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Allee effects and conspecific cueing jointly lead to conspecific attraction

Received: 30 December 2004 / Accepted: 16 March 2006 / Published online: 11 May 2006
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Abstract Conspecific attraction is the preferential settlement into habitat patches with conspecifics. To be a good proximate strategy, fitness gains from settling with conspecifics must outweigh the costs of higher conspecific densities, such as intraspecific competition. Two types of benefits have been proposed to explain conspecific attraction: Allee effects (i.e., positive density dependence) and conspecific cueing (using conspecifics as an indicator of habitat quality). I present empirical evidence for conspecific attraction in the settlement of the porcelain crab, *Petrolisthes cinctipes* Randall (Anomura: Porcellanidae). Previous work demonstrated that *P. cinctipes* experiences strong intraspecific competition and that both Allee effects and conspecific cueing are present in *P. cinctipes* life-history. I developed an empirically-based fitness model of the costs and benefits of settling with conspecifics. Based on this model, I simulated optimal settlement to habitat patches that varied in conspecific density and habitat quality, where the correlation between density and habitat quality determined the level of conspecific cueing. I tested whether Allee effects alone, conspecific cueing alone, or Allee effects and conspecific cueing together could provide an ultimate explanation for the proximate settlement behavior of *P. cinctipes*. The settlement simulation was consistent with empirical settlement only when Allee effects and conspecific cueing were both included. Three life-history features are critical to this conclusion: (1) fitness is maximized at intermediate density, (2) fitness depends on the decisions of previous settlers, and (3) conspecific density provides good

information about habitat quality. The quality of information garnered from conspecifics determines whether conspecific attraction is a good proximate strategy for settlement. I present a graphical illustration demonstrating how Allee effects and conspecific cueing work together to influence fitness, providing a conceptual framework for other systems.

Keywords Gregarious settlement · Habitat selection · *Petrolisthes cinctipes* · Habitat quality · Fitness trade-offs

Introduction

Conspecific attraction is an increase in the probability of settlement in the presence of conspecifics. It is a common phenomenon across taxa in both terrestrial and marine systems (Baltz and Clark 1999; Brown et al. 2000; Burke 1986; Doligez et al. 2002; Jensen 1989; Minchinton 1997; Muller et al. 1997; reviewed in Reed and Dobson 1993; Smith and Peacock 1990; Stamps 1988; Toonen and Pawlik 2001). For conspecific attraction to be a good settlement strategy, the costs associated with higher conspecific densities, such as intraspecific competition, must be outweighed by the benefits of settling with conspecifics. Previous studies have identified two types of benefits that may accrue to settlers: conspecifics may provide benefits directly via positive density dependence (i.e. Allee effects) or conspecifics may be indicators of habitat quality (i.e., conspecific cueing).

Allee effects are density-dependent increases in per capita fitness, such as: (1) lower per capita predation rate when surrounded by conspecifics (Bertness and Groszholz 1985; Highsmith 1982; Jensen and Armstrong 1991; Ray and Stoner 1994; Tegner and Levin 1983), (2) increased foraging success in a group of conspecifics (Buckley 1997; Clark and Mangel 1984), (3) decreased environmental stress near conspecifics (Bertness 1989), or (4) increased access to mates. Conspecific attraction in marine invertebrates (usually called “gregarious

Electronic Supplementary Material Supplementary material is available for this article at <http://www.dx.doi.org/10.1007/s00442-006-0419-y> and is accessible for authorized users.

Communicated by Craig Osenberg

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settlement”) is often attributed to Allee effects. For example, Highsmith (1982) documented that gregarious settlement of the sanddollar, *Dendraster excentricus*, to existing sanddollar beds resulted in decreased predation on settlers: adult sanddollars continuously rework the sediment making it unfit for the tube-forming predators of settlers. Similarly, Bertness and Grosholz (1985) demonstrated that high conspecific density decreases the risk of predation and mitigates the risk of ice scour in the gregariously settling mussel, *Geukensia demissa*. Regardless of the specific mechanism, Allee effects are increases in per capita fitness directly attributable to conspecific density (N).

Conspecific cueing is the use of conspecifics as an indicator of habitat quality: settler fitness is higher in patches with conspecifics because of higher intrinsic habitat quality (κ) in those patches, and not as a direct result of conspecific presence or behavior. By “intrinsic habitat quality”, I mean an environmental parameter (e.g., resource abundance) that influences density-independent growth rate. The effectiveness of conspecific cueing depends on the quality of information garnered from conspecifics, which increases with increasing positive correlation between conspecific density (N) and habitat quality (κ), $\rho_{N,\kappa}$. In the avian literature, conspecific attraction is widely attributed to conspecific cueing (or, more specifically, to “public information”: the use of conspecific performance as an indicator of habitat quality: Brown et al. 2000; Danchin et al. 2001; Doligez et al. 2002, 2004; Valone 1993, 1996). For birds choosing a breeding territory, conspecific performance is an important indicator of high-quality breeding sites, especially for inexperienced or failed breeders that lack individual information about breeding sites (Doligez et al. 2003, 2004). A recent review (Danchin et al. 2001) suggested that all reported cases of conspecific attraction are actually examples of public information.

For conspecific attraction to be a good proximate strategy, fitness should increase with increasing conspecific density over the natural density range. Previous studies emphasized either Allee effects or conspecific cueing, but few studies have jointly addressed these benefits and the concomitant costs of increased conspecific density. Here, I developed a model of the costs and benefits of settling with conspecifics in the intertidal porcelain crab, *Petrolisthes cinctipes*. First, I discuss the life history of *P. cinctipes*, including the empirical evidence for intraspecific competition, Allee effects in the form of decreased predation in the presence of conspecifics, and $\rho_{N,\kappa}$. I present new data on the empirical pattern of gregarious settlement in *P. cinctipes*. Second, based on the empirical evidence for costs and benefits, I developed a deterministic fitness model to predict individual fitness as a function of N with and without Allee effects. Third, based on this fitness model, I developed a stochastic settlement model in which incoming larvae optimally choose among habitat patches that vary in habitat quality (κ) and conspecific density (N). I compared the settlement distributions for three cases: Allee

effects only, conspecific cueing only, and both Allee effects and conspecific cueing. The settlement simulation is consistent with the empirical pattern of settlement only when Allee effects and conspecific cueing are both included. Finally, I present a graphical illustration of how Allee effects and conspecific cueing work together to influence fitness, providing a conceptual framework that can be applied to other systems.

Gregarious settlement in *P. cinctipes*

Costs and benefits of conspecifics

P. cinctipes is a filter-feeding porcelain crab that lives under rocks in cobblefields from Point Conception, California, USA to British Columbia, Canada. Larvae settle episodically from May to August and crabs reach densities in excess of 900 m^{-2} (Donahue 2004). Despite this aggregated distribution and feeding strategy, there is strong evidence for intraspecific competition in *P. cinctipes*. In a previous study (Donahue 2004), I demonstrated that individual growth rates decline with increasing density in both field enclosures and in laboratory experiments.

Previous studies (Jensen 1991; Jensen and Armstrong 1991) demonstrated that *P. cinctipes* settle preferentially with conspecifics rather than congeners and suggested that Allee effects contribute to this behavior. In a laboratory experiment, Jensen and Armstrong (1991) found that predation on recently settled *P. cinctipes* by the tidepool sculpin, *Oligocottus maculosus*, was lower in the presence of *P. cinctipes* adults. Settlers used adults as refuges by hiding underneath them. This Allee effect is a benefit that may accrue to settlers in the presence of adults.

Conspecifics as indicators of habitat quality

Settlers may also benefit from conspecific adults if conspecific density is an indicator of quality habitat. *P. cinctipes* are filter-feeders and, therefore, inorganic particulates decrease feeding efficiency: growth rates are lower when suspended particulates have a lower fraction of organic content (Donahue 2004). In a field experiment with long enclosures placed vertically in the intertidal, Jensen (1991) found that adult *P. cinctipes* actively chose mid-intertidal habitats over low-intertidal habitats and that low-intertidal habitats had a higher proportion of fine-grained inorganic sediment than did mid-intertidal habitats. In a randomized field experiment, Akins (2003) found that adult *P. cinctipes* strongly preferred rocks set on cobbles and pebbles, rather than rocks set on sand or a combination of sand and pebbles. In addition, Akins (2003) found a close association ($R^2=0.84$) between the overall abundance of *P. cinctipes* at a site and the percent of cobble habitat per rock. By settling with conspecific adults, settlers cue on habitat

with lower amounts of the fine sediments that interfere with filter feeding, thereby improving habitat quality.

Methods

Previous field studies demonstrated that *P. cinctipes* settle preferentially with conspecifics over congeners (Jensen 1991; Jensen and Armstrong 1991). Laboratory experiments on *P. cinctipes* larvae have found that newly metamorphosed megalopae settle within 2–4 days in the presence of adults, but wait for 2–3 weeks or more to settle without a cue from conspecifics (Jensen 1991). However, previous studies have not quantified the relationship between settlement and resident density over the wide range of crab densities observed in the field. To investigate this relationship, I manipulated crab density in field enclosures (for a description of the enclosures, see Donahue 2004) and tracked settlement to those enclosures during settlement pulses at Twin Coves (Sonoma County, California, 38°27.517'N, 123°8.683'W) in May and June of 2001. The total number of settlers to enclosures was higher in May (260 settlers) than in June (850 settlers).

Enclosures were randomly assigned to one of five treatments: control, zero, five, 30, or 60 crabs per enclosure. Each density treatment had eight replicates; there were seven control replicates (enclosures without lids). There was no difference between the control and the zero treatment, indicating that the mesh did not impede settling megalopae. Death of settlers by predation before sampling was unlikely because the enclosures excluded fish and crab predators and there is no evidence of cannibalism by adults on settlers in laboratory experiments (Donahue 2003; Jensen 1991). While sampling the experiment, I found that additional adult *P. cinctipes* had colonized under the enclosures and I counted them. I took advantage of this larger range of total crab densities (exceeding the natural density range found in the field) to estimate the relationship between settlement and total conspecific density, N . I also examined how colonizing crabs might influence the results of the settlement experiment.

To estimate the relationship between the number of settlers and total N (including experimental and colonizing crabs), I used a generalized linear model. The variance in the number of settlers per enclosure increased faster than the mean; therefore, I modeled the response variable as an over-dispersed Poisson random variable, estimating the over-dispersion parameter from the deviance (Dobson 2002). Transforming the response variable to meet normality assumptions was not an option because the purpose of the statistical model was to distinguish between a linear and nonlinear relationship between settlers and N ; a nonlinear transformation would introduce spurious nonlinearity into this relationship. For the same reason, I used an identity link function. First, I analyzed the two pulses separately testing whether settlement was a linear (N_{ij}) or nonlinear

(N_{ij}^2) function of N during each pulse. Second, I tested for interactions between Pulse and the linear and nonlinear components, using the following statistical model:

$$\text{Settlers}_{ij} \sim N_{ij} + N_{ij}^2 + \text{Pulse}_j + \text{Pulse}_j \times N_{ij} + \text{Pulse}_j \times N_{ij}^2, \quad (1)$$

where Settlers_{ij} is the number of settlers to enclosure i during settlement pulse j , Pulse_j is a nominal variable indicating May or June, and N_{ij} is the total density of conspecifics at enclosure i during settlement pulse j . In all cases, density was centered to reduce collinearity.

Crabs colonizing under the enclosures present a potential problem. If colonizing crabs are responding to habitat quality cues, then N and κ are no longer independent. I performed two analyses to understand how colonizing crabs might influence the results of the settlement experiment. First, I tested whether settlers responded similarly to colonizing and experimental crab densities. If settlers and colonizing crabs both select for habitat quality, then the number of settlers should be more strongly related to colonizing crabs than to experimental crabs. Using a generalized linear model with over-dispersed Poisson distribution similar to Eq. 1, I replaced density with separate terms for experimental crab density and colonizing crab density (Table 2). Both density terms were centered to reduce collinearity; there was no association between experimental and colonizing crab densities ($\rho = 0.13$, $P = 0.27$). Second, I analyzed the residuals of a competition experiment (reported in Donahue 2004) performed in these same enclosures for 2 months following the settlement experiment. These are the residuals of average individual growth rate per enclosure regressed on experimental crab density; the residuals could reflect variation in habitat quality among enclosures. I tested for an association between these residuals and the number of colonizing crabs in June.

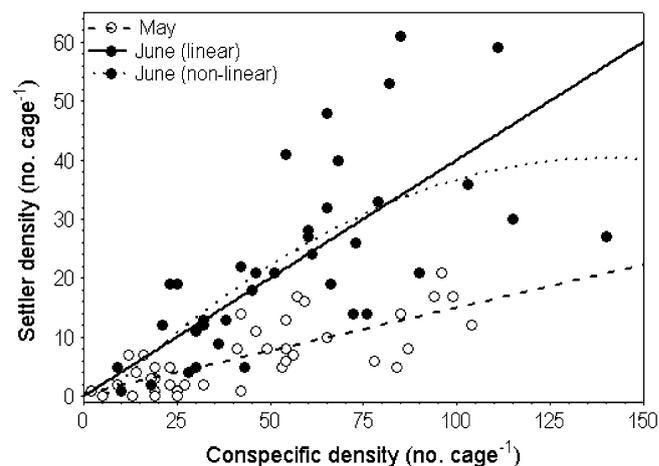


Fig. 1 Density of porcelain crab (*Petrolisthes cinctipes*) settlers versus total conspecific density (N) (see Table 1) in and under cages in May (open circles, dashed line) and in June (filled circles, solid and dotted lines)

Table 1 Generalized linear model of the number of settlers per enclosure with over-dispersed Poisson distribution and identity link. N_{ij} is the total density of crabs in and under an enclosure (centered to reduce collinearity); *Pulse* indicates the larval settlement pulses in May and June

	Estimate	SE	Wald	<i>P</i>
May only				
Intercept (centered)	6.91	0.940	54.1	< 0.00001
<i>N</i>	0.146	0.0225	42.2	< 0.00001
<i>N</i> ²	-0.0000161	0.000773	0.000434	0.983
June only				
Intercept (centered)	24.4	2.20	123	< 0.00001
<i>N</i>	0.377	0.0490	59.1	< 0.00001
<i>N</i> ²	-0.00223	0.00131	2.90	0.0888
May and June				
Intercept (centered)	15.7	1.11	198	< 0.00001
<i>Pulse</i>	-8.74	1.11	61.8	< 0.00001
<i>N</i>	0.261	0.0253	107	< 0.00001
<i>N</i> ²	-0.00112	0.000735	2.33	0.127
<i>N</i> × <i>Pulse</i>	-0.115	0.0253	20.8	< 0.00001
<i>N</i> ² × <i>Pulse</i>	0.00110	0.000735	2.26	0.133

Results

The number of settlers increased with conspecific density in both May (Table 1; Fig. 1, dashed line) and June (Table 1; Fig. 2, solid line), though the slope varied between pulses (Table 1, May and June). When the pulses were analyzed together, there was no evidence of nonlinearity (Table 1, May and June). When June was analyzed alone, there was a marginal deceleration of settlement at high conspecific densities (Table 1; Fig. 1, dotted line). There was no trend for nonlinearity in May when analyzed alone (Table 1) or when both pulses were analyzed together (Table 1).

In both May and June, settlers responded more strongly to the increasing density of experimental crabs than colonizing crabs (Table 2). In May, the nonlinear response of settlers to colonizing crabs was positive (i.e., accelerating) while the nonlinear response to experimental crabs was marginally negative (i.e., decelerating) (Table 2). In June, there was no nonlinear response to experimental or colonizing crabs (Table 2). The combined effect was that the nonlinear response to total crabs in both months together was nonsignificant (Table 1). There was a marginal negative association ($\rho = -0.35$, $P = 0.06$) between the residuals of the competition experiment and the number of colonizing crabs.

Table 2 Generalized linear model of the number of settlers per enclosure with over-dispersed Poisson distribution and an identity link. There was no correlation between experimental (number of crabs in the experimental treatments) and colonizing crabs (number of crabs that colonized under the enclosures). Both measures of crab density were centered to reduce collinearity. To ease interpretation, the two settlement pulses were analyzed separately

	Estimate	95% CI	Wald	<i>P</i>
May				
Intercept (centered)	7.84	(5.11, 10.6)	31.7	< 0.00001
Experimental crabs	0.231	(0.147, 0.315)	29.2	< 0.00001
Experimental crabs ²	-3.38×10 ⁻³	(-7.34, 0.573)×10 ⁻³	2.81	0.0938
Colonizing crabs	0.0898	(0.00347, 0.176)	4.16	0.0415
Colonizing crabs ²	0.00518	(0.000319, 0.010)	4.36	0.0367
June				
Intercept (centered)	26.9	(20.3, 33.4)	63.6	< .00001
Experimental crabs	0.612	(0.389, 0.836)	28.9	< .00001
Experimental crabs ²	-0.00620	(-0.0168, 0.00438)	1.32	0.251
Colonizing crabs	0.215	(0.0632, 0.367)	7.70	0.00552
Colonizing crabs ²	-0.00488	(-0.0113, 0.00158)	2.19	0.139

Model of fitness tradeoffs

Methods

To understand how Allee effects and conspecific cueing contribute to the empirical pattern of gregarious settlement in *P. cinctipes* (Fig. 1), I developed an empirically based model of settler fitness that quantifies the tradeoffs between competition, habitat quality, and Allee effects. In this model, competition is the negative effect of conspecifics on individual growth rate. Using the von Bertalanffy model as a starting point, the density-independent maximum growth rate (κ) is achieved at the smallest size and growth rate declines linearly with increasing size at rate δ . Adding competition to this basic model, growth rate decreases with increasing N at rate γ :

$$\frac{dL}{dt} = (\kappa - \gamma N) - \delta L_t,$$

where growth rate (dL/dt) is at its maximum (κ) when size (L) and N are equal to zero. I integrated this equation to find size as a function of time:

$$L(t) = L_0 + (L_\infty - L_0)(1 - e^{-\delta t}),$$

$$\text{where } L_\infty = \frac{(\kappa - \gamma N)}{\delta}, \quad (2)$$

where $L(t)$ is individual size at time t , L_0 is size at settlement, and L_∞ is the maximum size achieved. Therefore, competition results in a slower growth rate and a smaller maximum size. In a previous study on *P. cinctipes* competition (Donahue 2004), I found that density-independent growth rate varies with food availability, making it a suitable metric for habitat quality. Therefore, in the simulation of settlement distribution, I modeled variation in habitat quality as variation in the density-independent maximum growth rate κ . The parameters in this growth model were directly estimated from laboratory experiments testing the effect of density and food quality on *P. cinctipes* growth rate (Donahue 2004) (Table 3).

Higher predation risk for smaller, more recently settled individuals is common among marine organisms (Gosselin and Qian 1997; Hunt and Scheibling 1997; Moksnes et al. 1998; Ray-Culp et al. 1999). Therefore, I assumed that size-dependent predator attack rate, $\alpha(L_t)$, is an exponentially decreasing function of size:

$$\alpha(L_t) = \alpha_A + \alpha_S e^{-\beta_L L_t}, \quad (3)$$

where α_A is the predation rate on adult crabs, α_S is the increased predation risk for settlers, and β_L determines how quickly settlers outgrow this size-related risk. I estimated α_S from a field experiment (Akins 2003), which found a difference in the number of settlers between predator access and predator exclusion cages over the course of 2 weeks. I re-analyzed this data to estimate the daily attack rate on 1.5-mm-carapace width (CW) settlers and based α_S on this estimate. With no data available to estimate α_A , I assumed an adult mortality rate of 0.001 per day. Finally, I assumed that by the time crabs had reached reproductive size (~ 5.5 mm CW), mortality rates had declined to only 2 times higher than the background adult mortality of 0.001 (see Table 3 for parameter estimates).

There is an Allee effect in *P. cinctipes* fitness if settlers are protected from predation by hiding under adults (Jensen 1991). Jensen (1991) found that the overall attack rate of an intertidal sculpin (*O. maculosus*) on settlers declined 2.5 times in the presence of adults. With this Allee effect, the predator attack rate is a function of both size (as in Eq. 3) and N :

$$a(L_t, S_t, N) = \alpha_A + \left(\alpha_S e^{-\beta_R (N/S_t)} \right) e^{-\beta_L L_t}, \quad (4)$$

where α_A , α_S , and β_L , are defined as in Eq. 3, and β_R is the decline in settler predation risk as the ratio of adults to settlers increases, estimated from Jensen (1991). Predator abundance multiplies predator attack rate and is assumed to be constant. When Allee effects are included in the fitness model, the predator attack rate is Eq. 4; when Allee effects are excluded from the fitness model, the predator attack rate is Eq. 3.

Fecundity is closely related to size (346 eggs g^{-1} crab biomass, $R^2=0.89$, Donahue (2004)); therefore, I estimated fitness by survival to and size at the first reproductive season. Specifically, fitness was the probability of surviving to first reproduction multiplied by the size-dependent number of eggs. The probability of survival to first reproduction depends on the predator attack rate (Eq. 3 or 4) and the size at reproduction depends on competition and growth rate (Eq. 2). The sensitivity of the fitness model to its parameters was tested by changing each parameter by 20% and comparing this to the model with default values (Table 3).

Results

In the model lacking Allee effects (Eq. 3 for predator attack rate), fitness decreases monotonically with increasing N (Fig. 2a, b, dashed lines, left axis). Growth rate declines with increasing density and there is no density-dependent benefit of conspecifics. Therefore, fitness is maximized in the absence of conspecifics. In the model with Allee effects (Eq. 4 for predator attack rate), fitness is maximized at intermediate N (Fig. 2a, b, solid lines, right axis). This is a consequence of competition-predation tradeoffs: survivorship increases with N because adults protect settlers from predation, but growth rate declines with N due to competition.

The presence of other settlers decreases the Allee effect and contributes to competition (Fig. 2a, b). As the number of other settlers increases, individual fitness decreases (note difference in scale on the y-axis between Fig. 2a, b) and, in the model with Allee effects, the optimal density of adult conspecifics increases (note the

Table 3 Definitions, sources, and estimates (with SEs) of model parameters

Parameters	Source of estimate	Estimate
κ , maximum growth rate ^a	Donahue (2004) ^b	0.0136 (0.0124, 0.0149) day^{-1}
δ , change in growth rate with size	Donahue (2004) ^b	$5.98 (5.67, 6.29) \times 10^{-4} (\text{day mm})^{-1}$
γ , competition coefficient	Donahue (2004) ^b	$1.47 (0.517, 2.42) \times 10^{-4} (\text{day crab})^{-1}$
L_0 , size at settlement	Donahue (2004) ^b	1.5 mm
α_A , predation rate on adult crabs	No data	0.001 day^{-1}
α_S , increased predation for settlers	Akins (2003)	0.311 (0.229, 0.399) day^{-1}
β_R , decline in predation with N/S	Jensen (1991)	0.875 settler crab^{-1}
β_L , decline in predation with size	Calculated from α_A and α_S	0.873 (0.818, 0.918) mm^{-1}

^aServes as a surrogate for habitat quality

^bThese values are based on data from the high resource level treatment of the laboratory experiment in Donahue (2004) using the regression model. Individual growth rate $\sim \kappa - \gamma N_{ij} + \delta \text{InitialSize}$

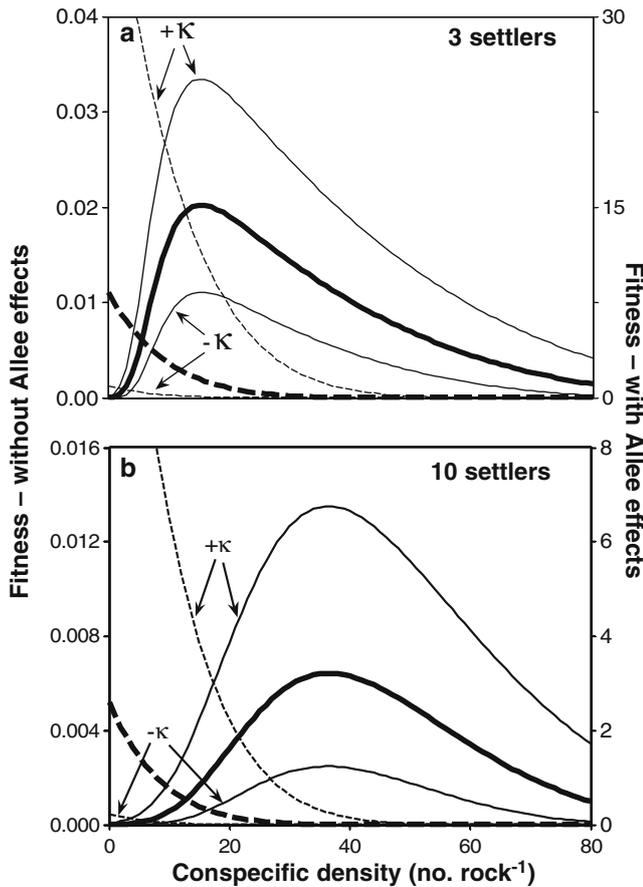


Fig. 2 Fitness as a function of adult N when there are **a** three or **b** ten settlers per rock. Without Allee effects (*left axis, dashed lines*), fitness declines monotonically with N . With Allee effects (*right axis, solid lines*), fitness is maximized at intermediate N . The *thin lines* illustrate the effect of increasing ($+\kappa$) or decreasing ($-\kappa$) density-independent maximum growth rate (κ) by 20%

shift in the location of the maximum between Fig. 2a, b). With or without Allee effects, variation in habitat quality (κ) causes density-independent variation in fitness (Fig. 2a, b, thin lines are $\pm 20\%$ of κ).

These patterns are not qualitatively changed by $\pm 20\%$ changes in parameter values. In the model with Allee effects (Fig. 2, solid lines, right axis), the position of the peak is most sensitive to changes in β_R and β_L , which change peak location $\sim 18\%$ for a 20% change in parameter value (see Electronic Supplementary Material, Fig. S1b). In the model lacking Allee effects (Fig. 2, left axis), the rate of decline is most sensitive to changes in κ , β_L , and α_S (see Electronic Supplementary Material, Fig. S1a).

Simulation of settlement distribution

Methods

To investigate how Allee effects and conspecific cueing contribute to the empirical pattern of settlement,

I simulated a pulse of 1,000 settlers optimally choosing among 100 habitat patches (=rocks) that varied in conspecific density (N) and habitat quality (κ). Adult conspecifics were gamma distributed [$N \sim \Gamma(2, 10)$] among habitat patches with parameters estimated from the empirical distribution of *P. cinctipes* among rocks at Twin Coves (Donahue 2004). Habitat quality (κ) varied normally across habitat patches based on the empirically estimated maximum growth (κ , Table 3). Conspecific cueing depends on the quality of information garnered from conspecifics, which is the correlation between habitat quality and conspecific density, $\rho_{N,\kappa}$. To vary $\rho_{N,\kappa}$, I used a bivariate Gaussian copula (Genest and MacKay 1986) to generate gamma-distributed density (N) and normally-distributed habitat quality (κ) from a pair of uniform random variables with a given correlation coefficient.

In the simulation, settlers arrive sequentially and choose the habitat patch that maximizes individual fitness, which depends on habitat quality, adult density, and the number of settlers already in the patch. The model assumes that individuals do not move once settled and that patch characteristics at settlement determine fitness at first reproduction. I tested whether suboptimal patch selection or incomplete information could influence the distribution of settlers. In the first case, settlers are unable to distinguish the “best” patch from a “good” patch and choose randomly from patches with fitness values within 10 or 25% of the best patch. In the second case, settlers have incomplete information, perhaps due to limited time or mobility, and choose optimally from a random subset (10 or 25%) of habitat patches.

I compared the settlement distributions resulting from three cases: (1) conspecific cueing only—adult conspecifics are associated with higher habitat quality ($\rho_{N,\kappa} > 0$) but do not change predator attack rate (Eq. 3); (2) Allee effects only—adult conspecifics are not associated with higher habitat quality ($\rho_{N,\kappa} = 0$) but do decrease predator attack rate (Eq. 4); and (3) both Allee effects and conspecific cueing—adult conspecifics are associated with higher habitat quality ($\rho_{N,\kappa} > 0$) and also decrease predator attack rate (Eq. 4). To compare these models with the empirical data, I analyzed the simulation data with a similar statistical model to that used for the field data.

Results

Without Allee effects, settlement is optimal at only a few patches that have low N but high κ (Fig. 3). Increasing $\rho_{N,\kappa}$ shifts the location of these patches along the density axis (Fig. 3a–c), but conspecific attraction remains a poor strategy because increases in habitat quality never offset competition from conspecifics. Neither suboptimal habitat selection nor incomplete information changed this underlying pattern; both moderately increased variation (Electronic Supplementary Material, Fig. S2).

With Allee effects, the settlement distribution depends strongly on the quality of information garnered from conspecifics. When there is no correlation or only moderate correlation between habitat quality and density, the settlement distribution reflects the underlying fitness model (Fig. 4a, b). In this case, settlement is maximal at intermediate N and the number of settlers is strongly quadratic in N (Table 4, $\rho_{N,\kappa}=0$, $\rho_{N,\kappa}=0.45$). Therefore, if conspecific density provides little information about habitat quality, then conspecific attraction would be a poor proximate strategy. As quality of information garnered from conspecifics improves (i.e., $\rho_{N,\kappa}$ increases), the decline in settlement at high density weakens until the distribution is increasing with N (Fig. 4c: $\rho_{N,\kappa}=0.9$). At high information quality ($\rho_{N,\kappa}=0.9$), the quadratic term is much weaker (Table 4) and appears saturating (Fig. 4c). With Allee effects and high-quality information from conspecifics, conspecific attraction is a good proximate strategy across the range of natural densities. Suboptimal habitat selection and incomplete information had little effect on the settlement distribution: both simply contribute additional variation to the underlying pattern (Electronic Supplementary Material, Fig. S3).

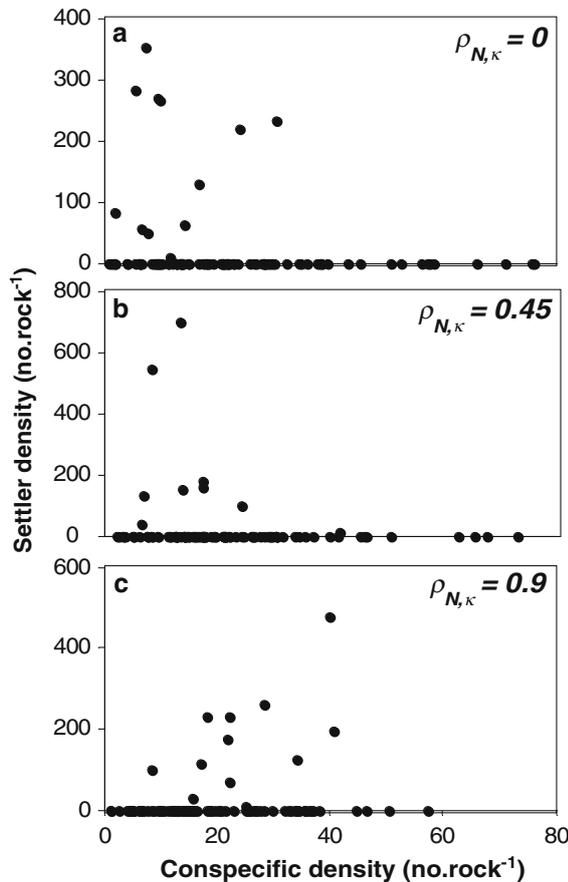


Fig. 3a–c Simulated settler density versus N when there are no Allee effects. The quality of information garnered from conspecifics varies with the correlation between habitat quality and N ($\rho_{N,\kappa}$): **a** $\rho_{N,\kappa}=0$, **b** $\rho_{N,\kappa}=0.45$, **c** $\rho_{N,\kappa}=0.9$

Discussion

In the field, settlement consistently increased with conspecific density (Fig. 1). There is marginal evidence for deceleration of settlement at high conspecific densities in June but this pattern is difficult to distinguish because the variance also increases with N . With or without deceleration at high conspecific densities, the empirical evidence indicates that *P. cinctipes* settlers use conspecific attraction as a settlement strategy across the entire range of biologically relevant densities.

The empirical settlement distribution is most closely matched by the model that includes both Allee effects and conspecific cueing with high information quality (Fig. 4c). For *P. cinctipes*, the Allee effect is a decrease in predation on settlers in the presence of conspecifics (Eq. 4) and correlation between habitat quality and conspecific density, $\rho_{N,\kappa}$. When there is little information garnered from conspecifics ($\rho_{N,\kappa}=0$), optimally choosing settlers avoid patches with high N because intraspecific competition outweighs the benefits of decreased predation (Fig. 4a). Increasing habitat quality offsets increasing intraspecific competition and settlement increases

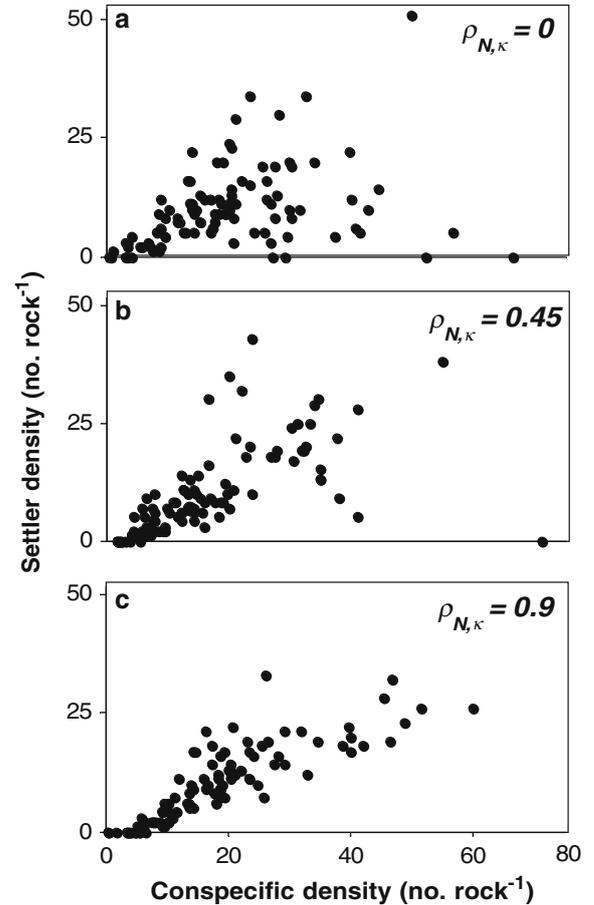


Fig. 4a–c Simulated settler density versus N when Allee effects contribute to fitness. The quality of information garnered from conspecifics varies with $\rho_{N,\kappa}$: **a** $\rho_{N,\kappa}=0$, **b** $\rho_{N,\kappa}=0.45$, **c** $\rho_{N,\kappa}=0.9$

Table 4 Analysis of simulation data. The number of settlers per “rock” was analyzed with a generalized linear model with overdispersed Poisson distribution and identity link to test for linear and nonlinear effects of conspecific density (N). $\rho_{N,\kappa}$ is the correlation between habitat quality and conspecific density

	Estimate (SE)		
	$\rho_{N,\kappa}=0$	$\rho_{N,\kappa}=0.45$	$\rho_{N,\kappa}=0.90$
Intercept (centered)	12.4 (0.842)	11.9 (0.701)	10.8 (0.314)
N	0.260 (0.0491)	0.460 (0.0312)	0.694 (0.0201)
N^2	-0.0137 (0.00153)	-0.0153 (0.00202)	-0.00601 (0.0016)

with density (Fig. 4c), similar to the empirical result (Fig. 1). Optimally choosing settlers show only a slight deceleration in settlement with increasing N (Table 4). Therefore, when conspecifics are the source of Allee effects and provide high-quality information, conspecific attraction is a good strategy over the range of natural densities.

The value of conspecific attraction as a good proximate settlement strategy depends ultimately on a strong, positive correlation between habitat quality and conspecific density. Conspecific density is likely to reflect underlying site quality through the movement of resident conspecifics to high-quality patches and/or the differential mortality of resident conspecifics in different-quality patches. While relatively sedentary, *P. cinctipes* adults do move between rocks and previous experiments demonstrate that they have distinct substrate preferences, even within the cobblefield habitat (Akins 2003; Jensen 1990, 1991). Therefore, by settling with conspecifics, *P. cinctipes* settlers choose habitat patches that are lower in fine-grained sediment. These patches are likely to have fewer suspended inorganic particles and a lower proportion of inorganic particles results in higher growth rate (Donahue 2004). However, maximum growth rate is not the only possible measure of habitat quality. Additional simulations that kept maximum growth rate constant but allowed predator density to negatively covary with N resulted in settlement distributions similar to those in Fig. 4. While there is no evidence for a negative correlation between predator density and conspecific density for *P. cinctipes* (unpublished data), this form of habitat quality may be more important for sessile organisms that settle gregariously. For these organisms, conspecifics may reflect underlying habitat quality through differential mortality due to predation. Both habitat selection by mobile species and differential mortality of mobile or sessile species will make N a good, temporally integrated predictor of habitat quality.

The response of settlers to colonizing and experimental crabs was similar, though the response to experimental crabs was stronger. If colonizing crabs are responding to local habitat quality, then the weaker response of settlers to colonizing crabs may indicate that

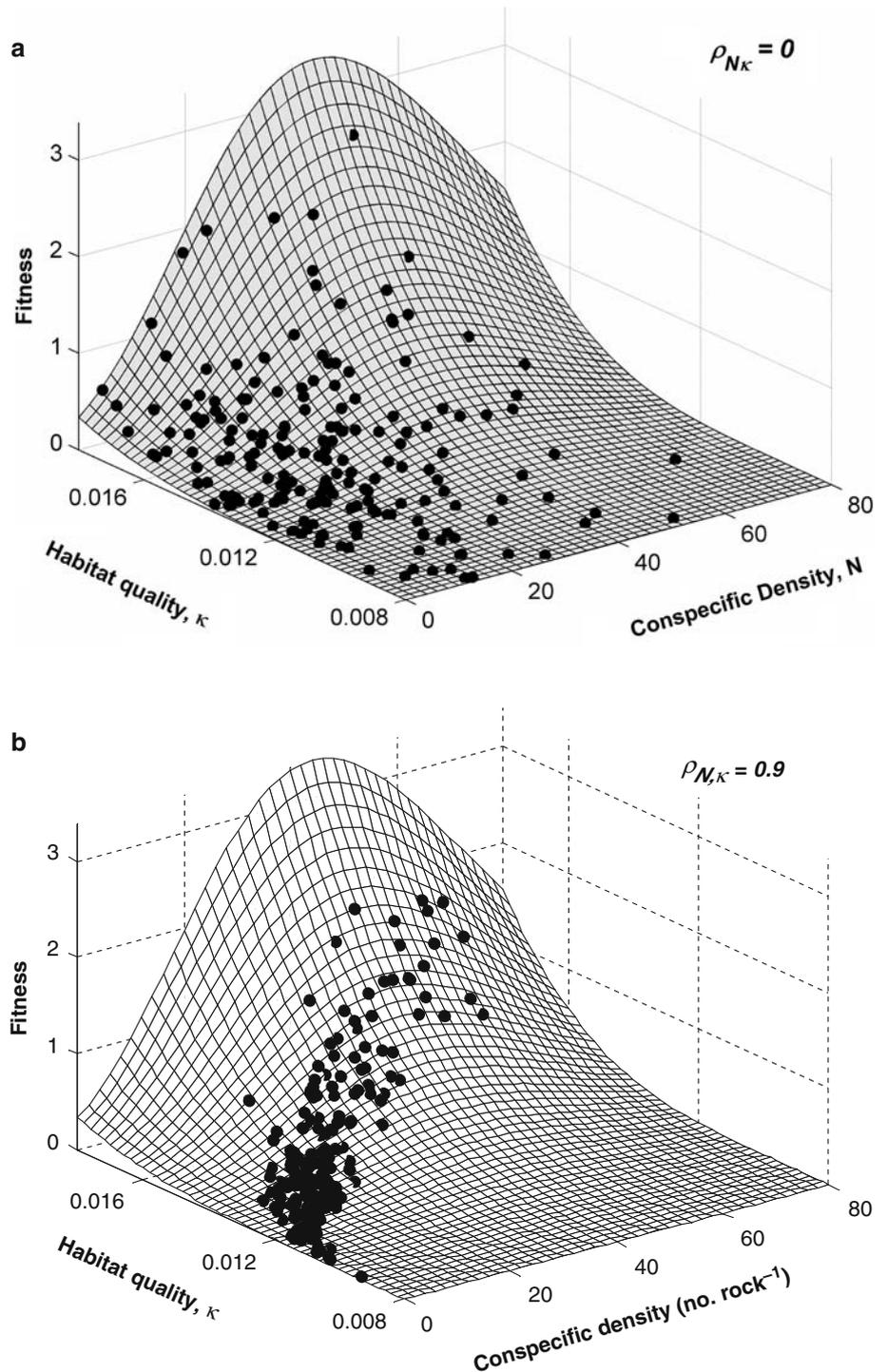
settlers are not responding directly to habitat quality. Instead, a stronger response to experimental crabs may be because the densities of experimental crabs were fixed for the length of the settlement period, while colonizing crabs increased to the measured density over the course of the settlement period. The marginally negative correlation between the residuals of the competition experiment (Donahue 2004) and colonizing crab density probably indicates competition between the colonizing crabs and the crabs in the competition experiment. There is no indication that colonizing crabs were responding to local habitat quality, though this cannot be ruled out. Only additional experiments that directly manipulate habitat quality could distinguish whether settlers respond to habitat quality separately from conspecific density.

The results of the simulation model were robust to behavioral limitations in optimal patch selection. Neither the inability to distinguish a “good” patch from the “best” patch (Electronic Supplementary Material, Figs. S2 and S3, left panels) nor the inability to sample all possible patches (Electronic Supplementary Material, Figs. S2 and S3, right panels) qualitatively changed the simulation results. In addition, the ability of crustaceans to accurately respond to chemical cues is well documented and indicates a sophisticated chemosensory apparatus that can adapt to varying levels of cue (Finelli et al. 2000; Zimmer et al. 1999). Many crab larvae are highly selective, delaying settlement in the absence of appropriate cues (reviewed in Forward et al. 2001; Pechenik 1990) and displaying dose-dependent responses to those cues (e.g., Fitzgerald et al. 1998; Pawlik 1992). Previous laboratory work on *P. cinctipes* demonstrated that competent larvae settle quickly in the presence of conspecific adults but will delay settlement for weeks without this cue (Jensen 1991). Jensen (1989) demonstrated that *P. cinctipes* will settle at a shore level typically occupied by a congener when conspecific adults are experimentally placed there. Therefore, *P. cinctipes* larvae are capable of selective settlement and the model is robust to modest deviations from optimal selection.

General implications

The case of gregarious settlement in *P. cinctipes* illustrates how consistent landscape characteristics (here, the correlation between habitat quality and conspecific density) can change habitat selection strategy. To illustrate this, Fig. 5 displays the fitness surface along habitat quality (κ) and conspecific density (N) axes for the model including Allee effects. Superimposed on the fitness surface is the distribution of 100 randomly generated habitat patches with low (Fig. 5a) or high (Fig. 5b) $\rho_{N,\kappa}$. The optimal settlement distribution (Fig. 4) reflects the projection of these patches onto the density axis. When $\rho_{N,\kappa}$ is low, habitat patches are selected from a broad range of the fitness surface (Fig. 5a) and settlement

Fig. 5 Fitness as a function of N and habitat quality (κ) including Allee effects. Randomly generated habitat patches are superimposed on the fitness surface when **a** $\rho_{N,\kappa} = 0$ and **b** $\rho_{N,\kappa} = 0.9$



reflects the underlying hump-shaped fitness surface (Fig. 4a). As $\rho_{N,\kappa}$ increases, habitat patches are selected from a narrower subset of the fitness surface (Fig. 5b) and settlement increases with N (Fig. 4c). Note that the underlying fitness surface does not change, but that $\rho_{N,\kappa}$ determines the subset of the fitness surface available to settlers. As a result of high $\rho_{N,\kappa}$ in the natural landscape, gregarious settlement is an optimal strategy across the entire range of biologically relevant densities of conspecifics.

Figure 5 also illustrates how this result is sensitive to the distribution of conspecifics and habitat quality. For example, if the average density in a patch were higher than the density at the fitness maximum, then the decelerating portion of the fitness surface would be more heavily represented in a random selection of patches. In reality, the mean density is lower than the density at the fitness maximum, and the distribution of patches is skewed to the increasing portion of the fitness surface.

Previous studies have investigated the importance of temporal autocorrelation in habitat quality as a factor in the use of public information (Danchin et al. 1998; Doligez et al. 2003). When public information is used in breeding site selection, failed breeders or sub-adults prospect at breeding sites in year t to garner information about breeding sites in year $t+1$. It is clear that temporal autocorrelation in site quality must be high for this to be a good strategy. In this model of *P. cinctipes*, the temporal autocorrelation of sites is subsumed in $\rho_{N,\kappa}$. The correlation between density and habitat quality is given by $\rho_{N,\kappa}$, but, within a patch, κ is constant from settlement to first reproduction when fitness is assessed (i.e., the temporal autocorrelation in κ is 1). Therefore, adults must be mobile enough to respond to changes in habitat quality on the year-to-year timescale, but sedentary enough to accurately reflect habitat quality on the within-year timescale. In fact, *P. cinctipes* adults move little unless disturbed: in surveys of the intertidal at high and low tide during the day and night, *P. cinctipes* are only visible when rocks are overturned (personal observation). When disturbed, however, they choose patches of higher quality (Jensen 1991). As long as conspecific density reflects habitat quality from settlement to first reproduction, then the assumption of the model is met.

While the model presented here is based on *P. cinctipes*, the principle it illustrates is dependent on three conditions. First, individual fitness must respond to both Allee effects and competitive effects, such that fitness is maximized at intermediate N . Several recent papers discuss both the importance of Allee effects to population dynamics (Courchamp et al. 1999; Greene 2003; Greene and Stamps 2001; Stephens and Sutherland 1999) and indicate that they are common in many populations. Second, early settlers must influence the fitness of subsequent settlers; in this model, early settlers compete with subsequent settlers both for food and for protection from predators. This is similar to a basic assumption of most habitat selection models (e.g., the ideal free distribution and its descendents), in which competitors change the fitness landscape. Third, fitness must increase with habitat quality; this is a truism when the appropriate environmental factor represents habitat quality. When these three conditions are in place, the spatial correlation between habitat quality and conspecific density will influence optimal behavior, and can make conspecific attraction a good proximate strategy across biologically relevant conspecific densities.

Consequences for population dynamics

In this model, conspecific attraction is a good proximate strategy only when there is moderate to high $\rho_{N,\kappa}$. Therefore, conspecific attraction results in higher population density in higher quality habitat patches,

i.e., positive covariance between environment and competition. Covariance between environment and competition (higher density in locations of higher per capita growth rate) changes population dynamics from the mean-field model and is an important mechanism of species coexistence (Chesson 2000; Snyder and Chesson 2003). Snyder and Chesson (2003) suggest local dispersal in a spatially varying but temporally constant environment as a mechanism generating covariance between environment and competition. Conspecific attraction may be a more robust mechanism to generate covariance between environment and competition because: (1) the mechanism and scale of dispersal does not matter as long as conspecific cueing is used in settlement, and (2) because N can be correlated with habitat quality even when the environment is changing (e.g., due to habitat selection or differential mortality of resident conspecifics).

The correlation between conspecific density and habitat quality also has important implications for ecologists looking for density dependence. Shima and Osenberg (2002) demonstrate that ecologists often fail to detect density dependence in correlative studies due to positive covariance between habitat quality and density; they call this “cryptic density dependence”. This study indicates that gregarious settlement may be an important mechanism for generating cryptic density dependence. In the model, density dependence due to competition is always present but it is offset by increasing habitat quality.

Conclusion

This study has elucidated one possible set of life history characteristics that make conspecific attraction a good proximate behavioral strategy. First, common to life history optimization models, there must be a tradeoff between fecundity and survival, resulting in an Allee model of fitness. Second, in common with habitat-selection models, individual fitness optimization is dependent on the choices of other individuals. Here, previous settlers influence fitness by increasing competition and changing predator attack rate. Finally, positive correlation between habitat quality and conspecific density must offset increasing competition. When these three conditions are in place, the spatial correlation between habitat quality and conspecific density will influence optimal behavior and can make conspecific attraction a good settlement strategy.

Acknowledgements I had valuable discussions on this work with J. Stamps, C. Lee, and J. Jones, who also commented on a draft of this manuscript. R. Toonen, S. Morgan, P. Chesson, M. Holyoak, L. Akins, B. Byrne, and two anonymous reviewers made helpful comments on earlier drafts. This research was conducted with support from the American Association of University Women, the Bodega Marine Laboratory, and the NSF Research Training Grant for Nonlinear Dynamics in Biology (DBI-9602226) awarded to the University of California, Davis.

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