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## Long-term survival and colony growth of *Acropora palmata* fragments transplanted by volunteers for restoration

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## Long-term survival and colony growth of *Acropora palmata* fragments transplanted by volunteers for restoration

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4 **Long-term survival and colony growth of *Acropora palmata* fragments**  
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6 **transplanted by volunteers for restoration**  
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8  
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42 **Key words:** coral reef, demography, Elkhorn coral, fragmentation, restoration  
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## ABSTRACT

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1. Many branching corals are fragmented by storms, which can serve as a mechanism of asexual reproduction for species that are able to reattach themselves to the substratum and form new colonies. Fragments can also be manually reattached as a means of reef restoration.

2. The growth and survival of 832 fragments of Elkhorn coral, *Acropora palmata*, that were transplanted for a restoration project in the British Virgin Islands was modeled.

3. Mortality was higher in the first year after transplanting than in subsequent years, perhaps reflecting stress from handling or failure of the attachment method.

4. Survival also varied with the year of transplantation (from 2005-2011), and was lowest in years with major storms (2007 and 2010).

5. Fragment survival increased with increasing initial size, with the largest fragments (surface area roughly 1,000cm<sup>2</sup>) faring substantially better than the smallest (roughly 10cm<sup>2</sup>) and average sized fragments (roughly 100cm<sup>2</sup>).

6. Colony size (surface area of live tissue) tended to decrease in size slightly in the first 3 months after being reattached, presumably due to stress from transplanting.

Subsequently, the surface area of surviving colonies tended to progressively increase over time, with fragments typically reaching 3,000 cm<sup>2</sup> after 7 years. Colony growth was, however, extremely variable and largely independent of initial colony size.

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3 7. Despite initial reductions in growth and survival due to transplanting, long-term  
4 survival of transplanted fragments was roughly comparable to that of natural colonies.  
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6 Transplanting fragments is thus a promising tool for grass-roots restoration projects.  
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## 10 11 INTRODUCTION

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14 As corals have progressively declined in abundance worldwide over the past 30 years  
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16 (Gardner *et al.*, 2003; Bellwood *et al.*, 2004), there has been an increasing interest in  
17  
18 developing methods to restore coral populations (Harriott and Fisk, 1988; Edwards  
19  
20 and Clark, 1998; Precht, 2006; Rinkevich, 2005, 2008). One approach to restoration is  
21  
22 seeding broken fragments from coral colonies on damaged reefs, or manually  
23  
24 reattaching fragments to the substratum. Coral colonies fragment naturally through  
25  
26 the actions of storms, bioerosion and predation, but fragmentation also occurs when  
27  
28 boats, divers and snorkelers collide with the reef (Woodley *et al.*, 1981; Rogers *et al.*,  
29  
30 1982; Bruckner and Bruckner, 2001, Hawkins *et al.*, 2005, ). Fragments used for  
31  
32 restoration include those generated naturally by storms, by unintentionally human  
33  
34 impact, and also created deliberately by pruning natural colonies (Rinkevich, 2005;  
35  
36 Precht, 2006).  
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44 The process of fragmentation is important to the natural demography of branching  
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46 scleractinian corals, as well as other branching colonial invertebrates on coral reefs  
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48 (Lasker, 1984; Wallace, 1985; Karlson, 1986; Lewis, 1991,). Under favourable  
49  
50 conditions, coral fragments may naturally reattach to the reef and form new colonies  
51  
52 (Smith and Hughes, 1999). This process of fragmentation and reattachment is  
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56 hypothesized to be an adaptive strategy for branching corals to colonize new habitats,  
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3 spread the risk of mortality, and circumvent mechanical limits on colony size  
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6 (Highsmith, 1982; Wallace, 1985).  
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9 For natural coral populations, population dynamic models based on individual body  
10  
11 size are often more accurate than are models based on age (Hughes, 1984). Because  
12  
13 individual corals are colonies of genetically identical modules, the importance of  
14  
15 colony size derives in part from the fact that colony growth is indeterminate and that  
16  
17 colonies can also shrink through the death of some modules (partial mortality)  
18  
19 (Connell, 1973). Analyses of growth and survival of naturally generated fragments  
20  
21 have focused on the fragments created in enormous numbers after major storms. The  
22  
23 fate of these fragments is independent of the parent colony (Highsmith, 1982) and  
24  
25 their chance of survival is typically very low (Tunncliffe, 1981; Fong and Lirman,  
26  
27 1995; Smith and Hughes, 1999). In some cases, larger fragments had an improved  
28  
29 chance of post-storm survival (Loya, 1976; Highsmith *et al.*, 1980), but others found no  
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31 effects of size (Lirman and Fong, 1997), or observed size-distributions consistent with  
32  
33 better survival of smaller fragments (Rogers *et al.*, 1982).  
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40 A comparable understanding of the demography of transplanted fragments is valuable  
41  
42 to assess the success of restoration projects. Variable effects of fragment size on  
43  
44 survival have been observed for artificially seeded fragments that were loose on the  
45  
46 substratum, with examples reported of size-dependence (Heyward and Collins, 1985;  
47  
48 Smith and Hughes, 1999; Bowden-Kerby, 1997, 2001) and size-independence (Bruno,  
49  
50 1998; Bowden-Kerby, 2001; Lindahl, 2003). The fate of fragments that have been  
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52 manually re-attached to the substratum also appears to be size-dependent in some  
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3 cases (Bowden-Kerby, 2001, Bruckner and Bruckner, 2001, Raymundo and Maypa,  
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5  
6 2004; Garrison and Ward, 2008, Okubo *et al.*, 2005, 2007, 2009) but not others  
7  
8 (Kobayashi, 1984; Yap *et al.*, 1998; Bowden-Kerby, 2001; Lindahl, 2003). The survival  
9  
10 and colony growth of fragments used for restoration can also be reduced by the  
11  
12 handling and disturbance involved in the transplanting process (Yap and Gomez, 1985;  
13  
14 Plucer-Rosario and Randall, 1987; Yap *et al.*, 1992; Forrester *et al.*, 2011) and survival  
15  
16 may also be reduced by the failure of methods used to reattach the fragment to the reef  
17  
18 (Borneman and Lowrie, 2001; Bruckner and Bruckner, 2001).

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23 Few studies have compared the relative effects of natural and transplant-related  
24  
25 influences on the demography of transplanted coral fragments. The objectives of this  
26  
27 study were thus to test the influence on colony growth and survival of: (1) the year  
28  
29 when fragments were transplanted, (2) the time elapsed since transplanting and (3)  
30  
31 the size of fragments. Differences in colony growth and survival among years should  
32  
33 reflect changes in natural conditions (e.g. storms, temperature anomalies) that  
34  
35 influence coral demography. Effects of elapsed time are hypothesized because stress  
36  
37 from handling fragments and failure of the attachment procedure should reduce  
38  
39 survival immediately after transplanting. Because most experimental transplanting  
40  
41 studies are of relatively short duration (one year or less), we tracked fragments over 7  
42  
43 years in order to assess the longer-term fate of transplanted corals (Harriott and Fisk,  
44  
45 1988; Edwards and Clark, 1998; Rinkevich, 2005; Precht, 2006).

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47  
48 The study species was the Elkhorn coral, *Acropora palmata* (Lamarck, 1816). *Acropora*  
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50 *palmata* is a major reef-building coral in the Caribbean, and was formerly the dominant  
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3 coral species in shallow wave-exposed areas (Goreau, 1959). During the 1980s and  
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5 1990s, *A. palmata* declined by 80-98% (Precht *et al.*, 2004), making it a priority  
6  
7 candidate for restoration and prompting its listing on the US Endangered Species Act,  
8  
9 the IUCN red list and CITES Appendix II. *Acropora palmata* has a branching  
10  
11 morphology and reproduces both asexually, by fragmentation, and sexually (Bak and  
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13 Engel, 1979; Dunne and Brown, 1980; Highsmith, 1982; Fong and Lirman, 1995.).  
14  
15 Post-storm survival of unattached fragments generated by hurricanes has been  
16  
17 reported as both size-dependent (Highsmith *et al.*, 1980) and size-independent  
18  
19 (Lirman and Fong, 1997; Lirman, 2000). Broken fragments of *A. palmata* have been  
20  
21 translocated and reattached in several restoration projects (Bruckner and Bruckner,  
22  
23 2001; Garrison and Ward, 2008; Williams and Miller, 2010; Forrester *et al.*, 2011), and  
24  
25 larger fragments are reported to survive better than smaller ones (Bruckner and  
26  
27 Bruckner, 2001, Garrison and Ward, 2008).

## 35 METHODS

### 38 **Study sites and transplanting methods**

39  
40 This study used 832 storm-generated *A. palmata* fragments that were transplanted to a  
41  
42 restoration site (0.4-1.6 m deep) on the leeward southern side of Guana Island, British  
43  
44 Virgin Islands (18°29'N, 64°35'W). The fragments were collected from three source  
45  
46 populations, all within 4 km of the restoration site. Conditions at the study sites are  
47  
48 described in detail elsewhere (Forrester *et al.*, 2012). Groups of fragments were  
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50 transplanted in July-August each year from 2005-2011 (Table 1).  
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3 Each year, student and volunteer divers searched for fragments at the source sites, and  
4 brought all fragments they found to the surface, except fragments that showed visual  
5 symptoms of disease (Williams *et al.*, 2006). Because all undiseased fragments  
6 encountered were collected, the distribution of fragment sizes should be  
7 representative of that present in the area. Once on the boat, fragments were  
8 submerged in bins of fresh seawater. Corals were then taken to the restoration site  
9 and transplanted within 2.5 hrs of collection (for further details see Forrester *et al.*,  
10 2011).

11  
12  
13 At the restoration site, divers attached fragments to the reef using one of three  
14 methods: (1) nylon cable ties (2) marine epoxy, or (3) hydrostatic cement. In a  
15 previous analysis, these three attachment methods were shown to have no effect on  
16 the growth and survival of the transplanted fragments (Forrester *et al.*, 2011). An  
17 independent study of *A. palmata* also found no differences between cable tied and  
18 epoxied fragments (Williams and Miller, 2010). To facilitate recognition and analysis  
19 of fragments over time, the location of fragments was mapped and a numbered tag was  
20 attached to the reef adjacent to each fragment.

### 21 22 23 **Monitoring fragments**

24  
25  
26 Fragments were monitored at intervals after transplanting. Each cohort (fragments  
27 transplanted in the same year) was monitored 3 and 12 months after transplanting,  
28 and then annually thereafter. The size of each coral fragment was estimated within a  
29 few days of transplanting and during all subsequent surveys. Colony size was  
30 measured as the surface area of live tissue (SAL) and estimated using two methods.  
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3 For small colonies with simple shapes, the surface area was traced from digital  
4 photographs of each surface using image analysis software (ImageJ) (Bythell *et al.*,  
5 2001; Abramoff *et al.*, 2004). For large colonies, with more complex 3-dimensional  
6 branching morphology, SAL was estimated from linear dimensions. SAL was estimated  
7 as  $[(L+W+H)/3]^2$ , where L, H and W are colony length, width and height respectively  
8 (Williams *et al.*, 2008).  
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### 17 **Analysis of survival**

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19 Differences in survival among years were tested to assess whether interannual  
20 differences in conditions influenced the success of transplanting. As a simple means of  
21 testing for a difference in survival among cohorts, a  $\chi^2$  test was used to compare the  
22 observed number of fragments that survived their first year against the number  
23 expected under the null hypothesis of equal survival in all years (Sokal and Rohlf,  
24 1995). The range of fragment sizes used was fairly consistent each year, and the mean  
25 initial size of fragments, did not differ among cohorts (ANOVA  $F_{6,825} = 1.72$ ,  $p = 0.12$ ;  
26 Table 1), so this analysis should be unaffected by bias in fragment sizes.  
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41 Additional tests examined the effect of initial fragment size on survival and whether  
42 survival was a function of time elapsed since transplanting. Data from all cohorts was  
43 pooled for this analysis, which is justifiable because the range of fragment sizes used  
44 was fairly consistent across cohorts (discussed above). Pooling cohorts permitted  
45 analysis of a large sample of fragments and allowed tracking of early cohorts for  
46 several years. For this analysis, simple parametric survival models appropriate for  
47 censored (i.e. incomplete) data on survival times were used (Lee, 1992; Kleinbaum,  
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3 2011). Survival times are uncertain in field studies because the exact timing of death is  
4 almost never observed. Regularly monitoring the fragments yielded estimates of  
5 survival time (the time elapsed between transplanting and death) that were either  
6 interval-censored (when a fragment died between two censuses) or right-censored  
7 (the fragments was still alive at the end of the study) (Lee, 1992).  
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15 Estimates of survival time are conservative because any coral that could not be  
16 positively identified was assumed to have died. There were no sexually produced *A.*  
17 *palmata* recruits at the restoration site; therefore transplants could not be confused  
18 with natural colonies. By the end of the study, however, there were 35 fragments at  
19 the site that could not be positively identified because they lacked a tag and/or were  
20 not in the location of an original fragment. Based on their locations and morphology,  
21 these fragments probably originated from *A. palmata* transplanted early in the study  
22 that were damaged by storms or boats, and then subsequently reattached to form a  
23 new colony.  
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38 To isolate the effect of time-elapsd since transplanting, three models for the time-  
39 dependence of survival were compared. The null exponential model assumes the  
40 instantaneous mortality rate is constant. The Weibull model allows the instantaneous  
41 mortality rate to either rise or decline monotonically as a function of time, whereas the  
42 log-logistic model allows the rate to either rise or decline over time, or to rise to a  
43 maximum then subsequently decline (i.e. a "hump" shaped pattern). A parameter was  
44 then added to these models to test for the effect of fragment size on survival.  
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3 The fit of data to each model was assessed by inspecting plots of the quantiles of the  
4 fitted distribution versus observed cumulative deaths, Cox-Snell residual plots  
5 (estimated cumulative mortality), and probability plots (failure times versus the  
6 quantiles of the chosen distribution) (Davison and Tsai, 1992; Waller and Turnbull,  
7 1992; Cohen, 1995). Relative model fit was also compared using Akaike's Information  
8 Criterion, corrected for small samples (AICc), using the convention that models differ  
9 in fit when their AICc values differ by more than 7 (Burnham and Anderson, 2002).

### 20 **Analysis of change in colony size**

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22 To assess the effect of initial fragment size on the net change in colony size due to the  
23 combined effects of loss (partial mortality) and gain (clonal reproduction) of polyps we  
24 modeled the change in SAL as a function of initial SAL using linear regression. We  
25 performed two analyses, in which the response variables were growth over 12 months  
26 and growth over 24 months respectively, because we had large sample sizes for these  
27 time intervals ( $n=653$  and  $238$  respectively).

## 38 **RESULTS**

### 41 **Analysis of survival**

42  
43 There were significant differences in first-year survival among cohorts ( $\chi^2=41.9$ ,  $df=1$ ,  
44  $p<0.0001$ ). The percentage of transplants surviving the first year was lower for the  
45 2007 and 2010 cohorts than for corals transplanted in other years (Table 2).

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47 When we pooled cohorts, both survival models allowing the instantaneous mortality  
48 rate to vary as a function of time since transplanting (log-logistic and Weibull) fit better  
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3 than the simpler model that assumes a constant mortality rate (exponential) (Table 3).  
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5 Of the two models allowing the mortality rate to vary over time, AICc values indicate  
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7 that the log-logistic model fit better than Weibull (Table 3). This ranking of relative  
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9 model fit based on AICc values was also consistent with inspection of diagnostic plots  
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11 for the three models (plots not shown).  
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15 Although the log-logistic allows for complex patterns of survival over time, the  
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17 mortality functions for both the Weibull and log-logistic models indicated a simple  
18  
19 decelerating mortality rate over time. Under both models, the mortality rate was high  
20  
21 in the first 12 months after transplanting and then relatively constant thereafter (plot  
22  
23 for best-fitting log-logistic function shown in Figure 1). For comparison to the data on  
24  
25 percent survival among cohorts, we converted the instantaneous mortality rates to  
26  
27 annual percent survival. This conversion requires the simplifying assumption that  
28  
29 instantaneous mortality is constant over time (and high) for year 1, and then constant  
30  
31 (but lower) thereafter (Figure 1). Under this simplifying assumption, roughly 56% of  
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33 fragments are expected to remain alive a year after transplanting but annual survival  
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35 increases to 68% for all subsequent years.  
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43 *Acropora palmata* fragments found at the source sites varied widely in initial size (2–  
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45 1016cm<sup>2</sup>), but most fragments were small (mean=108cm<sup>2</sup>) and 50 % of the fragments  
46  
47 were between 26 and 136cm<sup>2</sup> (Figure 2). For all three survival models we evaluated,  
48  
49 adding a term for the effect of initial fragment size improved model fit relative to the  
50  
51 comparable model lacking this covariate (Table 3). The parameter for fragment size  
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53 was always positive and significantly different from zero (Table 3), indicating that all  
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3 models predict increased survival of larger fragments. Adding a term for fragment size  
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5 to the survival models did not alter the relative fit of the three models, and both  
6  
7 parameters of the Weibull and log-logistic models were still statistically significant  
8  
9 (Table 3). This indicates separate effects both of time since transplanting and fragment  
10  
11 size on survival, i.e. poor initial survival was not simply a by-product of that fact that  
12  
13 fragments tended to be smaller when transplanted than afterwards.  
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18 To illustrate the effect of fragment size on survival, we used the best-fitting model (log-  
19  
20 logistic) to predict survival over time for three representative sizes of coral: 10cm<sup>2</sup>,  
21  
22 100cm<sup>2</sup>, and 1000cm<sup>2</sup> (sizes close to the smallest, average and largest fragments found  
23  
24 at our study site) (Figure 3). This plot shows a modest increase in expected survival as  
25  
26 coral size increases from 10-100cm<sup>2</sup>, but a dramatic improvement for 1000cm<sup>2</sup> corals.  
27  
28 For example, 10% of the smallest corals are expected to remain alive after 7 years. For  
29  
30 average sized corals, this figure increases to 19%, but 67% of the largest corals remain  
31  
32 alive after 7 years.  
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### 37 38 **Effects of initial colony size on colony growth**

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41 Considering only surviving colonies, the average fragment shrank slightly in size in the  
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43 first 3 months after being transplanted (Figure 4). Subsequently, surviving fragments  
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45 tended to progressively increase in size, albeit with substantial variation around the  
46  
47 trend (Figure 4).  
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50  
51 Linear regressions for survivors only, showed that the relationship between initial  
52  
53 colony size (SAL in cm<sup>2</sup>) and change in colony size was statistically significant for  
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55 change over 12 months ( $r^2=0.06$ ,  $F_{1,385}=25.6$ ,  $p<0.0002$ ), but not for change over 24  
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3 months ( $r^2=0.02$ ,  $F_{1,143}=2.79$ ,  $p=0.196$ ). Although the relationship was statistically  
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5 significant after 12 months, initial colony size (SAL in  $\text{cm}^2$ ) explained only a trivial  
6  
7 percentage of variation in colony growth in the first 12 and 24 months after  
8  
9 transplanting (6% and 2% respectively; Figure 5).  
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11

## 12 13 14 DISCUSSION

### 15 16 17 **Effects on survival of time elapsed since transplanting and year transplanted**

18  
19 For any fragment loose on the reef, survival depends on remaining at a favorable  
20  
21 location long enough for the colony to reattach itself to the reef (Tunncliffe, 1981;  
22  
23 Fong and Lirman, 1995; Smith and Hughes, 1999). For this reason, fragments  
24  
25 reattached manually for restoration have an initial advantage over loose fragments  
26  
27 (Lindahl, 2003; Forrester *et al.*, 2011). For example, at the sites from which we  
28  
29 collected *A. palmata*, only 2% (2 out of 102) of fragments left loose as controls  
30  
31 remained alive after 12 months, so their survival was far worse than transplanted  
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33 fragments (Forrester, unpublished data).  
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40 Survival in the first 12 months after transplanting varied considerably among the  
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42 seven years we transplanted corals (2005-2011). We attribute these interannual  
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44 differences partly to the effects of storms, whose ability to inflict severe episodic  
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46 mortality on *A. palmata* is well documented (Highsmith *et al.*, 1980; Woodley *et al.*,  
47  
48 1981; Rogers *et al.*, 1982). In the two years when survival to 12 months was lowest  
49  
50 (2007 and 2010), storms caused visible damage to the benthos and reef structure at  
51  
52 the site (a winter storm on 19-20 March 2008, and hurricane Earl on 30 August 2010  
53  
54 respectively). Interestingly, survival was highest in 2005 even though a warming event  
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3 caused mass bleaching throughout the Caribbean in autumn of that year. In addition  
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5 differing among years, pooling data across cohorts showed that survival was  
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7 consistently lower in the 12 months after transplanting than thereafter. Low initial  
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9 survival may be attributed partly to stress induced by the transplanting process (Yap  
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11 and Gomez, 1985; Plucer-Rosario and Randall, 1987; Yap *et al.*, 1992; Forrester *et al.*,  
12  
13 2011). Transplanting stress is further indicated by the fact that surviving fragments  
14  
15 tended to decrease in size in the first three months after transplanting, but  
16  
17 progressively increased in size thereafter. Another probable cause of low initial  
18  
19 survival is failure of the ties/epoxy/cement used to reattach the fragment (Borneman  
20  
21 and Lowrie, 2001; Bruckner and Bruckner, 2001). Deaths from attachment failure  
22  
23 should decline rapidly with elapsed time as fragments grow and form their own  
24  
25 connection with the substratum (Guest *et al.*, 2011) and we noted during monitoring  
26  
27 visits that, after 12 months, the tissues of virtually all surviving *A. palmata* fragments  
28  
29 had grown to contact the reef.  
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### 36 37 **Effects of initial colony size on growth and survival**

38  
39 We found that fragment survival improved with increasing colony size and, across the  
40  
41 size range of fragments at our sites, the very largest fragments survived far better than  
42  
43 did small and average-sized fragments. Our results are consistent with the analysis of  
44  
45 the survival of *A. palmata* fragments reattached to the reef with wire after a ship  
46  
47 grounding in Puerto Rico (Bruckner and Bruckner, 2001). Survivors after two years  
48  
49 (mean length=70cm) were significantly larger than fatalities (mean length=52cm),  
50  
51 indicating better survival of larger fragments. These ship grounding-generated  
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3 fragments (15-304cm long) were generally larger than the (presumably) storm-  
4  
5 generated fragments we transplanted (we expressed colony size as surface area but,  
6  
7 for comparison, our fragments ranged from 4-105cm long). Okubo and colleagues also  
8  
9 reported size-dependent survival of two Pacific species of *Acropora*. They pruned  
10  
11 small fragments from natural colonies of *A. formosa* (5, 10 and 20cm in length) and *A.*  
12  
13 *nasuta* (5 and 10cm in length) and cable-tied them to nails that had been hammered  
14  
15 part-way into the reef. Larger fragments of both species survived better than smaller  
16  
17 ones after 1 year and 3 years respectively (Okubo *et al.*, 2007, 2009). *Acropora*  
18  
19 fragments affixed to the substratum for restoration thus appear to consistently display  
20  
21 size-dependent survival.  
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27  
28 Survival is also commonly a positive function of size for natural coral colonies (Connell,  
29  
30 1973; Hughes and Jackson, 1985; Vermeij and Sandin, 2008). The survival of  
31  
32 transplanted fragments is likely to differ from that of natural colonies for at least three  
33  
34 reasons: (1) transplanting stress, (2) failure of the manual reattachment process, and  
35  
36 (3) microhabitat differences - the specific locations chosen by restoration practitioners  
37  
38 to attach fragments are likely to be different from locations selected by sexual coral  
39  
40 recruits (Hughes, 1984). Nonetheless, two mechanisms for increased survival with  
41  
42 larger size should apply equally to natural colonies and transplants: (1) a reduced  
43  
44 probability that predators, disease or abrasion can kill all polyps in a colony, and (2) an  
45  
46 improved ability to mobilize resources from unaffected polyps (Pearse and Muscatine,  
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48 1971; Hughes, 1984).  
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3 To the best of our knowledge, the only direct comparison between natural colonies and  
4 manually reattached fragments was made by Garrison and Ward (2008). They found  
5 no difference in survival of natural colonies and manually reattached fragments of  
6 *Acropora cervicornis* and *Porites porites*, though their samples were small enough that  
7 subtle differences in survival might not be detectable (n=15 transplants and n=15  
8 natural colonies per species). They were able to compare a larger sample of *A. palmata*  
9 (n=30 transplants and n=45 natural colonies) and found that natural colonies survived  
10 better than transplanted ones. Their natural colonies were, however, also larger on  
11 average than transplanted colonies so better survival may be a function of larger size.  
12 Further direct comparisons between natural colonies and manually reattached  
13 fragments would thus be valuable to test whether size-based demographic models  
14 developed for natural colonies (Hughes, 1984, Hughes and Jackson, 1985) might be  
15 modified to predict the fate of transplanted fragments.  
16  
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18 Although survival was size-dependent, we found the change in size of surviving *A.*  
19 *palmata* colonies to be independent of their initial size. In contrast, experimentally  
20 created fragments of *Acropora nasuta*, *Porites rus* and *P. cylindrica*, all displayed a  
21 positive relationship between size and colony growth after attachment to the reef (Yap  
22 *et al.*, 1998; Okubo *et al.*, 2009). For *A. nasuta*, this represented a trade-off between  
23 growth and reproduction, smaller fragments grew faster than larger ones at the  
24 expense of oocyte production (Okubo *et al.*, 2009). *A. palmata* reproduces sexually  
25 once per year, and we were not able to monitor spawning at our sites. Nonetheless,  
26 size-independence of colony growth in *A. palmata* presumably reflects the fact that,  
27 like all modular colonial organisms, coral colonies can shrink as well as grow over time  
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3 and at our sites, surviving colonies were just as likely to lose as they were to gain  
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5 polyps in any given time interval (Garrison and Ward, 2008). This matches the pattern  
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7 of growth reported for natural colonies *Agaricia agaricites*, whose colonies frequently  
8  
9 decreased as well as increased in size between monitoring events (Hughes, 1984).  
10  
11

### 12 13 **Implications for restoration**

14  
15  
16 For coral fragments transplanted and reattached to restore reefs, one useful measure  
17  
18 of their success is whether they grow and survive as well as natural colonies. Although  
19  
20 there were obvious impacts of the transplanting process, in terms of reduced colony  
21  
22 growth in the first 3 months and reduced survival in the first 12 months after  
23  
24 transplanting, it is encouraging that transplanting effects were of no greater magnitude  
25  
26 than year-to-year differences in survival from natural causes (e.g. storms). Beyond the  
27  
28 first year, fragment survival was reasonably high and, although differences in methods  
29  
30 preclude an exact comparison, long-term survival of the larger fragments we  
31  
32 transplanted appears roughly equivalent to the survival of large natural *A. palmata*  
33  
34 colonies in Florida (Williams and Miller, 2012). For practitioners, our results thus  
35  
36 suggest that demographic monitoring of restoration projects should focus on the first  
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38 year after transplanting.  
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45  
46 We used students and volunteers to transplant most fragments, rather than  
47  
48 professional scientists, in order to simulate a level of care and expertise that might be  
49  
50 expected in volunteer-based restoration projects. This restoration method depends on  
51  
52 locating a donor population of *A. palmata* with fragments suitable for transplanting.  
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56 Every year in our study area, we were able to locate enough fragments in a few days of  
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3 searching. Before starting the transplanting process, students and volunteers received  
4 training for one or two days on how to attach fragments to the reef, and on selecting  
5 suitable locations for attachment. The overall process of finding and transplanting  
6 fragments thus took less than a week, and so is feasible for projects using volunteers  
7 that have limited time to invest in conservation work. Simple, direct transplanting of *A.*  
8 *palmata* thus shows promise as a method usable by practitioners to restore local  
9 populations of endangered *A. palmata* on Caribbean reefs.  
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TABLE 1. Initial sizes (surface area of live tissue in cm<sup>2</sup>) of coral fragments, grouped by year transplanted. Displayed are number of corals transplanted (*n*), mean ( $\pm$ SE), minimum and maximum sizes.

Year	<i>n</i>	Mean	( $\pm$ SE)	Min.	Max.
transplanted					
2005	35	198	(37)	7	961
2006	19	78	(17)	2	300
2007	88	117	(16)	8	950
2008	254	106	(17)	15	823
2009	44	87	(22)	2	561
2010	135	79	(10)	4	1004
2011	257	113	(10)	12	1015

TABLE 2. Initial survival of corals transplanted in different years. \* indicates years when major storms impacted the site.

Year transplanted	Percent alive after 12 months
2005	85
2006	58
2007	21*
2008	50
2009	68
2010	30*
2011	70

TABLE 3. Estimates of model fit (AICc) and parameter estimates ( $\pm$  95% CI) for survival models fit to the data. We compared three survival models: exponential, Weibull, and log-logistic. Models were first fit without (a) and then with (b) a term for initial coral size as a covariate. The meaning of the parameters  $B1$  and  $B2$  is model-specific, as follows: for exponential  $B1$ =scale; for Weibull  $B1$ =shape and  $B2$ =scale; for log-logistic  $B1$ =scale and  $B2$ =location.

## (a) Models with no covariates

Survival				
model	AICc	$B1 \pm (95\% \text{ CI})$	$B2 \pm (95\% \text{ CI})$	
Exponential	1,848	$19.61 \pm (17.93-21.41)$		
Weibull	1,784	$0.74 \pm (0.70-0.77)$	$21.0 \pm (18.9-23.6)$	
Log-logistic	1,764	$1.01 \pm (0.95-1.08)$	$2.52 \pm (2.36-2.58)$	

## (b) Models with term for initial coral size

Survival				
model	AICc	$B1 \pm (95\% \text{ CI})$	$B2 \pm (95\% \text{ CI})$	Initial Size $\pm (95\% \text{ CI})$
Exponential	1,792	$15.51 \pm (12.77-18.39)$		$0.002 \pm (0.001-0.0035)$
Weibull	1,740	$1.35 \pm (1.28-1.39)$	$2.70 \pm (2.65-2.77)$	$0.003 \pm (0.002-0.004)$
Log-logistic	1,718	$0.99 \pm (0.98-1.02)$	$2.10 \pm (2.04-2.17)$	$0.003 \pm (0.002-0.004)$

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9 Fig. 1. Instantaneous mortality rate after transplanting for the best fitting log-logistic  
10 survival model. Dotted lines are 95% confidence intervals.  
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17 Fig. 2. Size distribution of coral fragments encountered at source sites and used for  
18 transplanting.  
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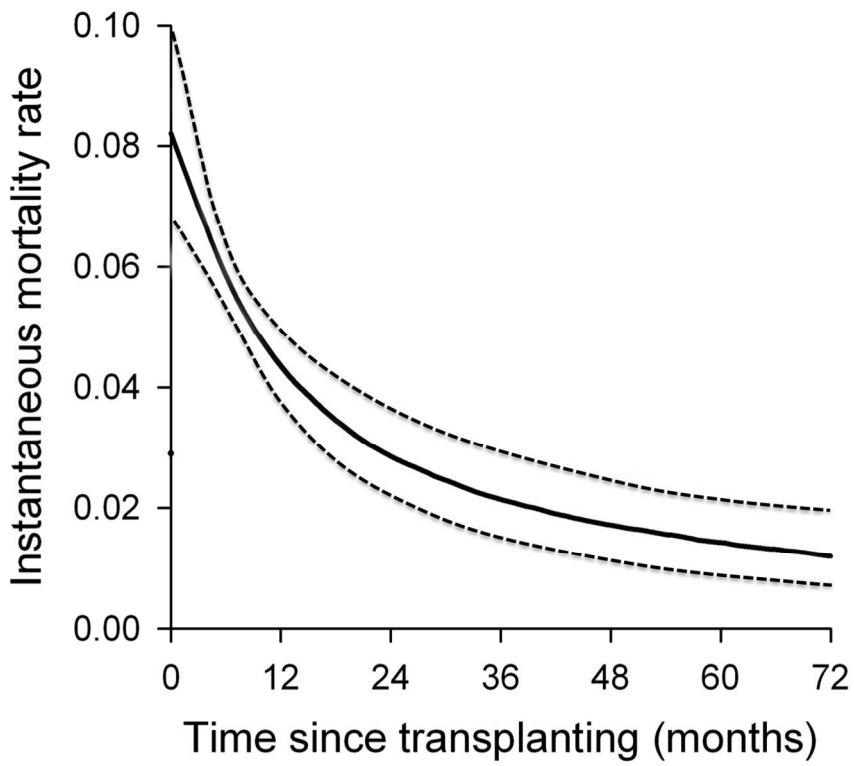
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25 Fig. 3. Survival as a function of time since transplanting for three representative sizes  
26 of transplanted corals. Sizes were selected to represent corals close to the smallest,  
27 average, and largest coral fragments found naturally at the site: 10, 100, and 1000cm<sup>2</sup>  
28 respectively. Solid lines are best-fit estimates from the log-logistic survival function  
29 and dotted lines are 95% confidence intervals.  
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41 Fig. 4. Mean colony size (mean SAL in cm<sup>2</sup> ±95%CI) of corals as a function of time since  
42 transplanting. Only corals that remained alive at each time were plotted.  
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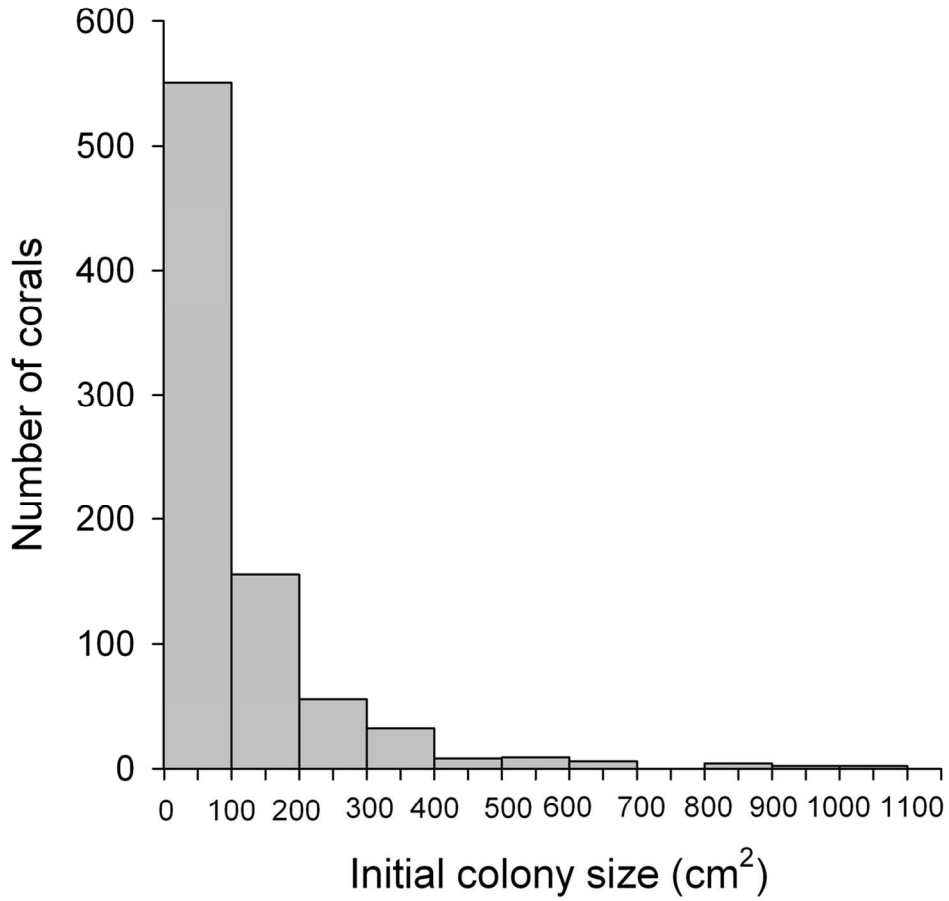
49 Fig. 5. Change in colony size (SAL in cm<sup>2</sup>) as a function of initial size. Data are plotted  
50 for growth over the first 12 months (a) and 24 months (b) since transplanting. Corals  
51 that survived the interval and those that did not are plotted separately, and a linear  
52 regression (solid line) with 95%CI (dotted lines) is fit through data for survivors only.  
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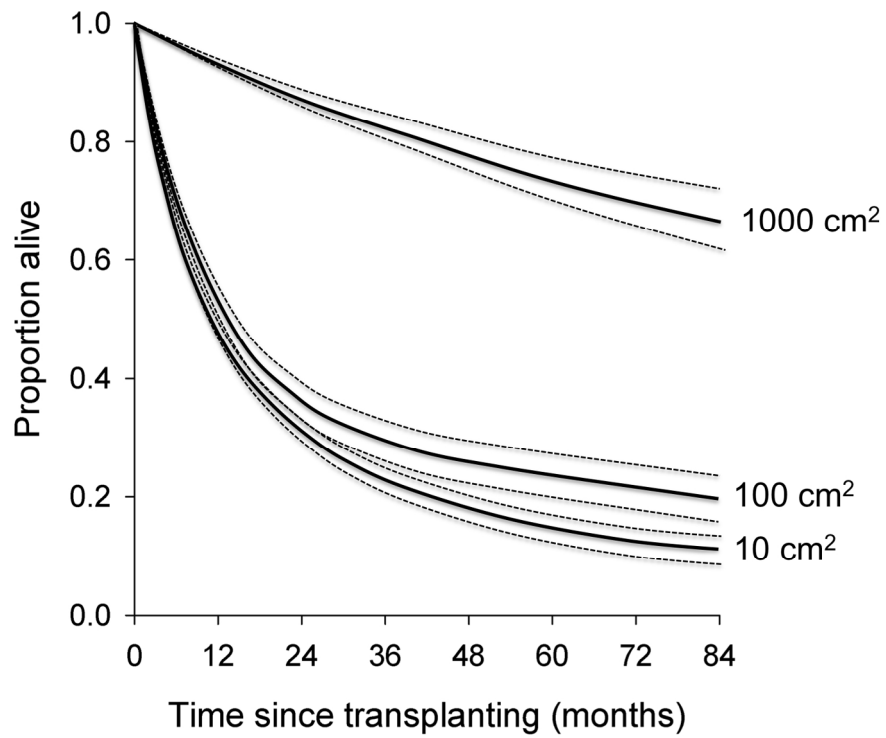


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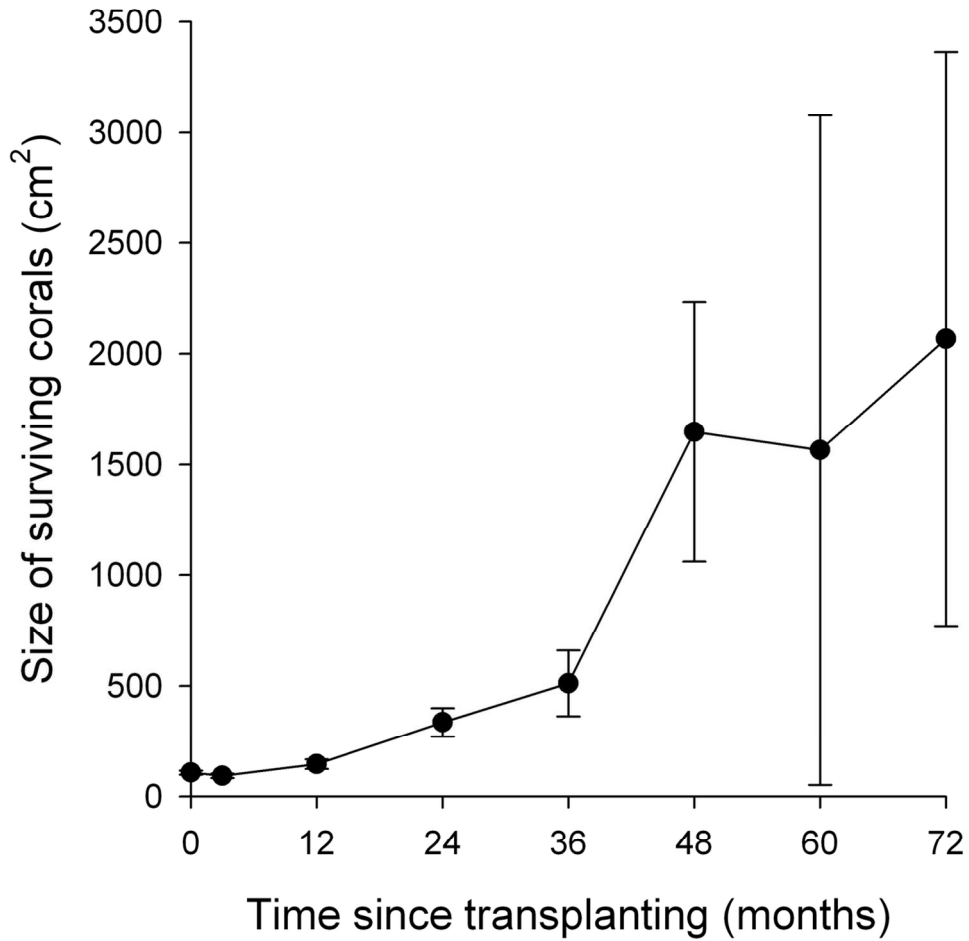


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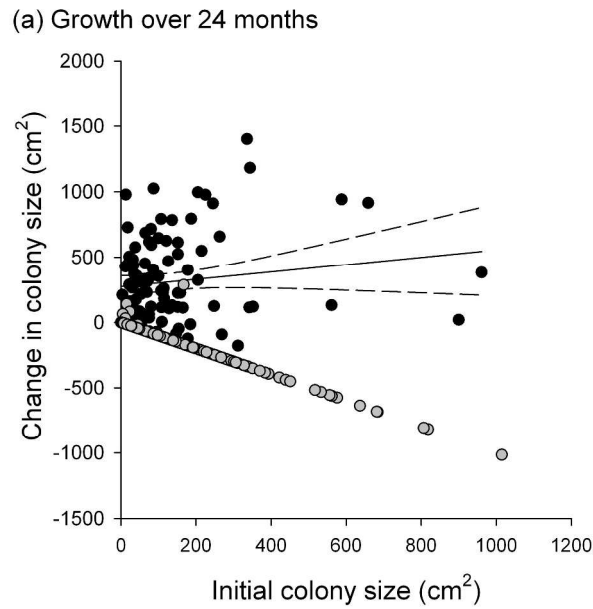
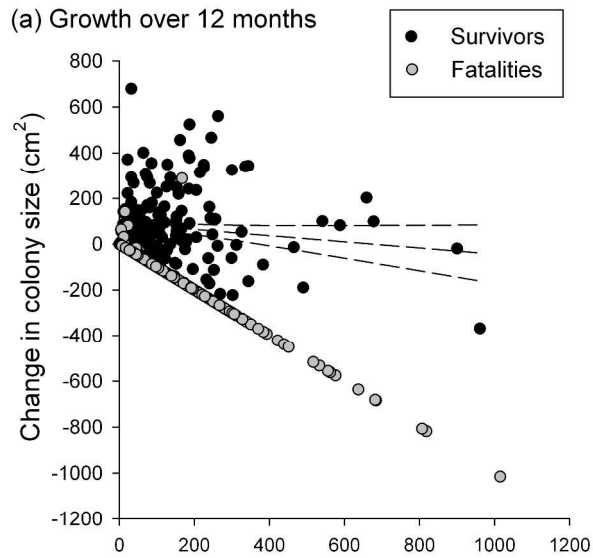


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