Spatially stochastic settlement and the coexistence of benthic marine animals

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Abstract. For sessile organisms, dispersal and recruitment are typically spatially stochastic, but there is little understanding of how this variability scales up to influence processes such as competitive coexistence. Here we argue that coexistence of benthic marine animals is enhanced by stochastic differences between species in the spatial distribution of larval settlement. Differentiation of settlement distributions among competitors results in intraspecifically aggregated settlement, which can reduce overall interspecific competition and increase overall intraspecific competition. We test for the components of this mechanism using a pair of subtidal invertebrates, and we find that the mean interspecific effect of the dominant competitor is substantially reduced by natural settlement variability. Using a simulation parameterized with experimental data, we find that variable settlement could play an important role in long-term coexistence between these species. This mechanism may apply broadly to benthic marine communities, which can be highly diverse and typically exhibit large settlement fluctuation over a range of scales.

Key words: aggregation; larval dispersal; marine; stochasticity; storage effect; supply-side ecology.

INTRODUCTION

A persistent challenge in ecology is to explain the maintenance of species diversity in communities where there is little opportunity for resource partitioning (Hutchinson 1961). Space-limited communities of benthic marine organisms have often been studied from this perspective. Evidence exists that coexistence is promoted by a variety of mechanisms, such as a colonization–competition tradeoff (Sousa 1979, Edwards and Stachowicz 2010), a tradeoff between competitive ability and tolerance of harsh abiotic conditions (Connell 1961), and a tradeoff between competitive ability and susceptibility to predation (Paine 1974). A dominant feature of these communities is spatial and temporal variability in the settlement of dispersing invertebrate larvae, and many studies have investigated the causes and consequences of this variability (reviewed in Caley et al. 1996, Underwood and Keough 2000). However, although settlement variation is suspected to influence the diversity of benthic marine animals (Sale 1977, Chesson and Warner 1981), it is generally unknown how local benthic interactions combine with variable settlement to affect whole-population outcomes such as competitive coexistence (Hixon et al. 2002). Our goal in this study is to test whether spatial settlement patterns may act as an additional coexistence mechanism in benthic communities.

One way in which settlement variation could affect coexistence is via a mechanism first proposed for communities of insects feeding on patchy, ephemeral resources (Atkinson and Shorrocks 1981, Ives and May 1985, Ives 1991, Inouye 1999). In these communities, females oviposit on ephemeral resources such as carcasses or rotting fruit, and the developing larvae experience competition for food within the resource patch. Models of competition in this kind of community have shown that coexistence can be facilitated if oviposition is intraspecifically aggregated, and if intraspecific aggregation is greater than interspecific aggregation (Ives 1991). Intraspecifically aggregated oviposition results in intraspecifically aggregated competition among larvae. As a result there is a population-wide increase in intraspecific competition, and a simultaneous population-wide decrease in interspecific competition. As is the case for all stabilizing coexistence mechanisms (Chesson 2000), an increase in intraspecific competition and a decrease in interspecific competition promote stable coexistence. If the effect of aggregation is strong enough, an inferior competitor can coexist with a superior competitor, without any niche partitioning beyond that created by aggregation (Atkinson and Shorrocks 1981, Ives and May 1985).

The processes underlying this mechanism, and the resultant effects on coexistence, may also apply to benthic marine communities. In many benthic systems, ephemeral resource patches (e.g., free space) are created by the mortality of benthic adults (e.g., Sousa 1979). For animal species, these patches are colonized by dispersing...
larvae, and in many communities the density of colonizing larvae is high enough to create substantial competition for space or food during the growth of newly settled individuals (e.g., Marshall and Keough 2003a). In those communities for which competition among neighboring settlers is important, aggregation during settlement should have effects similar to aggregated oviposition in insect communities.

A theoretical study by Berkley et al. (2010) has shown how intraspecific aggregation during larval settlement can permit coexistence, with no other source of niche partitioning. The key assumption of their model is that spatiotemporal variation in the processes affecting dispersal and settlement results in spatial patterns of settlement that are somewhat uncorrelated between competitors. This decoupling of competitors’ settlement patterns results in intraspecifically aggregated settlement. Consequently, competition among neighboring recruits for space or other resources is intraspecifically aggregated as well, which promotes coexistence for the reasons outlined above. Berkley et al. focus on turbulent coastal circulation as a mechanism that can decouple competitors’ settlement distributions (Berkley et al. 2010); this highlights the important fact that larval aggregation may be inadvertent, and that it is the realized patterns of settlement that determine population-wide coexistence. We will focus here on settlement variation at a small scale (centimeters to meters), which is apparently due to stochastic causes, in a benthic environment that is relatively homogeneous. The approach we take can therefore be seen as a field test of the consequences of settlement variation that is uncorrelated between competitors, variation which could be due to small-scale turbulent flow or other factors. However, we note that any cause of aggregation will have similar effects, such as aggregation due to species-specific settlement preferences in a heterogeneous environment.

Recent studies in benthic systems have shown that experimental intraspecific aggregation of established colonial organisms can reduce the overall strength of interspecific competition (Idjadi and Karlson 2007, Hart and Marshall 2009). Our study adds to this work by showing how aggregation and its effects can be consistently generated during larval settlement. This is an important component for understanding the effects of aggregation on coexistence, because theory has shown that aggregated settlement consistently promotes coexistence (Ives and May 1985, Potthoff et al. 2006), while aggregation due to localized growth or dispersal limitation can either promote or inhibit coexistence (Chesson and Neuhauser 2002, Bolker et al. 2003, Potthoff et al. 2006).

We will describe evidence that settlement variability facilitates coexistence among two common subtidal invertebrates in Bodega Harbor, California. In order to test whether settlement variability is important for the coexistence of these species, we show that the following conditions occur: (1) settlement varies stochastically in space, and competing species show distinct settlement distributions; (2) because the dominant competitor exhibits aggregated settlement, the average effect of this species on the inferior competitor is weakened. We also show that settlement variation increases the average strength of intraspecific competition, but for this pair of species the effect on intraspecific competition is negligible. We present additional evidence that settlement variation weakens interspecific competition, using an experimental manipulation of settlement performed in a similar community in Connecticut. Finally, we use a simulation of the Bodega Harbor system to assess the effect of this mechanism on long-term dynamics, and based on this simulation we argue that this mechanism may have an important effect on the persistence of benthic organisms.

**Materials and Methods**

Our approach to quantifying the importance of settlement variability for coexistence can be divided into four parts. First, we use observational data and competitor removals to quantify, for two focal species, the strength of intraspecific and interspecific competition as a function of settlement density. Second, we quantify natural settlement patterns to test for intraspecific and interspecific aggregation during settlement. Third, we combine the empirical competition functions with natural settlement patterns to estimate how variability in settlement alters the population-wide strength of intraspecific and interspecific competition. Fourth, we address the long-term effects of this coexistence mechanism using a simulation parameterized with our empirical estimates of competition and demographic rates. In addition, we use experimental data from a similar community in Connecticut as a further test of whether aggregated settlement of a dominant competitor reduces its negative effect on inferior competitors.

**Natural history.**—The sessile epibenthic invertebrate community in Bodega Harbor, California, USA is composed of solitary and colonial ascidians, encrusting and erect bryozoans, mussels, barnacles, hydroids, sea anemones, and sponges, all organisms with a sessile adult phase and a free-living pelagic larval phase. From June to December 2008 we monitored spatial and temporal variation in larval settlement for the entire community. We quantified the effect of competition on recruitment for the solitary ascidian *Ascidia ceratodes* (hereafter *Ascidia*) and the encrusting bryozoan *Watersipora subtorquata* (hereafter *Watersipora*). These species are common, late-successional dominants in the system (Nydam and Stachowicz 2007). Settlement of larvae in this community occurs primarily on uninhabited surfaces. Occupied space is therefore effectively preempted from settling larvae, and when free space becomes available it is rapidly colonized by settlement. *Ascidia* and other solitary ascidians grow away from the substrate and successfully recruited adults are largely invulnerable to competition for space. *Watersipora*
grows initially as a thin crust, and is most vulnerable to mortality from overgrowth at small sizes (Appendix A). A larger colony may experience partial overgrowth at its margins, while at the same time expanding into neighboring free space and growing away from the substrate. The effect of the life history traits of these two species is that the transition from a newly settled individual to the adult stage is most sensitive to competition, while established individuals are relatively resistant to competition. Accordingly, we focus on the effects of competition on juveniles, using artificial substrate as a proxy for space freed by mortality. We also quantify adult survival in order to project population dynamics under different scenarios. 

_Ascidia_ is a broadcast spawner with larvae likely competent to settle in 1–2 days (K. F. Edwards, _personal observation_), while _Watersipora_ broods coronate larvae which typically settle within 8 hours in the lab (Marshall and Keough 2003b). Dispersal for these species therefore occurs at a scale larger than the scale of sessile interactions, but at a scale small enough that populations within the harbor (roughly 4 km$^2$) are likely effectively closed. For purposes of simulation we therefore treat larvae as entering a global pool from which they are dispersed to free patches with some amount of between-patch variation.

_Data collection and competitor removals._—We monitored settlement by hanging PVC panels from a floating dock at Spud Point Marina, Bodega Bay, California. Panels measuring 10 × 10 cm were deployed on racks in groups of 8, face-down 1 m below the water surface. From June through August, we deployed 16–24 panels every 2–3 weeks, with all panels in a set located within 5 m of each other. Six sets of panels were deployed in total. The homogeneous treatment of the experimental substrate and its deployment in a relatively small area minimized the effect of environmental variation on settlement variation. At 4 weeks after deployment, panels were transported in coolers to the Bodega Marine Laboratory (~2 miles [3.2 km]). We randomly assigned panels to one of three treatments: Control, _Ascidia_ monoculture, or _Watersipora_ monoculture. We examined control panels under a dissecting microscope to count all newly settled individuals. For monoculture treatments, the focal species was counted and all heterospecific settlers were removed. We returned examined panels to Spud Point and monitored them every 2–4 weeks to maintain monoculture treatments and take photographs. In this and other experiments we have observed no sign that transport to the lab or experimental weeding increases the mortality of remaining settlers. Final cover and abundance data was taken at 14 weeks, at which time individuals of the focal species were large enough to resist further competition and reproduce. We will refer to individuals counted at 4 weeks as “settlers,” and individuals at 14 weeks as “recruits.”

In order to provide a broader test of the importance and generality of recruitment variation among sessile invertebrates, we reanalyzed data from a previously conducted field experiment performed in 2000, which involved similar species at Avery Point, Connecticut, USA (Stachowicz et al. 2002). In this experiment, we compared settlement and recruitment of subordinate species onto two groups of panels. The first group represented constant conditions of high cover (60%) of a dominant solitary ascidian, _Ciona intestinalis_. The second group of panels had the same mean cover of the dominant species as the first group, but percent cover varied among individual panels in order to simulate spatial variation in recruitment: half the panels had lower cover (20%) and half had higher cover (100%). The subordinate competitors in this experiment were an array of other ascidians. Treatments were created by densely settling _Ciona_ larvae onto panels in the lab and thinning to approximately 20% or 60% cover, or left at 100% cover. These communities ($N=8$ per cover treatment) were deployed in the field in mid-August and censused over 2 months using weekly photographs, which were later analyzed to assess percent cover of all subordinate species on each panel. For each subordinate species, we used a generalized linear model to compare the mean cover of that species in the constant recruitment treatment (60% cover) with the average cover across the 20% and 100% treatments (variable recruitment), to assess whether spatial variability in recruitment led to higher average cover of subordinates. We used a gamma error distribution with log link, which was appropriate because the data were necessarily non-negative, while recruitment was low enough (range 0–27%) that the upper bound of 100% was unimportant. We added 0.1 to the percent cover data, because the gamma distribution is only defined for positive values.

_Relating recruitment to settlement._—Larval settlement of _Ascidia_ and _Watersipora_ varied in space and time. The density or percent cover of a species at 14 weeks after panel deployment was a saturating function of the number of settlers present at 4 weeks (see Results). We fit a saturating exponential curve to quantify this nonlinearity while testing for an effect of competition on recruitment. Details of the estimation of this relationship are given in Appendix B. Exploratory analyses indicated that _Ascidia_ is the dominant competitor during recruitment, while _Watersipora_ is a weaker competitor. We therefore used our unmanipulated treatment to estimate the effect of _Ascidia_ on _Watersipora_. To quantify the effect of _Ascidia_ on _Watersipora_ recruitment, we first calculated _Watersipora_ per capita recruitment for each panel as (percent cover of _Watersipora_ at 14 weeks)/ (number of _Watersipora_ settlers at 14 weeks).

We then modeled _Watersipora_ per capita recruitment as an exponentially decreasing function of the abundance of _Ascidia_ settlers at 4 weeks. 

_Quantifying the magnitude of spatial settlement variation._—For the purposes of this study we wished to
examine spatial settlement variation while controlling for temporal trends. Across all time periods, the variance : mean ratio of settlers per plate ranged from 1.8 to 13.5 for Ascidia and from 0.8 to 12 for Watersipora, indicating substantial overdispersion compared to Poisson-distributed settlement. Accordingly, we modeled spatial variation for each species with the negative binomial distribution, using a generalized linear model with a factor to account for differences in mean settlement over time (Venables and Ripley 2002). The negative binomial fit effectively represented the observed spread of settler density (Appendix C), and fit much better than a model with Poisson error (ΔAIC = 301 for Ascidia, ΔAIC = 149 for Watersipora). For our analyses, we assume that the magnitude of settlement variation, i.e., the dispersion parameter in the negative binomial distribution, does not vary as a function of species' overall densities. This assumption has been of some importance in models of aggregated insect oviposition (Green 1986), and further evidence and discussion of this issue can be found in Appendix D.

Quantifying the effect of spatial settlement variation.— To quantify the effect of spatial settlement variation on interspecific and intraspecific competition, we combined our fitted models of recruitment as a function of settlement with our negative binomial models of spatial settlement variation. Effectively we asked, what is the predicted recruitment over an entire landscape under set variation. We used this method to quantify the effect of natural settlement variation on both intraspecific and interspecific competition. Further details of this method are given in Appendix E.

The method described above yields a point estimate for the effect of settlement variation on the strength of competition. In order to account for the uncertainty in our estimates of the competition curves and the negative binomial settlement fits, we used a bootstrap procedure to create confidence intervals for the effects of settlement variation on competition. For each bootstrap replicate, we resampled the rows of our data set with replacement (each temporal block was resampled separately). We then used the resampled data set to fit competition curves as in Fig. 1A–C, and to quantify settlement variation with the negative binomial distribution. Finally, using the method described above, we combined the competition curves with the fitted negative binomial parameters to estimate the effect of settlement variation on intraspecific and interspecific competition. We used this procedure to create 10 000 bootstrap replicates, from which we calculated adjusted percentile 95% confidence intervals using the boot package in R 2.11.0 (Davison and Hinkley 1997, Canty and Ripley 2010, R Development Core Team 2010). Very similar results were obtained using other forms of bootstrap confidence intervals.

Patch-based simulation.— It can be difficult to judge the long-term ecological effects of changes in recruitment caused by settlement variation. We therefore created a model based on field data that isolates the effect of this coexistence mechanism on the long-term persistence of the inferior competitor Watersipora. In order to directly parameterize the model with data from our competition experiment, we used a landscape divided into 10 000 patches, each 100 cm² in size (the same size as our experimental panels). We included two species representing Ascidia and Watersipora. We modeled time in discrete one-month steps, during which the following events occurred. (1) Larvae are produced in proportion to the total abundance of adults, and distributed randomly among patches according to a negative binomial distribution with mean \( r_i N_i \) and species-specific dispersion parameter \( \theta_i \), where \( r_i \) is the per capita fecundity of species \( i \) (settlers per unit abundance per month per 100 cm²), and \( N_i \) is the abundance of species \( i \).

(2) In each patch, the number of Ascidia larvae encountering free space is equal to (number of settling larvae) × (fraction of space unoccupied), rounded to the nearest integer. Then the number of successful recruits is determined according to the relationship in Fig. 1A. Finally, the amount of space occupied by those recruits is determined according to the empirical relationship between abundance and space
occupied for *Ascidia* (Appendix E: Fig. E1). (3) In each patch, any space not claimed by *Ascidia* recruitment is available to *Watersipora* larvae, and the number of larvae encountering free space is equal to (number of settling larvae) × (fraction of unoccupied space), rounded to the nearest integer. The amount of space occupied by those settlers is determined from the relationship in Fig. 2A. This form of competition between *Ascidia* and *Watersipora* does not directly use the relationship in Fig. 2C. Instead, it is assumed that *Watersipora* has no effect on *Ascidia*, and that *Watersipora* can therefore only occupy space not occupied by *Ascidia*. This assumption is reasonable based on our observations and the interspecific relationship shown in Fig. 2C, and it allows us to combine estimates of intraspecific competition, which are based on monoculture treatments (Fig. 2A, B), with interspecific effects.

(4) The age of all individuals is incremented one month (and individuals only reproduce at age 3 months or greater). (5) Adult individuals die randomly with some constant, species-specific probability.

We quantified coexistence with an invasibility analysis. The simulation first ran for 300 time steps with only *Ascidia* present, at which point a roughly constant abundance had been obtained. We then introduced 50 *Watersipora* individuals, and monitored per capita growth rate of *Watersipora* for 20 time steps. The average growth rate over this period estimates the low-density growth rate. This process was repeated three times for each combination of parameter values. *Ascidia* could invade *Watersipora* for all parameter values we considered, and therefore the ability of *Watersipora* to invade *Ascidia* determines whether the two species will tend to coexist.

We estimated demographic parameters from field data (K. F. Edwards, unpublished data). *Watersipora* fecundity was set to 0.8 settlers per month, per cm² occupied. *Ascidia* fecundity was set to 0.4 settlers per individual per month. We set spatial variation in *Watersipora* settlement using a negative binomial dispersion parameter equal to 8.17, estimated from field data. We varied spatial variation in *Ascidia* over a wide range (dispersion parameter: 1–200) to see how coexistence is affected by
clustering of the dominant competitor. *Ascidia* mortality rate was estimated as 0.125 mo\(^{-1}\), using survival analysis with data gathered by following individuals over time with photographs; *Ascidia* mortality appears to be caused primarily by senescence and/or disturbance. *Watersipora* mortality was estimated by following individuals with photographs and measuring partial overgrowth by competitors, senescence, and clonal spread of a colony into vacant neighboring areas. Partial overgrowth can be substantial, but is largely balanced by new growth. Since we are interested primarily in recruitment variability, we approximate the combination of processes affecting adult *Watersipora* with a single mortality rate, which we varied over different runs from 0.04 to 0.08 mo\(^{-1}\), the minimum value representing mortality from senescence only and the maximum representing mortality from senescence and partial overgrowth combined. Although this simulation is too simple to represent in detail the dynamics of these species, we have utilized field estimates of fecundity, mortality, competitive interactions, and settlement variation. The results should therefore give a reasonable first approximation of the importance of settlement variation for long-term dynamics.

**Results**

Removal of heterospecific competitors revealed a strong asymmetry in the competitive abilities of the focal species. *Watersipora* recruitment in the unmanipulated treatment was ~25% of recruitment when heterospecific competitors were removed (Fig. 1B), while *Ascidia* recruitment was not affected by heterospecifics (Fig. 1A). Furthermore, we found that *Watersipora* recruitment was predicted by *Ascidia* settlement (Fig. 1C), with survival declining to zero at ~30–40 *Ascidia* settlers per 100-cm\(^2\) panel. The role of *Ascidia* as a dominant competitor is consistent with our observation that *Ascidia* can displace or smother settlers of all other species on primary substrate as it grows, being vulnerable itself only at the smallest sizes. Likewise, the poor competitive ability of *Watersipora* is consistent with data showing strong size-dependence of over-
growth mortality, with settlers experiencing much higher mortality than older and larger colonies (Appendix A).

We found substantial spatial variation in larval settlement for both species (Fig. 1D; Appendix A: Fig. A2), with a typical CV of ~0.5. Importantly, among-panel variation was weakly negatively correlated between species ($r = -0.34$, $P = 0.021$; Fig. 1D). This variation occurred on a scale of 5 meters or less, with panels within 20 cm varying up to a factor of three in settlement of *Ascidia*. Because settlement variation is relatively large for each species (highly overdispersed compared to a Poisson distribution, Appendix C), and because settlement tends to be negatively correlated between species, the settlement distributions of these species result in intraspecific aggregation, but not interspecific aggregation (Ives 1991).

We estimated the effect of settlement variation on the overall strength of intraspecific and interspecific competition during recruitment. Intraspecific competition for *Ascidia* is relatively weak over the range of settlement densities we observed, because *Ascidia* recruitment increases approximately linearly with *Ascidia* settlement, but the abundance of adult *Ascidia* does begin to saturate at high settlement densities, presumably reflecting reduced survival due to intraspecific competition (Fig. 1A). Intraspecific competition is stronger for *Watersipora*, because the total amount of space occupied at 14 weeks begins to saturate at 100% at a settlement density of 30–40 per 100 cm$^2$ (Fig. 1B). Interspecific competition between *Ascidia* and *Watersipora* is estimated using the relationship in Fig. 1C. Fig. 2 shows the results of combining these statistical models of competition with observed settlement variation. Although the confidence intervals in Fig. 2A and B do not overlap zero, settlement variation has a very weak effect on the overall strength of intraspecific competition; when the mean settlement density is 30 settlers per 100 cm$^2$, *Ascidia* recruitment is reduced by ~3%, while *Watersipora* recruitment is reduced by ~5%. The effect of settlement variation on interspecific competition is much stronger; at a settlement density of 30 *Ascidia* settlers per 100 cm$^2$, recruitment of *Watersipora* is increased by ~800% in the presence of variable settlement (Fig. 2C). The difference in effect for intraspecific and interspecific competition appears to be due to strong per capita effects of *Ascidia* on *Watersipora*, but relatively weak per capita effects on conspecifics for each species.

We analyzed data from a separate experiment in Connecticut, in which manipulation of the density of recruits of a spatial dominant (*Ciona intestinalis*) mimicked the effects of settlement variation. We found that all three competitors that were monitored had greater recruitment when *Ciona* recruitment varied in space, compared to a treatment with no spatial variation but the same average density (Fig. 2D). *Botrylloides violaceus* recruitment increased by ~60% in the “variable” treatment, *Diplosoma listerianum* recruitment increased by ~300% in the “variable” treatment, and *Ascidia aspersa* had zero recruitment in the “constant” treatment. The effect was significant for *Diplosoma listerianum* (likelihood ratio $\chi^2_1 = 5.6$, $P = 0.017$) and *Ascidia aspersa* (likelihood ratio $\chi^2_1 = 4.1$, $P = 0.043$), but not *Botrylloides violaceus* (likelihood ratio $\chi^2_1 = 1.3$, $P = 0.25$).

In our patch-based simulation of competition between *Ascidia* and *Watersipora*, we found that the invasion rate of *Watersipora* in an *Ascidia* monoculture increased with increasing spatial variation in *Ascidia* settlement (i.e., increased aggregation), and the effect was sufficient for coexistence under very high spatial variation (Fig. 3) that was near the upper limit of that observed in nature. For parameter combinations where coexistence was not predicted, spatial variation still increased the low-density growth rate of *Watersipora*, making coexistence more feasible under natural conditions where multiple coexistence mechanisms likely operate.

**DISCUSSION**

Our results suggest that spatially stochastic settlement, in this case occurring at a small scale, can promote coexistence of benthic species. In the *Watersipora-Ascidia* system, *Ascidia* is a dominant competitor when recruiting to patches of free space (Fig. 1). Both species exhibit patchy settlement distributions that result in intraspecific aggregation (Appendix C), and these distributions are largely independent of each other, weakly negatively correlated on average (Fig. 1D). When the effect of *Ascidia* on *Watersipora* (Fig. 1C) is combined with the settlement distributions of these species (Appendix C: Fig. C1), it is predicted that the overall negative effect of *Ascidia* on *Watersipora* is much less under natural settlement variation, when compared to a hypothetical world with no settlement variation (Fig. 2C). In contrast, settlement variation is predicted to have weak effects on overall intraspecific competition during recruitment, for both species (Fig. 2A, B). The importance of settlement variation in altering the strength of interspecific competition is supported by our re-analysis of an experimental manipulation in the similar *Ciona* system (Fig. 2D). Here, three inferior competitors all benefited from variability in recruitment of another dominant solitary ascidian.

For the *Watersipora-Ascidia* system, the difference between interspecific and intraspecific competition results from differences in per capita effects, which manifest as differences in the nonlinearity of the curves in Fig. 1A–C. *Ascidia* has a strong per capita effect on *Watersipora*, because growing *Ascidia* completely overgrow neighboring young *Watersipora* colonies (K. F. Edwards and J. J. Stachowicz, *personal observations*). In contrast, competition between neighboring *Ascidia* tends to result in less attachment area per individual, without large effects on the survival or growth of individuals (K. F. Edwards and J. J. Stachowicz, *personal observations*). Intraspecific competition between *Watersipora* is...
somewhat stronger, because Watersipora at high density do begin to overgrow one another. However, Watersipora grows relatively slowly, and saturation of space at the time when we measured recruitment (14 weeks) only occurs at relatively high density. Therefore, it is possible that our analysis underestimates the total importance of settlement variation for intraspecific competition, for both species. This is because we have focused on competition during recruitment, and intraspecific density dependence may manifest more slowly than interspecific effects. Nonetheless, it is clear that strong asymmetric interspecific competition at early life stages should limit the coexistence of these species, in the absence of mechanisms that reduce the effects of Ascidia on Watersipora settlers.

When a species is at low density, its ability to persist and grow should be determined by the strength of interspecific effects, because interactions with conspecifics will be relatively rare. For this reason, a reduction in interspecific competition due to settlement variation should enhance the persistence of inferior competitors. This argument is supported by our simulation of long-term competition between Watersipora and Ascidia (Fig. 3). The model output indicates that an increase in settlement variation for Ascidia results in an increase in the invasion rate of Watersipora in an Ascidia monoculture (Fig. 3). Although the effect can be substantial over the natural range of settlement variation, highly aggregated settlement is required to produce coexistence. This simulation necessarily simplifies the population dynamics of these species, but we think it is reasonable to infer from these results that spatially variable settlement plays an important role in long-term coexistence for these species, and that this mechanism likely combines with others (such as temporal recruitment differentiation) to jointly maintain diversity in this system.

We have focused on the community consequences of variable settlement, but what processes cause the variation we observe? Our collection methods were designed to minimize environmental differences among patches, so that differences over space would be due to “stochastic” factors, rather than spatial niche differences. We therefore expect that the variation we observe is due to causes that operate over relatively homogeneous substrates and environmental conditions. Fluid dynamics in marine systems are complex, even in environments with low mean current velocity (Koehl 2007), and could create clumping in the supply of dispersing propagules. In addition, settling larvae of some species are known to respond to the presence of conspecifics or heterospecifics (Grosberg 1981, Pawlik et al. 1991). Preferential aggregation with conspecifics or avoidance of heterospecifics could lead to the moderate spatial segregation we observe, and the weak negative correlation between Ascidia and Watersipora may indicate a role for competitor avoidance. However, separate settlement experiments have not shown a strong avoidance of Ascidia by Watersipora (D. Claar, K. F. Edwards, J. J. Stachowicz, unpublished manuscript).

**Settlement variation over larger scales**

We have studied settlement variation at a small scale, among organisms with short enough dispersal that a harbor is likely a closed system. Our results suggest that small-scale variability, which is often treated as background “noise,” may have significant effects on species interactions. However, many benthic organisms disperse over much greater distances and show large settlement variation over a range of scales (e.g., Navarrete et al.)
2008). We think the coexistence mechanism we have described should be important over large spatial scales as well, because the components of the mechanism will still apply (Inouye 1999). If settlement varies stochastically at the scale of sites separated by kilometers, and species show different settlement distributions among sites, then population-wide interspecific competition should be reduced and intraspecific competition increased. This expectation is supported by a model of dispersal under realistically turbulent flow conditions (Berkley et al. 2010). This model shows that settlement variation can allow an inferior competitor to coexist with a superior competitor, because turbulent flow creates enough stochasticity during dispersal to differentiate competitors’ settlement distributions. In general, we expect that the importance of settlement variation will depend upon the amount of variation, the degree of difference in competitors’ distributions, and the ability of adults to preempt resources from juveniles.

Aggregation and coexistence

We have focused on stochastic settlement variation as a ubiquitous phenomenon that may affect coexistence in benthic marine systems. The mechanism we have described is related more generally to a large theoretical literature addressing the effects of intraspecific aggregation on coexistence (e.g., Ives and May 1985, Pacala 1986). An important theme of this work has been that the details of how aggregation arises and how competition operates are critical in determining whether aggregation promotes coexistence. For example, there are many models of plant competition in which aggregation arises from local dispersal, but this aggregation may promote or inhibit coexistence, depending on conditions such as the relative scales of intraspecific and interspecific competition, and whether competitors would coexist without dispersal limitation (Chesson and Neuhauer 2002, Murrell et al. 2002, Bolker et al. 2003). Dispersal distances are typically much larger for benthic animals than terrestrial plants (Kinlan and Gaines 2003), and even for animals with relatively short larval duration, dispersal is unlikely to be so limited as to produce the strong species segregation observed in some models of plant competition (Bolker et al. 2003).

Instead, for marine animals, aggregation during recruitment is more likely to arise from the various processes that can produce patchy or clumped settlement, such as larval behavior or complex fluid dynamics. Theoretical work by Potthoff et al. (2006) has shown that patchy dispersal and local dispersal have very different effects on coexistence. The effect of local dispersal varies, depending on environmental heterogeneity and relative competitive abilities, while patchy dispersal robustly promotes coexistence under different conditions, for the reasons we have outlined here. It therefore seems likely that nonrandom spatial distributions have different origins and consequences in terrestrial vs. marine systems, and further modeling work incorporating realistic dispersal processes in marine systems will help unravel the role of these processes in coexistence. Aggregation in benthic communities has also been addressed in experimental studies that manipulate the spatial distribution of established invertebrate colonies (Idjadi and Karlson 2007, Hart and Marshall 2009). These studies have found that intraspecific aggregation reduces the overall effects of interspecific competition on weaker competitors. In order to understand the long-term consequences of these effects, it will be important to understand how larval settlement and local colony growth jointly affect spatial distributions, and how these different sources of aggregation alter long-term dynamics.

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Literature Cited


R Development Core Team. 2010. R version 2.11.0. R Project for Statistical Computing, Vienna, Austria.


APPENDIX A
Size-dependent mortality of Watersipora (Ecological Archives E092-088-A1).

APPENDIX B
Estimation of recruitment as a function of settlement (Ecological Archives E092-088-A2).

APPENDIX C
Quantification of spatial settlement variation (Ecological Archives E092-088-A3).

APPENDIX D
Density independence of the negative binomial dispersion parameter (Ecological Archives E092-088-A4).

APPENDIX E
The effect of settlement variation on the strength of competition (Ecological Archives E092-088-A5).