

Non-contact competition in a sessile marine invertebrate: causes and consequences

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ABSTRACT: In marine benthic communities, phenotypic responses to contact competition are well resolved, but the causes and consequences of non-contact competition remain unclear. Here, we used the arborescent bryozoan *Bugula neritina* to firstly identify whether colonies change their phenotype as a result of non-contact competition, and then understand the mechanism behind the changes. Secondly, we determined the phenotypes that change in response to non-contact competition, with focus on changes in the feeding structure, viz. the lophophore. Lastly, we used a reciprocal transplant design to test whether phenotypic responses to non-contact competition reduce its negative effects. We found that phenotypic responses to non-contact competition were mediated by the biological effects of conspecific neighbours, but were also determined by the physical effects associated with increased density. Further, we found that colonies grown in high conspecific density environments were smaller (though more elongated for their size) and had smaller lophophores than colonies from low conspecific density treatments. However, we found no evidence that such phenotypic responses constituted adaptive plasticity; instead, individuals that experienced non-contact competition always performed worse than individuals that had not, and the effects of exposure to non-contact competition were additive. Our study suggests that non-contact competition is an important and persistent process in benthic marine communities, but that phenotypic plasticity, though present, does not buffer individuals from the negative effects of this process.

KEY WORDS: Phenotypic plasticity · Reciprocal transplant · Conspecific competition · Lophophore size · Phenotype–environment mismatch · *Bugula neritina*

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INTRODUCTION

Space is thought to be the most limiting resource for sessile marine invertebrates, and competition for it can be intense (Jackson 1977, Buss 1979, Connell 1983). Most work on responses to competition has focused on the effects of contact between competitors, and a wide variety of responses have been documented. For example, in corals, contact between conspecifics can reduce growth rate and can cause abnormal morphology (Rinkevich & Loya 1985), and interspecific competition can trigger extracoelenteric digestion along contact fronts (Romano 1990). In barnacles, contact with conspecific competitors induces

a tall 'hummocked' morphology that may improve access to suspended food particles (Bertness et al. 1998). Another common response to contact competition is the overgrowth of neighbouring organisms (Buss 1990, McKinney 1992). While examples of contact interactions have long been classic examples of competition, the causes and consequences of non-contact competition have been less explored.

Across a range of taxa, individuals in dense communities perform worse than individuals in sparse communities despite an absence of direct contact or the presence of free space (Hart & Marshall 2013). For example, the ascidian *Pyura stolonifera* and the bryozoan *Watersipora subtorquata* grow more slowly

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inside communities relative to individuals outside communities (Dalby 1995, Marshall & Keough 2009). Pairwise interactions in the absence of contact can also reduce performance; for example, the ascidians *Styela plicata* and *Microcosmus squamiger* and the bryozoans *W. subtorquata* and *Bugula neritina* can reduce each other's performance (Rius et al. 2010, Hart & Marshall 2013). Within species, increases in conspecific densities reduce survival, growth and reproduction across bryozoans, mussels and ascidians (Kautsky 1982, Fréchet & Bourget 1985, Marshall & Keough 2003, Gooley et al. 2010, Hart & Marshall 2013). Despite their apparent ubiquity, the underlying drivers of non-contact competition are unclear.

In the case of contact competition, space is clearly the limiting resource, but for non-contact competition, numerous factors are implicated. Mechanisms of non-contact competition include both biological mechanisms (e.g. food depletion: Merz 1984, Wildish & Kristmanson 1984, Petersen & Riisgård 1992, Svensson & Marshall in press; oxygen depletion: Altieri 2006, 2008, Ferguson et al. 2013; or allelopathy) and physical mechanisms (e.g. disrupted water flow: Buss & Jackson 1981, Okamura 1984, 1992). Since marine benthic communities consist mainly of sessile and immobile organisms, they have to create either self-generated feeding currents (Merz 1984) or other structures that allow them to effectively catch resources (reviewed by Jorgenson 1966, Hart & Strathmann 1994). Just as important as food capture, oxygen has recently been suggested to be an important limiting resource for sessile marine invertebrates, where the stress of low oxygen environments can alter community structure (Altieri 2006, Ferguson et al. 2013). Furthermore, water flow can affect marine communities by altering food availability (Arkema 2009) and changing species community composition (Palardy & Witman 2011, Palardy & Witman 2014). Disentangling the relative contributions of biological and physical mechanisms to non-contact competition has not yet been done. One way of disentangling these mechanisms is to use mimics (e.g. Young 1989, Nelson & Craig 2011) of sessile marine invertebrates to alter physical conditions (i.e. water flow) while controlling for biological effects (i.e. food depletion, oxygen consumption and allelopathic effects).

Another poorly studied aspect of non-contact competition is the extent to which phenotypic plasticity occurs in response to non-contact competition. While phenotypic plasticity in response to contact competition is obvious and well documented (e.g. Buss 1990),

the phenotypes that may change in response to non-contact competition are less obvious. Plant competition for light is a good analogue that may provide guides to likely phenotypic responses to non-contact competition in marine systems—both may involve exploitative competition for a diffuse resource. Plants grow taller and more elongate when surrounded by conspecifics (Harper 1977). For example, extensive research has focused on the shade-avoidance syndrome in terrestrial plants (Schmitt et al. 2003, Keuskamp et al. 2010): terrestrial plants often elongate their stems in response to the amount of reflected radiation from adjacent canopies (Ballaré et al. 1990, Gilbert et al. 1995, 2001, Weinig & Delph 2001, Devlin et al. 2003, Salter et al. 2003, Keuskamp et al. 2010). This elongation response allows individuals to escape shading and increase their interception of light. An analogue has been found in a marine invertebrate: the arborescent bryozoan *Bugula neritina* (hereafter referred to simply as *Bugula*). Gooley et al. (2010) found that exposure to high conspecific density altered growth form, whereby colonies at high densities were smaller, less fecund and more elongate. More nuanced responses other than growth form may also occur. Plant studies find that the light-harvesting ability of leaves and the morphology of leaves change in response to light availability. In marine invertebrates, feeding organs are analogous structures to leaves, and may also be able to change as a result of food availability. However, the extent to which feeding structures change in response to competition in marine invertebrates remains largely unexplored.

The fitness consequences of non-contact competition also remain poorly explored. Ultimately, our interest in any phenotypic response to non-contact competition lies in determining its capacity to reduce the negative effects of non-contact competition (i.e. to reduce negative density-dependence). Non-contact competition alters an individual's phenotype for a reason, that reason either being that the individual is 'actively' (i.e. adaptively) trying to outgrow the competition to reach more resources, or the individual is 'passively' responding to the poor environment. In plants, elongation responses appear to be adaptive, but whether the same is true in marine invertebrates is less clear. The assumption that any plastic changes in a phenotype are adaptive is problematic (Moran 1992, Schmitt et al. 1999, 2003). Phenotypes may only be considered adaptive if they perform better in their inductive environments relative to phenotypes that were induced in other environments, implying that the observed pattern of plasticity

across environments is maintained by selection (Kawecki & Ebert 2004). Reciprocal transplant experiments, whereby organisms with a particular environmentally induced phenotype are switched into a new environment where the original phenotype may be inappropriate (i.e. there is phenotype–environment mismatch), offer a useful way of testing this criterion. Despite the utility of the reciprocal transplant approach, however, it is rarely used to formally evaluate the performance consequences of phenotypic responses to competition (both contact and non-contact) in marine benthic communities. Instead, such plasticity is often assumed to be adaptive (e.g. Gooley et al. 2010).

Here, we addressed these important knowledge gaps regarding: (1) the mechanisms driving non-contact competition; (2) the fine-scale phenotypic responses to non-contact competition; and (3) whether phenotypic responses to non-contact competition are adaptive. We first explored the mechanisms of non-contact competition using a mimic experiment comparing the relative effects of live and artificial *Bugula* colonies on the performance of conspecifics. We then characterised the individual response of *Bugula* to increases in conspecific density by measuring changes in the food-capturing organ, the lophophore. Finally, we used a reciprocal transplant experiment to test whether these phenotypic responses to non-contact competition ameliorate its effects.

MATERIALS AND METHODS

Study species and site

Bugula is an arborescent bryozoan that can form dense populations in marine benthic environments (Keough 1989). At reproductive maturity, colonies release endotrophic larvae from conspicuous external brood chambers (Ostrovsky 2013). Larvae swim for minutes to hours before attaching permanently to the substrate where they metamorphose (Reed 1991, Burgess & Marshall 2011). After metamorphosis, new colonies form via branching modular growth, which is achieved by the asexual budding of zooids at the distal tips of branches. At various intervals along each branch, the colony bifurcates to form 2 new branches. Individual zooids along a branch can potentially produce eggs and feed by capturing suspended food particles from the water in a basket-like tentacle crown called a lophophore. The size of the lophophore influences the size of the food particles that can be ingested (Rubenstein & Koehl 1977, Win-

ston 1977, 1981). As space is limiting in these benthic environments (Jackson 1977, Buss 1979, Connell 1983), occupying a large area to obtain resources (i.e. food) is critical. In this study, we used colony size (bifurcation number and mass) and overall fecundity as our performance measures, as colony size is a proxy for space obtained and fecundity determines the number of offspring that a colony contributes to the next generation. Field work was conducted on floating pontoons located at East Coast Marina (27° 27' 33" S, 153° 11' 22" E), Moreton Bay, Queensland, Australia.

Expt 1. Mechanisms of non-contact competition: disentangling biotic vs. abiotic effects of density

To disentangle the biotic and abiotic effects of non-contact competition arising from conspecific density, we exposed focal settlers of *Bugula* to simultaneous manipulations of conspecific density itself, plus the type of neighbour within density treatments using plastic mimics (Fig. 1). By imitating the size and shape of live *Bugula* colonies, these mimics removed any biological effects of conspecifics while maintaining a similar physical disruption to water flow.

Density treatments with live conspecifics

To generate treatments representing different densities of live conspecifics, we hung pre-roughened sheets of acetate underwater at our field site for 2 wk to sample natural settlement. From these sheets, we selected established recruits with 2 bifurcations, cut the acetate around their bases and glued them into petri dishes in arrays of either 2 recruits per dish (the low-density treatment) or ~10 recruits dish⁻¹ (the high-density treatment), with 15 replicate dishes treatment⁻¹. To obtain focal settlers for these live density treatments, large reproductive colonies sampled from our field site were held in darkness for 48 h, then exposed to bright light to stimulate the release of larvae (Keough 1989, Allen et al. 2008). Larvae were settled onto another set of preroughened acetate sheets coated in natural biofilms to encourage settlement (Unabia & Hadfield 1999, Dahms et al. 2004). After 24 h, they were cut out and glued via their acetate bases into either the high-density treatment or the low-density treatment. Overall, the size of both the surrounding and focal colonies was the same throughout all of the experiments.



Fig. 1. Comparison between a live *Bugula neritina* colony (left) and a mimic colony (right)

Density treatments with mimic conspecifics

Plastic mimics of *Bugula* colonies were glued into another set of petri dishes at the same densities as the live density treatments, again with 15 replicate dishes treatment⁻¹. Focal settlers for these mimic density treatments were obtained and glued into dishes as described above for live density treatments.

Deployment and monitoring

All petri dishes across all 4 treatment groups (i.e. focal settlers exposed to high and low densities of live and mimic conspecifics) were transported to the field in insulated aquaria, where 1 replicate dish treatment⁻¹ was attached to each of the 15 PVC backing panels. Panels were submerged face down from floating pontoons to a depth of ~1 m below the water surface. Note that all treatments were over-inoculated initially, in the expectation that some stress-related mortality would arise from our experimental manipulations. After 2 d in the field, the densities of focal settlers were reduced to 1 ind. dish⁻¹, and the densities of conspecifics were reduced to either 1 dish⁻¹ in low-density replicates or 7 dish⁻¹ in high-density replicates. These densities reflected natural variation in the field (Allen et al. 2008). All dishes were monitored weekly to clear sediment and remove newly settled organisms.

The growth of each focal settler (eventually a focal colony) was monitored in the field by measuring its bifurcation number twice a week. Bifurcation number is an established and non-destructive estimate of colony size (Keough & Chernoff 1987) obtained by counting the number of times the longest branch of a

colony has bifurcated. After 20 d in the field, colonies were returned to the laboratory where colony size was measured as dry mass (colonies were left at room temperature for 2 wk to dryout, then weighed with a micro balance).

Expt 2. Characterising fine-scale phenotypic responses to non-contact competition

We characterised fine-scale phenotypic responses to non-contact competition in terms of lophophore size. We did so using 2 live density treatments, a high conspecific density with 9 established adults and a low conspecific density with 1 established adult, which were generated by the same methods described for Expt 1. In the field, 2 replicate petri dishes per density treatment were attached to each of 6 PVC backing panels and deployed as described for Expt 1.

After 24 d of growth in the field, colonies were returned to the lab to measure their overall size and lophophore volume. We were able to estimate lophophore volume by measuring tentacle crown diameter, base diameter, and tentacle length from digital photographs (Wendt 1996). Photographs were taken with a Tucsen 5MP camera attached to a dissection microscope and analysed in ImageJ (available at <http://rsbweb.nih.gov/ij>). At least 5 lophophores were measured per colony. To ensure that colony mass did not confound measures of lophophore size (e.g. if larger colonies had larger lophophores), we measured the lophophores from different sized colonies found in the same density treatment. Lophophore size was not significantly correlated with colony size ($r = 0.112$; $p = 0.418$).

Expt 3. Are phenotypic responses to non-contact competition adaptive?

To assess whether phenotypic responses to non-contact competition were adaptive, we repeated Expt 2, exposing a new set of focal settlers to high and low conspecific densities for 4 wk in the field. At this time, we counted the bifurcation number and fecundity (in terms of brood-chambers) of each focal colony non-destructively, and then transplanted it from its inductive environment into the alternate environment. The transplantation involved cutting colonies out from the acetate sheet they were growing on, and gluing them into a new density environment. For 1 of the 2 replicate colonies per treatment on each panel, the alternate environment had the same conspecific density as the inductive environment (i.e. transplantation was from low density to low density, or from high density to high density). For the remaining replicates on each panel, colonies that had previously grown at high conspecific densities were transplanted into a new low conspecific density environment and vice versa. The remaining colonies were also transplanted to account for any trauma effects of being handled (i.e. colonies from a low-density environment were transplanted into a new low-density environment, and colonies from a high-density environment were transplanted into a new high-density environment; for a schematic illustration, refer to Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m522p115_supp.pdf). After 3 wk, colonies were brought back to the laboratory to measure final colony size and fecundity (i.e. our performance measures).

Data analyses

All data were analysed with general linear models fitted in Systat 12.0. Full models were initially fitted to all interactions between categorical effects and reduced with regard to non-significant interactions as appropriate (Quinn & Keough 2002). Data on final colony mass from Expt 1 were analysed in a univariate analysis of variance (ANOVA) that included conspecific density (high vs. low density) and neighbour type (live vs. mimic colonies) as fixed categorical effects and panel as a random categorical blocking effect. Also from Expt 1, data on colony growth (i.e. bifurcation number) over time in the field were analysed in a repeated measures ANOVA that included these same categorical effects of conspecific density, neighbour type and panel.

Data on final colony mass and lophophore size from Expt 2 were analysed in a multivariate analysis of variance (MANOVA) that included conspecific density (high vs. low density) as a fixed categorical effect and panel as a random categorical effect. We used the Pillai trace as the multivariate test statistic (Quinn & Keough 2002) and univariate F -tests to indicate which of the response variables contributed to significant multivariate effects.

Data on final colony mass and fecundity from Expt 3 were analysed in a second MANOVA that included source density and final density as fixed categorical effects, and panel as a random categorical blocking effect. Again, we used the Pillai trace as the multivariate test statistic (Quinn & Keough 2002) and univariate F -tests to indicate which of the response variables contributed to significant multivariate effects.

RESULTS

Expt 1. Mechanisms of non-contact competition: disentangling biotic vs. abiotic effects of density

We detected independent effects of conspecific density and neighbour type on colony mass. Regardless of whether neighbouring colonies were mimic or live, higher conspecific density significantly reduced final colony size (Fig. 2, Table 1). Regardless of conspecific density, however, colony mass was also reduced significantly by exposure to live conspecifics

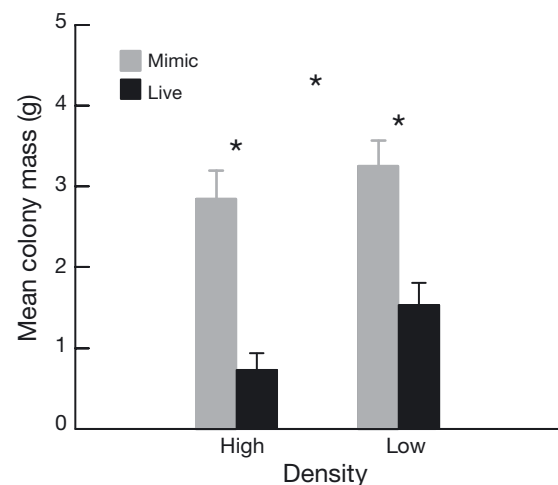


Fig. 2. Effect of conspecific density (high vs. low density) and neighbour type (live vs. mimic colonies) on the mean mass of *Bugula neritina* colonies. Asterisks above bars show that both density and neighbour type have a significant effect on the mass of *Bugula*. The interaction between conspecific density and neighbour type was not significant. Error bars: +SE

Table 1. ANOVA of colony mass of *Bugula neritina* in response to conspecific density (high vs. low density) and neighbour type (live vs. mimic colonies). Significant p-values (<0.05) are in **bold**

Effect	df	MS	F	p
Density	1	3.031	7.95	0.008
Type	1	23.201	60.845	<0.001
Density × Type	1	0.284	0.746	0.394
Panel	14	0.872	2.287	0.025
Error	33	0.381		

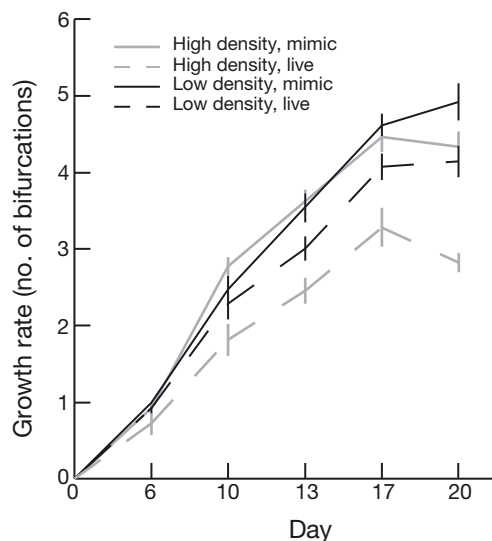


Fig. 3. Effect of conspecific density (high vs. low density) and neighbour type (live vs. mimic colonies) on the growth rate (measured as bifurcation number) of *Bugula neritina* colonies over time. Error bars: \pm SE

compared to mimics, implying that biotic effects (as opposed to abiotic, physical effects) of conspecifics are an important component of non-contact competition in this system (Fig. 2, Table 1).

In the repeated measures analysis of colony growth rate, we detected a significant effect of sampling day, whereby growth generally accelerated over time. This effect was largely consistent across density and neighbour treatments, although the density \times day interaction was marginally significant due to a tailing-off in the growth of colonies exposed to high densities toward the end of the sampling period (Fig. 3, Table 2). Regardless of time, we also detected a significant interaction between conspecific density and neighbour type on colony growth, whereby colonies exposed to low densities of live conspecifics showed an equivalent growth rate to colonies exposed to high densities of mimics, again indicating a biotic component to non-contact competition (Fig. 3, Table 2).

Table 2. Repeated measures ANOVA of colony growth rate (measured as bifurcation number) over time in *Bugula neritina* in response to conspecific density (high vs. low density) and neighbour type (live vs. mimic colonies). Significant p-values (< 0.05) are in **bold**

Effect	df	MS	F	p
Between colonies				
Density	1	0.845	16.885	<0.001
Type	1	2.078	41.513	<0.001
Density \times Type	1	0.333	6.65	0.015
Panel	13	0.116	2.309	0.027
Error	32	0.05		
Within colonies				
Day	4	8.052	445.574	<0.001
Day \times Density	4	0.039	2.134	0.080
Day \times Type	4	0.035	1.945	0.107
Day \times Density \times Type	4	0.009	0.518	0.722
Day \times Panel	52	0.02	1.107	0.319
Error	128	0.018		

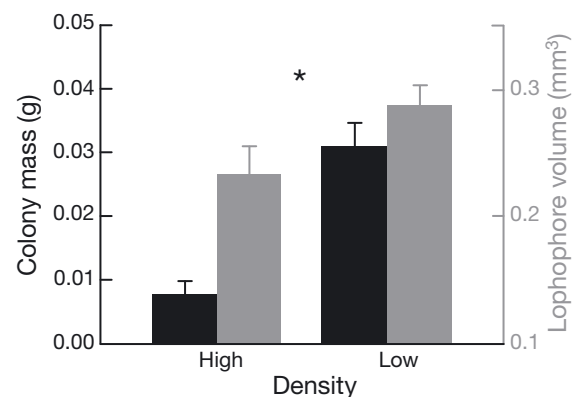


Fig. 4. Effect of conspecific density (high vs. low density) on the mean mass (black) and lophophore size (grey) of *Bugula neritina* colonies. The asterisk above the bars indicates a significant difference of both colony mass and lophophore volume when grown in different densities. Error bars: \pm SE

Expt 2. Characterising fine-scale phenotypic responses to non-contact competition

We detected a significant multivariate effect of conspecific density on the multivariate phenotypes of focal colonies (Fig. 4, Table 3). This effect was driven not only by the negative effect of density on colony mass (consistent with the results of Expt 1), but also by the finer-scale responses of colony lophophores. Specifically, colonies exposed to high conspecific densities had significantly smaller lophophores (thereby restricting them to feed on smaller food particles) than colonies exposed to lower densities (Fig. 4, Table 3). Given the lack of correlation between colony mass and lophophore volume (see 'Materials

Table 3. Multivariate ANOVA of colony mass and lophophore size of *Bugula neritina* in response to conspecific density (high vs. low density). Significant p-values (<0.05) are in **bold**

Effect	Pillai trace	df	F	p
Multivariate tests				
Density	0.949	2, 6	56.088	<0.0001
Panel	1.32	10, 14	2.716	0.043
Density × Panel	1.193	10, 14	2.068	0.104
Univariate tests				
Density				
Lophophore size		1	16.426	0.005
Colony mass		1	52.596	<0.0001
Panel				
Lophophore size		5	2.57	0.125
Colony mass		5	4.47	0.038

and methods: Expt 2.'), this result suggests a direct effect of conspecific density on the feeding apparatus of focal colonies.

Expt 3. Are phenotypic responses to non-contact competition adaptive?

We detected no evidence that phenotypic responses to non-contact competition were adaptive, which would have manifested as a significant source density × final density interaction whereby colony phenotypes expressed at low conspecific density performed better (i.e. attained higher mass and fecundity) at low density relative to high-density phenotypes, and colony phenotypes expressed at high density performed better at high density relative to low-density phenotypes. Instead, we found that focal colonies performed better upon transplantation to low conspecific densities, regardless of the prior density environment in which they were reared (Fig. 5, Table 4). The lack of phenotypic response in the transplanted environment suggests the inability to create a phenotype–environment mismatch, explaining our fitness results.

DISCUSSION

Expt 1. Mechanisms of non-contact competition: disentangling biotic vs. abiotic effects of density

We found evidence for both biological and physical mechanisms that reduce the performance of *Bugula* in the presence of conspecifics. Overall, the biological effect was much greater than the physical:

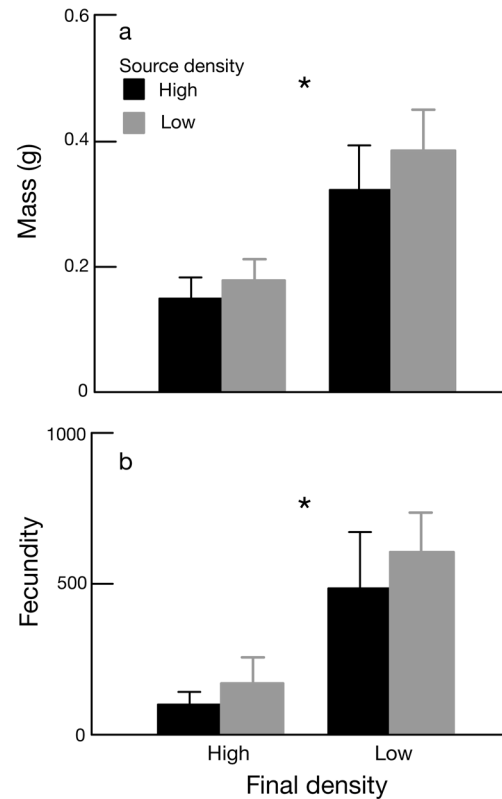


Fig. 5. Effect of transplantation from source environment (high density: black columns; low density: grey columns) to final environment (high or low density) on (a) mass and (b) fecundity of *Bugula neritina* colonies. Asterisks above bars indicate a significant effect of both colony mass and fecundity once colonies were exposed to their final density. All other effects were not significant. Error bars: +SE

colonies grew more slowly when adjacent to 1 live colony than to 7 mimic colonies (Fig. 2). Live colonies may reduce conspecific performance by either reducing the local availability of food (Buss & Jackson 1981), or via allelopathic effects (McGovern & Hellberg 2003, Lopanik et al. 2004). Initially, mimics may have increased the performance of focal individuals by reducing current flow, allowing colonies more time to catch food. However, our results show that once the focal individual had grown larger (~5 bifurcations in size), the growth rate of the focal individual in the high-density mimic treatment had slowed relative to the low-density mimic treatment (Fig. 3, Day 20). These results suggest that larger colonies are affected by a disrupted flow and other abiotic effects more so than smaller colonies from low-density environments. In comparison to our results, Okamura (1984) studied flow and feeding in arborescent colonies, and found that feeding in small colonies was reduced in high flow, but feeding in large colonies was unaffected by flow. Other studies, how-

Table 4. Multivariate ANOVA of colony mass and fecundity of *Bugula neritina* in response to transplantation from source environment (high or low density) to final environment (high or low density). Significant p-values (< 0.05) are in **bold**

Effect	Pillai trace	df	F	p
Multivariate tests				
Source density	0.023	2, 46	0.549	0.581
Final density	0.22	2, 46	6.489	0.003
Source density × Final density	0.02	2, 46	0.474	0.625
Panel	0.37	14, 94	1.526	0.117
Univariate tests				
Source density				
Colony mass		1	0.971	0.329
Fecundity		1	0.058	0.811
Final density				
Colony mass		1	11.345	0.002
Fecundity		1	9.32	0.004
Source density × Final density				
Colony mass		1	0.753	0.390
Fecundity		1	0.767	0.386
Panel				
Colony mass		7	2.063	0.066
Fecundity		7	1.344	0.251

ever, have suggested that flow has no effect on the feeding rate of arborescent colonies (Okamura 1990), but can have an effect on cilia-generated flow by the lophophore itself (McKinney et al. 1986). Feeding current interactions in bryozoans have been studied rather extensively (Winston 1979, Best & Thorpe 1986, reviewed by McKinney 1990); therefore, we will not go into much detail here. It is important to note that a high flow environment can interrupt cilia-generated feeding currents, thereby interrupting feeding in the colony itself (McKinney et al. 1986).

Expt 2. Characterising fine-scale phenotypic responses to non-contact competition

Morphological responses to increases in conspecific density have been studied in a number of bryozoans (Okamura 1984, 1992, Cancino & Hughes 1987, Allen et al. 2008, Gooley et al. 2010) as well terrestrial modular organisms (Harper 1977, Turkington et al. 1991, Linhart & Grant 1996). In these studies, the general response of organisms is a reduction in growth associated with density. Consistent with these studies, we found that colonies grown at high density have fewer bifurcations and weigh less than those grown at low density. Furthering the study of Gooley et al. (2010), we found that conspecific density also affects the mor-

phology of colony feeding structures (lophophores). We anticipated that our results would match that of a previous study by Thorpe et al. (1986), in which bryozoans under high food stress (analogous to the high-density treatment in our study) had larger lophophores. Surprisingly, we found the opposite pattern, in that colonies from high-density environments had smaller lophophores than colonies from low-density environments. This response parallels those of terrestrial plants to increased competition, with individuals often producing smaller leaves (the analogues of lophophores) at higher densities (Weiner et al. 1990, Berntson & Weiner 1991). However, caution must be exercised here, as in our study we only selected lophophores at random from within each *Bugula* colony, whereas in plants, the impacts of competition on leaf size can vary depending on their position along a branch (Jones 1999, Kaplan 2001).

There are a few reasons why colonies would produce smaller lophophores at high density. First, energy may be relocated away from lophophores (feeding) and allocated to internode elongation (growth), to allow colonies to escape their surrounding environment. Second, *Bugula* may show some other 'adaptive' growth response whereby they change their lophophore size to target different food sources at higher densities (Okamura 1987, 1990, Okamura & Partridge 1999, reviewed by Ostrovsky et al. 2002, Shunatova & Ostrovsky 2002). Presumably, this switch would be of limited value, however, given that all of the colonies at higher densities are similarly targeting food particles of smaller sizes. Ultimately, our reciprocal transplant experiment is one of the few ways in which to determine whether the responses we observed were adaptive.

Expt 3. Are phenotypic responses to non-contact competition adaptive?

In our reciprocal transplant, we used colony mass and fecundity (adjusted for mass) as our performance measures to test whether the morphological responses to competition that we observed were adaptive. It is possible that organisms with continuous, modular development (such as *Bugula*) will always be sensitive to environmental conditions and be capable of modifying their growth forms continuously (Hughes 2005).

To determine whether the phenotype of *Bugula* is adapted to its source environment, it would have to perform better in its inductive environment relative to a phenotype induced from another environment.

We found that the benefits of experiencing a low-density environment outweighed any costs of initially expressing the 'wrong' phenotype. This pattern was true regardless of whether a colony started or finished in a low-density environment. In other words, being in a lower-density environment was always a positive for performance, and there was no downside to having a high-density phenotype in a low-density environment. As such, it seems that the phenotypic plasticity we observed cannot compensate for the negative effects of increased density. Interestingly, the negative effects of increased density were persistent and additive: the more time spent at a high density, the greater the penalty on individual performance. An individual that was exposed to high density earlier in its life history still had much lower performance than an individual that had never experienced high density. These results suggest that like classical contact competition, non-contact competition can shape the trajectories of populations and communities in much the same way. Future studies should explore whether the phenotypic responses (specifically size) resulting from non-contact competition are able to reduce the effects of contact competition, focusing on the effects of size separate from density on competition in general (Giménez & Jenkins 2013).

Concluding remarks

The goal of this study was to determine the causes and consequences of non-contact competition in *Bugula neritina*. We found that the phenotype of *Bugula* was controlled more by its biological surroundings (neighbouring 'mouths') than by the physical surroundings (altered water flow). We also found that *Bugula* colonies grown in high-density environments had fewer bifurcations, weighed significantly less and had small lophophores compared to colonies grown in low-density environments. We were unable to determine whether the response of *Bugula* to conspecific density was adaptive, as the effects of experiencing a low-density environment outweighed any benefits of showing an alternate phenotype. These results suggest that if the phenotypic plasticity we observed is adaptive, it imperfectly buffers individuals from the negative effects of a high-density environment. Our study emphasises that phenotypic plasticity should not be assumed to be adaptive and that non-contact competition can have strong and lasting effects on the performance of benthic marine invertebrates.

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