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INTRASPECIFIC COMPETITION AND FACILITATION IN A NORTHERN ACORN BARNACLE POPULATION¹

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Abstract. The role of density-dependent mortality in shaping adult populations of the acorn barnacle, Semibalanus balanoides, was studied on a sheltered New England shore and revealed that high recruitment densities can have both positive and negative effects on barnacle survival. Recruitment greatly exceeded the capacity of the space to support adults in the three years of this study. At low tidal heights, recruits grew rapidly, experienced severe crowding, and rarely survived to reproduce. At higher tidal heights, individuals grew more slowly and were less affected by crowding, and many ($\approx 10\%$) survived to reproduce.

Recruit density was manipulated to examine crowding effects on survival. At low tidal heights, no recruits survived to reproduce at any density, due to intraspecific crowding, algal overgrowth, and predation. At intermediate tidal heights, lower recruitment decreased intraspecific crowding and increased survivorship, while at high tidal heights, lower recruitment decreased survivorship.

In the high intertidal habitat, *S. balanoides* survivorship was higher on boulders than on rock cobbles due to thermal buffering, and intraspecific crowding decreased rock and barnacle temperatures and facilitated survival. Shading high intertidal cobbles from solar radiation decreased maximum rock and barnacle temperatures, dramatically increased survivorship and eliminated the survivorship advantage of high densities.

High recruitment of *S. balanoides* can lead to massive density-dependent mortality in physically benign habitats, but in physically stressful habitats high recruitment density may buffer individuals from physical stress and facilitate survival. Variation in the nature of density-dependent interactions along environmental gradients may be important in generating pattern in many natural populations.

Key words: facilitation; intertidal ecology; intraspecific competition; New England; Semibalanus balanoides; thermal stress.

INTRODUCTION

The roles that intra- and interspecific competition play in shaping natural populations and communities has long been of interest to ecologists (Hairston et al. 1960, Strong et al. 1984). High population densities often result in competitive processes dictating natural distribution and abundance patterns (e.g., Buss 1986), but consumer pressure (Paine 1966, Harper 1969) and physical disturbance (Dayton 1971, Platt 1975) often reduce densities and minimize the importance of competition in nature. Limited recruitment (Underwood and Denley 1984, Roughgarden et al. 1987) and harsh physical conditions (Connell 1961a, Fowler 1986) also potentially limit population size, and reduce the impact of competitive phenomena on populations. High population densities, however, can also facilitate survival by buffering individuals from interspecific competitive pressures (Buss 1981), consumers (Atsatt and O'Dowd 1976), physical disturbance (Bertness and Grosholz 1985), and physiological stress (Hay 1981). Largely due to these contrasting effects of recruitment variation in natural populations and the variety of other factors that can independently or interactively influence pop-

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ulations, general statements relating recruitment density to population processes have been hard to make even in extensively studied systems (Connell 1985).

The study of plant and animal assemblages in hard substratum marine habitats has been valuable in understanding the interplay of biotic and physical factors in generating pattern in natural communities (e.g., Connell 1961b, Paine 1966, Dayton 1971). Sessile organisms in these systems are often space-limited, found along gradients of environmental harshness, and easily trackable and amenable to experimental manipulation. Acorn barnacles are conspicuous members of many temperate zone intertidal communities, dominating a distinct zone at intermediate to high tidal heights (Stephenson and Stephenson 1949). Within this habitat, barnacles compete intra- and interspecifically by crushing and/or overgrowing neighbors (Connell 1961a, Wethey 1983a), are limited from higher intertidal habitats by heat and desiccation (Connell 1961a, Wethey 1983b), and from lower intertidal habitats by predators and competitors (Connell 1972, Menge 1976).

In this paper, I examine the intraspecific densitydependent dynamics of the barnacle *Semibalanus balanoides* in a wave-sheltered southern New England bay. I document variation in recruitment and survivorship, investigate the role of density-dependent mortality in generating survivorship patterns across the intertidal habitat, and examine physical constraints on barnacle success. The results suggest that while high recruitment leads to intense intraspecific competition and massive mortality at lower tidal heights, at high tidal heights, high recruitment can buffer barnacles from thermal stresses and facilitate survivorship.

STUDY SITE

Fieldwork was carried out at the Haffenreffer Preserve of Brown University in Bristol, Rhode Island. Loose cobble substratum (100-625 cm², maximum length \times width) covers > 80% of the intertidal habitat, and large embedded boulders with a minimum diameter of 50 cm cover the remaining available space in the habitat. Wave action is minimal and cobble movement is generally confined to winter months and is not severe (see Methods: Experimental Manipulations of S. balanoides Densities). The area would be considered a protected bay habitat (Ricketts and Calvin 1968). Exposed rock surfaces are covered almost exclusively with Semibalanus balanoides and two algal crusts, Ralphsia verrucosa and Hildenbrandia rubra (Bertness et al. 1983, Bertness 1984). The most conspicuous mobile organisms in the community are the herbivorous snail Littorina littorea and the oyster drill Urosalpinx cinerea.

METHODS

The S. balanoides population at the study site was examined in 10×10 cm quadrats on boulder (>1 m diameter) surfaces. A third of these quadrats were placed at low (-0.1 to 0.0 m, relative to mean low water) tidal heights, a third at intermediate (0.0 to +0.5 m) tidal heights, and a third at high (+0.5 to 1.0 m) tidal heights. Quadrats were individually numbered with aluminum tags attached to 6-mm (quarter-inch) stainless steel corner screws. Quadrats were established in February 1985 and followed until September 1987. All quadrats were photographed monthly from March-September through 1986. In 1987 photographs were taken in April, after settlement, and in September. The only major barnacle predator at the site, Urosalpinx cinerea, was removed from boulders containing quadrats in 1985 and 1986. This was done to examine S. balanoides dynamics without predators present, but particularly since this predator was not present at the study site in 1984 during preliminary studies. In 1987, the quadrats were followed at natural predator densities. Quadrat photographs were projected to their actual size, S. balanoides were counted and percent cover estimates of barnacles were made with a clear plastic overlay with 50 random points. Photographs were taken frequently enough so that most barnacle deaths were verified by the presence of empty tests. Barnacle recruitment was operationally defined as the number of recruits present in the monitored plots 2 wk after settlement had ceased.

Since few S. balanoides in this population appeared

to survive longer than ≈ 16 mo, and individuals that survived their 1st yr experienced severe crowding from recruits during their 2nd yr, I examined the hypothesis that heavy recruitment limited the success of adult barnacles. In March 1985 I established 11 10 × 10 cm quadrats containing 1-yr-old individuals at intermediate and high tidal heights. These quadrats were cleared of *S. balanoides* recruits from 1985–1987, analyzed as described above, and compared with adjacent controls containing 1-yr-old individuals. Recruits were removed within 1 mo of settlement with a dissecting needle.

Surveys were taken in 1985 to quantify the influence of intraspecific crowding on S. balanoides morphology. On the first spring tide of each month from June to August, random cobbles with S. balanoides recruits were collected at high and low tidal heights. An additional set of cobbles with solitary individuals (not in physical contact with neighbors) was also collected each month. Outside basal and apical diameters, test heights, and thicknesses (measured at the base) were measured on 20-30 randomly chosen crowded and solitary individuals from each tidal height. Barnacle densities were determined by counting individuals in a 2×2 cm quadrat placed centrally over measured individuals. To minimize variation in these data, stunted individuals between hummocks (Barnes and Powell 1950) were systematically avoided in this survey, which was otherwise done randomly. A separate survey in June 1985 examined barnacle morphological variation as a function of tidal height and density. At high and low tidal heights, the morphology of individuals in as wide a range of densities as could be found were determined as described above.

Experimental manipulations of S. balanoides densities

To examine the influence of recruitment density on S. balanoides survivorship, recruit densities were manipulated on boulders and cobbles. In February 1987, 120 10 \times 10 cm quadrats were marked on boulders along a 300-m stretch of shoreline. Adult barnacles were removed from these quadrats. The quadrats were grouped in sets of three adjacent (<15 cm apart) quadrats with >10 sets placed at low, intermediate, and high tidal heights. Two weeks after recruitment ceased, recruits in two quadrats in each set were thinned. In one thinning quadrat in each set, a grid of 1.5×1.5 cm squares was placed over the area and all but ≈ 3 recruits in each square were removed to produce low recruit densities. To establish medium recruit densities, a grid of 0.7×0.7 cm squares was placed over quadrats and similarly thinned. This generated 10-15 sets of low, medium, and high recruitment density treatments at each tidal height, which were photographed 2 wk after thinning, and subsequently every month through September 1987. Initial recruitment densities in high-density treatments were similar among

the three tidal heights. Photographs were analyzed as described above. These quadrats were maintained free of *Urosalpinx cinerea*.

A separate experiment examined the influence of recruitment density on barnacle survivorship on cobbles in 1986 and 1987. At high and low tidal heights, 25-30 cobbles (250-625 cm², maximum length \times width, >7 cm thick) with a wide range of recruit densities, were individually marked in April and placed in predator exclusion pens, under shades to reduce solar heating, and in control areas. Two predator exclusion pens at each tidal height were constructed of 1 \times 1 cm galvanized hardware cloth walls 25 cm high, embedded into the substratum (Bertness 1984). Each pen was 1.5×1.5 m, topless, and maintained free of Urosalpinx cinerea. Shade treatments were 1×1 m canopies of a double layer of 6×6 -mm black plastic screening (Vexar) supported 25 cm above the ground by metal rods. Shades reduced solar radiation by $\approx 60\%$. Two shades were installed at each tidal height. Control areas were located adjacent to all treatments. In 1987, an additional treatment was run at the high tidal height. Twenty-five cobbles of the same size used in the other treatments were embedded in sand substratum underlying the cobble covering the beach to insulate them from thermal extremes. All cobbles were photographed monthly from April-September, and barnacles were counted in a centrally located 10×10 cm area on each cobble.

During the spring and summer months (April–September) <4% (n = 244) of the experimental cobbles were overturned (found upside down) by waves. This low frequency of rock rolling reflects the lack of wave action at the site. Of the cobbles marked in 1986, 32% (n = 118) were overturned between September 1986 and April 1987, indicating that winter disturbance exceeds summer disturbance. Less than 5% of the annual mortality of recruits on 1986 cobble, however, occurred during the winter, and this mortality did not influence the density-dependent *S. balanoides* survivorship patterns documented below in any substantial way.

Thermal relations

Since harsh physical conditions in the high intertidal habitat appeared to limit *S. balanoides* success, the thermal relations of *S. balanoides* were examined. Rock and barnacle temperatures were taken with a thermistor mounted in a hypodermic needle, and were highly repeatable $(\pm 1^{\circ}C)$. Barnacle body temperatures were taken by inserting the thermistor directly into barnacle tissue through the opercular plates. Rock surface temperatures were taken on bare rock surfaces.

Barnacle tissue temperatures were examined during summer daytime tidal exposures in 1985 and 1986. At low and high tidal heights, tissue temperatures were taken for solitary and crowded barnacles on cobble and boulder surfaces. Eight measurements were made in each situation every 60 min beginning 30 min after individuals were exposed by the receding tide and ending just before they were submerged by the ascending tide. Additional rock and barnacle temperatures were taken during daytime low tides on hot summer days in 1986 and 1987 to determine effects of rock size, shading, and barnacle crowding.

RESULTS

Recruitment and survival of S. balanoides in Mt. Hope Bay

At the study site S. balanoides recruitment began in late February and continued for a 2-4 wk period in each year of this study (Fig. 1). Annually, recruitment on boulder surfaces varied over twofold (P < .001, ANOVA), and was considerably higher in 1985 (31.2 \pm 1.9 barnacles/cm²) and 1986 (40.7 \pm 2.5 barnacles/ cm²) than in 1987 (17.8 \pm 2.5 barnacles/cm²). Recruitment to unoccupied space varied with tidal height (P < .01, ANOVA, each year). In each year, recruitment to unoccupied space increased with increasing tidal height, with high intertidal bare surfaces receiving 30-60% more recruits than low intertidal locations. Total recruitment, however, was highest in low intertidal locations in each year, since annual recruit survivorship decreased with decreasing tidal height, making unoccupied space during the settlement season more common in low intertidal habitats. Recruitment, however, was sufficiently high each year and at all tidal heights so that shortly (4-6 wk) after settlement and initial growth, barnacle cover was essentially 100% on all intertidal hard substratum surfaces.

Similar patterns of *S. balanoides* survivorship were seen in 1985 and 1986 (Fig. 1). In both years, recruit survival increased with increasing tidal height. Few recruits survived their 1st yr at low tidal heights (1985, 0.04%; 1986, 0.09%), whereas survivorship at intermediate (1985, 0.3%; 1986, 2.0%) and high (1985, 9.5%; 1986, 11.4%) tidal heights was markedly higher. Over 90% of the 1st-yr mortality at all tidal heights occurred during the spring and summer (May–September). Survivorship patterns generated by summer mortality were not altered by winter mortality (Fig. 1).

Effects of crowding on *S. balanoides* recruits varied conspicuously with tidal height. At low tidal heights, intraspecific crowding generated severe morphological modification of crowded individuals that was apparent by May. At higher tidal heights, this density-dependent morphological variation was not conspicuous until late June or July. In contrast to solitary individuals that are 2–4 times as wide at the base as they are tall, individuals in dense aggregations are often 4–8 times as tall as they are wide (Fig. 2, also see Barnes and Powell 1950, Wethey 1984). At low tidal heights, severely elongated individuals are crushed by the lateral growth of their neighbors (e.g., Connell 1961*a*). Massive mortality of severely elongated low intertidal individuals



FIG. 1. Semibalanus balanoides density and percent cover on boulder surfaces at the study site from March 1985 to March 1987. Data are from 10–15 100-cm² permanent quadrats at low, intermediate, and high tidal heights. Standard-error bars are visible only when they exceed the size of the symbols.

began in June and resulted in barnacle cover dropping from nearly 100% in early June to 60-70% by the beginning of July (Fig. 1). Death of severely elongated low intertidal individuals continued through the summer, and by September <20% of the space on low intertidal boulders was covered by *S. balanoides*. At high intertidal heights, crowding does not as frequently lead to the death of severely elongated individuals (see below), and by September barnacle cover was relatively high (30–60%, Fig. 1).

The influence of density stress on *S. balanoides* morphology is illustrated in Figs. 2 and 3 and Table 1. By June, at low tidal heights *S. balanoides* at densities of 5-8 barnacles/cm² were nearly as tall as they were wide (basal diameter), and were 2–4 times taller than they

were wide at higher densities (Fig. 3). At high tidal heights, individuals as tall as they were wide were only found at densities in excess of 10 barnacles/cm², and the most severely elongated individuals were only twice as tall as they were wide (Fig. 3). The temporal pattern of morphological modification of *S. balanoides* (Table 1) showed that: (1) at high and low tidal heights, density-induced morphological modification increased over time (P < .05, ANOVA), (2) density-induced morphological modification was much more severe at low than at high tidal heights (P < .01, ANOVA), and (3) elongated high-density individuals at low tidal heights are constructed of thin tests in comparison to solitary individuals (P < .01, ANOVA).

Differences in the morphological responses of S. bal-

anoides to crowding at high and low tidal heights likely reflected differences in growth rates across the intertidal habitat (Fig. 4). Barnacles in low intertidal habitats are submerged longer than at higher tidal heights and therefore have more available feeding time each tidal cycle.

Few recruits that survived their 1st yr survived an additional year (Fig. 5). At low tidal heights, no adults survived for longer than 14 mo, while at higher tidal heights, survival of 1-yr-olds through their 2nd yr was low ($6.4 \pm 2.9\%$) and did not differ between intermediate and high tidal heights (P > .20, ANOVA). No naturally occurring individuals in this population have ever been observed to survive to reproduce in a 3rd yr. Removal of *S. balanoides* recruits from intermediate and high intertidal height quadrats containing 1-yr-olds demonstrated that this high adult mortality is largely the result of competition with recruits (Fig. 5). When recruits were removed, over 20 times as many 1-yr-olds survived their 2nd yr in comparison to adjacent control quadrats.

Predators do not appear to play a dominant role in the population dynamics of *S. balanoides* in this population. The oyster drill, *Urosalpinx cinerea*, is the only common barnacle predator at the site. In 1987, I followed quadrats with natural *U. cinerea* densities and with *U. cinerea* removed. Recruitment was similar in control and predator removal quadrats at each tidal height (P > .50, ANOVA), and *S. balanoides* survivorship did not differ (P > .20, ANOVA) between control and predator removal quadrats at any tidal height. As observed in both predator removal and control areas in 1985 and 1986, few recruits survived until September at low tidal heights in 1987, while survi-



FIG. 2. Line drawings of density-induced morphological variation in *Semibalanus balanoides* at the study site. (A) typical solitary morphology, (B) elongated morphology of individuals in dense aggregations, (C) morphology of aggregations at high tidal heights where individuals are as tall as they are wide, and (D) morphology of aggregations at low tidal heights where individuals are 2–6 times as tall as they are wide.



FIG. 3. The influence of density on *Semibalanus bala-noides* morphology (test height/basal diameter) at low and high tidal heights. Data are from a survey taken in June 1985.

vorship increased markedly with increasing tidal height. The lack of strong predator effects in this population is surprising, since U. cinerea is a voracious barnacle predator (Carriker 1955, Katz 1985). However, it is confined to low and intermediate tidal heights and is only a seasonal intertidal resident at the study site. Urosalpinx cinerea is conspicuous in the intertidal region from the middle of June through September, reaching maximum densities in July (low tidal height $47.2 \pm 4 \text{ drills/m}^2$, intermediate tidal height 5.6 ± 3.1 drills/m²). It is virtually absent in the high intertidal habitat, and appears to migrate into the subtidal habitat in the winter. While U. cinerea consumes a substantial portion of recruits at intermediate and low tidal heights in the late summer, it does not appear to influence the intertidal distribution of S. balanoides substantially. The reason for this paradox seems to be that at high barnacle recruitment densities, when this predator arrives in the intertidal habitat, most barnacles at lower tidal heights are severely crowded and committed to a morphology that will ultimately result in massive mortality whether they are eaten or not.

Experimental manipulations of S. balanoides density

To analyze results from the density manipulations of recruits, summer (April–September) survivorship was examined as a function of initial density, with initial densities grouped by thinning treatments. In lowdensity treatments (<3 recruits/cm²), essentially all individuals developed solitary morphologies, and barnacle cover rarely exceeded 50% of the available space. In medium- (5–10 recruits/cm²) and high- (=control, >11 recruits/cm²) density treatments, virtually all individuals developed crowded morphologies and covered 100% of the available space by June.

At low tidal heights on boulders, no recruits survived until September at any density (Fig. 6). At this tidal height, density effects were apparent in June and July

Measure†	June	July	August
	High intertidal z	one	
Solitary barnacles			
Morphology index	$\begin{array}{c} 0.36 \pm 0.01 \\ (0.23 0.55) \end{array}$	$\begin{array}{c} 0.34 \pm 0.01 \\ (0.28 0.42) \end{array}$	$\begin{array}{c} 0.33 \pm 0.01 \\ (0.25 0.51) \end{array}$
Shell thickness (mm)		$\begin{array}{c} 0.30\pm0.01\\ (0.200.44)\end{array}$	$\begin{array}{c} 0.35 \pm 0.04 \\ (0.25 - 0.46) \end{array}$
Crowded barnacles			
Morphology index	$\begin{array}{c} 0.42 \pm 0.07 \\ (0.09 {-} 2.17) \end{array}$	$\begin{array}{c} 0.80 \ \pm \ 0.05 \\ (0.44 1.49) \end{array}$	$\begin{array}{c} 0.82 \pm 0.07 \\ (0.5\text{-}2.2) \end{array}$
Shell thickness (mm)		$\begin{array}{c} 0.38 \pm 0.02 \\ (0.20 0.56) \end{array}$	$\begin{array}{c} 0.41 \pm 0.02 \\ (0.24 0.66) \end{array}$
	Low intertidal z	one	
Solitary barnacles			
Morphology index	$\begin{array}{c} 0.31 \pm 0.001 \\ (0.22 0.59)^{-1} \end{array}$	$\begin{array}{c} 0.30 \pm 0.01 \\ (0.140.37) \end{array}$	$\begin{array}{c} 0.33 \pm 0.01 \\ (0.26 0.44) \end{array}$
Shell thickness (mm)		$\begin{array}{c} 0.55 \pm 0.02 \\ (0.40 0.82) \end{array}$	$\begin{array}{c} 0.66 \pm 0.04 \\ (0.401.00) \end{array}$
Crowded barnacles			
Morphology index	$\begin{array}{c} 1.64 \pm 0.18 \\ (0.37 4.94) \end{array}$	$\begin{array}{c} 2.25 \pm 0.15 \\ (0.75.02) \end{array}$	$\begin{array}{r} 2.42 \pm 0.17 \\ (1.044.56) \end{array}$
Shell thickness (mm)		$\begin{array}{c} 0.35 \pm 0.01 \\ (0.26 0.43) \end{array}$	$\begin{array}{c} 0.36 \pm 0.02 \\ (0.140.50) \end{array}$

TABLE 1. Results of 1985 Semibalanus balanoides morphology survey.* Data are means ± 1 se, with ranges in parentheses. All sample sizes are 20-30.

* For each tidal height and sampling date, data for crowded individuals were obtained from a random survey of barnacle morphologies, while solitary individuals were nonrandomly located and defined as individuals not in direct physical contact. † Morphology index = shell height/basal diameter. Shell thickness was measured randomly at the base.

when the survivorship of low-density individuals was over twice that of high-density individuals, but by September recruits at all densities had died. Most of the late summer mortality at this level appeared to be the result of overgrowth and smothering by the algal crust *Ralphsia verucosa* (Bertness et al. 1983). By August essentially all low intertidal hard surfaces are covered by *R. verucosa* at the study site, including *S. balanoides* tests and opercular plates. Vigorous seasonal growth of *R. verucosa*, however, is primarily restricted to low intertidal levels, and did not appear to influence recruit survival at higher tidal heights.

At medium and high tidal heights, recruit density influenced survivorship differentially (P < .05, AN-OVA, density × tidal height interaction). At intermediate tidal heights, high recruitment led to severe crowding, and <12% of the recruits at natural densities survived until September (Fig. 6). At this tidal height, reducing densities increased *S. balanoides* survivorship 3–4 fold (Fig. 6). In contrast, at high tidal heights, the survivorship of *S. balanoides* at low densities was less than that of crowded individuals (Fig. 6).

On cobbles no *S. balanoides* survived at the low tidal height in either 1986 or 1987 (Fig. 6), showing that barnacle mortality was independent of recruitment density, benthic predators, and solar radiation. As was seen on boulder surfaces, recruits that survived until July (primarily solitary individuals) were overgrown and killed by *Ralphsia verrucosa*.

At high tidal heights, survival of recruits on cobbles was less than half that on boulders (Fig. 6). Predator exclusion did not influence recruit survivorship (P > .50, ANOVA), but recruit density strongly influenced survivorship (P < .001, ANOVA). High recruitment increased survivorship compared to low recruitment. This effect, however, was much stronger on cobbles than on boulders. On cobbles, no solitary recruits survived the summer, while on boulders, survival of low-density recruits was nearly 20% (Fig. 6).

Buffering cobble from thermal extremes in the high intertidal zone by shading or embedding them in substratum (Fig. 6) increased the survival of recruits 2–3 fold compared to controls, and led to higher survival than on boulder surfaces (Fig. 6). Most importantly, in contrast to the total mortality of solitary barnacles on control cobbles, recruit mortality on shaded and embedded cobbles increased (P < .01, ANOVA) with increasing recruit density (Fig. 6). This strongly suggests that moderate to high recruitment buffers *S. balanoides* from physical stress in the high intertidal habitat.

Rock and barnacle temperature relations

In the summers of 1985–1986, I surveyed barnacle and rock temperatures eight times during midday low tide exposures. On days that were cool or had heavy cloud cover, rock and barnacle temperatures were similar on cobble and boulder surfaces, and solitary and crowded barnacle temperatures were virtually identical (M. D. Bertness, *personal observation*). During low tide exposures on hot, cloudless days, however, temperatures reached by *S. balanoides* accurately mirrored the

mortality patterns of recruits in the high intertidal habitat (Fig. 7). Semibalanus balanoides body temperatures reached higher levels at higher tidal heights, were higher for individuals on cobbles than for individuals on boulders, and were consistently higher for solitary than for crowded individuals. Body temperatures of barnacles on cobble and boulder surfaces directly reflected the thermal properties of rocks of different sizes (Fig. 8). Loose cobbles heat rapidly when exposed to solar radiation during low tides, while larger rocks are buffered from thermal change by their mass. Cobbles embedded in substratum were consistently cooler than loose cobbles unable to conduct heat efficiently with the substratum (Fig. 9). Loose cobbles under shades were cooler (P < .05, ANOVA) than cobble exposed to direct solar radiation and exposed boulder surfaces (Fig. 9), suggesting that solar radiation dictates substratum temperatures.

Thomas (1987) recently constructed a thermal budget (sensu Gates 1980) for S. balanoides, which showed that substratum surface temperature is the single most important determinant of barnacle body temperature under essentially all natural field conditions. She found that rock surface temperature accurately predicted >90% of the natural variation in S. balanoides body temperatures, and that barnacle crowding per se did not significantly influence the thermal balance of S. balanoides. The thermal advantage of crowded S. balanoides over solitary individuals appears to be the result of the effect that dense barnacle aggregations have on rock surface temperatures (Fig. 9). While the temperatures of solitary and crowded S. balanoides on cobble and boulder surfaces did not differ (P > .10, AN-OVA) from adjacent rock surfaces, rock surface temperatures adjacent to solitary individuals were higher (P < .05, ANOVA) than those adjacent to crowded individuals on cobble and boulder surfaces. These data suggest that by shading or in some other



FIG. 4. Mean basal diameter (\pm sE) of solitary *Semibal-anus balanoides* at low, intermediate, and high tidal heights in 1986. Each point represents 20–30 randomly chosen individuals.



FIG. 5. Survivorship of 1-yr-old Semibalanus balanoides at the study site in 1985 and 1986 (mean \pm sE) at intermediate and high tidal heights (pooled). Data are presented for unmanipulated quadrats in 1985 (n = 28) and 1986 (n = 28), and for quadrats where recruits were removed beginning in the spring of 1985 (n = 11).

manner influencing rock surfaces, aggregations of barnacles reduce rock surface temperatures and therefore buffer their own major thermal input. This effect is greater on thermally labile cobble surfaces than on boulder surfaces (P < .05, ANOVA rock size × barnacle density interaction), suggesting that barnacle aggregations buffer individuals from thermal stress more effectively on cobbles than on boulders.

DISCUSSION

Intraspecific competition and facilitation in S. balanoides

At the high recruitment densities documented in this study, S. balanoides recruits at densities that exceed adult holding capacity by over an order of magnitude. Recruitment of this magnitude is common for S. balanoides (D. S. Wethey, personal communication), and results in intense intraspecific spatial competition (Barnes and Powell 1950, Connell 1961a, Wethey 1983b). The morphology of S. balanoides is severely affected by density stress, and can result in tall, thinwalled individuals, vulnerable to being crushed by growing neighbors (e.g., Connell 1961a), but dependent on neighbors for structural support. These dense aggregations are extremely fragile, and can lead to the death of all participating individuals. In the population that I have studied, the death of individuals in dense aggregations is triggered when the most crowded participants are killed by the lateral expansion of their neighbors (Connell 1961a). Death of these individuals exposes primary free space, but when members of aggregations are extremely elongated, neighboring individuals appear to be incapable of taking advantage of new free space. Lateral expansion of the test at the base seems to be precluded in elongated individuals, since their body tissues are not in contact with the substratum (Wethey 1984). Without the structural support of neighbors, elongated individuals are extremely vulnerable to further lateral expansion of neighbors, since they have a relatively small base of attachment (Fig.



FIG. 6. Survivorship of Semibalanus balanoides in the recruitment-density manipulation experiment as of September. Density treatments were: low = <3 recruits/cm², medium = 4–10 recruits/cm², and high = >11 recruits/cm². Sample sizes are given for each treatment above standard-error bars. Data from boulder surfaces are from 1987. Cobble data from 1986 and 1987 are pooled. Controls represent the pooled data from unmanipulated and predator-removal areas, which did not differ significantly (P > .30, ANOVA). Some cobbles at the high tidal height were shaded and some were embedded in the sand substratum.

2). These individuals are ultimately pushed off the substratum by neighbors, and this process continues until essentially all of the individuals in these aggregations have died. This appears to occur independently of waves or other physical disturbances in the wave-sheltered population I have examined, since crushed tests and live elongated individuals that have been dislodged from the surface by neighbors often remain in place for weeks before being washed away. At low tidal heights, growth rates are high, and this process occurs rapidly (within 10-15 wk) and appears to be responsible for the death of most recruits. At high tidal heights growth rates are reduced, resulting in less drastic density-induced morphological modification and subsequent mortality at similar densities. In slower growing high intertidal aggregations, the death of crowded individuals generally does not lead to the death of neighbors, since they are not severely elongated, are able to take advantage of newly generated free space, and are not as dependent on their neighbors for structural support. The result of this crowding process is that in habitats with high recruitment and individual growth rates (i.e., good habitats), few individuals survive to reproduce, while survivorship is increased at identical densities in habitats where individual growth rates are reduced (i.e., poorer habitats) and a substantial number of recruits survive to reproduce.

In the S. balanoides population I studied, densitydependent intraspecific crowding appears to be responsible for most barnacle death at low and intermediate tidal heights independent of other biotic and physical pressures. At low tidal heights, most individuals at natural recruitment densities succumbed to density stress before July (>50%). Barnacles that survive

until late summer at low tidal heights are killed by predators, overgrowth by algal crusts, or further crowding. Consequently, few individuals survive at low tidal heights regardless of recruitment density. At intermediate tidal heights, growth rates are reduced, fewer individuals succumb to intraspecific spatial competition, and predators and algal crusts are relatively rare. At this tidal level, high recruitment reduces *S. balanoides* survivorship (Fig. 6).

At high tidal heights, physical stress becomes the dominant factor limiting the success of S. balanoides (Connell 1961b, Wethey 1983b). Recruits at high tidal heights have reduced growth rates (Fig. 4), intraspecific crowding does not lead to the drastic morphological modifications (Fig. 3), and death caused by crowding is greatly reduced (Fig. 6). At high tidal heights, factors that influence the temperatures reached by S. balanoides during tidal exposures on hot summer days appear to dictate mortality patterns. The dominant factor influencing barnacle heating in the habitat I have examined is the mass of the substratum to which individuals are attached. Large boulders are buffered from thermal extremes by their mass (Fig. 8), and during low tide exposures on hot summer days, barnacles on boulders remain cooler than individuals on thermally



FIG. 7. Semihalanus balanoides tissue temperatures during a daytime low tide exposure in July 1986. Data are given for solitary and crowded individuals on boulder and cobble surfaces. Each point represents the mean of 8–10 measurements. Standard errors are smaller than the symbols.



FIG. 8. Rock surface temperatures in the high tidal zone at the study site as a function of rock size. Data were taken on a hot summer day in July 1986 after the rocks had been uncovered by the tide for ≈ 3 h. None of the rocks sampled had >10% barnacle cover.

labile cobbles (Fig. 7). Cobbles embedded in substratum are buffered from thermal extremes by rock-substratum conductance and remain cooler than loose cobble (Fig. 9). Barnacle mortality patterns accurately mirror these thermal differences. Recruit mortality on loose cobble surfaces is much greater than on boulders or embedded cobbles (Fig. 6). In addition, shading cobbles from solar heating reduces rock and barnacle temperatures (Fig. 9) and drastically increases barnacle survivorship (Figs. 6 and 9). Thermal stress or factors closely linked to thermal stress, e.g., desiccation, appear to dictate S. balanoides success in the high intertidal habitat. In contrast to the strong interspecific crowding mortality at lower tidal heights, at high tidal heights, medium and high densities buffer individuals from thermal extremes and facilitate survival, compared to low den-sities. Dense aggregations of barnacles lead to cooler rock surface temperatures (Figs. 7 and 9). Since rock surface temperature is the primary determinant of barnacle tissue temperature (Thomas 1987), crowded barnacles have lower tissue temperatures than solitary barnacles on thermally stressful days (Fig. 7; M. D. Bertness, personal observation). This thermal buffering of aggregated individuals appears to be an important determinant of survival in the high intertidal habitat. Dense aggregations of barnacles lowered rock surface temperatures more effectively on thermally labile cobble than on more thermally stable boulder surfaces (Fig. 9), and crowding facilitated survival of S. balanoides on cobbles more effectively than on boulders (Fig. 6). In addition, when cobbles were shaded from solar heating or embedded in the substratum buffered from thermal extremes, the survivorship advantage of crowded individuals was lost (Fig. 6).





FIG. 9. Rock surface and barnacle tissue temperatures as a function of barnacle crowding, rock size, and the cobble treatments from the recruit density manipulation experiment. Sample sizes are given above bars; standard errors are too small to be legible. Data were taken during a low tide exposure in August 1987 after the rocks had been uncovered by the tide for 2–3 h. For the data on barnacle and rock temperatures on cobble and boulder surfaces as a function of barnacle density, all cobbles monitored were of similar size ($\approx 300 \text{ cm}^2$, length × width), boulders were >0.75 m in diameter, and rock surface temperatures of shaded, embedded, and loose cobbles were taken in the high tidal level manipulations (see Fig. 6).

Population consequences of density-dependent mortality effects

If density-dependent intraspecific competition and facilitation processes commonly influence barnacle populations, populations that routinely experience different levels of recruitment could exhibit markedly different within-population patterns of distribution. Recruitment variation in organisms with planktonic larvae is common (Underwood and Denley 1984), and in barnacles, can be strongly influenced by oceanographic and biotic processes (Kendall et al. 1982, Gaines et al. 1985, Gaines and Roughgarden 1987). In populations with low recruitment, barnacle success may be increased at lower tidal heights due to decreased intraspecific competition, but decreased at high tidal heights due to increased thermal stress mortality. In populations routinely experiencing heavy recruitment, intense spatial competition may reduce the success of individuals at low tidal heights, but increase survival at higher tidal heights. Effects of recruitment variation on intraspecific factors influencing distributions, however, likely are minimized at lower tidal heights, since interspecific competition and predation frequently dictate populations at lower tidal levels (e.g., Connell 1961b, Menge 1976).

Among populations, the relative importance of intraspecific competition and facilitation processes in influencing mortality patterns may vary markedly. In habitats where individual growth rates are high, density-dependent intraspecific competition likely plays a more important role in generating patterns of distribution and abundance than in populations with lower growth rates. In physically benign habitats, densitydependent intraspecific facilitations may be reduced or inconspicuous. In this vein, the density-dependent processes influencing barnacle populations in open coast and sheltered bay environments may differ markedly. In inland bays, climatic conditions are more extreme than in open coast environments, since they are not thermally buffered by oceanic weather conditions (Ricketts and Calvin 1968). In addition, sessile organisms in open coast environments tend to live on large rock faces, while in sheltered bays, cobble and smaller boulder habitats are more common. Large rock faces in open coast habitats may further buffer sessile organisms from thermal extremes.

Density-dependent facilitation processes in physically harsh environments may be more widespread than is generally believed, and often contribute to population patterns of distribution and abundance. In terrestrial plant (Fowler 1986) and sessile marine plant and animal (Connell 1972, Menge and Sutherland 1976) communities, intra- and interspecific competitive processes are less important in generating pattern in physically stressful habitats than in physically benign habitats. In addition, while population responses to environmental conditions have traditionally been assumed to be density independent (Hairston et al. 1960), recent studies suggest that this is often not the case (Hay 1981, Taylor and Littler 1982, Bertness and Grosholz 1985, Peterson 1985). Group benefits may frequently generate population and community pattern in physically stressful habitats. Hay (1981) has shown that in high coral reef flat habitats, dense algal assemblages facilitate survival by reducing desiccation stress, while in less physically rigorous habitats, algal competition becomes a prevalent force in these algal communities. In desert plant communities (Muller 1953, Niering et al. 1963) and in the primary plant succession of Mt. St. Helens (Wood and Del Moral 1987), both physically harsh habitats, plant-plant facilitations have been identified as important processes in generating community pattern.

If high population densities frequently facilitate survival in physically harsh environments, but limit the success of individuals in physically benign environments, our understanding of density-dependent population dynamics may be in need of revision. While much research has focused on elucidating the role of competitive interactions in shaping natural populations (Strong et al. 1984), most of this work has not paid close attention to reciprocal interactions between organisms and their physical environment, and has not been designed to examine group facilitation effects explicitly. Group facilitation in the barnacles examined in this paper was only apparent when densities were

artificially manipulated, warning us that positive density effects may be important in assemblages, but not necessarily conspicuous. Future efforts to understand density-dependent phenomena in nature should equally weigh competitive and facilitation hypotheses, and consider potential interactions between organisms and their physical environment.

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