

Size-dependent competition in a gregarious porcelain crab *Petrolisthes cinctipes* (Anomura: Porcellanidae)

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ABSTRACT: Studies of competition in benthic marine organisms have focused on sessile filter-feeders and mobile grazers, to the neglect of mobile filter-feeders, including porcelain crabs. The present study demonstrates intraspecific competition in *Petrolisthes cinctipes* (Randall) (Porcellanidae: Anomura). *P. cinctipes* settles gregariously and lives in high-density, multi-size aggregations. Studies of gregarious species often identify the benefits of aggregation without quantifying the concomitant costs; this study quantifies these costs. In field and laboratory experiments, *P. cinctipes* growth rates declined with increasing conspecific density and this decline was more severe for smaller individuals. *P. cinctipes* also fed less frequently at high density, and this effect was more pronounced for smaller individuals. This indicates that size-dependent agonistic interactions in *P. cinctipes* have effects on feeding rate and, ultimately, on growth rate. Resource levels were manipulated in laboratory experiments by using filtered and unfiltered seawater. The effect of resource level also depended on size: smaller crabs were more sensitive to changes in food level. Thus, conspecific density and food availability both affected growth rate in a size-dependent manner. Therefore, the costs of aggregation are more extreme for recruits than for adult crabs; recruits suffer more from competition, but may also benefit more if conspecific cueing results in settlement to sites with higher food availability.

KEY WORDS: Intraspecific competition · Size-dependent competition · Porcelain crab · Filter feeding · Gregarious settlement · Aggregation

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INTRODUCTION

Studies of competition in marine systems have focused on 3 guilds that differ in mobility and feeding strategy. (1) Sessile, filter-feeding invertebrates of the rocky intertidal compete fiercely for space, resulting in radical changes in morphology and high mortality (Connell 1961, Bertness 1989, Wootton 1993, Bertness et al. 1998, Connolly & Roughgarden 1998). (2) Among filter- or deposit-feeding, soft-bottom infauna with limited mobility, studies have demonstrated exploitative competition for food (Peterson 1982, Wenngren & Olafsson 2002) and, occasionally, competition for space (Peterson & Andre 1980). In contrast to sessile invertebrates of the rocky shore, competition among soft-

bottom infauna typically results in decreased individual growth rate and fecundity, but rarely in mortality (Peterson & Black 1993). Finally, (3) mobile grazers in the rocky intertidal or shallow subtidal (Menge 1976, Underwood et al. 1983, Branch 1984, Chow 1989, Schmitt 1996) usually compete exploitatively for food, resulting in decreased growth and fecundity.

Mobile filter-feeders, including many anomuran crabs and ophiuroids, fall between these guilds. Although mobile filter-feeders are abundant in many marine habitats, there has been little work on the presence and nature of competition in these organisms. Whereas studies on sessile filter-feeders have demonstrated competition for food (Peterson 1982, Cote et al. 1994) and space (Connell 1961, Bertness 1989,

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Bertness et al. 1998, Menge 2000), competition among mobile filter-feeders could be mitigated by movement. Increased mobility could also change the predominant mechanism of competition from interference competition for space to exploitative competition for food.

Behaviors that result in aggregation, like gregarious settlement, can enhance competition. Gregarious settlement is the preferential settlement in a patch with conspecifics over an equivalent patch without conspecifics (reviewed in: Burke 1986, Pawlik 1992). Researchers of gregarious settlement have proposed several benefits to this behavior (Burke 1986, Stamps 1988, Raimondi & Keough 1990, Pawlik 1992, Krug & Zimmer 2000, Toonen & Pawlik 2001a), including (1) information about habitat quality (or 'habitat cueing') (Raimondi 1988, Jensen 1989, Muller et al. 1997, Mullineaux et al. 2000), (2) reduced risk of predation (Highsmith 1982, Tegner & Levin 1983, Bertness & Grosholz 1985, Jensen & Armstrong 1991, Peterson & Black 1993, Ray & Stoner 1994), (3) facilitation (reduced suffocation risk: Bertness & Grosholz 1985; reduced desiccation risk: Bertness 1989), and (4) access to mates (e.g. barnacle copulation: Burke 1986; fertilization of broadcast spawners: Metaxas et al. 2002). However, studies of gregarious species often identify the particular benefits of aggregation without quantifying the competitive costs.

Among the 3 benthic guilds for which competition is well studied, gregarious settlement is common among sessile filter-feeders and soft-bottom infauna (e.g. Bertness & Grosholz 1985, Raimondi 1988, Nielsen & Franz 1995, Minchinton 1997, Toonen & Pawlik 2001b), but is rare among mobile grazers (Burke 1986). Among the mobile organisms that settle gregariously are a few snails (Burke 1986) and porcelain crabs, including *Petrolisthes cinctipes* (Jensen 1989, M. J. Donahue unpubl. data). Because sessile organisms choose a settlement site only once, settlement is a high risk event, which may select more strongly for gregariousness. For mobile organisms, the costs and benefits of aggregation seem less dramatic because immediate costs may be mitigated by movement. Despite this, *P. cinctipes* settles gregariously and individuals remain in high-density aggregations as adults. This pattern of aggregation in *P. cinctipes*, despite its mobility, might indicate that competition is weak.

Gregarious settlement can also lead to size-structured interactions. In some organisms, arriving larvae are attracted to conspecific adults, resulting in multi-size aggregations; in others, e.g. barnacles (Bertness 1989), larvae settle gregariously with a cohort of other settlers. If competition is size dependent and settlement produces multi-size aggregations, then analysis of competition must take both size distribution and density into account (Werner & Gilliam 1984). If

different size-classes exploit different resources, then settlers will not compete with adults and the costs of gregarious settlement will be diminished. However, if the outcome of interference competition is determined by size, multi-size aggregations will have the opposite effect: juveniles will pay a high price for settling with larger conspecifics.

Resource availability can also change competitive interactions: high resource levels may decrease exploitative competition if the feeding apparatus is saturated, while low food levels may increase aggressive, interference interactions (Hazlett et al. 1975). Resource availability can affect small and large individuals differently, since small individuals are often more sensitive to low resource levels due to higher metabolic demands (Peters 1983). For filter-feeders, it is difficult to manipulate resource levels without adding unnatural food. In my experiments, I used filtered and unfiltered seawater as food treatments to maintain realism.

Using laboratory and field experiments, I estimated the effects of conspecific density, food availability, and size on individual growth and feeding rates in a mobile filter-feeder, *Petrolisthes cinctipes*. To connect these growth rates with fitness outcomes, I examined the relationship between body size and fecundity for *P. cinctipes*.

MATERIALS AND METHODS

Natural history and site description. *Petrolisthes cinctipes* lives in cobblefields and mussel beds from Point Conception, California, USA, to British Columbia, Canada (Morris et al. 1980). Adult *P. cinctipes* are highly aggregated, reaching densities of 950 m⁻² (see Fig. 1). Megalopae settle preferentially with conspecifics over congeners, reinforcing the zonation of *Petrolisthes* species in the intertidal (Jensen 1989, Jensen & Armstrong 1991). Megalopae are ~1.5 mm in carapace width (CW) at settlement, females are reproductive at ~5 mm CW, and the maximum size of *P. cinctipes* is ~20 mm CW.

Petrolisthes cinctipes move only when disturbed, and movement is size dependent: when a rock is turned, adults move quickly away, but recruits do not move at all (author's pers. obs., Jensen 1990). During both high and low tide, day and night, crabs can only be found under rocks and are never seen moving from rock to rock. A mark-recapture survey indicated that most *P. cinctipes* move very little (<0.5 m) in 24 h, even after the disturbance of mark and release, although 1 crab moved 8 m (author's unpubl. data). This short-term survey matched the findings of Jensen (1990) and Jensen & Armstrong (1991), who found that most *P. cinctipes* moved very little, but a few moved from

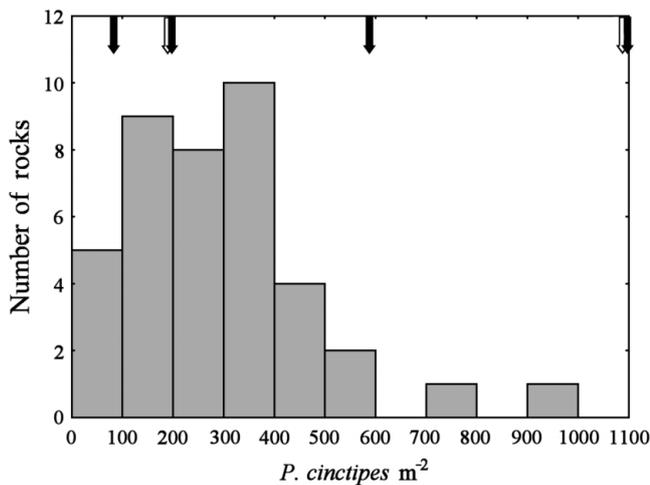


Fig. 1. *Petrolisthes cinctipes*. Histogram of crab density at Twin Coves: number of rocks (0.1 to 0.15 m²) with a given range of crab density. Solid arrows indicate the density treatments in the field experiment; open arrows indicate the density treatments in the laboratory experiment

10 to 20 m (out of an experimental patch into nearby habitat) over the course of a month.

The field experiment was performed at Twin Coves, a pair of small coves (0.5 km wide at the mouth) along a stretch of exposed coast in Sonoma County, California, USA (38° 27.517' N, 123° 8.683' W). The intertidal area is a cobblefield; most cobbles are from 800 to 1600 cm² (longest length by width) and are interspersed with large boulders.

Site survey. In March 2001, I performed a preliminary survey of *Petrolisthes cinctipes* density to determine an appropriate range of treatment densities. In August 2002, I conducted a more thorough survey of 40 rocks at Twin Coves. A 40 m transect was placed parallel to the shore at ~0.2 m above MLLW, which is in the middle of the *P. cinctipes* zone. At 1 m intervals along the transect, the nearest rock of the target size (0.05–0.15 m²) was overturned into a plastic tub and all crabs >0.2 mm CW on or under the rock were collected and counted. Rocks below the target size were frequently tumbled by wave action and, consequently, *P. cinctipes* were rarely found underneath them. Rocks above the target size were too large and unwieldy to sample effectively, though they did have *P. cinctipes* underneath them. Habitable rock area was estimated using a piece of Vexar[®] mesh (mesh size 4.5 cm) as a grid to measure the area of each rock in contact with the substrate.

Field experiment. To assess the impact of intraspecific competition on *Petrolisthes cinctipes*, I tracked the growth of crabs caged at different densities at Twin Coves. Each of 32 cylindrical cages was constructed

from 25 cm diameter PVC pipe. A 10 cm length of pipe formed the base, the bottom of which was covered with Vexar mesh (mesh size 4.7 mm); a 3 cm length of pipe formed the lid, the top of which was covered with mesh. The lid was secured to the base with cable ties, which allowed access to the cage without detaching the mesh. Three mesh-covered windows (15 × 6 cm) in the base increased flow. The cages were haphazardly placed at least 3 m apart between 0.15 and 0.30 m above MLLW (mean low, low water), in the center of the *P. cinctipes* zone, each containing 3 small cobbles. Cage placement deliberately avoided tidepools or areas with standing water at low tide. It was often necessary to move several small cobbles to fit the cage snugly on the substrate (coarse sand and small rocks); this procedure assured that the rocks in the cage were at the same height as surrounding rocks and also prevented cages from being displaced by waves.

To evaluate the effect of density on growth rate, 5 crabs were tracked in each of 8 replicates of 4 density treatments, for a total of 32 cages. I collected, measured (CW) and wet weighed (after drying with Kim-wipes) 160 *Petrolisthes cinctipes* sized 5.5 to 6.5 mm CW. Each crab was randomly assigned to one of 4 density treatments that fell within the range of densities measured in the field (Fig. 1), i.e. 5, 10, 30, 60 crabs cage⁻¹; replicates of each treatment were randomly assigned to 8 cages. It is difficult to track crustacean growth for a long period since any tag on their carapace will be molted. Since this experiment was to run longer than a molt cycle for crabs of this size, I established the density treatments by adding larger crabs (>10 mm CW). Thus, if the tracked crabs molted and lost their tags, they could still be distinguished by size.

After 70 d, I sampled the experiment by collecting the 5 tracked crabs from each cage and reweighing them. Most of the tracked crabs had molted and were indistinguishable from one another. Therefore, I calculated the average individual growth rate per day (AvgIGR) for the 5 crabs in each cage according to the formula:

$$\text{AvgIGR} = \frac{\frac{1}{5} \sum \ln W_{\text{final}} - \frac{1}{5} \sum \ln W_{\text{initial}}}{70 \text{ d}} = \frac{\ln(W_{\text{final}}/W_{\text{initial}})}{70 \text{ d}}$$

(where W is crab biomass) and regressed this against density (STATISTICA 6.1, StatSoft 2002, available at www.statsoft.com). This response variable translates easily to growth equations and has a simple interpretation: the intercept of the regression is the relative growth rate in the absence of competitors and the slope is the decline in relative growth rate with each additional competitor.

Laboratory Expt I: effect of competition on growth rate. To assess the effects of food and density on the

growth rate of 4 size-classes of crabs, I performed a laboratory experiment crossing 2 food levels by 2 densities. Each of these 4 treatments was replicated in eight 6 l aquaria for a total of 32 aquaria. This experiment was run for 72 d (18 September to 29 November 2001) at the Bodega Marine Laboratory.

To maintain realism, I used raw and filtered seawater as the different food treatments (Lenihan et al. 1996), rather than adding an artificial food source that could dramatically change both food quantity and quality. Filtered seawater was processed through a sand filter, a 300 μm filter bag, a settling tank, and (to ensure that food quality decreased, as well as particle size) a few hundred mussels; the raw water was unprocessed. This approach had the advantage that food components included only those in the field, but the disadvantage that food treatments were difficult to control and varied with the quality of intake water (see 'Sediment, organic matter, and chlorophyll in the laboratory and field'). Each water type was split through a manifold to flow into 16 aquaria; flow rates varied from 1 to 2 l min^{-1} into each aquarium. Jensen (1990) and Molenock (1976) hypothesized that *Petrolisthes* spp. compete for high-quality feeding spots characterized by high flow. Therefore, each aquarium contained a half-brick, propped up ~ 1 cm on one side; the incoming water was oriented underneath this brick to create variation in flow within the aquarium. To account for variation in flow across the manifold positions, aquarium placement was re-randomized every 3 to 4 d when the crabs were measured.

I designed the density treatments to correspond to the densities of 10 and 60 crabs cage^{-1} found in the field experiment (Fig. 1). I collected crabs in 5 size-classes (A: 3.5 to 4.5 mm, B: 6.5 to 7.5 mm, C: 9.0 to 11.0 mm, D: 12.5 to 14.5 mm, E: >16.0 mm) and imposed 2 density treatments at size-class ratios approximating those in the field. Low-density aquaria had 6 crabs in the ratio 2:2:1:1:0 (A:B:C:D:E); high-density aquaria had 35 crabs in the ratio 12:12:5:5:1. One individual in the largest size-class (>16 mm) was included in the high-density treatment to reflect size distributions in the field. However, this resulted in an unbalanced design, and this size-class was excluded from all analyses.

All crabs were marked with bee tags ('queen marking kit', The Bee Works), weighed, measured (CW), and randomly assigned to 1 of the 4 treatments (high/low density \times high/low food). Every 3 to 4 d for 72 d, each aquarium was cleaned and sampled; any individuals that had molted were remeasured, reweighed, and retagged. Any dead or missing crabs were noted and replaced.

At the end of the experiment, individual growth rate (IGR) per day was calculated for each crab: $\text{IGR} =$

$[\ln(W_{\text{final}}) - \ln(W_{\text{initial}})] / \text{no. of days}$. The analysis used only the 487 crabs that had been in the aquarium for at least 36 d between initial and final measurements and had retained both chelipeds during that time. The 36-d cutoff balanced the need for a sufficient treatment exposure and inclusion of sufficient replicates of smaller crabs, because smaller crabs lost their chelipeds more frequently (see below). With this cutoff, there was no effect of the number of days in the experiment on either individual growth rate ($p > 0.6$) or ranked individual growth rate ($p > 0.8$) when added to the model below. To analyze the effect of density (D), food level (F), size-class (S), and aquarium (A) on IGR, I used the general linear model (GLM): $\text{IGR} \sim D + F + S + (D \times F) + (D \times S) + (F \times S) + (D \times F \times S) + A(D \times F) + \epsilon$, in which $A(D \times F)$ is the error term for D, F, and $D \times F$, and ϵ is the error term for S, $D \times S$, $F \times S$, and $D \times F \times S$.

There was significant non-normality and heteroscedasticity in the data. I solved this by analyzing ranked IGR and using the natural logarithm of initial weight ($\ln W_{\text{initial}}$) as a continuous variable instead of the categorical variable size (S). The residuals of the ranked, transformed model met the assumptions of normality and homogeneity of variance. There were no differences in the overall significance of the transformed model compared to the original model. I present significance values for the transformed, ranked model. However, to ease interpretation, the figures are plotted using IGR and categorized by size-classes. To understand the responses of different size-classes, I re-analyzed each size-class separately, using the model: $\text{IGR} \sim D + F + (D \times F) + A(D \times F) + \epsilon$. Size-classes A, B, and C met the assumptions, while D remained heteroscedastic and the results should be considered with caution.

To compare the laboratory and field data, I regressed IGR versus numerical density for high- and low-food treatments separately using only Size-class B, which was closest in size to the crabs in the field experiment. I compared the intercepts (growth without competition) and slopes (competitive effect) between the high-food laboratory experiment, the low-food laboratory experiment, and the field experiment with t -tests.

Cheliped loss is another potential cost of agonistic interactions. Limb regrowth often results in a slowing of somatic growth and/or a decrease in fecundity and may decrease competitive ability (Juanes & Smith 1995). Limb loss may also be size dependent, such that small individuals lose and regrow claws more easily than larger individuals (Juanes & Smith 1995). To evaluate the size dependence of this behavior, I analyzed the frequency of limb loss in a logistic regression in which lost cheliped was the binomial response variable and food, density, and $\ln W_{\text{initial}}$ were predictor variables. These 3 variables and their interactions

were evaluated with best subset model building, using likelihood ratio tests and the Akaike information criterion (Burnham & Anderson 1998). The overall model fit is reported using R^2_L , which is the proportion of variation described in the best model compared to that described by the saturated model. Of 667 total crabs in the experiment, 85 crabs had lost a cheliped. Because of the relatively few cases of cheliped loss to consider, I did not test for an aquarium effect in this regression.

Petrolisthes spp. autotomize limbs very easily, suggesting that autotomy has a low cost for a filter-feeder that uses only modified maxillae for feeding (Wasson et al. 2002). Of the 85 crabs that lost a cheliped during the experiment, I had growth rates for 21 individuals both with and without the cheliped (i.e. the crab either lost its cheliped during the experiment or molted into a new cheliped during the experiment). Using a paired *t*-test, I tested for the effect of cheliped loss on IGR and on CW growth rate. If cheliped loss inhibits feeding (physically or due to competitive interactions), then both measures of growth rate should be negatively affected; if growth is reallocated to regrow the missing cheliped, then only the carapace growth rate should be negatively affected.

To more carefully examine the effects of food, density, and cheliped loss on growth rate, I restricted my analysis to Size A crabs, because most (57 out of 85) crabs that lost chelipeds were from Size-class A. I used a GLM with food, density, and cheliped loss as the main factors and density \times cheliped loss and food \times cheliped loss as crossed factors. I did not include food \times density or food \times density \times cheliped loss interactions, because of the low numbers of crabs with missing chelipeds in each treatment and because food \times density was non-significant in the ANOVA on Size A crabs.

Sediment, organic matter, and chlorophyll in the laboratory and field. To estimate the effectiveness of the food treatments and to compare those food treatments to field conditions, I measured the percent organic matter and the amount of chlorophyll *a* (chl *a*) in water samples from the 2 food treatments and the field. On each of 2 d, I collected three 1 l samples each of laboratory-filtered seawater, laboratory-raw seawater, and Twin Coves seawater (collected on a rising tide in ~ 1.5 m of water). The laboratory samples were collected and processed on the same day, but field samples were collected on another day (within a week of the laboratory samples); this was sufficient to see how laboratory treatments compared to food levels in the field. I filtered each sample to find the particulate matter in 3 fractions: 1 to 250 μm , 250 to 500 μm , and 500 to 1000 μm . For the 2 larger fractions, I filtered 1 l of seawater through stacked sieves and rinsed the sieves with deionized water into pre-weighed drying tins. For the smallest fraction (1 to 250 μm), I filtered

400 ml through a 250 μm sieve and then onto a pre-weighed, 1 μm quantitative glass-fiber filter (GF/D). Each of these samples was dried, weighed, ashed, and reweighed for dry weight and ash-free dry weight. Dry weight and transformed percent organic matter were analyzed in a MANOVA, with day nested in seawater source and fraction (GLM module, STATISTICA 6.1, StatSoft 2002).

I also performed a fluorometric analysis of chl *a* and phaeophytin. From each sample, I filtered 100 ml of <250 μm filtrate onto 1 μm quantitative glass-fiber filters (GF/D) and immediately froze them. To ensure that these measurements were comparable between days and water sources, all fluorometry was performed on a single day according to standard procedures with acetone (American Public Health Association 1995). I analyzed chl *a* and phaeophytin ($\mu\text{g l}^{-1}$) in a MANOVA, with day nested in water source and fraction. Chl *a* was square-root transformed to meet the assumptions of MANOVA.

Laboratory Expt II: effect of density on feeding behavior. In order to understand the mechanism of competition, I tested how crab density affects feeding behavior. Using the same densities and size-class ratios as described in 'Laboratory Expt I', I set up 5 low-density and 5 high-density aquaria with individually marked crabs. To facilitate observations, these aquaria were placed in a different room from the competition experiment, where they could be seen from all sides. Because the experiment lasted for only 1 night and treatments could not be randomized across any flow differences, the aquaria were systematically interspersed along the manifold that divided seawater among treatments. Aquaria were supplied with filtered seawater, so there was no food treatment in this experiment; flow rates were from 1 to 2 l min^{-1} . The 2 density treatments were established 1 d previous to the start of the experiment to allow crabs to acclimate. Crabs are more active at night; therefore, I sampled the experiment 5 times from 1 afternoon until the next morning (every 3 to 4 h), using a dim red light during the night samples. For each sample, I checked whether each crab was or was not feeding. I analyzed the fraction of observations in which each crab was seen feeding, *p*, as $\text{Logit}(p+0.5) = D + S + D \times S + A(D) + \epsilon$ and tested for effects of density, size, and aquarium, where aquarium was nested in density, plus the interaction of density and size. In addition to main effects, the comparisons of interest were across density within each size-class; these planned comparisons were tested using a Bonferroni adjustment for multiple comparisons.

Relationship between fecundity and biomass. The field and laboratory growth experiments were designed to test the effect of density on growth rate and resulting individual biomass. However, it is essential to

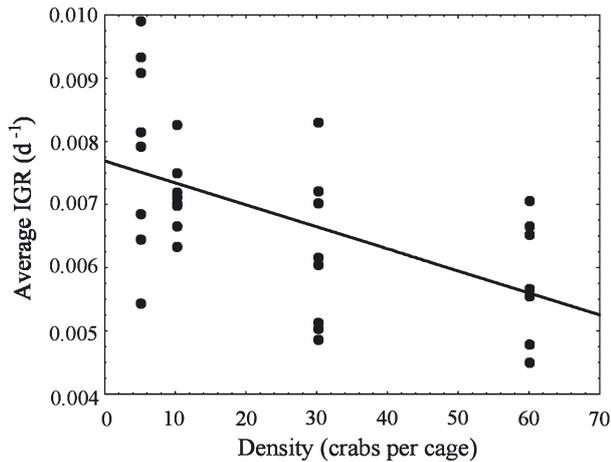


Fig. 2. *Petrolisthes cinctipes*. Average individual growth rate (IGR) from the field experiment. Average IGR is for the 5 tracked individuals in each cage; each point represents 1 cage. Overall regression is significant ($p = 0.0007$; $R^2 = 0.32$). Intercept of the regression ($\beta_0 = 7.5 \times 10^{-3} \pm 0.28 \times 10^{-3}$ [SE], $p < 0.0001$) corresponds to the daily multiplicative growth rate in the absence of competition. Slope of the regression corresponds to the competitive effect of each crab added to the cage ($\beta_1 = -3.5 \times 10^{-5} \pm 1.0 \times 10^{-5}$ [SE], $p < 0.001$)

connect biomass with fecundity to extrapolate from growth rate to population effects. In February 2001, I collected 182 ovigerous females from Twin Coves and 3 other cobblefields in Sonoma County (Salt Point, Timber Cove, and Fort Ross). From 37 crabs, I estimated the relationship between clutch size (number of eggs) and clutch dry weight ($R^2 = 0.98$, $p \ll 0.001$, 0.104 ± 0.005 mg egg $^{-1} \pm 95\%$ CI). I dried and weighed

Table 1. MANOVA on total dry weight and percent organic weight with seawater source, size fraction of particles, and day as factors

Effect	Wilk's λ	F	df _{effect}	df _{error}	p
Intercept	0.0045	3516	2	32	<0.0001
Day (Source \times Fraction)	0.3694	2.3	18	64	0.008
Source	0.5508	5.6	4	64	0.0007
Fraction	0.0624	48.0	4	64	<0.0001
Source \times Fraction	0.5173	3.1	8	64	0.005

the clutches of the remaining 145 crabs, calculated clutch size based on clutch dry weight, then estimated the relationship between crab biomass and clutch size using regression.

RESULTS

Site survey

Petrolisthes cinctipes is highly aggregated, with an average density of 294 ± 30 m $^{-2}$ (mean \pm SE) and a maximum density of 950 m $^{-2}$ (Fig. 1).

Field experiment

Average individual daily growth rate declined significantly with increasing density ($p < 0.001$, $R^2 = 0.32$; Fig. 2). The regression parameters can be used to estimate the effects of competition. The intercept of the

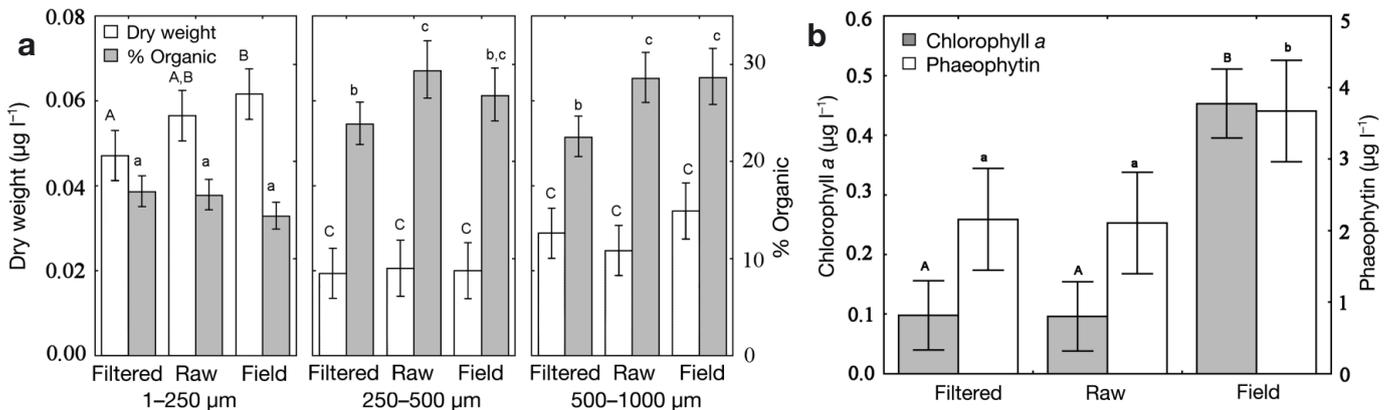


Fig. 3. Particulate matter, chlorophyll *a*, and phaeophytin in filtered, raw, and Twin Coves (field), seawater ($\pm 95\%$ CI). (a) Total dry weight is plotted on the left axis with open bars; upper-case letters indicated homogeneous groups (post hoc Tukey's HSD, $p < 0.05$). Back-transformed percent organic matter is plotted on the right axis with filled bars; lower-case letters indicate homogeneous groups (post hoc Tukey's HSD, $p < 0.05$). See Table 1 for results of MANOVA on total dry weight and percent organic matter. (b) Chl *a* concentration (left axis, filled bars, upper-case letters) and phaeophytin (right axis, open bars, lower-case letters) were higher in the field than in the laboratory (Wilk's $\lambda = 0.11$, $p \ll 0.0001$). Letters indicated homogeneous groups (post hoc Tukey's HSD, $p < 0.005$)

Table 2. General linear model of ranked individual growth rate with the continuous variable ln initial weight (ln InitWt) and the factors food, density, and aquarium (aqua) nested in food \times density. Aqua (food \times density) is the error term for food, density, and food \times density

Effect	SS	df	MS	F	p
Intercept	23 227 945	1	23 227 945	1490	<0.001
Aqua (Food \times Density)	391662	28	13 988	0.899	0.617
Food	82 602	1	82 602	5.91	0.022
Density	863 780	1	863 780	61.8	<0.001
ln InitWt	2 613 445	1	2 613 445	168.0	<0.001
Food \times Density	8 870	1	8 870	0.634	0.433
Food \times ln InitWt	51 963	1	51 963	3.34	0.068
Density \times ln InitWt	87 221	1	87 221	5.61	0.018
Food \times Density \times ln InitWt	2 074	1	2 074	0.133	0.715
Error	7 017 308	451	15 559		

regression ($\beta_0 = 7.5 \times 10^{-3} \pm 0.28 \times 10^{-3}$ [SE], $p < 0.0001$) corresponds to the daily relative growth rate in the absence of competition: $R = e^{\beta_0} = 1.008$. The slope of the regression corresponds to the competitive effect on relative growth rate of each additional crab in the enclosure ($\beta_1 = -3.5 \times 10^{-5} \pm 1.0 \times 10^{-5}$ [SE], $p < 0.001$).

Sediment, organic matter, and chlorophyll in the laboratory and field

Filtration to establish differing laboratory food treatments was only partially effective; percent organic matter was lower in filtered seawater compared to raw seawater for the 250 to 500 μm and 500 to 1000 μm fractions (Tukey's honest significant difference [HSD], $p < 0.025$; Fig. 3a). However, there was no difference in total dry weight between raw and filtered seawater for any fraction (Table 1, Fig. 3a). There were also no differences in chl *a* or phaeophytin between the raw and filtered seawater (Fig. 3b). Overall, filtered seawater contained the same food quantity (total dry weight) as raw seawater, but lower food quality (percent organic weight) at larger particle sizes.

Field samples had higher levels of chl *a* and phaeophytin than did the laboratory samples (Fig. 3b). For small particle sizes, field samples had higher total dry weight than the filtered laboratory samples, but there was no difference for larger particle sizes (Fig. 3a). For large particle sizes, field samples had a higher percent organic matter compared to filtered seawater (Fig. 3a). Overall, the trend was for

field samples to have higher food quantity than the filtered laboratory samples at small particle sizes, but higher food quality at large particle sizes.

Laboratory Expt I: effect of density and food on growth rate

IGR declined with density (Table 2, Fig. 4: Panels I & II vs III & IV) and increased with food level (Table 2, Fig. 4 Panels II & IV vs I & III). There was no effect of aquarium and no food \times density or food \times density \times initial weight interactions (Table 2). Overall,

IGR declined with initial weight, but there was a significant density \times initial weight interaction and a marginally significant food \times initial weight interaction (Table 2). Based on the individual size-class ANOVAs, the food \times initial weight interaction arose because only Size-class B showed a marginally significant (Size B, +22%) increase in IGR with increased food (Table 3). The density \times initial weight interaction arose because

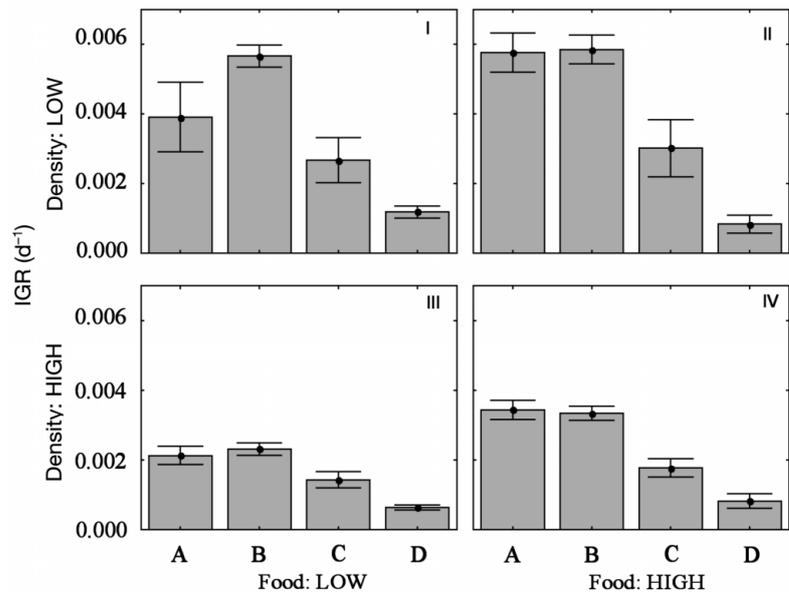


Fig. 4. *Petrolisthes cinctipes*. Individual growth rate by size-class, density, and food level from the laboratory experiment with standard error. There were significant declines in IGR with decreasing food (Panels II & IV to I & III) and with increasing density (Panels I & II to III & IV). There was a significant effect of initial weight (categorized here as A: 3.5 to 4.5 mm, B: 6.5 to 7.5 mm, C: 9.0 to 11.0 mm, D: 12.5 to 14.5 mm carapace width) and significant initial weight \times food and initial weight \times density interactions. IGR decreases with decreasing food for Size-classes A and, marginally, B; IGR decreases with increasing density for Size-classes A, B, and C

Table 3. Separate ANOVAs on individual growth rate (IGR) within each size-class: $IGR \sim D + F + (D \times F) + A(D \times F)$. There were no significant interactions between food and density and no significant effects of aquarium (Table 2). Effect sizes are the percent change in IGR from low to high levels of the given effect. The F -statistic and associated p -value are the main effects from each ANOVA. Size-class D did not meet the assumption of homoscedasticity

Effect	Size-class	Effect size (%)	F	p
Food	A	24	1.34	0.26
	B	22	2.98	0.09
	C	9	0.29	0.6
	D	11	0.09	0.77
Density	A	-47	16.1	<0.001
	B	-51	76.4	<0.001
	C	-45	7.58	0.011
	D	-29	1.38	0.25

only Size-classes A (-47%), B (-51%), and C (-45%) had significant declines with increasing density (Table 3).

The propensity to lose a cheliped was higher for smaller crabs (Likelihood Ratio Test [LRT], $\ln W_{\text{initial}}$, $p < 0.001$) and, for these smaller crabs, the propensity to lose a cheliped was higher when food was scarce (LRT, $\text{food} \times \ln W_{\text{initial}}$, $p = 0.02$). The logistic regression model with $\ln W_{\text{initial}}$ and $\text{food} \times \ln W_{\text{initial}}$ was the best model by the Akaike information criterion; the overall regression accounted for 94% of the variance compared to the saturated model (i.e. $R^2_L = 0.94$). For individual crabs, IGR was higher for a crab without its cheliped than with its cheliped (paired t -test, $p = 0.007$; Fig. 5); however, the growth in CW was marginally lower without its cheliped than with it (paired t -test, $p = 0.08$; Fig. 5). In the analysis of growth rate of Size A crabs, including

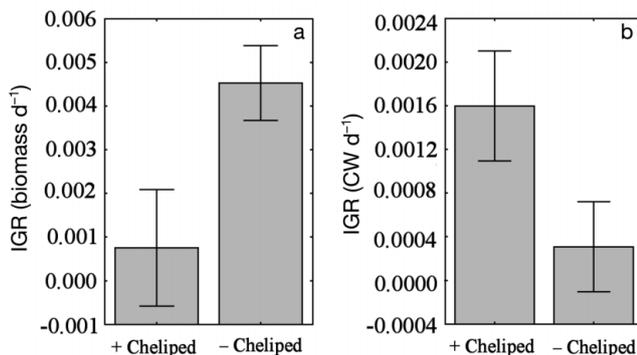


Fig. 5. *Petrolisthes cinctipes*. Paired comparisons of individual growth rate (IGR) in terms of (a) biomass and (b) carapace width (CW) with and without chelipeds in the laboratory growth experiment. There is a significant difference in biomass growth rate (paired t -test, $p = 0.007$) and a marginally significant difference in carapace width growth rate (paired t -test, $p = 0.08$). Means and standard errors are plotted

Table 4. Comparison of individual growth rate (IGR) and competitive effect (decline in IGR per competitor) between high- and low-food laboratory experiments and the field experiment. The laboratory data are for Size-class B only. Compared to either laboratory treatment, growth was higher (t -test, $p < 0.05$) and competition was lower (t -test, $p < 0.02$) in the field. There is no difference between high- and low-food laboratory treatments for growth rate or competitive effect (t -test, $p > 0.2$). Note that all table values are $\times 10^{-3}$

Experiment	Growth rate (95 % CI) (without competitors $\times 10^{-3}$)	Competitive effect (95 % CI) (per unit competitor $\times 10^{-3}$)
Field	7.69 (0.64)	-0.0349 (0.0189)
Laboratory-high food	6.368 (1.21)	-0.0865 (0.0469)
Laboratory-low food	6.353 (0.93)	-0.115 (0.0372)

Table 5. Effects of size and density on frequency of feeding. Aqua (density) is the error term for density and size \times density

Effect	SS	df	MS	F	p
Intercept	10.77	1	10.77	31.82	<0.0001
Density	4.83	1	4.83	5.92	0.041
Aqua (Density)	6.53	8	0.82	2.41	0.017
Size	3.07	3	1.02	3.03	0.031
Size \times Density	0.34	3	0.11	0.14	0.935
Error	61.93	183	0.34		

those with lost chelipeds, IGR decreased with density (GLM, $p < 0.001$), similar to the analysis excluding crabs with lost chelipeds (Table 3). There was a marginally significant increase in IGR with food (GLM, $p = 0.06$), in contrast to the analysis that excluded crabs with lost chelipeds (Table 3). Cheliped loss also resulted in a marginally significant increase in growth rate (GLM, $p = 0.06$), similar to the results of the paired t -test. Density \times cheliped loss and food \times cheliped loss interactions were non-significant (GLM, $p > 0.4$).

Comparison between laboratory and field results

Compared to either laboratory treatment, growth was higher and competition was lower in the field (Table 4). There was no difference between high- and low-food laboratory treatments in growth rate or competitive effect (Table 4).

Laboratory Expt II: effect of density on feeding behavior

Crabs fed less frequently at high density (Table 5, Fig. 6), and smaller crabs fed less frequently than larger crabs (Table 5, Fig. 6). At high density, Size A

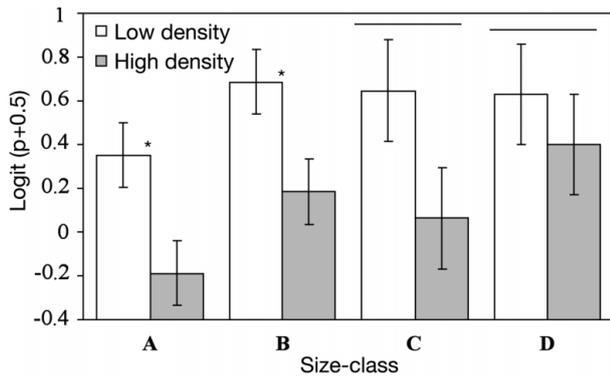


Fig. 6. *Petrolisthes cinctipes*. Feeding rate by density and size-class (\pm SE). Feeding rate was lower for crabs at high density and increased with crab size (Table 5). * = significant Bonferroni-adjusted planned comparisons across density within size, and horizontal lines indicate no significant difference between densities. Post hoc comparisons among size-classes indicated that Size-class A feeds significantly less than the other 3 size-classes (least significant difference = LSD test, $p < 0.04$)

crabs fed 66% less ($p = 0.007$) and Size B crabs fed 40% less ($p = 0.012$) than at low density (Fig. 6). Size C crabs fed 50% less at high density, but this difference was not significant ($p = 0.04$: non-significant with Bonferroni correction). The 15% decrease in the feeding rate of Size D crabs at high density was also non-significant ($p = 0.45$). Because there were fewer crabs in Size-classes C and D, the power to detect an equivalent difference in feeding rate with density was lower (exact power calculations are difficult because of the unbalanced, nested design). The density \times size interaction was non-significant ($p = 0.8$), but the power to

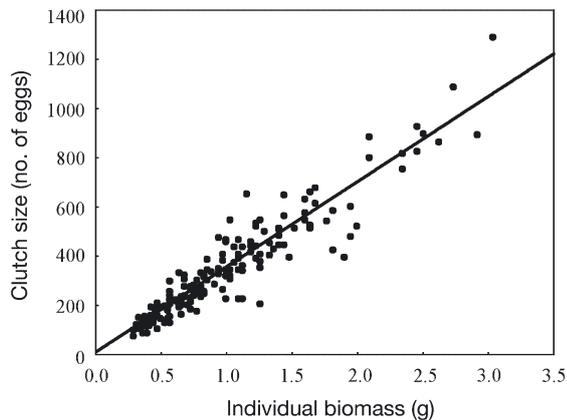


Fig. 7. *Petrolisthes cinctipes*. Fecundity as a function of wet biomass. Fecundity increased significantly with individual biomass ($R^2 = 0.89$, $p < 0.0001$). The intercept was not significantly different from zero and the slope equalled 346 eggs g^{-1} . Crabs were collected in February 2001 from 4 cobblefield sites in Sonoma County, CA, USA

detect such an interaction was low (< 0.30). There was a significant aquarium effect in this experiment ($F_{8,183} = 2.4$, $p = 0.017$); the feeding rate was related to aquarium placement on the manifold and tended to be higher in higher flow aquaria. The effects of flow rate on the feeding behavior of filter-feeders has been documented in several studies (Sanford et al. 1994, Achituv & Pedrotti 1999, Genovese & Witman 1999). The laboratory growth-rate experiment took place in another facility with less variable flow, and I randomized aquaria across the manifold every 3 to 4 d to avoid these systematic effects.

Relationship between biomass and fecundity

Crab biomass was an excellent predictor of crab fecundity ($R^2 = 0.89$, $p < 0.001$; Fig. 7); the intercept was not significantly different from zero. Once it reaches reproductive size, a female crab bears 346 eggs g^{-1} of biomass.

DISCUSSION

In both the laboratory and the field, *Petrolisthes cinctipes* is negatively affected by conspecific density (Figs. 2 & 4). Extrapolating from the daily growth rates in the field, a 5.5 mm crab will grow to 14.2 mm (95%CI: 13.1, 15.3) by the next year without competitors, but only to 11.0 mm (95%CI: 10.3, 11.6) with 60 competitors, equivalent to high-density rocks in the field. This has a striking effect on fecundity (Fig. 7): the lone crab will bear 1080 eggs (95%CI: 853, 1363), whereas the crowded crab will bear only 503 (95%CI: 420, 601).

Size-specific effects of density and food

The overall effect of density on IGR decreased with size (Fig. 4, Table 3). Small crabs may be more strongly affected by agonistic interactions than large crabs; this is supported by the decreasing effect of density on feeding rate with size (Fig. 6) and by the increased tendency for smaller crabs to lose chelipeds. Molenock (1976) found that size was a determining factor in agonistic interactions: for a pair of interacting *Petrolisthes cinctipes*, the larger crab usually initiated the interaction and the larger crab won space in >70% of interactions.

Size also mediated the effect of resource availability on growth rate: smaller crabs suffered more from low food levels (Table 3, Fig. 4). Smaller organisms have higher metabolic demand per unit biomass than larger

organisms and may be more sensitive to changes in food level (Peters 1983). Comparing density effect (change in IGR due to density) to food effect (change in IGR due to food) showed that the growth rates of Size A, B, C, and D crabs were ~2.9-, 3.5-, 8.0-, and 3.2-fold more affected by density than food. The stronger effect of density than food in this experiment is not surprising, because density was increased 6-fold, while the food treatment decreased food quality (percent organic matter) by only ~10%. However, food does seem to be important in cheliped loss: low food increased the probability of cheliped loss in small crabs and food had a marginally significant effect on growth rate when the analysis included crabs missing chelipeds.

There was no significant interaction between food level and density in the laboratory experiment (Table 2, Fig. 4), though the power to detect such an interaction was low. Regardless, it would not be correct to infer that competition is generally unaffected by resource level, because competition decreases with increasing size. For example, in a low-food year, newly settled crabs will grow more slowly and therefore suffer from stronger competition for a longer period. In a good-food year, however, a newly settled crab may quickly grow to a size where the competition it suffers is reduced.

Another indirect interaction between food and density may be mediated by limb loss. For small crabs, the prevalence of limb loss is higher when food is low. Though crabs seem to compensate for limb loss by increasing growth rate, this additional growth is allocated to limb replacement and not to an increase in carapace width (Fig. 5). Crabs that have lost chelipeds may take longer to outgrow size dependent competitive effects. Wasson et al. (2002) demonstrate the effectiveness of autotomy for predator avoidance in *Petrolisthes* spp. They also suggest that filter-feeders may have lower costs to autotomy, because they do not use their chelipeds to feed. The present study gives merit to the Wasson et al. (2002) hypothesis: *P. cinc-tipes* grew faster when a cheliped was missing, possibly indicating an increase in food intake, which could hasten cheliped regrowth. However, cheliped loss is not without costs, since it slows carapace growth.

Comparing exploitative and interference competition

Several studies have partitioned the relative effects of exploitative and interference competition (Anholt 1990, Fradkin 1995, Schmitt 1996, Josefson 1998). These effects cannot be strictly distinguished from these experiments, but some conclusions seem reason-

able. In this study (author's pers. obs.) and in that of Jensen (1990), crabs appeared to congregate in areas of high flow in the aquarium and vie for position using the agonistic behaviors described by Molenock (1976). Several studies have demonstrated that flow rate affects feeding behavior and feeding efficiency in porcelain crabs (Trager et al. 1992, Trager & Genin 1993, Achituv & Pedrotti 1999) and in barnacles (Trager et al. 1992, 1994, Sanford et al. 1994). Since feeding efficiency varies with flow rate, crabs may be competing for good filter-feeding locations.

However, the decline in feeding rate with density is also consistent with exploitative competition. Many filter-feeders increase their feeding rate with food availability (Sanford et al. 1994), and Hartman & Hartman (1977) found a positive relationship between the concentration of amino acids in seawater and the number of *Petrolisthes cinc-tipes* feeding. If crabs reduce their resources by feeding, then the decrease in feeding rate could simply be a response to lower food levels imposed by higher density. This is possible but seems unlikely since the high flow rate into the aquaria (1 to 2 l min⁻¹) should have greatly exceeded the ability of *P. cinc-tipes* to draw down its resources. Achituv & Pedrotti (1999) found a maximum clearance rate of 0.286 l crab⁻¹ h⁻¹ for *Porcellana longicornis* (Anomura: Porcellanidae) clearing an algal suspension. While exploitative and interference mechanisms for the decline in feeding rate with density are not mutually exclusive, the interference mechanisms are probably stronger in this case.

Comparing competition between the laboratory and field

Competitive effects were generally lower in the field than in the laboratory. There are many possible explanations for this, including: (1) food availability, (2) size differences between laboratory and field crabs, (3) changes due to captivity, (4) size-structured interactions, and (5) complexity of the environment. (1) Overall food levels were higher in the field than in the laboratory, which could have resulted in decreased exploitative competition or aggressive interference interactions. Though there was no overall interaction between food availability and competition in the laboratory experiment (Table 2), the growth rate of Size B crabs was more strongly affected by density when food was low than when food was high (Fig. 4). For this size-class (which was most similar to that in the field), the higher food levels in the field could have mitigated the effects of competition. (2) Crabs in the field experiment were ~1 mm CW smaller than laboratory Size-class B. Since the relative effect of density increased from Size

A to Size B in the laboratory experiment (Table 3), this could help explain the stronger competition in the laboratory. (3) Crab behavior or physiology might have changed due to captivity in the laboratory experiment (Houlihan & Mathers 1985). However, this would generally be expected to decrease aggressive interactions as physical performance declines in captivity. (4) Size-structured interactions should have increased, rather than decreased, competitive effects in the field compared to the laboratory, since larger crabs were used to impose the field density treatments. Finally, (5) the laboratory aquaria, with a single half-brick and single inflow tube per aquarium, provided a less complex environment than the field cages. The cages were filled with 3 cobbles and probably had more high-flow spots than did the aquaria. This may have resulted in a stronger competitive hierarchy in the laboratory aquaria than in the field enclosures. Overall, higher food availability in the field (Fig. 3) and increased habitat complexity in field cages compared to aquaria are the most likely causes for decreased competition in the field compared to the laboratory.

Trade offs related to gregarious settlement

Petrolisthes cinctipes megalopae settle gregariously as incoming megalopae (Jensen & Armstrong 1991, M. J. Donahue unpubl. data) and the adults are highly aggregated as adults (Fig. 1). Although they compete strongly (Figs. 2 & 4), there are also benefits to gregarious settlement, including habitat cueing (Raimondi 1988, Jensen 1989, Muller et al. 1997, Mullineaux et al. 2000), reduced predation risk (Highsmith 1982, Tegner & Levin 1983, Bertness & Grosholz 1985, Jensen & Armstrong 1991, Peterson & Black 1993, Ray & Stoner 1994), facilitation (Bertness & Grosholz 1985, Bertness 1989), and access to mates (Burke 1986, Metaxas et al. 2002). In addition, Jensen & Armstrong (1991) showed that adult *P. cinctipes* protected settlers from predation by intertidal fishes and that, by settling with conspecifics, *P. cinctipes* settlers choose habitat preferred by adults. In another study (M. J. Donahue unpubl. data), I quantitatively compare the costs and benefits accrued to gregariously settling *P. cinctipes* and demonstrate that the competitive costs of settling with adults can be offset only when benefits include both decreased predation and increased habitat quality.

CONCLUSIONS

At first glance, *Petrolisthes cinctipes* would not seem to compete strongly: it settles gregariously, lives awash in its food, and is mobile. This study demonstrates that,

despite these characteristics, competition is an important feature in the life history of *P. cinctipes*. Competition among filter-feeders has been well documented for space-limited sessile invertebrates (reviewed in Branch 1984) and for soft-bottom infauna (e.g. Peterson & Andre 1980, Peterson 1982), but the present study draws new attention to mobile filter-feeders such as *P. cinctipes*.

Petrolisthes cinctipes densities vary widely from rock-to-rock within cobblefield sites (Fig. 1) and from site-to-site (M. J. Donahue unpubl. data). This spatial variation in density means that not all crabs experience the same level of competition. A site that receives high larval supply due to coastal features (Wing et al. 1995, 1998a,b) may have diminished fecundity due to intense post-settlement competition that decreases the growth rate. This interaction between spatially varying larval supply and post-settlement density dependence can influence the dynamics and stability of metapopulations (Chesson 1998). When considering *P. cinctipes* dynamics on the metapopulation scale, aggregation has an overall negative effect on crab growth rate due to competition, but a positive effect on local recruitment due to gregarious settlement and decreased predation. Future work will focus on how intraspecific competition in *P. cinctipes*, as demonstrated in this study, interacts with spatial variation in density to influence local and regional dynamics.

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