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

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

46 globally for the past 40 years (De'ath et al. 2012, Jackson et al. 2014). In response to coral declines,  
47 coral restoration has grown rapidly in popularity and is now practiced worldwide by many non-profit  
48 groups and government agencies, but a global analysis suggests that coral reefs are the most  
49 expensive ecosystem to restore per unit-area (de Groot et al. 2013, Bayraktarov et al. 2016).

50 Restoration of sessile foundation species such as trees, seagrasses, mangroves, and corals  
51 often involves transplanting individuals to degraded sites (e.g., Putz et al. 2001, Rinkevich 2005,  
52 Lewis 2009, Paling et al. 2009). Transplanted individuals are usually small and may include seeds or  
53 propagules, juveniles, cuttings, and asexual fragments. We used asexual coral fragments derived from  
54 adults in wild populations, the most widely used approach for coral restoration projects (Rinkevich  
55 2005, Precht 2006, Edwards and Gomez 2007, Edwards 2010, Johnson et al. 2011, Young et al. 2012,  
56 Chavanich et al. 2014). Protocols for transplanting fragments can be classified into those which: 1)  
57 transplant individuals harvested directly from wild populations (hereafter direct transplanting); or 2)  
58 culture wild fragments in a “nursery” for some time before transplanting (hereafter *nursery-*  
59 *outplanting*).

60 We compared the time- and cost-effectiveness of two direct transplanting approaches, referred  
61 to as “direct-loose” and “direct-attached” methods respectively. In the direct-loose approach,  
62 fragments are simply placed on the substratum at the restoration site (e.g., Bowden-Kerby 1997,  
63 Lindahl 1998, Bowden-Kerby 2001, Lindahl 2003). This approach mimics the fate of asexual  
64 fragments generated by storms or broken from parent colonies by human activity (e.g., Fong and  
65 Lirman 1995, Smith and Hughes 1999). Tissue growth occasionally re-attaches these fragments to the  
66 substratum, in which case they may form a new colony (e.g., Tunnicliffe 1981). Although past  
67 research shows the survival of direct-loose transplants can be poor (e.g., Bak and Crieens 1981,  
68 Knowlton et al. 1981, Mercado-Molina et al. 2014), this method has been used in several restoration  
69 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<sup>2</sup> in area and HG was roughly 800 m<sup>2</sup>. 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  $\geq 40$  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 ( $TLD_{\text{final}}/TLD_{\text{initial}}$ ). 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 ( $TLD_{\text{final}}/TLD_{\text{initial}}$ ) 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 ( $TLD_{\text{final}}/TLD_{\text{initial}}$ ) 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  $\times$  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).

227 **Discussion**

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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304

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476

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 ( $TLD_{\text{final}}/TLD_{\text{initial}}$ ), 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).