Persistence of an isolated population of the temperate coral *Plesiastrea versipora*

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1   **Persistence of an isolated population of the temperate coral *Plesiastrea versipora***

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3   **Running head:** Population dynamics of *Plesiastrea versipora*.

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9

10   **Abstract**

11   Successful establishment of new populations outside present geographical ranges requires

12   the capacity for species to both disperse to and persist in isolated patches. By definition,

13   dispersal to such patches is typically rare or sporadic, making individual-level growth and

14   survival and self-recruitment key to population persistence. To better understand the

15   demographic processes that lead to the long-term establishment of species in isolated

16   patches, I studied a genetically isolated population of the reef coral *Plesiastrea versipora*

17   in Sydney Harbour. I hypothesized that persistence of the population was due to either high

18   levels of reproduction and self-recruitment or high levels of growth and survivorship that

19   could buffer population decline. I used a size-based adaption of the Leslie matrix model to

20   combine field-measured demographic rates and size structure data in order to quantify

21   intrinsic population growth rate and sensitivies to changes in demographic contributions

22   of different size classes. The results show that persistence of *P. versipora* population relies

23   mostly on yearly survival, especially in larger more fecund colonies, and is less reliant on

24   recruitment. The 'persistent' demographic strategy identified in this study may be key to

25   establishing new sub-populations outside native ranges as well as maintaining existing

26   populations during periods of environmental change, especially when dispersal is

27   diminished or unpredictable.

28

29   **Keywords:** Population modeling, growth rate, survivorship, recruitment, *Plesiastrea*

30   *versipora*, dispersal

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32

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Introduction

The success of sub-populations outside species' native ranges is conditional upon the intrinsic capacity for population growth in a new patch. This intrinsic capacity represents a balance between adding individuals to the population (via recruitment) and taking individuals away (via mortality). Despite the importance of demographic approaches for understanding the persistence of populations, recent studies purporting geographical range shifts in association with environmental changes are largely observational, and therefore the dynamics or persistence of new populations cannot be quantified. For example, increased connectivity between the Great Barrier Reef and South East Coast of Australia due to the incursion of the East Australian current has allowed the dispersal and recruitment of various reef corals and fishes to higher latitude locations (Figueira & Booth 2010, Hobbs 2010), but whether these species will persist is largely unknown; for example, reef fishes rarely survive the cooler winters, resulting in ephemeral populations that are reliant on an external source of recruits (Figueira & Booth 2010). Similarly, based on a long record of historical observations, four reef-building corals have demonstrated pole-ward range expansions along the Japanese coast since the 1930s (Yamano et al. 2011). These studies provide evidence that environmental change has led to an increasing number of species moving towards and persisting at edges of their geographic ranges. However the demographic requirements that facilitate these range expansion observations are not understood. A demographic approach would elucidate the requirements for long-term population persistence of species outside their known ranges as well as the potential future changes to present day geographical ranges.

The persistence of a localized population in the marine environment requires adequate recruitment of individuals, which occurs primarily during the pelagic larval stage. During this stage, larvae can be passively and actively mobile and can potentially travel and settle some distance away from natal populations. Population size and structure can vary greatly due to variations that arise in the larval stage (Caley et al. 1996). Such variation is driven by the interaction of oceanography with larval behavior and biological traits (Sponaugle et al. 2002, Kinlan et al. 2005, Luiz et al. 2012, Luiz et al. 2013). For instance, dispersal of larvae depends on the flow, speed and direction of ocean currents, which may augment or impede dispersal patterns (Shanks et al. 2003, Cowen & Sponaugle 2009), while topographical complexity can potentially redirect flows and create dispersal barriers (e.g.

68   protruding headlands that create large scale gyres; Sponaugle et al. 2002). In addition,

69   often, individual dispersal abilities and behavior such as duration in the larval phase

70   (Shanks et al. 2003, Lindsay 2012), swimming ability and orientation (Fisher et al. 2000,

71   Sponaugle et al. 2002) and depth range (Sponaugle et al. 2002) may influence the capacity

72   for larvae to disperse. This variation in larval dispersal ability can limit species' range sizes

73   but also the flow of recruits into existing populations and new patches. However, despite

74   successful dispersal capabilities of larvae, settlement and establishment often depends on

75   settlement choice and specific environmental cues that may hinder the opportunity for

76   recruitment.

77

78   Populations at range edges are likely to be more sensitive to recruitment, because dispersal

79   from native populations is usually rare or sporadic (Cowen & Sponaugle 2009). It has

80   previously been assumed that due to high connectivity in the marine environment, owing

81   to ocean currents and duration of larvae in the pelagic stage, dispersal of recruits to distant

82   populations can be achieved (Tanner et al. 1996, Roberts 1997). However, since the

83   concentration of larvae declines with increasing distance between populations as the result

84   of diffusion and mortality (Cowen et al. 2000), distant populations are unlikely to be

85   frequently replenished and maintained by external recruits. Distant populations that

86   become isolated typically rely on self-recruitment for population growth (Sponaugle et al.

87   2002, Swearer et al. 2002, Baums et al. 2005).

88

89   Various demographic tradeoffs have been observed in corals that contribute to the

90   maintenance of a population with limited recruitment. For instance, poorly self-recruiting

91   populations that experience diverse environmental conditions may rely on survivorship

92   instead (i.e. the storage effect (Warner & Chesson 1985)). This in turn enables a population

93   to accumulate adults when conditions become favorable (Edmunds 2000, Hughes &

94   Tanner 2000, Kersting & Linares 2012). In addition, studies have shown size-dependent

95   survivorship in long-lived organisms, where the probability of survivorship of a coral

96   colony increases with size (Tanner et al. 1996, Glassom & Chadwick 2006), demonstrating

97   the importance of survival in juvenile corals during the early growth stage. Such tradeoffs

98   may benefit the long-term persistence of isolated populations outside their normal ranges

99

100   Population models provide a useful framework for examining demographic tradeoffs. .

101   Such models incorporate individual-level rates of growth, survivorship and recruitment to

102 estimate properties of populations, such as intrinsic growth rate, and enable the

103 quantification of a population's sensitivity to changes in age-, size- or stage-based

104 demographic rates. Intrinsic growth rate is given by the dominant eigenvalue (λ) and

105 'elasticity' is characterised by the sensitivity of the eigenvalue to relative changes in the

106 demographic contributions (Roughgarden 1998). The importance of individual-level

107 growth, survivorship and fecundity can be quantified by these model sensitivities (Caswell

108 1989, Easterling et al. 2000). While size-based population models have previously been

109 used to understand the population dynamic of corals (e.g. Hughes 1984), this is the first

110 study which will specifically address population dynamics of a temperate coral species in

111 order to understand the ecological attributes for persisting in an isolated setting.

112

113 *Plesiastrea versipora* (Lamarck, 1816) is a hermatypic coral species characterized by a

114 geographic range that extends from Japan to South Australia. It is one of a few species of

115 reef coral found at high latitudes, beyond the limiting range for most tropical species

116 (Rodriguez-Lanetty et al. 2001). Corals in high latitude environments tend to experience

117 greater fluctuations in light and temperature conditions compared to the relatively stable

118 conditions experienced by species closer to the equator (Burgess et al. 2009). At the

119 highest latitude where *P. versipora* is located (Port Phillip Bay, Victoria, Australia) the

120 annual temperature ranges between 10-21 degrees Celsius. Several sub populations of *P.*

121 *versipora* occur within the Sydney Harbour region, but the overall abundance of this

122 species is unknown. Populations in Sydney Harbour were established as a result of an

123 independent historical in which populations continued to persist over many generations.

124 However, due to the enclosed and branching nature of the Harbour that create dispersal

125 barriers, gene flow is restricted between other populations along the East Australian coast,

126 leading to geographical isolation and possibly genetic divergence. For these reasons, *P.*

127 *versipora* is a useful species for studying and understanding the demographic requirements

128 for range expansion in terms of population persistence in isolated patches.

129

130 This study used a size-based adaption of the Leslie matrix (Leslie 1945) to assess the

131 population dynamics of *P. versipora* specifically located at Fairlight Beach, Sydney

132 Harbour region, Australia. A size-based model was used because corals can undergo

133 several individual-level trajectories that unitary organisms cannot, such as shrinkage,

134 fragmentation and partial mortality (Hughes 1984). For this reason, size is a much better

135 descriptor of demographic rates than age. To determine the demographic mechanisms

136 allowing *P. versipora* to persist in isolated patches, I hypothesized that populations
137 receiving little or no external supply of recruits, must either have:
138 (a) High levels of self-recruitment and/or
139 (b) High levels of survivorship.
140 Population dynamics *P. versipora* was quantified using field estimates of growth rates,
141 mortality rates, fecundity and recruitment, in order to gain insight into the underlying
142 demographic processes that maintain the *P. versipora* population. The study provides a
143 baseline for understanding population resilience in temperate areas and subsequently the
144 likelihood of the persistence of other coral species given range fragmentation under global
145 climate change.
146
147 **Methodology**
148
149 *Study site and field measurements*
150 Demographic rates and size structure were measured for the Sydney Harbour population of
151 *Plesiastrea versipora* at Fairlight Beach, Australia (151°16'32"E, 33°48'1"S). The Fairlight
152 Beach population is the largest of three known sub-populations within the harbor, with
153 high abundances between depths of 5 and 10 meters on the rocky sandstone shelf spanning
154 the bay. The two other, much less abundance sub-populations occur in similar habitats at
155 Camp Cove and Little Manly. Given limitations with replication at these sites, I assumed
156 that the field measurements at Fairlight Beach were representative of the entire Sydney
157 Harbour population.
158
159 To estimate individual demographic rates, three 10 m permanent transects were attached to
160 the rocky substrate on December 7th 2012 (Fig. 1). Transects were censused both after
161 they were attached and one year later on December 13th 2013. The census consisted of 20
162 x 1 m^2 quadrats placed consecutively along each side of the permanent transect line. Four
163 photographs were taken of quadrants within each quadrat, resulting in 80 photographs for
164 each transect. Photographs were corrected for barrel distortion and colonies of *P. versipora*
165 were numbered and outlined using ImageJ. The scale for estimating colony planar area
166 was based on a 25 cm section of the quadrat found in each quadrant photograph. Colonies
167 that died over the year were recorded and new colonies in 2013 less than 10 cm^2 that were
168 clearly not present in 2012 were recorded as recruits. To increase the number of colonies
169 for calculating population size structure, a series of additional 20 x 2 m belt transects were

170   run and 350 colonies were photographed with 10 x 10 cm scale plates. Photographs were

171   corrected for barrel distortion and colonies outlined using ImageJ. Planar areas were

172   estimated based on a 10 cm scale plate.

173

174   *Population matrix modeling*

175

176   Properties of the population were estimated using a size-structured Leslie matrix model

177   (Hughes 1984, Caswell 1989). All colony areas were log10 transformed and size structure

178   data were used to delineate seven equally spaced size classes spanning the range of planar

179   areas in the population (Fig. 2). Size class I was defined as the recruitment class, ranging

180   between 3.16 to 10cm^2. No colonies were observed for size classes VI and VII, but classes

181   were included to allow for potential growth in the model.

182

183   To parameterize the growth component of the matrix model, size of colonies in the second

184   year were modeled as a linear function of size in the initial year using the *lm* function in

185   the statistical software R (R Development Core Team). The probability of moving from a

186   given size class in the initial year to neighboring size classes in the second year was then

187   estimated by calculating the normal probability distribution from the linear model for the

188   initial year size class mid-points, and then numerically summing the parts of this

189   distribution that fell into the prescribed size class bins (Table 1; Supplementary material

190   1).

191

192   To parameterize the survival component, survival of colonies in the second year was

193   modeled as a function of size in the initial year using a generalized linear model (function

194   *glm* in R) with binomial response and logit link function. Similarly to growth, the

195   binomial probability distribution of yearly survival for size class midpoints was summed

196   for size class bins (Supplementary material 1).

197

198   Given that fecundity per polyp is independent of colony size (Madsen et al. 2014) and the

199   population was considered closed (i.e. not influenced by external recruitment), recruitment

200   was modeled as a function of colony size, given by:

201   Recruitment $= qx$

202   Where x is colony size and q is the number of successful recruits per unit area of coral that

203   fell into size class 1 at t+1. q was estimated in two ways. First, the year's field observed

204   number of recruits was divided by the total area of coral within the permanent transects to

205   give a *short-term* estimate of q. Second, by finding the *q* that gave the best-fit between the

206   model eigenvector (i.e. stable size distribution) and the empirical population size structure

207   measured in the field to give a *long-term* estimate of *q (*Fig.2). The fit was assessed using

208   maximum log-likelihood and the function *optim* in R (Supplementary material 1). The

209   latter recruitment calculation gives the best estimate of the mean recruitment that give rise

210   to the empirical size structure at the study site.

211

212   The growth, survival and recruitment components were combined to form the transition

213   matrix (M), where:

$$M = growth \times survival + recruitment$$

214   The intrinsic growth rate of the population is given by the dominant eigenvalue (λ), which

215   was calculated using the function *eigen* in R. The relative effects of matrix transition

216   probabilities on the intrinsic growth rate (i.e. elasticities) were calculated using the *elas*

217   function in the *popbio* package in R (Stubben and Milligan 2007)

218

219   **Results**

220

221   5 size classes were derived from the 350 colonies measured independently and another 2

222   larger size classes to allow for potential growth (Fig 2). Size structure indicated majority of

223   colonies fell into size class II and III with the lowest proportion of colonies in size class V.

224   Of the 84 colonies tracked on the permanent transect, five were dead after a year.

225   Additionally, 11 new recruits were found. Asexual reproduction and fusion was not

226   observed in the field after one year. For the 79 colonies found in both years, their planar

227   areas were log-transformed and the best-fit relationship between areas a t and t+1 was

228   (Table 2; Fig. 3**)**:

229

$$X_{t+1} = 0.29 \times 10^{0.87 x_t}$$

230

231   where the positive intercept showed positive growth on average when colonies are small,

232   but the exponent below 1 indicates slower growth for larger individuals until a maximum

233   size is reached (i.e., where the mode lines crosses the unity line in Fig. 3).

234

235   Overall, yearly survivorship was high at approximately 95%. There was also a significant

236   relationship between colony size and survivorship (p=0.0124, *df*=71) (Table 2; Fig. 4),

237   where larger colonies were more likely to survive.

238

239   The empirically-derived short-term recruitment parameter *q* was 0.0051 where every 1 m^2

240   of coral cover contributed 5.1 recruits on average in the following year. The recruitment

241   parameter derived from fitting the model eigenvector to the empirical size structure was

242   estimated to be lower at *q* = 0.0015, where every 1 m^2 of coral cover contributed 1.5

243   recruits on average in the following year.

244

245   The final transition matrix indicated that corals tended to stay in the same size class after

246   each year (Fig. 5). However, smaller colonies were more likely to grow and move to the

247   larger sizes. Whereas, medium size colonies were more likely to stay in the same size

248   class, while larger colonies had a higher probability of shrinking to smaller size classes.

249

250   The dominant eigenvalue based on the short-term recruitment parameter was λ=1.071

251   suggesting a doubling of the unconstrained population every 10 years. The dominant

252   eigenvalue for this population, based on the model-derived long-term recruitment

253   parameter, was λ=1.023, suggesting a doubling of the unconstrained population every 30

254   years.

255

256   Using the long-term recruitment parameter, model elasticities indicated λ to be particularly

257   sensitive to growth and survivorship in size classes III and IV (Fig. 6). Moreover,

258   elasticities indicated recruitment was relatively unimportant to population intrinsic growth

259   rate. Results were similar for empirically derived short-term recruitment (Supplementary

260   material 2).

261

262   **Discussion**

263

264   The intrinsic demographic capacities for isolated populations to grow are largely

265   dependent on tradeoffs associated with survivorship and recruitment. This study used a

266   size-based population model to assess these trade-offs in a genetically isolated population

267   of the temperate coral species *Plesiastrea versipora*. It was found that the majority of the

268   colonies tended to remain in the same size class after one year. Additionally, the field

269   calibrated transition matrix indicated the long-term population growth rate was λ=1.023
270   with a relatively slow doubling of unconstrained densities every 30 years. Since the
271   population growth was characterized by relatively low rates of recruitment (Fig. 6) and
272   survivorship increased with larger size classes (Fig. 4), this support the hypothesis that *P.*
273   *versipora* populations in isolated patches are characterized by high survivorship. The
274   population also appears to be largely independent of recruitment. The results of this study
275   are as discussed below.

276

277   Population size structure of *P. versipora* appears to be independent of the normal size
278   frequency distribution for corals despite the exclusion of colonies below 3.16cm^2.
279   Population size structure is likely species-specific and variation between species can be
280   explained by differences in life histories processes such as growth, partial mortality, whole
281   colony mortality and recruitment (Meesters et al. 2001). This was observed in Meesters
282   (2001) where size structure patterns were consistent for the same species across different
283   sites but not consistent among different species.

284

285   Elasticity analysis indicated the persistence of this population was largely dependent on
286   survivorship (Fig. 6). Population growth (λ) was most sensitive to survivorship in size
287   classes III and IV and to a lesser extent size class II, suggesting that small changes in the
288   survival of these classes would critically impact population growth the most. Similar trends
289   in size specific mortality in corals have been found in previous studies where the highest
290   probability of whole colony mortality mostly occurred in smaller colonies (Connell 1973,
291   Hughes 1984, Babcock 1991). However these trends are not always limited to whole
292   colony mortality; Babcock (1991) showed partial mortality, particularly in larger size
293   classes, also contributed a significant proportion of overall tissue loss. As a corollary,
294   larger classes with partial mortality would be expected to show higher survivorship
295   because a proportion of a colony would remain unaffected (Hughes & Jackson 1980,
296   1985). Since *P. versipora* may exist as the result of sporadic recruitment events, survival in
297   larger classes therefore, may be crucial and key to the persistence of this population.

298

299   The survival rate for this study was approximately 95 percent (~5% mortality) indicating
300   the *P. versipora* population is stable. Mortality was significantly higher in smaller colonies
301   (Fig. 4). This result seems consistent with the annual survivorship rates in previous
302   literature, suggesting increased survivorship as a function of colony size (Hall & Hughes

303   1996, Harriott et al. 2002, Vermeij & Sandin 2008). Harriott et al. (2002) also documented

304   low mortality rates between 0.7 and 2.0 corals/m^{-2}/yr^{-1} for corals in the Solitary Islands

305   Marine Park, but reported high mortality rates for encrusting, planulating species. Since *P.*

306   *versipora* colonies can range from encrusting to massive forms (Burgess et al. 2009), the

307   relationship between growth and survivorship is remains inconclusive.

308

309   Results indicated mortality was 5 percent, however this may likely be underestimated due

310   to discrepancies in photographs that limit visibility and locality of colonies over the study

311   period. Juvenile survivorship is highly variable over space and time (Irizarry-Soto & Weil

312   2009), such that survivorship may be driven by the interaction with other organisms and

313   habitat quality (Glassom & Chadwick 2006). Sources of mortality in high latitude benthic

314   communities have been attributed to competition with macroalgae species and filter

315   feeders as well as cold water and high nutrient influxes (Richmond 1993, Kleypas et al.

316   1999, Harriott et al. 2002). During censuses, *P. versipora* colonies were surrounded by

317   macroalgae and filter feeders, but the proportion of macroalgae to coral planar areas was

318   not empirically defined. It is unknown whether macroalgae has impact on colony radial

319   growth. Furthermore, given that photographs were taken with poor lighting, it was difficult

320   to accurately identify all survivors after one year. Survivorship exhibited for larger corals

321   was 100 percent, but does not account for individual colony tissue loss resulting from

322   partial mortality, which would otherwise contribute to overall mortality rates (Hughes &

323   Jackson 1980). To account for the possible discrepancies within the data, mortality rate

324   was also increased by 10 percent in the final transition matrix. The resulting dominant

325   eigenvalue was λ=0.923 with suggested population half-life of 9 years. This confirms that,

326   even with a temporary increase in mortality the population is able to persevere for a

327   number of years.

328

329   The elasticity analysis indicated recruitment was relatively unimportant compared to the

330   survivorship of colonies in terms of population persistence. This was a good sign given

331   that the recruitment rate was quite low with an average of 1.5 recruits/m^{-2}/yr^{-1}, consistent

332   with species characterized by high longevity in high latitudes (Nozawa et al. 2006,

333   Kersting & Linares 2012). Result showed similarities with that of subtropical coral

334   communities in Solitary Islands Marine Park, where recruitment rates averaged 1.3 to 1.8

335   recruits/m^{-2}/yr^{-1} (Harriott et al. 2002). But was relatively high compared to the cold water

336   species *Cladocora caespitosa* where the recruitment rate was between 0.31 and 0.33

337 recruits/m^{-2} /yr^{-1}. Comparatively, annual recruitment is greater for tropical corals, with
338 recruitment ranging between 1.7 and 12.7 recruits m^{-2} yr^{-1} (Connell et al. 1997). However it
339 should be pointed out that comparisons between the recruitment rates across studies are
340 somewhat ambiguous due to differences in assumptions and methodologies (Harriott &
341 Banks 1995).

342

343 Recruitment in the marine environment varies greatly on spatial and temporal scales
344 (Connell 1997). For example, habitat substrate type and orientation as well as presence of
345 other organism on substratum surfaces may influence larval settlement preferences in
346 corals (Glassom & Chadwick 2006). Similarly, variation in environmental conditions such
347 as seawater temperature, water quality and flow may influence larval settlement (Caley et
348 al. 1996). Due to those reasons, recruitment rates are expected to vary depending if
349 favorable conditions are met. Although fitting the eigenvector to the *P. versipora*
350 population size structure that has accumulated over many years of recruitment events gives
351 the recruitment estimate, interannual variation and seasonal patterns in recruitment rates
352 are expected and corresponds to good and bad years of reproductive output (Connell et al.
353 1997, Glassom & Chadwick 2006). Considering the latter, this study also estimated actual
354 recruitment rates of *P. versipora* based on field observations (short-term). The resulting
355 recruitment rate was 5.1 recruits m^{-2} yr^{-1}, which is considerably higher than the long-term
356 recruitment estimate and perhaps linked to a good year. This also had a significant affect
357 on the population growth rate, where $\lambda=1.071$ with a suggested doubling of the population
358 every 10 years. Peak in recruitment may very well be the result of greater surface areas
359 available for settlement and reduced algal activity coupled with favorable environmental
360 conditions.

361

362 This study found the resilience of *P. versipora* in Sydney Harbour was attributed to the
363 faster growth of smaller colonies that reduces early life mortality rates and very high
364 survivorship in larger, slow growing colonies, which together buffered low recruitment
365 rates. Although, isolated populations are generally expected to be self-recruiting (Swearer
366 et al. 2002), it seems *P. versipora* colonies at Fairlight beach is not reliant on high levels of
367 recruitment for persistence, but rather high survivorship. Furthermore, given that the
368 population is geographically isolated accentuating bottlenecks in gene flow (Rodriguez-
369 Lanetty & Hoegh-Guldberg 2002), survival in larger colonies seems to be the key limiting
370 factor in determining population persistence.

371

372 The next step would be to assess the population dynamics of *P. versipora* over multiple

373 generations that take into account extrinsic factors such as environmental conditions that

374 decouple the effects of change. It is possible that the intrinsic population growth predicted

375 from model reflected a good year, but does not denote possible changes in population

376 dynamics that reflect ecological and environmental variables that would occur over

377 multiple years. This is important since populations in coastal temperate locations are

378 subjected to greater variation in conditions that reflect environmental and anthropological

379 perturbations (Halfar et al. 2005, Halpern et al. 2008). Furthermore, there are limitations

380 associated with this population model, which include the assumption that populations are

381 'closed' and not influenced by external recruits and the practicality of estimating

382 recruitment rate in terms of size structure rather than the latter observed recruitment.

383 Ideally, the population model used in this study can be augmented to understand the

384 population dynamics of other isolated metapopulations within the Sydney region and their

385 connectivity in terms of recruitment.

386

387 The success of sub-populations outside species' present geographical ranges is conditional

388 on the intrinsic capacity for a population to grow in a new patch and is made up of

389 variations in mortality and recruitment. This study has shown that a population modeling

390 approach can provide useful insight into the important demographic strategy that allow

391 isolated coral reef populations to persist outside native ranges. The demographic fate of an

392 individual or population can be accurately predicted using size related classification

393 Finally, it can be elucidated from this study that the dispersal of marine organisms to

394 temperate locations, resulting in regional isolation, may require population-specific

395 survival strategies (Baums et al. 2005). More specifically, high level of survivorship that

396 buffers low recruitment as well as rapid juvenile growth. In summary, this is the first study

397 that specifically addressed the persistence of corals in temperate locations using population

398 models and may contribute to the testing of population parameters among other sites.

399

403

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533

534   **Tables**

535 **Table 1:** *P. versipora* size classes given by unconstrained colony planar areas.

Size class	Planar areas (cm^2)
I	3.16 – 10
II	10 – 31.62
III	31.62 – 100
IV	100 – 316.23
V	316.23 – 1000
VI	1000 – 3162.28
VII	3162.28 - 10000

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Table 2. Results from linear models for growth and survivorship

	df	SE	*p*
Growth	43	0.844	<0.005
Survivorship	71	2.010	0.0124

541

542   **Figure legends**

543   Figure 1: Aerial view of Fairlight beach, Sydney Harbour, Australia. Solid lines represent

544   transects 1, 2 and 3

545

546   Figure 2: Proportion of colonies in each size class. Line indicates best fit for size structure

547   with the model eigenvector for q= 0.0015 recruits/cm^2. Shaded parts indicate upper and

548   lower 95 % confidence intervals.

549

550   Figure 3: Linear regression of *Plesiastrea versipora* colony growth at Fairlight beach. Each

551   individual graph point represents a colony's size at t and one year later at t+1. Solid lines

552   represents mean model estimate and light grey lines indicate 95 % confidence intervals.

553   The dotted line is the unit line that indicates unchanged colony size.

554

555   Figure 4: Logistic regression of *Plesiastrea versipora* survivorship as a function of colony.

556   Each point represents an individual colony's size at time t and if it survived (1) or died (0)

557   at t+1. Solid line is the model mean fit and dashed lines are 95 % confidence intervals

558

559   Figure 5: Transition matrix of size class probabilities for *Plesiastea versipora* for model-

560   derived recruitment q = 0.00015 recruits/cm^2. The top row represents yearly recruitment

561   attributed to each size class. The main diagonal is the yearly probability of colonies

562   remaining in the same size class. Cells above this diagonal indicate shrinkage or

563   fragmentation and those below the diagonal indicate growth to larger size classes.

564

565   Figure 6. Elasticity analysis quantifying the sensitivity of lambda (λ) to changes in cell

566   probabilities weighted by their magnitude. Red shading indicates higher levels of

567   sensitivity to change.

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FIGURES

Figure 1

Figure 2

Colony growth

Figure 3

Survival
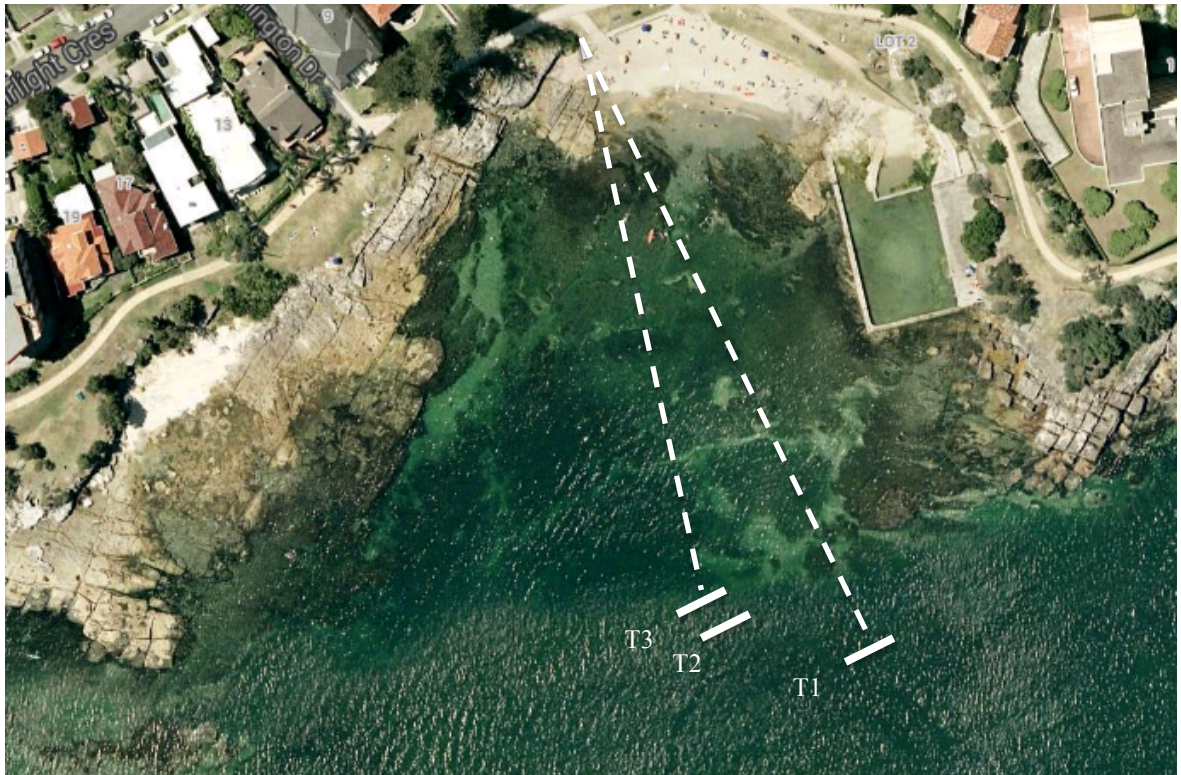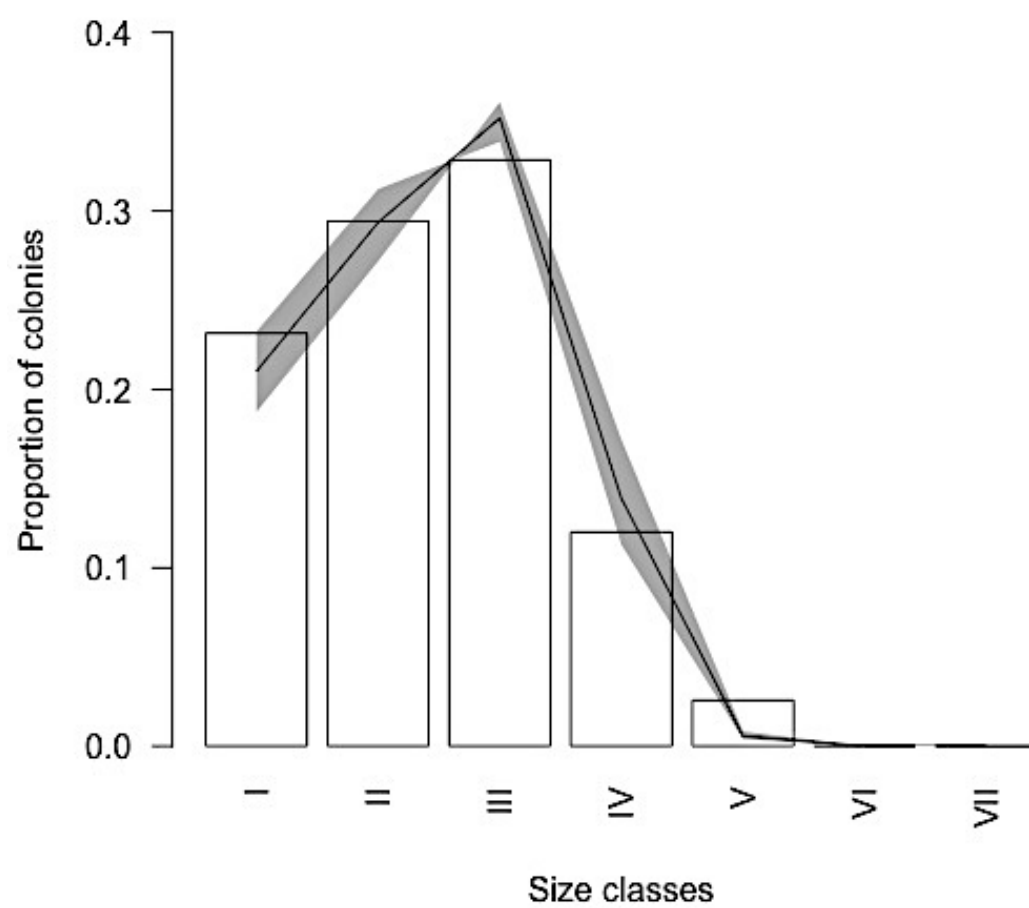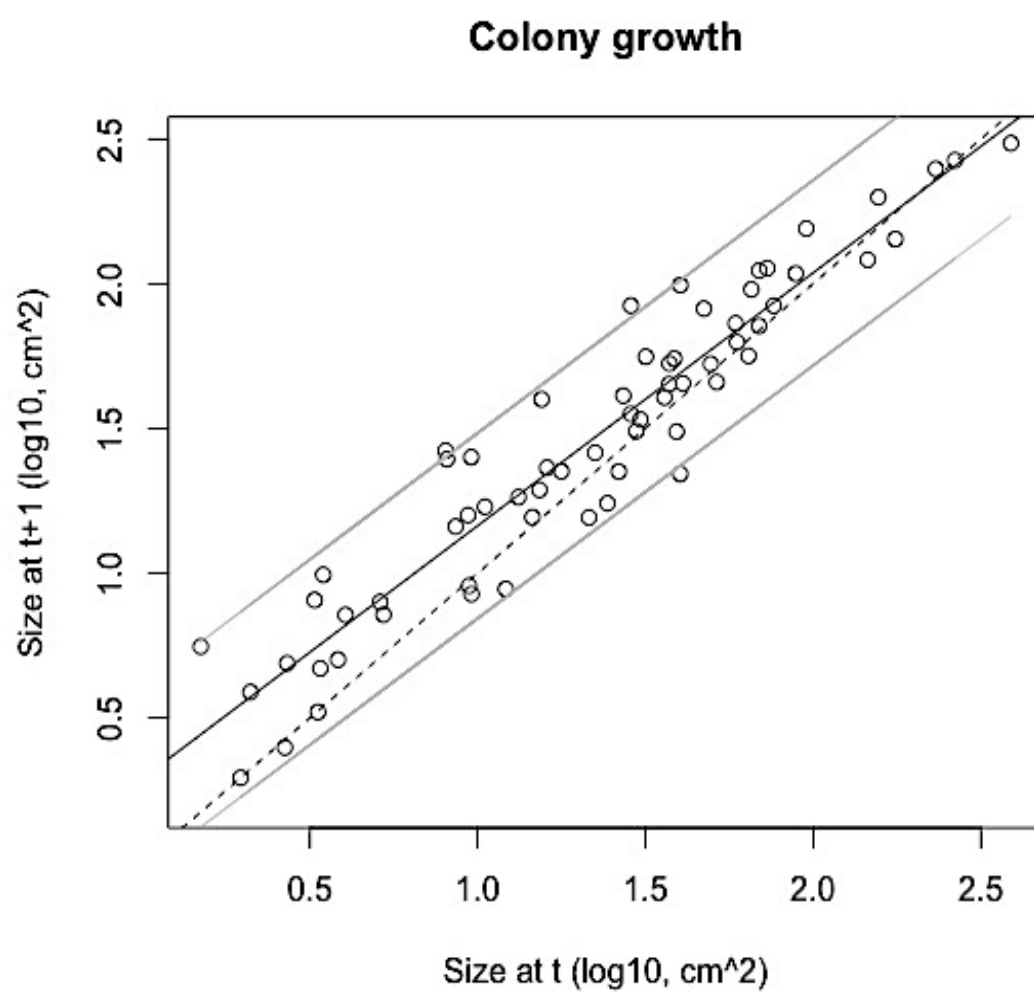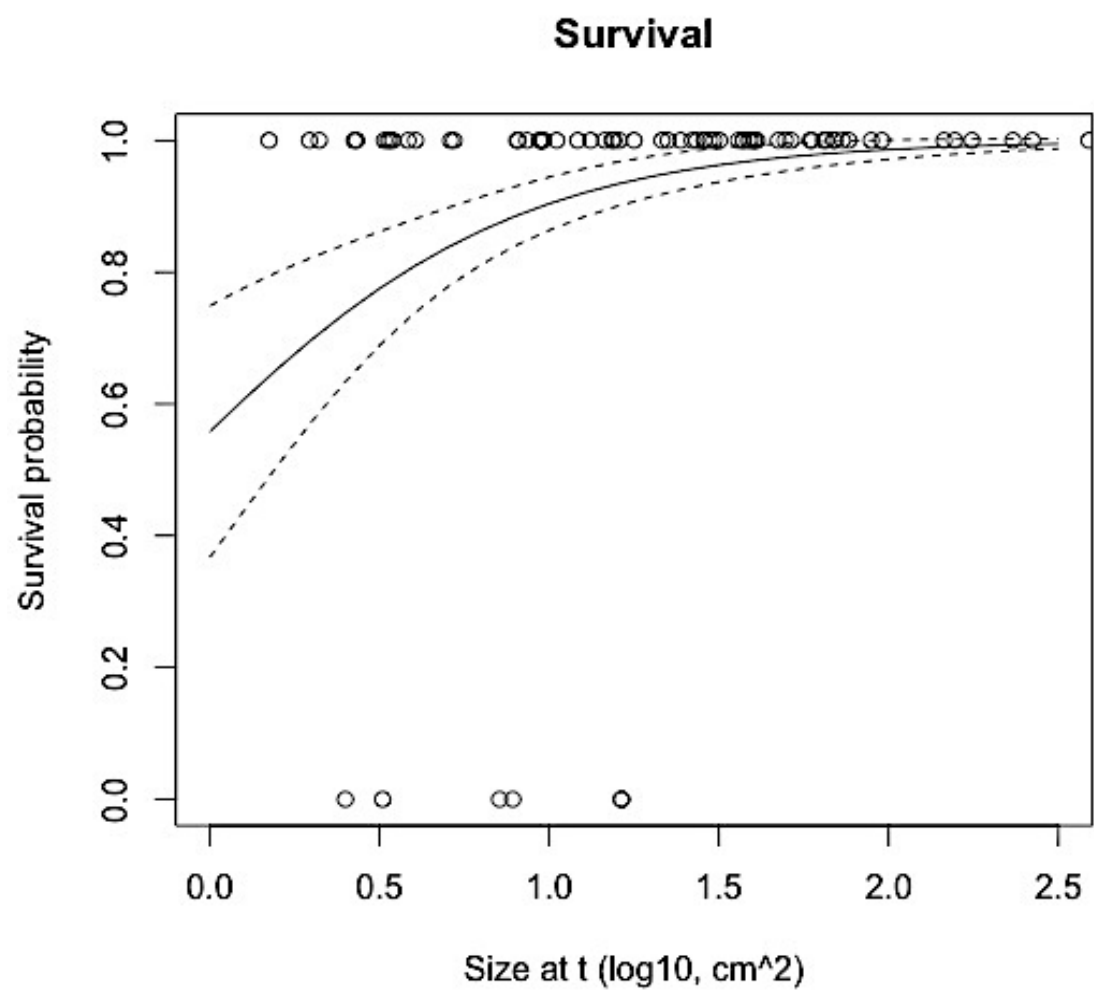
Figure 4

Coral transition matrix

	_	=	≡	≳	<	≤	≦
I	0.643	0.027	0.085	0.269	0.849	2.686	8.494
II	0.216	0.869	0	0	0	0	0
III	0	0.071	0.964	0.001	0	0	0
IV	0	0	0.013	0.989	0.009	0	0
V	0	0	0	0.001	0.988	0.055	0
VI	0	0	0	0	0	0.944	0.205
VII	0	0	0	0	0	0	0.794

Figure 5

22

Coral elasticity matrix

	_	=	≡	≧	<	≦	≦≦
I	0.039	0.002	0.009	0.011	0.001	0	0
II	0.023	0.131	0	0	0	0	0
III	0	0.021	0.342	0	0	0	0
IV	0	0	0.012	0.364	0	0	0
V	0	0	0	0.002	0.043	0	0
VI	0	0	0	0	0	0	0
VII	0	0	0	0	0	0	0

Figure 6

Supplementary material 1

R Script for population matrix modeling

Packages

if (!"popbio" %in% rownames(installed.packages())) install.packages("popbio", repos="http://cran.csiro.au", dependencies=TRUE)

library(popbio)

if (!"stats4" %in% rownames(installed.packages())) install.packages("stats4", repos="http://cran.csiro.au", dependencies=TRUE)

library(stats4) # for mle

Size structure

Input size structure data based on planar areas of unconstrained colonies

ss = read.delim("data/sizestructure_output.txt", as.is = T)

hh = hist(log10(ss$area_T), breaks = seq(-0.5, 4, 0.5))

Smaller classes 1 -3 were grouped due to undersampling of these classes

hh = hh$counts

hh[3] = sum(hh[1:3])

hh = hh[3:9]

Population size classes given by log10

This means that the "recruitment" class is 3 to 10 cm^2 (or 10^0.5 to 10^1 is log10 space)

ends = seq(0.5, 4, 0.5)

mids = seq(0.75, 3.75, 0.5)

Growth

Input of individual demographic rates, i.e. colony planar areas for 2012 and 2013

tag_dat = read.delim("data/Colony_areas_outlined.txt", as.is = T)

x = tag_dat$x[!is.na(tag_dat$y)]

y = tag_dat$y[!is.na(tag_dat$y)]

Planar areas for 2012 and 2013 log transformed.

```
x = log10(x)
y = log10(y)
mod <- lm(y ~ x)
```

Parameterization of the growth component of the matrix model using a linear function; Roman numerals represent size classes.

```
lm(x, y, xlab = "Size at t (log10, cm^2)", ylab = "Size at t+1 (log10, cm^2)", main = "Colony growth")
abline(mod)
abline(0, 1, lty = 2)
lines(x, predict(mod, list(x)) + 1.96*sd(residuals(mod)), col=("grey"))
lines(x, predict(mod, list(x)) - 1.96*sd(residuals(mod)), col=("grey"))

G = matrix(0, length(mids), length(mids))
rownames(G) = colnames(G) = 1:length(mids)
rownames(G) = colnames(G) = c("I", "II", "III", "IV", "V", "VI", "VII")

for (x in 1:length(mids)) {
  z = seq(-0.5, 4, 0.001)
  p = dnorm(z, predict(mod, list(x=mids[x])), sd(residuals(mod))/2)
  for (y in 1:length(mids)) {
    G[y,x] = sum(p[z >= mids[y]-0.25 & z < mids[y]+0.25])/sum(p)
  }
}
```

Growth matrix

```
image2(G, mar=c(1,3.5,5,1), box.offset=.1)
title("Growth matrix", line=2.5)
```

Survivorship

Parameterization of the survivorship component of the matrix model using a general linear model with a binomial response and logistic function of the initial year

```
tag_dat$x_log10 <- log10(tag_dat$x)
```

```
sur_mod = glm(Survival ~ x_log10, family = binomial, data = tag_dat)
summary(sur_mod)
ss = seq(0, 2.5, 0.1)

est <- predict(sur_mod, list(x_log10=ss), type="response", se.fit=TRUE)

plot(Survival ~ x_log10, data = tag_dat, xlim=c(0, 2.5))
lines(ss, est$fit)
lines(ss, est$fit + est$se.fit, lty=2)
lines(ss, est$fit - est$se.fit, lty=2)

pred = sur_mod$coef[1] + sur_mod$coef[2] * mids
est <- exp(pred) / (1 + exp(pred))

S = matrix(est, length(mids), length(mids), byrow = T)
rownames(S) = colnames(S) = 1:length(mids)
rownames(S) = colnames(S) = c("I", "II", "III", "IV", "V", "VI", "VII")
```

Survival matrix
image2(S, mar=c(1,3.5,5,1), box.offset=.1)
```
title("Survival matrix", line=2.5)
```

Recruitment
Recruitment was modeled as a function of colony size; q was estimated in two ways
Recruitment based on field observations
```
recr <- 11
total_area_pop <- sum(dat[,3], na.rm=T)
q_field <- recr/total_area_pop
```

Recruitment best fitted to model stable and field size structure.
Fit was assessed using the maximum log likelihood function optim

```
R <- function(q) {
```

```
 R = matrix(0, length(mids), length(mids))

 R[1,] = q * 10^mids

 rownames(R) = colnames(R) = 1:length(mids)

 return(R)

}


fit <- function(q) {

 M = G*S+R(q) # growth x survival + recruitment

 pre = abs(Re(eigen(M)$vectors[,1])) / sum(abs(Re(eigen(M)$vectors[,1])))

 obs = hh #/ sum(hh)

#  bb <- barplot(c(obs / sum(obs)), ylim=c(0, 0.4))

#  lines(bb[1:7], pre)

 return(-sum(obs * log(pre)))

}
```

The number of successful recruits per unit area of corals into class 1 in t+1 is given by q

```
q = optimise(fit, c(0.0001, 0.01))$minimum

q_mle = mle(fit, start=list(q=2))


q = q_mle@coef

q_ci=confint(q_mle)

sum(dat[,3], na.rm=TRUE) * q

sum(dat[,3], na.rm=TRUE) * q_ci[1]

sum(dat[,3], na.rm=TRUE) * q_ci[2]


bb <- barplot(c(hh / sum(hh)), ylim=c(0, 0.4), names.arg=c("I", "II", "III", "IV", "V", "VI",
"VII"), las=2, col="white", ylab="Proportion of colonies", xlab="Size classes")

M = G*S+R(q) # growth x survival + recruitment

pre = abs(Re(eigen(M)$vectors[,1])) / sum(abs(Re(eigen(M)$vectors[,1])))


Ml = G*S+R(q_ci[1]) # growth x survival + recruitment

prel = abs(Re(eigen(Ml)$vectors[,1])) / sum(abs(Re(eigen(Ml)$vectors[,1])))

Mu = G*S+R(q_ci[2]) # growth x survival + recruitment

preu = abs(Re(eigen(Mu)$vectors[,1])) / sum(abs(Re(eigen(Mu)$vectors[,1])))
```

polygon(c(bb, rev(bb)), c(prel, rev(preu)), col=rgb(0, 0, 0, 0.4), border=NA)

lines(bb[1:7], pre)

Recruitment matrix

image2(R(q_ci), mar=c(1,3.5,5,1), box.offset=.1)

title("Recruitment matrix", line=2.5)

Final transition model

M = G*S+R(q_field)

x survival + recruitment

rownames(M) = colnames(M) = 1:length(mids)

rownames(M) = colnames(M) = c("I", "II", "III", "IV", "V", "VI", "VII")

Mu <- G*S+R(q_ci[2])

rownames(Mu) = colnames(Mu) = 1:length(mids)

Ml <- G*S+R(q_ci[1])

rownames(Ml) = colnames(Ml) = 1:length(mids)

Transition matrix

image2(M, mar=c(1,3.5,5,1), box.offset=.1)

title("Coral transition matrix", line=2.5)

The estimated population intrinsic growth rate was given by dominant eigenvalue

lam = Re(eigen(M)$values[1])

lamu = Re(eigen(Mu)$values[1])

laml = Re(eigen(Ml)$values[1])

The number of years it would take an unconstrained population to double in size

years_double = log(2)/log(lam)

years_doubleu = log(2)/log(lamu)

years_doublel = log(2)/log(laml)

Increased mortality

Mortality increased by 10 percent in the final transition matrix

M_im = G*(S*0.9)+R(q)

x survival + recruitment

rownames(M_im) = colnames(M_im) = 1:length(mids)

Mu_im <- G*(S*0.9)+R(q_ci[2])

rownames(Mu_im) = colnames(Mu_im) = 1:length(mids)

Ml_im <- G*(S*0.9)+R(q_ci[1])

rownames(Ml_im) = colnames(Ml_im) = 1:length(mids)

Final transition matrix with increased mortality

image2(M_im, mar=c(1,3.5,5,1), box.offset=.1)

title("Coral transition matrix, increased mortality", line=2.5)

Resulting dominant eigenvalue after increasing mortality

lam_im = Re(eigen(M_im)$values[1])

lamu_im = Re(eigen(Mu_im)$values[1])

laml_im = Re(eigen(Ml_im)$values[1])

The resulting number of years it would take an unconstrained population to double in size after increasing mortality

years_half = log(0.5)/log(lam_im)

years_halfu = log(0.5)/log(lamu_im)

years_halfl = log(0.5)/log(laml_im)

Elasticity

This is the sensitivity of the eigenvalue to changes in the demographic contributions

elas = elasticity(M)

image2(elas, mar=c(1,3.5,5,1), log=FALSE)

rownames(M) = colnames(M) = 1:length(mids)

rownames(M) = colnames(M) = c("I", "II", "III", "IV", "V", "VI", "VII")

title("Coral elasticity matrix", line=2.5)

Supplementary material 2

Coral elasticity matrix

	_	=	≡	≳	<	≤	≦
I	0.085	0.012	0.026	0.013	0.001	0	0
II	0.052	0.223	0	0	0	0	0
III	0	0.04	0.356	0	0	0	0
IV	0	0	0.014	0.169	0	0	0
V	0	0	0	0.001	0.009	0	0
VI	0	0	0	0	0	0	0
VII	0	0	0	0	0	0	0

Supplementary material 3.a

Colony planar areas (cm^2) for 2012 and 2013, 'NA' indicates colonies not present.

2012	2013	Survival			
			5.115119588	7.943739859	1
37.30336136	53.00569522	1	2.66208331	2.499522764	1
30.56114099	33.94972632	1	10.51114613	16.96088754	1
40.16950236	22.0068747	1	2.100269409	3.881642526	1
22.38951077	26.06858978	1	9.421891357	9.044410115	1
24.3720643	17.42881545	1	9.582721793	8.462317214	1
NA	20.48995298	1	2.702892932	4.881526824	1
26.3507183	22.4476169	1	16.30708888	NA	0
1.965459956	1.963660986	1	37.20787528	44.9599367	1
14.55795857	15.61367541	1	264.7637839	267.0346177	1
28.60354206	35.52144854	1	36.03012749	40.4948233	1
12.12442339	8.813509455	1	21.47831209	15.57190122	1

5.23832188	7.18523621	1
8.598973811	14.49161379	1
NA	1.625585763	1
NA	2.643523698	1
NA	3.44701441	1
17.76765782	22.47211067	1
27.16484549	41.04660419	1
40.91959425	45.24701849	1
39.1690296	30.83715945	1
64.21406834	56.32861887	1
8.099071683	24.75736579	1
3.463516532	9.868814411	1
16.09585475	23.14024655	1
9.358764033	15.86721909	1
NA	5.261555855	1
3.395512483	4.685733465	1
1.493744097	5.576474649	1
15.28349016	19.39375232	1
38.54248508	55.09537524	1
15.50694647	39.86979324	1
NA	2.645292741	1
NA	2.301330999	1
88.7740582	108.3796743	1
NA	5.035042166	1
NA	2.649445635	1
69.00741331	71.49927871	1
145.5429039	120.963363	1
4.037758031	7.171844466	1
175.8265276	142.6202478	1
49.54631138	52.818652	1
3.341427309	3.313118424	1
NA	5.859820086	1
3.229650697	NA	0
7.80122555	NA	0

58.73956448	72.90735144	1
NA	7.311895943	1
76.28078809	83.92645158	1
65.44533733	95.58973366	1
95.41078249	155.0801232	1
156.467323	198.9978956	1
28.61827924	84.08971961	1
69.06675153	111.05489	1
13.23777537	18.30194169	1
3.265177951	8.072717196	1
40.191661	98.93210197	1
9.565448352	25.15470793	1
8.024893577	26.49410974	1
73.03123846	113.1188261	1
51.59122466	45.71204687	1
59.3265188	62.80494563	1
232.1702821	249.2712152	1
29.70637088	30.97687618	1
3.83435151	5.027631596	1
31.7220799	55.96849807	1
47.26018869	81.99649151	1
388.822845	305.8117941	1
2.505595831	NA	0
0.147502617	NA	0
16.34211076	NA	0
7.138531416	NA	0

Supplementary material 3.b

Size structure given by planar areas of unconstrained colonies

Colony no.	Area
1	15.18327821
2	4.324705918
3	42.63932904
4	1.019824475
5	30.09062596
6	14.24034118
7	6.51150429
8	11.19674994
9	1.745766573
10	11.85500753
11	7.368063462
12	108.5011555
13	9.457650123
14	77.36237833
15	23.37822147
16	42.22303557
17	49.83971527
18	32.12951511
19	48.15230835
20	76.76691824
21	59.32175581
22	2.659327359
23	36.50439503
24	2.916366126
25	5.444270572
26	3.087298928

27	2.847947675	77	3.69868063	127	17.08726841
28	13.42692637	78	35.56179488	128	50.08842753
29	26.65306924	79	9.373330065	129	19.71809412
30	52.72256633	80	17.00043078	130	16.79456898
31	5.546968892	81	106.318241	131	23.40566324
32	1.201523066	82	8.574950745	132	64.35217097
33	42.17297551	83	42.75465478	133	5.7735256
34	149.1340433	84	1.639328609	134	11.03360384
35	11.41741582	85	6.850078968	135	15.75970909
36	71.38799168	86	9.891354375	136	199.0285731
37	13.00455035	87	41.15979285	137	180.3836159
38	3.443219214	88	27.81645288	138	442.9061997
39	87.97702211	89	1.480222592	139	11.88056744
40	121.802725	90	9.352262918	140	7.695924341
41	31.88854598	91	5.16904958	141	32.79191845
42	119.2046012	92	8.208199217	142	16.75909012
43	21.09209511	93	16.72630187	143	43.36786506
44	2.582591008	94	7.094093869	144	22.03488552
45	30.50782072	95	17.46520053	145	46.73123602
46	138.8754196	96	7.719061845	146	9.671613972
47	42.46919657	97	75.49965042	147	59.32726966
48	1.061952463	98	24.32844629	148	24.82821598
49	3.389555373	99	22.06122637	149	9.403517655
50	18.97166556	100	1.823817105	150	5.654105337
51	291.333672	101	48.61080995	151	17.8682507
52	19.38063246	102	28.32491214	152	12.12343134
53	6.094182825	103	193.7225581	153	8.535254903
54	56.92925842	104	4.678931269	154	180.7045313
55	41.56295062	105	8.660749594	155	22.39890327
56	475.2922482	106	2.53199089	156	44.87463078
57	34.77789133	107	13.25525674	157	37.29022345
58	28.99732602	108	43.27710211	158	25.24404943
59	1.785689286	109	1.509931926	159	43.47854882
60	72.6664423	110	8.650364476	160	25.41889082
61	17.18072998	111	67.22083825	161	11.20231964
62	23.04844535	112	15.36331794	162	9.339434856
63	69.83620112	113	30.24393803	163	44.51276939
64	57.20801419	114	81.38434224	164	12.97154271
65	0.416799175	115	8.471506837	165	37.7068026
66	3.277695863	116	11.41204319	166	18.69537704
67	8.788278868	117	80.99990058	167	32.14941114
68	3.54271268	118	13.71363625	168	11.07857268
69	11.78683238	119	6.715353179	169	2.279135173
70	8.559345307	120	12.51823729	170	55.01810512
71	17.02594763	121	59.24545599	171	132.2170882
72	5.706439439	122	3.661555768	172	261.9249301
73	2.845373443	123	34.99780652	173	14.45737838
74	2.089463236	124	23.88746217	174	8.262079526
75	7.112711701	125	84.92124132	175	11.92158337
76	5.04873786	126	11.87366465	176	9.889646382

177	84.56608151	227	43.96924202	277	47.24849925
178	466.0842575	228	126.0599866	278	44.76819096
179	11.49383129	229	32.67319618	279	267.2718593
180	135.0736609	230	20.76933525	280	74.44223012
181	189.4209771	231	15.89697779	281	108.1540299
182	11.18050807	232	55.25983757	282	5.017545267
183	99.09338347	233	70.96410314	283	99.36162083
184	45.67729974	234	92.57584109	284	113.1862286
185	310.3527849	235	67.46036689	285	29.16495095
186	259.241703	236	9.794114201	286	269.7595177
187	11.42267864	237	25.38825893	287	166.7871733
188	90.28573884	238	66.08104457	288	33.20528069
189	75.4152881	239	185.8644102	289	25.0722128
190	67.33081253	240	59.08583336	290	47.45467846
191	58.17170111	241	130.7473538	291	58.34850918
192	61.33459374	242	38.41350081	292	69.45858653
193	59.76496369	243	40.59384167	293	21.70627162
194	27.96158639	244	227.6805449	294	16.45910431
195	40.90018476	245	30.39970203	295	1.739977579
196	44.93275469	246	107.5879208	296	3.68289085
197	76.46882569	247	28.63741784	297	2.310353161
198	67.58346026	248	29.29649843	298	0.612671995
199	56.89780019	249	62.50559961	299	5.418676893
200	53.57749257	250	48.12310877	300	4.857369186
201	39.6601663	251	17.18382162	301	36.36118011
202	56.16994182	252	42.74501556	302	28.0327605
203	27.21790806	253	27.73829282	303	36.65338923
204	38.4316712	254	18.32467304	304	4.512724588
205	347.7352743	255	33.36268455	305	21.33816031
206	16.57844141	256	10.24137638	306	57.21794845
207	62.83374965	257	180.4912235	307	19.77012782
208	185.794839	258	41.72503145	308	5.553057094
209	103.4342816	259	6.152091293	309	11.76491713
210	48.91979744	260	22.21472044	310	31.09710052
211	114.9362916	261	18.86606554	311	6.630767471
212	25.82013281	262	14.6343327	312	11.14666529
213	48.99824033	263	29.69355685	313	59.08289515
214	18.35786857	264	15.7715941	314	4.798215399
215	29.06633078	265	64.57045511	315	17.41657091
216	53.2086647	266	12.50310714	316	3.067624398
217	30.98277916	267	55.37737466	317	3.735802011
218	36.6885756	268	83.55314412	318	7.035740479
219	49.19815147	269	27.3046348	319	2.477151147
220	85.91485753	270	31.34699465	320	6.121865268
221	15.70490937	271	36.81586316	321	2.442844607
222	15.21335942	272	147.1024927	322	43.52231022
223	49.391109	273	30.04185109	323	42.19775434
224	90.83584624	274	50.12665762	324	16.30513341
225	7.597336737	275	79.29677061	325	19.09832966
226	34.72679344	276	727.6128582	326	17.78118991

327	29.29808717
328	2.502093443
329	12.63319347
330	57.08535784
331	117.9634678
332	105.6363342
333	122.3174965
334	99.3448537
335	58.84133843
336	60.09749274
337	25.58415028
338	100.4643813
339	359.5738182
340	443.5175434
341	167.3121674
342	299.053776
343	195.7382021
344	250.8314971
345	31.82477239
346	324.6725914
347	350.4470732
348	156.8184716
349	66.68345826
350	131.0205121