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# Revisiting Connell: Competition but not as we know it.

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1 **Title:** Revisiting Connell: Competition but not as we know it.

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7 **Running head:** *Intra and interspecific competition*

8

9 **Abstract**

10 Space is one of the primary limiting resources for organisms on the intertidal rocky shore. This paper  
11 examined the effect of reduced density on key traits (mortality and growth) on the intertidal barnacles,  
12 *Chthamalus montagui* and *Semibalanus balanoides*, on the mid-shore in Plymouth, UK. Intra- and  
13 interspecific treatments comprising of *C. montagui* and *S. balanoides* were manipulated to reduce densities  
14 at two similar sites. Changes in mortality and operculum growth were assessed over an 8-week period using  
15 digital photography. Covariates of growth included nearest neighbour distance, competition between  
16 closest pairs and initial size. Conflicting patterns were observed when comparing growth rates between  
17 treatments and sites. At Site 1, interspecific treatments had a lower growth rate than intraspecific  
18 treatments, whereas at Site 2, interspecific growth rates were higher. ANCOVA showed that nearest  
19 neighbour distance had no significant effect on growth, but when comparing differences in growth of  
20 closest neighbouring pairs, *C. montagui* treatment showed evidence of competition whereas *S. balanoides*  
21 did not. ANCOVA analysis indicated no difference in growth between each outcome of pair competition,  
22 suggesting winners are initially bigger than losers. Comparisons of mortality between treatments indicated  
23 mortality over time with no significant differences observed between treatments, but response surface  
24 methodology (RSM) revealed no effects of competition on mortality of *S. balanoides*, but negative effects  
25 of both intra- and interspecific competition on *C. montagui* survivorship. Examination of natural  
26 populations of barnacles in the mid-shore indicated there was strong spatial variation in growth rates,  
27 perhaps driven by small-scale differences within sites.

28

29 **Keywords:** Barnacles; rocky shore; competition; growth; nearest neighbour distance; coexistence; rsm.

30



31 **INTRODUCTION**

32 The effect of competition on natural populations and community dynamics has long been of interest to  
33 ecologists (Connell, 1961a,b; Tilman, 1982; Strong et al. 1984), especially the role of intraspecific and  
34 interspecific resource competition as determining factors of the structure of both terrestrial and marine  
35 populations (Hart & Marshall, 2009; Caro et al. 2011; Shinen & Navarrete, 2014).

36  
37 Competition acts as an important feedback loop that controls population density and growth rate of the  
38 population and individuals (Begon et al. 2006). Intraspecific competition between individuals of the same  
39 species commonly leads to mortality when the resources needed to sustain them, such as food and space,  
40 become limiting (Moore, 1935; Hixon et al. 2002; Begon et al. 2006; Knights et al. 2010). This mechanism  
41 can be described by a logistic growth model which describes the negative effect of population size on  
42 growth rate until the carrying capacity is reached (birth rate equals death rate) and resources are no longer  
43 limited (Hixon et al. 2002; Neal, 2004). While changes in population size is the emergent result, intraspecific  
44 competition may in fact alter survivorship at the scale of the individual rather than a the population level,  
45 for example, as neighbouring individuals compete for a resource (Begon et al. 2006) reducing their growth  
46 and size (Hixon et al. 2002).

47  
48 In addition to intraspecific competition, population size has also been shown to be dependent on  
49 interspecific interactions. The Lotka-Volterra model (Lotka, 1925; Volterra, 1926) states when two species  
50 occur together, the growth rates of both species are affected by the presence of each other (*sensu*  
51 'interference competition', Neal, 2004) as a result of direct competition for the same resource which  
52 affects their growth or survival (Reece et al. 2011; Feldhamer et al. 2007). This can affect the distribution  
53 and abundance of different species in natural communities. Gause (1934) used laboratory experiments to  
54 observe resource competition between two closely related species, namely *Paramecium caudatum* and  
55 *Stylonychia mytilus*. When grown separately, each population grew rapidly before reaching asymptote at  
56 their carrying capacity ( $k$ ), yet when both species co-occurred, growth rates were reduced and the carrying  
57 capacity was lower. Moreover, *S. mytilus* appeared to partially outcompete *P. caudatum*, evident as greater  
58 reductions in the growth of *P. caudatum* than *S. mytilus*.

59  
60 A comparison of the relative strengths of intra- and interspecific competition provides an indication of how  
61 species may coexist. The Lotka-Volterra model (Lotka, 1925; Volterra, 1926) suggests that species co-exist  
62 when intraspecific competition is stronger than interspecific competition (Connell, 1983; Ying et al. 2014);  
63 the competitively superior species is 'self-limited' by competition between individuals below a density  
64 threshold that is necessary to eliminate the other species (Connell, 1983). If the competitively superior  
65 species is not 'self-limited', then the weaker competitor may be eliminated unless external sources of  
66 mortality, such as predation or disturbance, limit the population of the superior species (Shinen &

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67 Navarrete, 2014). While a well-established principle, recent studies have suggested that species are not 'co-  
68 existing' *per se*, but instead a species is slowly driving another to extinction (Siepielski & McPeck 2010;  
69 Shinen & Navarrete, 2014). Nonetheless, the relative strength of competition is important to determine if  
70 we are to predict the possibility of co-existence between species and understand changes in the density of  
71 competing species (Connell, 1983).

72

73 Barnacles have long been used to test hypotheses of intra- and interspecific competition (e.g. Connell,  
74 1961a,b; Wethey, 1983; Jenkins et al. 2008) and have been shown to demonstrate both intra- and  
75 interspecifically by crushing or overgrowing neighbours (Connell, 1961a,b; Wethey, 1983; Jenkins et al.  
76 2008). In intertidal systems, barnacles are excluded from higher regions of the shore by physical stress (e.g.  
77 desiccation) and reduced in number on lower shore heights by biological control (e.g. predation and  
78 competition). Their small size, dense concentrations and intertidal location make barnacles an ideal model  
79 organism for manipulation in field experiments (Leslie, 2005; Lopez et al. 2014). For instance, the survival of  
80 individuals can be determined accurately by simply mapping the position of all the members of a  
81 population and then following the same individuals by regular censuses (Connell, 1961b).

82

83 Space is one of the primary limiting resources for barnacles on the intertidal rocky shore (Connell, 1961a,b;  
84 Leslie, 2005). At high densities, intraspecific competition for space may negatively affect survival, cause  
85 changes in growth rates, and reduce reproductive activity (Barnes & Powell, 1950; Lopez et al. 2014) and  
86 success (Hansson et al. 2003). In contrast, high densities have been reported to facilitate survival by  
87 buffering individuals from interspecific competitive pressures, consumers, physical disturbance and  
88 physiological distress (Bertness, 1989; Leslie, 2005). It is suggested that barnacles in dense aggregations  
89 grow more slowly than adjacent isolated individuals as food in the water flowing over the surface is shared  
90 among more individuals (Moore, 1935).

91

92 In a seminal study by Connell (1961a), it was found that barnacles within the mid-intertidal zone undergo  
93 significant interspecific competition. Undertaken on the Isle of Cumbrae in the Firth of Clyde, Connell  
94 demonstrated interspecific competition between two co-existing species, *Chthamalus stellatus* (now  
95 recognised as *Chthamalus montagui* and referred to as *C. montagui* herein, see Southward 1976) and  
96 *Semibalanus balanoides*. *Chthamalus montagui* generally occurred above *S. balanoides* and was shown to  
97 be able to settle lower on the shore, but was unable to survive as a result of being eliminated by *S.*  
98 *balanoides* over a 1-yr period. Connell argued that the short supply of a common resource caused the  
99 exclusion of *C. montagui* as space for attachment and growth was limited, and the poor survival of *C.*  
100 *montagui* in the lower shore was as a result being outcompeted by the faster growing species, *S.*  
101 *balanoides* (Connell, 1961a).

102

## Intra and Interspecific competition

103 This paper revisits Connell's study (1961a), re-testing his assumptions of intra- and interspecific  
104 competition by way of manipulated densities and combinations of *S. balanoides* and *C. montagui*. The  
105 study aims to determine whether (1) growth rates vary between intra- and interspecific treatments, and (2)  
106 if survival rate varies between intra- and interspecific treatments over time. Small-scale effects on growth  
107 between closely interacting (neighbouring) individuals are also tested.

108

## 109 **MATERIALS AND METHODS**

110 The study was carried out at Mount Batten, Plymouth, UK (Fig. 1) between September and December 2014.  
111 Mount Batten is a headland of limestone protruding into Plymouth Sound (see Knights et al. 2016 for  
112 description of the area). Two sites on the shore were identified and defined as limestone rock surfaces of  
113 similar aspect, gradient, tidal exposure and orientation (approx. south-west facing; see Figure 1 and  
114 [www.EMODnet.eu](http://www.EMODnet.eu) for more information) where *Semibalanus balanoides* and *Chthamalus montagui* are  
115 locally abundant and coexist in the mid-shore. Locations were at the same tidal height and separated  
116 by >50 m. The study area was intentionally limited in order to reduce variability caused by differences in  
117 tidal exposure, salinity, temperature and light (Connell, 1961b).

118

119 To test for evidence and strength of intraspecific and interspecific competition in CM and SB, three  
120 treatments were established in areas characterised by 100% cover of adult barnacles. Intraspecific  
121 treatment patches contained either SB or CM, and interspecific (mixed) treatment patches contained both  
122 species. Patches were 5 x 5 cm and located randomly within the mid-shore (determined using tide-tables)  
123 where both species are roughly equally abundant. The location of each patch was recorded using GPS  
124 (Garmin eTrex10, USA) and barnacles were removed from each patch using forceps to manipulate the  
125 density and occurrence of species within each patch (Fig. 2B and D) to allow a response surface  
126 experimental design to be used (see Inouye 2001) to test hypotheses about competition. The area around  
127 each 5cm<sup>2</sup> patch was cleared of all barnacles using a paint scraper to reduce the likelihood of edge effects  
128 (Volkenborn et al. 2007). Each quadrat (N = 30 per site) was photographed (Panasonic DMC-FS16) prior to  
129 the removal of any barnacles, following manipulation at Time 0 and subsequently at 2, 4, 6 and 8-wk post-  
130 manipulation. Photographs were used to calculate density (and therefore mortality) and to estimate  
131 individual growth over time.

132

### 133 *Estimates of growth rate by species and treatment*

134 Growth was measured as the change in the length of the operculum over time (Wetthey, 1983; Jenkins et al.  
135 2008, Burrows et al. 2010), rather than the total length of the barnacle (rostro-carinal) as this metric can be  
136 severely affected by crowding, as well as other micro-topographical features of the rock surface.  
137 Operculum length of individual barnacles was measured using a photograph (e.g. Fig. 2B) that had been  
138 scaled in the image analysis programme, ImageJ (Schneider et al. 2012), and individuals geo-referenced

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139 allowing their growth to be tracked over time. Average growth rate (per species and per 2-wk period) was  
140 calculated for each patch and treatment type.

141

### 142 *Mortality of barnacles*

143 Barnacle mortality was measured using images from Time-0 and after 8-wk. Images of patches were  
144 overlaid with one-another so that individual barnacles could firstly be identified, speciated (in mixed  
145 patches) and a binary code applied to whether they were dead (0) or alive (1) after 8-wk. Individuals were  
146 identified as dead by the absence of opercular plates. These data were then used to calculate proportional  
147 mortality of each species in each patch.

148

### 149 *Growth and distance from a neighbour*

150 Photographs were also used to calculate the nearest neighbour distances (NND) of all barnacles in a patch.  
151 Images were imported in ArcGIS (ArcInfo 10.2.2), georeferenced and a point applied to the centre of each  
152 barnacle in an image. The ordinal distance between the centre of all barnacles were calculated using the  
153 spatial analysis toolkit (nearest neighbour tool) and NNDs used as a covariate to test the hypothesis that  
154 shorter NNDs would lead to a reduction in operculum growth as a result of competition.

155

### 156 *Evidence of 'winners' and 'losers' in intraspecific patches*

157 To determine if small-scale intraspecific competition occurs between barnacles in close proximity to each  
158 other, barnacles closest to each other (based on NND) were paired to test if either individual was  
159 outcompeting its 'pair' (measured as a difference in growth rate). Individuals were classified as the 'winner'  
160 and 'loser' based on growth rate differences; the individual that grew more was the 'winner'. When no  
161 evidence of growth rate differences was seen (i.e. equal growth in paired individuals), the contest was  
162 considered a 'draw'. The operculum length of each barnacle at the start of the experiment was also used as  
163 a covariate to account for potential differences in growth rate based on starting size (Moore, 1939).

164

## 165 **Statistical Analysis**

166 Growth rates were compared using an orthogonal 2-factor ANOVA with the factors: (1) Site (2 levels,  
167 random), and (2) Treatment (3 levels: CM only, SB only, CM+SB (mixed)). The outcome of paired  
168 competitions as determined by growth rate was also tested using 2-factor ANOVA with the factors: (1)  
169 Outcome (3 levels: Win, Lose or Draw), and (2) Treatment (2 levels: CM only, SB only). Significant  
170 differences between means were compared using post-hoc pairwise comparisons (Tukey HSD, 'car'  
171 package).

172

173 The effect of NND on operculum growth was testing using Analysis of Covariance (ANCOVA) with the fixed  
174 factors, Treatment (3 levels: CM only, SB only, CM+SB (mixed)), Outcome (see above) and continuous

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175 covariate (NND in mm). Step-wise model simplification of the maximal ANCOVA model was used to test  
176 between slope and intercept parameters for the relationship between growth and initial size (covariate)  
177 and categorical factor levels. Akaike Information Criteria (AIC) was used determine the best-fitting model  
178 (Burnham and Anderson 2007).

179  
180 Change in barnacle density and mortality over 8 wk between treatments was compared using linear mixed  
181 effects models (lmer) with an auto-regression (1) correlation structure to account for possible temporal  
182 autocorrelation effects. Local regression (loess) was used to describe change in average density over time  
183 between treatments. For all analyses above, data were tested for residual normality and homoscedasticity  
184 prior to statistical analyses, and in cases of significance ( $p < 0.05$ ), data were log transformed.  
185 Multicollinearity was examined using the variance inflation factor (VIF), values of which were  $<10$ , and  
186 therefore unlikely to affect regression outcomes (O'Brien 2007).

187  
188 To test for evidence of intraspecific and interspecific competition, mortality within plots was compared  
189 using a response surface method (after Box et al. 2005; see Inouye 2001, Lenth 2016 and Fig 7D for mixture  
190 details) and ANOVA tests. The effect of CM and SB density on mortality of CM and SB was modelled using  
191 first-order polynomial regression models and ANOVA tests,  $R^2$  for goodness-of-fit and plotted using  
192 perspective plots.

193  
194 All analyses were performed using the software *R* (R Core Team, 2016) using the R packages, '*graphics*',  
195 '*lme4*' (Bates et al. 2015) and '*rsm*' (Lenth 2009).

196

## 197 **RESULTS**

### 198 **Variation of operculum growth in relation to treatment (Tr) and site (Si)**

199 There was marked spatial variation in operculum growth rates among treatments between sites (Table 1, Si  
200 x Tr,  $p < 0.0001$ ). In intraspecific treatments, CM grew ~16% more at Site 2 than Site 1, whereas for SB, the  
201 pattern was reversed with SB growing ~21% more at Site 1 than 2 (Figure 3). In the interspecific treatment  
202 containing both barnacle species, average growth was significantly higher (~44%) at Site 2 than Site 1. A  
203 comparison of the three treatments across sites indicated little variation in operculum growth at Site 1  
204 irrespective of treatment, whereas at Site 2, growth was highest in the CM + SB and CM only treatments,  
205 and lowest in the SB only treatment (Figure 3).

206

### 207 **Variation in operculum growth in relation to nearest neighbour distance**

208 When data were combined within a single analysis without consideration of barnacle 'pairings', there was  
209 no effect of nearest neighbour distance on the operculum growth of an individual in any of the treatments  
210 (Table 2, NND,  $p > 0.01$ ). Operculum growth was highly variable, especially when NNDs were short ( $<5\text{mm}$ )



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211 (Figure 4) and individuals located further away from a neighbour (i.e. large NND) showed no significant  
212 increase in growth in comparison to those with barnacles closer to them.

213

214 However, when barnacles were 'paired' to those closest to each other and classified as either a 'winner',  
215 'loser' or 'draw' based on their growth after 8-wk, ANOVA indicated significant differences in growth  
216 between treatment (Table 3, Outcome x Treatment,  $p < 0.05$ ). In general, losers grew 60% less than  
217 individuals classified as winners. Post-hoc comparisons revealed clear differences in growth between  
218 winners, losers and drawing individuals within CM and SB treatments (Figure 5). In the CM treatment,  
219 winners grew significantly more than individuals who lost, but losers also grew more than those paired  
220 individuals who drew. In the SB treatment, winners grew significantly more than individuals who lost or  
221 drew, but there were no significant differences between losing individuals and drawing pairs (Figure 5).

222

### 223 **Effect of operculum size on growth over time**

224 Growth was dependent on the initial size of the barnacle (at Time-0) and the outcome of the 'competition'  
225 between paired individuals (Table 4,  $p < 0.01$ ). The ANCOVA revealed that the slopes were parallel but the  
226 intercepts (starting body size) were significantly different, indicating that the initial operculum size affected  
227 the outcome of the contest i.e. a larger individual was more likely to 'win' a contest (Figure 6). There was a  
228 negative relationship between growth and initial operculum size suggesting smaller individuals had a  
229 greater scope-for-growth than larger individuals.

230

### 231 **Variation in survival of barnacles in relation to time (Ti) and treatment (Tr)**

232 There was a significant decrease in survival over time (Table 5, Ti,  $p < 0.001$ ). Overall there was a 57%  
233 decrease in total barnacle survival after 8-wk, although densities approached asymptote after 4-wk  
234 suggesting a period of rapid early mortality of individuals (0 - <4-wk) followed by relatively little mortality  
235 (Figure 7). There was no significant difference in survival between the three treatments over time (Table 5,  
236 Figure 7).

237

### 238 **Response Surface Methodology (RSM) for testing competition**

239 Fitting a response surface model indicated that in mixed plots, the density of both CM and SB had a  
240 significant effect on the mortality of CM (Table 6,  $p < 0.05$ ). Mortality was highest when (i) CM occurred at  
241 intermediate densities ( $\sim 40$  individuals per  $25\text{cm}^2$ ) in conjunction with high ( $\sim 60$  individuals per  $25\text{cm}^2$ )  
242 densities of SB, or (ii) when densities of CM were low and SB were absent (Table 6, Figure 8). In contrast,  
243 model reduction revealed no significant effect of CM density or SB density on SB mortality ( $F_{1,13}=0.5983$ ,  
244  $p=0.45$ ) suggesting no negative effects of intra- or interspecific competition on SB at the patch scale.

245

246 **DISCUSSION**

247 The results of this study demonstrate that *Semibalanus balanoides* and *Chthamalus montagui* show strong  
248 spatial variation in operculum growth in areas where their distributions overlap in their intertidal. The  
249 composition of the patch - either a single species (CM or SB only) or a mixture of both species (CM + SB) -  
250 had a greater influence on growth than density. A comparison of the growth of all individuals in a patch  
251 with consideration of distance between individuals (nearest neighbour distance) suggested little or no  
252 competition was occurring between individuals, but comparisons at smaller spatial scales focusing on pairs  
253 of individuals neighbouring each other revealed clear 'winners' and 'losers' in terms of individual growth  
254 with few 'draws'. An individual with a larger operculum from the outset of a paired competition tended to  
255 result in that individual 'winning' the growth competition, although larger individuals tended to grow less  
256 than smaller conspecifics. Comparing mortality rates at the patch level using a surface response method  
257 suggests that CM are undergoing competition, both with conspecifics and SB, whereas SB show no  
258 evidence of mortality related to competition.

259  
260 Connell (1961a) investigated growth rates of intertidal barnacles, discovering growth rates of *S. balanoides*  
261 were greater than that of *Chthamalus montagui*. While direct interactions between *S. balanoides* and *C.*  
262 *montagui* have not been investigated, based on Connell's findings it was predicted that *S. balanoides* would  
263 have a higher operculum growth rate than *C. montagui* when co-existing. Treatments containing only a  
264 single species (CM or SB) indicated considerable variation in operculum growth depending on location.  
265 Differences in growth were not consistent across species, with growth of *C. montagui* greater at Site 2 over  
266 Site 1, and for *S. balanoides*, greater at Site 1 over Site 2. This differentiation may be due to relatively small-  
267 scale spatial variation in resource availability between sites located on Mount Batten shore. In previous  
268 studies, spatial heterogeneity of biotic and abiotic conditions that vary among-rocks within a shore has  
269 been found to influence fluctuations in population growth (Fukaya et al. 2013). This is especially important  
270 in temperate regions, where seasonal fluctuations have been shown to affect growth; in the summer,  
271 population growth rates are strongly affected by regional-scale fluctuation, whereas in winter growth is  
272 affected more by rock-scale fluctuation (Fukaya et al. 2010). Given Connell (1961a) carried out his study in  
273 spring/summer and this study undertaken in the autumn (fall), rock-scale fluctuations may have influenced  
274 the results. Lopez et al. (2010) also showed variation in morphological structures (e.g. filtration and  
275 respiration) due to spatial-temporal fluctuations in biotic and abiotic factors including density and wave  
276 exposure. Such variation may also account for some of the variation in individual growth rates and explain  
277 the differences here.

278  
279 Shinen and Navarrete (2014) indicated that in the two barnacle species, *Notochthamalus scabrosus* and  
280 *Jehlius cirratus*, growth rates were largely consistent and independent of occurring together or separately.  
281 Certainly, in this study, growth rates of *C. montagui* at Site 1 was largely the same irrespective of it

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282 occurred in isolation or in combination with *S. balanoides*. In contrast, the growth of *S. balanoides* was  
283 marginally greater when occurring in isolation than when occurring with *C. montagui* although clear  
284 significant differences could not be determined. Connell (1961a) reported differences in growth between  
285 intraspecific and interspecific treatments, where he showed the average growth of *C. montagui* was higher  
286 when independent of *S. balanoides* (Connell, 1961a). In contrast, at Site 2 the average growth of individuals  
287 in the interspecific treatment (CM + SB) was higher than when *S. balanoides* occurred on its own and the  
288 growth of *C. montagui* occurring in isolation marginally lower, contradicting Connell's findings (1961a).  
289 Location, even at relatively small spatial scales, appears to play an important role in the effect of  
290 interspecific interactions (Sandford & Menge, 2001). Thus, the experimental area - a unique shore on the  
291 Isle of Cumbrae in the Firth of Clyde, Scotland - and level of replication used in Connell's study (1961a) may  
292 therefore be less representative of general interaction strength implications than previously thought. The  
293 mechanisms that alter growth rates in interspecific treatments remain unclear, but it is suspected that  
294 differences in microhabitats, which vary greatly in their degree of physical stress, may be related to  
295 differences in growth as this environmental heterogeneity creates distinct selection regimes (Schmidt &  
296 Rand, 1999; Schmidt et al. 2015) and this should be explored further to tease apart differences.

297  
298 Many studies have shown high densities of organisms can negatively affect growth if resources are limited  
299 due to increased competition (Barnes & Powell, 1950; Connell, 1961a,b; Leslie, 2005; Lopez et al. 2014).  
300 Here, including nearest neighbour distance (NND) between all individuals had no effect on growth  
301 (although growth was highly variable) suggesting that resources were not limited in this instance at scale of  
302 a patch to the extent that competition was reduced and both species were able to co-exist (Gerwing et al.  
303 2016). Higher densities of organisms has been shown to facilitate growth as the complex structure that is  
304 formed (e.g. mussel hummocks) can buffer individuals from physical disturbance, consumers and  
305 physiological stress (Bertness, 1989; Leslie, 2005) and elevate individuals exposing them to higher particle  
306 fluxes (Bertness et al. 1998). Our results for *C. montagui* indicate some support for these mechanisms, with  
307 individuals on average exhibiting increased growth in areas of higher density.

308  
309 The relative strength (importance) of intraspecific and interspecific competition has long been debated,  
310 with intraspecific competition often implicated as the main driver of negative effects (e.g. reductions in  
311 growth) through competition for resources between closely matched individuals (Moore, 1935; Hixon et al.  
312 2002; Begon et al. 2006). Here, there were significant differences in growth between neighbouring pairs of  
313 *C. montagui* and *S. balanoides* indicating clear winners and losers at small-spatial scales. As early as 1939,  
314 Moore demonstrated that the initial size of a *S. balanoides* could influence its growth. Here, initial  
315 operculum size was a good predictor of whether an individual would win, lose or draw a contest, with  
316 larger individuals tending to win a contest over smaller counterparts. There was also a difference in growth

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317 potential, with individuals with a smaller operculum size growing more than larger conspecifics within  
318 contest categories.

319

320 Differentiation between winners and losers helps to partition much of the variability in growth at the patch  
321 level. Interestingly, while there were relatively few 'drawn' contests, where they occurred, growth in *C.*  
322 *montagui* was greatly reduced in drawn contests such that growth was lower than the 'loser' in a contest  
323 where there was a clear winner and loser. In *S. balanoides*, growth of the 'loser' or those featuring in a  
324 'drawn' contest exhibited similar but reduced growth in comparison to a 'winning' individual. These results  
325 suggest that competition occurs at the spatial scale of individuals, rather than at the patch level, requiring  
326 comparisons to be made at the scale of individuals if we are to be able to detect the effect of competition  
327 on patch dynamics. Given the differences in growth of *C. montagui* and *S. balanoides* as a result of  
328 individual contests suggests that there may be differences, perhaps in the morphology or physiological  
329 requirements of the two species, that alters the strength of mechanisms such as interference competition  
330 (Shinen and Navarrete, 2010) allowing *S. balanoides* to be more successful than *C. montagui* when  
331 occurring in close proximity with conspecifics. This explanation is supported by the comparison of mortality  
332 rates between species, which show negative effects of competition on CM, but not SB.

333

334 Interspecific competition can also have a negative effect on a species survival (Connell, 1961a; Wethey,  
335 1983; Jenkins et al. 2008). Connell (1961a) showed direct competition between *S. balanoides* and *C.*  
336 *montagui* and indicated crowding was an important cause of death of *C. montagui*. Crowding can lead to an  
337 elongation of the calcareous and exoskeleton structures (Bertness et al, 1998; Lopez et al. 2007), especially  
338 in *S. balanoides*, which have been shown to grow tall, thin-walled and dependent on neighbours for  
339 structural support (Connell, 1961a). Aggregations can be extremely fragile (Bertness, 1989) such that water  
340 motion (e.g. from wave exposure) can reduce barnacle survival (Connell, 1961b; Gaylord, 1999). Reductions  
341 in density, through mechanisms such as disturbance or predation (Knights et al, 2012), can increase survival  
342 and reduce competition between or within species (Bertness, 1989; Bracewell et al, 2013). Here, no  
343 difference in the rate of survival of SB between intraspecific and interspecific treatments was found  
344 suggesting that density of individuals in interspecific plots was sufficiently low to reduce the impacts of  
345 direct competition between the two species, increasing survivorship of both species within the patch.

346

347 In summary, this study suggests small-scale spatial distribution of organisms, the density and composition  
348 of species within a patch plays an important role in determining the strength (or lack of) intraspecific and  
349 interspecific competition in intertidal communities. The results show clear variability in the outcome of  
350 contests between individuals of the same and different species related to these factors and indicates that  
351 an evaluation of the mechanism at the scale of a patch may not capture the effects of those processes

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352 effectively. The role of competition in the affecting the structure and functioning of intertidal shores is  
353 clearly important, however, the mechanisms may not be as generic as previously thought.

354

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359

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484 = 5).

485

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506

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510 Inouye (2001).

511

512 **Figure 3.** Mean ( $\pm$ SE; n=5) log growth of barnacle opercula in three treatments: CM + SB (mixed species  
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515 significant differences between 'treatment x site' combinations (p<0.01).

516

517 **Figure 4.** Scatterplot of operculum growth in individual barnacles after 8-wk in relation to distance (mm)  
518 from its nearest neighbour. Different treatment combinations are shown: *Semibalanus balanoides* +  
519 *Chthamalus montagui* (white); *Chthamalus montagui* only (grey); and *Semibalanus balanoides* only (black).

520

521 **Figure 5.** Growth of barnacles who 'win' (white), 'lose' (grey) or 'draw' (black) in a contest with their  
522 nearest neighbour in intraspecific competition treatments (*Chthamalus montagui* (CM) and *Semibalanus*  
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524 different letters indicates significant differences between groups (p<0.05).

525

526 **Figure 6.** Relationship between initial operculum size (mm) and growth after 8-wk for barnacles that 'win'  
527 (white circles, dashed line), 'lose' (grey circles, dotted line), and 'draw' (black circles, solid line). Significant  
528 regressions are shown (p < 0.05).

529

530 **Figure 7.** Panel plot showing survival over time (weeks) for each treatment combination in 10 replicate  
531 quadrats: Mixed (CM + SB), CM (*Chthamalus montagui*) and SB (*Semibalanus balanoides*). A LOESS  
532 smoother with a span of 1 was fitted to aid visual interpretation.

533 **Figure 8.** Response surface plot of *Chthamalus montagui* proportional mortality in 25cm<sup>2</sup> plots after 8-wk.

534

535

536

537 **TABLES**

538 **Table 1.** ANOVA of operculum growth (mm) in relation to site and treatment at Mount Batten, Plymouth, in  
 539 2014.

Source	Df	MS	F	P
Site (Si)	1	0.03	2.91	0.089
Treatment (Tr)	2	0.16	17.21	<0.0001****
Si x Tr	2	0.16	17.88	<0.0001****
Residual	777	0.009		

540

541 **Table 2.** Analysis of covariance (ANCOVA) of barnacle operculum growth in relation to nearest neighbour  
 542 distance and treatment (SB only; CM only; CM + SB).

Source	df	MS	F	P
Treatment ( <i>Tr</i> )	2	2.944	3.79	<0.05*
Nearest neighbour distance (NND)	1	2.253	2.90	0.089
Residual	816	0.776		

543

544 **Table 3.** Analysis of Variance (ANOVA) of barnacle growth in relation to outcome (win, lose, draw) and  
 545 intraspecific treatments (SB and CM).

Source	df	MS	F	P
Outcome (Ot)	2	0.5707	37.59	< 0.001***
Treatment (Tr)	1	0.0465	3.062	0.0810
Ot x Tr	2	0.0460	3.028	< 0.05*
Residual	355	0.0152		

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550 **Table 4.** Analysis of Covariance (ANCOVA) of barnacle growth in relation to initial size and outcome (win,  
551 lose, draw).

Source	df	MS	F	P
Outcome (Ot)	2	0.56084	42.057	<0.001***
Initial size (In)	1	0.52175	39.126	<0.001***
Residual	455	0.01334		

552

553

554 **Table 5.** Linear mixed effects model summary testing the effect of time (Ti) and intraspecific treatment on  
555 survival.

Source	Value	Std. Error	DF	P
(Intercept)	55.41037	7.15	135	< 0.001 ***
Time (Ti)	-5.27866	1.37	135	< 0.001 ***
<i>Chthamalus montagui</i> (CM)	11.05549	9.52	135	0.2473
<i>Semibalanus balanoides</i> (SB)	1.50183	9.52	125	0.8748
Ti × CM	0.52012	1.93	125	0.7884
Ti × SB	2.25671	1.93	135	0.2454

556

557 **Table 6.** Response Surface Model Fitting (ANOVA) of *Chthamalus montagui* and *Semibalanus balanoides*  
558 barnacle survival in mixed treatments.

Source	Df	MS	F	P
Model (CM mortality)	2	0.394	5.19	<b>0.024*</b>
Residual	12	0.076		
Lack of fit	12	0.076		
Model (SB mortality)	2	0.059	0.65	0.54
Residual	12	0.092		
Lack of fit	12	0.092		

559

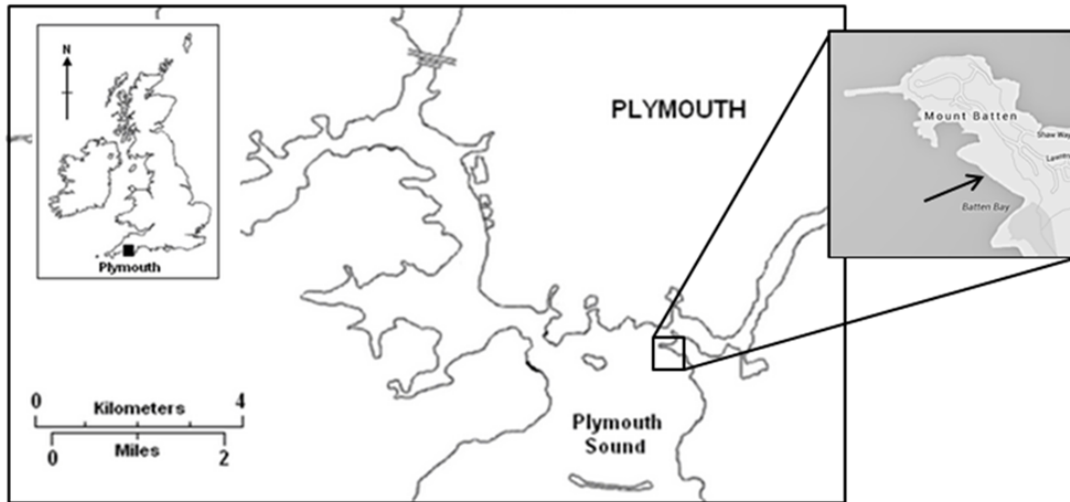
$R^2$  (CM) = 0.38

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561

562 **FIGURES**

563



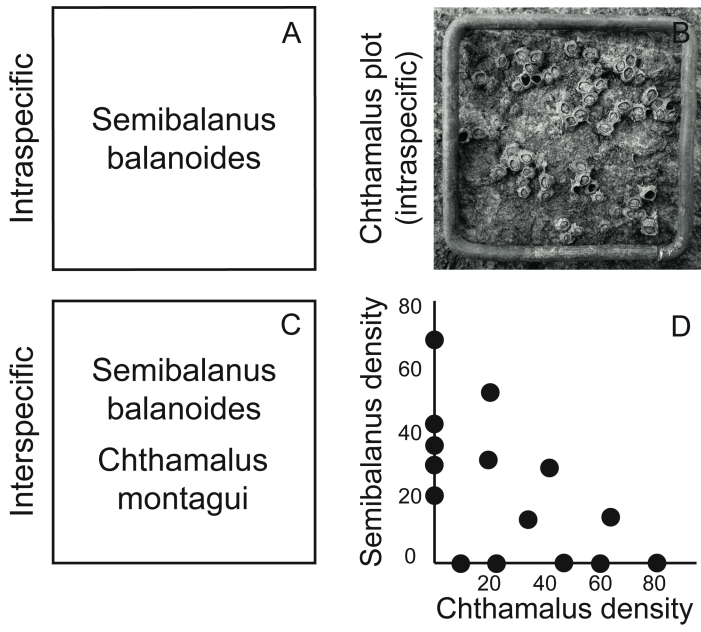
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565 **Fig. 1**

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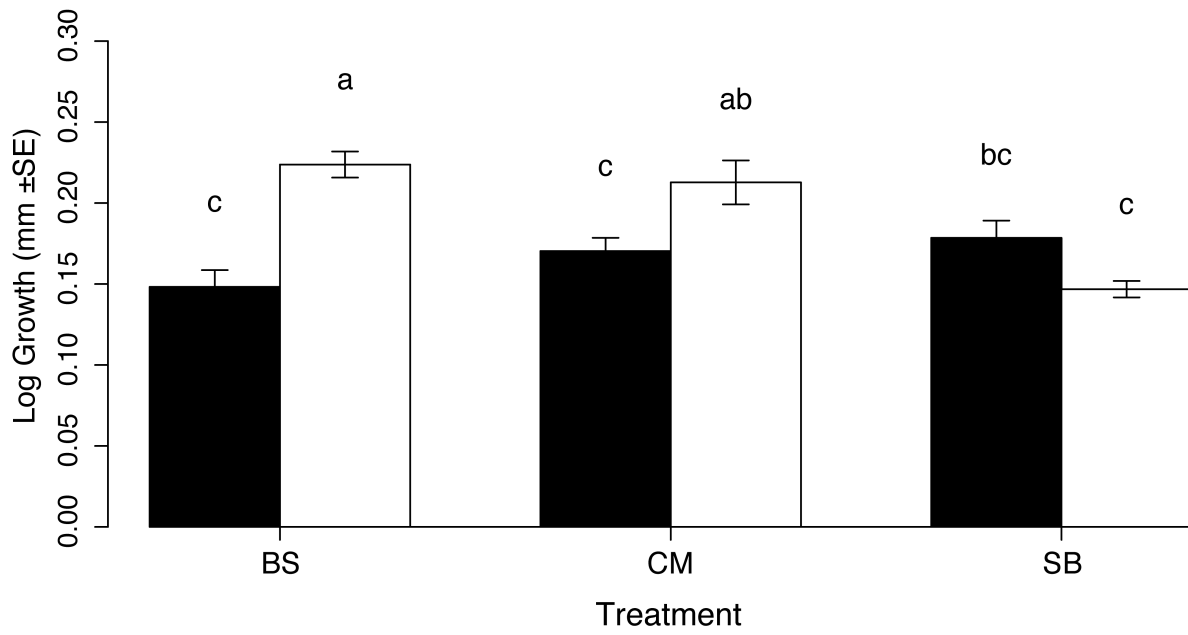
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569 Fig. 2

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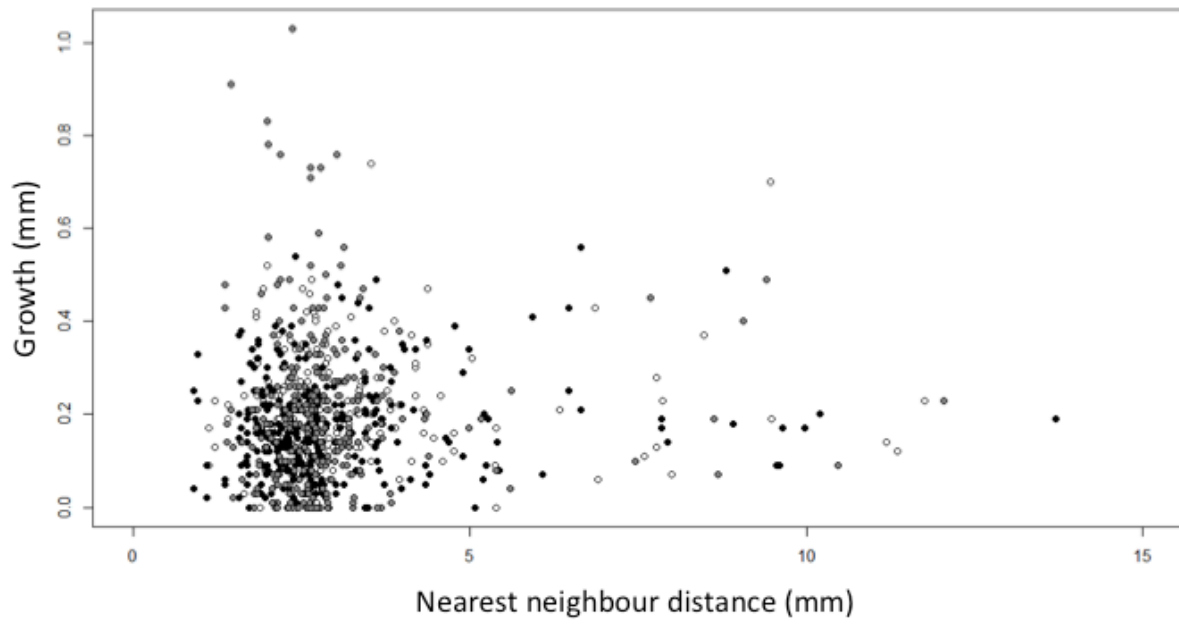
572 **Fig. 3**

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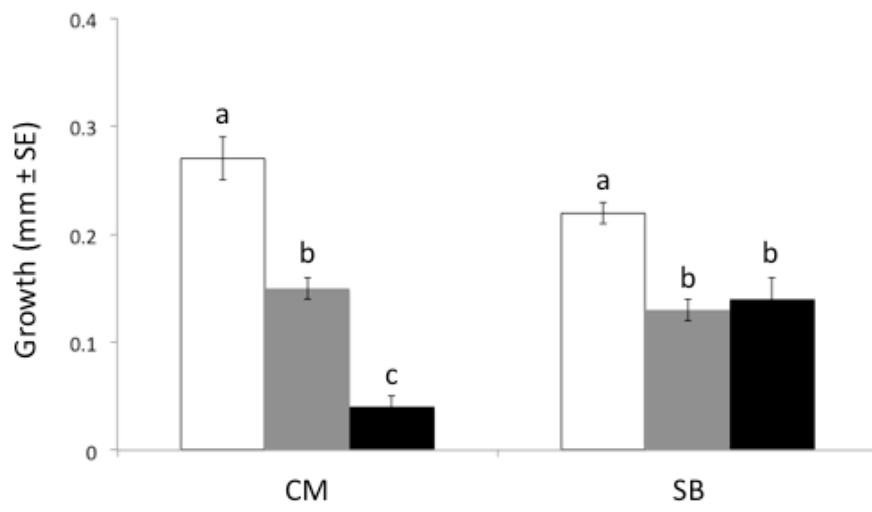
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577 **Fig. 4**

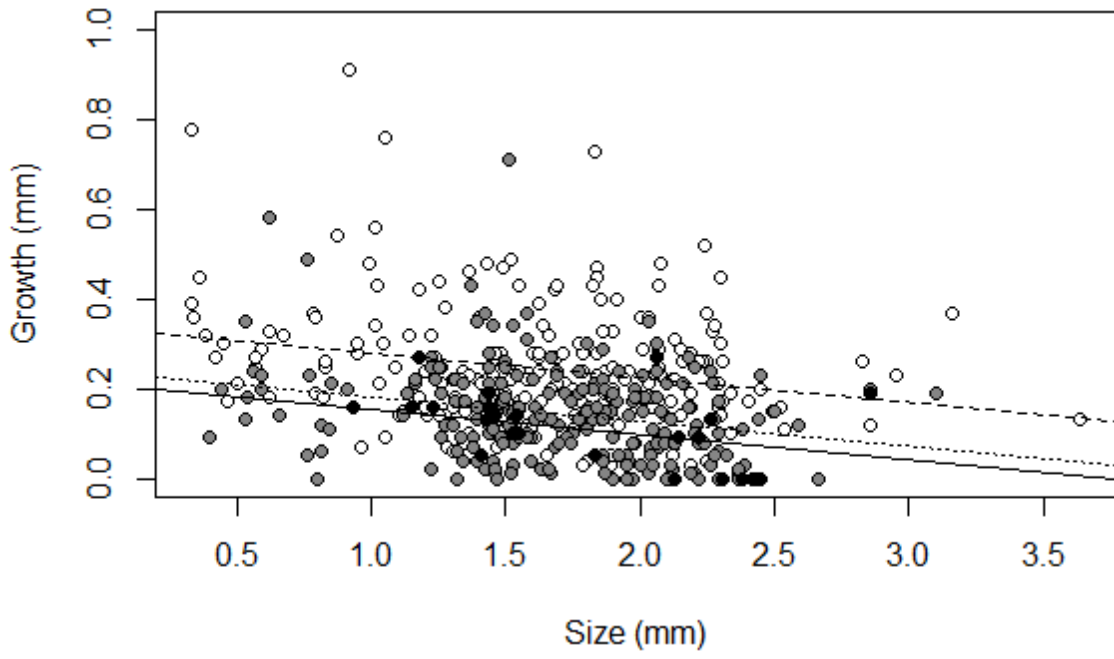
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580 **Fig. 5**

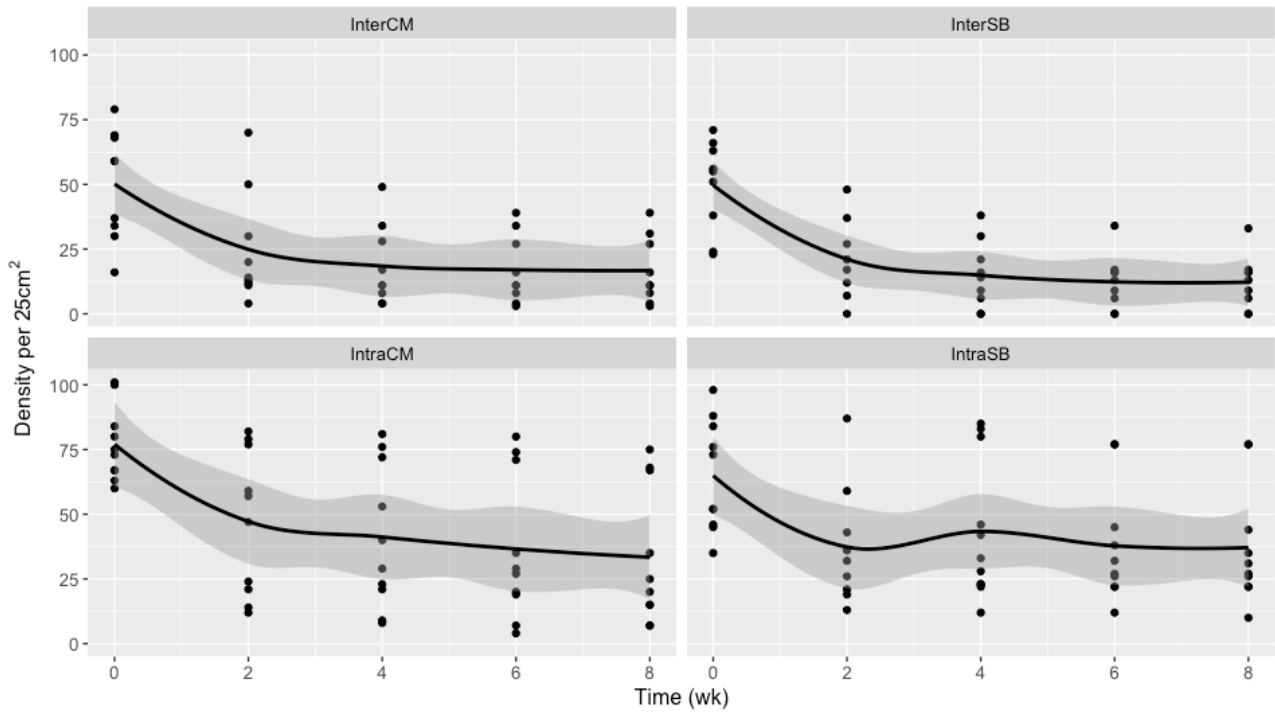
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583 **Fig. 6**

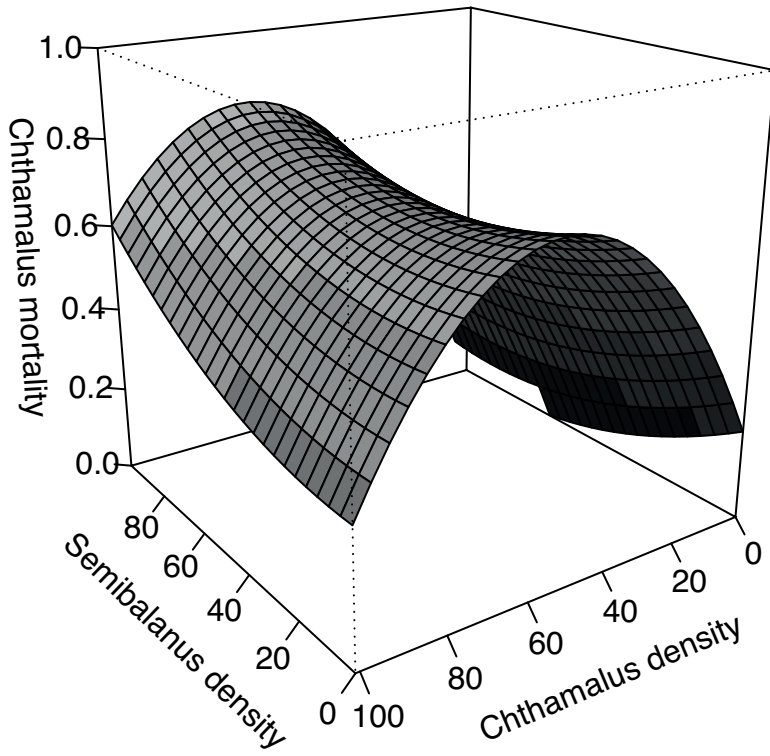
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586 **Fig. 7**

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589 **Fig. 8**

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