Comparing the Efficiency of Nursery and Direct Transplanting Methods for Restoring Endangered Corals

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Comparing the Efficiency of Nursery and Direct Transplanting Methods for Restoring Endangered Corals

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Abstract

Restoration of plants, corals, and other sessile species often involves transplanting individuals to sites chosen for rehabilitation. Transplanted individuals are sometimes harvested directly from wild populations (direct transplanting), and sometimes propagated or cultured in a “nursery” before being transplanted (nursery outplanting). The ecological effectiveness and cost-efficiency of these methods have rarely been compared, so we performed an experiment to address this. Coral fragments, *Acropora cervicornis* (n = 780), were collected and assigned to one of three treatments: 1) directly transplanted to a restoration site and placed loose on the reef; 2) directly transplanted and manually attached to the reef; 3) moved to a nursery site near the restoration site for three months before being transplanted and manually attached to the reef. Treatment 1 was inefficient simply because these corals survived poorly. After 15 months, the survival and growth of corals assigned to treatments 2 and 3 was similar. The nursery method (3) was more expensive and time-consuming than direct transplanting (2), so treatment 2 yielded twice as many surviving corals per hr of work invested and three times as many survivors per dollar of set-up costs as treatment 3. The net production of live coral tissue per hr or per dollar invested was also greatest for direct-attached transplants. Cost- and
time-efficiency are important considerations for practitioners seeking to maximize the area of reef
rehabilitated and, in this case study, were maximized by bypassing a nursery stage.

**Keywords:** *Acropora*, cost-benefit, growth, staghorn coral, survival, tissue production

**Restoration Recap**

- We present a case study using the coral *Acropora cervicornis* that uses the money and time
  required to restore populations as a simple way to compare the efficiency of alternate restoration
  methods.
- Transplanting fragments without affixing them to the reef was the simplest and cheapest method,
  but poor fragment survival made this method inefficient.
- The growth and survival of directly transplanted fragments that were affixed to the reef was
  similar to that of fragments that spent three months in a nursery before transplanting. However,
  because the nursery took extra time and money to set up, it was less efficient than direct
  transplanting.
- Because cost- and time-efficiency calculations may be specific to species, location, and
  procedural detail, further tests are needed to generalize about methodological efficiency.
  Practitioners are thus encouraged to weigh the costs and benefits of different protocols on a case-
  by-case basis.

Despite the fact that time and money for restoration is limited, there have been relatively few
comparative analyses of the cost-effectiveness of restoration protocols (Benayas et al. 2009, Aronson
et al. 2010, de Groot et al. 2013). Such analyses are of particular value for corals, which are the
foundation species for the most biologically diverse marine ecosystem, yet have been in decline
globally for the past 40 years (De'ath et al. 2012, Jackson et al. 2014). In response to coral declines, coral restoration has grown rapidly in popularity and is now practiced worldwide by many non-profit groups and government agencies, but a global analysis suggests that coral reefs are the most expensive ecosystem to restore per unit-area (de Groot et al. 2013, Bayraktarov et al. 2016).

Restoration of sessile foundation species such as trees, seagrasses, mangroves, and corals often involves transplanting individuals to degraded sites (e.g., Putz et al. 2001, Rinkevich 2005, Lewis 2009, Paling et al. 2009). Transplanted individuals are usually small and may include seeds or propagules, juveniles, cuttings, and asexual fragments. We used asexual coral fragments derived from adults in wild populations, the most widely used approach for coral restoration projects (Rinkevich 2005, Precht 2006, Edwards and Gomez 2007, Edwards 2010, Johnson et al. 2011, Young et al. 2012, Chavanich et al. 2014). Protocols for transplanting fragments can be classified into those which: 1) transplant individuals harvested directly from wild populations (hereafter direct transplanting); or 2) culture wild fragments in a “nursery” for some time before transplanting (hereafter nursery-outplanting).

We compared the time- and cost-effectiveness of two direct transplanting approaches, referred to as “direct-loose” and “direct-attached” methods respectively. In the direct-loose approach, fragments are simply placed on the substratum at the restoration site (e.g., Bowden-Kerby 1997, Lindahl 1998, Bowden-Kerby 2001, Lindahl 2003). This approach mimics the fate of asexual fragments generated by storms or broken from parent colonies by human activity (e.g., Fong and Lirman 1995, Smith and Hughes 1999). Tissue growth occasionally re-attaches these fragments to the substratum, in which case they may form a new colony (e.g., Tunnicliffe 1981). Although past research shows the survival of direct-loose transplants can be poor (e.g., Bak and Criens 1981, Knowlton et al. 1981, Mercado-Molina et al. 2014), this method has been used in several restoration projects (e.g., Lindahl 1998, 2003) and its relative simplicity makes it a useful benchmark against...
which to evaluate more elaborate and expensive methods. More common, however, is the direct-
attached method wherein transplanted coral fragments are manually secured to the substratum.

Securing fragments increases the probability that they will subsequently grow to self-attach to the
reef (e.g., Guest et al. 2011) and so improves their long-term survival (e.g., Forrester 2011, Forrester
et al. 2014), but the benefit of this improved survival has rarely been weighed against the increased
time and money required (Edwards et al. 2010).

We also compared direct transplants to nursery outplants. Nursery outplanting has been
widely adopted, and typically involves the culturing fragments in sheltered inshore nursery sites away
from reefs (Epstein et al. 2003, Rinkevich 2005). Nursery cultivation usually involves constructing
structures to hold or suspend the coral fragments, plus regular cleaning and maintenance of the
nursery apparatus, so almost certainly requires a greater investment of time and money per coral than
direct transplanting. Nurseries have been advocated for multiple reasons (Rinkevich 2005, 2014), but
we evaluated only their hypothesized benefits for fragment growth and survival. These benefits are
predicted because fragments in nurseries can be positioned for exposure to favorable flow and
lighting conditions, and isolated from the harmful effects of sediment, competitors, predators, and
pathogens present on the reef (Epstein et al. 2003). Direct comparisons among these protocols are
limited (for an exception see de la Cruz et al. 2015), so our objective was to quantify the cost- and
time-efficiency of the two methods to test whether the expected higher survival of nursery outplants
offsets the increased costs of cultivation.

Methods

Study Species

We studied staghorn corals, *Acropora cervicornis* (Lamarck, 1816), formerly a major reef-building
coral in Caribbean at intermediate depths (5-15 m). This species suffered a particularly acute decline
region-wide since the 1980s (Jackson et al. 2014), which prompted its listing under the US
endangered species act, the IUCN red list, and CITEs Appendix II (National Marine Fisheries Service
2006). Fragmentation and reattachment is an important mechanism of asexual reproduction for this,
and other branching coral species (Highsmith 1982). Fragments are generated naturally by storms,
unintentionally when boats and people collide with reef, and deliberately when colonies are pruned
for restoration (Johnson et al. 2011, Young et al. 2012). Fragments generated from each of these
sources grow quickly and have been used for both direct transplanting and nursery outplanting
(Johnson et al. 2011, Young et al. 2012). Acropora cervicornis is the species most commonly used
species for reef restoration in the Caribbean (Young et al. 2012, Schopmeyer et al. 2017), and
Acropora is the most widely used genus for restoration globally (Edwards and Gomez 2007,
Rinkevich 2014).

Source and Restoration Sites

To increase generality of the outcome, we used two study sites, Harris Ghut (HG) and Muskmelon
Bay (MB), both of which were near Guana Island, British Virgin Islands: (Figure S1). MB was
roughly 420 m² in area and HG was roughly 800 m². Both sites are wave-protected fringing reefs,
close to horizontal in profile, with relatively low rugosity (1.6-1.9 based on the chain method
([Alvarez-Filip et al. 2009]) and low total coral cover (5-10%). Although A. cervicornis is now rare
on both reefs (<0.2% cover), their depth (5-7 m) and leeward location (Goreau 1959, Bak 1977), plus
local eyewitness accounts from the 1980s, suggest they are suitable habitat. We collected 780
"fragments of opportunity" for the study (Johnson et al. 2011, Young et al. 2012). Fragments were
sourced from two leeward reefs (2-7 m deep) that were 2-4 km from the restoration sites and support
recovering A. cervicornis populations (Figure S1). Fragments were collected on snorkel, placed in
bins of seawater on a boat, and then taken directly to the restoration sites. At the restoration site,
fragments were placed temporarily on the reef for 1-6 days, after which they were assigned to one of the treatments to start the experiment (start dates ranged from 13-19 Aug 2013). Although variable, time between transport and the start of the experiment was equal among treatments so it did not affect the outcome.

**Experimental Design**

Fragments were randomly assigned to one of three treatments (Figure S2): 1) Direct-loose transplants (n = 138 at HG, n = 45 at MB); 2) Direct-attached transplants (n = 225 at HG, n = 81 at MB); and 3) Nursery-outplants (n = 183 at HG, n = 108 at MB).

In August, we constructed three line nurseries at MB and four at HG (see Johnson et al. 2011, Griffin et al. 2012). Nurseries were placed in sandy protected areas, 7-10 m deep, 25-40 m inshore from each restoration reef (Figure S3). Each nursery consisted of a rigid outer PVC frame (2m x 2 m or 2m x 3m), from which we strung rows of monofilament line spaced 25-cm apart. The nursery-outplant fragments were hung from the monofilament at 25-cm intervals using plastic-coated wire (Figure S4). Each nursery was anchored using concrete blocks and suspended vertically using subsurface buoys so that the corals were 5-7 m deep. Nurseries were not maintained after set-up, but there was no obvious subsequent overgrowth by fouling organisms.

In August, we placed the direct-loose fragments on the reef, and the direct-attached fragments were secured to the reef using cable ties (see Garrison and Ward 2008) tied to masonry nail anchors (see Lirman et al. 2014). Twelve weeks later (24-27 October 2014), the nursery-outplants were removed from the nursery and secured to the reef using cable ties. We ensured that fragments from different treatments were interspersed at each site, and were at roughly equal densities (all fragments were ≥ 40 cm apart). When corals from all treatments were first moved to the reef, we photographed them, mapped their location and secured a numbered identification tag to the reef nearby (Figure S2).
We monitored the survival and growth of the coral fragments after 12 weeks (26-29 October 2013), after 24 weeks (19-21 January 2014) and after 64 weeks (26-28 October 2014).

*Acropora cervicornis* fragments can grow to form a tissue connection with the reef within 8 weeks of transplanting (e.g., Bowden-Kerby 2001), so corals from all treatments had time to self-attach to the reef and experience ecological conditions on the reef (Guest et al. 2011, Forrester et al. 2014).

Because direct-loose fragments were not attached to the substratum, they could potentially be moved by currents. To track their survival, we thus searched the entire site and the area within 5 m of the perimeter in case fragments had been moved out of the site. Each time the fragments were monitored, we took several photographs of each fragment encountered and, using the maps and previous photographs, we attempted to identify each loose fragment based on its location and appearance. Relatively few fragments disappeared during the study (direct-loose: n = 10, direct-attached: n = 3, nursery-outplants, n = 2). When calculating survival, corals that disappeared were assumed to have died.

**Measuring Fragment Survival**

We compared the survival of fragments between treatments and sites using the non-parametric Kaplan-Meier survival model (Lee 1992, Kleinbaum and Klein 2011). Because periodic monitoring yields a record of whether a coral is alive on each census date, estimates of survival time were thus either interval-censored (when a fragment died between two censuses) or right-censored (when the fragment was still alive at the end of the study) (Lee 1992). Separate survival curves were fit for each treatment × site combination, and the survival parameters were judged different if their 95% confidence intervals did not overlap.
Measuring Fragment Growth and Tissue Production

*Acropora cervicornis* colonies are composed of cylindrical branches whose diameter varies much less than their length, so we summed the length of all branches, excluding areas of dead tissue, as a simple estimate of colony size (hereafter TLD, see Figure 5 and Shinn (1966)). To assess colony growth, we compared the mean TLD of surviving colonies among treatments (a fixed effect) and sites (a random effect) at the start and end of the experiment using a two-factor analysis of variance (ANOVA). The ANOVA model included the two main effects and their interaction. Before conducting the analyses, we checked whether the data met the assumptions of ANOVA (TLD data at the end of the experiment were heteroscedastic and so were log_{10} transformed to meet the assumption of equal variances).

To assess how much new live tissue was produced per coral, we also calculated net tissue production over the course of the study (TLD_{final}/TLD_{initial}). To measure TLD divers took photographs of each coral from different angles to capture images of each branch, with a ruler in the frame to provide a scale. We later used image analysis software (ImageJ) to measure each branch (Abramoff et al. 2004). To check of the accuracy of the photographic method, divers also measured a subset of the corals (n = 102) in the field using a flexible tape measure (Figure S6). There was a close relationship between the direct field (x) and photographic (y) TLD measurements (linear regression: (n = 102, range of TLD = 2-173 cm, y = 5.51 + 0.78x, r^2 = 0.91), suggesting that measurement error did not obscure differences between treatments (Figure 2) (Kiel et al. 2012).

Quantifying the Outcome of the Restoration in Terms of Time and Cost Invested

To evaluate the time and cost-efficiency of the three restoration methods, the time needed to establish each coral on the reef was quantified (hrs per coral; Table S1). We logged each step of the restoration process at the field site (Table S1), but excluded accessory tasks such as washing SCUBA gear and
filling tanks. Time to complete tasks common to all methods, such as searching donor sites for fragments, was divided according to the number of corals involved per treatment.

We also calculated the local purchase price of materials needed to establish each coral at the restoration site in US$ per fragment, which included materials for attaching corals to the reef and materials for the nursery frames (Table S2). We excluded some costs that were common to all methods (e.g., SCUBA and snorkel equipment for participants, and bins to hold fragments while being transported in the boat), and others that are context- and location-specific (e.g., air travel to the project site, food, and accommodation costs) (Edwards et al. 2010). We also excluded the time and cost invested in the scientific monitoring such as attaching tags, measuring, and photographing corals because this is not essential for practical restoration projects.

We then calculated coral survival and tissue production as a function of the time invested and money spent on materials. To measure return on time invested, we calculated the number of surviving corals at the end of the study that were produced per hr of initial set-up time (survivors after 64 weeks per hr). We also calculated the net production of coral \((\text{TLD}_{\text{final}}/\text{TLD}_{\text{initial}})\) per hr of initial set-up time.

To measure return based on financial cost, we calculated the number of surviving corals at the end of the study that were produced per dollar of materials (survivors after 64 weeks per US$) and net coral production \((\text{TLD}_{\text{final}}/\text{TLD}_{\text{initial}})\) per dollar of materials.

**Results**

**Survival**

At both sites, survival of loose fragments was significantly lower than that of nursery and directly attached fragments by the end of the study (Figure 1 and Figure S7). Survival of corals from the latter two treatments was site-dependent (Figure S7). In Harris Ghut, nursery fragments survived significantly better than directly attached fragments while suspended on the nursery frames, but this
initial advantage was subsequently overturned and, at the end of the experiment, survival did not differ between the two treatments (Figure S7). In Muskmelon Bay, however, the survival of nursery outplants was significantly lower than that of directly attached fragments throughout (Figure S7). Pooling sites to give a project-wide overview revealed no overall difference in the survival of direct-attached fragments and nursery-outplants (Figure 1).

**Growth of Surviving Fragments**

At the start of the experiment, fragments did not differ in size among treatments or sites (ANOVA: p > 0.05 for main effects and interaction term; Figure 1 and Figure S8). At the end of the experiment, however, direct outplants at Muskmelon Bay had grown significantly larger than all other groups of fragments (ANOVA: treatment × site interaction; $F_{2,300} = 4.18, p = 0.016$; Fig. S9). Although the differences between restoration treatments were site-specific, pooling sites to give a study-wide overview revealed that direct-attached fragments generally reached larger sizes than nursery-outplants and direct-loose fragments (Figure 2).

**Return on Investment**

Even though directly transplanted loose fragments took little time to place on the bottom, the fact that they survived so poorly meant that there were few survivors and very little return on investment (Figures 3 and 4). For the remaining two treatments, survival was similar but nursery-outplants received a greater investment of time and money per coral than direct-attached fragments. Consequently, direct transplanting produced roughly twice as many surviving corals per hr invested, and three times as many survivors per dollar, as the nursery treatment (Figure 3). Because direct-transplants grew slightly faster than nursery-outplants, the differential in return on investment was magnified further when expressed as net tissue production (Figure 4).
The poor survival of loose transplants is consistent with most previous studies of loose fragments (e.g., Bowden-Kerby 1997, Lindahl 1998, Smith and Hughes 1999, Bowden-Kerby 2001, Forrester 2011), suggesting that this method would only become efficient if fragments were extremely plentiful and securing fragments to the reef was very expensive and time-consuming. Because hurricane damage to branching corals can create enormous numbers of fragments, most of which die in the subsequent months (e.g., Knowlton et al. 1981), the immediate aftermath of a major storm might create a situation favoring this method. Other agents of extensive local damage, such as a major boat grounding, might also create conditions for this method to be cost- and time-efficient.

Because nursery outplants and direct-attached transplants had similar survival, our results did not support the hypothesis that time in a nursery improves the subsequent survival of transplanted corals (Epstein et al. 2003). Broadly similar findings were reported in the only other direct comparison of these methods we know of (dela Cruz et al. 2015). While in nurseries, fragments of two non-branching Pacific corals survived better than equivalent direct transplants, but this advantage dissipated when corals from the nursery were then placed on the reef alongside direct outplants (dela Cruz et al. 2015).

Although the overall survival of nursery outplants and direct-attached transplants was similar in our study, we did observe differences between the two treatments in apparent causes of death. A macroalgal bloom (Dictyota spp.) coincident with the start of the study appeared to smother many direct transplants but had no effect on fragments while they were in the nursery, which supports the hypothesis that being on the reef places direct-transplants at risk from negative species interactions (Forrester et al. 2012, Johnston and Miller 2014, Miller et al. 2014, Casey et al. 2015). Both groups of corals were vulnerable to human impacts, but from different activities. In Muskmelon Bay, some
direct-transplants were apparently killed by boat anchoring, while some nursery corals died as a result of physical damage to the nursery frames (we believe the frames were damaged inadvertently by fishing nets). Future studies are needed to test whether other agents of coral mortality differentially impact nursery outplants and direct transplants. Both groups are vulnerable to storms, predators, climate-induced bleaching events, and disease epidemics (e.g., Garrison and Ward 2008, Shaish et al. 2010a, b, Forrester et al. 2014), and more direct comparisons are needed to quantify their relative importance and quantitative effects.

We also found that the costs of restoration differed among the three methods tested. A cross-ecosystem comparison revealed that coral reefs are typically the most expensive habitat to restore per unit area (de Groot et al. 2013, Bayraktarov et al. 2016), which raises the concern that high costs will limit all coral restoration projects to rehabilitating tiny areas relative to the vast swaths of degraded reef (Mumby and Steneck 2008). For that reason, all three methods we selected for comparison were relatively simple and inexpensive because we assumed low-cost protocols may be more readily adopted by non-specialists and scaled-up to restore large areas of reef. Although material costs are rarely quantified, other materials that have been used to stabilize transplanted corals and construct nurseries appear to vary widely in cost (Bayraktarov et al. 2016). For example, the cable ties and nails we used to affix corals to the reef are similar to string and wire in having a relatively low cost per-coral, whereas other frequently used alternatives such as epoxy and hydrostatic cement are more expensive. Likewise, the pvc and fishing line we used to construct nursery frames is likely cheaper than some other options, such as epoxy-coated rebar.

Perhaps the most important decision we made to reduce costs was to keep corals in the nursery for a short time and perform no maintenance. An abridged nursery phase has been tested occasionally (dela Cruz et al. 2015), but the most studies have kept corals in the nursery far longer, regularly cleaned the nursery apparatus, removed encroaching predators, excised diseased tissue, and
even provided supplemental feeding (Rinkevich 2005, Precht 2006, Edwards and Gomez 2007, Edwards 2010, Johnson et al. 2011, Young et al. 2012, e.g., Chavanich et al. 2014, Toh et al. 2014). Additional explicit comparisons between methods are thus needed to test if our preference for simplicity was justified, or whether the greater expense and labor requirements of these more elaborate and extended nursery methods are outweighed by substantial improvements in coral survival and tissue production.

Our analysis represents a simple and partial assessment of the costs and benefits of restoration. We compared costs based on the direct investments of time and money necessary to set-up and maintain a project because these costs are important for practitioners and non-profit groups to consider when allocating their limited resources (de Groot et al. 2013). The assessment of project costs could be expanded to include other costs, such as damage to the donor site (though we suggest this cost was negligible in our study) and the opportunity cost from benefits forgone in the absence of restoration (Spurgeon 2001, de Groot et al. 2013). There is also scope for improvement in our analysis of the benefits of restoration. Like most previous analyses, the benefit of our restoration was measured based only on the demography of the transplanted coral species (Rinkevich 2005, Precht 2006, Edwards 2010, Johnson et al. 2011, Young et al. 2012, Schopmeyer et al. 2017). While comparing unit benefits per coral after a semi-arbitrary endpoint is a reasonable starting point (Edwards et al. 2010), and can be expanded in innovative ways (Rinkevich 2015), we urgently need longer-term assessments of benefits based on how the entire ecological community responds to the restoration (e.g., Cabaitan et al. 2008, Yap 2009, Merolla et al. 2013, dela Cruz et al. 2014). This would allow use of well-established frameworks for the valuation of ecosystem services (Kumar 2010, ten Brink 2011), and so provide a more comprehensive measure of the monetary value of restored reefs (de Groot et al. 2012, de Groot et al. 2013).
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Figures

Figure 1. Survival of coral fragments (±95% CI) in each of the experimental treatments: directly attached transplants, nursery outplants, and direct-loose transplants.

Figure 2. Mean TLD (±95% CI) of surviving coral fragments over time in each of the experimental treatments: directly attached transplants, nursery outplants, and direct-loose transplants.

Figure 3. Return on investment, based on coral survival, for each experimental treatment. Absolute survival at the end of the experiment is shown as a benchmark for comparison (top plot). Return on investment is plotted as the number of survivors per hr invested (middle plot) and the number of survivors per dollar invested (lower plot).

Figure 4. Return on investment, based on the net production of coral tissue (TLD_{final}/TLD_{initial}), for each experimental treatment. Raw means for net production at the end of the experiment are shown as a benchmark for comparison (top plot). Return on investment is plotted as net production per hr invested (middle plot) and net production per dollar invested (lower plot).