

## POSITIVE INTRASPECIFIC EFFECTS TRUMP NEGATIVE EFFECTS IN HIGH-DENSITY BARNACLE AGGREGATIONS

HEATHER M. LESLIE<sup>2</sup>

*Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA*

**Abstract.** High-density aggregations of conspecifics have long been presumed to have negative effects on individual fitness, yet this has not been adequately tested for multiple life history traits in the field. Here I report a series of investigations that comprehensively evaluate the influence of conspecific density on key traits (survival, growth, and reproduction) in the intertidal barnacle *Balanus glandula*. Density was manipulated in mid-intertidal barnacle populations living on both natural rock surfaces and on settlement plates, and monitored in natural populations. Survival was positively related to density: populations at the lowest density level were 19 times more likely to experience  $\geq 95\%$  mortality than those at the highest level. In contrast, growth and individual reproductive output were negatively related to density: animals at lower experimental densities (16–50 adult barnacles/100 cm<sup>2</sup>) grew to 1.6 times the diameter of individuals living at higher densities (200–460 adult barnacles/100 cm<sup>2</sup>), and larger barnacles produced larger brood masses than smaller individuals. Overall, the frequency of brooding barnacles in experimental and natural populations was greatest at intermediate densities. Estimation of the basic reproductive rate for the experimental animals on the settlement plates indicated that the primary effect of increased conspecific density was enhanced survival, and consequently, a larger mean number of larvae produced per original recruit. Thus in this case, the positive intraspecific effects of high-density aggregations outweighed the negative effects. My results demonstrate that key life history traits may not have similar responses to changes in density, and provide a strategy for evaluating the relative importance of positive vs. negative intraspecific interactions.

*Key words:* *Balanus glandula*; barnacles; competition; conspecific density; facilitation; intertidal.

### INTRODUCTION

The role of density-dependent processes in population and community dynamics has long been an important area of investigation (Hixon et al. 2002). Until recently, ecologists have emphasized the roles of negative interactions, e.g., competition, predation, and the effects of abiotic stress, in structuring biological populations and communities (Bruno et al. 2003). Nevertheless, facilitation, such as when one organism ameliorates stressful abiotic or biotic conditions for another, also can play an important role (Connell and Slayter 1977, Menge and Farrell 1989, Bertness and Callaway 1994, Bertness et al. 1999).

The focus on negative interactions has been particularly pervasive in the presumed negative relationship between conspecific density and individual fitness (Stephens and Sutherland 1999, Bruno et al. 2003). Increasingly, however, ecologists have documented the roles of positive intraspecific interactions in population and community dynamics, e.g., where conspecifics liv-

ing at high densities survive, grow, or reproduce better than their more isolated counterparts (Lynch 1978, Bertness and Leonard 1997, Callaway and Walker 1997, Courchamp et al. 1999, Bruno et al. 2003).

Here I focus on rocky intertidal marine communities, which have served as a particularly rich testing ground for evaluating the relative importance of negative vs. positive interactions. In rocky intertidal ecosystems, considerable knowledge of population and community dynamics exists, and organisms can be manipulated in field experiments with relative ease. Space is one of the primary limiting resources in these systems, particularly for sessile species (Connell 1961, Lubchenco and Menge 1978, Paine and Levin 1981).

For barnacles, for example, intraspecific competition for space can result in reduced growth rates and even death (Barnes and Powell 1950, Connell 1961, Dayton 1971, Menge 1976, Bertness 1989). Yet possible positive effects of high-density barnacle aggregations include increased settlement and recruitment (Knight-Jones 1953, Wetthey 1984, Raimondi 1988, Bertness et al. 1999), increased survival (Bertness 1989), improved feeding efficiency (Bertness et al. 1998), and greater reproductive output (Wu 1980, Wetthey 1984). To date, investigations of the effects of increased conspecific density on barnacles and other species have focused primarily on a single response, and especially on re-

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<sup>1</sup> Present address: Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544 USA. E-mail: hleslie@princeton.edu

recruitment. In marine populations in particular, earlier life history phases (e.g., larval production, planktonic larval or juvenile stages) have been less studied, in part because of the logistical difficulties of tracking organisms with complex life histories.

Here I report a series of studies that develop a more comprehensive approach. I evaluated the influence of conspecific density on multiple life history traits in the intertidal barnacle *Balanus glandula* by measuring responses across several life stages, from recruitment through larval production. Density was manipulated in barnacle populations living on both settlement plates and on natural rock surfaces, and tracked in natural populations.

#### METHODS

The studies were conducted in the mid-intertidal zone at Bob Creek (BC) and Fogarty Creek (FC), two exposed rocky intertidal sites in Oregon, USA. FC is located at 44.84° N, 124.06° W; BC is located at 44.24° N, 124.11° W. The mean tidal range at these sites is ~1.8 m (data from Yaquina Bay, Bar at Entrance).<sup>2</sup> The acorn barnacle *Balanus glandula* occupies both primary and secondary space in the mid-intertidal zone, which spans +1.5 to 2 m above mean lower low water (MLLW) at these sites (H. Leslie, *unpublished data*). Air and water temperatures at each site were recorded every 30 minutes with Onset StowAway TidbiT loggers (Onset Computer Corporation, Bourne, Massachusetts, USA) deployed at +2 m above MLLW. The program SiteParser (B. Helmuth, *unpublished data*) was used to extract daily high air temperatures from the temperature records.

#### *Settlement plate experiment*

Barnacles of a known age were maintained at standardized densities on plastic settlement plates, after Sanford and Menge (2001). The plates were made of a 6.35 mm thick opaque gray polyvinyl chloride (PVC), which was cut into 100-cm<sup>2</sup> squares and attached to the substrata with 6.35 cm long stainless steel lag screws. Each plate had one of four configurations of shallow pits (1 mm in diameter, 0.3 mm deep) spaced at regular intervals. (See Appendix A for specifications.) Barnacles prefer to settle in these pits rather than on the smooth surface of the plates (Connell 1985, Sanford and Menge 2001), which enabled me to control recruit densities.

In late June 2002, I deployed 160 plates at Strawberry Hill, <1 km north of BC. To facilitate concurrent settlement, the plates were distributed within a 16-m<sup>2</sup> area in the low intertidal zone (+1 m above MLLW). In early July 2002, settlement was observed. In mid-August 2002, once the juvenile barnacles were ~2 mm in basal diameter, the plates were sorted in the laboratory to remove those with low numbers of recruits.

The remaining 100 plates were sorted randomly into 25 blocks of four plates (one of each density level), and out-planted to the BC mid-intertidal zone (+2 m above MLLW) over a 50-m stretch of exposed shoreline. Plates were photographed monthly to track survival and growth of the original recruits. I removed new recruits as needed to maintain the density levels. Whelks (primarily *Nucella emarginata*) were removed from the 400-cm<sup>2</sup> area around each plate to minimize predation effects, although the snails were rarely observed in the vicinity of the experiment.

In April 2003, when the original *B. glandula* recruits were nine months old, the plates were collected and photographed in the laboratory. Based on photographs, original recruits were identified. Density per 100 m<sup>2</sup> (i.e., per plate) was quantified in the laboratory. The density of potentially reproductively mature animals at the experiment's end included both survivors (i.e., those barnacles from the original cohort) and younger animals with basal diameters of ≥4 mm who recruited subsequently. These younger individuals were large enough to potentially compete and mate with the original survivors (*personal observation*).

The original recruits were dissected to quantify growth, morphology, and reproductive condition after storage at -20°C for several months. I measured the dimensions (height, basal diameter, and opercular diameter) of each barnacle. As all barnacles were of similar age and size at the beginning of the experiment, basal diameter was used as a measure of relative growth. Basal diameter, rather than shell volume, was used as an index of growth, as a barnacle growing under crowded conditions often does not occupy the entire vertical extent (i.e., height) of its shell (*personal observation*). Also, basal diameter can be directly measured, whereas shell volume is an estimated, and therefore less accurate, quantity. Changes in morphology were quantified as the ratio of barnacle height to basal diameter, as less crowded animals have truncated cone-shaped shells and low ratios, and more crowded individuals have more columnar forms and higher ratios (see Appendix B). I noted if each animal had a brood (conspicuous yellow or dark brown egg lamellae), unfertilized ovarian material (viscous, yolky yellow material), or no evident female reproductive tissue within the mantle cavity (Barnes and Barnes 1956, Walker 1992). A brood and unfertilized ovarian material co-occurred within the same animal in some instances; in these cases, individuals were scored as "brooding."

To quantify individual biomass allocation, I then dissected each individual, separated the shell, body, and female gonadal (brood and ovarian) tissues, and quantified their dry masses, after drying them at 50°–55°C for ≥48 hours. Masses stabilized after 48 hours (H. Leslie, *unpublished data*). The number of larvae per brooding barnacle was estimated as a function of barnacle diameter and shape ( $\ln[\text{number of larvae}] = 4.590 + 0.304[\text{basal diameter}] + 0.505[\text{height:basal diameter}]$ )

<sup>2</sup> (<http://tidesonline.nos.noaa.gov/>)

based on animals sampled from natural populations in this region (Multiple linear regression:  $n = 138$  barnacles,  $R^2 = 0.44$ ,  $F = 53.500$ ,  $P < 0.0001$ ,  $df = 2, 135$ ). For full details, see Leslie (2004).

#### *Natural rock surface experiment*

Before deploying the plate experiment, I conducted a similar manipulation on natural rock surfaces. In May 2001, I cleared three sets (i.e., blocks) of two 400-cm<sup>2</sup> plots in the mid-intertidal zone (+2 m above MLLW) at BC and FC. The sites were chosen to bracket a known gradient in nearshore primary productivity, as the coastal waters adjacent to BC have consistently higher phytoplankton concentrations (measured as chlorophyll *a*, a proxy for primary production) relative to FC (Menge et al. 1997).

Following *B. glandula* recruitment in early July 2001, one plot of each block was randomly selected as the "thinned" treatment, while the other was classified as "natural." For the next seven months, I maintained the "thinned" treatment by manually removing barnacles in order to create plot densities considerably less than those in the "natural" plots (see Appendix C). Plots were photographed monthly to track barnacle densities, survival, and growth. Individuals as small as 2 mm basal diameter may brood larvae (*personal observation*), so density per 100 cm<sup>2</sup> was estimated based on counts of all *B. glandula*  $\geq 2$  mm in basal diameter in replicate subsamples of the plots.

In February 2002, I collected a haphazard subsample of the seven-month-old original recruits from each plot. *B. glandula* reproduces throughout the year in Oregon's mid-intertidal zone (Leslie 2004), so the results of the two experiments are comparable. Animals were frozen on dry ice in the field, and stored at  $-20^{\circ}\text{C}$  until laboratory processing. I then dissected them to quantify growth, morphology, and reproduction, as described above.

#### *Field surveys*

To evaluate the relevance of the density manipulations to natural populations, I collected individuals from natural *B. glandula* mid-intertidal populations at BC and FC in April 2003. I ran a 50-m transect through the center of the zone, and collected all barnacles within 12 randomly selected 100-cm<sup>2</sup> quadrats. Animals were frozen in the field on dry ice, and stored at  $-20^{\circ}\text{C}$  until laboratory processing. Barnacles with  $\geq 2$  mm basal diameters were counted to estimate density per 100 cm<sup>2</sup>. Up to 50 animals per quadrat were measured and scored for reproductive condition, as described previously.

#### *Statistical analyses*

Analysis of variance models (ANOVAs) were constructed to evaluate the effects of density, site, and block on several response variables. Block was considered a random factor, and variance components were

estimated using the restricted maximum likelihood estimation (REML) method. REML is considered more reliable than the traditional Expected Mean Squares approach (Quinn and Keough 2002). Linear regression was used to examine relationships between continuous variables. Treatment groups were compared via Tukey-Kramer HSD tests based on least square means estimated from the relevant main effect or interaction term ( $P < 0.05$ ).

In the plate experiment, there were many cases of 100% mortality. Consequently, I also analyzed the per capita mortality data as a contingency table by comparing those plates that experienced  $\geq 95\%$  mortality vs. those with lower mortality rates (Ramsey and Schaffer 1997, Quinn and Keough 2002). Also, I eliminated the plates with fewer than three survivors for the growth and reproduction analyses. This resulted in three remaining blocks, with three replicate plates for each of the three higher density levels. All but two individuals died at the lowest density level, precluding growth and reproduction analyses for this density. For the analyses of individual-level reproduction only, means for the second lowest density level (81 pits per plate) were averaged across two replicate plates, as the third plate had only one brooding barnacle on it. Inclusion of the third replicate did not qualitatively change the results.

All analyses were conducted with JMP IN 4.0 (SAS Institute 2001). Statistical tables are presented in Appendices A–E, as are supplementary figures. Given the small sample sizes available to test most hypotheses, I report marginal effects ( $P < 0.1$ ). Upon inspection of residuals, the data were transformed ( $\ln(y)$  for data sets with values  $> 1$  and  $\ln(1 + y)$  for data sets with values  $< 1$ ) to meet ANOVA assumptions. If transformations did not improve the spread of the data, untransformed values were used. ANOVA is generally robust to violations of most assumptions, provided the data set is balanced (Underwood 1997, Quinn and Keough 2002).

## RESULTS

### *Settlement plate experiment*

The mean number of recruits per 100 cm<sup>2</sup> differed among the four density levels in August 2002, as did the number of adult barnacles at the end of the experiment (Fig. 1A–B, Table 1A; Appendix D: Table D1, parts a and b). As expected from the random allocation of plates to each block, recruit density did not vary among blocks (Appendix D: Table D1, part a).

The number of survivors was strongly affected by density (Fig. 1C, Table 1A; Appendix D: Table D1, part c). Animals living at the lowest density level were 19 times (95% confidence interval, 4–103 times) more likely to experience  $\geq 95\%$  mortality than those living at the highest density level ( $\chi^2$  test:  $\chi^2 = 26.745$ ,  $P < 0.0001$ ; Appendix D: Table D2).

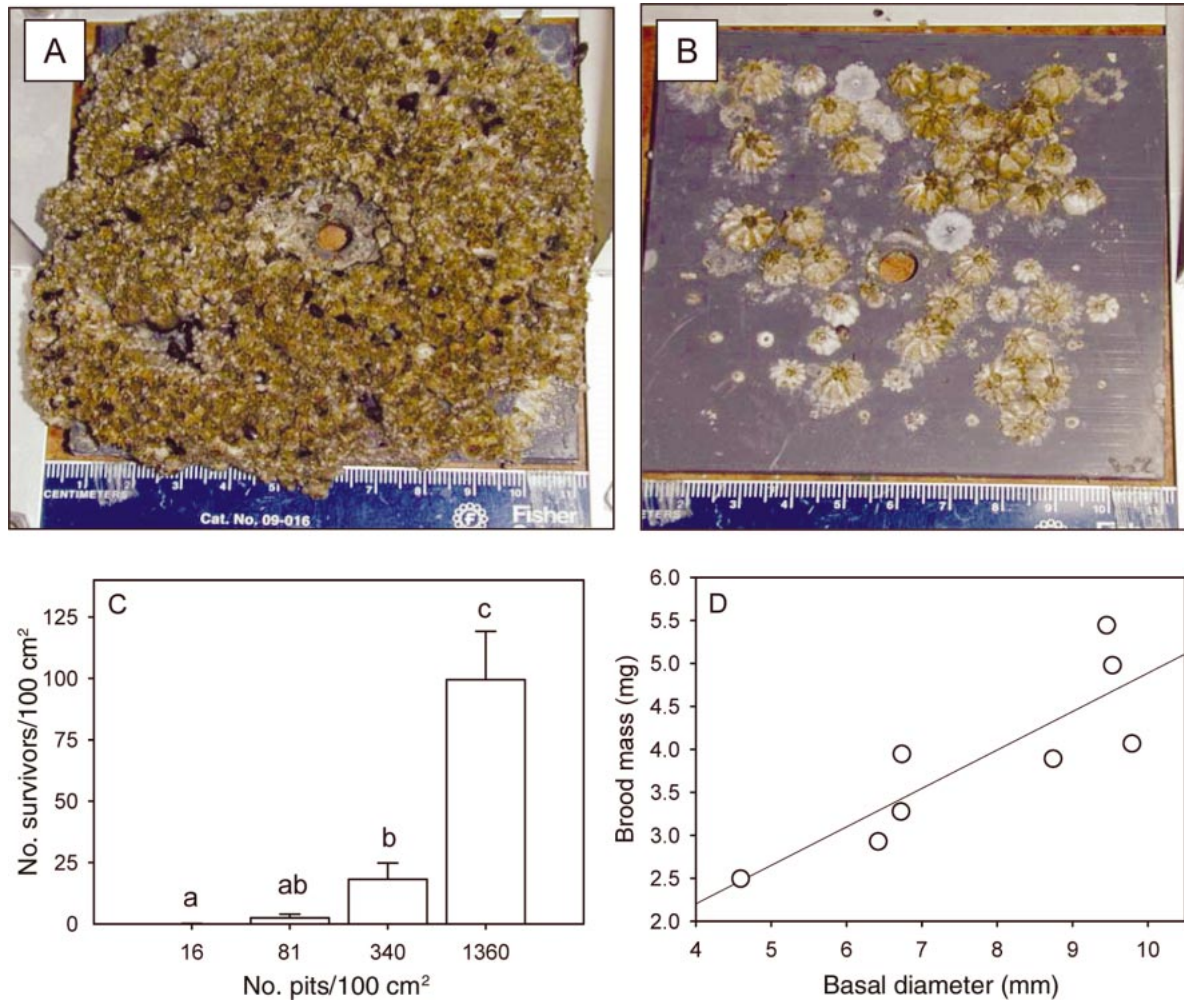


FIG. 1. Representative plates with (A) 1360 pits/100 cm<sup>2</sup> vs. (B) 81 pits/100 cm<sup>2</sup>. (C) Number of survivors/100 cm<sup>2</sup> relative to density. Means with dissimilar letters are significantly different (Tukey-Kramer test on ln-transformed values,  $P < 0.05$ ). Means + SE are shown ( $n = 24-25$  plates per level). For the lowest level, the values [ $0.118 + 0.081(\text{survivors}/100 \text{ cm}^2)$ ] were too small to be visible. (D) Barnacle brood mass related to barnacle size in the plate experiment [ $\ln(y) = -0.426 + 0.868 \ln(x)$ ;  $R^2 = 0.78$ ,  $F = 21.827$ ,  $df = 1, 6$ ,  $P = 0.003$ ]. Untransformed plate-level means are shown ( $n = 8$  plates, with 3–8 barnacles sampled per plate).

Animals living at the second lowest density (81 pits per plate) grew 1.6 times (95% CI, 0.9–2.2 times) larger than barnacles living at the highest density (1360 pits per plate) (Figs. 1A–B, 2A; Appendix D: Table D1, part d;  $F = 191.788$ ,  $P < 0.001$ ,  $df = 2, 4$ ). As density increased, shell morphology changed as well, becoming proportionally taller (Fig. 2B; Appendix D: Table D1, part e;  $F = 5.840$ ,  $P = 0.039$ ,  $df = 2, 6$ ). Surprisingly, individual allocation to shell and somatic and reproductive tissues was not affected by conspecific density (Appendix D: Table D3). Consequently, I report the overall mean dry masses, averaged across density levels (Table 2A).

Size-specific reproduction increased with basal diameter. As the median basal diameter per plate doubled from 5 to 10 mm, there was a 1.83-mg (95% CI, 1.33–2.50 mg) increase in median brood dry mass (Fig. 1D).

In other words, barnacles living at lower densities were larger and therefore had larger brood masses. The estimated number of larvae brooded per barnacle was strongly related to brood mass size (Fig. 3A), and the estimated number of larvae produced per barnacle tended to decrease with higher densities (Appendix D: Table D4, part a).

Brooding frequencies increased with density (Appendix D: Table D4, part b). No barnacles were brooding at the lowest conspecific density, where mortality was so high. But when the lowest density level was omitted from the analysis, there was no relationship between brooding frequency and conspecific density among the three higher densities. Overall, brooding frequencies averaged  $51 \pm 14\%$  (mean  $\pm$  SE) among the three higher density levels (Appendix D: Table D4, part c).

TABLE 1. Barnacle densities in the three studies (A–C) encompassed a comparable range (no./100 cm<sup>2</sup> ± SE).

Density	Recruits	Adults†	Survivors
A) Plate experiment (at BC)‡			
16 pits/100 cm <sup>2</sup>	8 ± 1	3 ± 1	0 ± 0
81 pits/100 cm <sup>2</sup>	49 ± 4	16 ± 4	2 ± 2
340 pits/100 cm <sup>2</sup>	169 ± 14	129 ± 24	18 ± 7
1360 pits/100 cm <sup>2</sup>	770 ± 84	329 ± 32	99 ± 20
B) Natural surface experiment			
BC, thinned (site, treatment)		50 ± 7	
FC, thinned		53 ± 6	
BC, natural		203 ± 94	
FC, natural		461 ± 44	
C) Natural population surveys			
BC		113 ± 36	
FC		65 ± 28	

Notes: (A) Plate experiment densities of recruits in August 2002, and reproductively mature adults and survivors, April 2003 ( $n = 24$ – $25$  plates per density level). (B) Natural rock surface experiment densities, February 2002 ( $n = 3$  plots per treatment). (C) Natural population densities, April 2003 ( $n = 12$  quadrats per site).

† In Study A, the count of adults included all barnacles  $\geq 4$  mm in basal diameter. In Studies B and C, the counts included all barnacles  $\geq 2$  mm in basal diameter.

‡ BC = Bob Creek; FC = Fogarty Creek. See *Methods* for site details.

#### Natural rock surface experiment

At the termination of the density manipulation on natural rock surfaces, barnacle populations in natural (i.e., unthinned) plots were 4–9 times more abundant than those in the thinned plots (Table 1B; Appendix D: Table D5, part a;  $F = 68.498$ ,  $P = 0.0001$ ,  $df = 1, 6$ ). Barnacle densities were 2 times (0.6–14 times) higher in the FC natural than in the BC natural plots due to differences in recruitment and postrecruitment survival (*personal observation*).

Barnacles in the thinned treatments grew to 1.6 times (95% CI, 0.9–3.0 times) the diameter and exhibited a less crowded morphology than those in the natural treatments (Fig. 2C–D; Appendix D: Table D5, parts b and c). Barnacles in the FC natural plots were smaller and more crowded than those in the other treatments. Although there was no effect of density on mean individual biomass allocation per plot (as observed in the previous experiment), these responses were greater at BC than FC (Appendix D: Table D6). Consequently, I present the estimated individual allocation by site (Table 2B).

There was no relationship between brood mass and barnacle size (i.e., basal diameter) in this experiment, perhaps because barnacle densities and thus morphology were less controlled than in the plate experiment. Neither density nor site had any effect on the estimated number of larvae produced per barnacle (results not shown).

Brooding frequency varied inconsistently among the treatments (Appendix D: Table D5, part d, site  $\times$  density interaction term;  $F = 24.270$ ,  $P = 0.003$ ,  $df = 1, 6$ ). The mean brooding frequency in the FC natural plots was  $23 \pm 7\%$ , whereas in the other three treat-

ments (i.e., FC thinned, BC natural, BC thinned), it was  $56 \pm 3\%$  (mean  $\pm$  SE). In the FC natural plots, *B. glandula* lived at much higher densities, developed a more crowded morphology, and brooded at lower frequencies than animals in the other treatments. Note that the FC natural plot densities exceeded those in the highest level of the plate study (Table 1).

#### Field surveys

Surveys of mid-intertidal natural populations of *B. glandula* at BC and FC indicated that densities at BC were marginally higher than those at FC (Table 1C; one-way ANOVA on ln-transformed data:  $F = 3.526$ ,  $P = 0.07$ ,  $df = 1, 22$ ). As density increased in the natural populations, shell morphology changed as in the experiments, with higher mean ratios (of barnacle height to basal diameter) at higher densities (Appendix E: Fig. E1). There was no relationship between mean barnacle size and density, which makes sense given that the sampled animals were a mix of multiple size and age classes. Nor was there a relationship between the estimated number of larvae per individual and density.

Brooding frequency was not influenced by density or site. The overall mean brooding frequency was  $23 \pm 4\%$  (mean  $\pm$  SE), and individual rates per quadrant ranged from 0% to 58%. There was a strong association between mean barnacle size and brooding frequency, however (Fig. 3B). In quadrats where mean barnacle size was  $\geq 4$  mm in basal diameter, the frequency of brooding barnacles increased markedly, suggesting that this was a reasonable lower limit for quantifying reproductively mature barnacles.

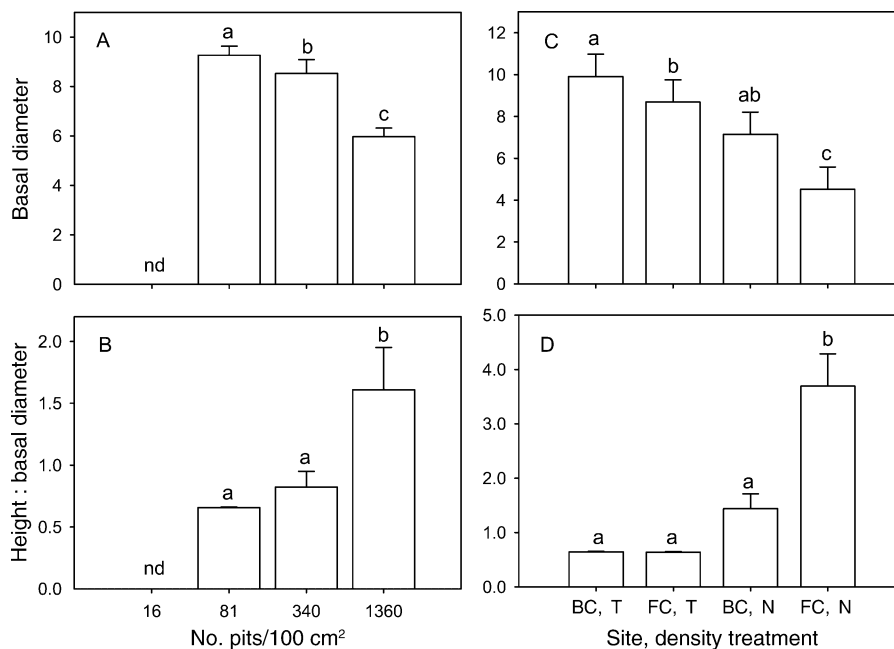


FIG. 2. Influence of density on barnacle growth and morphology in (A, B) the plate experiment and (C, D) the natural surface experiment. Key to abbreviations: BC = Bob Creek, FC = Fogarty Creek; T = thinned treatments, N = natural treatments of the natural rock experiment. Means + SE are shown ( $n = 3$  plates, with 9–10 barnacles subsampled per plate;  $n = 3$  plots per site, 28–42 barnacles subsampled per plot); nd = no data. Means with dissimilar letters above the bars are significantly different (Tukey-Kramer tests,  $P < 0.05$ ).

*Evaluating the net effect of increased density on barnacle fitness*

To integrate the observed positive and negative effects of conspecific density, I employed a standard life table approach. Both individual fitness and population persistence are linked to the basic reproductive rate,  $R_0$ .  $R_0$  can be calculated as the sum of the mean number of larvae produced per original recruit during each life stage (i.e.,  $R_0 = \sum l_x m_x$ ), where  $l_x$  is the proportion of original recruits surviving to the adult stage and  $m_x$  is the number of larvae produced per surviving individual in the adult stage. While age- or size-specific repro-

ductive output data are not available in this case (precluding calculation of a full life table), I used the data on survival and the estimated number of larvae produced per individual barnacle from the settlement plate experiment to estimate the mean number of larvae produced per original recruit ( $l_x m_x$ ) for one stage. I refer to this stage as the “reproductively mature adult stage” (Table 3). The mean number of larvae ( $l_x m_x$ ) provides a means of assessing the net effect of density on survival, growth, and reproduction in *B. glandula*. The mean number of larvae produced per original recruit increased with density, indicating that the positive ef-

TABLE 2. Estimated biomass allocation (mean ± SE) per barnacle for the (A) plate and (B) natural surface experiments.

Site	Somatic tissue		Female gonad†		Shell organics‡		Brood biomass (mg)
	Biomass (mg)	%	Biomass (mg)	%	Biomass (mg)	%	
A) Plate experiment							
BC	2.74 ± 0.26	37	3.19 ± 0.38	43	1.56 ± 0.14	21	3.88 ± 0.35
B) Natural rock surface experiment							
FC	1.82 ± 0.22	47	1.23 ± 0.09	32	0.81 ± 0.13	21	1.72 ± 0.28
BC	3.42 ± 0.34	49	2.23 ± 0.29	32	1.35 ± 0.12	19	2.90 ± 0.27

Notes: (A) Plate experiment values were averaged across the three higher density levels ( $n = 8-9$  replicate plates, with 3–10 barnacles subsampled per plate). (B) Natural surface experiment values were averaged across the two density levels at each site ( $n = 6$  replicate plots, with 28–42 barnacles subsampled per plot). Percentages were estimated from the sum of somatic, female gonad, and shell organic biomass.

† Includes both brooding and nonbrooding individuals.

‡ Shell organic matter biomass calculations assumed that 1% of shell dry mass was organic (after Wethey [1984]).

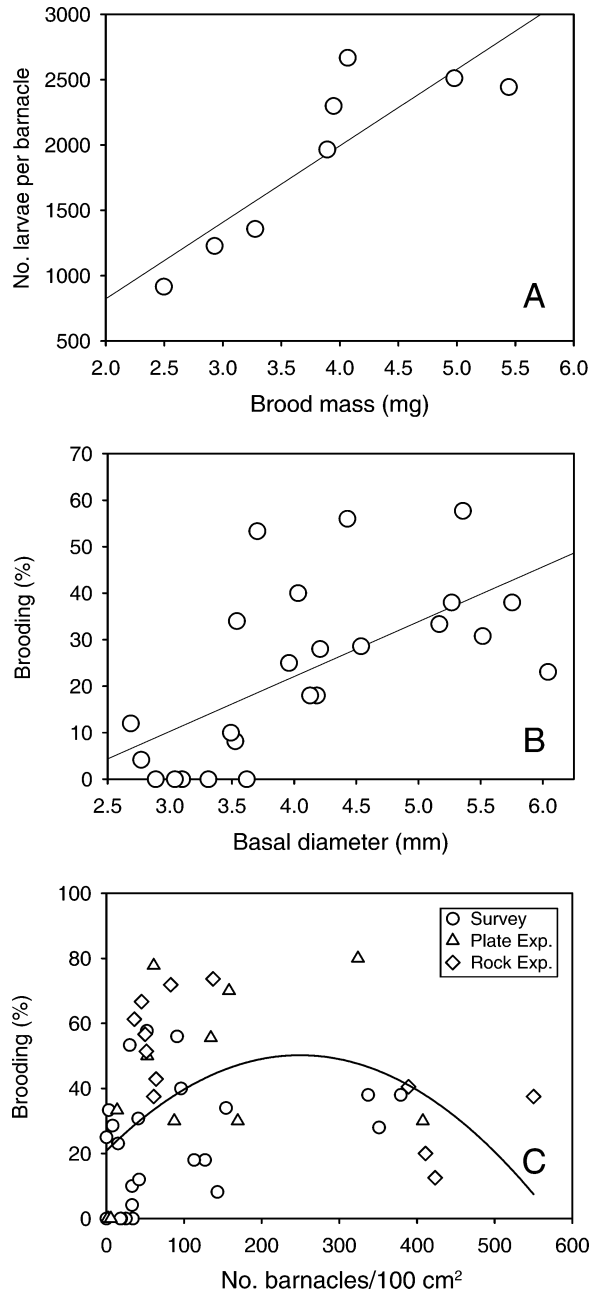


FIG. 3. Reproductive output in the experimental and natural populations. (A) Estimated number of larvae per barnacle relative to brood mass in the plate experiment ( $\ln(y) = 5.642 + 1.400 \ln(x)$ ;  $R^2 = 0.84$ ,  $F = 30.729$ ,  $df = 1, 6$ ,  $P = 0.002$ ). Untransformed plate-level means are shown ( $n = 8$ , with 3–8 barnacles subsampled per plate). (B) Brooding frequency relative to barnacle size in the mid-intertidal natural populations surveyed at FC and BC in April 2003 ( $y = -25.13 + 11.80x$ ;  $R^2 = 0.40$ ,  $F = 14.381$ ,  $df = 1, 22$ ,  $P = 0.001$ ). Quadrat-level means are shown ( $n = 24$ ). (C) Brooding frequency was maximized at intermediate densities; data from the three studies were combined ( $y = 0.209 + 0.002x - 0.0000047x^2$ ;  $R^2 = 0.15$ ,  $F = 4.021$ ,  $df = 2, 45$ ,  $P = 0.025$ ). Quadrat, plate, and plot-level means are shown ( $n = 48$ ).

fects of high-density aggregations outweighed the negative effects in the plate experiment (Table 3, last column).

#### DISCUSSION

##### *Density's strong and variable effects on key life history traits*

Density had strong although variable effects on multiple life history traits of the intertidal barnacle *B. glandula*. In summary, increased densities increased survival, decreased growth and individual reproductive output, and had no observable effect on individual biomass allocation (Table 4). Population-level reproductive output varied, as outlined in the following paragraphs.

The fact that increased density resulted in increased survival suggests that intraspecific facilitation played a stronger role than competition in this context. This is intriguing given that the emphasis regarding intraspecific interactions in gregarious species has largely been on the negative effects. Positive intraspecific effects (also known as facilitative, cooperative, or Allee effects) can occur for a number of reasons, including the existence of minimum threshold densities for mating and habitat modification (Stephens and Sutherland 1999). In barnacles, positive intraspecific interactions have been observed primarily under conditions deemed to be at the more severe end of an environmental stress gradient (Bertness 1989, Bertness et al. 1999). In Bertness' (1989) barnacle study in New England, for example, high intertidal temperatures on large rocks (most comparable to the broad intertidal benches at BC) reached 38°C during daytime low tides. During the first two months of the plate experiment (August–October 2002), when most of the mortality occurred, the daily high air temperature at BC was 16.8°–18.5°C (95% confidence interval), although isolated daily highs of 30.6°C (13 August) and 25.3°C (15 September) were recorded. These data suggest that the abiotic conditions during the plate experiment in Oregon were not as severe as those observed in New England. Yet positive interactions were observed in both cases, suggesting that facilitation may occur over broader environmental gradients than previously thought.

Density negatively influenced barnacle growth rates in both experiments. Barnacles at lower experimental densities grew to a mean diameter 1.6 times greater than those animals at higher experimental densities. At higher densities, barnacle height:diameter ratios increased, as well. This relationship between density and morphology also was observed in the surveys of natural populations. Previous investigators have documented similar changes in growth and barnacle shell morphology (Barnes and Powell 1950, Knight-Jones 1953, Bertness 1989, Lopez and Gonzalez 2003).

Density also negatively influenced individual reproduction. Barnacles living at lower densities produced

TABLE 3. Comparison of the reproductive rates ( $R_0 = l_x m_x$ ) of barnacles at different densities in the plate experiment. Means are shown ( $n = 25$  for  $l_x$  and  $n = 3$  for  $m_x$ ).

Density (no. pits/100 cm <sup>2</sup> )	Proportion of original recruits surviving to adult stage ( $l_x$ )	Larvae produced per surviving individual in adult stage ( $m_x$ )	Larvae produced per original recruit in adult stage ( $l_x m_x$ )
16	0.020	0	0.000
18	0.038	2538	96.090
340	0.079	1922	151.541
1360	0.149	1480	221.018

larger brood masses, and these heavier broods were composed of a greater number of larvae than lighter broods. Other investigators have reported similar trends. Wethey (1984) observed that in natural populations of *B. glandula*, barnacles living at low densities had larger brood masses than those at higher densities. In experiments with *Semibalanus balanoides*, Hills and Thompson (2003) found that increased densities led to decreased larval production per individual. In an observational study with *Jehlius cirratus*, a chthamaloid barnacle in Chile, Lopez and Gonzalez (2003) also concluded that solitary animals produced more larvae per individual.

In terms of population-level reproduction, the individual studies indicated little relationship between brooding frequency and conspecific density. But when data from all three studies were combined, I observed a unimodal relationship between conspecific density and brooding (Fig. 3C). Barnacles living at very low densities (as in the lowest level of the plate experiment) and at very high densities (as in the FC natural plots) had low brooding frequencies. Brooding frequencies varied with increased densities, but overall, seemed to be maximized at intermediate densities. This result makes sense given the presence of both negative and positive intraspecific interactions: at very low densities, barnacles are unable to fertilize one another, whereas at very high densities, the effects of competition likely outweigh the positive effects of the dense aggregations. Information on both individual and population-level measures of reproduction is needed to understand population dynamics and the mechanisms underlying population regulation and persistence.

Surprisingly, I did not observe an overall shift in biomass allocation with density, even though larger animals produced larger brood masses. This was likely

a function of small sample sizes. With larger sample sizes, I expect that mean brood mass and ovarian tissue mass per individual would be greater in animals living at lower densities than in animals living at higher densities, provided that the animals were within fertilization distance of one another.

My results correspond with those reported for a number of other taxa with varying life histories. Large colonies of encrusting bryozoans, another marine organism with a sessile adult form, have higher survival, growth, feeding, and reproductive rates than smaller colonies (Pratt 2004). Juvenile damselfish living in the presence of larger conspecifics had higher growth rates than those living where larger conspecifics were absent, probably due in part to the reduced predation risk in a larger sized group (Booth 2004). Reproductive success in the desert wildflower *Lesquerella fendleri* increased strongly with the local density of conspecifics, perhaps due to increased visitation from pollinators (Roll et al. 1997). Negative density-dependent interactions among conspecifics clearly play major roles in many, if not all, marine, terrestrial, and freshwater systems, as well (Morin 1986, Shaw 1986, Peterson and Black 1993, Forero et al. 2002).

Understanding the contexts in which variation in conspecific density leads to shifts in key life history traits and overall fitness has great ecological significance. It also is important for the development of effective conservation strategies (Stephens and Sutherland 1999). Recovery of species that have been reduced to low densities, elimination of invasive species, and even ecosystem and landscape-scale conservation often involve manipulation of population numbers. To design and execute such manipulations successfully, we need to understand how they are likely to affect the short-

TABLE 4. Summary of mean responses to increased density.

Study	Survival	Growth	Biomass allocation	No. larvae per barnacle	Brood mass size (mg)	Brooding frequency
Plate experiment	increased	decreased	no change	decreased	decreased	increased, but similar at higher densities
Natural rock surface experiment	...†	decreased	no change	no change	no change	similar overall, but decreased at very high densities
Field surveys	...	...	...	no change	...	no change

† Ellipses (...) indicate that no data are available.



and long-term dynamics of populations, communities, and ecosystems.

#### *Integrating information on multiple traits*

My results also highlight the importance of considering multiple life history traits when assessing the influence of positive and negative intraspecific interactions on individual fitness, and provide a model for how to do that empirically by combining field experiments and observations of natural populations. By integrating information on multiple traits, I was able to evaluate the relative importance of the positive and negative intraspecific interactions underlying each of these responses. Calculation of the mean number of larvae produced per original recruit suggests that overall increased density led to increased fitness. Consideration of only one response—survival, growth, individual or population-level reproductive output—would have generated a very different picture of the net effect of increased conspecific densities on fitness.

While a number of investigations have evaluated the positive and negative density-dependent effects on particular life history traits, these studies rarely have assessed the net effect of density on fitness, either qualitatively or quantitatively (for an exception, see Peterson and Black 1993). Additional studies that integrate information on multiple traits across several life stages will advance understanding of population dynamics and contribute to more ecologically informed conservation and management strategies.

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#### APPENDIX A

Settlement plate specifications are available in ESA's Electronic Data Archive: *Ecological Archives* E086-145-A1.

#### APPENDIX B

A photograph illustrating the influence of conspecific density on barnacle shell morphology is available in ESA's Electronic Data Archive: *Ecological Archives* E086-145-A2.

#### APPENDIX C

A photograph of the natural surface density experiment is available in ESA's Electronic Data Archive: *Ecological Archives* E086-145-A3.

#### APPENDIX D

Statistical tables detailing responses in the plate and natural surface experiments are available in ESA's Electronic Data Archive: *Ecological Archives* E086-145-A4.

#### APPENDIX E

A figure showing the association between density and barnacle morphology in natural barnacle populations is available in ESA's Electronic Data Archive: *Ecological Archives* E086-145-A5.