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Revisiting Connell: competition but not as we know it

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

Keywords: Barnacles, rocky shore, competition, growth, nearest neighbour distance, coexistence, rsm

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INTRODUCTION

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

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

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

A comparison of the relative strengths of intra- and interspecific competition provides an indication of how species may coexist. The Lotka–Volterra model (Lotka, 1925; Volterra, 1926) suggests that species co-exist when intraspecific competition is stronger than interspecific competition (Connell, 1983; Ying *et al.*, 2014); the competitively superior species is 'self-limited' by competition between individuals below a density threshold that is necessary to eliminate the

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other species (Connell, 1983). If the competitively superior species is not 'self-limited', then the weaker competitor may be eliminated unless external sources of mortality, such as predation or disturbance, limit the population of the superior species (Shinen & Navarrete, 2014). While a well-established principle, recent studies have suggested that species are not 'co-existing' *per se*, but instead a species is slowly driving another to extinction (Siepielski & McPeek, 2010; Shinen & Navarrete, 2014). Nonetheless, the relative strength of competition is important to determine if we are to predict the possibility of co-existence between species and understand changes in the density of competing species (Connell, 1983).

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

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

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

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

MATERIALS AND METHODS

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

To test for evidence and strength of intraspecific and interspecific competition in CM and SB, three treatments were established in areas characterized by 100% cover of adult barnacles. Intraspecific treatment patches contained either SB or CM, and interspecific (mixed) treatment patches contained both

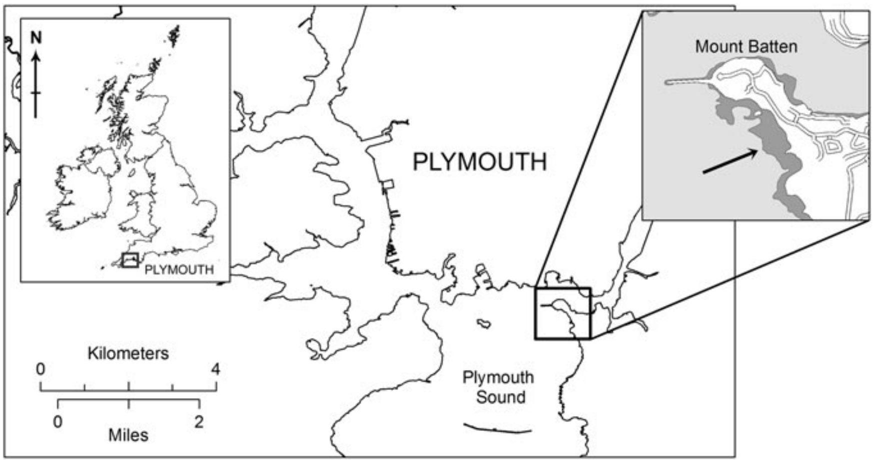

Fig. 1. Geographic location of the study in Plymouth, UK. Inset: the intertidal rocky shore at Mount Batten (50°21′N 4°07′W).

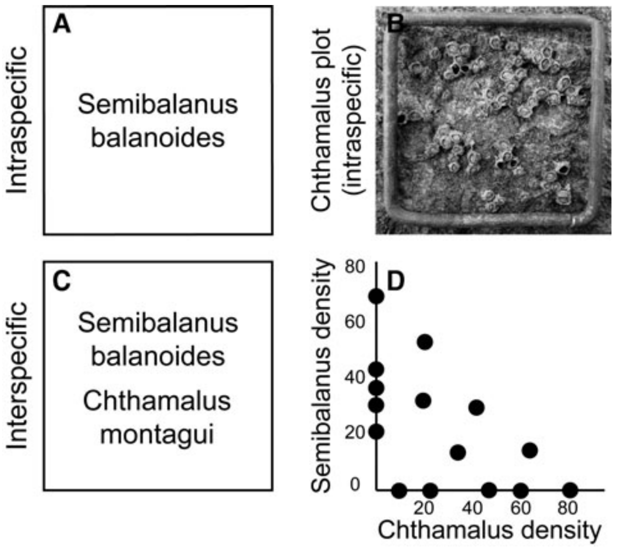

Fig. 2. Schematics and photograph of $5\ cm^2$ manipulative treatment plots used to test for evidence of intraspecific (A, B – *Chthamalus montagui* only) and interspecific (C) competition and (D) the response surface experimental design with example species densities in each patch at Time-0 as recommended by Inouye (2001).

species. Patches were 5 × 5 cm and located randomly within the mid-shore (determined using tide-tables) where both species are roughly equally abundant. The location of each patch was recorded using GPS (Garmin eTrex10, USA) and barnacles were removed from each patch using forceps to manipulate the density and occurrence of species within each patch (Figure 2B, D) to allow a response surface experimental design to be used (see Inouye, 2001) to test hypotheses about competition. The area around each $5cm^2$ patch was cleared of all barnacles using a paint scraper to reduce the likelihood of edge effects (Volkenborn *et al*., 2007). Each quadrat ($N = 30$ per site) was photographed (Panasonic DMC-FS16) prior to the removal of any barnacles, following manipulation at Time 0 and subsequently at 2, 4, 6 and 8 weeks post-manipulation. Photographs were used to calculate density (and therefore mortality) and to estimate individual growth over time.

Estimates of growth rate by species and treatment

Growth was measured as the change in the length of the operculum over time (Wethey, 1983; Jenkins *et al*., 2008, Burrows *et al*., 2010), rather than the total length of the barnacle (rostro-carinal) as this metric can be severely affected by crowding, as well as other micro-topographical features of the rock surface. Operculum length of individual barnacles was measured using a photograph (e.g. Figure 2B) that had been scaled in the image analysis programme, ImageJ (Schneider *et al*., 2012), and individuals geo-referenced allowing their growth to be tracked over time. Average growth rate (per species and per 2-week period) was calculated for each patch and treatment type.

Mortality of barnacles

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

Growth and distance from a neighbour

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

Evidence of 'winners' and 'losers' in intraspecific patches

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

Statistical analysis

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

The effect of NND on operculum growth was testing using Analysis of Covariance (ANCOVA) with the fixed factors, Treatment (3 levels: CM only, SB only, CM + SB (mixed)), Outcome (see above) and continuous covariate (NND in mm). Step-wise model simplification of the maximal ANCOVA model was used to test between slope and intercept parameters for the relationship between growth and initial size (covariate) and categorical factor levels. Akaike Information Criteria (AIC) was used determine the best-fitting model (Burnham & Anderson, 2004).

Change in barnacle density and mortality over 8 weeks between treatments was compared using linear mixed effects models (lmer) with an auto-regression (1) correlation structure to account for possible temporal autocorrelation effects. Local regression (loess) was used to describe change in average density over time between treatments. For all analyses above, data were tested for residual normality and

Table 1. ANOVA of operculum growth (mm) in relation to site and treatment at Mount Batten, Plymouth, in 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 × Tr	2	0.16	17.88	$<0.0001^{****}$
Residual	777	0.009		

homoscedasticity prior to statistical analyses, and in cases of significance ($P < 0.05$), data were log transformed. Multicollinearity was examined using the variance inflation factor (VIF), values of which were <10, and therefore unlikely to affect regression outcomes (O'Brien, 2007).

To test for evidence of intraspecific and interspecific competition, mortality within plots was compared using a response surface method (after Box *et al.*, 2005; see Inouye, 2001, Lenth, 2009 and Figure 7D for mixture details) and ANOVA tests. The effect of CM and SB density on mortality of CM and SB was modelled using first-order polynomial regression models and ANOVA tests, R^2 for goodness-of-fit and plotted using perspective plots.

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

RESULTS

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

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

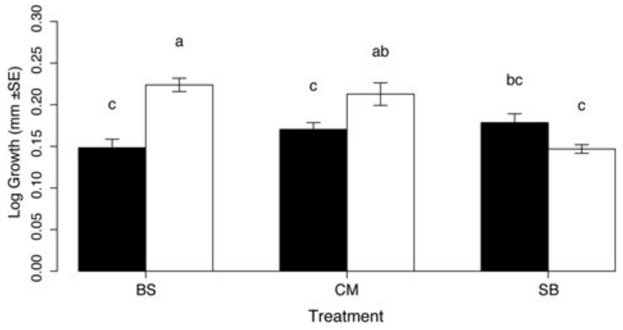

Fig. 3. Mean (±SE; N = 5) log growth of barnacle opercula in three treatments: CM + SB (mixed species plots), CM (*Chthamalus montagui* only) and SB (*Semibalanus balanoides* only) at two sites after 8 weeks. Post-hoc pairwise comparison results are shown as letters above columns, where different letters indicates significant differences between 'treatment × site' combinations ($P < 0.01$).

Variation in operculum growth in relation to nearest neighbour distance

When data were combined within a single analysis without consideration of barnacle 'pairings', there was no effect of nearest neighbour distance on the operculum growth of an individual in any of the treatments (Table 2, NND, $P > 0.01$). Operculum growth was highly variable, especially when NNDs were short (<5 mm) (Figure 4) and individuals located further away from a neighbour (i.e. large NND) showed no significant increase in growth in comparison to those with barnacles closer to them.

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

Effect of operculum size on growth over time

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

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

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

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

Source	df	MS	*F*	*P*
Treatment (Tr)	2	2.944	3.79	$<0.05^{*}$
Nearest neighbour distance (NND)	1	2.253	2.90	0.089
Residual	816	0.776		

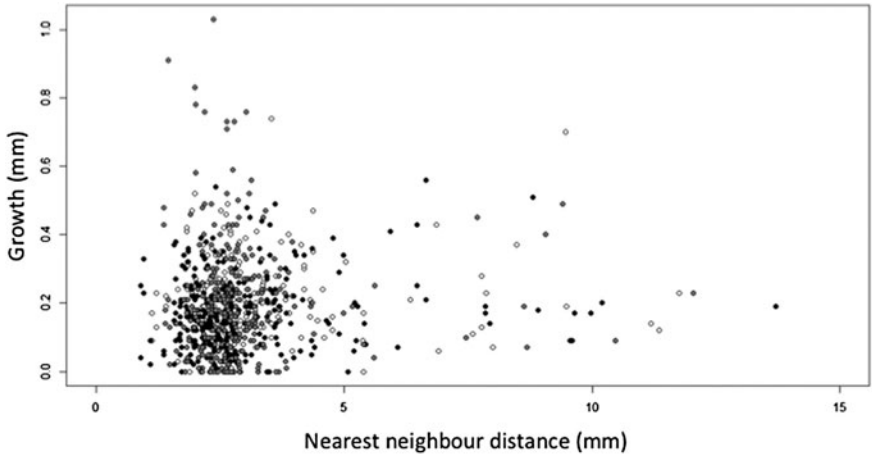

Fig. 4. Scatterplot of operculum growth in individual barnacles after 8 weeks in relation to distance (mm) from its nearest neighbour. Different treatment combinations are shown: *Semibalanus balanoides* + *Chthamalus montagui* (white); *Chthamalus montagui* only (grey); and *Semibalanus balanoides*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

Table 3. Analysis of Variance (ANOVA) of barnacle growth in relation to outcome (win, lose, draw) and 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	0.081
Ot × Tr	2	0.0460	3.028	$<0.05^{*}$
Residual	355	0.0152		

Response Surface Methodology (RSM) for testing competition

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

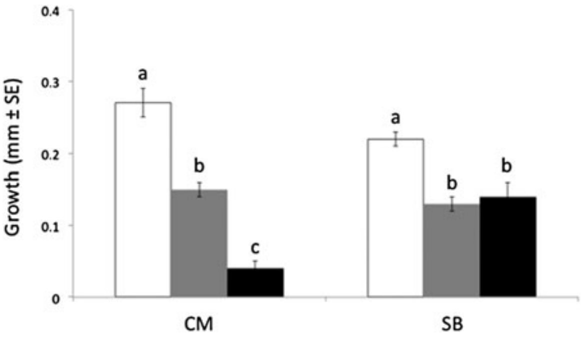

Fig. 5. Growth of barnacles who 'win' (white), 'lose' (grey) or 'draw' (black) in a contest with their nearest neighbour in intraspecific competition treatments (*Chthamalus montagui* (CM) and *Semibalanus balanoides* (SB)). Post-hoc pairwise comparison outcomes are shown as letters above columns, where different letters indicates significant differences between groups ($P < 0.05$).

DISCUSSION

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

Connell (1961a) investigated growth rates of intertidal barnacles, discovering growth rates of *S. balanoides* were greater than that of *Chthamalus montagui.* While direct interactions between *S. balanoides* and *C. montagui* have not been investigated, based on Connell's findings it was predicted that *S. balanoides* would have a higher operculum growth rate than *C. montagui* when co-existing. Treatments containing only a single species (CM or SB) indicated considerable variation in operculum growth depending on location. Differences in growth were not consistent across species, with growth of

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

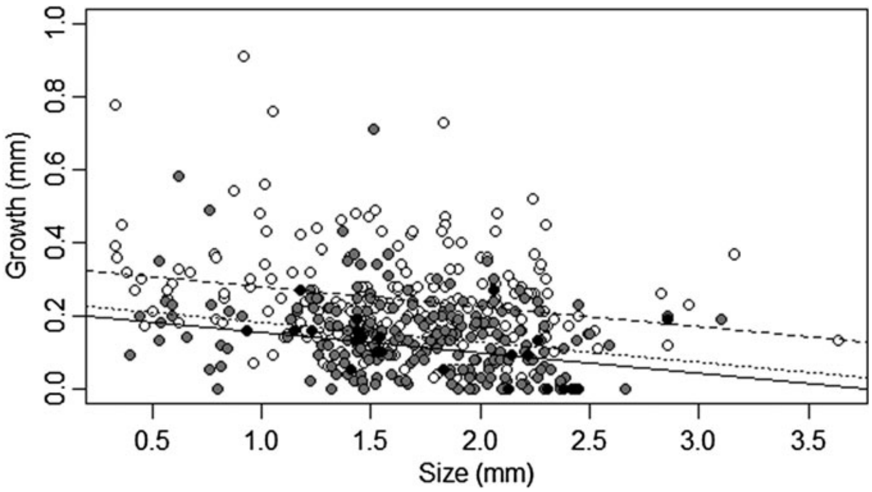

Fig. 6. Relationship between initial operculum size (mm) and growth after 8 weeks for barnacles that 'win' (white circles, dashed line), 'lose' (grey circles, dotted line), and 'draw' (black circles, solid line). Significant regressions are shown ($P < 0.05$).

C. montagui greater at Site 2 over Site 1, and for *S. balanoides*, greater at Site 1 over Site 2. This differentiation may be due to relatively small-scale spatial variation in resource availability between sites located on Mount Batten shore. In previous studies, spatial heterogeneity of biotic and abiotic conditions that vary among rocks within a shore has been found to influence fluctuations in population growth (Fukaya *et al*., 2013). This is especially important in temperate regions, where seasonal fluctuations have been shown to affect growth; in the summer, population growth rates are strongly affected by regional-scale fluctuation, whereas in winter growth is affected more by rock-scale fluctuation (Fukaya *et al*., 2010). Given Connell (1961a) carried out his study in spring/summer and this study was undertaken in the autumn, rock-scale fluctuations may have influenced the results. López *et al.* (2010) also showed variation in morphological structures (e.g. filtration and respiration) due to spatial-temporal fluctuations in biotic and abiotic factors including density and wave exposure. Such variation may also account for some of the variation in individual growth rates and explain the differences here.

Shinen & Navarrete (2014) indicated that in the two barnacle species, *Notochthamalus scabrosus* and *Jehlius cirratus*, growth rates were largely consistent and independent of occurring together or separately. Certainly, in this study, growth rates of *C. montagui* at Site 1 was largely the same irrespective of whether it occurred in isolation or in combination with *S. balanoides*. In contrast, the growth of *S. balanoides* was marginally greater when occurring in isolation than when occurring with *C. montagui* although clear significant differences could not be determined. Connell (1961a) reported differences in growth between intraspecific and interspecific treatments, where he showed the average growth of *C. montagui* was higher when independent of *S. balanoides* (Connell, 1961a). In contrast, at Site 2 the average growth of individuals in the interspecific treatment (CM + SB) was higher than when *S. balanoides* occurred on its own and the growth of *C. montagui* occurring in isolation was marginally lower, contradicting Connell's findings (1961a). Location, even at relatively small spatial scales, appears to play an important role in the effect of interspecific interactions (Sandford & Menge, 2001). Thus, the experimental area – a unique shore on the Isle of Cumbrae in the Firth of Clyde, Scotland – and level of replication used in Connell's study (1961a) may therefore be less representative of general interaction strength implications than previously thought. The mechanisms that alter growth rates in interspecific treatments remain unclear, but it is suspected that differences in microhabitats, which vary greatly in their degree of physical stress, may be related to differences of growth as this environmental heterogeneity creates distinct selection regimes (Schmidt & Rand, 1999; Schmidt *et al*., 2015) and this should be explored further to tease apart differences.

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

Source	Value	SE	df	*P*
(Intercept)	55.41037	7.15	135	<0.001***
Time (Ti)	−5.27866	1.37	135	<0.001***
Chthamalus montagui (CM)	11.05549	9.52	135	0.2473
Semibalanus balanoides (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

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

The relative strength (importance) of intraspecific and interspecific competition has long been debated, with intraspecific competition often implicated as the main driver of

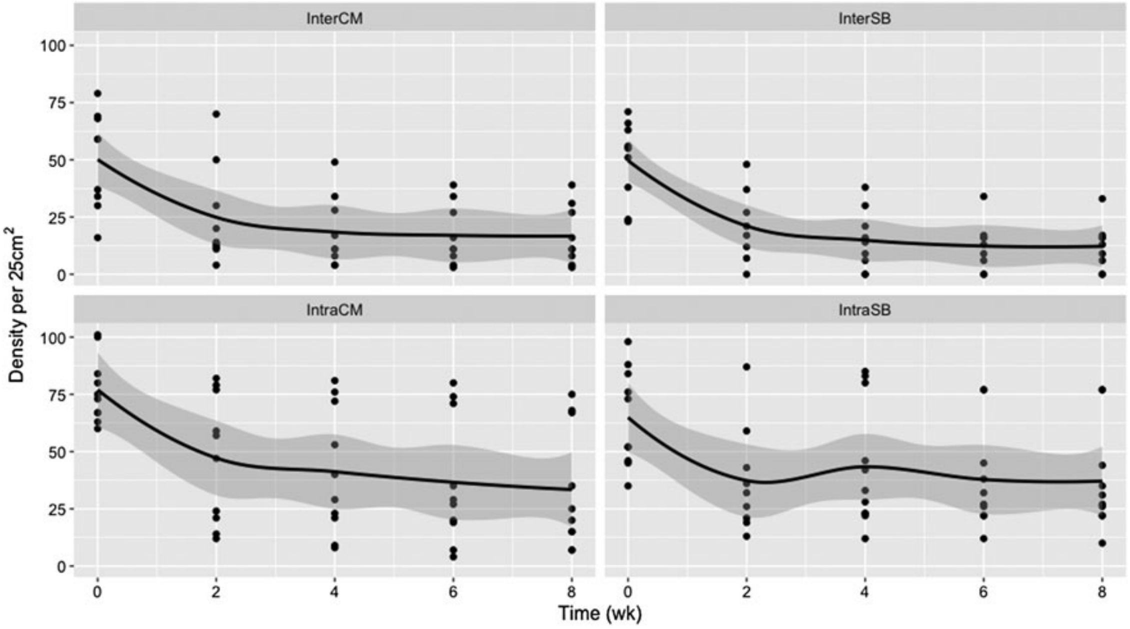

Fig. 7. Panel plot showing survival over time (weeks) for each treatment combination in 10 replicate quadrats: Mixed (CM + SB), CM (*Chthamalus montagui*) and SB (*Semibalanus balanoides*). A LOESS smoother with a span of 1 was fitted to aid visual interpretation.

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

Source	df	MS	*F*	*P*
Model (CM mortality)	2	0.394	5.19	0.024*
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		

R^2 (CM) = 0.38.

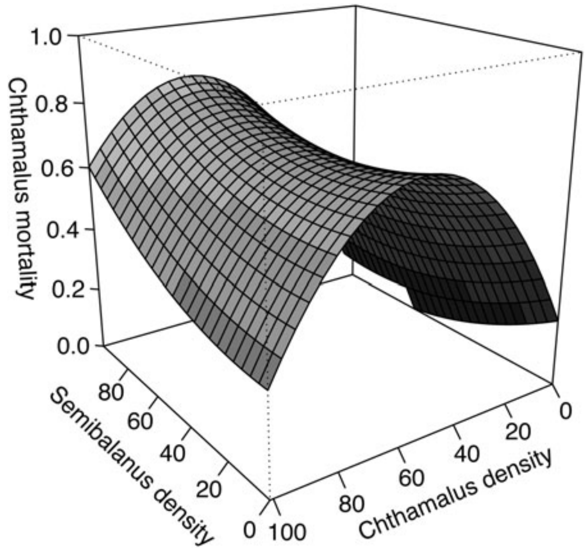

Fig. 8. Response surface plot of *Chthamalus montagui* proportional mortality in 25 cm^2 plots after 8 weeks.

negative effects (e.g. reductions in growth) through competition for resources between closely matched individuals (Moore, 1935; Hixon *et al*., 2002; Begon *et al*., 2006). Here, there were significant differences in growth between neighbouring pairs of *C. montagui* and *S. balanoides* indicating clear winners and losers at small-spatial scales. As early as 1939, Moore demonstrated that the initial size of a *S. balanoides* could influence its growth. Here, initial operculum size was a good predictor of whether an individual would win, lose or draw a contest, with larger individuals tending to win a contest over smaller counterparts. There was also a difference in growth potential, with individuals with a smaller operculum size growing more than larger conspecifics within contest categories.

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

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

In summary, this study suggests small-scale spatial distribution of organisms, the density and composition of species within a patch play an important role in determining the strength (or lack of) intraspecific and interspecific competition in intertidal communities. The results show clear variability in the outcome of contests between individuals of the same and different species related to these factors and indicates that an evaluation of the mechanism at the scale of a patch may not capture the effects of those processes effectively. The role of competition in affecting the structure and functioning of intertidal shores is clearly important, however, the mechanisms may not be as generic as previously thought.

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