

Effectiveness of different nursery designs for the restoration of the threatened coral *Acropora cervicornis* in Culebra, Puerto Rico

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SUMMARY

The threatened staghorn coral *Acropora cervicornis* is an important reef-builder species in the Caribbean. Its ecological importance and critical status have prompted efforts to restore degraded populations. In this respect, nursery-based programmes have effectively propagated *A. cervicornis* and helped to increase population sizes. Despite many advances in low-cost coral nursery designs, there is still a need to increase productivity while reducing costs. This study evaluates *A. cervicornis* demographic performance in two propagation structures: floating trees (FT) and floating horizontal frames (HF). Two equal-sized fragments were collected from 50 healthy staghorn coral colonies. Each fragment was placed into an FT or HF design. Survival, growth, branching, and productivity were recorded for seven months. To address the cost-effectiveness of the coral propagation techniques, we compared the total cost of producing corals between the two designs. Survival was similar, with 91% and 92% of the coral fragments surviving in the FT and HF, respectively. Although colonies in HF nurseries grew faster and produced more branches than those in FT nurseries, these differences were not statistically significant. Likewise, productivity did not differ statistically between nursery designs despite fragments in HF nurseries being 1.5 times more productive than those in FT nurseries. Because of the similarity in demographic performance, the selection of nursery designs could be based solely on their cost-effectiveness. In this respect, the cost-effectiveness analysis shows that producing corals using HF costs about 70% less than FT. Thus, we conclude that floating horizontal frame (HF) nurseries are better for propagating *A. cervicornis* and accelerating coral restoration activities.

BACKGROUND

The health of Caribbean coral reef ecosystems has been deteriorating steadily since the late 1970s and early 1980s. Unfortunately, degraded coral reefs have shown little, to no, sign of natural recovery (Raymundo et al., 2007; Boström-Einarsson et al., 2020). The current state of most coral reefs, with increasing pressure from human activities and natural forces (e.g., hurricanes), presents an ominous future. Losing the many services that coral reefs provide puts the socioeconomic situation of millions of people living across tropical coastlines at risk, especially in under-industrialised island nations (Hernández-Delgado et al., 2014). In response, the field of coral reef restoration has emerged. Coral reef restoration aims to boost coral reef conditions by, among other actions, increasing the population size of reef-forming stony (Scleractinia) corals through the outplanting of nursery-reared colony fragments (Lindahl, 2003; Bayraktarov et al., 2020; Vardi et al., 2021). Outplanting (taking corals from the nursery back into the wild) nursery-reared corals not only increases the probability of population persistence (Mercado-Molina et al., 2015a) but also leads to higher biodiversity (Yap et al., 2009; dela Cruz et al. 2014; Chomitz et al., 2023) and improves ecosystems services (Bayraktarov et al., 2019).

The last decade has seen valuable gains in the fundamental knowledge of active coral reef restoration, especially in the techniques to propagate corals sexually and asexually. For instance, many *in-situ* aquaculture techniques, such as benthic blocks, floating coral farms, rope suspension, and frame tables, have been developed not only to propagate coral species but also to improve coral demographic performance (Shafir et al., 2010; Hernández-Delgado et al., 2014; Omori, 2019; Bernal et al., 2023). Researchers have been able to raise coral colonies in land-based nurseries from field-collected gametes and successfully outplant them back to the reef (Chamberland et al., 2015; Banaszak et al., 2023). In addition, it has been demonstrated that recreating optimal environmental conditions (i.e., temperature, light exposure, and hydrodynamics) in state-of-the-art *ex-situ* propagation facilities accelerates coral growth and improves colony micro-fragment survival (Knapp, et al. 2022). Altogether, the advances gained have promoted the implementation of coral gardening (e.g., the cultivation of corals in propagation units, *in-situ* or *ex-situ*, for restoration purposes) as a tool to aid in the recovery of coral reef health (Lindahl, 2003; dela Cruz et al., 2014; Boström-Einarsson et al., 2020).

In the Caribbean, one of the most common species used in coral reef restoration is the threatened branching staghorn coral *Acropora cervicornis*. This coral has been favored due to its rapid growth, critical ecological roles (i.e., habitat for fish, high calcium carbonate deposition), and ease of propagating via fragmentation. Caribbean staghorn coral populations, however, have collapsed during the past decades, forcing it to be listed as a threatened species under the US Endangered Species Act. (Bruckner & Hourigan, 2000). Indeed, *A. cervicornis* has disappeared from many coral reefs in Puerto Rico, where it was previously common (Weil et al., 2002).

Despite the significant improvements and innovations in low-tech *A. cervicornis* propagation techniques, the cost of running an aquaculture program still poses a major barrier to sustainability (Omori, 2019), especially for community-based programmes. Therefore, if coral gardening is to increase coral production, it is essential to balance operational costs and productivity. The first step to attaining such a goal is to determine the aquaculture techniques that favor the growth and survival of nursery-reared corals. Many floating and fixed-to-the-bottom nurseries have been compared in Puerto Rico (Hernández-Delgado et al., 2014; Griffin et al., 2012), Florida (O'Donnell et al., 2017), and the Dominican Republic (Calle-Triviño et al., 2020). These studies agree that floating nurseries are a better approach to raising *A. cervicornis* because colonies showed faster growth rates and lower mortality (O'Donnell et al., 2017; Hernández-Delgado et al., 2014). Among floating units, tree-like nurseries have commonly been used to propagate *A. cervicornis* (Nedimyer et al., 2011). Besides enhancing coral demographic performance (compared to benthic structures), tree-like nurseries also have the advantage of reducing the damaging effect of waves due to their ability to move in the water column. However, the benefits of using tree-like propagation units come at the cost of

reduced space to grow corals which limits nurseries' productivity; for instance, each tree unit holds 50 fragments compared to other structures, such as a benthic table, that can accommodate up to 100 colonies (Hernández-Delgado et al., 2014).

An evaluation of nursery designs to select the best approach that enhances coral demographics while increasing cost-effectiveness (i.e., a higher number of corals produced) is essential to improve local restoration efforts. However, most studies measuring the demography of nursery-grown corals lack the details required for managers to make informed decisions about replicating nursery designs (Maurer et al., 2022). Details such as coral farms' productivity, material costs, labour hours, and equipment needed to install and maintain the propagation units are necessary to determine overall cost-effectiveness. This study analysed and compared the cost-effectiveness of propagating *A. cervicornis* colonies in two floating units based on the orientation (vertical trees vs. horizontal frames) and the number of colony fragments that can be grown in each unit. The results of this study will help coral ecologists and managers determine the best approach for restoration efforts and make informed decisions about replicating nursery designs.

ACTION

Study area: This study was carried out in Culebra, an island municipality located approximately 27 km east of Puerto Rico (Fig. 1). Culebra is an archipelago consisting of the main island and twenty-three smaller keys (Haeselbarth, 1903). These islands are arid, as they have no rivers or streams. Culebra is characterized by having an irregular topography resulting in a long, intricate shoreline, and almost 80% of the island's area is volcanic rock from the Cretaceous period (Haeselbarth, 1903). The island is approximately 11 by 8 km, and its coastline is marked by cliffs, sandy coral beaches, and mangrove



Figure 1. The study was performed at Punta Melones Reef (18°18'23.5"N, -65°18'52.2" W), located in the western side of island municipality of Culebra, Puerto Rico. The figure also shows the spatial arrangement of *in-situ* nurseries based on design.

forests (Haeselbarth, 1903). The specific study site is located at Punta Melones (PMEL) reef (18°18'23.5" N, 65°18'52.2" W) on the west coast of Culebra. PMEL is part of the US National Oceanographic Atmospheric Administration (NOAA) Habitat Blueprint Focus Area and has also been designated by Puerto Rico's Department of Natural and Environmental Resources (PR-DNER) as an area of coral reef conservation priority. Less than 5% of the reef's bottom is covered by corals. Furthermore, coral species diversity is low, dominated by *Porites astreoides* and *P. porites* (Santiago-Padua et al., 2023). PMEL has been selected for an active nursery and restoration project run by the local non-profit community-based organization Sociedad Ambiente Marino (SAM) due to its social, economic, and ecological importance.

Construction and placement of nurseries: Floating tree nurseries (FT; Fig. 2A) consisted of a central 2.54 cm-wide PVC pipe intersected by five fiberglass rods (Nedimyer et al., 2011). Each rod was pre-drilled with ten holes, 10 cm apart, from which coral fragments were suspended using thin metal wire (Nedimyer et al., 2011). Thus, each FT unit supported 50 colonies. FT nurseries were identified with a numbered tag and secured to the seabed using paracord rope tied to two duckbill anchors. The horizontal frame nurseries (HF; Fig. 2B) consisted of a 1.5 m² square-shaped "table" made from 3.81 cm-wide PVC pipes. Corals were suspended from a thin metal wire approximately 1 m off the bottom. Each HF unit supported 100 colonies. HF nurseries were identified with a numbered tag and secured to the seabed using paracord rope tied to four duckbill anchors. Plastic tubing was used to protect the rope from abrasion as it passed through the metal shackle on the duckbills. SAM deployed 20 nurseries (ten of each design, Fig. 1), employing six divers over two days, resulting in 16 labor hours per diver. Nurseries were clustered based on type (Fig. 1) at a depth of ~ 8 m over a sandy bottom adjacent to seagrass beds and approximately 150 m from the front reef. The distance between nurseries was ~ 2 m, whereas clusters were separated by ~ 5 m. Despite the distance between clusters, there was no apparent variability in environmental conditions (e.g., similar water transparency, temperature, and sandy bottom). SAM chose the nursery site based on depth, accessibility, and protection from human interference (e.g., tourist activities).

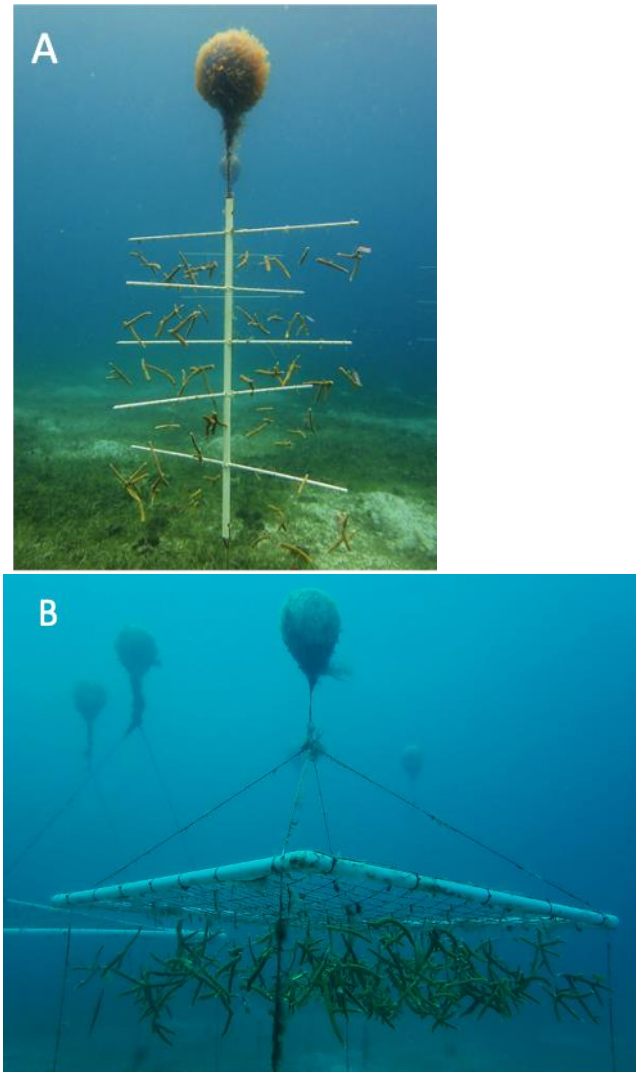


Figure 2. *In-situ* nursery designs: A) Floating Tree (FT); B) Horizontal Frame (HF)

Coral harvesting: We surveyed and identified 50 healthy donor colonies of *A. cervicornis* at Punta Soldado (PSO) coral nurseries (18° 16' 48.8" N, -65° 17' 19.8" W) run by SAM. Donor colonies were non-diseased or bleached colonies with more than five branches ≥ 10 cm in total linear length (Mercado-Molina et al., 2013). Branch sizes were determined from *in-situ* photographs (scale-by-side) taken using an Olympus Tough TG-6 Waterproof Camera before collection. Then, using pliers, two branches of equal size (~15 cm) were collected from each of the 50 coral donors and placed in independent plastic bags inside baskets that were later brought to the boat. By selecting donor colonies >300 cm in size, we ensured that the total number of branches ($n = 2$; ~ 30 cm of live tissue) collected from each donor colony represented less than 15% of its total live tissue (Mercado-Molina et al., 2013). During the boat ride from PSO to

PMEL, approximately 15 minutes, fragments were under constant shade and running seawater in order to reduce physiological stress. At PMEL, fragments were tagged and placed evenly in each type of nursery (i.e., 5 for each of the 20 nurseries) and allowed to grow for seven months (see Fig. 3). The placement of the coral fragments within each of the propagation units was random. Each colony clone was represented in each of the two methodologies tested to correct for possible genetic effects on coral demographic performance. Hence, each colony fragment was considered independent among colonies growing in the same nursery unit but matched pairs based on genotypic identity when comparing between nurseries (see statistical analysis section below).

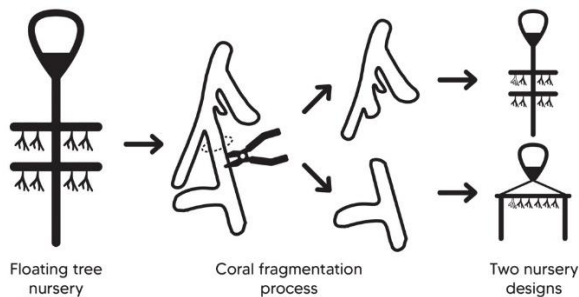


Figure 3. Coral fragmentation and placement in FT and HF nurseries. Two branches of equal size (~15 cm) were cut from 50 healthy donor colonies using pliers. Fragments from the same colony were tagged with the same identification number and assigned to one of each type of nursery; each donor colony was represented in each of the two methodologies used.

Data collection: The demographic performance of *A. cervicornis* was compared between the nursery designs by means of survival, growth, branching, and productivity. A colony was considered dead if no live tissue was evident. Coral colonies were photographed *in-situ*, and qualitatively assessed monthly from September 2021 to April 2022. When photographing coral colonies, the branches extending towards or away from the camera in the “Z” axis cannot be fully appreciated. To minimize this error, we photographed all coral colonies from different angles. In this way, we ensured that all branches were photographed in their full extension. To estimate the rate of coral growth, images of each colony were processed using the software Coral Point Count with Excel extensions (CPCe) (Kohler & Gill, 2006). Both initial and final sizes were measured as the sum of the linear length of live tissue in all branches, subtracting partial mortality from the total size when appropriate. The change in linear extension (final length – initial length) was then calculated and expressed as cm/day. Branch production was quantified as the number of new branches produced by

fragments. Branch counts were performed using the same images used to calculate colony growth. We also calculated coral productivity as the new tissue produced (final length – initial length) / initial length) divided by the number of months, expressed as cm/month. The nursery site required a monthly visit to visually inspect the integrity of nurseries and remove biofouling, such as filamentous algae and encrusting fire coral (*Millepora alcicornis*). Unfortunately, the study was halted after seven months because an outbreak of the algae *Cottoniella filamentosa* overgrew and killed many of the corals growing on the nursery units.

Cost-effectiveness analysis: The framework for calculating the cost of coral reef restoration based on asexually produced transplants was established by Edwards et al. (2010). The cost of asexual propagation was computed from the time of fragment collection to *in-situ* nursery rearing for 7 months (see Table 1). We performed the cost-effectiveness analysis by breaking down the costs of coral gardening in the following phases: (1) construction and placement of the nurseries; (2) collection and placement of coral fragments in the nurseries; (3) maintenance and monitoring (Table 2). In each phase, we itemized costs such as materials, equipment, labour hours (i.e., time input by personnel), dive gear rental, air-SCUBA tanks, boat use, car rental, and housing. Labour hours were expressed as person x hours (Table 1) since pay rates differ greatly between countries around the world. In order to calculate the costs per nursery unit, the total costs per nursery design were divided by the number of nursery units (i.e., Total costs of HF design / 10 units = cost per nursery unit). To calculate the cost of producing a coral, the cost per nursery unit was divided by the number of corals produced by unit (i.e., Cost of HF unit / 100 corals = cost of producing a coral). Results were expressed as the percent difference between the costs of rearing corals using FT and HF nursery designs.

Statistical analyses: The Kaplan-Meier test was used to determine whether the pattern of survivorship varied statistically between nursery designs. Because the study design permitted us to pair samples (e.g., same genets), growth, branching rates, and productivity were compared using the non-parametric Wilcoxon signed rank test. All statistical analyses were based on a sample size of 90 (FT: n = 45; HF: n = 45) because one FT with the five tagged colonies was lost, forcing us to remove their respective clones growing in the HF from the analyses. The open-source software R version 4.1.0 was used to perform the statistical analyses.

Table 1. Restoration project phases, comparison of labour hours between project plans expressed as person x hour, and details included in cost-effectiveness analysis.

Restoration project phase	Persons	Hours	Total hours	Items considered
I. Collection and placement of fragments in nurseries	5	8	40	1a. Equipment and consumables needed to collect fragments from donor colonies and establish them in nurseries. 1b. Labor and diving/boat time needed to collect fragments from donor colonies and establish them in nurseries.
II. Nursery deployment				2a. Equipment and consumables needed to construct 10 floating trees and 10 horizontal frame nurseries. 2b. Labor and diving/boat time needed to build and deploy 10 floating trees and 10 horizontal frame nurseries.
Floating Tress	4	6	24	
Horizontal Frames	4	10	40	
III. Maintenance and monitoring for 7 months				3a. Equipment and consumables needed; and 3b. labour, diving, and boat time needed to maintain 1,500 fragments and monitor 100 fragments in nurseries for 7 months.
<i>Maintenance</i>				
Floating Trees	2	14	28	
Horizontal Frames	2	10.5	21	
<i>Monitoring</i>				
Floating Trees	2	28	56	
Horizontal Frames	2	21	42	

CONSEQUENCES

Coral demography: Survival curves did not differ between FT and HF nurseries (KM log-rank test, $\chi^2 = 0$, $p = 0.90$; Fig. 4). At the end of the study period, 91% and 92% of the coral fragments survived on FT and HF, respectively. On average, colonies in HF nurseries grew 1.53 times faster than those in FT nurseries. However, growth rates did not differ significantly ($V=358$, $p = 0.07$), indicating that corals grew at a similar rate in both nursery designs. Fragments of *A. cervicornis* grew at mean rates of 0.047 ± 0.058 (\pm SD; median = 0.043) cm/day in FT nurseries and 0.072 ± 0.062 (\pm SD; median 0.007) cm/ day when growing in HF nurseries (Fig. 5a). Branch dynamics were also similar in both nursery designs. Coral colonies produced on average 0.24 ± 0.27 (\pm SD; median = 0.200) new branches per fragment per month at FT and 0.25 ± 0.18 (\pm SD; median = 0.243) at HF ($V=333$, $p = 0.428$; Fig. 5b). Fragment productivity was 1.49 times higher in HF treatments (FT: was 0.076 ± 0.083 [\pm SD; median = 0.083]; HF: 0.113 ± 0.093 [\pm SD; median = 0.123]), but as was the case for growth and branching, the difference was not statistically different ($V= 369$, $p = 0.10$; Fig. 5c).

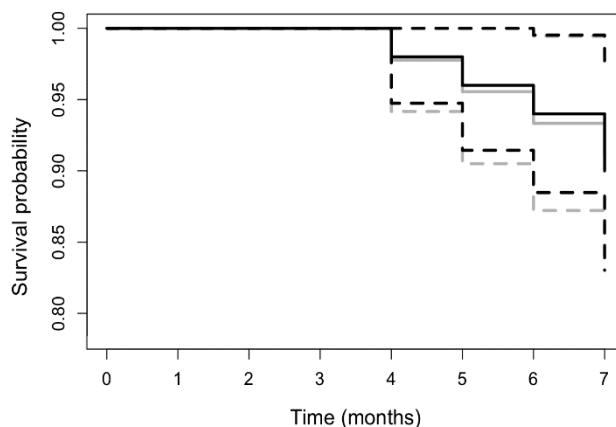


Figure 4 Comparison of the survival probability of *A. cervicornis* between FT (grey) and HF (black) nurseries with 95% lower and upper confidence intervals (CI) shown as the dotted lines. Sample size = 90, FT: n = 45; HF: n=45).

Table 2. The difference in costs between nursery designs tested between restoration project phases.

Restoration project phase	Cost and % difference
I. Build and set up 20 <i>in-situ</i> coral nurseries (10 FT and 10 HF)	FT = \$3,939.60 HF = \$4,793.40 19.6%
II. Collection and placement of fragments in nurseries	FT = \$1,495.91 HF = \$1,495.91 0%
III. Maintenance and monitoring for 7 months	FT = \$10,817.86 HF = \$9,418.74 13.8%
<i>Cost per nursery unit</i>	FT = \$1,625.34 HF = \$1,570.80 3.4%
<i>Cost of rearing a coral</i>	FT = \$32.51 HF = \$15.71 69.7%

COSTS

Nursery cost-effectiveness: The total costs of harvesting and rearing 1,500 corals for 7 months in 20 coral nurseries were split between 27% of the budget for the construction and placement of nurseries, 10% for the collection and placement of fragments in nurseries, and 63% for maintenance and monitoring. Breaking down by nursery design, the costs of collecting and placing fragments in nurseries (Phase I) were the same for each. Building and setting up the nurseries (Phase II) was 20% less for FT, whereas maintenance and monitoring costs (Phase III) were 14% less for HF design (see Table 2). The time divers spent conducting monitoring of coral fragments and removing biofouling from each nursery design contributed to this difference. Overall, FT costs 3.4% less than HF per nursery unit. However, because HF can hold twice as many colonies as FT, producing a coral with HF was 70% cheaper than growing it on FT (see Table 2).

DISCUSSION

A variety of techniques have been adopted to grow and propagate *A. cervicornis* with floating nurseries considered a better approach than benthic-based structures because coral fragments show faster growth rates and lower coral mortality (O'Donnell et al., 2017; Hernández-Delgado et al., 2014). Colony position on

floating nurseries was hypothesized by O'Donnell et al. (2017) to influence coral growth due to the possible combined effects of light availability, sources of heterotrophic nutrition, and increased water flow. Similarly, Maneval et al. (2021) reported that fragments on floating frames had slightly higher growth rates probably because the arrangement of the corals may have reduced competition for food, as all fragments experience similar exposure to currents. Accordingly, floating nursery types have become the preferred approach to propagate branching corals, including *A. cervicornis*.

Different floating nursery designs within the same habitat may influence coral demographics and cost effectiveness. Corals growing in vertical-frame nurseries have been shown to have significantly higher growth rates than those growing in tree-shaped nurseries (Maneval et al., 2021). However, in our study, corals growing in FT and HF nurseries did not differ significantly in survival, growth rates, branch production, or productivity. Although such findings indicate that both floating designs perform similarly, they still support the results of Maneval et al. (2021) that corals growing in tree-shaped nurseries do not outperform those growing in frames.

Survivorship of fragments in both nurseries was relatively high (more than 90%), similar to other studies that compared survival between propagation structures, including floating units (Griffin et al., 2012; Maurer et al., 2022). Such high survival rates support the contention that floating structures are an appropriate approach to propagating corals for reef restoration activities.

On the contrary, estimated growth and branching rates were lower than previously reported for corals growing in suspended or benthic units in Culebra, Puerto Rico (Hernández-Delgado et al., 2014). It is unclear what factor(s) may account for the observed difference, but it is known that growth in *A. cervicornis* is driven by the interaction between genes and the environment (Million et al., 2022). Thus, it is possible that we were growing distinct coral genotypes under distinct environmental conditions to that of Hernández-Delgado et al. (2014). Growth and branching were especially slow during the first months of the study. Studies have shown that total linear extension is often slower in the initial phases of nursery culture experiments (Hernández-Delgado et al., 2014) as new branches appear after a month following fragmentation. A possible explanation for such a result could be "handling stress" that slows growth rates and makes coral fragments more susceptible to changes in prevailing environmental conditions (Yap et al., 1992; Clark & Edwards, 1995; Mercado-Molina et al., 2015b).

Coral demographics were similar in both nursery designs, making selection a cost-effective decision. The cost-effectiveness analysis showed that corals growing in

HF cost 70% less than those growing in FT. HF units are a more productive and economically suitable approach because they can double the number of fragments available in nurseries, reducing the overall cost of producing a coral. Nursery design can influence not only coral growth rates but also the efficiency of data collection and the time required to perform maintenance (Maneval

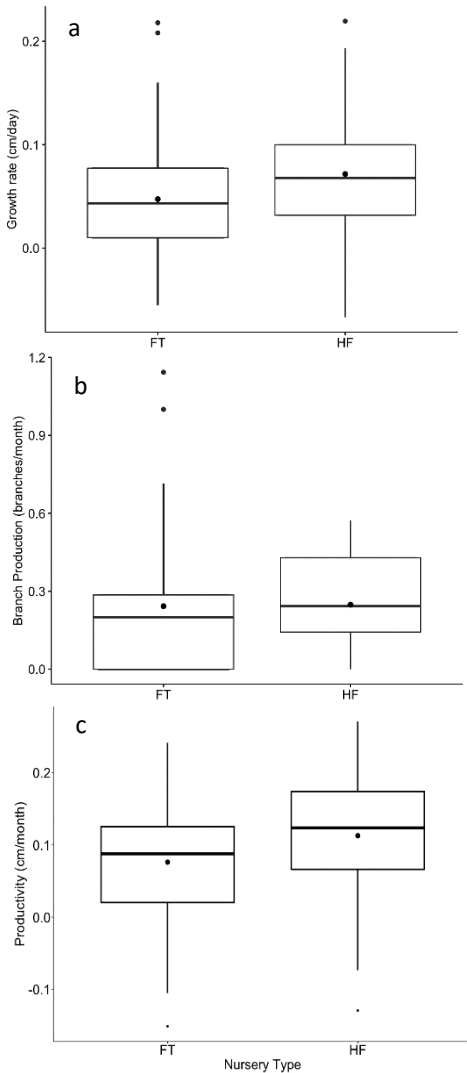


Figure 5 Comparison between a) growth rate; b) branch production; c) productivity of *A. cervicornis* between FT and HF nurseries. Dots within the box represent the mean values and dots outside the box represent outlier values. The upper and lower part of the box represents the interquartile range (Q1-Q3) and the line in the middle of the box represents the median value. The length of whiskers represents the quartiles maximum and minimum of quartiles. Sample size = 90, FT: n = 45; HF: n=45).

et al., 2021). Time spent on nursery maintenance is important for non-profit organizations to reduce costs associated with the restoration project. In this study, the horizontal frames proved to be more practical, with divers reporting less maintenance time and easier removal of fouling agents compared to tree-shaped nurseries. It is important to highlight that maintenance time may vary since fouling depends on the site location, the presence of fouling organisms, and the species that may predate them (Maurer et al., 2022).

Additional support for choosing horizontal frame structures for coral gardening is their resistance to wave impact from storms. Floating coral nurseries run by SAM withstood the onslaught of the storm surge much better than benthic units (Hernández-Delgado et al., 2014). Colonies growing on floating nurseries have lower probability of breakage when disturbed because the entire colony can move in response to disturbance (O'Donnell et al., 2017). In addition, HF design requires more anchors than FT, giving the nursery additional stability to resist storm waves more efficiently. Indeed, an FT unit went missing in the fifth month of this study, probably due to increased wave action in that period. Since we did not lose any HF units, we infer that the HF design is more suitable for withstanding tropical storms. However, more data is needed to determine the relative resistance of distinct floating designs to site-specific weather conditions.

To conclude, our findings indicate that *A. cervicornis* growing in FT and HF nurseries perform similarly, showing approximately equal demographic results. However, based on productivity, HF may be the preferred option to propagate *A. cervicornis*. HF is more cost-effective as it supports twice the number of coral fragments, resulting in twice the amount of tissue available for fragmentation for future restoration projects. Therefore, the type of nursery to propagate corals should be carefully considered when developing restoration plans. In this sense, the results of this study can help coral ecologists and managers make an informed decision about what nursery designs should be replicated as part of their restoration efforts.

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