 9 to 142 recruits per SU, and a settlement rate of approximately 3.75%. In total, 611 recruits were assigned to DO, 620 to FN, and 644 to AF. *P. strigosa* recruits displayed substantially higher initial mortality than *D. labyrinthiformis*, with 96–99% mortality seen across treatments in the first 6 months and no AF recruits surviving to 1 year (Fig. 4C). Survival was significantly different among all investment treatments (*K-M*: $\chi^2 = 32.1$, $p < 0.01$; FN vs. DO $p < 0.01$, FN vs. AF $p < 0.01$, DO vs. AF $p < 0.01$). Similar to *D. labyrinthiformis* recruits, *P. strigosa* recruits initially reared in the FN treatment exhibited significantly higher survival than AF and DO corals (Fig. 4C). After 1 year of investment, FN recruits (6.5% survival; $n = 40$ corals) were 10 times more likely to survive than DO (0.65% survival; $n = 4$ corals) (Fig. 4C). Following the investment period, *P. strigosa* survival declined by approximately 50% annually in both FN and DO, diminishing to 0% for DO and 0.65% ($n = 4$ corals) for FN at 45 months (Fig. 4C).

Initial scores of *Orbicella faveolata* recruits ranged from 1 to 78 recruits per SU with an average of 23.22 (SD = 18.0), and an approximate settlement rate of 2.51%. In total, 205 recruits were assigned to DO, 221 to FN, and 201 to AF. *O. faveolata* SUs were scored at 1 year, at which time only five coral recruits remained. Three of these corals were reared in FN and two were in DO, representing 1.4 and 1.0% survival respectively, with no

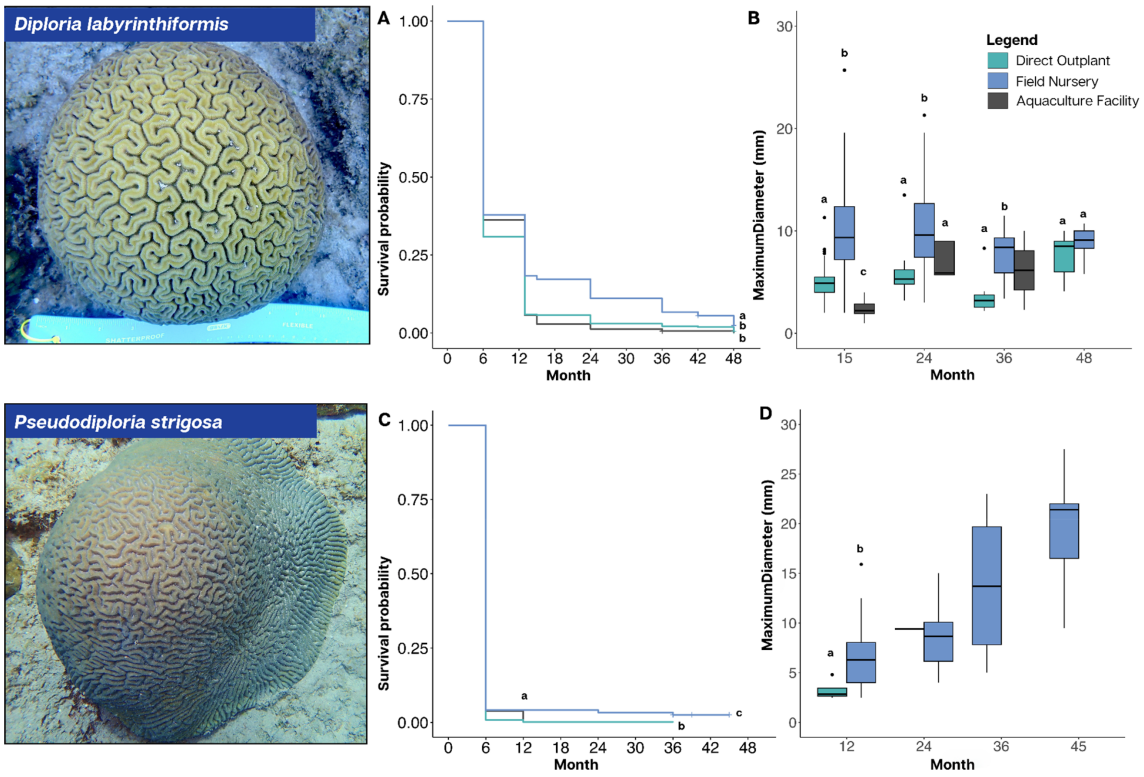


Figure 4. Survival and maximum diameter of sexually propagated *Diploria labyrinthiformis* and *Pseudodiploria strigosa* reared at three levels of investment: direct outplant (DO, teal), in situ field nursery (FN, blue), ex situ aquaculture facility (AF, black). Kaplan–Meier survival analysis for (A) *D. labyrinthiformis* and (C) *P. strigosa*. Letters next to lines indicate statistically different survival ($p < 0.05$) between treatments determined via Log-Rank post hoc pairwise comparison. Boxplots of juvenile colony size, maximum diameter (mm) by investment treatment at each monitoring time point for (B) *D. labyrinthiformis* and (D) *P. strigosa*. Letters indicate statistically different ($p < 0.05$) colony sizes between treatment groups and were determined by Welch's *t* test with post hoc comparison.

O. faveolata recruits surviving in the AF treatment (Table S3). While FN corals were not outplanted and monitored further, full mortality was observed in DO by 24 months (Table S3).

Recruit Diameter

At 15 months, *D. labyrinthiformis* mean maximum colony diameter (mm) differed significantly among all treatments (Welch's *t* test with pairwise post hoc comparison, $p < 0.01$). FN corals reached a mean maximum diameter of 10.0 mm ($n = 66$ corals, SD = 4.43), whereas DO- and AF-reared corals averaged 5.0 mm ($n = 35$ corals, SD = 1.93) and 2.3 mm ($n = 10$ corals, SD = 0.866), respectively (Fig. 4B). Following outplanting to reef plots, only AF juveniles displayed an increase in mean colony size from 15 to 24 months (Fig. 4B). At this time point, FN juvenile corals maintained a significantly higher mean maximum colony diameter of 10.26 mm ($n = 34$ corals, SD = 4.48) in comparison to DO and AF corals, 5.97 mm ($n = 11$ corals, SD = 2.71) and 7.06 mm ($n = 5$ corals, SD = 1.78) respectively (DO vs. FN $p < 0.01$, DO vs. AF $p = 0.6$, FN vs. AF $p = 0.03$). Interestingly, at 36 months of age (2 years following outplanting of FN and AF), mean maximum diameter decreased across all treatments, though FN juvenile corals mean maximum diameter remained significantly higher than DO corals (DO vs. FN $p < 0.01$) (Fig. 4B). This trend reversed at 48 months, with FN and DO mean colony size increasing to 8.78 mm ($n = 5$ corals, SD = 1.90) and 7.52 mm ($n = 5$ corals, SD = 2.41), respectively (DO vs. FN $p = 0.4$).

After 1 year of investment treatments, *P. strigosa* recruit colony size differed significantly between FN and DO corals ($p < 0.01$), with FN corals reaching a mean maximum diameter of 6.66 mm ($n = 40$ corals, SD = 2.99) in comparison to DO corals, which grew to 3.25 mm ($n = 4$ corals, SD = 1.05) (Fig. 4D). FN juvenile mean colony size continued to increase throughout the entirety of the study, measuring 8.58 mm ($n = 22$ corals, SD = 2.85) and 13.7 mm ($n = 12$ corals, SD = 6.99) at 24 and 36 months, respectively (Fig. 4D). Notably, at 36 months, half of the surviving *P. strigosa* juvenile cohort were on average triple the colony size of the other half, measuring a mean maximum diameter of 20.07 mm ($n = 6$ corals, SD = 2.26) and 7.3 mm ($n = 6$ corals, SD = 2.24) respectively (Fig. 4D). At 45 months, the mean maximum diameter reached 19.38 mm ($n = 5$ corals, SD = 6.76) (Fig. 4D).

The three surviving FN *O. faveolata* reached a mean maximum diameter of 2.53 mm (SD = 0.289) at 1 year, while the two surviving DOs measured at 1.9 and 3.0 mm.

Seeding Unit Yield and Cost Analysis

Restoration costs of directly outplanting to reef (DO) were the least expensive, totaling $31,741.52 for 4000 SUs. Restoration costs incorporating a 1-year rearing phase totaled $55,115.58 and $80,105.03 for in situ nursery (FN) and AF investment treatments, respectively (Fig. 5A & 5C). Costs of preparation, gamete collection, hatchery, outplanting, and monitoring stages were nearly identical across rearing methods (Table S2). Thus, differences in costs among treatments are due to costs associated with the rearing phase. Rearing was the most expensive stage for FN and AF, representing 42 and 61% of total costs, respectively (Table S2). Labor was the most expensive cost category for all treatments, making up 63% (DO), 65% (FN), and 75% (AF) of costs.

At 1 year, nine DO and FN SUs retained a minimum of one *D. labyrinthiformis* coral (100% yield), while only five AF SUs retained at least one living coral (56% yield), but this difference was not significant (Fig. 5B; Fisher's exact test with pairwise post hoc comparison, $p > 0.25$). DO was the least expensive method ($7.94 per SU) at this time point (Fig. 5A), but the most cost-effective method changed over time as yield dropped in all treatments. FN had the highest yield and therefore the lowest cost per SU in years two (100% yield; $13.78) and three (89% yield; $15.50) (Fig. 5A & 5B). By year 4, yield remained highest in FN (50%) but DO had a narrowly lower cost per SU ($23.81 for DO vs. $27.56 for FN). Differences in yield were only significant between FN and AF treatments in year 3 (Fig. 5B, FN vs. AF $p < 0.05$). AF SUs had the highest cost at all time points.

With the exclusion of the final 45-month time point ($p = 0.06$), yield was significantly higher in the FN treatment than the DO and AF treatments for *P. strigosa* (Fig. 5D). AF had 0% yield in year 1, while DO decreased to 0% yield by year 3 (Fig. 5D; DO vs. FN and FN vs. AF $p < 0.01$). FN was the most economical method throughout the study, retaining 57% yield in year 4 with a cost of $24.11 per SU (Fig. 5C).

SU yield for *O. faveolata* was low across treatments. In year 1, DO yield was 22%, FN yield was 33%, and AF yield was 0%. DO had the lowest cost per SU at $35.71, but yield fell to zero by 24 months (Table S3).

Discussion

Determining the restoration potential of coral propagation techniques is vital for effective implementation. The scale at which commonplace practices (i.e. asexual fragmentation and outplanting) act is insufficient to match the scale of the current climate change crisis (Bellwood et al. 2019; Bruno et al. 2019). Given the limitations of conventional asexual propagation techniques (limited scale and genetic diversity), coral sexual propagation has been suggested as a technique with the potential to overcome these limitations, though a scarcity of information exists on long-term viability in the Caribbean (Chamberland et al. 2015, 2017; Henry et al. 2021). To our knowledge, this is the longest study (4 years) to examine the ecological and economic effectiveness of sexually propagated corals in the Caribbean and highlights the benefits of a post-settlement in situ nursery rearing phase for two brain coral species, *Diploria labyrinthiformis and Pseudodiploria strigosa*.

In Situ Nursery Confers Survival and Growth Advantages to Sexually Propagated Corals

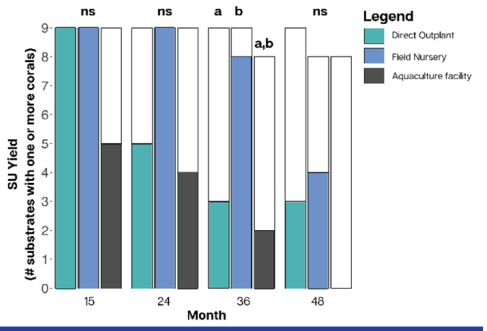
While brain corals *D. labyrinthiformis* and *P. strigosa* retained juvenile survival throughout the study, a post-settlement bottleneck was observed across treatments at 6 months (63–69 and

Diploria labyrinthiformis

A

Rearing method	Restoration cost of 4,000 SUs (USD)	1 Year		2 Years		3 Years		4 Years	
		SU yield (%)	SU cost (USD)	SU yield (%)	SU cost (USD)	SU yield (%)	SU cost (USD)	SU yield (%)	SU cost (USD)
Direct outplant	31,741.52	100	7.94	56	14.28	33	23.81	33	23.81
In situ nursery	55,115.58	100	13.78	100	13.78	89	15.50	50	27.56
Aquaculture facility	80,105.03	56	36.05	44	45.06	25	80.11	0	-

B



Pseudodiploria strigosa

C

Rearing method	Restoration cost of 4,000 SUs (USD)	1 Year		2 Years		3 Years		4 Years	
		SU yield (%)	SU cost (USD)	SU yield (%)	SU cost (USD)	SU yield (%)	SU cost (USD)	SU yield (%)	SU cost (USD)
Direct outplant	31,741.52	22	35.71	11	71.42	0	-	0	-
In situ nursery	55,115.58	89	15.50	78	17.72	63	22.05	57	24.11
Aquaculture facility	80,105.03	0	-	0	-	0	-	0	-

D

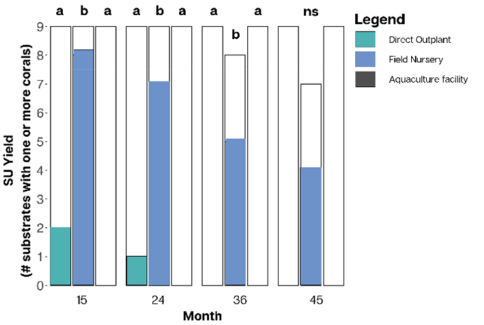


Figure 5. Cost table and SU yield of *Pseudodiploria strigosa* and *Diploria labyrinthiformis*. (A, C) Total cost, SU yield (%), and cost per SU for each rearing method at 1, 2, 3, and 4 years of age. Assumes 4000 SUs produced. All costs are in U.S. dollars. (B, D) SU yield (# substrates) of each investment treatment over the course of the study. Statistical differences were determined by Fisher's exact test with pairwise post hoc analysis and are letter denoted.

96–99%, respectively). This aligns with previous sexual propagation studies, with high post-settlement mortality occurring in the first year (reviewed in Omori 2019). Despite initial mortality, sexually propagated brain corals assigned to 1 year of in situ nursery rearing displayed survival benefits that persisted in the 3 years post-outplanting and were found to be significantly larger in size when compared to directly outplanted and AF-reared recruits. We hypothesize that the in situ nursery provides protection from stressors found on algae-dominated reefs while conferring benefits of in situ rearing. In situ nursery tables protect juvenile corals from antagonistic features that characterize degraded reefs such as benthic competition (Arnold & Steneck 2011), sedimentation (Speare et al. 2019), predation (Gallagher & Doropoulos 2017), hypoxia (Mallon et al. 2023), and microbialization (Vermeij et al. 2009) while maintaining natural temperature, pH, light, flow, nutrients, and access to symbionts. Although no microbial, physical, or chemical parameters were recorded, water column restoration structures have been found to hold lower microbial load and to be more impervious to low-oxygen diel swings than nearby degraded reefs (Baer et al. 2023). For these reasons, an intermediate nursery rearing phase for sexually propagated corals prior to outplanting is increasingly supported as an essential practice (e.g. Guest et al. 2014; Ligson et al. 2021; Humanes et al. 2021).

Regardless of initial investment, fleshy macroalgae, turf algae, *Ramicrusta*, fire coral, and sponges were observed to play a direct role in slowing and even reversing juvenile coral colony growth once outplanted onto the reef site. Interestingly, while 1 year of in situ rearing conferred increased survival and colony size in both brain corals, performance differed once outplanted to the reef. At 4 years, 1.8% ($n = 6$ corals) of *D. labyrinthiformis* juveniles remained, with no increases in colony size post-outplanting. Notably, while only 0.65% ($n = 4$ corals) of *P. strigosa* juveniles remained, mean colony size continued to increase following outplanting. Growth rates of these two species are reportedly similar (Van Moorsel 1988; Chamberland et al. 2017); thus, we hypothesize this difference in growth rates indicates that *P. strigosa* overcame a size-dependent mortality threshold, a life history trait that is well documented in juvenile corals (Raymundo & Maypa 2004; Vermeij & Sandin 2008; Ferrari et al. 2012). *Orbicella faveolata*, which faced 100% recruit mortality by year 2, proved to be an ineffective species for sexual restoration in this study. While it is recognized that results are inevitably biased by cohort effects, this mortality rate (99–100%) is commonly observed in *O. faveolata* sexual propagation efforts (Alvarado-Chacón et al. 2020) and is concurrent with low natural recruitment rates (Hughes & Tanner 2000). Results highlight the importance of considering species-specific life history traits when strategizing restoration. Based on this report, we recommend maintaining sexually propagated brain corals for 1 year or longer on in situ nursery structures. Further research is required to determine

species-specific size-to-escape thresholds and the most effective nursery grow-out time periods.

In Situ Nursery Efforts and Brain Coral Species Are the Most Cost-Effective Multi-Year Investment

Understanding the economic investment needed to restore habitat is crucial to successfully planning and implementing restoration projects. SU yield calculations and cost analyses provide applicable insights for restoration practitioners that are essential for scalable implementation. The most cost-effective method for *D. labyrinthiformis* changed over the course of the multi-year study, highlighting the importance of long-term monitoring. For *D. labyrinthiformis*, in situ nursery rearing resulted in a higher yield but a similar cost to direct outplanting; for *P. strigosa*, in situ nursery rearing was the only method that yielded surviving juveniles by the end of the study. These results suggest that a greater initial investment may yield a greater long-term return. *O. faveolata* had the highest cost of the three species at 1 year, ranging between $34 and $42 per SU. While these values were not considerably different from the ranges seen in the brain corals at 1 year, the 100% mortality of directly outplanted *O. faveolata* seen at 2 years rendered propagation of this species to be all cost with no return. SU cost was comparable to other studies, which have found SUs retaining at least one coral to be $5.30–325 USD at 1–3 years of age (Chamberland et al. 2015; reviewed in Omori et al. 2019). The most effective way to reduce this cost is by improving SU yield via increased survival during the early recruit stage (<1 year). Husbandry techniques such as feeding, co-rearing, and symbiont acquisition stand to greatly increase survival and thus cost-effectiveness (reviewed in Omori et al. 2019). Cost-effectiveness can also be improved by identifying and reducing the most expensive cost categories. In this study, labor was the highest cost category across all treatments; therefore, reducing restoration steps and manual labor holds the potential to decrease cost per SU.

High operational costs and eventual complete mortality rendered the AF rearing an extremely expensive investment (> $80,000 USD) with no return. These results do not suggest that land-based facilities hold no potential for successfully scaling coral sexual propagation but do represent realistic obstacles to establishing controlled aquaculture facilities on small islands with limited resources. Facilities utilized in this study were established in 2020, only months before the start of this study. During the investment period, the facility faced multitudinous operational issues, including insufficient operating equipment, island-wide power failures, and staffing shortages. Diel temperature generally fluctuated by 1.5°C, rising at peak daylight hours, with a maximum recorded swing of 4.4°C in December 2020. Colder months elicited substantial temperature fluctuations (±2.8°C) as systems were equipped with chillers but no heaters and were unable to maintain temperatures at night. Salinity was also highly variable as staff was managing a newly running closed system. Temperature and salinity are known to affect coral recruit survival (Vermeij et al. 2006; Randall & Szmant 2009), and despite monthly SU cleaning, these variable physical (light and temperature) and chemical (salinity and pH) conditions inevitably contributed to the low to no survival observed across species. Additionally, survival rates could likely have been improved and costs reduced by feeding recruits (Conlan et al. 2017) and introducing herbivores to the tanks earlier in the study and in greater quantities. While survival rates may be increased with improved facilities control and additional husbandry, the high cost of operating an AF requires greatly increased survival rates and yield to make it an economically viable technique, with Chamberland et al. (2015) reporting 2.5-year-old SUs to be over 20 times more costly when reared in an AF compared to directly outplanted on reef.

These findings highlight the importance of multi-year monitoring for restoration research. Future cost scenarios should examine how to further decrease costs per SU by either increasing recruit survival and thereby SU yield, or reducing costs associated with the most expensive restoration stages and cost categories. The highest cost categories will vary by program and region, and program-specific cost-effectiveness analyses are recommended to identify where reductions can be most beneficial on an individual program basis. Additionally, standardizing methods of cost evaluations across programs is recommended to allow for cross-programmatic comparisons.

Additive stressors have largely shifted Caribbean reefs to algae-dominated systems, characterized by increased hypoxia (Altieri et al. 2017; Candy et al. 2023), microbialization, and disease (Vega Thurber et al. 2008; Haas et al. 2016; Becker et al. 2024), all of which are known detriments to coral recruit survival (Vermeij et al. 2009; Williamson et al. 2022; Mallon et al. 2023). Ultimately, it is important to recognize that sexual propagation alone is not a viable restoration strategy for restoring algae-dominated reefs to calcifying scleractinian coral-dominated systems. Nonetheless, substrate unit yield and cost-effectiveness of 4-year-old juveniles suggest that outplanting of sexually propagated corals is a viable addition to the coral restoration toolkit, and that implementing an in situ nursery rearing stage should be considered when scaling up sexual propagation efforts for future reef restoration.

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Supporting Information

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

Table S1. Spawning metadata table.
Table S2. Specific cost breakdowns per coral recruit investment treatment.
Table S3. *Orbicella faveolata* cost table.
Figure S1. Map of St. Croix, USVI.
Figure S2. Seeding unit diagram and described outplanting technique.
Figure S3. Treatment temperature data.
Supplement S1. Symbiodiniaceae algal cell isolation.

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