Spatial arrangement affects population dynamics and competition independent of community composition

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Abstract. Theory suggests that the spatial context within which species interactions occur will have major implications for the outcome of competition and ultimately, coexistence, but empirical tests are rare. This is surprising given that individuals of species in real communities are typically distributed nonrandomly in space. Nonrandom spatial arrangement has the potential to modify the relative strength of intra- and interspecific competition by changing the ratio of conspecific to heterospecific competitive encounters, particularly among sessile species where interactions among individuals occur on local scales. Here we test the influence of aggregated and random spatial arrangements on population trajectories of competing species in benthic, marine, sessile-invertebrate assemblages. We show that the spatial arrangement of competing species in simple assemblages has a strong effect on species performance: when conspecifics are aggregated, strong competitors perform poorly and weaker competitors perform better. The effect of specific spatial arrangements depends on species identity but is also strongly context dependent. When there are large differences in species competitive ability, aggregated spatial arrangements can slow competitive exclusion, and so nonrandom spatial arrangement can work synergistically with other trade-off based mechanisms to facilitate coexistence.

Key words: aggregation; coexistence; competition; intraspecific competition; interspecific competition; segregation; sessile invertebrate; spatial.

INTRODUCTION

A central tenet of traditional coexistence theory (derived from Lotka-Volterra models of interspecific competition) is that, for coexistence to occur, intraspecific competition must be stronger than interspecific competition (Chesson 2000, Adler et al. 2007). Support for this requirement stems from niche theory: conspecifics are more similar to each other than to heterospecifics, and so should compete more strongly (Abrams 1983). While there is substantial theoretical and empirical evidence for niche-based mechanisms of coexistence (Chase and Leibold 2003), empirical support for intraspecific competition being stronger than interspecific competition is equivocal (Goldberg and Barton 1992, Silvertown and Wilson 2000). However most considerations of the relative strength of intra- and interspecific competition have neglected an important element of competition in natural systems: the arrangement of competing species in space.

Organisms are typically distributed nonrandomly in space yet theoretical studies often assume otherwise. For example, theoretical models of interspecific interactions often rely on a mean-field assumption, which subsumes all abiotic and biotic heterogeneity into a single global average for analytical tractability (Law et al. 2000).

Classic examples that contain the mean-field assumption include Lotka-Volterra models of two-species competition: interactions between species *i* and *j* are expressed as the product of their mean densities $N_i \times N_j$, which essentially requires that there be an equal probability of interspecific and intraspecific competitive encounters. There may be some circumstances when the mean-field assumption would be appropriate such as when physical factors cause strong mixing of interacting species (e.g., open-water plankton communities), however, in most ecological scenarios, the restrictive conditions of the mean-field assumption are unlikely to apply (Law et al. 2000).

Communities that are most likely to depart from the requirements of the mean-field assumption are those of plants and other sessile organisms. Many studies have described the pattern of individual plants across landscapes and these studies show that individuals of different species are generally arranged nonrandomly in space (e.g., Watt 1947, Herben et al. 2000). Furthermore, sessile species such as plants interact over relatively short distances and most strongly with only their immediate neighbors (e.g., Tyler and D' Antonio 1995). The combination of local interactions and nonrandom arrangement in space produces a situation where the local environment that individual organisms experience can be very different from the mean environment averaged across the entire community. Although we have some understanding of the processes

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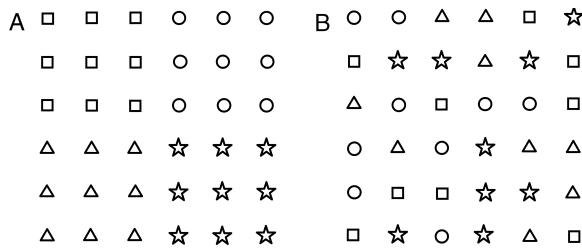
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Fɪɢ. 1. Schematic representation of experimental treatments for examining the effects of spatial arrangement on performance in the field. Panel A represents an aggregated treatment; and panel B represents a random treatment. Different shapes represent different species. Note that for both treatments, the actual arrangement differed from replicate to replicate.

that generate nonrandom spatial pattern in communities (Pacala and Levin 1997), we have only a limited understanding of the consequences of these patterns for community dynamics. However, the effect of spatial pattern on evolutionary and ecological dynamics could be substantial (Pacala and Deutschman 1995, Murrell et al. 2001, Hubbell 2006).

Importantly, nonrandom arrangement of interacting species provides a simple mechanism that would satisfy the requirement for coexistence that intraspecific competition be stronger than interspecific competition (Stoll and Prati 2001). If a species aggregates in space, then this necessarily increases the number of conspecific interactions relative to heterospecific interactions and, therefore, increases the strength of intraspecific competition relative to interspecific competition (Shmida and Ellner 1984, Pacala 1986). This scenario could facilitate coexistence without necessarily invoking more complex phenomena such as niche differentiation (Shmida and Ellner 1984). Several theoretical models support the idea that species aggregations should facilitate coexistence in both mobile animals (Atkinson and Shorrocks 1981, Hanski 1981, Ives and May 1985) and in plants (Silvertown et al. 1992, Pacala and Levin 1997, Murrell et al. 2002). Silvertown et al. (1992) constructed a cellular automaton model based on field-calibrated competition coefficients among five species of grasses. They showed community dynamics were dependent on the arrangement of plants in space and so could not be predicted from the competitive hierarchy alone. When species were randomly arranged, competitive subordinates were rapidly excluded, but when species were aggregated in monospecific bands, exclusion was slowed or prevented (Silvertown et al. 1992). Pacala (1997) and Pacala and Levin (1997) use spatial models of Lotka-Volterra competition to show that species aggregation can reduce the likelihood of exclusion but these results conflict with a more recent version of these models which showed that coexistence may be less likely when species are aggregated (Neuhauser and Pacala 1999, Chesson and Neuhauser 2002). Debate continues in the theoretical literature regarding the importance of

intraspecific aggregation to coexistence (e.g., Chesson and Neuhauser 2002, Murrell et al. 2002) but the scarcity of empirical data hampers the resolution of this debate.

Nowhere is the arrangement of competing individuals likely to be more important than for benthic, sessile assemblages in marine environments. These communities are characterized by intense local competition for space among immediate neighbors that often differ strongly in competitive ability (Sebens 1986, Buss 1990). Furthermore, nonrandom spatial arrangement of species is a feature of these communities as a result of the patchy distribution of larvae in the plankton, small-scale hydrodynamics, and the colonization behavior of larvae (Keough 1983). While there is a long history of studies of interspecific competition in sessile marine invertebrate assemblages, there have been very few studies that have addressed the influence of spatial structure on competitive outcomes (Idjadi and Karlson 2007). Here, we experimentally manipulate the arrangement of competing species of colonial marine invertebrates. We show that the spatial arrangement of competing species may slow competitive exclusion but that the advantages of different spatial arrangements are context dependent.

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We manipulated the spatial arrangement of four competing species in a single competitive arena to determine how arrangement early in assembly affects competitive outcomes. The experiment was done twice with two different sets of four competing species arranged in two different treatments (Fig. 1, Appendix A). In the first treatment, individuals were randomly arranged with respect to each other. In the second treatment, individuals of the different species were conspecifically aggregated, which reduced the ratio of inter- to intraspecific contacts. Both runs of the experiment were done within Manly Boat Harbour, Queensland, Australia (27°27′ S, 153°11′ E).

To collect experimental individuals, we allowed natural settlement onto roughened 0.25 mm thick PVC sheets that were attached to the underside of 6 mm thick PVC plastic backing panels suspended from floating pontoons at a depth of 1 m. We allowed natural settlement to occur over three weeks after which we removed the PVC film from the backing panels and transported them to the laboratory in containers of cool, aerated seawater. To manipulate the spatial arrangement of recruits, we cut the PVC film around experimental individuals with a scalpel. We then used superglue to attach the small pieces of PVC film, each with a single recruit, in the desired position on a settlement plate. We arranged recruits on a regular 6×6 grid on each settlement plate. In the aggregated treatment, nine individuals of a single species were aggregated in a corner of the grid. In the random arrangement, individual recruits of each species were assigned a location on the grid using a random number

table (Fig. 1, Appendix A). In the aggregated treatment, species did not always have the same "neighbors," and in the random treatment, the actual location of individuals of each species differed among replicates.

There were some differences between the experimental trials. In the first trial, we used two arborescent bryozoans *Bugula neritina* and *Bugula stolonifera* and two encrusting bryozoans *Watersipora subtorquata* and *Celloporaria* sp. Experimental individuals were attached to black Perspex settlement plates ($100 \times 100 \times 6$ mm) with 1 cm between each recruit. There were five replicate settlement plates for each treatment. The settlement plates were attached, and randomly arranged, to a 60×60 cm, 6 mm thick PVC backing panel using stainless steel screws. The backing panel was suspended facedown from a floating pontoon at a depth of 1 m. After one month, we recorded survival and measured the final size of each individual. For the arborescent bryozoans, we counted the number of bifurcations on each colony's longest branch as a measure of colony size, which is a standard measure in *Bugula* spp. (Keough and Chernoff 1987). For the encrusting bryozoans, we took digital photographs and measured colony area using image processing software (ImagePro Express v5.1; Media Cybernetics, Bethesda, Maryland, USA).

In the second trial, we used a different set of species and a slightly different experimental setup. The four species were the encrusting bryozoans *W. subtorquata* and *Celloporaria* sp., an unidentified, encrusting, colonial ascidian, *Didemnum* sp., and an unidentified sponge in the family Microcionidae. The treatments were the same as in the first trial, but in the second trial we attached recruits to a 6×6 cm grid in the middle of a larger ($200 \times 200 \times 6$ mm) gray PVC plastic settlement plate. There was less space between competitors in the second trial (1 vs. 1.5 cm) and more room to grow outside the experimental competitive arena. One replicate of each treatment was attached to a single backing panel. There were eight replicates for a total of eight backing panels. We took digital photographs of each settlement plate each week for four weeks. To take the photographs, we briefly removed each backing panel from the water. The area of individual colonies was measured from the photographs using image processing software (Image-Pro Express v5.1). We measured total area for *Didemnum* sp. because individuals of this species rapidly grew together and could not be distinguished.

Analyses

We were initially interested in the aggregate performance of each species within each arrangement. To assess performance we calculated the total size of each species on each settlement plate. To be able to formally compare the response of species with different growth forms in trial 1 (arborescent and encrusting) in a single analysis, we used a simple numerical transformation to standardize size measurements among species. We did this by dividing each species' total size in each replicate by that species maximum total size across both treatments. Trial 1 was then analyzed using three-way ANOVA with treatment and species as fixed factors and settlement plate as a random, blocking factor. Trial 2 was analyzed using repeated-measures ANOVA with treatment and species as fixed factors, and time as a fixed, repeated factor.

To determine if differential survival could explain differences in species performance, we compared survival of individuals between treatments. We were able to assess survival directly in trial 1 using a generalized linear model with a logit link and binomial errors. We could not easily use survival as a dependent variable in trial 2 because there was substantial fragmentation of colonies in this trial. Therefore, we used the number of colonies (fragments) as a dependent variable in a repeated-measures ANOVA with treatment as a fixed factor and time as a fixed, repeated factor. These analyses were done separately for each species.

We also determined whether spatial arrangement qualitatively changed the effect of competition on surviving individuals in a population. We were interested in differences between treatments in the relative contribution of individuals to overall size. To do this we estimated the degree of size inequality among colonies in each treatment using the Gini (G) coefficient (Weiner and Solbrig 1984). The Gini coefficient takes the value 0 when all individuals are the same size (perfect equality), and has a theoretical maximum of 1 when all but one individual in the population has size equal to zero (perfect inequality). We were not initially interested in the absolute values of G, but rather in differences between treatments in the relative contribution of individuals to overall size. For trial 1, we calculated G for each replicate and then did a two-way ANOVA on log-transformed data (to meet ANOVA assumptions) to test for differences among treatment/species combinations. For trial 2, we calculated G for each species in each treatment at week three and then used two-way ANOVA (treatment fixed and backing panel random) to compare G between treatments for each species. Data at week three were used to avoid large numbers of missing values at week four, and because the largest differences in overall size between treatments were observed at week three. All calculations and statistical analyses were done using Systat v11 (Systat Software, Chicago, Illinois, USA) and R v2.7.1 (*available online*).[2]

RESULTS

Spatial arrangement affected performance in both trials, although results were different between trials and between species in trial 2. Species in trial 1 grew more when arranged randomly (Fig. 2, Appendix B: Table B1), and this effect was strongest in *W. subtorquata* (Fig. 2). The difference in total size among treatments could not
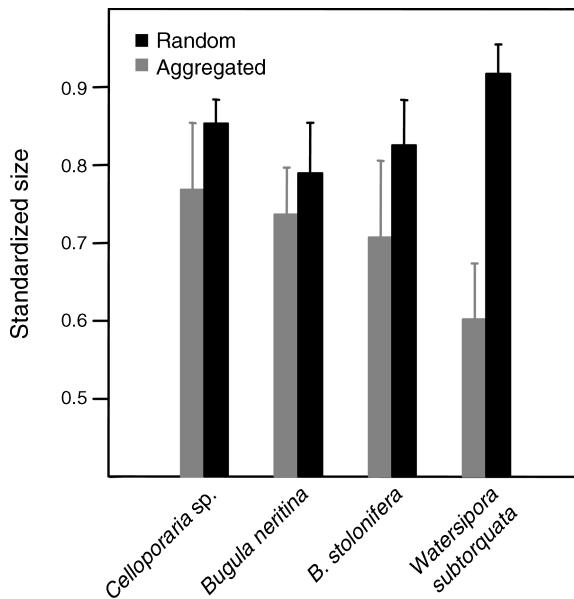
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[2] ⟨www.r-project.org⟩

FIG. 2. The influence of spatial arrangement (random vs. aggregated) on total size (the sum of size of all individuals on a replicate plate) among four competing species in trial 1. Note that size has been standardized for each species for ease of comparison (see *Materials and methods* for details).

be explained by differential survival; survival was high in both treatments (>88%) and there was no evidence that either treatment ($\chi^2 = 0.000$, df $= 1$, $P = 0.999$) or species ($\chi^2 = 2.836$, df $= 3$, $P = 0.418$) influenced survival. Furthermore, there was no evidence for any differences in size inequality among treatments or between species (Appendix B: Table B2).

For the analysis of total area in the second trial, there was a significant, three-way interaction between time, species, and treatment ($F_{9, 165} = 2.811$, $P = 0.029$) and so we analyzed each species separately. All species increased substantially in size in the first two weeks and there was little or no difference in performance among the treatments for any species during this time (Fig. 3). The ascidian *Didemnum* sp. was the only species that continued to increase in size throughout the experiment in both treatments. The other species either decreased in size dramatically (*W. subtorquata* and *Celloporaria* sp.) or stayed approximately the same (Microcionid sponge) after two weeks. Spatial arrangement strongly affected the performance of all of the species from three weeks in the field onwards, but the strength and direction of these effects varied among species (Fig. 3, Appendix B: Table B3). The total area of *Didemnum* sp. was ~20% greater when individuals were randomly arranged (Fig. 3A, Appendix B: Table B3). In contrast, *Celloporaria* sp. and the Microcionid sponge performed better in the aggregated treatment (Fig. 3B, C, Appendix B: Table B3b, c). Although *Celloporaria* sp. decreased in size in both treatments, the decrease in size was less severe in the aggregated treatment.

Despite strong effects of arrangement on *W. subtorquata* performance in trial 1, there was no effect of arrangement on this species in trial 2 (Fig. 3D, Appendix B: Table B3d).

For the sponge, *W. subtorquata* and *Celloporaria* sp. there was no evidence that differential survival or fragmentation could explain the differences observed among treatments (Appendix B: Table B4, Fig. B1). Furthermore, there was no evidence for any difference in size inequality between the treatments for any of these species in trial 2 after three weeks in the field (Appendix B: Table B5).

DISCUSSION

The spatial arrangement of competing species in simple assemblages has a strong effect on species performance. The effect of specific spatial arrangements depends on species identity, but is also strongly context dependent—a finding that is consistent with empirical studies in other systems (Monzeglio and Stoll 2005, Turnbull et al. 2007). While the influence of local-scale, spatial arrangement on community dynamics has been theorized for some time (e.g., Shmida and Ellner 1984), this is one of few empirical studies to clearly demonstrate a strong effect of ecological pattern on ecological process (Murrell et al. 2001, Rejmanek 2002). Our results also inform theoretical arguments (Chesson and Neuhauser 2002, Murrell et al. 2002) about the ability of aggregated spatial arrangements to facilitate coexistence among competing species. Consistent with previous studies (Stoll and Prati 2001, Idjadi and Karlson 2007), our results suggest that when conspecifics are aggregated, strong competitors perform poorer and weaker competitors perform better. The effects of spatial arrangement will therefore slow exclusion when there are large differences in species competitive ability (Fig. 3; Idjadi and Karlson 2007), and are likely to work synergistically with other mechanisms (e.g., trade-off based mechanisms) to facilitate coexistence (Idjadi and Karlson 2007).

In the first experiment, all four species performed better when randomly arranged (Fig. 2) indicating that intraspecific competition is stronger than interspecific competition in this simple community. Among the few empirical tests of species aggregation on performance, our finding that aggregation did not favor a single species is unique (Stoll and Prati 2001, Monzeglio and Stoll 2005). However, in an elegant study that assessed the effects of natural spatial structure on coexistence in seven species of sand-dune annuals, Turnbull et al. (2007) demonstrated that when intraspecific competition is strong relative to interspecific competition, most species in the community are likely to benefit from being randomly arranged. Among the four species included in our experiment there were two different functional groups: arborescent and encrusting bryozoans. These two functional groups have very different growth forms and space requirements, which should
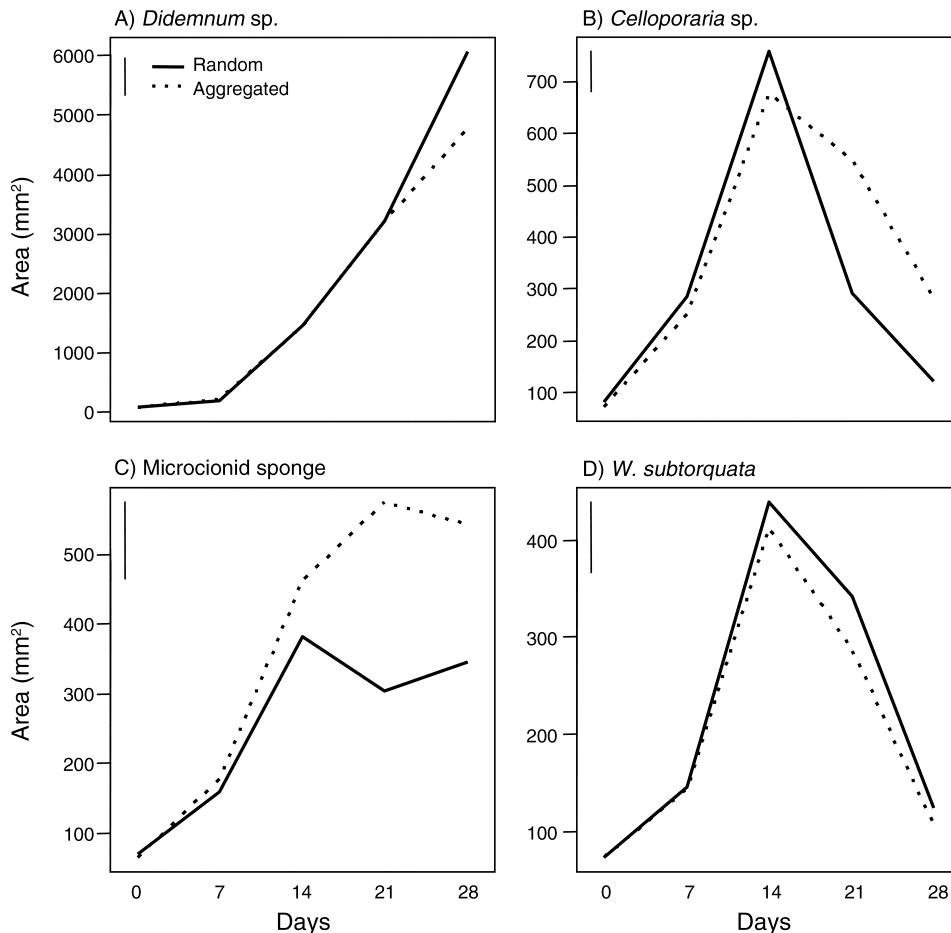
FIG. 3. The effect of spatial arrangement on total size (the sum of size of all individuals on a replicate plate) over time in four competing species in trial 2: (A) *Didemnum* sp., (B) *Celloporaria* sp., (C) microcionid sponge, and (D) *Watersipora subtorquata*. Error bars are shown in the top left corner of each plot. Note that the appropriate errors for these figures are the within-subjects square-root of MS error as shown in Table B3 (for an explanation of why this error is appropriate, see Quinn and Keough [2002:506]).

limit resource-use overlap and therefore the overall strength of interspecific competition in this community. Consequently, there may have been advantages to avoiding intraspecific competition within aggregations because intraspecific competition was likely to be strong relative to interspecific competition in this community.

The advantages of different arrangements were not consistent among the species in the second experiment. Similar to all the species in the first experiment, *Didemnum* sp. performed better when randomly arranged relative to when it was aggregated (Fig. 3A). In contrast, the Microcionid sponge and *Celloporaria* sp. performed better when aggregated (Fig. 3B, C), and there was no advantage in either treatment for *W. subtorquata* (Fig. 3D). The influence of the different spatial arrangements can be interpreted in terms of the relative strength of interspecific and intraspecific competition for each species. Colonial ascidians tend to be strong interspecific competitors in sessile invertebrate assemblages (Russ 1982, Keough 1984) and this was also

the case in our experiment where *Didemnum* sp. rapidly expanded to a very large size and readily grew over other species (Fig. 3). Consequently, individuals of *Didemnum* sp. with a heterospecific neighbor could grow essentially unimpeded but had less opportunity for growth when neighbors were conspecific. Sponges also tend to be strong interspecific competitors in these assemblages (Russ 1982, Buss 1990), but the Microcionid sponge in our experiment was unable to compete effectively with *Didemnum* sp. The sponge preempted free space early in both treatments but to a much greater extent when exposed to less interspecific competition with *Didemnum* sp. in the aggregated arrangement. Bryozoans, in contrast, are generally weak competitors (Russ 1982, Keough 1984, Buss 1990) and our results support this generalization: both species decreased in size after two weeks in the field. The two species of bryozoan in our experiment are weedy species that exploit free space early in community assembly but disappear in older assemblages when they are out-competed by larger,

longer-lived species (S. P. Hart, *personal observation*). Because bryozoans are weak competitors, there is a clear advantage to avoiding strong interspecific competition by limiting heterospecific encounters in the aggregated arrangement, although this was only advantageous for *Celloporaria* sp. in our experiment. Our results corroborate theoretical results (Shmida and Ellner 1984, Tilman 1994, Murrell et al. 2001, 2002) and are consistent with several other empirical studies that demonstrate that strong competitors perform better when inter-dispersed with heterospecifics whereas weak competitors perform better when intraspecifically aggregated (Stoll and Prati 2001, Monzeglio and Stoll 2005, Turnbull et al. 2007).

Competitive superiority within the experimental community not only affected the direction of the effects of spatial arrangement among the different species, it also affected the magnitude of the effects of spatial arrangement: spatial arrangement had a stronger effect on poorer competitors than strong competitors in our experiments (Fig. 3). That arrangement has a stronger effect on poor competitors appears to be a consistent pattern emerging from empirical work (Norris et al. 2001a, b, Monzeglio and Stoll 2005, Turnbull et al. 2007), but we await further studies to assess the generality of this pattern.

There was no evidence for differences in survival or fragmentation rates among treatments for any species in either trial (Appendix B: Table B4, Fig. B1). Furthermore, our assessment of size-inequality suggests that the relative contribution of individuals to overall size was not substantially altered by the different spatial arrangements (Appendix B: Tables B2, B5). Together, these results suggest that the effects of intra- and interspecific competition are quantitatively, but not qualitatively different; the two forms of competition do not appear to generate differences in survival or population size structure, but do, however, alter the capacity for individuals to grow. Therefore, the benefits associated with being randomly arranged (trial 1) or aggregated (trial 2) appear to be driven by an increase in growth across all individuals.

The two encrusting bryozoans, *Celloporaria* sp. and *W. subtorquata*, were included in both experiments and yet the advantage of different spatial arrangements changed between runs (Figs. 2 and 3). These results suggest that the influence of spatial arrangement is context dependent. Other studies have also demonstrated different effects of arrangements on the same species in different contexts and these differences have been attributed to changes in the competitive hierarchy in different situations (Stoll and Prati 2001, Monzeglio and Stoll 2005, Turnbull et al. 2007). We believe that our results also suggest that the benefit of different arrangements will depend on the relative strengths of inter- and intraspecific competition. Interspecific competition was likely to be weak in the first experiment because of the inclusion of different functional groups but was strong in the second experiment because of the presence of the dominant ascidian (*Didemnum* sp.) competitor. However, we recognize that other factors also differed between the experiments and so this suggestion requires further examination.

Mechanisms of the effect of species arrangement

There are two principal mechanisms by which intraspecific aggregation can benefit poor competitors: (1) simple spatial segregation whereby the strength of interspecific competition is reduced by reducing heterospecific encounters (Pacala 1997); and (2) aggregation of a strong competitor increases the strength, and therefore cost, of intraspecific competition, which reduces its effectiveness as an interspecific competitor (Murrell et al. 2001). Most studies assume the first mechanism is primarily responsible for facilitating coexistence among competing species (Stoll and Prati 2001, Monzeglio and Stoll 2005) and this mechanism is almost certainly operating in our experiments. However, the effectiveness of the ascidian as an interspecific competitor was also reduced in our study (i.e., mechanism 2), but not because of a cost of intraspecific competition per se (for corals see Idjadi and Karlson 2007), but rather because of an inherently spatial mechanism. Aggregation of the ascidian reduces the effective perimeter from which it can expand into heterospecific territory such that aggregation in and of itself limits the expansion of the strong competitor and provides poorer competitors with extra time and space to grow (cf. Neuhauser and Pacala 1999, Chesson and Neuhauser 2002). This has the same effect as a "cost of competition," namely, reducing the per capita effectiveness of the ascidian as an interspecific competitor. Ultimately, to determine the relative importance of the different mechanisms by which aggregation may favor poor competitors, experiments that vary the strength of intraspecific competition for the superior competitor independently of the number of heterospecific contacts are required (e.g., Idjadi and Karlson 2007).

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Reports

APPENDIX A

Photographs of experimental treatments in trial 2 after one week in the field (*Ecological Archives* E090-101-A1).

APPENDIX B

ANOVA tables and figure showing the effects of spatial arrangement on size, size inequality, and number of surviving colonies for both trials (*Ecological Archives* E090-101-A2).