Density-associated recruitment mediates coral population dynamics on a coral reef

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1 # **Density-associated recruitment mediates coral**

2 # **population dynamics on a coral reef**

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15 **Abstract**

16 Theory suggests that density-associated processes can modulate community resilience following declines

17 in population size, and here we show their presence in two scleractinian populations on the outer reef of

18 Moorea, French Polynesia, which are rapidly increasing in population size following the effects of two

19 catastrophic disturbances. Between 2006 and 2010, 93% of the coral cover was killed by crown of thorns

20 sea stars, in 2010 the dead coral skeletons were removed by a cyclone, and in 2011 and 2012 high coral

21 recruitment initiated community recovery. Coral recruitment was associated with coral cover, with the

22 relationship differing between two coral genera that are almost exclusively broadcast spawners in

23 Moorea. Acroporids recruited at low densities, and were positively association with cover of *Acropora*,

24 whereas pocilloporids recruited at high densities, and were negative association with cover of

25 *Pocillopora*. Our results show there are conditions favoring recovery of contemporary corals reefs

26 following large disturbances, specifically to promote rapid increases in population size through

27 recruitment that is associated with coral abundance. Because these relationships differ in direction

28 between two common and important genera of corals, they can mediate temporal shifts in taxonomic

29 composition of coral communities.

30

31 *Key words: Density dependence; recovery; Scleractinia; synecology; French Polynesia.*

32

Introduction

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

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

58 Declines in coral cover are common throughout the tropics (Bruno and Selig 2007, Schutte et al.

59 2010; Jackson et al. 2014), but only a few reefs in recent times have been found to recover

60 following major disturbances (e.g., Adjeroud et al. 2009; Graham et al. 2011; Gilmour et al.

61 2013). Poor recruitment of scleractinian corals has been proposed as a leading reason for

62 incomplete population recovery following major disturbances (Arnold and Steneck 2011;

63 Gilmour et al. 2013), but this outcome could be a result of multiple processes acting on one or

64 more coral life stages. Disturbances and the recovery of coral communities are normal aspects

65 of the biology of coral reefs (Pearson 1981; Nystrom et al. 2000), and when such events are

66 coincident with long-term ecological studies, there is the opportunity to use them as "natural

67 experiments" to study the processes associated with the development of coral communities.

68 The outer reefs of Moorea, French Polynesia (Fig. 1a), provide such an opportunity, because

69 their ecological history is particularly well known (e.g., Galzin and Pointier 1985; Berumen and

70 Pratchett 2006; Adjeroud et al. 2009; Adam et al. 2011). Most recently these reefs suffered

71 catastrophic damage from crown of thorns sea stars over 2006–2009 (Kayal et al. 2012), and

72 then were impacted by a cyclone in 2010 (Adam et al. 2011). Based on sampling conducted in

73 2015, it is clear that these communities are recovering exceptionally quickly (described below).

74

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,

4

85 population recovery. We discuss the potential roles of such effects in determining the

86 community structure of scleractinians as the reefs of Moorea recover from two major

87 disturbances.

88

89 **Materials and Methods**

90

91 *Overview*

92 Given the local- and region- scale importance of *Pocillopora* and *Acropora* in the tropical Pacific,

93 we focused on their populations in Moorea using data collected at the Moorea Coral Reef, Long-

94 Term Ecological Research site (http://mcr.lternet.edu). These data describe the percentage

95 cover of corals (2005 to 2014), the density of juvenile corals (colonies ≤ 40-mm diameter from

96 2005 to 2014), and the abundance of coral recruits on settlement tiles (2008 to 2014), and

97 together we use them to describe community dynamics on the outer reef before and after two

98 major disturbances that unfolded over several years. These data were used to explore the

99 statistical signal of the relationships between population size and a demographic property

100 (here, recruitment), and using these results, we evaluate the possibility that causal processes

101 arising from organism interactions regulate local population size of *Pocillopora* and *Acropora*.

102

103 The most recent disturbances affecting the outer reefs (10-12 m depth) of Moorea prior to

104 2006, were bleaching and a cyclone in 1991 that reduced coral cover to 22.5%, and bleaching in

105 1994, 2002, and 2003 that ultimately had little impact on coral cover (Adjeroud et al. 2009). By

106 2005 however, at 10-m depth on the outer reef, coral covered 38 ± 2% (mean ± SE, n = 6 sites)

107 of the benthos (Adam et al. 2011), with *Pocillopora* and *Acropora* the dominant coral genera

108 (37% of the coral; http://mcr.lternet.edu). By 2006, high population densities of the

109 corallivorous seastar *Acanthaster planci* were recorded on the reefs of Moorea (Kayal et al.

110 2012), and by 2009 they had reduced coral cover on the outer reef to 10 ± 4% (mean ± SE, n = 6

5

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 ≤ 3.4% mean coral cover at 10-m and 17-m depths (n = 40 quadrats

114   at two sites for both depths; Fig. 1c).

115

116   *Coral community structure*

117   Starting in April 2005, coral community structure was quantified using photoquadrats (0.5 ×

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*.

127

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 ~ 80 y^{-1}). To place the changes in

135   populations of *Pocillopora* and *Acropora* at these two sites in a broader context, specifically

6

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).

140

Juvenile corals

142 Starting in April 2005, juvenile corals ≤ 40-mm diameter were quantified in situ to genus, using

143 0.5 × 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.

148

Coral recruits

150 Coral recruits were assayed using unglazed terracotta tiles (15 × 15 × 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 ∼ 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

7

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^{-1}, pooled between sites, from

164 2008 to 2014) were summed (corals tile^{-1} y^{-1} based on $\sim$ 60 tiles).

165

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^{-1})

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^{-1}. 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

8

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.

194

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.,

9

214 and where significant associations were detected the functional relations were described by

215 Model II regression (described below).

216

217 Association between coral cover and density of early life stage corals (i.e., juveniles and

218 recruits) was evaluated following a 3-step procedure. First the best model describing the

219 relationship between the two random variables was chosen according to an Akaike information

220 criterion (AIC) approach (Akaike 1978). Linear, exponential, and power models were tested for

221 each set of data, and the model providing the lowest AIC value was chosen to provide the best

222 description of the relationship between the variables. Second, the statistical association

223 between the variables was evaluated using Pearson correlations and variables transformed to

224 correspond to the relationship that best described the data (as selected by lowest AIC values).

225 Third, where the two variables were significantly associated, the functional relationship

226 between them was described using Model II regression techniques because of the random

227 nature of both variables (Sokal and Rohlf 2012). In this procedure, the slope of the relationship

228 was determined by the method of standard major axis (SMA) (Sokal and Rohlf 2012; R software,

229 command "lmodel2").

230

231 Pearson correlations were calculated using a 1-year lag for recruitment and a 1–2 years lag

232 (depending on genus) for juveniles relative to the year in which adult cover was measured. For

233 example, correlations for recruitment paired recruit density in each year with coral cover the

234 previous year, and correlations for juveniles paired juvenile density in each year either with

235 coral cover in the previous year (i.e., a 1 y lag for *Pocillopora spp*), or with coral cover two years

236 before (i.e., a 2 y lag for *Acropora spp*). A lagging approach was used because we reasoned that

237 an effect of adult population size (i.e., coral cover) on recruits and juveniles would only be

238 detectable after the passage of sufficient time to allow these small life stages to be enumerated.

239 The settlement tiles used to assess recruitment were deployed for ~ 6 months at each sampling,

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 ~ 2 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., ~ 4 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

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

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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

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

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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).

298

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^{-1}), and in 2012 the highest density of recruits was

301   recorded (8.2 corals tile^{-1}; Fig. 3b, left panel). Likewise, the highest density of juvenile

302   *Pocillopora* spp. (12.6 juveniles 0.25 m^{-2}; 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^{-1}) and juveniles

308   (from 12.62 to 4.74 juveniles 0.25 m^{-2}).

309

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

13

316 following 3 years (pairwise comparison: 2011 < 2012 < 2013 < 2014, p < 0.001). The

317 density of juvenile *Acropora* spp. differed among years (RM-ANOVA, $F_{9,711}$ = 250.1, p <

318 0.001), with changes among years that were similar to those affecting the cover of *Acropora*

319 spp. from 2005 to 2009 (pairwise comparison: 2005 = 2006 = 2007, p > 0.050; 2007 > 2008,

320 p < 0.001; 2008 > 2009, p < 0.001). A decrease in density of *Acropora* spp. juveniles

321 occurred from 2009 to 2010 (pairwise comparison: 2009 > 2010, p < 0.001) followed by an

322 increase from 2010 to 2012 (pairwise comparison: 2010 < 2011 < 2012, p < 0.001). From

323 2012 to 2014, density of *Acropora* spp. juveniles gradually decreased (pairwise comparison:

324 2012 > 2013 > 2014, p < 0.01). For acroporid recruits, densities recorded in

325 August/September differed among years (ANOVA, F_{6206} = 4.06, p < 0.001), but post hoc

326 analyses showed that this effect was due to high recruitment in 2012 (TukeyHSD, 2008 =

327 2009 = 2010 = 2011, p > 0.050; 2011 < 2012, p < 0.001; 2012 > 2013, p < 0.001; 2013

328 =2014, p > 0.05).

329

330 Like *Pocillopora*, *Acropora* spp. was effectively removed from the outer reef by 2010 (cover

331 < 0.01%), but unlike *Pocillopora*, densities of *Acropora* spp. juveniles and acroporid recruits

332 have remained low in the following years (mean values of 0.21 juveniles 0.25 m^{-2} $y^{-1}$and 0.68

333 recruits $tile^{-1}$ y^{-1}, respectively). Although acroporid recruits were found at a relatively high

334 mean density of 1.65 corals $tile^{-1}$ in 2012, in 2014 the density of juvenile *Acropora* spp. and

335 acroporids recruits both were low (0.10 m^{-2} and 0.27 corals $tile^{-1}$, respectively) (Fig. 3c, left

336 panel).

337

338 For *Acropora* spp., the AIC analysis showed that the relationships between adult cover and

339 density of coral recruits and juveniles were best described by power, curves (Table 1).

340 However, the association between coral cover and density of recruits was not significant (for

14

341 Log-Log transformed data, r = 0.29, df = 5, p > 0.1), although the association between coral

342 cover and density of juveniles was significant (for Log-Log transformed data, r = 0.96, df =

343 7, p < 0.01). Model II regression described the-best fit functional relation for juvenile density

344 on coral cover with a power curve having an exponent of 0.41 (Fig 3c, right panel).

345

Discussion

347

348 We investigated the dynamics of an ongoing recovery of a coral community on the outer reef of

349 Moorea after disturbances reduced coral on the outer reef > 92% (from 38% in 2005 to 3% in

350 2011). Using census data, we quantified recruitment of *Pocillopora* spp. and *Acropora* spp., the

351 two most abundant coral genera on the outer reefs of Moorea, with the objective of describing

352 the dynamics of coral community staging a remarkable recovery from catastrophic damage.

353 The broad-reaching scope of this recovery is revealed by the overall coral cover in 2014 relative

354 to 2005, the cover of the two dominant genera (*Acropora* and *Pocillopora*) over the same period,

355 and a strong trend towards restoration of the full generic coral composition (for scleractinians

356 and *Millepora*) in 2014 relative to 2005. By focusing on *Pocillopora* spp. and *Acropora* spp.

357 during this recovery period we were able to contrast two important genera that share a

358 spawning reproductive strategy, but which differ in reproductive timing in this location.

359 *Pocillopora* spp. reproduces during an extended period lasting several months (Gleason 1996;

360 Adjeroud et al. 2007; Edmunds et al. 2010) whereas *Acropora* spp spawns in a discrete mass

361 spawning event (Carroll and Harrison 2006). Our results show different directions of density

362 association between coral cover and both recruits and juveniles in these two genera, which may

363 be associated with their contrasting reproductive phenologies.

364

365 Our study cannot test for cause-and-effect relationships that drive the density association we

366 report, however the associations are consistent with the hypothesis that different density-

15

367 dependent relationships (positive or negative) involving recruitment of *Pocillopora* spp. and

368 *Acropora* spp. modulate the recovery of coral populations on this outer coral reef community.

369 For *Pocillopora* spp., our results show a negative association between cover and density of

370 recruits, which is consistent with a causal mechanism involving negative density dependence

371 modulating recruitment of *Pocillopora* spp. In contrast, for acroporids we found a positive

372 association between cover and density of juveniles, which is consistent with a causal

373 mechanism involving positive density-dependence modulating recruitment of *Acropora* spp.

374 While there was no association between cover and density of recruits this outcome may reflect

375 the low density of recruits of this genus (< 1.65 recruit tile^{-1}), and the limited capacity of the

376 small target areas of settlement tiles to detect them. Different reproductive strategies, as shown

377 by *Acropora* spp. and *Pocillopora* spp. in Moorea, can result in different recovery dynamics

378 following major disturbances, and understanding the mechanisms mediating these dynamics is

379 likely to be one important part of the puzzle in determining the coral community structure of

380 future reefs. On coral reefs in the Indo-Pacific, *Pocillopora* spp. and *Acropora* spp. are

381 characterized by different life history strategies, with *Pocillopora* spp. generally having a high

382 population turnover and *Acropora* spp. showing slower population dynamics (Darling et al.

383 2012). Species characterized by populations with fast turnover are well known for their ability

384 to colonize recently-disturbed habitats (Grime 1977; Grime and Pierce 2012), whereas species

385 forming population characterized by slow dynamics tend to dominate in favorable

386 environments, but have slow recovery capacities (Darling et al. 2012).

387

388 Our results document profound changes affecting the outer reefs of Moorea in quick succession

389 within a decade, and describe a sequence of events that have turned a reef with high coral cover

390 into a pavement of rock, and then back to a coral-dominated community within a few years. The

391 recovery has been fueled by recruitment of pocilloporid and acroporid corals displaying

392 contrasting recovery dynamics that may reflect different mechanisms of population regulation

393 by members of these genera. Previously, recovery dynamics for coral communities on the outer

16

394 reefs of Moorea have been reported (Adjeroud et al. 2009), and these are similar to the present

395 results in describing large declines in coral cover following multiple disturbances between 1991

396 and 2006, followed by rapid recovery of coral cover. This earlier description of the reefs of

397 Moorea showed that the recovered coral community differed in relative abundance of coral

398 genera compared to that described initially (Adjeroud et al. 2009), and while this again may be

399 the case as the reefs continue to recover, the coral community developing in the first 4 y after

400 the most recent disturbance does not support this possibility (Fig. 2).

401

402 In Moorea, there is evidence that *Pocillopora* spp. recruits throughout much of the year (Gleason

403 1996; Adjeroud et al. 2007; Edmunds et al. 2010), which suggests that their larvae are the

404 products of a lengthy period of reproduction and may be consistently present in the seawater

405 flowing over the outer reefs. Although the brooding pocilloporid *P. damicornis* (Stoddart and

406 Black 1985) is occasionally seen on the outer reefs of Moorea (PJ Edmunds personal

407 observation), the majority of the pocilloporids on the outer reefs of Moorea (*P. meandrina*, *P.

408 verrucosa*, and *P. eydouxi*) are spawners (Harrison and Wallace 1990; Sier and Olive 1994;

409 Hirose et al. 2011; Schmidt-Roach et al. 2012). Throughout the Indo-Pacific, *P. meandrina, P.

410 eydouxi* and *P. verrucosa* are characterized by a spawning reproductive strategy (Schmidt-Roach

411 et al. 2012), although brooding by *P. verrucosa* has been recorded in the Phillipines (Villanueva

412 et al. 2008), and brooding by *P. meandrina* has been recorded in Enewetak (Stimson 1978).

413 Therefore, it is likely that the pocilloporid recruits we detected on the reefs of Moorea are the

414 products of external fertilization with pelagic larval durations (PLD) varying from hours-to-days

415 depending on the species (Harrison and Wallace 1990; Jones et al. 2009). Given the potential

416 PLD of *Pocillopora* spp. larvae, the short distance between near-by islands around Moorea (e.g.,

417 Tahiti lies 17 km east), the speed of prevailing surface currents (30 – 50 cm s^{-1}, Martinez et al

418 2006), and the high fecundity of *Pocillopora* spp. (Sier and Olive 1994), it is likely that at least

419 Tahiti supplies some of the *Pocillopora* spp. larvae recruiting to the reefs of Moorea (Magalon et

420 al. 2005). Critically, however, the extent to which this inferred larval transport occurs will

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

18

447 effect could generate a trophic shadow (sensu Porter 1976) that deters recruitment through

448 food limitation in downstream locations. Alternatively, upstream corals could create a "wall of

449 mouths" (sensu Fabricius and Metzner 2004) from their numerous branches and polyps that

450 could consume a wide diversity of planktonic organisms, including larvae. Second, it is possible

451 that host–specific biotic interactions could cause positive density dependent mortality of coral

452 larvae and coral recruits. This mechanism could be analogous to the ways by which, in tropical

453 forests, pathogens on young seedlings of the tree *Shorea quadrinervis* cause highest mortality in

454 areas of high adult density, where transmission of pathogens presumably is most likely

455 (Blundell and Peart 2004). On coral reefs, a negative association between coral cover and the

456 abundance of juvenile corals has been recorded for the Caribbean coral *Siderastrea radians* by

457 Vermeij (2005), and a waterborne factor, whose effect became stronger as coral cover

458 increased, has been hypothesized as an explanation (Vermeij and Sandin 2008). According to

459 Marhaver et al. (2013), conspecific recruits settling downstream of the Caribbean coral *Orbicella*

460 *faveolata* were negatively affected by microbial flora associated with adult colonies, resulting in

461 a negative density dependent effect on recruitment. Conceivably, similar effects could modulate

462 recruitment of *Pocillopora* spp. in Moorea.

463

464 Different life history traits typically drive differential recovery dynamics of populations

465 following disturbances (Stearns 1997), and in Moorea differential timing of reproduction in

466 *Acropora* spp. versus *Pocillopora* spp. may be important in facilitating contrasting patterns of

467 density association in recruitment. In this location, *Acropora* spp. mass spawns between

468 September and November (Carrol and Harrison 2006), and the highest recruitment of

469 acroporids occurs from December to March (Adjeroud et al. 2007). In contrast, pocilloporids

470 tend to recruit year-round on the reefs of Moorea (Gleason 1996; Adjeroud et al. 2007;

471 Edmunds et al. 2010), suggesting that reproduction in this family is not constrained to a single

472 period each year (Sier and Olive 1994). The trends for variation in population density reported

473 here for *Acropora* spp. are different from those for *Pocillopora* spp. For the Acroporidae, we

19

474 found positive density association based on the *Acropora* spp. cover, with the effect weak for

475 recruits and strong for juveniles (Fig. 2c right panel). This pattern suggests that, at a local scale

476 (i.e., < 10 km scale), recruitment may be supported by near-by adult colonies (i.e., self-seeding).

477 This mechanism should be accentuated by the temporally constrained reproduction of *Acropora*

478 (i.e., with September-November spawning in Moorea) that would make their larvae available for

479 settlement during only short periods each year. Effectively, this could constrain the supply of

480 acroporid larvae to the outer reefs of Moorea, and dampen the potential for among-island

481 connectivity (sensu Black et al. 1991).

482

483 Together, our results underscore the potential importance of density dependence and its role in

484 determining population size (Herrando-Pérez et al. 2012), in understanding the response of

485 contemporary coral communities to disturbances. By exploiting this realm of ecological theory

486 to augment our understanding of the coral communities of Moorea, we make the case that

487 density dependence is associated with population-level responses of two coral genera to

488 disturbances acting over the spatial scale of the present analysis. However, the implications of

489 our results are limited by their grounding in correlation rather than cause-and-effect, and

490 addressing this limitation is an important goal of future research. This task will not be easy

491 however, as it will require large-scale manipulative experiments in which the density of adult

492 corals, juvenile corals, and coral recruits are modified in an orthogonal design. Such an

493 approach may no longer be acceptable in an era when so many coral reefs have degraded and

494 the permitting framework for manipulative experimentation is highly restrictive.

495 Notwithstanding the limitations of our study, our results are likely to have broad application to

496 other coral reefs, because the genera studied are representative of large functional groups of

497 corals having different life-history strategies (i.e., extended reproduction throughout the year

498 versus temporally restricted reproduction). Moreover, our findings may also apply to other

499 reefs that operate as part of larger metapopulations linked through hydrodynamic connectivity

500 in which the likelihood of recovery following disturbances is determined, in part, by density

20

501 dependent mechanisms. If the trends we describe have a mechanistic basis, then the recovery

502 dynamics of denuded reefs may be driven by corals with life-history strategies characterized by

503 protracted periods of reproduction and strong potential through pelagic larvae for connectivity

504 among nearby reefs.

505

514

References

516

517 Akaike H (1978) A Bayesian Analysis of the minimum AIC procedure. Ann Inst Stat Math 30: 9–14

518

519 Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ, Carpenter RC, Bernardi G (2011) Herbivory,

520 connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. PLoS ONE

521 **6**(8): e23717. [doi:10.1371/journal.pone.0023717]

522

523 Adjeroud M, Penin L, Carrol A (2007) Spatio-temporal heterogeneity in coral recruitment around Moorea,

524 French Polynesia: implications for population maintenance. Mar Ecol Prog Ser 341 (2007) 204–218

525

526 Adjeroud M, Michonneau F, Edmunds PJ, Chancerelle Y, Lison de Loma T, Penin L,. Thibaut L, Vidal-Dupiol

527 J, Salvat B, Galzin R (2009) Recurrent disturbances, recovery trajectories, and resilience of coral

528 assemblages on a South Central Pacific reef. Coral Reefs 28: 775–780

529

530 Arnold SN, Steneck RS (2011) Settling into an increasingly hostile world: the rapidly closing "recruitment

531 window" for Corals. PLoS ONE 6(12): e28681. [doi:10.1371/journal.pone.0028681]

532

533 Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429: 827-

534 833

535

536 Bence JR (1995) analysis of short time series: correcting for autocorrelation. Ecology 76:628-639

537

538 Berumen ML, Pratchett MS (2006) Recovery without resilience: persistent disturbance and long-term

539 shifts in the structure of fish and coral communities at Tiahura reef, Moorea. Coral Reefs 25: 647-653

540

541 Black KP, Moran PJ, Hammond LS (1991) Numerical models show coral reefs can be self-seeding. Mar

542 Ecol Prog Ser 74: 1-11

543

544 Blundell AG, Peart DR (2004) Density-dependent population dynamics of a dominant rain forest canopy

545 tree. Ecology 85: 704-715

546 Bramanti L, Iannelli M, Fan TY, Edmunds PJ (2015) Using demographic models to project the effects of

547 climate change on scleractinian corals: Pocillopora damicornis as a case study. Coral Reefs 34: 505–515 [doi

548 10.1007/s00338-015-1269-z]

549

550   Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and

551   subregional comparisons. PLoS ONE 2: e711. [doi:10.1371/journal.pone.0000711]

552

553   Carroll AG, Harrison PL (2006) Sexual reproduction of *Acropora* reef corals at Moorea, French Polynesia.

554   Coral Reefs 25: 93–97

555

556   Clarke KR, Gorley RN (2006) Primer v6: user manual/tutorial. PRIMER-E, Plymouth

557

558   Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. Trends

559   Ecol Evol 14 (10): 405-410

560

561   Darling E, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of

562   reef corals from species traits. Ecol Lett 15: 1378-138

563

564   Edmunds PJ, Leichter J, Adjeroud M (2010) Landscape-scale variation in coral recruitment in Moorea,

565   French Polynesia. Mar Ecol Prog Ser 414: 75–89

566

567   Fabricius KE, Metzner J (2004) Scleractinian walls of mouths: predation on coral larvae by corals. Coral

568   Reefs 23: 245-248

569

570   Fan TY, Li JJ, Ie SX, Fang LS (2002) Lunar periodicity of larval release by Pocilloporid corals in southern

571   Taiwan. Zool Stud 41: 288–294

572

573   Galzin R, Pointier JP (1985) Moorea Island, Society Archipelago. Proc 5th Int Coral Reef Symp 1: 73-102

23

574

575 Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett M (2013) Recovery of an isolated coral reef system

576 following severe disturbance. Science 340: 69-71. [doi: 10.1126/science.1232310]

577

578 Gleason M (1996) Coral recruitment in Moorea, French Polynesia: the importance of patch type and

579 temporal variation. J Exp Mar Biol Ecol 207: 79-101

580

581 Graham NAJ, Nash KL, Kool JT (2011) Coral reefs recovery dynamics in a changing world. Coral Reefs

582 30:283–294

583

584 Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to

585 ecological and evolutionary theory. Am Nat 111: 1169–1194

586

587 Grime JP, Pierce S (2012) The evolutionary strategies that shape ecosystems, 7th edn. Wiley-Blackwell,

588 Oxford, UK

589

590 Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In:

591 Dubinsky Z (ed) Ecosystems of the world: coral reefs. Elsevier, Amsterdam, pp 133–207

592

593 Herrando-Pérez S, Delean S, Brook BW, Bradshaw CJA (2012) Density dependence: an ecological tower of

594 Babel. Oecologia 170: 585-603

595

596 Hixon MA, Pacala SW, Sandin SA (2002) Population regulation: historical context and contemporary

597 challenges of open vs. closed systems. Ecology 83:1490–1508

598

599 Hirose M, Obuchi M, Hirose E, Reimer JD (2011) Timing of spawning and early development of *Palythoa*

600 *tuberculosa* (Anthozoa, Zoantharia, Sphenopidae) in Okinawa, Japan. Biol Bull 220:23–31

601

602 Jackson JBC, Donovan M, Cramer K, Lam V (2014) Status and trends of caribbean coral reefs: 1970-2012,

603 Global Coral Reef Monitoring Network, IUCN, Gland Switzerland, 2014

604 Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Hoppen MJH, Willis BL (2009) Larval retention

605 and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral

606 Reefs 28: 307-325

607

608 Kayal M, Vercelloni J, Lison de Loma T, Bosserelle P, Chancerelle Y, Geoffroy S, Stievenart C, Michonneau

609 F, Penin L, Planes S, Adjeroud M (2012) Predator Crown-of-Thorns starfish (*Acanthaster planci*) outbreak,

610 mass mortality of corals, and cascading effects on reef fish and benthic communities. PLoS ONE 7:

611 e47363. [doi:10.1371/journal.pone.004736]

612

613 Kough AS, Paris CB (2015) The influence of spawning periodicity on population connectivity. Coral Reefs

614 [doi: 10.1007/s00338-015-1311-1]

615

616 Kim K, Lasker HR (1997) Flow-mediated resource competition in the suspension feeding gorgonian

617 *Plexaura homomalla* (Esper). J Exp Mar Biol Ecol 215: 49-64

618

619 Kohler KE, Gill SM (2006) Coral point count with excel extensions (CPCe): a visual basic program for the

620 determination of coral and substrate coverage using random point count methodology. Comput Geosci

621 32: 1259–1269

622

623 Magalon H, Adjeroud M, Veuilee M (2005) Patterns of genetic variation do not correlate with geographical

624 distance in the reef-building coral *Pocillopora meandrina* in the South Pacific. Mol Ecol 14: 1861–1868

625

626 Marhaver KL, Vermeij MJA, Rohwer F, Sandin SA (2013) Janzen-Connell effects in a broadcast-spawning

627 caribbean coral: distance-dependent survival of larvae and settlers. Ecology 94:146–160

628

629 Martinez E, Maamaatuaiahutapu K, Payri C, Ganachaud A (2006) *Turbinaria ornata* invasion in the

630 Tuamotu Archipelago, French Polynesia: ocean drift connectivity. Coral Reefs 26: 79–86

631

632 Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated

633 environment. Trends Ecol Evol 15: 413–417

634

635 Pearson RG (1981)Recovery and Recolonization of Coral Reefs. Mar Ecol Progr Ser 4:105-122

636

637 Pickett STA, Kolasa J, Armesto JJ, Collins SL (1989) The Ecological Concept of Disturbance and Its

638 Expression at Various Hierarchical Levels. Oikos 54 (2): 29-136

639

640 Porter JW (1976) Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals.

641 Am Nat 110: 731-742

642

643 Pratchett MS, Anderson KD, Hoogenboom MO, Widman E, Baird AH, Pandolfi JM, Edmunds PJ, Lough JM

644 (2015) Spatial, temporal, and taxonomic variation in coral growth—implications for the structure and

645 function of coral reef ecosystems. Oceanogr Mar Biol (53).

646

647 Richmond RH (1987) Energetics, competency, and long-distance dispersal of planula larvae of the coral

648 *Pocillopora damicornis*. Mar Biol 93: 527-533

649

650 Schmidt-Roach S, Miller KJ, Woolsey E, Gerlach G, Baird AH (2012) Broadcast spawning by *Pocillopora*

651 species on the Great Barrier Reef. PLoS ONE 7: e50847. [doi:10.1371/journal.pone.0050847]

652

653 Schutte VG, Selig ER, Bruno JF (2010) Regional spatio-temporal trends in Caribbean coral reef benthic

654 communities. Mar Ecol Prog Ser 402: 115–122

655

656 Sier CJS, Olive PW (1994) Reproduction and reproductive variability in the coral *Pocillopora verrucosa*

657 from the Republic of Maldives. Mar Biol 118:713-722

658

659 Sokal RR, Rohlf FJ (2012) Biometry: the principles and practice of statistics in biological research. 4th

660 edition. WH Freeman and Co.: New York. 937 pp.   ISBN: 0-7167-8604-4 or 978-0-7167-8604-7.

661

662 Stearns S (1997) The Evolution of Life-Histories. Oxford University Press, Oxford

663

664 Stimson JS (1978) Mode and timing of reproduction in some common hermatypic corals of Hawaii and

665 Enewetak. Mar Biol 48: 173-184

666

667 Stoddart JA, Black R (1985) Cycles of gametogenesis and planulation in the coral *Pocillopora damicornis*.

668 Mar Ecol Prog Ser 23: 154-164

669

670   Vermeij MJA (2005) Substrate composition and adult distribution determine recruitment patterns in a

671   Caribbean brooding coral. Mar Ecol Prog Ser 295:123–133

672

673   Vermeij MJA, Sandin A (2008) Density-dependent settlement and mortality structure the earliest life

674   phases of a coral population. Ecology 89:1994–2004

675

676   Veron JEN (2000) Corals of the world; Stafford-Smith M, editor. Townsville: Australian Institute of Marine

677   Science. 463 p

678

679   Villanueva R, Yap H, Montaño M (2008) Timing of planulation by pocilloporid corals in the northwestern

680   Philippines. Mar Ecol Prog Ser 370: 111–119

681

682   Warner RR, Hughes TP (1988) The population dynamics of reef fishes. In: Proceedings of the

683   International Coral Reef Symposium (6), pp. 149-155. From: 6th International Coral Reef Symposium, 8-

684   12 August 1988, Townsville, QLD, Australia.

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687

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^{-1}; 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

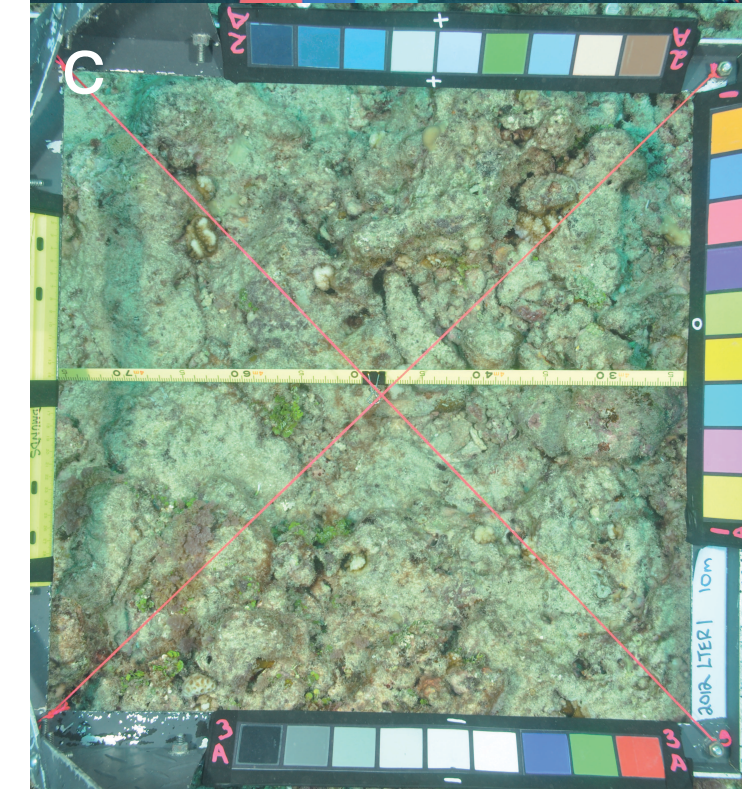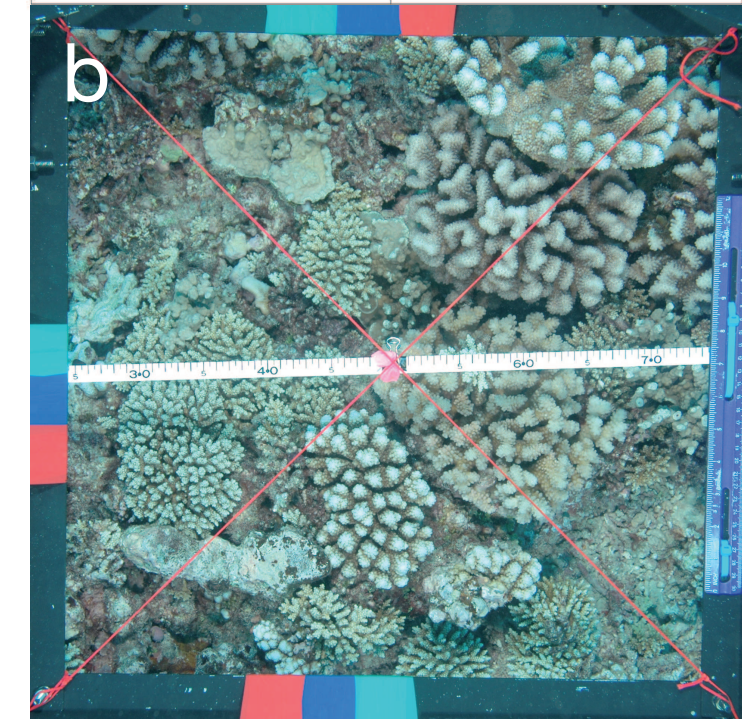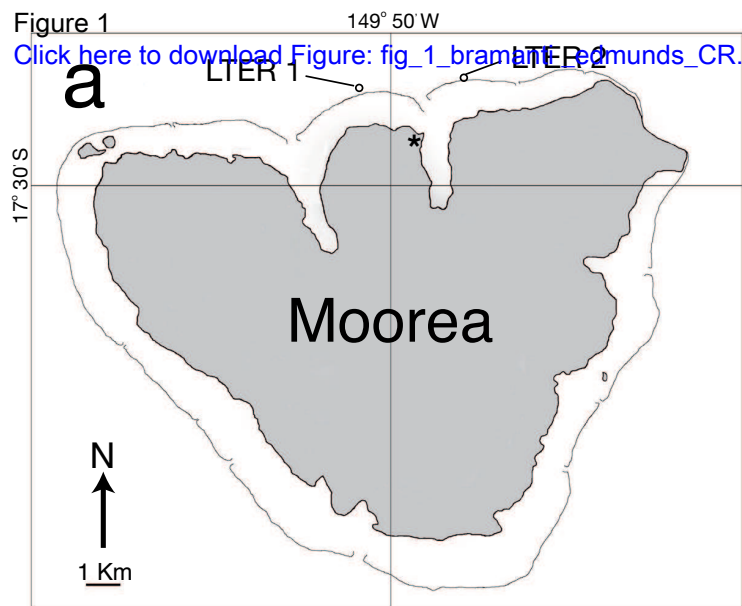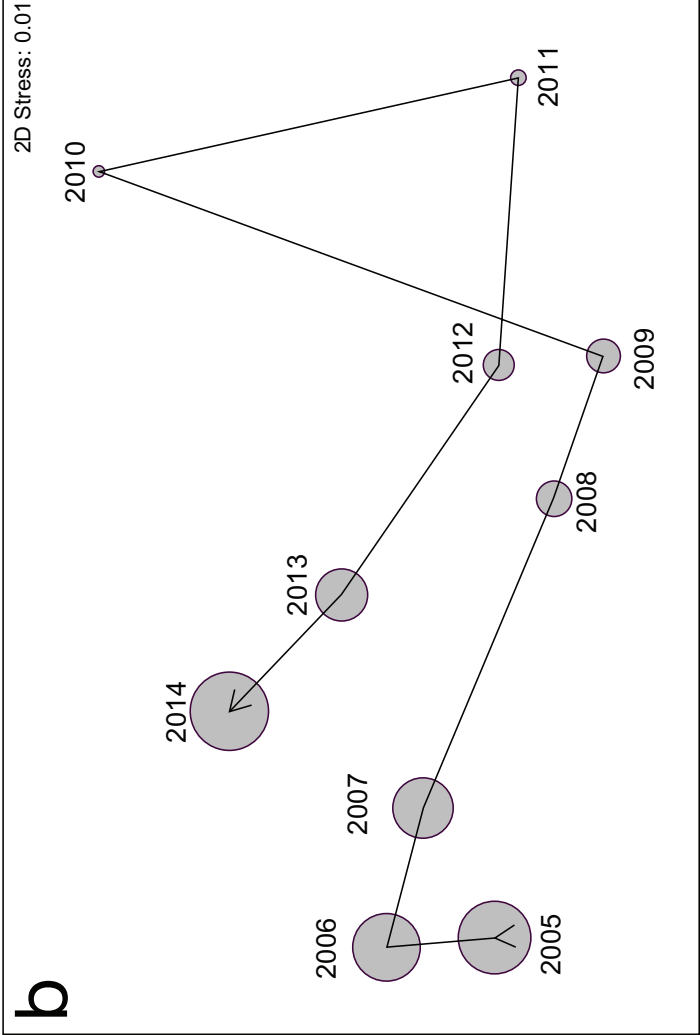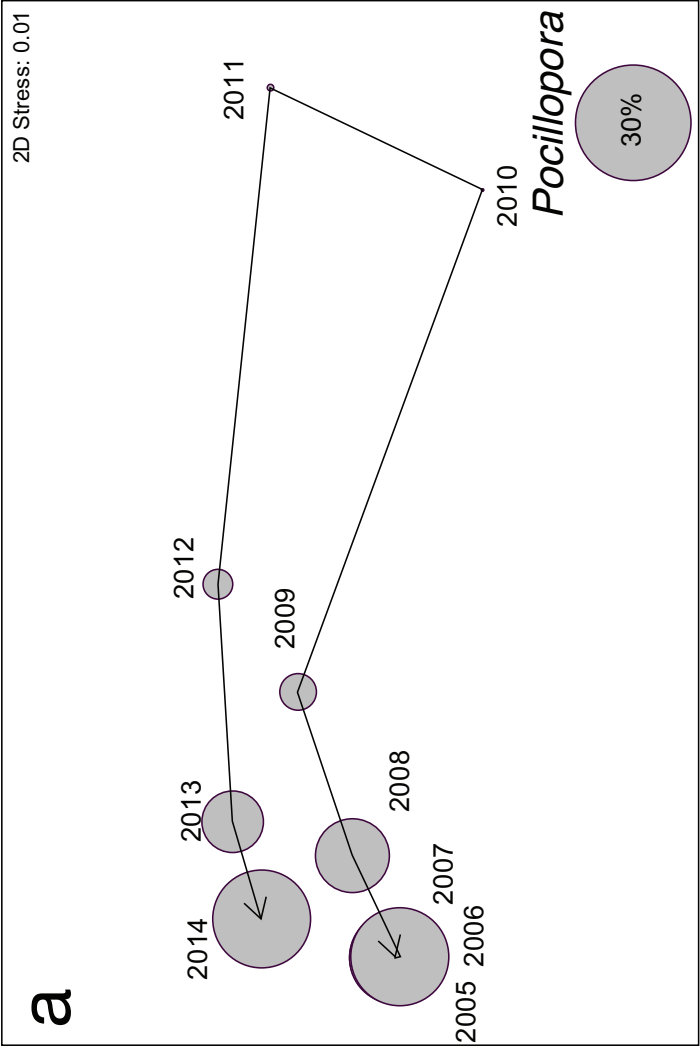709 density of juveniles (r = 0.96, p < 0.01, n = 9).

Figure 1

Figure 1

Figure 2
Click here to download Figure: fig_2_bramanti_edmunds_CR.eps

a) Island-wide
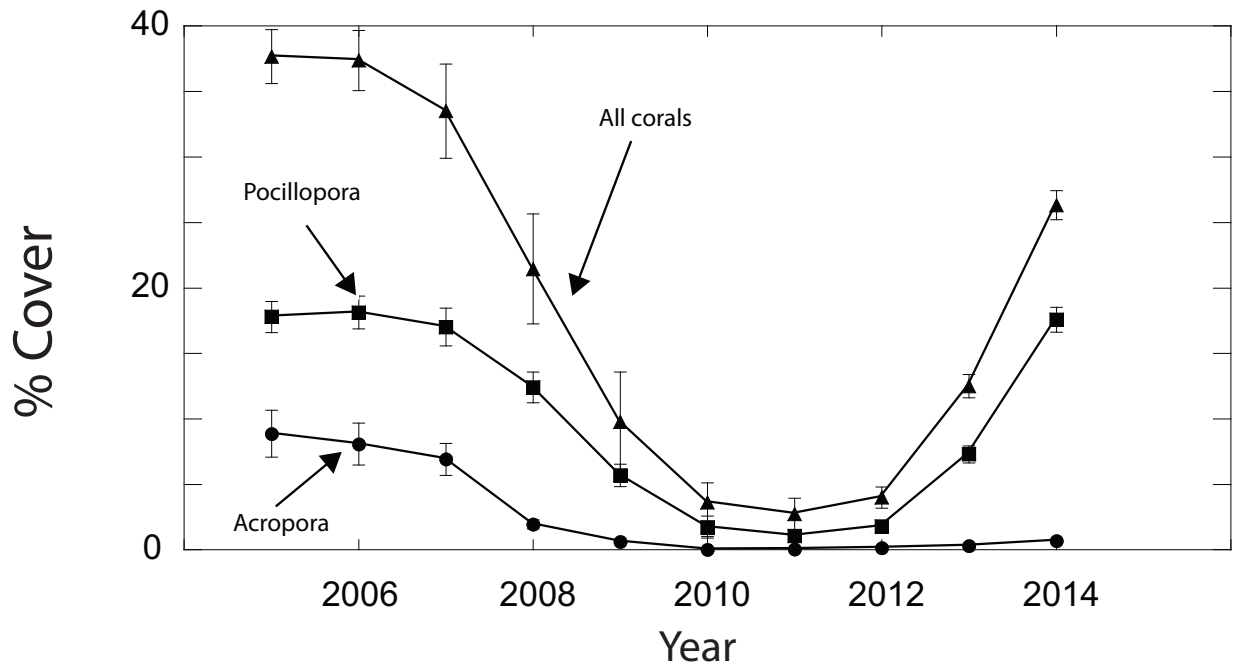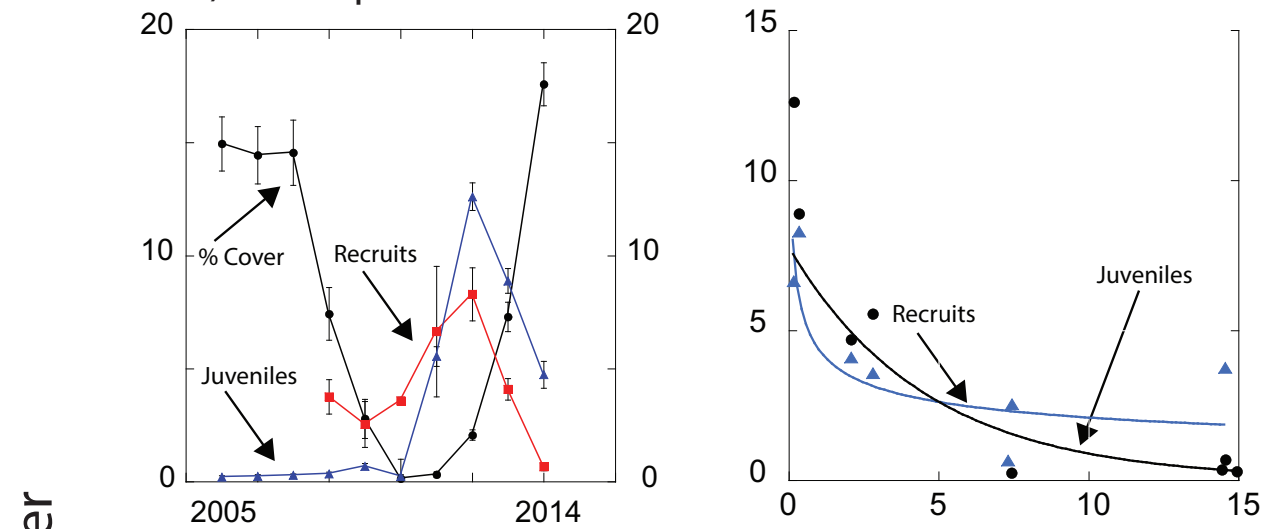
b) Pocillopora

c) Acropora

% Cover

Year

% Cover
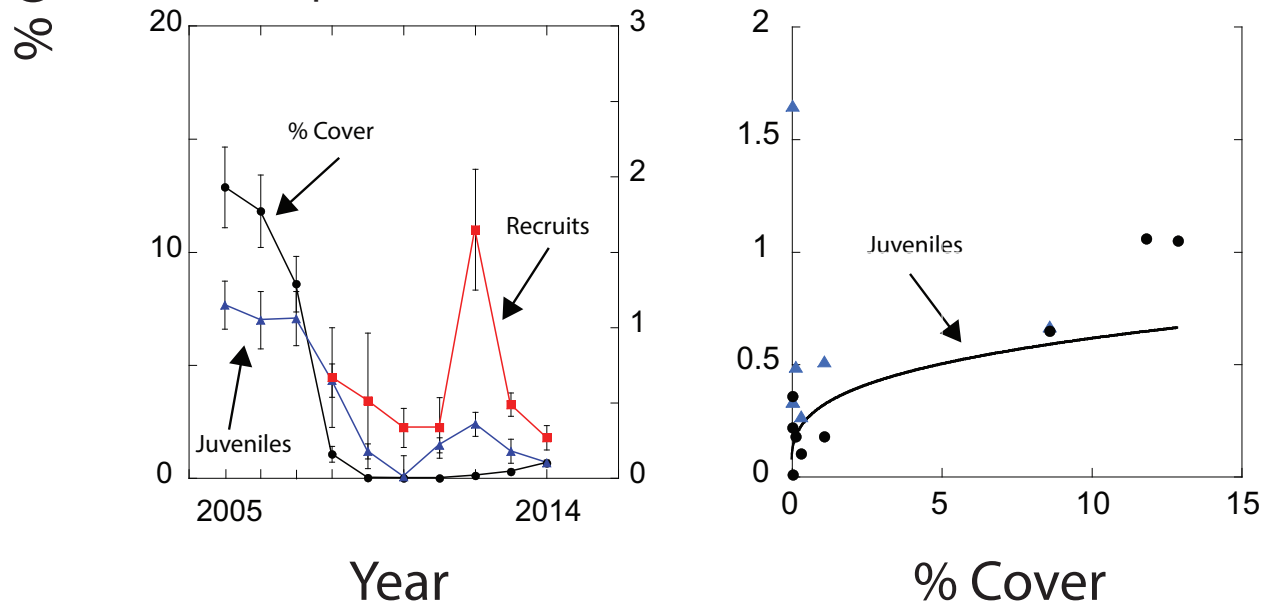
Juveniles 0.25 m⁻² or recruits tile⁻¹

Table 1
Click here to download Table: Tab_1_bramanti_edmunds_CR.docx

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 variab;e	**Model**	**AIC value**
Pocillopora spp.	Adults/recruits	Linear	11.8
		Power	**6.3**
		Exponential	8.7
	Adults/juveniles	Linear	22.3
		Power	15.9
		Exponential	**2.52**
Acropora spp.	Adults/recruits	Linear	-8.55
		Power	**-9.23**
		Exponential	-8.59
	Adults/juveniles	Linear	-38.5
		Power	**-39.3**
		Exponential	-31.2