

1 **Density-associated recruitment mediates coral**  
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4 **population dynamics on a coral reef**

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15 **Abstract**

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3 16 Theory suggests that density-associated processes can modulate community resilience following declines  
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5 17 in population size, and here we show their presence in two scleractinian populations on the outer reef of  
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7 18 Moorea, French Polynesia, which are rapidly increasing in population size following the effects of two  
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9 19 catastrophic disturbances. Between 2006 and 2010, 93% of the coral cover was killed by crown of thorns  
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11 20 sea stars, in 2010 the dead coral skeletons were removed by a cyclone, and in 2011 and 2012 high coral  
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13 21 recruitment initiated community recovery. Coral recruitment was associated with coral cover, with the  
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15 22 relationship differing between two coral genera that are almost exclusively broadcast spawners in  
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17 23 Moorea. Acroporids recruited at low densities, and were positively association with cover of *Acropora*,  
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19 24 whereas pocilloporids recruited at high densities, and were negative association with cover of  
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21 25 *Pocillopora*. Our results show there are conditions favoring recovery of contemporary corals reefs  
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23 26 following large disturbances, specifically to promote rapid increases in population size through  
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25 27 recruitment that is associated with coral abundance. Because these relationships differ in direction  
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27 28 between two common and important genera of corals, they can mediate temporal shifts in taxonomic  
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29 29 composition of coral communities.  
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35 31 *Key words: Density dependence; recovery; Scleractinia; synecology; French Polynesia.*  
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33 **Introduction**

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35 Density dependence affects a wide variety of mechanisms structuring populations and  
36 communities, with positive and negative dependence accelerating or impeding (respectively)  
37 biological processes as population density increases (Courchamp et al. 1999). Recruitment is  
38 often affected by density dependence, with positive effects arising from the enhancement of  
39 population-level fecundity and recruitment by high densities of adults, and negative effects  
40 arising from conspecific interactions such as competition (Hixon et al. 2002). While most  
41 examples of density dependence are statistical reflections of the association between  
42 population density and demographic rates (Warner and Hughes 1988), their ecological value  
43 lies in the insights they provide into the causal relationships between these properties,  
44 particularly in the extent to which they affect population regulation (Hixon et al. 2002).

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46 Evaluating the impacts of disturbances on community structure is a central goal of ecology, and  
47 disturbance effects therefore are deeply engrained in ecological theory (Pickett et al. 1989;  
48 Nystrom et al. 2000). In recent years however, especially on coral reefs, investigations have  
49 focused more keenly on disturbances linked to climate change, and the possible dramatic  
50 outcomes of such effects (Bellwood et al. 2004). In ecological theory, the increased prevalence  
51 of large changes in the community structure of coral reefs implies that regulatory mechanisms  
52 preventing such change now are less well developed than once was the case, and moreover,  
53 they suggest that once changes in community structure are initiated, they tend to be extreme.  
54 In other words, the stability and resilience of coral communities may have declined in recent  
55 decades (Nystrom et al. 2000).

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58 Declines in coral cover are common throughout the tropics (Bruno and Selig 2007, Schutte et al.  
1  
2 59 2010; Jackson et al. 2014), but only a few reefs in recent times have been found to recover  
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4 60 following major disturbances (e.g., Adjeroud et al. 2009; Graham et al. 2011; Gilmour et al.  
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6 61 2013). Poor recruitment of scleractinian corals has been proposed as a leading reason for  
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8 62 incomplete population recovery following major disturbances (Arnold and Steneck 2011;  
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10 63 Gilmour et al. 2013), but this outcome could be a result of multiple processes acting on one or  
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12 64 more coral life stages. Disturbances and the recovery of coral communities are normal aspects  
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14 65 of the biology of coral reefs (Pearson 1981; Nystrom et al. 2000), and when such events are  
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16 66 coincident with long-term ecological studies, there is the opportunity to use them as “natural  
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18 67 experiments” to study the processes associated with the development of coral communities.  
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20 68 The outer reefs of Moorea, French Polynesia (Fig. 1a), provide such an opportunity, because  
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22 69 their ecological history is particularly well known (e.g., Galzin and Pointier 1985; Berumen and  
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24 70 Pratchett 2006; Adjeroud et al. 2009; Adam et al. 2011). Most recently these reefs suffered  
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26 71 catastrophic damage from crown of thorns sea stars over 2006–2009 (Kayal et al. 2012), and  
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28 72 then were impacted by a cyclone in 2010 (Adam et al. 2011). Based on sampling conducted in  
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30 73 2015, it is clear that these communities are recovering exceptionally quickly (described below).  
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75 Here we describe the population dynamics underlying the rapid recovery of the coral  
76 community on the outer reef of Moorea, and show that the recovery is driven by recruitment of  
77 *Pocillopora* and *Acropora* that are some of the most abundant corals in the Indo-Pacific (Veron  
78 2000), including Moorea (Adjeroud et al. 2009). On the outer reefs of Moorea, broadcast  
79 spawning characterizes all the *Acropora* and most of the *Pocillopora* (Sier and Olive 1994;  
80 Harrison and Wallace 1990; Magalon et al. 2005; Carroll and Harrison 2006), and while the  
81 brooding coral *P. damicornis* (Richmond 1987; Fan et al. 2002) is found in Moorea, it is rarely  
82 encountered on the outer reefs. Our analyses reveal strong associations between densities of  
83 early life stages (recruits and juvenile colonies) and overall coral cover, suggesting that density  
84 dependence could serve as a mechanism mediating recruitment of these genera and ultimately,

85 population recovery. We discuss the potential roles of such effects in determining the  
1 86 community structure of scleractinians as the reefs of Moorea recover from two major  
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3 87 disturbances.  
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## 10 89 **Materials and Methods**

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### 15 91 *Overview*

17 92 Given the local- and region- scale importance of *Pocillopora* and *Acropora* in the tropical Pacific,  
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19 93 we focused on their populations in Moorea using data collected at the Moorea Coral Reef, Long-  
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21 94 Term Ecological Research site (<http://mcr.lternet.edu>). These data describe the percentage  
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23 95 cover of corals (2005 to 2014), the density of juvenile corals (colonies  $\leq$  40-mm diameter from  
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25 96 2005 to 2014), and the abundance of coral recruits on settlement tiles (2008 to 2014), and  
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27 97 together we use them to describe community dynamics on the outer reef before and after two  
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29 98 major disturbances that unfolded over several years. These data were used to explore the  
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31 99 statistical signal of the relationships between population size and a demographic property  
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33 100 (here, recruitment), and using these results, we evaluate the possibility that causal processes  
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35 101 arising from organism interactions regulate local population size of *Pocillopora* and *Acropora*.  
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43 103 The most recent disturbances affecting the outer reefs (10-12 m depth) of Moorea prior to  
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45 104 2006, were bleaching and a cyclone in 1991 that reduced coral cover to 22.5%, and bleaching in  
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47 105 1994, 2002, and 2003 that ultimately had little impact on coral cover (Adjeroud et al. 2009). By  
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49 106 2005 however, at 10-m depth on the outer reef, coral covered  $38 \pm 2\%$  (mean  $\pm$  SE,  $n = 6$  sites)  
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51 107 of the benthos (Adam et al. 2011), with *Pocillopora* and *Acropora* the dominant coral genera  
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53 108 (37% of the coral; <http://mcr.lternet.edu>). By 2006, high population densities of the  
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55 109 corallivorous seastar *Acanthaster planci* were recorded on the reefs of Moorea (Kayal et al.  
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57 110 2012), and by 2009 they had reduced coral cover on the outer reef to  $10 \pm 4\%$  (mean  $\pm$  SE,  $n = 6$   
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111 sites) (Adam et al. 2011; Kayal et al. 2012). Waves from Cyclone Oli in February 2010 removed  
112 virtually all of the dead coral skeletons left by *A. planci* on the north shore, and surveys of these  
113 reefs in April 2010 revealed  $\leq 3.4\%$  mean coral cover at 10-m and 17-m depths ( $n = 40$  quadrats  
114 at two sites for both depths; Fig. 1c).

### 116 *Coral community structure*

117 Starting in April 2005, coral community structure was quantified using photoquadrats ( $0.5 \times$   
118  $0.5$  m) recorded in annual increments at 6 sites at 10-m depth on the outer reefs of Moorea  
119 (Fig. 1 b, c). A single 40-m transect is marked permanently at each site, and 40  
120 photoquadrats are recorded annually at fixed positions that initially were randomly selected.  
121 Images were analyzed using CPCe software (Kohler and Gill 2006) with 200 dots (10 pixel  
122 diameter) randomly placed on each image, and under which scleractinians (and *Millepora*)  
123 were scored to genus and quantified as percentage cover. Island-wide trends in coral  
124 community structure were described using sites as replicates ( $n = 6$ , with 2 sites on each of  
125 the three shores) and three categories of benthic organism of direct relevance to the present  
126 analysis: overall cover of scleractinians, cover of *Pocillopora* and cover of *Acropora*.

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128 The population dynamics of *Pocillopora* and *Acropora* were described in detail using two  
129 sites (LTER 1 and 2) on the north shore of Moorea (Fig 1a), where coral cover, the density of  
130 juvenile corals, and coral recruitment are measured with at least annual resolution. The sites  
131 on the southeast and southwest shores were not included in this portion of the analysis, as  
132 sampling is more limited in these locations that are less accessible from the marine laboratory  
133 where our research is based. In this portion of the analysis, photoquadrats were treated as  
134 replicates and pooled between LTER1 and LTER2 ( $n \sim 80 \text{ y}^{-1}$ ). To place the changes in  
135 populations of *Pocillopora* and *Acropora* at these two sites in a broader context, specifically

136 the extent to which the coral community have recovered since the *Acanthaster planci*  
137 outbreak and Cyclone Oli, the among-year similarity in the coral communities (scleractinian  
138 and *Millepora*) at LTER1 and LTER2 was described with genus resolution for 10 years using  
139 non-metric multidimensional scaling (MDS).

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#### 141 *Juvenile corals*

142 Starting in April 2005, juvenile corals  $\leq 40$ -mm diameter were quantified in situ to genus, using  
143  $0.5 \times 0.5$  m quadrats placed at the same positions as the photoquadrats. Fragments generated  
144 by breakage were excluded by focusing on juvenile colonies that had a clear basal attachment to  
145 the substratum without fractured edges or dead portions. Likewise, fission products were  
146 avoided by counting small colonies that were composed of new skeleton rather than portions of  
147 an antecedent framework.

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#### 149 *Coral recruits*

150 Coral recruits were assayed using unglazed terracotta tiles ( $15 \times 15 \times 1$  cm) secured  
151 individually at 10-m depth at the two north shore sites (LTER 1 and 2) (similar to Edmunds et  
152 al. 2010). At each site, fifteen tiles were attached independently to the reef with a  $\sim 1$  cm  
153 microhabitat beneath and each tile positioned approximately horizontal. Tiles were first  
154 deployed at 10 m depth on the outer reef in January 2007, and thereafter were exchanged in  
155 August/September and January/February. They were bleached, dried, and scored on all  
156 surfaces (top, bottom, and edges) for coral recruits that were identified to family. Pocilloporids  
157 in Moorea are represented by one genus, while acroporids are represented by *Acropora* spp.,  
158 *Astreopora* spp., and *Montipora* spp. *Astreopora* spp. and *Montipora* spp. have typically occurred  
159 at relatively low cover on the outer reefs (Adjeroud et al. 2009; Edmunds et al. 2010). For  
160 *Acropora* spp. and *Pocillopora* spp. therefore, recruits identified to family are likely to provide  
161 an effective estimate of the additions through sexual reproduction of new individuals to support

162 population growth of these two genera. To estimate annual coral recruitment, mean recruit  
163 densities at each of two samplings per year ( $n = 30$  tiles sampling<sup>-1</sup>, pooled between sites, from  
164 2008 to 2014) were summed (corals tile<sup>-1</sup> y<sup>-1</sup> based on  $\sim 60$  tiles).

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#### 166 *Data analysis*

167 To test for changes over time in cover of corals and density of juvenile corals one-way repeated  
168 measures ANOVA (RM-ANOVA) were used in which Time was the main (repeated) factor with  
169 10 levels (from 2005 to 2014), coral cover (arcsin transformed) and density of juvenile corals  
170 were the dependent variables (in separate univariate tests), and photoquadrats ( $\sim 80$  year<sup>-1</sup>)  
171 were the statistical replicates. RM-ANOVAs were performed using R software (package “ez”,  
172 command “ezANOVA”).

173

174 As settlement tiles were exchanged in August/September and January/February, annual  
175 recruitment was estimated by summing the mean density of recruits across both sampling  
176 periods within each year. Each measure of recruitment therefore was based on the number of  
177 recruits encountered on two batches of  $\sim 30$  tiles y<sup>-1</sup>. This procedure was necessary to evaluate  
178 recruitment that occurred within the minimal sampling interval for coral cover and density of  
179 juvenile corals (i.e., 1 year), but it had the limitation of providing no measure of error and  
180 precluded inferential analyses of annual recruitment. To test for changes in density of recruits  
181 over time, an inferential test was applied to the single sampling period in each year with the  
182 highest recruitment (August/September), when individual settlement tiles could be used as  
183 statistical replicates. Using this subset of recruitment data, one-way ANOVA (R software,  
184 command “aov”) was used to test for differences in recruitment over time (7 years between  
185 2008 and 2014) using the density of acroporid and pocilloporid recruits as dependent variables  
186 in separate univariate analyses. For the analyses of adult coral cover, and density of both  
187 juvenile corals and recruits, when the main effect of Time was statistically significant, post hoc



188 analyses were performed using either pairwise comparisons (for RM-ANOVA) or Tukey HSD  
189 test (for the one-way ANOVA). For all statistical tests, the assumptions of normality and  
190 homoscedasticity were evaluated through graphical analysis of residual. For RM-ANOVA, the  
191 assumption of sphericity was verified by Mauchly test. When the Mauchly test was significant  
192 (i.e., the null hypothesis of sphericity was rejected), a Greenhouse-Geisser correction was  
193 applied to the data.

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195 To place the population dynamics of *Pocillopora* and *Acropora* over 2005–2014 in a broader  
196 context of changes in the overall coral community, the similarity among years based on coral  
197 cover by genus and site (LTER1 and LTER2) was evaluated within a MDS framework using  
198 Primer-E v 6 software (Clarke and Gorley 2006). In this analysis, coral cover was  $\log(x + 1)$   
199 transformed, similarities among years evaluated by the method of Bray-Curtis, and the results  
200 displayed with MDS using multiple restarts of 100 iterations until stress stabilized and  
201 ordinations were repeatable.

202  
203 We tested for density-association phenomena by exploring the relationships among coral cover  
204 and the density of both juvenile and recruiting corals as determined using data collected over  
205 multiple years (i.e., a time-series). The analyses of time-series data are prone to artifacts arising  
206 from autocorrelation, and in tests of temporal trends and associations between two time series,  
207 these effects can elevate the risks of Type I errors and create biases in describing the linear  
208 relationships between variables (Bence 1995). Prior to testing for density association, we  
209 therefore tested for autocorrelation using a Durbin-Watson procedure (implemented in R  
210 software, command “dw.test”). As none of the time series data were significantly autocorrelated  
211 ( $P > 0.05$ ), density association was evaluated using Pearson correlations to test for relationships  
212 between coral cover (a proxy for population size) and the densities of juvenile corals and coral  
213 recruits (annualized). Separate analyses were conducted for *Pocillopora* spp. and *Acropora* spp.,

214 and where significant associations were detected the functional relations were described by  
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2 215 Model II regression (described below).  
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8 217 Association between coral cover and density of early life stage corals (i.e., juveniles and  
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10 218 recruits) was evaluated following a 3-step procedure. First the best model describing the  
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12 219 relationship between the two random variables was chosen according to an Akaike information  
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14 220 criterion (AIC) approach (Akaike 1978). Linear, exponential, and power models were tested for  
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16 221 each set of data, and the model providing the lowest AIC value was chosen to provide the best  
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18 222 description of the relationship between the variables. Second, the statistical association  
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20 223 between the variables was evaluated using Pearson correlations and variables transformed to  
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22 224 correspond to the relationship that best described the data (as selected by lowest AIC values).  
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24 225 Third, where the two variables were significantly associated, the functional relationship  
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26 226 between them was described using Model II regression techniques because of the random  
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28 227 nature of both variables (Sokal and Rohlf 2012). In this procedure, the slope of the relationship  
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30 228 was determined by the method of standard major axis (SMA) (Sokal and Rohlf 2012; R software,  
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32 229 command "lmodel2").  
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41 231 Pearson correlations were calculated using a 1-year lag for recruitment and a 1–2 years lag  
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43 232 (depending on genus) for juveniles relative to the year in which adult cover was measured. For  
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45 233 example, correlations for recruitment paired recruit density in each year with coral cover the  
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47 234 previous year, and correlations for juveniles paired juvenile density in each year either with  
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49 235 coral cover in the previous year (i.e., a 1 y lag for *Pocillopora spp*), or with coral cover two years  
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51 236 before (i.e., a 2 y lag for *Acropora spp*). A lagging approach was used because we reasoned that  
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53 237 an effect of adult population size (i.e., coral cover) on recruits and juveniles would only be  
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55 238 detectable after the passage of sufficient time to allow these small life stages to be enumerated.  
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59 239 The settlement tiles used to assess recruitment were deployed for ~ 6 months at each sampling,  
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240 and the recruits appearing on these times suggested a lag of 6-12 months provided a  
241 conservative estimate of the time necessary to capture the recruitment signal from each  
242 spawning event. For juvenile corals, a 2 y lag was applied to *Pocillopora* spp. and a 1 y lag to  
243 *Acropora* spp., because they grow at different rates. Assuming juvenile *Pocillopora* spp. grow at  
244  $\sim 2 \text{ cm y}^{-1}$  (Bramanti et al. 2015; Pratchett et al. 2015), a 2 y lag therefore provides a  
245 conservative means to test for an association between the density of juveniles and coral cover.  
246 Juvenile *Acropora* spp. grow faster (i.e.,  $\sim 4 \text{ cm y}^{-1}$  [Pratchett et al. 2015]) than juvenile  
247 *Pocillopora* spp., and therefore the relationship between the density of juvenile *Acropora* spp.  
248 and coral cover was tested with a 1 y time lag.

249

## 250 **Results**

### 251 *Community recovery*

252 In 2005, mean coral cover (averaged across 6 sites on 3 shores) at 10 m depth on the outer  
253 reefs of Moorea was 40%, with 20% cover of *Pocillopora* spp. and 10% cover of *Acropora*  
254 spp. (Fig. 3a). In 2011, after major disturbances affecting these reefs (*Acanthaster planci*  
255 outbreak [Kayal et al. 2012] and Cyclone Oli [Adam et al. 2011]), the lowest mean coral  
256 cover detected in this study was recorded (2.7%; Fig 3a). By 2012, mean coral cover had  
257 increased to 4.0%, and the increase intensified in 2014 (when mean coral cover reached  
258 26.3%). The increase in coral cover from 2012 to 2014 was mainly driven by *Pocillopora*  
259 spp., which increased in mean cover from 1.8% (2012) to 17.6% (2014), whereas mean  
260 *Acropora* spp. cover remained  $< 1\%$ .

261

262 In a broader context, the MDS plots displaying coral community structure based on mean  
263 coral cover by genus at LTER1 and LTER2 (both on the north shore) revealed the large  
264 extent to which the community was perturbed from 2005 to 2010, and the high degree to  
265 which it had recover by 2014 (Fig. 2). Relative to the coral community structure in 2005 as

266 evaluated by the Bray Curtis similarity, by 2014 the community was 68% similar to the initial  
267 condition at LTER1, and 70% similar at LTER2.

268

### 269 *Pocillopora* population

270 For *Pocillopora* spp. (Fig. 3b, left panel), cover changed over time (RM-ANOVA,  $F_{9,711} =$   
271 256,  $p < 0.001$ ), with no change between 2005 and 2007 (pairwise comparison: 2005 = 2006,  
272 2006 = 2007, 2005 = 2007, all  $p > 0.050$ ) but a decline between 2007 and 2010 (pairwise  
273 comparison: 2007 > 2008; 2008 > 2009; 2009 > 2010, all  $p < 0.001$ ). *Pocillopora* cover did  
274 not change between 2010 and 2011 ( $p > 0.050$ ), but it increased between 2011 and 2014  
275 (pairwise comparison: 2011 < 2012,  $p < 0.001$ ; 2012 < 2013,  $p < 0.001$ ; 2013 < 2014,  $p <$   
276 0.001). For juvenile *Pocillopora* spp., densities varied over time (RM-ANOVA,  $F_{9,711} = 250$ ,  
277  $p < 0.001$ ), with no change between 2005 and 2010 (pairwise comparison: 2005 = 2006 =  
278 2007 = 2008 = 2009 = 2010, all  $p > 0.05$ ) but an increase following 2010 when the lowest  
279 cover of *Pocillopora* spp. was recorded (pairwise comparison: 2010 < 2011; 2011 < 2012, all  
280  $p < 0.001$ ). In 2013 and 2014, the density of juvenile *Pocillopora* spp. decreased relative to  
281 2012 (pairwise comparison: 2012 > 2013 > 2014,  $p < 0.001$ ). For pocilloporid recruits,  
282 densities recorded in August/September differed among years (ANOVA,  $F_{6,206} = 4.29$ ,  $p <$   
283 0.01), with similar densities in 2008 and 2010, an increase from 2011 to 2012, and a decrease  
284 in 2013 and 2014 (Tukey HSD, 2008 = 2009 = 2010,  $p > 0.050$ ; 2010 < 2011,  $p < 0.001$ ;  
285 2011 < 2012,  $p < 0.001$ ; 2012 > 2013 > 2014,  $p < 0.001$ ).

286

287 For *Pocillopora* spp., the AIC analyses showed that the relationship between adult cover and  
288 density of coral recruits was best described by a power curve, and the relationship between  
289 adult cover and the density of juvenile corals by a negative exponential relationship (Table  
290 1). Pearson correlations revealed a significant negative relationship between coral cover and

291 the density of recruits (for Log-Log transformed data,  $r = -0.83$ ,  $df = 5$ ,  $p < 0.05$ ), and  
292 between coral cover and density of juvenile colonies (for Log-Linear transformed data,  $r = -$   
293  $0.97$ ,  $df = 6$ ,  $p < 0.01$ ). Model II regression provided the best-fit lines describing the  
294 functional relationships between these variables, with the exponent for the power curve (i.e.,  
295 the slope on linearized axes for recruits on cover) having a value of  $-0.45$  (Fig 3b, right  
296 panel), and constant in the exponential relationship (i.e., the slope on linearized axes for  
297 juveniles on cover) having a value of  $-0.93$  (Fig 3b, right panel).

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299 The lowest *Pocillopora* spp. cover in 2010 (0.2%) was followed in 2011 by a high density of  
300 pocilloporid recruits (6.7 corals tile<sup>-1</sup>), and in 2012 the highest density of recruits was  
301 recorded (8.2 corals tile<sup>-1</sup>; Fig. 3b, left panel). Likewise, the highest density of juvenile  
302 *Pocillopora* spp. (12.6 juveniles 0.25 m<sup>-2</sup>; Fig. 3b, left panel) was recorded in 2012, 2 y after  
303 the cover of this genus was at a minimum. As density of recruits and juvenile colonies was  
304 negatively associated with *Pocillopora* spp. cover (Fig. 3b, right panel), recruitment began in  
305 earnest when this coral virtually was extirpated from the outer reef. Increased *Pocillopora*  
306 spp. cover in 2012 (from 0.33% to 2.07%) and 2013 (from 2.07% to 7.30%) was followed in  
307 2013 and 2014 by decrease in density of recruits (from 8.29 to 0.67 corals tile<sup>-1</sup>) and juveniles  
308 (from 12.62 to 4.74 juveniles 0.25 m<sup>-2</sup>).

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#### 310 *Acropora* population

311 For *Acropora* spp. (Fig 3c, left panel), cover changed over time (RM-ANOVA,  $F_{9,711} =$   
312  $227.3$ ,  $p < 0.001$ ), with similar cover from 2005 and 2007 (pairwise comparison: 2005 = 2006  
313 = 2007,  $p > 0.05$ ) and decreases between 2007 and 2009 (pairwise comparison: 2007 > 2008;  
314 2008 > 2009, all  $p < 0.001$ ). Between 2009 and 2011, *Acropora* spp. cover remained at ~  
315 0.02% (pairwise comparison: 2009 = 2010 = 2011;  $p > 0.050$ ), but gradually increased in the

316 following 3 years (pairwise comparison: 2011 < 2012 < 2013 < 2014,  $p < 0.001$ ). The  
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2 317 density of juvenile *Acropora* spp. differed among years (RM-ANOVA,  $F_{9,711} = 250.1$ ,  $p <$   
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4 318  $0.001$ ), with changes among years that were similar to those affecting the cover of *Acropora*  
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6 319 spp. from 2005 to 2009 (pairwise comparison: 2005 = 2006 = 2007,  $p > 0.050$ ; 2007 > 2008,  
7  
8  
9 320  $p < 0.001$ ; 2008 > 2009,  $p < 0.001$ ). A decrease in density of *Acropora* spp. juveniles  
10  
11 321 occurred from 2009 to 2010 (pairwise comparison: 2009 > 2010,  $p < 0.001$ ) followed by an  
12  
13 322 increase from 2010 to 2012 (pairwise comparison: 2010 < 2011 < 2012,  $p < 0.001$ ). From  
14  
15 323 2012 to 2014, density of *Acropora* spp. juveniles gradually decreased (pairwise comparison:  
16  
17 324 2012 > 2013 > 2014,  $p < 0.01$ ). For acroporid recruits, densities recorded in  
18  
19 325 August/September differed among years (ANOVA,  $F_{6206} = 4.06$ ,  $p < 0.001$ ), but post hoc  
20  
21 326 analyses showed that this effect was due to high recruitment in 2012 (TukeyHSD, 2008 =  
22  
23 327 2009 = 2010 = 2011,  $p > 0.050$ ; 2011 < 2012,  $p < 0.001$ ; 2012 > 2013,  $p < 0.001$ ; 2013  
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25 328 =2014,  $p > 0.05$ ).

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33 330 Like *Pocillopora*, *Acropora* spp. was effectively removed from the outer reef by 2010 (cover  
34  
35 331 < 0.01%), but unlike *Pocillopora*, densities of *Acropora* spp. juveniles and acroporid recruits  
36  
37 332 have remained low in the following years (mean values of 0.21 juveniles  $0.25 \text{ m}^{-2} \text{ y}^{-1}$  and 0.68  
38  
39 333 recruits  $\text{tile}^{-1} \text{ y}^{-1}$ , respectively). Although acroporid recruits were found at a relatively high  
40  
41 334 mean density of 1.65 corals  $\text{tile}^{-1}$  in 2012, in 2014 the density of juvenile *Acropora* spp. and  
42  
43 335 acroporids recruits both were low ( $0.10 \text{ m}^{-2}$  and  $0.27$  corals  $\text{tile}^{-1}$ , respectively) (Fig. 3c, left  
44  
45 336 panel).

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47 337  
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49 338 For *Acropora* spp., the AIC analysis showed that the relationships between adult cover and  
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51 339 density of coral recruits and juveniles were best described by power, curves (Table 1).  
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53 340 However, the association between coral cover and density of recruits was not significant (for  
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341 Log-Log transformed data,  $r = 0.29$ ,  $df = 5$ ,  $p > 0.1$ ), although the association between coral  
1  
2 342 cover and density of juveniles was significant (for Log-Log transformed data,  $r = 0.96$ ,  $df =$   
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4 343  $7$ ,  $p < 0.01$ ). Model II regression described the-best fit functional relation for juvenile density  
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7 344 on coral cover with a power curve having an exponent of 0.41 (Fig 3c, right panel).  
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## 12 346 **Discussion**

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17 348 We investigated the dynamics of an ongoing recovery of a coral community on the outer reef of  
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19 349 Moorea after disturbances reduced coral on the outer reef > 92% (from 38% in 2005 to 3% in  
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21 350 2011). Using census data, we quantified recruitment of *Pocillopora* spp. and *Acropora* spp., the  
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23 351 two most abundant coral genera on the outer reefs of Moorea, with the objective of describing  
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25 352 the dynamics of coral community staging a remarkable recovery from catastrophic damage.  
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28 353 The broad-reaching scope of this recovery is revealed by the overall coral cover in 2014 relative  
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30 354 to 2005, the cover of the two dominant genera (*Acropora* and *Pocillopora*) over the same period,  
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32 355 and a strong trend towards restoration of the full generic coral composition (for scleractinians  
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34 356 and *Millepora*) in 2014 relative to 2005. By focusing on *Pocillopora* spp. and *Acropora* spp.  
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36 357 during this recovery period we were able to contrast two important genera that share a  
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38 358 spawning reproductive strategy, but which differ in reproductive timing in this location.  
39

42 359 *Pocillopora* spp. reproduces during an extended period lasting several months (Gleason 1996;  
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44 360 Adjeroud et al. 2007; Edmunds et al. 2010) whereas *Acropora* spp spawns in a discrete mass  
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46 361 spawning event (Carroll and Harrison 2006). Our results show different directions of density  
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48 362 association between coral cover and both recruits and juveniles in these two genera, which may  
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50 363 be associated with their contrasting reproductive phenologies.  
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57 365 Our study cannot test for cause-and-effect relationships that drive the density association we  
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59 366 report, however the associations are consistent with the hypothesis that different density-  
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367 dependent relationships (positive or negative) involving recruitment of *Pocillopora* spp. and  
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2 368 *Acropora* spp. modulate the recovery of coral populations on this outer coral reef community.  
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4 369 For *Pocillopora* spp., our results show a negative association between cover and density of  
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6 370 recruits, which is consistent with a causal mechanism involving negative density dependence  
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8 371 modulating recruitment of *Pocillopora* spp. In contrast, for acroporids we found a positive  
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10 372 association between cover and density of juveniles, which is consistent with a causal  
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12 373 mechanism involving positive density-dependence modulating recruitment of *Acropora* spp.  
13  
14 374 While there was no association between cover and density of recruits this outcome may reflect  
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16 375 the low density of recruits of this genus ( $< 1.65$  recruit tile<sup>-1</sup>), and the limited capacity of the  
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18 376 small target areas of settlement tiles to detect them. Different reproductive strategies, as shown  
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20 377 by *Acropora* spp. and *Pocillopora* spp. in Moorea, can result in different recovery dynamics  
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22 378 following major disturbances, and understanding the mechanisms mediating these dynamics is  
23  
24 379 likely to be one important part of the puzzle in determining the coral community structure of  
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26 380 future reefs. On coral reefs in the Indo-Pacific, *Pocillopora* spp. and *Acropora* spp. are  
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28 381 characterized by different life history strategies, with *Pocillopora* spp. generally having a high  
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30 382 population turnover and *Acropora* spp. showing slower population dynamics (Darling et al.  
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32 383 2012). Species characterized by populations with fast turnover are well known for their ability  
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34 384 to colonize recently-disturbed habitats (Grime 1977; Grime and Pierce 2012), whereas species  
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36 385 forming population characterized by slow dynamics tend to dominate in favorable  
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38 386 environments, but have slow recovery capacities (Darling et al. 2012).

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49 388 Our results document profound changes affecting the outer reefs of Moorea in quick succession  
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51 389 within a decade, and describe a sequence of events that have turned a reef with high coral cover  
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53 390 into a pavement of rock, and then back to a coral-dominated community within a few years. The  
54  
55 391 recovery has been fueled by recruitment of pocilloporid and acroporid corals displaying  
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57 392 contrasting recovery dynamics that may reflect different mechanisms of population regulation  
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59 393 by members of these genera. Previously, recovery dynamics for coral communities on the outer  
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394 reefs of Moorea have been reported (Adjeroud et al. 2009), and these are similar to the present  
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2 395 results in describing large declines in coral cover following multiple disturbances between 1991  
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4 396 and 2006, followed by rapid recovery of coral cover. This earlier description of the reefs of  
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6 397 Moorea showed that the recovered coral community differed in relative abundance of coral  
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8 398 genera compared to that described initially (Adjeroud et al. 2009), and while this again may be  
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10 399 the case as the reefs continue to recover, the coral community developing in the first 4 y after  
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12 400 the most recent disturbance does not support this possibility (Fig. 2).

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19 402 In Moorea, there is evidence that *Pocillopora* spp. recruits throughout much of the year (Gleason  
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21 403 1996; Adjeroud et al. 2007; Edmunds et al. 2010), which suggests that their larvae are the  
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23 404 products of a lengthy period of reproduction and may be consistently present in the seawater  
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25 405 flowing over the outer reefs. Although the brooding pocilloporid *P. damicornis* (Stoddart and  
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27 406 Black 1985) is occasionally seen on the outer reefs of Moorea (PJ Edmunds personal  
28  
29 407 observation), the majority of the pocilloporids on the outer reefs of Moorea (*P. meandrina*, *P.*  
30  
31 408 *verrucosa*, and *P. eydouxi*) are spawners (Harrison and Wallace 1990; Sier and Olive 1994;  
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33 409 Hirose et al. 2011; Schmidt-Roach et al. 2012). Throughout the Indo-Pacific, *P. meandrina*, *P.*  
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35 410 *eydouxi* and *P. verrucosa* are characterized by a spawning reproductive strategy (Schmidt-Roach  
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37 411 et al. 2012), although brooding by *P. verrucosa* has been recorded in the Phillipines (Villanueva  
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39 412 et al. 2008), and brooding by *P. meandrina* has been recorded in Enewetak (Stimson 1978).  
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42 413 Therefore, it is likely that the pocilloporid recruits we detected on the reefs of Moorea are the  
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44 414 products of external fertilization with pelagic larval durations (PLD) varying from hours-to-days  
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46 415 depending on the species (Harrison and Wallace 1990; Jones et al. 2009). Given the potential  
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48 416 PLD of *Pocillopora* spp. larvae, the short distance between near-by islands around Moorea (e.g.,  
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50 417 Tahiti lies 17 km east), the speed of prevailing surface currents (30 – 50 cm s<sup>-1</sup>, Martinez et al  
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52 418 2006), and the high fecundity of *Pocillopora* spp. (Sier and Olive 1994), it is likely that at least  
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54 419 Tahiti supplies some of the *Pocillopora* spp. larvae recruiting to the reefs of Moorea (Magalon et  
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56 420 al. 2005). Critically, however, the extent to which this inferred larval transport occurs will  
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421 depend on the degree of synergy among a large number of factors including the seawater  
422 currents, the fecundity of corals in each spawning event, the exact timing and duration of the  
423 spawning event (see Kough and Paris 2015), and the availability of suitable settlement surfaces  
424 when competent larvae arrive at the reef surface. Given the serendipitous nature of the  
425 likelihood of these factors conspiring to promote the transport of coral larvae among these  
426 islands, it is possible that the connectivity signal vested in different cohorts of coral recruits  
427 could differ very greatly.

428  
429 In addition to the potential for coral recruits on Moorea to originate in more distant locations  
430 (like Tahiti), *Pocillopora* spp. and *Acropora* spp. are also present in the back reef of Moorea  
431 (Edmunds et al. 2010), and colonies in this location also could provide larvae that recruit to the  
432 outer reef. Cross-reef transport of fish larvae and their delivery to the outer reef is known to  
433 occur in Moorea (Adam et al. 2011), for when the outer reef was depleted of coral in 2010,  
434 population growth of macroalgae was suppressed by the migration of parrotfish from the  
435 lagoon and back reef to the outer reef community (Adam et al. 2011). Elucidating the absolute  
436 roles of local versus more distant sources of pocilloporid and acroporid larvae in supporting  
437 coral recruitment on the outer reefs of Moorea must be a research priority to understand the  
438 extent to which population connectivity on a scale of 10's of kilometers modulates local-scale  
439 reef recovery.

440  
441 On the outer reefs of Moorea and at high population densities of *Pocillopora* spp., negative  
442 density-dependent mechanisms may underlie the association between cover and recruitment.  
443 While it was beyond the scope of this study to test for a mechanistic basis to this association for  
444 *Pocillopora* spp., there are at least two possibilities that could be relevant. First, high densities  
445 of branched adult colonies could deplete waterborne resources (such as zooplankton) that are  
446 necessary to sustain downstream recruits and juvenile colonies (Kim and Lasker 1997). This

447 effect could generate a trophic shadow (sensu Porter 1976) that deters recruitment through  
1  
2 448 food limitation in downstream locations. Alternatively, upstream corals could create a “wall of  
3  
4 449 mouths” (sensu Fabricius and Metzner 2004) from their numerous branches and polyps that  
5  
6 450 could consume a wide diversity of planktonic organisms, including larvae. Second, it is possible  
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9 451 that host-specific biotic interactions could cause positive density dependent mortality of coral  
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11 452 larvae and coral recruits. This mechanism could be analogous to the ways by which, in tropical  
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13 453 forests, pathogens on young seedlings of the tree *Shorea quadrinervis* cause highest mortality in  
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15 454 areas of high adult density, where transmission of pathogens presumably is most likely  
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18 455 (Blundell and Peart 2004). On coral reefs, a negative association between coral cover and the  
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20 456 abundance of juvenile corals has been recorded for the Caribbean coral *Siderastrea radians* by  
21  
22 457 Vermeij (2005), and a waterborne factor, whose effect became stronger as coral cover  
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24 458 increased, has been hypothesized as an explanation (Vermeij and Sandin 2008). According to  
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27 459 Marhaver et al. (2013), conspecific recruits settling downstream of the Caribbean coral *Orbicella*  
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29 460 *faveolata* were negatively affected by microbial flora associated with adult colonies, resulting in  
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31 461 a negative density dependent effect on recruitment. Conceivably, similar effects could modulate  
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33 462 recruitment of *Pocillopora* spp. in Moorea.

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40 464 Different life history traits typically drive differential recovery dynamics of populations  
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42 465 following disturbances (Stearns 1997), and in Moorea differential timing of reproduction in  
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44 466 *Acropora* spp. versus *Pocillopora* spp. may be important in facilitating contrasting patterns of  
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46 467 density association in recruitment. In this location, *Acropora* spp. mass spawns between  
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49 468 September and November (Carrol and Harrison 2006), and the highest recruitment of  
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51 469 acroporids occurs from December to March (Adjeroud et al. 2007). In contrast, pocilloporids  
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53 470 tend to recruit year-round on the reefs of Moorea (Gleason 1996; Adjeroud et al. 2007;  
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55 471 Edmunds et al. 2010), suggesting that reproduction in this family is not constrained to a single  
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58 472 period each year (Sier and Olive 1994). The trends for variation in population density reported  
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60 473 here for *Acropora* spp. are different from those for *Pocillopora* spp. For the Acroporidae, we  
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474 found positive density association based on the *Acropora* spp. cover, with the effect weak for  
1 recruits and strong for juveniles (Fig. 2c right panel). This pattern suggests that, at a local scale  
2 475 (i.e., < 10 km scale), recruitment may be supported by near-by adult colonies (i.e., self-seeding).  
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4 476 This mechanism should be accentuated by the temporally constrained reproduction of *Acropora*  
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6 477 (i.e., with September-November spawning in Moorea) that would make their larvae available for  
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8 478 settlement during only short periods each year. Effectively, this could constrain the supply of  
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10 479 acroporid larvae to the outer reefs of Moorea, and dampen the potential for among-island  
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12 480 connectivity (sensu Black et al. 1991).  
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21 483 Together, our results underscore the potential importance of density dependence and its role in  
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23 484 determining population size (Herrando-Pérez et al. 2012), in understanding the response of  
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25 485 contemporary coral communities to disturbances. By exploiting this realm of ecological theory  
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27 486 to augment our understanding of the coral communities of Moorea, we make the case that  
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29 487 density dependence is associated with population-level responses of two coral genera to  
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31 488 disturbances acting over the spatial scale of the present analysis. However, the implications of  
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33 489 our results are limited by their grounding in correlation rather than cause-and-effect, and  
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35 490 addressing this limitation is an important goal of future research. This task will not be easy  
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37 491 however, as it will require large-scale manipulative experiments in which the density of adult  
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39 492 corals, juvenile corals, and coral recruits are modified in an orthogonal design. Such an  
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41 493 approach may no longer be acceptable in an era when so many coral reefs have degraded and  
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43 494 the permitting framework for manipulative experimentation is highly restrictive.  
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48  
49 495 Notwithstanding the limitations of our study, our results are likely to have broad application to  
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51 496 other coral reefs, because the genera studied are representative of large functional groups of  
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53 497 corals having different life-history strategies (i.e., extended reproduction throughout the year  
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55 498 versus temporally restricted reproduction). Moreover, our findings may also apply to other  
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57 499 reefs that operate as part of larger metapopulations linked through hydrodynamic connectivity  
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59 500 in which the likelihood of recovery following disturbances is determined, in part, by density  
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501 dependent mechanisms. If the trends we describe have a mechanistic basis, then the recovery  
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2 502 dynamics of denuded reefs may be driven by corals with life-history strategies characterized by  
3  
4 503 protracted periods of reproduction and strong potential through pelagic larvae for connectivity  
5  
6 504 among nearby reefs.  
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9 505

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26 513 interests.  
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688 **Figures legends**

689

690 **Fig. 1.** Map of Moorea showing study sites (a) and representative photoquadrats (0.5 × 0.5 m) from 10 m  
691 depth in 2005 (b) and 2013 (c).

692

693 **Fig 2.** Non-metric multidimensional scaling plots showing the similarity of coral community structure  
694 among 10 years between 2005 and 2014 for LTER1 (a) and LTER2 (b), both at 10 m depth. Plots were  
695 prepared from mean coral cover by year for scleractinians and *Millepora*, that were  $\log(x + 1)$   
696 transformed prior to preparing resemblance matrices by the method of Bray Curtis; ordinations were  
697 generated from multiple restarts of 100 iterations. Bubbles for each year are scaled to show percentage  
698 cover of *Pocillopora* spp.

699

700 **Fig. 3.** Coral community structure from 2005 to 2014). (a) Island-wide community structure based on 6  
701 sites (2 sites shore<sup>-1</sup>; mean ± SE, n = 6); (b) Abundance of *Pocillopora* spp. on the north shore (LTER 1 and  
702 LTER2, Fig. 1). Left panel: cover (mean ± SE, left ordinate), density of juvenile colonies (mean ± SE, right  
703 ordinate), and density of recruits (summed within each year, right ordinate, 2008-2014). Right panel:  
704 relationships between cover of *Pocillopora* spp. and density of juvenile *Pocillopora* spp ( $r = 0.97$ ,  $p < 0.01$ ,  
705  $n = 8$ ), and pocilloporid recruits ( $r = 0.83$ ,  $p < 0.05$ ,  $n = 7$ ) using a time lag of 2 y; (c) Abundance of  
706 *Acropora* spp. on the north shore (LTER 1 and LTER2). Left panel: cover (mean ± SE, left ordinate),  
707 density of juvenile colonies (mean ± SE, right ordinate), and density of acroporid recruits (summed  
708 within each year, right ordinate, 2008-2014). Right panel: relationships between cover of *Acropora* and  
709 density of juveniles ( $r = 0.96$ ,  $p < 0.01$ ,  $n = 9$ ).

Figure 1  
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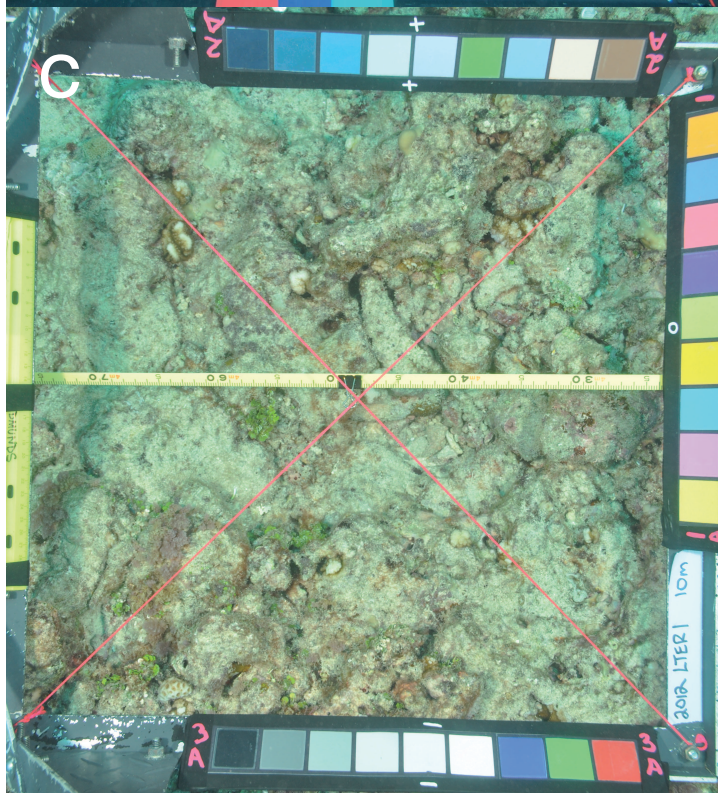
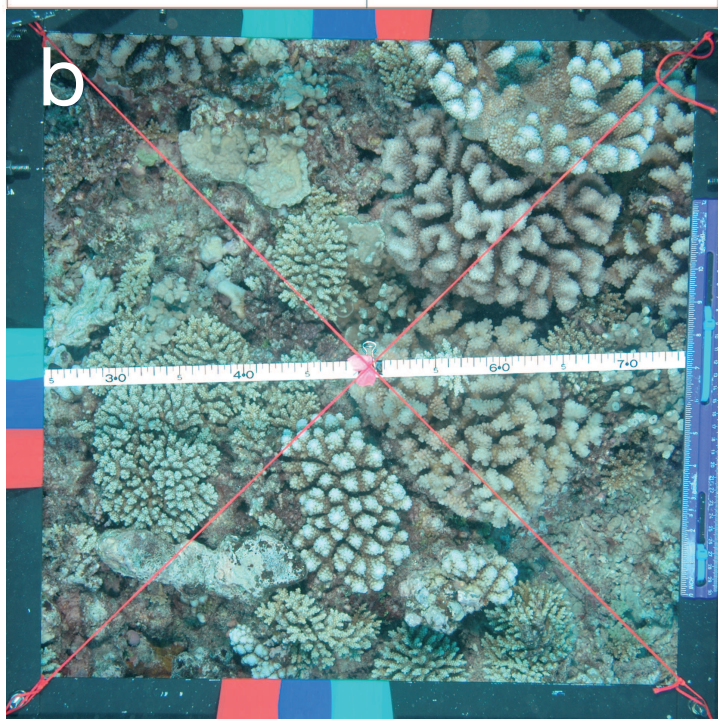
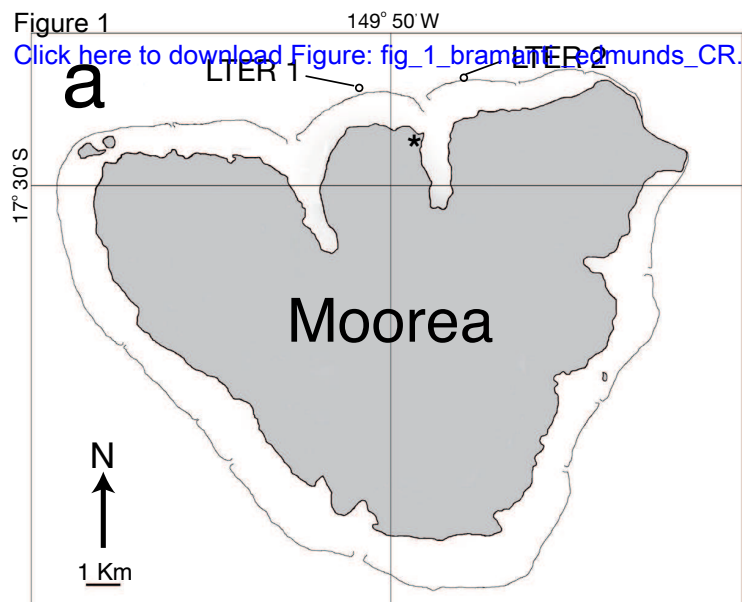


Figure 2

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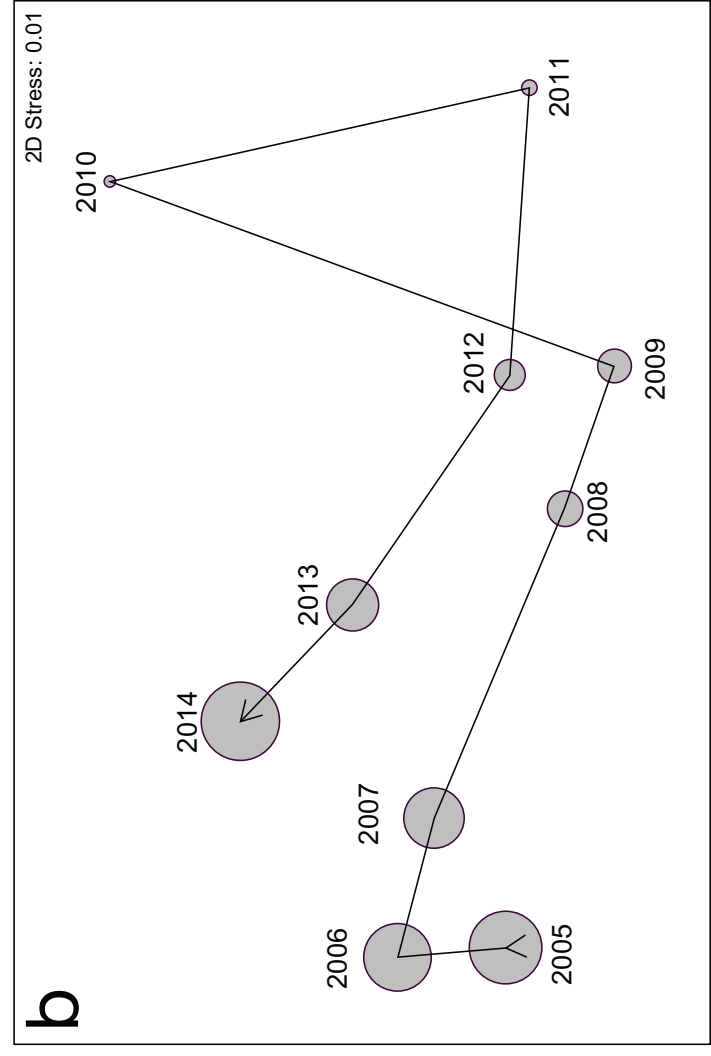
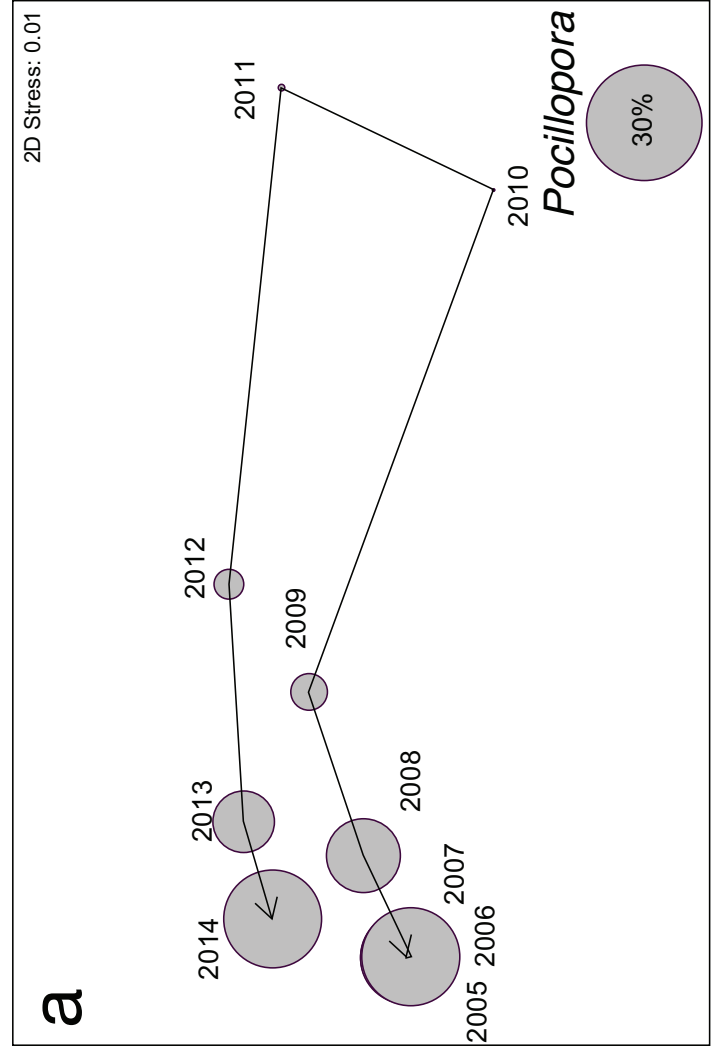
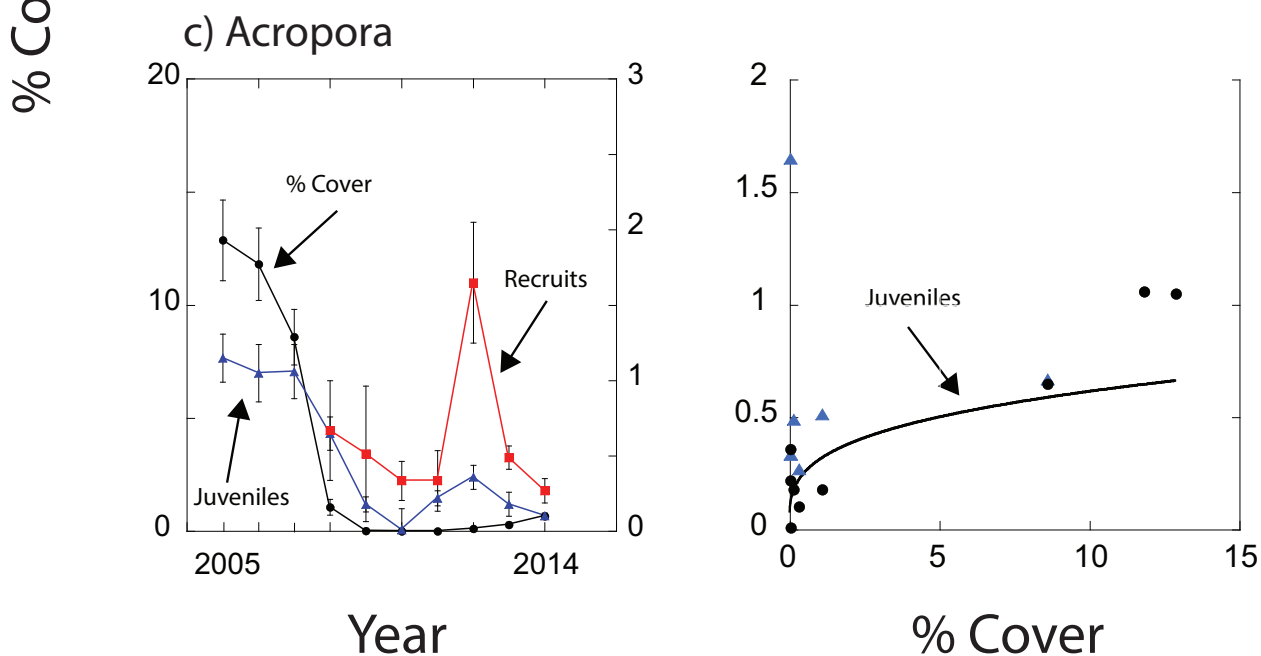
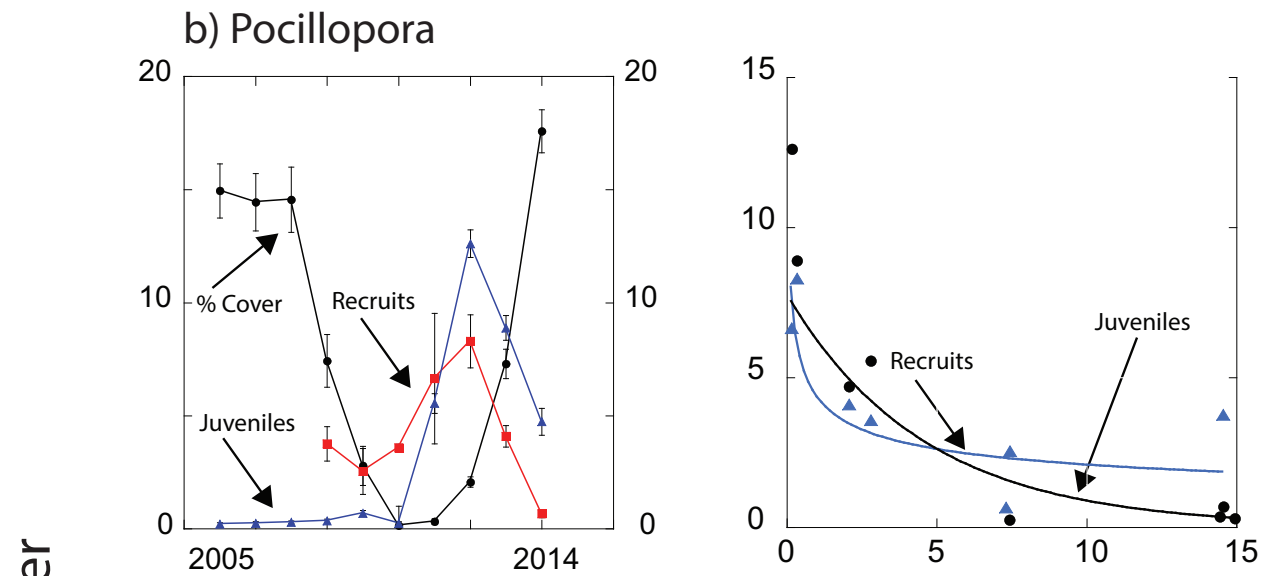
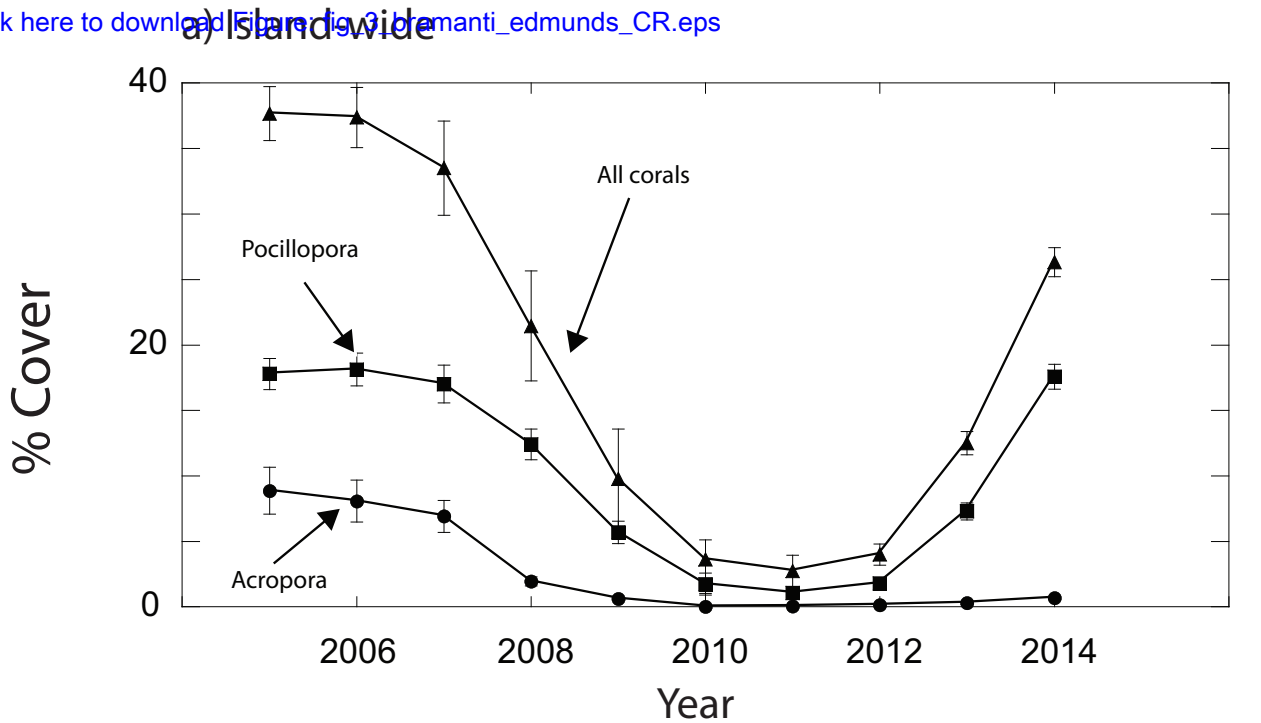


Figure 3  
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Juveniles 0.25 m<sup>-2</sup> or recruits tile<sup>-1</sup>



Table 1. Akaike Information Criterion (AIC) values for the three models tested (linear, power and exponential). The model with the lowest AIC value (in bold) was chosen to describe the relationship between adult (x axes) and recruit or juveniles (y axes) for *Pocillopora spp* and *Acropora spp*.

Genus	Dependent variable	Model	AIC value
<i>Pocillopora spp.</i>	Adults/recruits	Linear	11.8
		Power	<b>6.3</b>
		Exponential	8.7
	Adults/juveniles	Linear	22.3
		Power	15.9
		Exponential	<b>2.52</b>
<i>Acropora spp.</i>	Adults/recruits	Linear	-8.55
		Power	<b>-9.23</b>
		Exponential	-8.59
	Adults/juveniles	Linear	-38.5
		Power	<b>-39.3</b>
		Exponential	-31.2