Natural Resources Science Faculty Publications

Natural Resources Science

6-1-2019

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

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1   RESEARCH ARTICLE

2   **Comparing the Efficiency of Nursery and Direct Transplanting Methods for Restoring**

3   **Endangered Corals**

4

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7

8   Abstract

9   Restoration of plants, corals, and other sessile species often involves transplanting individuals to sites

10   chosen for rehabilitation. Transplanted individuals are sometimes harvested directly from wild

11   populations (direct transplanting), and sometimes propagated or cultured in a "nursery" before being

12   transplanted (nursery outplanting). The ecological effectiveness and cost-efficiency of these methods

13   have rarely been compared, so we performed an experiment to address this. Coral fragments,

14   *Acropora cervicornis* (n = 780), were collected and assigned to one of three treatments: 1) directly

15   transplanted to a restoration site and placed loose on the reef; 2) directly transplanted and manually

16   attached to the reef; 3) moved to a nursery site near the restoration site for three months before being

17   transplanted and manually attached to the reef. Treatment 1 was inefficient simply because these

18   corals survived poorly. After 15 months, the survival and growth of corals assigned to treatments 2

19   and 3 was similar. The nursery method (3) was more expensive and time-consuming than direct

20   transplanting (2), so treatment 2 yielded twice as many surviving corals per hr of work invested and

21   three times as many survivors per dollar of set-up costs as treatment 3. The net production of live

22   coral tissue per hr or per dollar invested was also greatest for direct-attached transplants. Cost- and

23   time-efficiency are important considerations for practitioners seeking to maximize the area of reef

24   rehabilitated and, in this case study, were maximized by bypassing a nursery stage.

25

26

27   **Restoration Recap**

28   •   We present a case study using the coral *Acropora cervicornis* that uses the money and time

29   required to restore populations as a simple way to compare the efficiency of alternate restoration

30   methods.

31   •   Transplanting fragments without affixing them to the reef was the simplest and cheapest method,

32   but poor fragment survival made this method inefficient.

33   •   The growth and survival of directly transplanted fragments that were affixed to the reef was

34   similar to that of fragments that spent three months in a nursery before transplanting. However,

35   because the nursery took extra time and money to set up, it was less efficient than direct

36   transplanting.

37   •   Because cost- and time-efficiency calculations may be specific to species, location, and

38   procedural detail, further tests are needed to generalize about methodological efficiency.

39   Practitioners are thus encouraged to weigh the costs and benefits of different protocols on a case-

40   by-case basis.

41

42   Despite the fact that time and money for restoration is limited, there have been relatively few

43   comparative analyses of the cost-effectiveness of restoration protocols (Benayas et al. 2009, Aronson

44   et al. 2010, de Groot et al. 2013). Such analyses are of particular value for corals, which are the

45   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

70 which to evaluate more elaborate and expensive methods. More common, however, is the direct-

71 attached method wherein transplanted coral fragments are manually secured to the substratum.

72 Securing fragments increases the probability that they will subsequently grow to self-attach to the

73 reef (e.g., Guest et al. 2011) and so improves their long-term survival (e.g., Forrester 2011, Forrester

74 et al. 2014), but the benefit of this improved survival has rarely been weighed against the increased

75 time and money required (Edwards et al. 2010).

76   We also compared direct transplants to nursery outplants. Nursery outplanting has been

77 widely adopted, and typically involves the culturing fragments in sheltered inshore nursery sites away

78 from reefs (Epstein et al. 2003, Rinkevich 2005). Nursery cultivation usually involves constructing

79 structures to hold or suspend the coral fragments, plus regular cleaning and maintenance of the

80 nursery apparatus, so almost certainly requires a greater investment of time and money per coral than

81 direct transplanting. Nurseries have been advocated for multiple reasons (Rinkevich 2005, 2014), but

82 we evaluated only their hypothesized benefits for fragment growth and survival. These benefits are

83 predicted because fragments in nurseries can be positioned for exposure to favorable flow and

84 lighting conditions, and isolated from the harmful effects of sediment, competitors, predators, and

85 pathogens present on the reef (Epstein et al. 2003). Direct comparisons among these protocols are

86 limited (for an exception see dela Cruz et al. 2015), so our objective was to quantify the cost- and

87 time-efficiency of the two methods to test whether the expected higher survival of nursery outplants

88 offsets the increased costs of cultivation.

89 **Methods**

90 *Study Species*

91 We studied staghorn corals, *Acropora cervicornis* (Lamarck, 1816), formerly a major reef-building

92 coral in Caribbean at intermediate depths (5-15 m). This species suffered a particularly acute decline

93 region-wide since the 1980s (Jackson et al. 2014), which prompted its listing under the US

94 endangered species act, the IUCN red list, and CITEs Appendix II (National Marine Fisheries Service

95 2006). Fragmentation and reattachment is an important mechanism of asexual reproduction for this,

96 and other branching coral species (Highsmith 1982). Fragments are generated naturally by storms,

97 unintentionally when boats and people collide with reef, and deliberately when colonies are pruned

98 for restoration (Johnson et al. 2011, Young et al. 2012). Fragments generated from each of these

99 sources grow quickly and have been used for both direct transplanting and nursery outplanting

100 (Johnson et al. 2011, Young et al. 2012). *Acropora cervicornis* is the species most commonly used

101 species for reef restoration in the Caribbean (Young et al. 2012, Schopmeyer et al. 2017), and

102 *Acropora* is the most widely used genus for restoration globally (Edwards and Gomez 2007,

103 Rinkevich 2014).

104 *Source and Restoration Sites*

105 To increase generality of the outcome, we used two study sites, Harris Ghut (HG) and Muskmelon

106 Bay (MB), both of which were near Guana Island, British Virgin Islands: (Figure S1). MB was

107 roughly 420 m^2 in area and HG was roughly 800 m^2. Both sites are wave-protected fringing reefs,

108 close to horizontal in profile, with relatively low rugosity (1.6-1.9 based on the chain method

109 ([Alvarez-Filip et al. 2009]) and low total coral cover (5-10%). Although *A. cervicornis* is now rare

110 on both reefs (<0.2% cover), their depth (5-7 m) and leeward location (Goreau 1959, Bak 1977), plus

111 local eyewitness accounts from the 1980s, suggest they are suitable habitat. We collected 780

112 "fragments of opportunity" for the study (Johnson et al. 2011, Young et al. 2012). Fragments were

113 sourced from two leeward reefs (2-7 m deep) that were 2-4 km from the restoration sites and support

114 recovering *A. cervicornis* populations (Figure S1). Fragments were collected on snorkel, placed in

115 bins of seawater on a boat, and then taken directly to the restoration sites. At the restoration site,

116   fragments were placed temporarily on the reef for 1-6 days, after which they were assigned to one of

117   the treatments to start the experiment (start dates ranged from 13-19 Aug 2013). Although variable,

118   time between transport and the start of the experiment was equal among treatments so it did not affect

119   the outcome.

120   *Experimental Design*

121   Fragments were randomly assigned to one of three treatments (Figure S2): 1) Direct-loose transplants

122   (n = 138 at HG, n = 45 at MB); 2) Direct-attached transplants (n = 225 at HG, n = 81 at MB); and 3)

123   Nursery-outplants (n = 183 at HG, n = 108 at MB).

124   In August, we constructed three line nurseries at MB and four at HG (see Johnson et al. 2011,

125   Griffin et al. 2012). Nurseries were placed in sandy protected areas, 7-10 m deep, 25-40 m inshore

126   from each restoration reef (Figure S3). Each nursery consisted of a rigid outer PVC frame (2m x 2 m

127   or 2m x 3m), from which we strung rows of monofilament line spaced 25-cm apart. The nursery-

128   outplant fragments were hung from the monofilament at 25-cm intervals using plastic-coated wire

129   (Figure S4). Each nursery was anchored using concrete blocks and suspended vertically using

130   subsurface buoys so that the corals were 5-7 m deep. Nurseries were not maintained after set-up, but

131   there was no obvious subsequent overgrowth by fouling organisms.

132   In August, we placed the direct-loose fragments on the reef, and the direct-attached fragments

133   were secured to the reef using cable ties (see Garrison and Ward 2008) tied to masonry nail anchors

134   (see Lirman et al. 2014). Twelve weeks later (24-27 October 2014), the nursery-outplants were

135   removed from the nursery and secured to the reef using cable ties. We ensured that fragments from

136   different treatments were interspersed at each site, and were at roughly equal densities (all fragments

137   were ≥ 40 cm apart). When corals from all treatments were first moved to the reef, we photographed

138   them, mapped their location and secured a numbered identification tag to the reef nearby (Figure S2)

139   (Forrester 2011). We monitored the survival and growth of the coral fragments after 12 weeks (26-29

140   October 2013), after 24 weeks (19-21 January 2014) and after 64 weeks (26-28 October 2014).

141   *Acropora cervicornis* fragments can grow to form a tissue connection with the reef within 8 weeks of

142   transplanting (e.g., Bowden-Kerby 2001), so corals from all treatments had time to self-attach to the

143   reef and experience ecological conditions on the reef (Guest et al. 2011, Forrester et al. 2014).

144   Because direct-loose fragments were not attached to the substratum, they could potentially be

145   moved by currents. To track their survival, we thus searched the entire site and the area within 5 m of

146   the perimeter in case fragments had been moved out of the site. Each time the fragments were

147   monitored, we took several photographs of each fragment encountered and, using the maps and

148   previous photographs, we attempted to identify each loose fragment based on its location and

149   appearance. Relatively few fragments disappeared during the study (direct-loose: n = 10, direct-

150   attached: n = 3, nursery-outplants, n = 2). When calculating survival, corals that disappeared were

151   assumed to have died.

152   *Measuring Fragment Survival*

153   We compared the survival of fragments between treatments and sites using the non-parametric

154   Kaplan-Meier survival model (Lee 1992, Kleinbaum and Klein 2011). Because periodic monitoring

155   yields a record of whether a coral is alive on each census date, estimates of survival time were thus

156   either interval-censored (when a fragment died between two censuses) or right-censored (when the

157   fragment was still alive at the end of the study) (Lee 1992). Separate survival curves were fit for each

158   treatment × site combination, and the survival parameters were judged different if their 95%

159   confidence intervals did not overlap.

160   *Measuring Fragment Growth and Tissue Production*

161   *Acropora cervicornis* colonies are composed of cylindrical branches whose diameter varies much less

162   than their length, so we summed the length of all branches, excluding areas of dead tissue, as a simple

163   estimate of colony size (hereafter TLD, see Figure 5 and Shinn (1966)). To assess colony growth, we

164   compared the mean TLD of surviving colonies among treatments (a fixed effect) and sites (a random

165   effect) at the start and end of the experiment using a two-factor analysis of variance (ANOVA). The

166   ANOVA model included the two main effects and their interaction. Before conducting the analyses,

167   we checked whether the data met the assumptions of ANOVA (TLD data at the end of the experiment

168   were heteroscedastic and so were $\log_{10}$ transformed to meet the assumption of equal variances).

169   To assess how much new live tissue was produced per coral, we also calculated net tissue

170   production over the course of the study ($TLD_{final}/TLD_{initial}$). To measure TLD divers took photographs

171   of each coral from different angles to capture images of each branch, with a ruler in the frame to

172   provide a scale. We later used image analysis software (ImageJ) to measure each branch (Abramoff et

173   al. 2004). To check of the accuracy of the photographic method, divers also measured a subset of the

174   corals (n = 102) in the field using a flexible tape measure (Figure S6). There was a close relationship

175   between the direct field (x) and photographic (y) TLD measurements (linear regression: (n = 102,

176   range of TLD = 2-173 cm, y = 5.51 + 0.78x, r^2 = 0.91), suggesting that measurement error did not

177   obscure differences between treatments (Figure 2) (Kiel et al. 2012).

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

179   To evaluate the time and cost-efficiency of the three restoration methods, the time needed to establish

180   each coral on the reef was quantified (hrs per coral; Table S1). We logged each step of the restoration

181   process at the field site (Table S1), but excluded accessory tasks such as washing SCUBA gear and

182   filling tanks. Time to complete tasks common to all methods, such as searching donor sites for

183   fragments, was divided according to the number of corals involved per treatment.

184   We also calculated the local purchase price of materials needed to establish each coral at the

185   restoration site in US$ per fragment, which included materials for attaching corals to the reef and

186   materials for the nursery frames (Table S2). We excluded some costs that were common to all

187   methods (e.g., SCUBA and snorkel equipment for participants, and bins to hold fragments while

188   being transported in the boat), and others that are context- and location-specific (e.g., air travel to the

189   project site, food, and accommodation costs) (Edwards et al. 2010). We also excluded the time and

190   cost invested in the scientific monitoring such as attaching tags, measuring, and photographing corals

191   because this is not essential for practical restoration projects.

192   We then calculated coral survival and tissue production as a function of the time invested and

193   money spent on materials. To measure return on time invested, we calculated the number of surviving

194   corals at the end of the study that were produced per hr of initial set-up time (survivors after 64 weeks

195   per hr). We also calculated the net production of coral ($TLD_{final}/TLD_{initial}$) per hr of initial set-up time.

196   To measure return based on financial cost, we calculated the number of surviving corals at the end of

197   the study that were produced per dollar of materials (survivors after 64 weeks per US$) and net coral

198   production ($TLD_{final}/TLD_{initial}$) per dollar of materials.

199   **Results**

200   *Survival*

201   At both sites, survival of loose fragments was significantly lower than that of nursery and directly

202   attached fragments by the end of the study (Figure 1 and Figure S7). Survival of corals from the latter

203   two treatments was site-dependent (Figure S7). In Harris Ghut, nursery fragments survived

204   significantly better than directly attached fragments while suspended on the nursery frames, but this

205 initial advantage was subsequently overturned and, at the end of the experiment, survival did not

206 differ between the two treatments (Figure S7). In Muskmelon Bay, however, the survival of nursery

207 outplants was significantly lower than that of directly attached fragments throughout (Figure S7).

208 Pooling sites to give a project-wide overview revealed no overall difference in the survival of direct-

209 attached fragments and nursery-outplants (Figure 1).

210 *Growth of Surviving Fragments*

211 At the start of the experiment, fragments did not differ in size among treatments or sites (ANOVA: p

212 > 0.05 for main effects and interaction term; Figure 1 and Figure S8). At the end of the experiment,

213 however, direct outplants at Muskmelon Bay had grown significantly larger than all other groups of

214 fragments (ANOVA: treatment × site interaction; $F_{2,300} = 4.18$, $p = 0.016$; Fig. S9). Although the

215 differences between restoration treatments were site-specific, pooling sites to give a study-wide

216 overview revealed that direct-attached fragments generally reached larger sizes than nursery-outplants

217 and direct-loose fragments (Figure 2).

218 *Return on Investment*

219 Even though directly transplanted loose fragments took little time to place on the bottom, the fact that

220 they survived so poorly meant that there were few survivors and very little return on investment

221 (Figures 3 and 4). For the remaining two treatments, survival was similar but nursery-outplants

222 received a greater investment of time and money per coral than direct-attached fragments.

223 Consequently, direct transplanting produced roughly twice as many surviving corals per hr invested,

224 and three times as many survivors per dollar, as the nursery treatment (Figure 3). Because direct-

225 transplants grew slightly faster than nursery-outplants, the differential in return on investment was

226 magnified further when expressed as net tissue production (Figure 4).

Discussion

227

228   The poor survival of loose transplants is consistent with most previous studies of loose fragments

229   (e.g., Bowden-Kerby 1997, Lindahl 1998, Smith and Hughes 1999, Bowden-Kerby 2001, Forrester

230   2011), suggesting that this method would only become efficient if fragments were extremely plentiful

231   and securing fragments to the reef was very expensive and time-consuming. Because hurricane

232   damage to branching corals can create enormous numbers of fragments, most of which die in the

233   subsequent months (e.g., Knowlton et al. 1981), the immediate aftermath of a major storm might

234   create a situation favoring this method. Other agents of extensive local damage, such as a major boat

235   grounding, might also create conditions for this method to be cost- and time-efficient.

236   Because nursery outplants and direct-attached transplants had similar survival, our results did

237   not support the hypothesis that time in a nursery improves the subsequent survival of transplanted

238   corals (Epstein et al. 2003). Broadly similar findings were reported in the only other direct

239   comparison of these methods we know of (dela Cruz et al. 2015). While in nurseries, fragments of

240   two non-branching Pacific corals survived better than equivalent direct transplants, but this advantage

241   dissipated when corals from the nursery were then placed on the reef alongside direct outplants (dela

242   Cruz et al. 2015).

243   Although the overall survival of nursery outplants and direct-attached transplants was similar

244   in our study, we did observe differences between the two treatments in apparent causes of death. A

245   macroalgal bloom (*Dictyota* spp.) coincident with the start of the study appeared to smother many

246   direct transplants but had no effect on fragments while they were in the nursery, which supports the

247   hypothesis that being on the reef places direct-transplants at risk from negative species interactions

248   (Forrester et al. 2012, Johnston and Miller 2014, Miller et al. 2014, Casey et al. 2015). Both groups of

249   corals were vulnerable to human impacts, but from different activities. In Muskmelon Bay, some

250   direct-transplants were apparently killed by boat anchoring, while some nursery corals died as a result

251   of physical damage to the nursery frames (we believe the frames were damaged inadvertently by

252   fishing nets). Future studies are needed to test whether other agents of coral mortality differentially

253   impact nursery outplants and direct transplants. Both groups are vulnerable to storms, predators,

254   climate-induced bleaching events, and disease epidemics (e.g., Garrison and Ward 2008, Shaish et al.

255   2010a, b, Forrester et al. 2014), and more direct comparisons are needed to quantify their relative

256   importance and quantitative effects.

257   We also found that the costs of restoration differed among the three methods tested. A cross-

258   ecosystem comparison revealed that coral reefs are typically the most expensive habitat to restore per

259   unit area (de Groot et al. 2013, Bayraktarov et al. 2016), which raises the concern that high costs will

260   limit all coral restoration projects to rehabilitating tiny areas relative to the vast swaths of degraded

261   reef (Mumby and Steneck 2008). For that reason, all three methods we selected for comparison were

262   relatively simple and inexpensive because we assumed low-cost protocols may be more readily

263   adopted by non-specialists and scaled-up to restore large areas of reef. Although material costs are

264   rarely quantified, other materials that have been used to stabilize transplanted corals and construct

265   nurseries appear to vary widely in cost (Bayraktarov et al. 2016). For example, the cable ties and nails

266   we used to affix corals to the reef are similar to string and wire in having a relatively low cost per-

267   coral, whereas other frequently used alternatives such as epoxy and hydrostatic cement are more

268   expensive. Likewise, the pvc and fishing line we used to construct nursery frames is likely cheaper

269   than some other options, such as epoxy-coated rebar.

270   Perhaps the most important decision we made to reduce costs was to keep corals in the

271   nursery for a short time and perform no maintenance. An abridged nursery phase has been tested

272   occasionally (dela Cruz et al. 2015), but the most studies have kept corals in the nursery far longer,

273   regularly cleaned the nursery apparatus, removed encroaching predators, excised diseased tissue, and

274   even provided supplemental feeding (Rinkevich 2005, Precht 2006, Edwards and Gomez 2007,

275   Edwards 2010, Johnson et al. 2011, Young et al. 2012, e.g., Chavanich et al. 2014, Toh et al. 2014).

276   Additional explicit comparisons between methods are thus needed to test if our preference for

277   simplicity was justified, or whether the greater expense and labor requirements of these more

278   elaborate and extended nursery methods are outweighed by substantial improvements in coral

279   survival and tissue production.

280   Our analysis represents a simple and partial assessment of the costs and benefits of

281   restoration. We compared costs based on the direct investments of time and money necessary to set-

282   up and maintain a project because these costs are important for practitioners and non-profit groups to

283   consider when allocating their limited resources (de Groot et al. 2013). The assessment of project

284   costs could be expanded to include other costs, such as damage to the donor site (though we suggest

285   this cost was negligible in our study) and the opportunity cost from benefits forgone in the absence of

286   restoration (Spurgeon 2001, de Groot et al. 2013). There is also scope for improvement in our

287   analysis of the benefits of restoration. Like most previous analyses, the benefit of our restoration was

288   measured based only on the demography of the transplanted coral species (Rinkevich 2005, Precht

289   2006, Edwards 2010, Johnson et al. 2011, Young et al. 2012, Schopmeyer et al. 2017). While

290   comparing unit benefits per coral after a semi-arbitrary endpoint is a reasonable starting point

291   (Edwards et al. 2010), and can be expanded in innovative ways (Rinkevich 2015), we urgently need

292   longer-term assessments of benefits based on how the entire ecological community responds to the

293   restoration (e.g., Cabaitan et al. 2008, Yap 2009, Merolla et al. 2013, dela Cruz et al. 2014). This

294   would allow use of well-established frameworks for the valuation of ecosystem services (Kumar

295   2010, ten Brink 2011), and so provide a more comprehensive measure of the monetary value of

296   restored reefs (de Groot et al. 2012, de Groot et al. 2013).

297

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477   **Figures**

478   Figure. 1. Survival of coral fragments ($\pm$95% CI) in each of the experimental treatments: direct-

479   attached transplants, nursery outplants, and direct-loose transplants.

480   Figure. 2. Mean TLD ($\pm$95% CI) of surviving coral fragments over time in each of the experimental

481   treatments: directly attached transplants, nursery outplants, and direct-loose transplants.

482   Figure. 3. Return on investment, based on coral survival, for each experimental treatment. Absolute

483   survival at the end of the experiment is shown as a benchmark for comparison (top plot). Return on

484   investment is plotted as the number of survivors per hr invested (middle plot) and the number of

485   survivors per dollar invested (lower plot).

486   Figure. 4. Return on investment, based on the net production of coral tissue ($TLD_{final}/TLD_{initial}$), for

487   each experimental treatment. Raw means for net production at the end of the experiment are shown

488   as a benchmark for comparison (top plot). Return on investment is plotted as net production per hr

489   invested (middle plot) and net production per dollar invested (lower plot).