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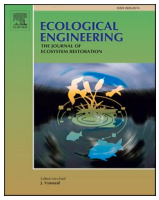

Some like it dirty: Less frequent nursery cleaning can reduce reef restoration costs with limited negative effects on coral performance

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ABSTRACT

Coral gardening is a reef restoration technique in which corals are first grown in nurseries and then outplanted onto degraded reefs. However, coral gardening does not yet achieve restoration at ecologically-relevant scales due to associated high costs. Coral nurseries are often manually cleaned to remove biofouling and improve coral performance, although putative benefits of this costly activity remain unconfirmed. We quantified the benefits and costs of various cleaning frequencies to identify the most cost-effective coral nursery approach at a study site with low herbivorous fish biomass. During this one-year study, nurseries were either cleaned weekly, monthly, quarter-yearly or never. Nurseries contained four coral species in three fragment sizes to examine species- and size-specific effects. Coral production (combined coral growth and fraction live coral tissue) and associated costs were quantified. No significant differences in coral production were found across cleaning frequencies and this result was consistent among coral species and fragment sizes. Therefore, no cleaning was clearly identified as the most cost-effective option. Costs could be further reduced by selecting fast-growing corals (e.g. *Acropora*) and stocking nurseries with large fragments, as these contributed most to coral production. The resulting minimum production cost is then US$0.26 per fragment including dive, wage and material costs for the building, deployment and filling of nurseries and sourcing of corals. For this study location and potentially many others with a similar or higher fish biomass, less frequent cleaning can substantially reduce reef restoration costs without having negative impacts on coral nursery production.

1. Introduction

Half of the world's live corals have been lost over the past decades by a combination of stressors including unsustainable fishing, pollution and climate change, thereby impairing the provision of numerous ecosystem services to coastal citizens (Eddy et al., 2021). To preserve coral reefs, a combination of climate action, effective local management and restoration is advocated (Knowlton et al., 2021). Coral gardening is a commonly-applied reef restoration technique in which coral stock is first grown in nurseries and then outplanted onto degraded reefs (Rinkevich, 1995). Coral gardening is applied by thousands of practitioners worldwide, but large-scale projects are rare due to the high associated costs (Boström-Einarsson et al., 2020; Bayraktarov et al., 2019). A frequently reported cost is the maintenance of coral nurseries: SCUBA divers are regularly deployed at ocean-based nurseries to remove biofouling (e.g. macroalgae) that might otherwise compete with corals for light and space (Edwards et al., 2010; Vaughan, 2021; Ferse et al., 2021). However, the presumed benefits of these costly cleaning activities have never been experimentally validated. Rather, earlier research has shown that herbivorous fish can play an important role clearing the biofouling from coral nurseries, thereby reducing costs and improving coral performance (Frias-Torres and Van de Geer, 2015; Knoester et al., 2019).

Quantifying the additional costs and benefits of nursery cleaning by divers allows for the identification of a more cost-effective nursery approach. Cleaning costs include labour and equipment (e.g. diving equipment, consumables such as brushes as well as vessel use for offshore nurseries) which increase with increasing cleaning frequency. Cleaning benefits include any increases in coral growth or survival due to the removal of competing biofouling (McCook et al., 2001). The most cost-effective cleaning approach maximizes coral performance benefits while minimizing the cleaning frequency. This study aimed to determine a more cost-effective cleaning frequency for coral nurseries at an ongoing restoration project in Kenya by quantifying the growth and survival benefits as well as associated costs of various cleaning regimes.

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Coral nurseries were subjected to either weekly, monthly, quarter-yearly or no cleaning for a full year. The nurseries contained four branching coral species (*Acropora* cf. *muricata, Acropora verweyi, Pocillopora verrucosa* and *Porites cylindrica*) in three different size classes to identify any species- or size-specific effects. We hypothesized that monthly cleaning would generally be most cost-effective, as this frequency is typically applied by restoration projects worldwide (Johnson et al., 2010; Edwards et al., 2010; Vaughan, 2021). We expected that longer optimal cleaning intervals would be found for highly competitive, fast growing coral species (e.g. *Acropora* spp.) and that shorter intervals would be optimal for smaller coral fragments, which tend to be easily overgrown by competing fouling organisms (Forsman et al., 2006). Overall, this complete and transparent cost-benefit analysis also helps to better inform conservationist about the general, often poorly reported costs of coral reef restoration, thereby allowing more informed choices between various conservation strategies.

2. Methods

2.1. Area description

This study was performed from October 2018 to October 2019 at Firefly House Reef (−4.6505, 39.3866) near Shimoni, Kenya. The reef is situated in a kilometre-wide sea strait that is subjected to semi-diurnal tides, with tidal differences of up to four meters. Average sea surface temperatures range from 25 °C in August to 29 °C in April. However, water temperatures peaked above 30 °C in April 2019, resulting in a temperature anomaly of six degree heating weeks (Liu et al., 2006). Hard coral cover at the study site averaged around 50% and was dominated by branching and massive growth forms of *Porites*, with also substantial cover of *Acropora*, *Montipora* and *Echinopora* (Knoester et al., 2023a). Macroalgal cover was low on the reef (4%), but has been shown to accumulate on coral nursery structures placed at this site (Knoester et al., 2023d). The reef was shallow (1–3 m depth; all depths are expressed at low tide), with seagrass meadows in shallow water and sand plains deeper. The biomass of non-cryptic, diurnally-active fish totalled to 200 kg ha^{-1}, of which herbivorous fish composed 70 kg ha^{-1} (Knoester et al., 2023b). A coral nursery forming part of an ongoing restoration project (Knoester et al., 2023c) was positioned about 20 m off the reef on sandy substrate. For this experiment, 12 new nursery structures were added at the same site.

2.2. Experimental setup

The nursery structures followed the coral tree design (Fig. 1) of Nedimyer et al. (2011). The plastic structure consisted of a vertical PVC (polyvinylchloride) trunk, holding six horizontal PPR (polypropylene) pipes. As the PPR pipes were crossing the central PVC trunk, this resulted in a total of 12 PPR branches. Each branch held five monofilament loops in which coral fragments could be hung, totalling to 60 fragments per tree. The coral tree was kept afloat by a 20 L buoy and anchored by two 15 kg concrete sinkers.

The 12 coral trees were deployed on a mixed sand and seagrass patch at around three meters depth and each tree was appointed randomly to one of four cleaning frequencies, resulting in three replicate trees per treatment. Each side of a tree was filled with one of four coral species in random order: either *Acropora* cf. *muricata, Acropora verweyi, Pocillopora verrucosa* or *Porites cylindrica* (Fig. 1). These species were locally abundant and represent different life history strategies for branching corals (Darling et al., 2017): both *Acropora* species are highly competitive and grow quickly, *Pocillopora verrucosa* is a generalist species and *Porites cylindrica* is a weedy species that opportunistically colonizes disturbed areas. For each species, the nursery was stocked with fragments that were cut using wire cutters into one of three different size classes, again in random order: fragments were either small (length < 3.5 cm), medium (3.5–6.5 cm) or large (> 6.5 cm). Each cleaning frequency *

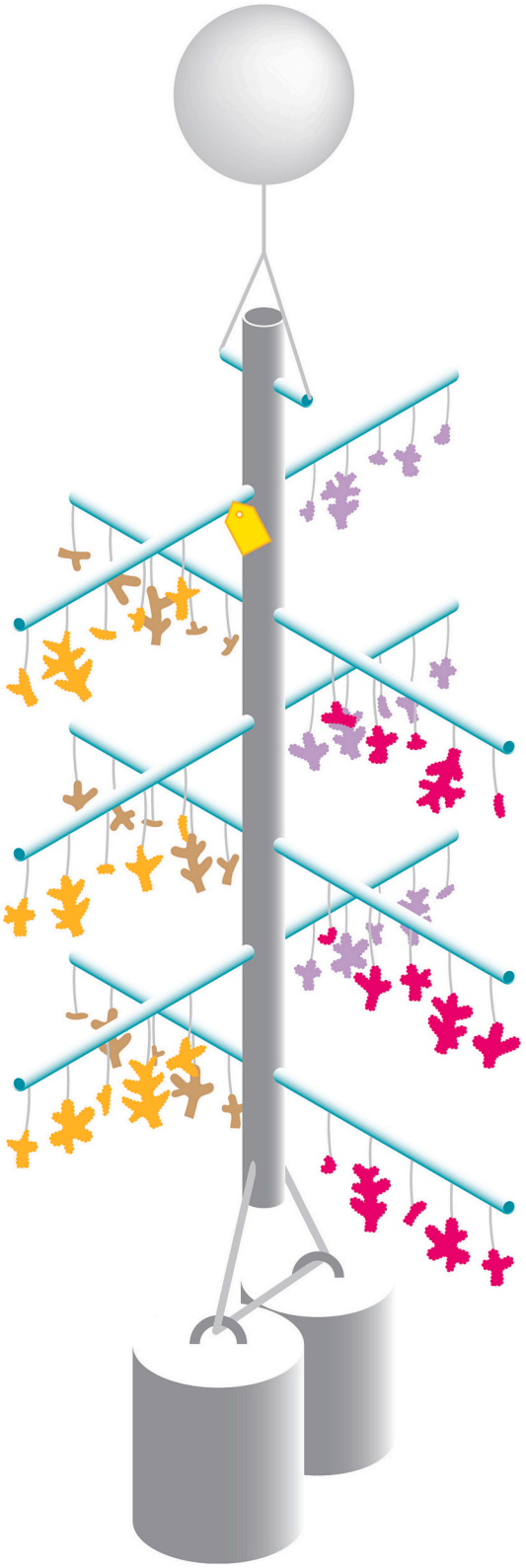

Fig. 1. A schematic drawing of a coral tree nursery. A nursery was filled with four different coral species, one on each side. Three different fragment start sizes were randomly distributed per side for each species. Five replicate fragments of each species x size combination were used within one nursery, totalling to 60 coral fragments per nursery. The yellow label in combination with systematic counting was used to identify each individual coral fragment for repeated measurements. Artwork by Vrijlansier. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species * size combination had 15 replicate fragments, nested within three coral trees. A total of 720 coral fragments were used in this study.

Trees were either cleaned weekly, monthly, quarterly or not at all throughout the one-year experiment. Cleaning entailed SCUBA divers removing all biofouling from the PPR branches with small handheld brushes (for macroalgae, tunicates and soft corals) or pliers (for barnacles). In addition, toothbrushes were used to remove biofouling from the monofilament loops (Fig. S1A-C in supplementary data Appendix A). The PVC trunk, buoy and sinkers were not cleaned.

2.3. Monitoring

Every other month (see Fig. S2 for exact dates), two scaled pictures were taken of each fragment at perpendicular angles to monitor coral performance. These pictures were used to measure the fragment's length (*l*), widest width (*w1*) and perpendicular width (*w2*) in cm using ImageJ (Ferreira and Rasband, 2012). Only live coral tissue was measured. These values were used to calculate the ecological volume (EV) each fragment occupied (Shafir et al., 2006; Knoester et al., 2019). The increase in EV over time (*t*) is expected to be exponential and therefore a specific growth rate (SGR) was calculated using:

$$SGR = ln\frac{EV_t}{EV_{t-1}} \Big/ t-(t-1) \quad \textbf{(1)}$$

Where *t* is expressed in days and SGR in days^{-1}. The same pictures were used to visually estimate the percentage of live coral tissue cover for each fragment. Only completely healthy fragments were used at the start of the experiment (i.e. live coral tissue cover of 100%).

2.4. Performance indicators

Effects of cleaning frequency, coral species and fragment size on culture efficiency were determined by analysing three coral performance indicators: coral growth, percentage live tissue cover and nursery production (i.e. absolute increase in EV). Growth was represented by the SGR of healthy fragments, healthy being defined as fragments having a live tissue cover ≥80% (analogous to Knoester et al., 2023d). This way, the effects of growth could be evaluated independently of decreases in live coral tissue cover. For live tissue cover and production the entire dataset was used. Nursery production was calculated as the increase in (live) EV per coral fragment after one year of culture. Production thus incorporates both changes in coral growth and live tissue cover. Throughout the study, 96 out of 720 coral fragments were lost mainly due to fishing gear entanglement and these fragments were excluded from the analyses (see Table S1 for details). Throughout the study, 17 coral fragments suffered from skeletal predation by fish. As this was considered natural and did not influence the outcomes of statistical analyses, these fragments were kept included in calculations to give the most realistic estimations for coral productivity at the study site.

2.5. Statistical analyses

For all three performance indicators, the effects of cleaning frequency, coral species and fragment size were investigated using R Studio (R Core Team, 2022). The effects over time were not statistically investigated as including this factor led to overfitting of some models. Therefore, only the start and end values were used to determine the three coral performance metrices. The developments over time are presented visually in the supplementary materials for growth (Fig. S2) and live tissue cover (Fig. S3). To test for the effects of cleaning frequency, coral species and fragment size on coral growth, the SGR of healthy fragments was fit using a linear mixed-effects model from the *nlme* package (DebRoy, 2006). Coral tree was included as random factor to account for the non-independence of multiple fragments in the same structure. To test for the effects of the same three factors on percentage live coral tissue (at the end of the experiment), a beta regression model with logit link from the *betareg* package was fit (Cribari-Neto and Zeileis, 2010), as this model accounts for the proportional nature of the live tissue cover data. Fragments in the same tree were averaged on live coral tissue cover to improve model fit. For coral production, the change in EV of all fragments was fit using an *nlme* linear mixed-effects model, again with coral tree as random factor. All model assumptions were validated by visual inspection of residual plots. For all models, Wald Chi-Squared tests from the *car* package (Fox and Weisberg, 2018) were used to determine the significance of the three fixed factors and their interactions. Where relevant, pairwise comparisons were made with Tukey adjustments using the *emmeans* package (Lenth, 2020).

2.6. Cost-benefit calculations

The total costs (expressed in US dollars in 2024) to establish and maintain a coral nursery tree with 60 fragments in Kenya was comprised of $Cost_{structure}$: the material and wage costs to build a coral tree ($22.87, Table S2), $Cost_{deployment}$: the wage and dive costs to fill a coral tree with fragments ($13.21, Table S3), $Cost_{corals}$: the initial costs to acquire 60 coral fragments of the appropriate start size (ranging between $0.02 and $15.16 depending on fragment size, coral species and prior cleaning frequency, see Table S4) and $Cost_{cleaning}$: the wage and dive costs associated with cleaning a tree ($6.61 per visit, Table S5). The cost to grow a single fragment ready for harvesting and outplanting was calculated as:

$$Cost_{fragment} = \frac{Cost_{structure} * t_{nursery}}{t_{structure}} + Cost_{deployment} + \frac{Cost_{corals}}{n_{rounds}} + \frac{Cost_{cleaning} * t_{nursery}}{t_{cleaning}} / 60 \quad \textbf{(2)}$$

Where $t_{nursery}$ is the duration a coral fragment spends in the nursery, which influences both the total structure and cleaning costs: a coral fragment with an extended $t_{nursery}$ (either through low growth or reduced live coral tissue) will result in higher structure costs, because a nursery structure can be used for less growth cycles before it wears out ($t_{structure}$: set to 5 years, or 1825 days). In addition, based on the various cleaning intervals ($t_{cleaning}$: either 7, 30, 91 days or none), more cleaning visits are needed throughout a longer nursery period, resulting in higher cleaning costs. Reworking Eq. 1, $t_{nursery}$ was calculated as:

$$t_{nursery} = \frac{ln\frac{EV_{end}}{EV_{start}}}{ln\frac{EV_t}{EV_0}} \Big/ t \quad \textbf{(3)}$$

In which $t_{nursery}$ presents the days needed for a coral fragment to grow from its start volume (EV_{start}) to the desired end volume (EV_{end}). Based on the fragment size class and length, EV_{start} was either set at 3 cm^3 (small), 30 cm^3 (medium) or 300 cm^3 (large) - comparable to the actual start volumes used in the experiment. EV_{end} was set at $EV_{start} + 300$, thus indicating when a fragment had grown sufficiently that a fist-sized chunk of coral (e.g. ~8 cm length x 5 cm diameter) could be harvested, while leaving a chunk of the original fragment size behind to regrow again. Fragment growth rates were determined from the actual average start (EV_0) and end (EV_t) values as measured in this study (with *t* being the duration of the experiment: 371 days), split per cleaning frequency, coral species and fragment size. Lastly, as $Cost_{corals}$ is only incurred when establishing a nursery structure for the first time (in consecutive nursery rounds, the initial size will still remain after the grown chunk of coral has been harvested), the contribution of this cost to the total costs will thus decrease as nurseries are used for more grow-out rounds (n_{rounds}). Here, n_{rounds} was set at 10, assuming a coral nursery for a specific species is harvested 10 times before being discontinued.

3. Results

3.1. Coral growth

Cleaning frequency had negligible effects on coral growth rate: both the main effect of cleaning frequency and the three-way interaction between cleaning frequency, coral species and fragment size were not significant. While coral growth was influenced by a significant interaction between the effects of cleaning frequency and coral species ($X^2 = 23.70$, $df = 9$, $p = 0.005$), subsequent post-hoc analysis did not reveal significant differences between cleaning frequencies for any of the four species (Fig. 2A). Similarly, while a significant interaction was found between cleaning frequency and fragment size ($X^2 = 13.09$, $df = 6$, $p = 0.042$), the post-hoc analysis showed no significant differences between cleaning frequencies for any of the three fragments sizes (Fig. 3A). In contrast, consistent patterns were found across fragment sizes, as the relative growth rate of small fragments were significantly higher than medium-sized fragments, which in turn had higher relative growth rates than large fragments (Fig. S4A). Only *A. verweyi* deviated from this pattern as small fragments grew relatively slowly and were therefore on par with medium-sized fragments, explaining the significant interaction found between coral species and fragment size ($X^2 = 24.57$, $df = 6$, $p < 0.001$). A comparison on the main effect of species showed that *A.* cf. *muricata* grew fastest (0.010 ± 0.0003 d^{-1}, mean specific growth rate ± SE), *P. cylindrica* slowest (0.007 ± 0.0003 d^{-1}) and *A. verweyi* (0.008 ± 0.0002 d^{-1}) and *P. verrucosa* (0.009 ± 0.0002 d^{-1}) reached intermediate growth rates.

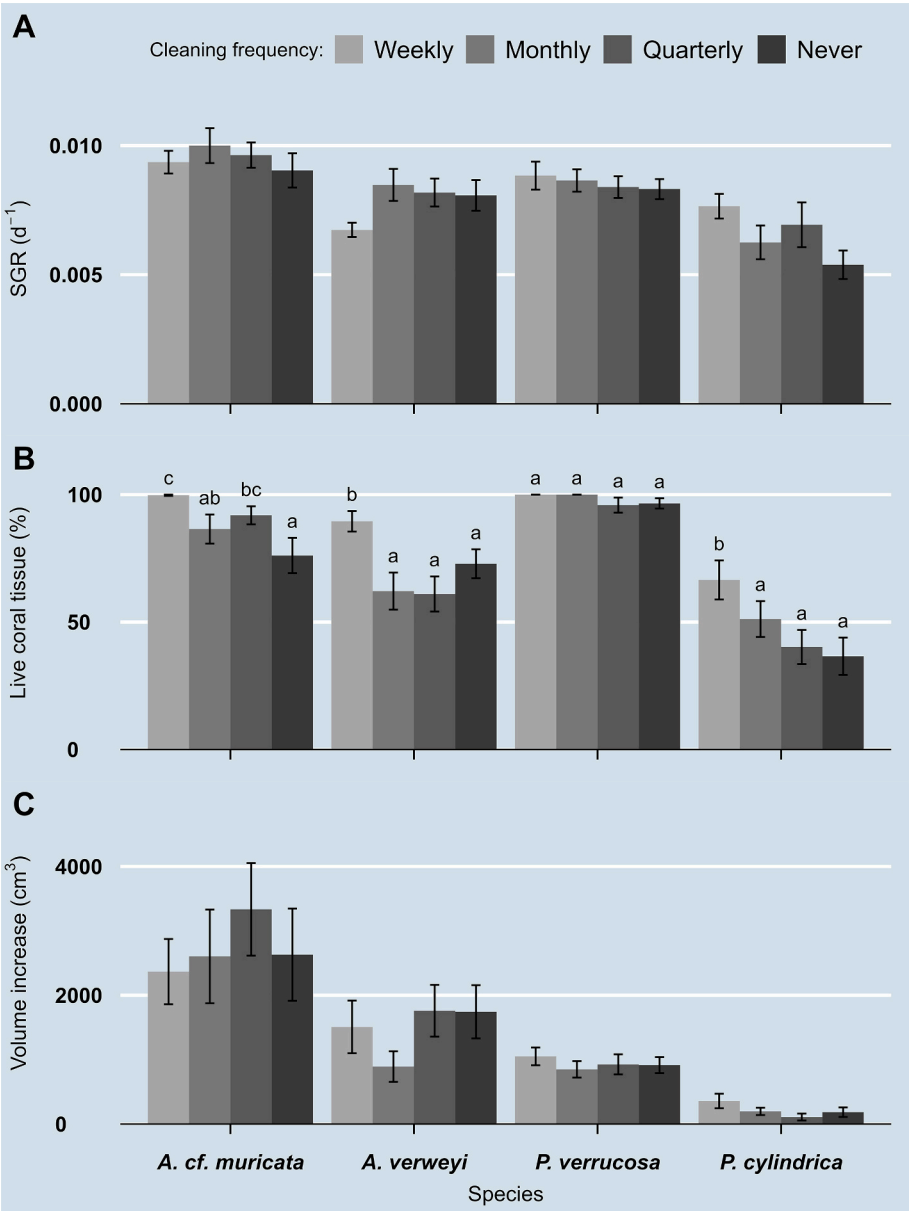

Fig. 2. Coral performance compared between cleaning frequencies for each coral species. The species are *Acropora* cf. *muricata*, *Acropora verweyi*, *Pocillopora verrucosa* and *Porites cylindrica*. A Average specific growth rate (SGR) over the full 1-year study period. B Live coral tissue at the end of the 1-year experiment. C Absolute increase in ecological volume (EV) between the end and start of the 1-year experiment. Error bars denote standard error. Non-matching lower-case letters indicate significant differences ($P < 0.05$) between cleaning frequencies within each species. Data has been pooled over the three different fragment size categories, so $n = 45$ (nested within 3 nurseries per cleaning * species combination).

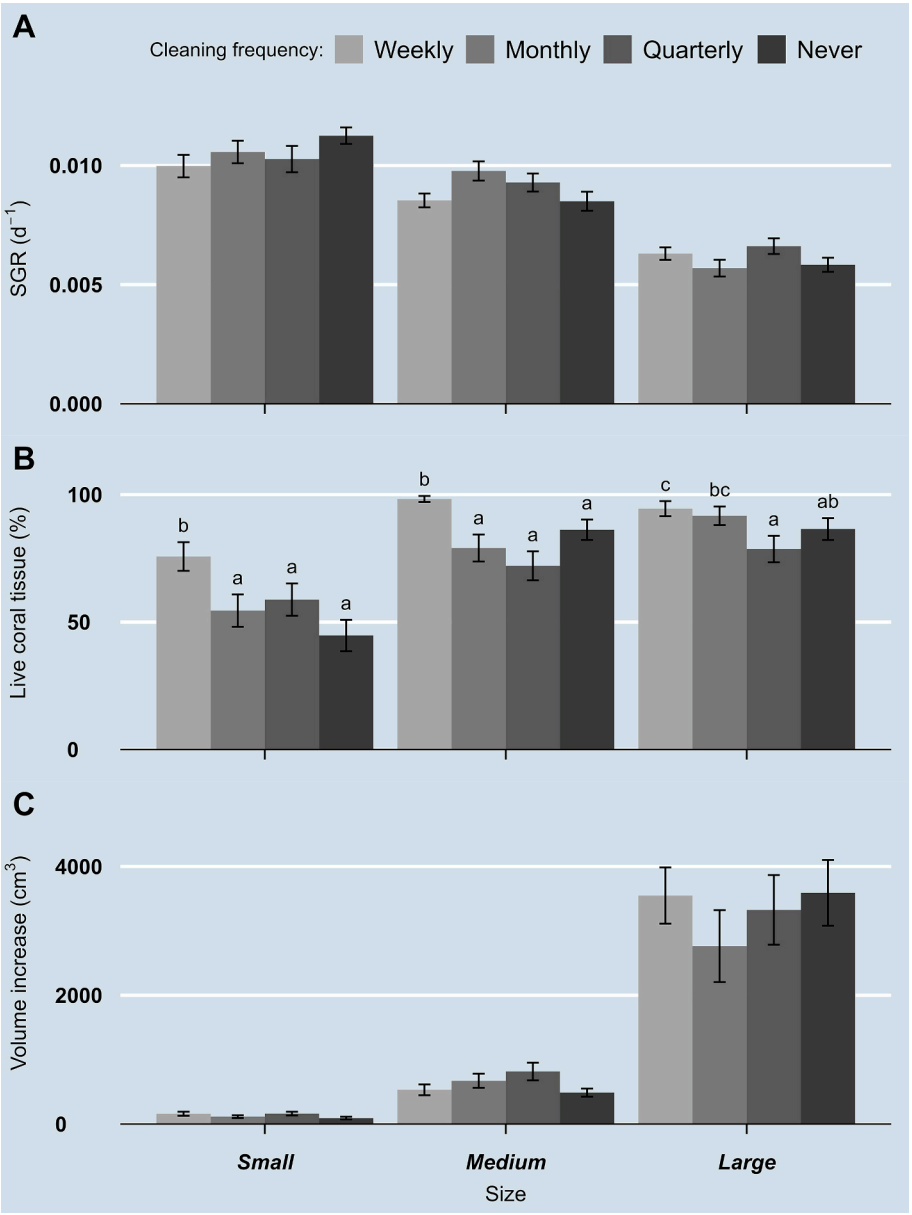

Fig. 3. Coral performance compared between cleaning frequencies for each fragment size category. A Average specific growth rate (SGR) over the full 1-year study period. B Live coral tissue at the end of the 1-year experiment. C Absolute increase in ecological volume (EV) between the end and start of the 1-year experiment. Error bars denote standard error. Non-matching lower-case letters indicate significant differences ($P < 0.05$) between cleaning frequencies within each size category. Data has been pooled over the four different coral species, so $n = 60$ (nested within 3 nurseries per cleaning * size combination).

3.2. Live tissue cover

A significant three-way interaction was found between the effects of cleaning frequency, coral species and fragment size on the percentage of live coral tissue cover ($X^2 = 41.42$, $df = 18$, $p = 0.001$), indicating that the effect of cleaning frequency on live coral tissue showed a different pattern across fragment sizes among the coral species. This three-way interaction is visualised in Fig. S5, but mainly the two-way interactions are discussed here for clarity, with deviations from the three-way interaction highlighted. Coral fragments that were cleaned weekly had typically higher live coral tissue cover than fragments that received less frequent cleaning (Fig. 2B). This pattern was consistent for all species except *P. verrucosa*, for which cleaning had no effect on live coral tissue cover (Fig. 2B), explaining the significant two-way interaction between species and cleaning frequency ($X^2 = 18.17$, $df = 9$, $p = 0.033$). The higher live coral tissue at weekly cleaning was largely consistent across fragment sizes (Fig. 3B) and the interaction between cleaning and size was indeed not significant. However, while the benefits of weekly cleaning were found for medium-sized fragments of *P. cylindrica*, this was not the case for small and large fragments. For both *Acropora* species only the small fragments profited from weekly cleaning (Fig. S5). Across species, small fragments had the lowest live coral tissue cover, except again for *P. verrucosa*, which had a consistently high live tissue cover across all three size classes, explaining the significant interaction between fragment size and species ($X^2 = 24.97$, $df = 6$, $p < 0.001$). Overall, live coral tissue cover was higher for the weekly cleaning than all other cleaning frequencies, differed between the species (*P. verrucosa* > *A.* cf. *muricata* > *A. verweyi* > *P. cylindrica*) and was lower for small fragments compared to both medium and large fragments.

3.3. Coral production

The influence of cleaning frequency on coral production was minimal: no significant differences among cleaning frequencies were found for any of the species (Fig. 2C), nor was the three-way interaction or the main effect of cleaning frequency significant. Only the interaction between cleaning frequency and fragment size was just significant ($X^2 = 12.77$, $df = 6$, $p = 0.047$), but post-hoc analysis did not show any differences in production between cleaning frequencies for any of the sizes (Fig. 3C). In contrast, very clear patterns emerged by comparing the different fragment sizes with each other. In contrast to the patterns found for relative growth rates, large fragments attained much higher absolute increases in volume than small fragments, with medium-sized fragments having slightly, but significantly higher increases than small fragments (Fig. S4C). Only *P. cylindrica* deviated from this pattern as both small and medium fragments showed equally low production, explaining the significant interaction found between size and species ($X^2 = 248.36$, $df = 6$, $p < 0.001$). Overall, production differed between species (*A.* cf. *muricata* > *A. verweyi* > *P. verrucosa* > *P. cylindrica)* and sizes (large > medium > small).

3.4. Cost-benefit analysis

The cost effectiveness analysis showed a very clear and consistent pattern: not cleaning was invariably the most cost-effective option, regardless of coral species or fragment size (Fig. 4). For *A.* cf. *muricata*, *A. verweyi* and *P. verrucosa*, which would need an estimated nursery time of between 295 and 313 days to reach the targeted end volume, the total cost without cleaning was $0.26–0.27 per fragment. For *P. cylindrica*, which required a much longer 637 days to reach target volume due to lower growth rates and reduced live coral tissue cover, the costs totalled $0.29 per fragment without cleaning. Across all four species, cleaning on a quarterly or monthly basis both doubled the costs to grow a fragment. Increasing the cleaning frequency from a monthly to a weekly regime

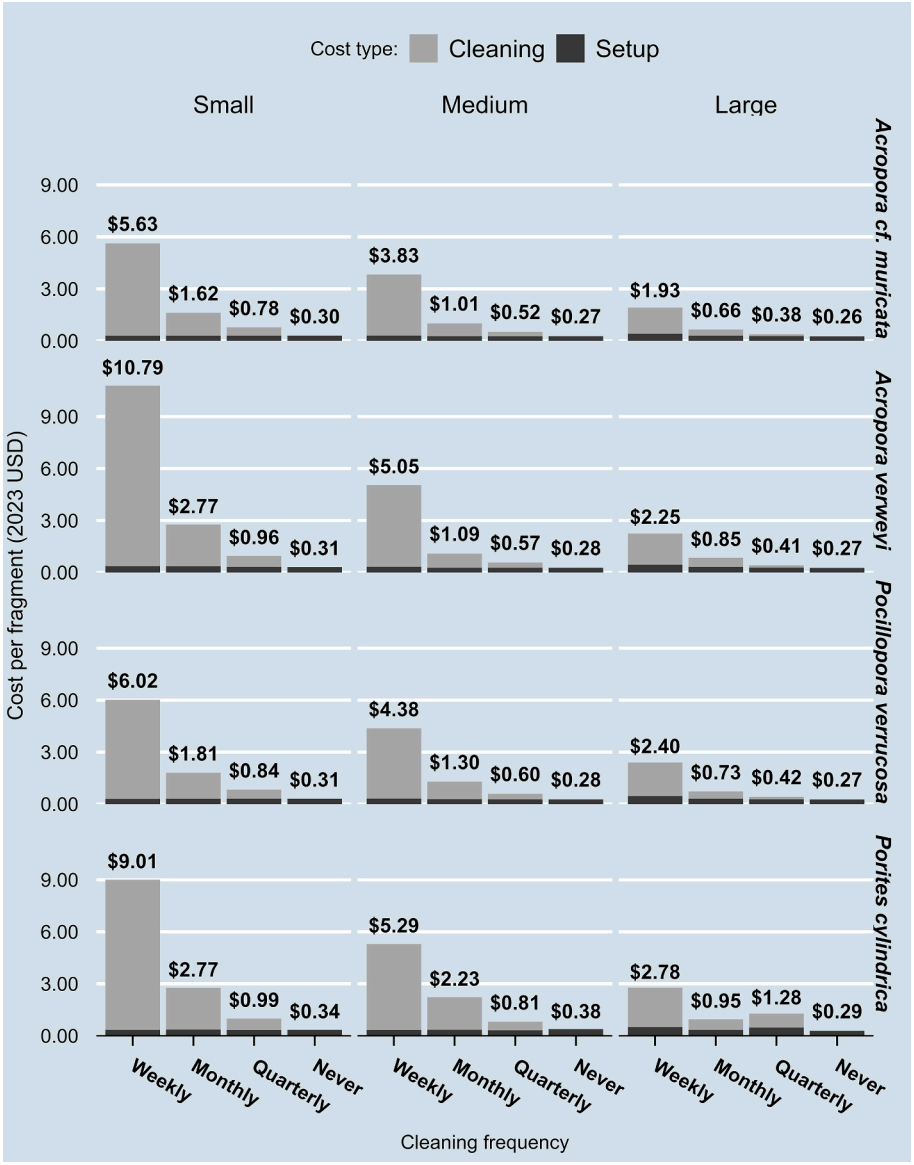

Fig. 4. Average costs to culture a single full-grown coral fragment, split per fragment size, coral species and cleaning frequency. Costs are based on measured production rates and project costs. Project costs are split between required setup costs to establish a nursery (including materials, corals, diving equipment, deployment and wages) and cleaning costs (including diving equipment and wages). The numbers above each bar are the total costs (sum of setup and cleaning costs). As slower growing corals can be cultured less efficiently with the same setup, setup costs can differ between coral species. As setup costs were also linked to fragment size and cleaning frequency to provide the initial batch of corals, setup costs can vary between cleaning frequencies and initial fragment size used.

would additionally triple the costs, up to a maximum average cost of $10.79 per fragment. These increases in costs with increasing cleaning frequency were much steeper for smaller fragments. For example, the relative increase in price from never cleaning to weekly cleaning was 7–10 fold for large fragments, 14–18 fold for medium fragments and 19–35 fold for small fragments (Fig. 4).

4. Discussion

This study aimed to quantify the costs and benefits of manual nursery cleaning by divers to identify a more cost-effective approach. No cleaning was consistently most cost-effective across all examined coral species and fragment sizes. This was contrary to our expectations that at least some cleaning, as commonly applied by restoration projects worldwide (Edwards et al., 2010; Vaughan, 2021; Ferse et al., 2021), would be beneficial, especially for smaller and competitively weaker corals. The absence of cleaning benefits for coral growth and only minor improvements in live coral tissue cover at weekly cleaning (for some species and sizes) clearly did not justify the high costs associated with cleaning in this study. The relatively low cost to establish a coral nursery ($22.87 per tree, lasting five years) compared to the relatively high costs of cleaning ($6.61 per tree, for each trip), reveal that the most cost-effective approach is to establish nurseries without cleaning. Replacement of dead fragments will prove more cost effective than aiming to increase survival through frequent cleaning. Assuming similar conditions and prices, strong reductions in nursery costs can be attained by restoration projects if they switch from the commonly-practiced monthly cleaning to no cleaning. Given the lower production and thus longer nursery durations for smaller fragments, such a change in cleaning regime would result in especially strong cost reductions for small fragments (up to nine-fold) compared to medium (up to six-fold) and large fragments (up to three-fold). Even without cleaning, starting with small fragments is still slightly more expensive because it takes longer before they reach the optimal size for outplanting so a nursery structure can be used for less growth cycles before it wears out. Overall, the absolute lowest costs to culture a fragment were achieved by using a combination of large starting sizes and no cleaning, resulting in a minimum total production cost of $0.26–0.29 per fragment, depending on the species.

Before these results are generalized to other reef restoration projects, the following five points regarding site-specific conditions and methodology have to be taken into account. Firstly, the role of natural herbivores. The study site was specifically chosen for its low herbivorous fish biomass, so that any benefits of cleaning could be clearly quantified. As the herbivorous fish biomass at this reef (70 kg ha^{-1}) was considerably lower than the worldwide average at fished (205 kg ha^{-1}) and protected (564 kg ha^{-1}) reefs (Edwards et al., 2014), benefits of manual cleaning will likely be even less pronounced at many other reefs worldwide and, therefore, manual cleaning is also unlikely to be cost-effective elsewhere. Although the coral tree nursery design typically excludes bottom-dwelling invertebrates, we saw sea urchins temporarily climb and feed on fouling in the coral trees after seagrass had been overgrazed in the surrounding area (Fig. S1E). The more natural herbivores can be used to omit the need for human cleaning in coral nurseries, the higher the cost-effectiveness of restoration efforts (Frias-Torres and Van de Geer, 2015). The competitive interactions between fouling and corals might be different in areas with a higher nutrient load, but the effect of natural herbivores has been shown to be more important to control primary producers and therefore fouling (Burkepile and Hay, 2006). Secondly, the composition and effects of fouling. Even though fouling has not been directly quantified in this study (but see Fig. S1A–C), macroalgae have been shown to proliferate in an earlier herbivore-exclusion study in the same area (Knoester et al., 2019). The potentially severe competitive interactions between fouling and corals (McCook et al., 2001) might have been limited in the coral tree nursery design, where the coral fragments are separated from most fouling by the thin monofilament line. Indeed, the nursery design itself appears an effective approach to prevent the need for manual cleaning. Thirdly, the effects of coral species and life history traits. While each coral species may react somewhat differently, the largely similar responses to cleaning for the range of studied coral species within three distinct life history strategies (Darling et al., 2017), make it likely that these results can be applied to numerous other branching coral species. Fourthly, the influence of environmental conditions. This study was performed during a thermal anomaly which bleached *P. verrucosa* fragments (Fig. S1D) and limited growth across all species from April to June (Fig. S2) and theoretically could have changed the competitive interactions between fouling and corals (Smith et al., 2022). Over the course of the one-year experiment, though, no influence was found on the need for manual cleaning due to the quick recovery in growth rates (Fig. S2). Lastly, in this study, coral trees were cleaned intensively to remove all fouling. This might have been more costly than needed and it cannot be excluded that this negatively influenced coral fragments due to handling stress. On the other hand, the advantages of cleaning found for live tissue cover of small, vulnerable coral fragments make this less likely. Also, less thorough cleaning would even further reduce any benefits of manual cleaning.

Considering all points above, it is likely that the results obtained in this study can be applied more widely to other reef restoration projects. We therefore would like to recommend other projects operating under similar conditions to experiment with reducing their cleaning frequency and intensity. If the minor reductions in live tissue cover of small fragments are not a major issue, the saved costs will likely amply compensate for these losses. Of course, periodic visits to inspect coral nurseries are still recommended for maintenance and monitoring, even when cleaning is no longer part of routine operations. Further cost reductions might be possible by using larger starting sizes of fragments, thereby capitalizing on the exponential increase in coral production over time. Interestingly, such an approach contradicts the microfragmentation concept developed for massive corals (Forsman et al., 2015), which aims to make use of the high relative growth rates of small fragments. Potentially, the drop in growth rate over time is steeper for massive corals than for branching corals and this would then need a separate cost-benefit analysis. Of course the choice of initial coral fragment size also depends on the amount of starting material available. Following the most cost-effective approach of large fragments and no cleaning reported here and an outplant density of four corals per square meter, the minimum nursery costs to outplant one hectare of coral reef in this study ($10,400–11,600, depending on species) fall well below the median costs ($32,900, corrected for inflation) as reported by Bayraktarov et al. (2019). This study has illustrated several ways how coral nursery costs can be reduced, most notably by reducing commonly-used cleaning regimes, and we hope such optimizations will make reef restoration a more cost-effective conservation technique.

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CRediT authorship contribution statement

E.G. Knoester: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **M.H. Groenendijk:** Writing – review & editing, Methodology, Investigation. **A.J. Murk:** Writing – review & editing, Supervision, Conceptualization. **R. Osinga:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data and code used for analysis is available as an archived Github repository on: https://github.com/ewoutknoester/OptimalCleaningInterval.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2024.107209.

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