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Population dynamics of the ribbed mussel, *Geukensia demissa*: The costs and benefits of an aggregated distribution

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Summary. Although mussel beds are common in many intertidal habitats, the ecological significance of the aggregated distribution of mussels has not been examined. The ribbed mussel, *Geukensia demissa*, is found in dense aggregations on the seaward margin of many salt marshes in New England. Here, we examine the population structure of *G. demissa* in a New England salt marsh and investigate experimentally the costs and benefits of aggregation.

Size, growth rate, and settlement rates of mussels decrease with increasing tidal height, whereas survivorship and longevity increase with increasing tidal height. Winter ice dislodges mussels from the substratum, resulting in mortality over all size classes, whereas crab predation results in the mortality of smaller mussels. The intensity of each of these mortality agents decreases with increasing tidal height. Effects of intraspecific competition on individual growth and mortality also decrease with increasing tidal height.

At high densities, individual growth rates were reduced, with depression of growth rates most pronounced on smaller individuals. Mortality from sources other than intraspecific crowding, however, was reduced at high mussel densities, including mortality due to winter ice and crab predators. As a result, our data suggest that the mussel population at our study site would be reduced by 90% in only five years and no juveniles would survive through their second year without an aggregated distribution.

Juveniles settle gregariously with or without adults present. The aggregated distribution of settlers and the post-settlement movement of smaller mussels to favorable microhabitats result in size and age class segregation within the population. This probably reduces intraspecific competition for food, while maintaining the survivorship advantages of an aggregated distribution.

Mussel beds are a conspicuous feature of many intertidal habitats, on both hard and soft substrata (Seed 1976). They have been studied extensively on rocky shores (Seed 1969a, b; Harger 1968, 1970, 1972; Paine 1971, 1974; Suchanek 1978; Paine and Levin 1981), where they often form dense bands at middle and low intertidal tidal heights. The lower

intertidal limit of the distribution of mussels on many rocky shores has been shown to be set by predators (Paine 1971, 1974; Menge 1976), whereas the upper intertidal limit of mussel beds appears to generally be set by physical stress (Suchanek 1978; Peterson 1979a). Physical disturbance is also a potent mediator of mussel bed dynamics (Paine and Levin 1981, Suchanek 1978). In the absence of predators and physical disturbance, mussels usually outcompete other sessile fauna and flora for primary substratum space (Paine 1971, 1974; Menge 1976).

Much less attention has been given to mussels that inhabit soft-bottom or intertidal grass habitats, even though, like the mussels found on hard substrata, they often dominate certain intertidal zones in the form of dense beds. In contrast to the information available for mussels found on hard substrata, most work on mussels that inhabit soft sediment has been directed at their role in nutrient dynamics (Kuenzler 1961a, b; Jordan and Valiela 1982), and aspects of their growth and shell form (Lent 1967a, b; Lutz and Castagna 1980; Brousseau 1984). Little work has been done on the dynamics and structure of mussel populations in soft sediment environments (Seed 1980; Stiven and Kuenzler 1979).

The ecological problems faced by sessile organisms in soft- and hard-substratum habitats are markedly different (Peterson 1979b). On hard substratum, living space in suitable habitats is often in short supply (Connell 1961; Jackson 1977) and successful primary space holders must be good either at competing for existing space, or locating new space in the system. In soft-bottom habitats, space is not generally limiting (Peterson 1979b), but disturbance is common (Woodin 1978) and stable substratum is often at a premium (Orth 1977; Woodin 1978). On hard substratum, mussels are commonly the competitive dominants in spatial competition (Paine 1971, 1974; Menge 1976), whereas in soft-bottom habitats, mussels stabilize substratum and minimize physical disturbance (Bertness 1984).

Juvenile mussels settle in association with conspecifics or move after settlement into association with conspecifics (Bayne 1976; Seed 1976). The resulting mussel matrix can close disturbance-generated free spaces on rocky shores (Paine and Levin 1981) and soft sediment habitats (Bertness 1984) without the recruitment of juveniles. Space occupation can occur in both habitats simply as the product of the individuals actively moving into free space or being pushed into open space by tightly packed conspecifics. In both hard- and soft-bottom habitats, therefore, matrix-

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forming mussels behave much as clonal organisms in their ability to occupy space without intervening sexual reproduction episodes (Jackson 1977). Clonal organisms are thought to be better spatial competitors on hard substratum than are solitary organisms due to their ability to invade space vegetatively (Jackson 1977). Similarly, in soft substratum, organisms that grow vegetatively (marsh cordgrass, mangroves, turtle grass, etc.) appear to dominate and stabilize substratum (Orth 1977).

Unlike truly clonal or primarily vegetatively reproducing organisms, however, mussels within an aggregation are probably not genetically similar, and have no mechanism to translocate nutrients between individuals. Mussels in an aggregation, therefore, probably incur costs in competing with conspecifics. The success of mussel aggregations, however, suggests that these potential costs are less than the advantages gained by individuals in group participation.

In this paper, we examine the structure and dynamics of a population of the ribbed mussel, *Geukensia demissa*. This mussel is a conspicuous member of salt marsh communities on the east coast of North America, and is generally found in aggregations. Here, we describe the size and age structure of a *Geukensia* population in a sheltered New England salt marsh, experimentally examine the importance of predation, intraspecific competition, physical disturbance, and recruitment in structuring the population, and evaluate the costs and benefits of their aggregated distribution.

Study site

The salt marsh examined in this study is a small embayment (~0.8 ha) of Smith Cove in Barrington, Rhode Island (Bertness 1984). The seaward border is characterized by a band of tall-form *Spartina alterniflora* ~5 m wide, ranging from 0.1 to 1.0 m mean tidal height. Below 0.1 m mean tidal height the substratum consists of fine mud devoid of emergent vegetation and sessile fauna (Bertness 1984). Above the tall-form *S. alterniflora*, a zone of short-form *S. alterniflora* ~3 m wide extends to the mean high water line (1.2 m mean tidal height). The marsh area above mean high water is dominated by *Spartina patens*. The ribbed mussel, *Geukensia demissa*, is found in a dense band on the seaward edge of the marsh. *Geukensia* is not found below the seaward edge of the marsh, and mussel density drops off dramatically with increasing tidal height. Throughout this paper the seaward edge of the marsh, typically covered with a dense matrix of *G. demissa* will be referred to as the marsh edge (0.1 to 0.6 m mean tidal height), the remaining tall-form *S. alterniflora* zone as the marsh flat and the the marsh area dominated by short-form *S. alterniflora* as the short *S. alterniflora* zone (Bertness 1984).

Physical disturbance is an important consideration in New England salt marsh habitats (Redfield 1972). During most winters (December–February), an ice sheet covers marsh embayments. In mild winters the ice cover is thin, short-lived and does little apparent physical damage. In colder winters, an ice sheet often 10–20 cm thick can cover sheltered marshes for >8 weeks, and often results in extensive damage to the marsh habitat. When the ice melts in the spring, ice incorporated in the marsh substratum is lifted by the tides and often results in large portions of marsh substratum (including grasses and mussels) being torn intact from the marsh and rafted on the ice sheet throughout

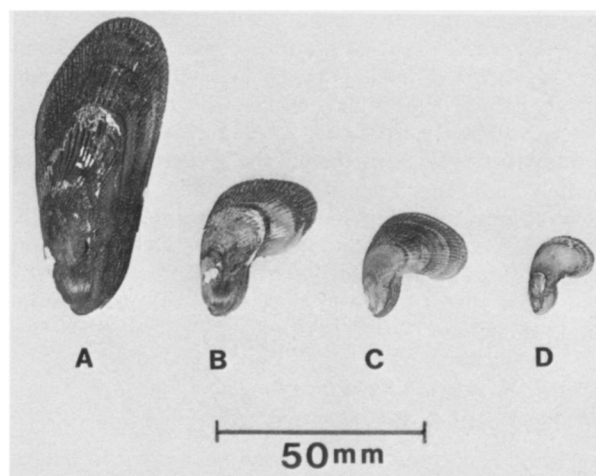


Fig. 1. Illustration of the normal shell shape found in *Geukensia demissa* (A) and three examples of the distorted shells (B, C, D) found in dense mussel aggregations that have angles of shell growth > 30°

the marsh. In addition, mussels, individually or in clumps, are often pulled from the substratum by ice and are generally stranded below the marsh edge in soft sediment (Hardwick-Witman, in press). Mussels deposited in soft sediment without attachment surfaces generally die after sinking in the sediment. The marsh edge is most strongly damaged by winter ice. At our study site, from June 1981 to September 1983, 5% of the marsh edge habitat was damaged, as evidenced by holes left in the marsh substrate, whereas <0.1% of the marsh flat showed signs of ice damage (Bertness, in preparation). Holes left by ice rafting generally range from 0.5 to 1.0 m in diameter and are rapidly recolonized by marsh grass and mussels. Small (<0.5 m diameter) holes on the marsh edge close within one year by the invasion of adult mussels, whereas small holes on the marsh flat are reinvaded within a year by the vegetative growth of *S. alterniflora* (Bertness 1984, unpublished data).

Methods

To examine the population structure and distribution of *Geukensia*, a series of quadrats were sampled in May 1981. A 625 cm² (25 × 25 cm) metal frame was haphazardly placed at 10 m intervals on the marsh edge, flat, short *S. alterniflora*, and *S. patens* zones. In each zone, 12–16 quadrats were sampled. Within each quadrat all mussels and substratum (excavated to 10 cm) were washed through a 2 mm sieve. Percent cover of mussels in each zone was estimated by laying a 0.25 m² grid of 100 25 cm² (5 × 5 cm) cells over each quadrat and counting the number of cells with mussels present.

For each mussel sampled, length was measured with calipers (±0.1 mm), and each mussel was aged by counting external growth rings (Seed, 1969b). In New England, the pronounced growth bands of *Geukensia* accurately record annual growth (Brousseau 1984). We have followed >4,000 marked mussels at our study site for a two-year period and without exception growth bands were found to be the product of rapid summer growth, followed by minimal winter growth and continued shell thickening (Bertness, in prep.). Nonseasonal growth lines are easily distinguished from the annual bands.

We also measured the angle of shell growth with a protractor ($\pm 5^\circ$), since many of the mussels in the population had severely distorted shells (Fig. 1). We defined the angle of shell growth as the angle between the hinge line and the posterior growing tip of the shell, measured from the umbo. Individuals with distorted shells were only found at extremely high mussel densities, suggesting that shell distortion was the result of interspecific crowding. Therefore, in addition to quantifying the incidence of shell distortion in the population, we also tested experimentally the hypothesis that shell distortion was the result of intraspecific crowding (see below).

Effects of tidal height and conspecific density on adult mussel growth and mortality

In May 1981, 2500 individual *Geukensia* ranging in length from 30 to 100 mm were collected from the marsh edge. Each mussel was measured, aged, and then numbered with a small plastic tag and a color-coded paint mark on the growing posterior edge of the shell. These mussels were divided into 25 similar groups of 100 mussels. Five groups were placed in the field in each of the following treatments: 1) high density on the marsh edge, 2) low density on the marsh edge, 3) high density on the marsh flat, 4) low density on the marsh flat, and 5) low density in the short *S. alterniflora* zone. Mussels were placed in the field in their natural position and attached to the substratum and one another within two days with no observable mortality or movement. In high density treatments, 100 mussels were confined to a 25×25 cm area, a density ($1600/\text{m}^2$) similar to that found naturally on the marsh edge. In low density treatments, 100 mussels were haphazardly placed over a 0.5×0.5 m area, a density ($400/\text{m}^2$) similar to that found on the marsh flat. Each treatment was located on marsh substratum where other mussels had been locally removed. Replicates were spaced at 5 m intervals along an otherwise undisturbed 25 m stretch of the marsh.

Each treatment was initially placed in the field in May 1981 and then sampled in September 1981, May 1982, and September 1982 so that growth and mortality could be partitioned into "summer" (May–September) and "winter" (September–May) components. At each sampling date, all mussels in each experimental area were collected; unmarked mussels (immigrants and recruits) were measured and aged, and marked mussels were measured, aged, and scored as either alive or dead. More than 90% of all marked mussels were accounted for on each sampling data. Shell margin expansion, measured from the initial posterior margin to the new posterior margin (± 0.1 mm) was measured for each individual at each sampling date, and will be used as a growth measure for comparative purposes. After each census the mussels were returned to the field with new individuals marked to replace mussels that had died during the previous time interval to reestablish desired densities in each treatment.

Juvenile mussel growth and survivorship

Greater mobility and difficulty in relocating small individuals made the above, infrequently sampled experiment inappropriate for assessing juvenile mussels. Thus, we designed a smaller, more frequently monitored experiment to assess juvenile growth and mortality in relation to tidal height, adults, and predators.

Replicate treatments of 20 juveniles were placed in the following treatments: 1) uncovered substratum without adults, 2) covered substratum without adults, 3) uncovered substratum with adults at marsh edge density, and 4) covered substratum with adults at marsh edge density. Five replicates of each treatment were placed in the marsh edge, flat, and short *S. alterniflora* zone in June 1982. A similar size range of mussels was used for each replicate, and each mussel was measured and painted on its posterior edge. Replicates consisted of a 15 cm diameter flower pot imbedded flush with the marsh surface. All pots were filled to within 2 cm of their top edge with ambient substratum. In treatments without adult mussels, a 10 mm mesh plastic screen was attached to the sediment surface to provide attachment points for the mussels. In treatments with adult mussels, adults (individuals > 60 mm in length) were placed in the pots and juveniles were allowed to attach to the adults. Covered treatments, designed to exclude mussel predators, were fitted with 10 mm mesh plastic screen covers which prevented access to larger predators, but did not reduce mussel feeding efficiency or increase sedimentation (see below).

Each replicate was inspected every other day for movement of mussels out of the pots and evidence of predation. Juveniles that moved out of their assigned treatment were measured and replaced, and the crushed shells of juveniles that had been preyed upon were removed and measured. After 6 weeks the growth of all surviving individuals was measured as posterior shell expansion.

In the above experiment, many juveniles appeared to die as a result of being covered by sediment. Juveniles initially observed attached below the surface in soft sediment with only their posterior tip protruding, would later be found completely buried in the sediment, dead, and with no signs of predator damage. Since we observed this type of mortality primarily on the marsh edge, we quantified differences in sedimentation among marsh zones in a way that mimicked sedimentation in the interstitial spaces occupied by mussels. We implanted plastic test tubes (18.5 mm diameter \times 120 mm long) in the substratum for one week in each marsh zone, and then dried and weighed the accumulated sediment in each tube.

To examine the hypothesis that the shell distortion observed in the population was the result of intraspecific crowding, a separate experiment was performed. One hundred juveniles (20–30 mm in length) were placed on the marsh edge in each of the following treatments: 1) maximum adult density ($2000/\text{m}^2$), 2) low adult density ($200/\text{m}^2$), and 3) without adults on substratum with a plastic screen attachment surface. Flower pots were used as described above, with five replicates each with 20 juveniles for each treatment. All juveniles were marked before the experiment and only juveniles with 'normal' shell morphology (angle of growth $24\text{--}26^\circ$, Fig. 1a) were used. Replicates were placed in the field in May and recovered four months later, when each juvenile was measured for posterior shell margin growth, and the angle of shell growth (initial and final).

Juvenile recruitment

To examine the distribution of recent *Geukensia* recruits, core samples (6.5 cm diameter \times 20 cm long) were taken in the marsh edge, flat and short *S. alterniflora* zones from

June to November 1983. 10–15 haphazardly located cores were taken monthly in each zone. Cores were washed through a 2 mm sieve and all mussels were aged and measured. Mussels without an annual growth band were considered juveniles. To examine the microdistribution of juvenile *Geukensia*, five larger (15 cm diameter \times 20 cm deep) cores were taken on the marsh edge and flat and dissected in the laboratory. The age and length of each mussel, the point of attachment of the byssal threads (other mussels, grass stems, etc.), and the size, age and distance of neighboring mussels were recorded.

Since examination of the microdistribution of *Geukensia* suggested that juveniles settled in association with conspecifics or the stems of *Spartina alterniflora*, a field experiment was performed to examine settlement preferences. In July 1982 five 0.25 m² quadrats of each of the following treatments were established: 1) mussel removal on the marsh edge, 2) grass removal on the marsh edge with mussels replaced at natural density, 3) mussel and grass removal on the marsh edge, 4) disturbance controls on the marsh edge, where mussels were removed, and then replaced, 5) addition of mussels on the marsh flat to marsh edge densities (1500/m²), 6) mussel removal on the marsh flat, 7) grass removal on the marsh flat, 8) mussel and grass removal on the marsh flat and 9) disturbance controls on the marsh flat. In grass removal replicates, the above and below-ground portions of *S. alterniflora* were removed. After 18 months, 5–6 core samples (6.5 cm \times 20 cm) were taken in each quadrat and examined for juveniles as described above.

Post-settlement mussel movement and habitat selection

Since our examination of mussel microhabitats suggested that mussels were capable of movement and possibly discriminating between microhabitats, we investigated post-settlement mussel movement and habitat selection. We cleared five 1 m² areas in the short *S. alterniflora* zone by removing all emergent vegetation and mussels. In the center of each area we implanted a 12 cm diameter flower pot, and around its circumference we implanted six other pots of the same size 10 cm from the perimeter of the central pot. The central pot was filled with ambient substratum with all grass stems and mussels removed (bare substratum). In each area, the peripheral pots contained: 1) 100 juvenile *Geukensia* (<30 mm in length) on bare substratum, 2) 25 adult *Geukensia* (>70 mm in length) on bare substratum, 3) substratum without mussels, but with *S. alterniflora* stems and root mat, 4) bare substratum with bamboo stakes imbedded in the substratum to mimic *S. alterniflora* stems (20/pot, 10 mm diameter), and 5) substratum without grass stems or mussels. The position of the peripheral pots was randomized among the five areas. We placed five marked mussels of each of the following size classes, 10–15 mm, 15–20 mm, 20–25 mm, 25–30 mm, 30–35 mm, and 35–40 mm in the central pot and examined movement away from the initial pot. Mussels attached to the substratum in the central pot within one or two hours. Mussels were considered to have moved only if they moved entirely out of the central pot. We replicated this experiment 10 times, each for a 4 day test period. Distance moved from the central pot was measured conservatively as the distance between where an individual was attached after four days and the margin of the central pot. We recovered >90%

of the juveniles tested. Mussels attached in natural positions with their anterior end embedded in the substratum in one of the peripheral pots at the end of each 4 day replicate were scored as having chosen the substratum in the new location.

All data were analyzed using the SAS-82 statistical package (Statistical Analysis System 1982). Standard normalizing procedure (Zar 1974) were performed as necessary. Standard error is reported throughout as a measure of variation.

Results

Population structure

Mussel density decreased markedly with increasing tidal height from the marsh edge to the *Spartina patens* zone. On the marsh edge, *Geukensia* density ranged from 640 to 1936 mussels/m² ($n=17$) with a mean of 1235.7 ± 88.0 mussels/m². Mussels were significantly clumped (variance/mean = 6.71, $P < 0.01$, X^2 , Pielou 1969) and covered $96.2 \pm 2.0\%$ ($n=25$) of available surfaces. On the marsh flat, mussel densities were less than half that of the marsh edge, ranging from 160 to 1040 mussels/m² ($n=16$) with a mean of 449.9 ± 64.8 mussels/m². In this zone, mussels were highly clumped (variance/mean = 9.39, $P < 0.01$, x^2) and covered $56.3 \pm 8.0\%$ ($n=25$) of the available substratum. In the short *S. alterniflora* zone, mussels were comparatively rare, with densities ranging from 32 to 124 mussels/m² ($x = 68.8 \pm 10.0$, $n=11$). Percent cover of mussels in the short *S. alterniflora* zone was $5.2 \pm 1.0\%$ ($n=25$) and the mussels were not clumped (variance/mean = 1.03, $P > 0.50$, x^2). In the *S. patens* zone mussel density ranged from 0 to 40 mussels/m² ($x = 2.0 \pm 2.1$ mussels/m², $n=12$), percent cover of mussels was $0.5 \pm 0.45\%$ ($n=25$), and the mussels were clumped (variance/mean = 2.48, $P < 0.05$, x^2).

Geukensia length and age data for each marsh zone are given in Fig. 2. Mean mussel length varied significantly ($P < 0.0001$, ANOVA) among marsh zones. This pattern reflects a general decrease in mussel size with increasing tidal height, but is complicated by the lack of small mussels at high tidal heights (Fig. 2). The largest mussel found in each zone decreased with increasing tidal height: edge 117.0 mm, flat 98.6 mm, short *S. alterniflora* 94.0 mm, and *S. patens* 75.6 mm.

Mean mussel age (determined by annual growth rings) increased significantly ($P < 0.0001$, ANOVA) with increasing tidal height (Fig. 2). This pattern is the result of both the lack of younger mussels in the higher tidal zones and the presence of older mussels at higher tidal heights.

Growth curves generated from age/size plots for mussels in each tidal zone suggest that mussel growth rate decreases significantly ($P < 0.0001$, ANOVA) with increasing tidal height (Fig. 3).

In addition to live mussels, many dead mussels with their valves still attached together were found in our samples. Since dead mussel shells appear to dissolve rapidly (within 1 or 2 years) in the acidic marsh substratum, dead in situ mussels appear to represent individuals that have died recently. 9.3% and 6.5%, respectively, of all mussels found on the marsh edge and flat were dead, while only 0.8% of the mussels found in the short *S. alterniflora* zone and 1.1% of the mussels found in the *S. patens* zone were dead. The size and age of dead mussels did not differ signifi-

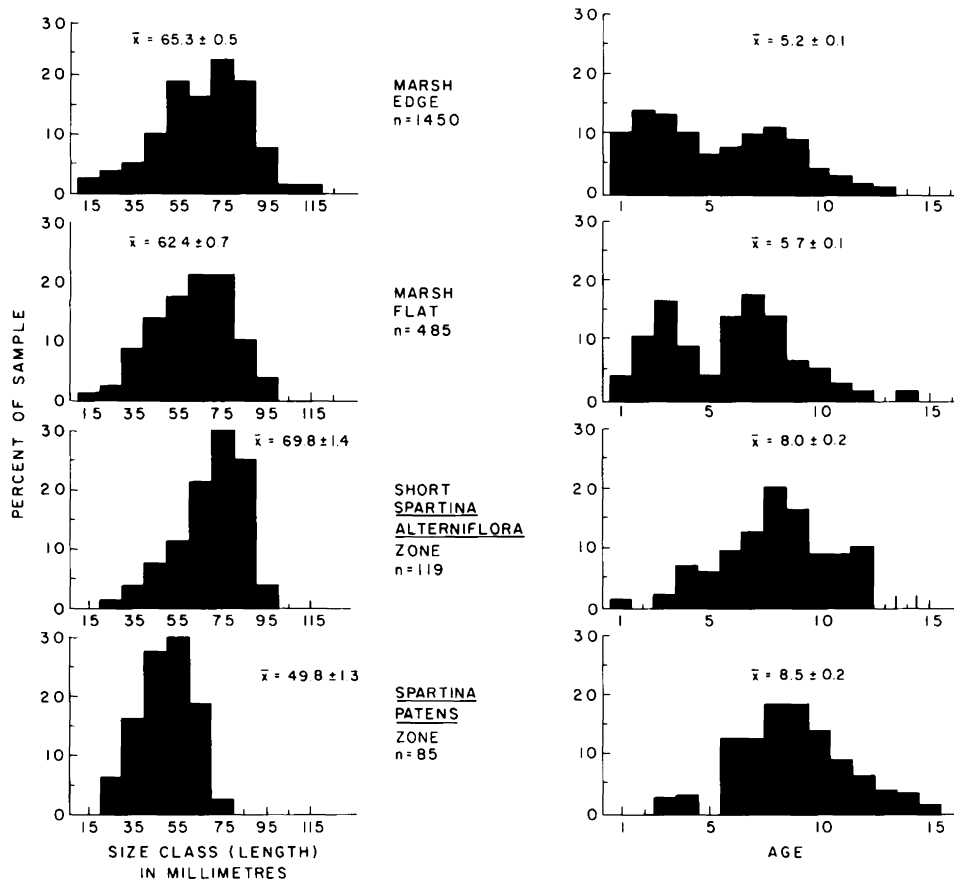


Fig. 2. Size (length in mm) and age distribution of *Geukensia demissa* from the marsh edge, marsh flat, short *S. alterniflora*, and *S. patens* zones (\pm S.E.). Mussel ages were determined by annual growth bands

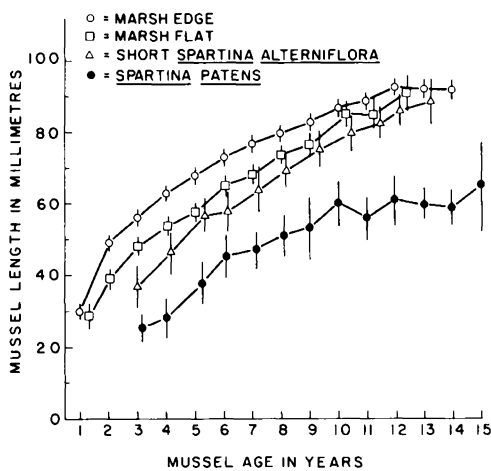


Fig. 3. Growth curves for *Geukensia demissa* in each marsh zone constructed from growth band age estimates. All points represent > 10 individuals and standard errors are presented as vertical bars

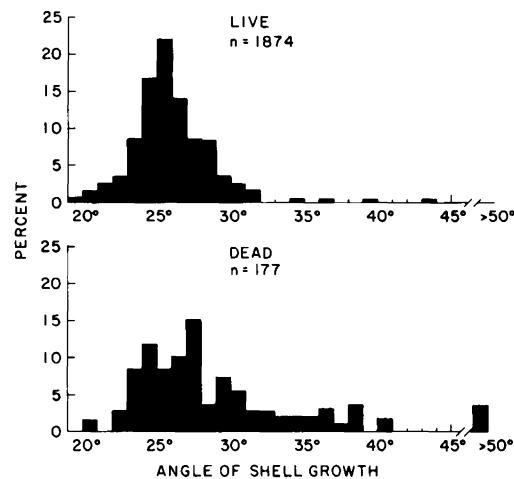


Fig. 4. Angle of shell growth of living *Geukensia demissa* and *G. demissa* found dead, but with their valves still attached together. Data are from the population survey with all habitats pooled

cantly from living mussels in each zone ($P > 0.20$, ANOVA for each zone). Little importance can be attributed to the frequency at which dead shells are found in the different habitats since the marsh zones may differ in the probability that an empty shell will be washed away or dissolved. The shape of shells found dead in situ, however, showed a striking pattern in contrast to living mussels.

The angle of shell growth of live mussels did not vary with shell length ($P > 0.50$, ANOVA), but did differ among tidal heights ($P < 0.01$, ANOVA). *Geukensia* on the marsh

edge grow at more of an angle ($28.1 \pm 0.1^\circ$) than mussels at any other tidal height ($p < 0.05$, Scheffe test). The angle of shell growth did not differ among mussels on the marsh flat ($25.4 \pm 0.1^\circ$), short *S. alterniflora* zone ($26.4 \pm 0.3^\circ$), and *S. patens* zone ($25.8 \pm 0.3^\circ$).

The distribution of the angle of shell growth of living and dead *Geukensia* from the population census is given in Fig. 4, combining individuals from all tidal heights. While only 3.5% of living mussels had highly distorted ($> 30^\circ$ shell angle) shells, significantly more ($P < 0.001$, G

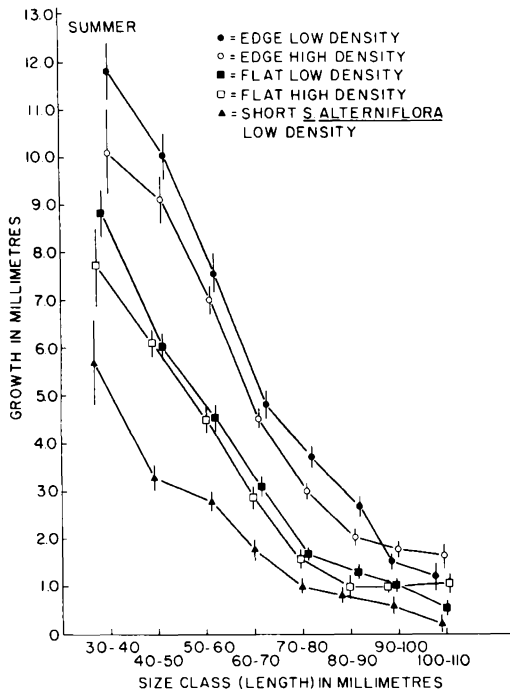


Fig. 5. Summer growth (posterior shell expansion) of mussels in the adult density manipulations in the marsh edge (circles), marsh flat (squares), and short *S. alterniflora* (triangles) zones. All points represent >10 individuals and vertical bars are standard errors. Results from both years of the experiment are pooled

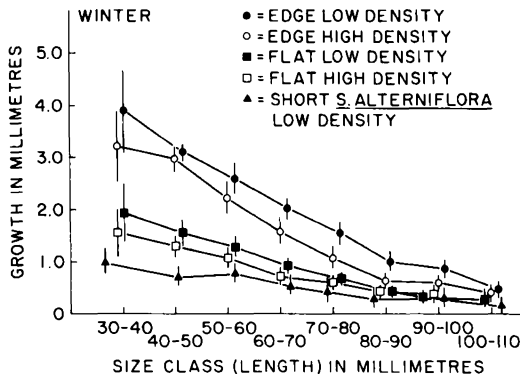


Fig. 6. Winter growth (posterior shell expansion) of mussels in the adult density manipulations. Symbols and conditions as in Fig. 5

test) of the dead shells (28.2%) had shells growing at an angle >30°, suggesting that mussels with strongly bent shells are more likely to die than mussels without severely bent shells.

Adult density manipulations

Mussel growth during the summer months (Fig. 5, May–August) far exceeded winter growth (Fig. 6, September–April) and did not differ during either the winter or summer between years (size × year ANOVA by season, $P > 0.50$ for year). Therefore, we analyzed summer and winter growth separately (size class × tidal height × density ANOVA), pooling data from 1981 and 1982.

Summer and winter mussel growth (Figs. 5 and 6) re-

Table 1. Survivorship of mussels in the adult density manipulations on the marsh edge, marsh flat, and short *S. alterniflora* habitats. See text for methods. The data was analyzed with a 4-way factorial ANOVA (habitat × treatment × season × year): habitat, $P < 0.0001$; treatment, $P < 0.005$; season, $P > 0.50$; year, $P < 0.001$; Habitat × Treatment × Season × Year interaction, $P < 0.001$. Density contrasts are given below

Habitat	Season	High density treatments (n)	Low density treatments (n)	Scheffé test
Edge				
	Summer 1981	70.0 ± 1.0(5)	74.0 ± 2.5(5) ^a	NSD*
	Summer 1982	69.8 ± 3.0(5) ^a	83.0 ± 3.4(5)	$P < 0.001$
	Winter 1981	73.6 ± 2.8(5)	54.2 ± 5.1(5) ^{a,b}	$P < 0.001$
	Winter 1982	81.8 ± 3.6(5) ^a	75.6 ± 1.7(5) ^b	NSD*
Flat				
	Summer 1981	73.4 ± 6.1(5) ^{a,b}	80.6 ± 3.0(5) ^a	NSD*
	Summer 1982	88.0 ± 1.4(5) ^b	83.3 ± 2.3(5)	NSD*
	Winter 1981	87.8 ± 2.1(5) ^a	70.4 ± 2.8(5) ^a	$P < 0.001$
	Winter 1982	86.4 ± 2.9(5)	75.2 ± 4.7(5)	$P < 0.01$
Short <i>Spartina</i>				
	Summer 1981	—	85.0 ± 3.1(5)	—
	Summer 1982	—	80.0 ± 1.4(5)	—
	Winter 1981	—	82.2 ± 3.0(5)	—
	Winter 1982	—	83.6 ± 2.5(5)	—

* NSD = no significant difference

^a $P < 0.05$, Scheffé test between seasons within density level, habitat, and years

^b $P < 0.05$, Scheffé test between years within density level, season, and habitat

vealed similar patterns: 1) growth decreased with increasing size ($P < 0.001$); 2) growth decreased with increasing tidal height ($P < 0.001$); 3) mussels at low densities grew more than mussels at high densities ($P < 0.001$); 4) the growth of all sizes of mussels was similarly affected by tidal height (size class × tidal height interaction, $P > 0.50$); and 5) the growth of smaller mussels was depressed more than that of larger individuals at high densities (size class × density interaction, $P < 0.05$).

Survivorship in the adult density manipulations (Table 1) was significantly affected by tidal height ($P < 0.001$), mussel density ($P < 0.01$), and year ($P < 0.01$), but not season ($P > 0.50$). Survivorship increased with tidal height (edge $72.3 \pm 1.6\%$, flat $80.6 \pm 1.5\%$, short *S. alterniflora* $82.9 \pm 1.3\%$), and was higher in 1982 ($80.7 \pm 1.1\%$) than in 1981 ($74.7 \pm 1.6\%$). Survivorship was also higher at high mussel density ($78.9 \pm 1.5\%$) than at low mussel density ($75.5 \pm 1.3\%$). The effect of density on mussel survivorship, however, was strongly influenced by season (density × season interaction, $P < 0.001$), with the interaction between density and season most pronounced on the marsh edge (Table 1). In the summer, survivorship was generally greater at low mussel densities, whereas in the winter survivorship was greater at high densities (Table 1). This suggests that in the summer, when growth rates are high (Figs. 5 and 6), high densities may lead to intraspecific competition resulting in mussel mortality, while in the winter when growth is minimal and most mussel deaths appear to be attributable to winter ice effects, high mussel densities may protect mussels from mortality.

To examine the effect of density on mussels of different

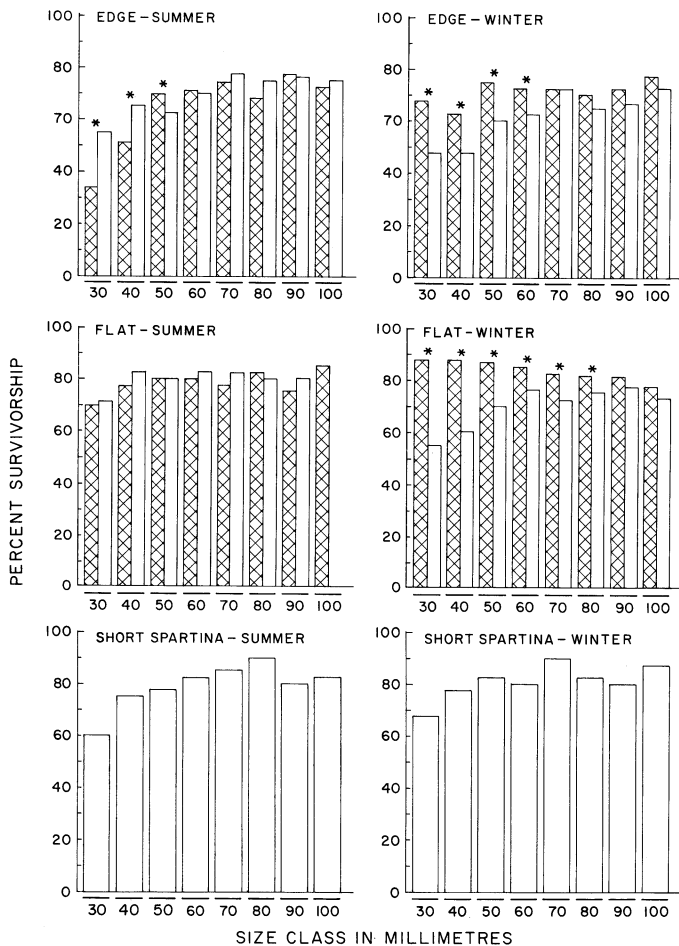


Fig. 7. Mussel survivorship by size class in the adult density manipulations partitioned by habitat and season. Crosshatched bars are high densities, open bars are low densities. Data is not given for cases with <15 individuals. An asterisk indicates a significant ($P < 0.05$, G test) difference between high and low density treatments

sizes, we compared the survivorship of mussels by 10 mm size classes between high and low density treatments, (Fig. 7). In the summer on the marsh edge, smaller mussels (30–49 mm) survived better at lower densities, while density did not significantly affect the survivorship of mussels >60 mm in length (Fig. 7). In the winter on the marsh edge, smaller mussels (30–69 mm) had lower survivorship at low mussel density, while density did not significantly affect the survivorship of mussels >70 mm in length. On the marsh flat, density did not affect the survivorship of any mussel size class in the summer, while in the winter the survival of all mussel size classes <90 mm in length was greater at high densities than at low densities (Fig. 7). This suggests that density effects on mussel survivorship are most pronounced on smaller mussels.

Juvenile mussel growth and survivorship experiments

Growth rates of juvenile mussels with and without adult conspecifics at each tidal height are given in Fig. 8. Covered and uncovered replicates were pooled, since the covers did not affect growth rates ($P > 0.25$, ANOVA). Juvenile growth was affected (size class \times tidal height \times treatment ANOVA) by size ($p < 0.001$), tidal height ($P < 0.001$), and

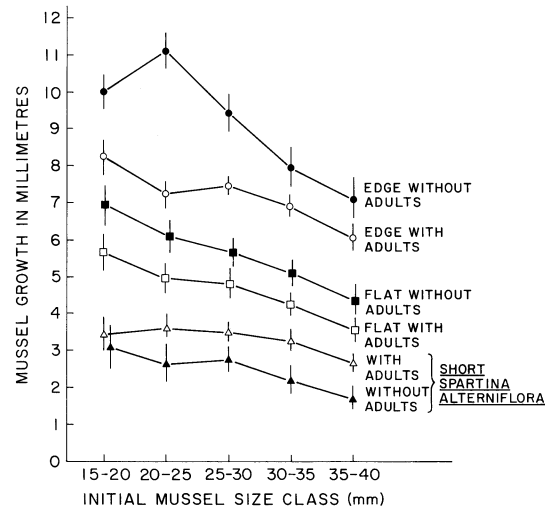


Fig. 8. Growth (posterior shell expansion) in the juvenile mussel experiment by size class and treatment. circles are treatments on the marsh edge; squares, the marsh flat; and triangles, the short *S. alterniflora* zone. Solid symbols are treatments without adults present, open symbols are treatments with adults. Vertical bars are standard errors

the presence of adults ($P < 0.001$). Growth decreased with increasing size and tidal height, and was reduced in the presence of adults on the marsh edge and flat (Fig. 8). As was the case with the adult density manipulations, the growth of smaller individuals was more strongly affected by high densities of adults, than were larger juveniles (Fig. 8). In the short *S. alterniflora* zone, however, juveniles grew significantly more in the presence of adults than when adults were not present in all ($P < 0.01$, Scheffe test, each case) but the smallest (15–20 mm) size classes. The most likely explanation for this reversal in the effect of conspecific density on individual growth is that while adults reduce the availability of food to juveniles at lower tidal heights (marsh edge and flat), in the higher intertidal short *S. alterniflora* zone, the presence of adults may have reduced physical stress (heat and desiccation) on the juveniles, and thus facilitated their growth.

Survivorship and mortality data from the juvenile mussel experiment are presented in Table 2, with mortality partitioned into juveniles whose shells had been broken by predators, and juveniles that were found dead, but with no signs of shell damage. We recovered >90% of all juveniles used in the juvenile survivorship experiment, and most losses that did occur were due to individuals losing their identifying paint mark.

Juvenile survivorship (Table 2) was significantly affected by tidal height ($P < 0.001$), covers over the replicates ($P < 0.001$), and the presence of adults ($P < 0.001$). Survivorship: 1) increased with increasing tidal height (edge $84.8 \pm 3.0\%$, flat $94.2 \pm 1.8\%$, short *S. alterniflora* $99.0 \pm 0.2\%$); 2) was higher in covered ($96.9 \pm 1.0\%$) than uncovered ($89.6 \pm 2.2\%$) replicates; and 3) was higher in the presence of adults ($99.5 \pm 0.2\%$) than when adults were absent ($86.2 \pm 2.3\%$). Shell-crushing mortality decreased with increasing tidal height with no crushed shells found in the short *S. alterniflora* zone. Shell-crushing mortality was not observed in covered replicates, and was reduced by an order of magnitude when adults were present (Table 2). Juvenile deaths without shell damage decreased with

Table 2. Juvenile survivorship from pots placed in the marsh edge, marsh flat, and short *S. alterniflora* habitats with and without adults and mesh covers which excluded large predators. See text for methods. The data was analyzed with a 3-way factorial ANOVA (habitat \times covers \times adults) on survivorship, crushed shell, and intact dead shell data separated. For each of these variables the results were similar: habitat, $P < 0.05$; Covers, $P < 0.005$; Adults, $P < 0.001$; Habitat \times Covers \times Adult interaction, $P < 0.001$. Further contrasts are given below

Habitat	Treatment	Percent survivorship	Percent crushed	Percent ^a dead	Percent accounted for (no. of replicates)
Edge	Covered	with adults	100%	0	90% (5)
		without adults	$90.0 \pm 1.5\%$ ^c	$10.0 \pm 1.5\%$ ^{b,c}	79% (5)
	Uncovered	with adults	$99.0 \pm 1.0\%$ ^b	0	86% (10)
		without adults	$67.5 \pm 1.8\%$ ^{a,c}	$1.0 \pm 0.6\%$ ^c	77% (10)
Flat	Covered	with adults	100%	0 ^b	98% (5)
		without adults	$93.3 \pm 3.5\%$ ^c	$6.6 \pm 3.5\%$ ^b	95% (5)
Short <i>S. alterniflora</i>	Covered	with adults	100%	0	93% (5)
		without adults	$99.0 \pm 1.0\%$	$1.0 \pm 1.0\%$	98% (5)
	Uncovered	with adults	$99.5 \pm 0.5\%$	$0.5 \pm 0.5\%$	95% (10)
		without adults	100%	0	90% (5)

^a Juveniles scored as "dead" only include those that died with no evidence of shell damage

^b $P < 0.05$, Scheffé Test between otherwise similar treatments with and without adults

^c $P < 0.05$, Scheffé Test between otherwise similar treatments with and without covers

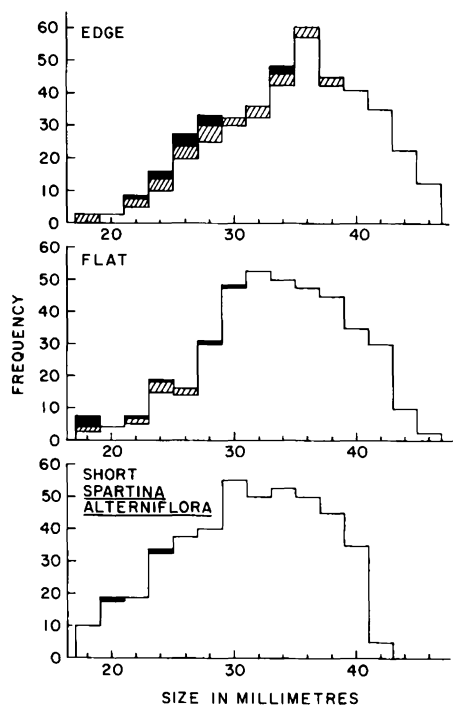


Fig. 9. Size distribution of mussels in the juvenile experiment that survived (□), were crushed by predators (▨), or died without shell damage (■) for each marsh habitat. See text for details

increasing tidal height (suggesting that heat and desiccation were not responsible for these deaths), were more common in covered than uncovered replicates, and were less common in the presence of adults than when adults were present (Table 2).

The size distribution of surviving juveniles and juveniles that were recovered crushed or dead, but without shell damage, are given in Fig. 9. Most mortality at each tidal height involved smaller individuals. On the marsh edge, where the sample size of dead mussels was large enough to test the relationship between mussel size and mortality, juveniles that died without evidence of shell damage were significantly ($P < 0.05$, *t*-test) smaller ($x = 27.7 \pm 2.0$ mm, $n = 10$) than individuals that survived ($x = 34.2 \pm 0.3$ mm, $n = 352$). Similarly, crushed shells were significantly ($P < 0.01$, *t*-test) smaller ($x = 28.4 \pm 0.9$ mm, $n = 42$) than mussels that survived ($x = 34.2 \pm 0.3$, $n = 352$).

Juveniles that died without shell damage appeared to have died due to sediment suffocation, and were more commonly seen on the marsh edge than at higher tidal heights (Table 2). Sedimentation decreased by over 5 orders of magnitude with increasing tidal height, with the largest decrease between the marsh edge and marsh flat ($P < 0.001$, ANOVA).

Results of the juvenile shell shape experiment showed that the angle of shell growth was influenced by intraspecific crowding ($P < 0.001$, ANOVA). Juveniles on bare substratum ($26.8 \pm 0.3^\circ$, range $24\text{--}33^\circ$, $n = 45$) and with a low density of adult conspecifics ($26.6 \pm 0.3^\circ$, range $23\text{--}31^\circ$, $n = 55$) did not differ ($P > 0.50$ Scheffé test) in the angle of shell growth, while juveniles from the high density adult treatments had a significantly higher ($P < 0.01$, Scheffé test, both

Table 3. Results of the juvenile *Geukensia* settlement survey (unmanipulated controls) and the juvenile settlement substrate preference experiment. Mussels without annual growth bands were considered to be settlers. Juvenile densities are given as juveniles/core sample (65. cm diameter). Settlement survey (unmanipulated control) cores were taken from August 1982–September 1983. Cores in manipulated substrates were taken in August 1983, 18 months after the substrate had been manipulated. The variance/mean ratio of juvenile density is presented to test for aggregation. See text for further methods and statistics

Habitat	Treatment	Juvenile length in mm \pm S.E. (n)	Juvenile density/core	
			$\bar{x} \pm$ S.E. (n)	Variance/mean ratio
Edge				
Control survey	(unmanipulated control)	—	2.17 \pm 0.3 ^a (79)	3.28 ^b
	Adult removal	12.1 \pm 0.7 (37)	0.59 \pm 0.2 ^a (27)	2.30 ^b
	Grass removal	12.7 \pm 1.6 (11)	0.42 \pm 0.1 ^a (26)	0.97
	Adult and grass removal	—	0 \pm 0 ^a (27)	1.00
	Disturbance control	10.6 \pm 0.5 (63)	2.41 \pm 0.5 (26)	2.54 ^b
Flat				
Control survey	(unmanipulated control)	—	0.34 \pm 0.1 (95)	1.78 ^b
	High density adults	7.1 \pm 1.5	0.30 \pm 0.1 (23)	1.03
	Low density adults	7.9 \pm 1.2 (6)	0.25 \pm 0.1 (24)	1.12
	Adult removal	7.5 \pm 0.4 (8)	0.25 \pm 0.1 (24)	1.52 ^b
	Grass removal	8.76 \pm 2.1 (3)	0.11 \pm 0.2 (28)	1.70 ^b
Adult and grass removal		—	0 \pm 0 ^a (26)	1.00
Short <i>Spartina alterniflora</i>				
Control survey	(unmanipulated control)	—	0.04 \pm 0.02 (96)	0.97
<i>Spartina patens</i>				
Control survey	(unmanipulated control)	—	0 \pm 0 (50)	—

^a $P < 0.05$, Scheffé test with control within habits

^b Juveniles significantly clumped ($P < 0.05$, χ^2 test, Pielou 1969)

cases) angle of growth ($29.1 \pm 0.3^\circ$, range $25\text{--}35^\circ$, $n = 54$). Only 4.2% of the juveniles from treatments without a high density of adults had shells growing at marked angles ($> 30^\circ$), while 12.9% of the juveniles with a high density of adults had shell growth angles of $> 30^\circ$ after only 3 months.

Juvenile recruitment

The natural density of juvenile mussels was over six times greater on the marsh edge than on the marsh flat, and was close to an order of magnitude greater on the marsh flat than in the short *S. alterniflora* zone (Table 3). No juvenile mussels were found in the 50 cores taken in the *S. patens* zone. Both tidal height ($P < 0.001$) and treatment ($P < 0.001$) significantly affected successful juvenile settlement (habitat \times treatment ANOVA; $P > 0.50$ interaction, Table 3).

On the marsh edge, removal of mussels and grass each significantly reduced *Geukensia* recruitment ($P < 0.05$, Scheffé test, each case) in relation to control areas. Removing either adult mussels or grass affected juvenile recruitment similarly ($P > 0.50$, Scheffé test), while removing both mussels and grass significantly reduced recruitment ($P < 0.05$, Scheffé test, both cases) in comparison to removal of either mussels or grass separately. This suggests that juveniles settle selectively with structural elements in the marsh substratum, rather than having a specific settlement preference for adults or grass stems. On the marsh flat,

removal of both mussels and grass stems significantly reduced juvenile recruitment in comparison to control areas ($P < 0.05$, Scheffé test), while the separate removal of mussels and grass stems or the addition of mussels did not significantly influence juvenile recruitment ($P > 0.10$, Scheffé test, each case).

Juveniles had a highly clumped distribution on both the marsh edge and flat (Table 3). We often found two or more recent settlers (< 10 mm in length) directly attached to one another in the cores. No clear pattern, however, is evident between the degree of clumping and the presence of adult conspecifics, indicating juvenile clumping is independent of the presence of adults (Table 3).

Examination of the microdistribution of *Geukensia* showed that the point of byssal thread attachment (Fig. 10A) varied significantly with mussel size ($P < 0.001$, G test). Small mussels were generally found attached to other mussels, while larger mussels were almost always found attached to *S. alterniflora*.

Neighboring conspecifics showed a strong positive relationship between both the size (Fig. 10B) and age of nearest neighbors. On both the marsh edge ($r^2 = 0.91$, $P < 0.01$) and flat ($r^2 = 0.94$, $P < 0.01$) and considering both the marsh edge and flat mussels combined (Fig. 10B, $r^2 = 0.95$, $P < 0.001$), neighboring mussels tended to be of similar size. As would be expected, neighboring mussel ages were also positively correlated on the marsh edge ($r^2 = 0.78$, $P < 0.05$), marsh flat ($r^2 = 0.92$, $P < 0.02$), and considering mussels from both habitats together ($r^2 = 0.85$, $P < 0.05$).

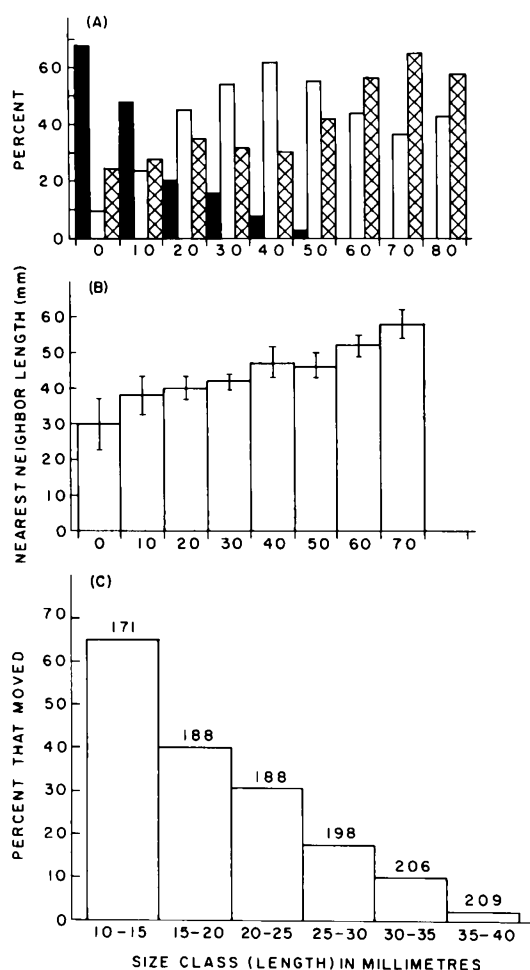


Fig. 10. **A** Point of byssal thread attachment of mussels on the marsh edge and flat by size class. Sample sizes are >30 for each size class. Less than 1% of the mussels were not attached to either other mussels (■), *S. alterniflora* stems (□), or *S. alterniflora* rhizomes (▨). **B** Nearest mussel neighbor size by mussel size class. Sample size are >30 for each size class and vertical bars are standard errors. **C** Percent of mussels that moved in the mussel mobility/habitat selection experiments by size class. Sample sizes are given for each size class

Post-settlement mussel movement and habitat selection

Our examination of juvenile mussel movement and habitat selection revealed that movement decreases with increasing mussel size and that juvenile mussels are capable of making post-settlement habitat selection decisions. Of the 1160 *Geukensia* ranging in size from 10 to 40 mm in length that we tested, 26% showed measurable movement over the four-day test periods. Movement ranged from 1 to 37 cm, with mussels that moved ($n=302$), moving an average of 8.41 ± 0.55 cm over the 4-day test period. Small mussels moved more frequently than larger mussels ($P < 0.0001$, *G*-test) with over half (63.7%) of the juveniles 10–15 mm in length moving. Only 3.3% of the mussels 35–40 mm in length moved (Fig. 10C). In the substratum choice experiment, juveniles showed a significant ($P < 0.001$, *G*-test) preference for substratum with either mussels or grass stems present. Of the mussels that moved and attached to one of the substratum types offered ($n=51$), 51.3% chose substratum with other juvenile mussels present, 27.4% chose substratum with adult mussels, 29.4% chose substratum

without mussels or grass stems, and 2% chose substratum without mussels or grass stems, but with bamboo stakes. The lack of juveniles attaching to substrate with bamboo stakes appeared to reflect that the bamboo stakes did not have root and rhizome structures, and not that the juveniles had a specific preference for attaching to *S. alterniflora*. These results demonstrate that smaller mussels are not only capable of considerable mobility, but that they are capable of discriminating and choosing where they attach. While our sample size is too small to expect a statistical difference, these results also hint that juvenile *Geukensia* attach to other juveniles in preference to adult conspecifics.

Discussion

In the *Geukensia* population we have examined, the distribution and abundance of individuals as well as the age and size structure of the population appear to be a complex product of interactions among juvenile settlement, growth, and biological and physical factors that vary across the marsh habitat. *Geukensia* abundance is greatest on the marsh edge, and is apparently maintained by the selective settlement of juveniles (Table 3). Mussels on the marsh edge have higher growth rates than mussels at higher tidal heights (Figs. 5 and 6) probably because mussels on the marsh edge are covered by the tide more often and can feed longer (Kuenzler 1961a). As a result, mussels on the marsh edge reach larger sizes (Fig. 2) and most likely have higher age-specific reproductive outputs (Suchanek 1981).

Geukensia, however, is subject to a number of mortality agents which diminish in importance with increasing tidal height, including physical disturbance, predation, and intraspecific competition. In the population we have examined, most physical disturbance is due to winter ice which pulls mussels individually or in clumps from the marsh surface, eventually depositing them haphazardly across the marsh basin. Most mussels transported by ice rafts die, either by being stranded too high on the marsh to survive, or more commonly by being deposited in the soft substratum below the marsh edge where, without structural support for attachment, they suffocate in the sediment. Our results suggest that: 1) winter mortality affects all sizes of mussels, but that smaller mussels are the most vulnerable (Table 1, Fig. 7), 2) winter mortality decreases with increasing tidal height in the marsh (Table 1), and 3) mussels at low densities are more vulnerable to removal by winter ice than mussels at high densities (Table 1, Fig. 7).

Predation on *Geukensia* is also more intense on the marsh edge than at higher tidal heights, but only affects smaller individuals (Table 2, Fig. 9). In our experiments, no mussels larger than 36.2 mm were crushed by predators and in three years of casual observation at the study site, no mussel larger than ~50 mm has been found that appeared to have died as the result of a shell crushing predator attack. If 40 mm in length is accepted as the largest sized mussel that is generally preyed upon, then most mussels in this population reach a size refuge from predation by the time they are two years old (Fig. 3).

Predation on mussels at our study site appeared to primarily be due to the blue crab *Callinectes sapidus* which regularly forages on the marsh during high tide and has been previously shown to be an important mussel predator (Seed 1980). Other potential mussel predators at the study site include other crabs, killifish, birds and raccoons. Of

the other predatory crabs, the rock crab *Carcinus maenas* will readily crush smaller *Geukensia* in the laboratory, but is rare at the site, and *Sesarma reticulatum* does not consume mussels in the laboratory. Similarly, the killifish, *Fundulus heteroclitus*, which is the only common predatory fish at the study site does not consume mussels in the laboratory, and does not appear to do so in the field. We have observed mallard ducks, *Anas platyrhynchos*, herring gulls, *Larus argentatus* and crows, *Corvus brachyrhynchos*, preying on mussels at our study site, but bird predation does not appear to be common, or an important factor in the distribution and abundance of *Geukensia*. Raccoons, *Procyon lotor*, are present at the study site, and we have often found their tracks in the short *S. alterniflora* zone adjacent to our predation experiments. The absence of predation on mussels in the short *S. alterniflora* zone where raccoons are present (Table 2), suggests that they are not important mussel predators at our site.

Intraspecific competition reduces the growth rate of *Geukensia* at high mussel densities (Fig. 5, 6, and 8), has more marked effects on smaller mussels than larger individuals (Figs. 5 and 8), and often results in death, particularly in the case of smaller individuals (Fig. 7). In our summer high density mussel treatments on the marsh edge, more mussels died than at either lower densities on the marsh edge or at any density at higher tidal heights (Table 1). This was not the case during the winter months when mussel growth rates were reduced (Figs. 5 and 6), and most mussel mortality occurred at low densities (Table 1), suggesting that the importance of intraspecific competition in the growth and survivorship of *Geukensia* decreases with increasing tidal height.

On the marsh flat, growth rates of mussels are reduced (Figs. 5 and 6) and physical disturbance and predation mortality are not as severe as on the marsh edge (Tables 1 and 2). Mussels are strongly aggregated, density is approximately a third of that on the marsh edge, and only a fifth as many mussels recruit to the marsh flat as on the marsh edge (Table 3). On the marsh flat, intraspecific crowding does not result as often in mussel deaths as on the marsh edge (Table 1, Fig. 7).

In the higher intertidal short *S. alterniflora* and *S. patens* zones, mussel growth rates were severely reduced (Fig. 3), mortality was negligible (Tables 1 and 2), and mussels were more long-lived than lower in the intertidal zone (Fig. 2). Few mussels are found at these high tidal heights and settlement of juveniles is negligible (Table 3). There are two explanations for the presence of mussels at these higher tidal heights which do not assume that they represent the survival of infrequent settlers. First, the intertidal height of the substratum changes over time and is affected by the presence of mussels. Accumulation of root material, peat and sediment can result in increases in tidal height in one year's time, and mussels stimulate belowground grass growth and marsh accretion (Bertness 1984). Without mussels, vertical marsh accretion on the marsh flat is ~ 0.66 cm/year, while with mussels present accretion nearly doubles to ~ 1.16 cm/year (Bertness 1984). Since most mussels live longer than eight years, during the life of an individual the tidal height of their habitat could increase by as much as 10 cm. For mussels on the marsh flat, this could result in beginning life at marsh flat tidal heights, but ending up living at short *S. alterniflora* tidal heights. We suggest that changing tidal heights within the marsh explains to a large degree the pres-

ence of mussels in the short *S. alterniflora* zone. This is a less satisfactory explanation for the presence of mussels in the *S. patens* zone, however, since marsh accretion decreases dramatically with increasing tidal height (Ranwell 1964).

We suggest that most mussels in the *S. patens* zone did not initially settle there, but were transplanted by winter ice rafts. We annually see examples of individuals and aggregates of mussels landing in the *S. patens* zone after being rafted by ice, and have observed that these relocated mussels often attach to the substratum and survive. This would explain the greater variance in the size of mussels of identical age in the *S. patens* zone in contrast to lower marsh habitats (Fig. 3).

Costs and benefits of the aggregated distribution of Geukensia

Our analysis of the effects of conspecifics on the success of individual mussels demonstrates that individuals have reduced growth rates and presumably reduced fecundity (Suchanek 1978) as a consequence of living in a dense matrix of conspecifics. Smaller mussels are affected by crowding more than larger mussels, both in terms of growth rate depression and mortality. All other common mortality agents, however, were reduced by group living.

High density aggregations of *Geukensia* appear to be less vulnerable to winter ice dislodgment than mussels at lower densities. This is probably due to the strength of communal attachment to the substratum and the effect of dense aggregations of mussels on belowground plant root production. In dense aggregations, mussels are attached to the substratum not only by their own byssal threads, but also by the byssal attachment of neighboring mussels which bind to the substratum as well as to their neighbors. The result is that groups of mussels are more firmly attached to the substratum than solitary individuals. Second, dense mussel aggregations may augment soil nutrients and stabilize substrata, and thereby increase the production of cordgrass roots and rhizomes to which the mussels attach (Bertness 1984). Since *S. alterniflora* roots and rhizomes are responsible for binding marsh sediments and peat into a dense root mat, increased belowground production most likely reduces the probability of winter ice damage.

The presence of conspecifics also reduced the vulnerability of smaller mussels to predators and suffocation by sediment (Table 2). Adults appear to reduce predation on juveniles by passively providing spatial refuge. In association with adults, juveniles live below the protruding shell margins of the adults and apparently out of the reach of most predators. In providing protection from sediment burial, larger mussels simply appear to provide a vertical surface on which smaller mussels can climb and remain above the sediment surface (Lent 1967a).

The mechanism that leads to the aggregated distribution of *Geukensia* does not appear to be simple. Since mussels in aggregations are more likely to survive than solitary mussels, aggregation distribution could simply be the product of random settlement followed by the differential mortality of solitary individuals. While this must contribute to the distribution of *Geukensia*, it would not appear to account for the non-random distribution of recent settlers (Table 3) or the size/age class segregation (Fig. 10B) found in the mussel population. *Geukensia* settle in an aggregated distri-

bution with or without adult mussels present (Table 3). Furthermore, smaller mussels are capable of considerable mobility (Fig. 10C) and preferentially attach to hard substrata such as other juveniles, adult mussels, and cordgrass stems. These abilities imply that juvenile mussels can select favorable microhabitats for their growth and survival.

Size class segregation within the mussel population is probably the result of one or a combination of two likely mechanisms. First, size segregation could be the product of contagious settlement and the subsequent selection of microhabitats away from large adults which reduce the growth rates of juveniles. It is unlikely that juvenile mussels affect each other's food supply as much as larger adults do, since the filtering rate of *Geukensia* increases with increasing body size (Jordan and Valiela 1982). A second possible mechanism for the establishment and maintenance of size class segregation is that adult mussels filter and eat planktonic juveniles before they settle (Woodin 1976). That this occurs in our population is likely. Jordan and Valiela (1982) have calculated that in a salt marsh of similar size, but with fewer mussels, the mussel population filters all the water which comes into the marsh basin during each tidal cycle. This is equally probable at our study site. If adults do not discriminate between food in the water column and planktonic conspecifics, and if the larvae can not avoid adult feeding currents, cannibalism may be important in our population. Cannibalism of juveniles by adults could generate the observed size class segregation in the population without invoking gregarious settlement or post-settlement habitat selection. That juveniles are found in an aggregated distribution without adults present (Table 3), however, argues that size class segregation in the population is at least in part an active behavioral process.

Whatever the mechanism of the size class segregation in the population studied, the result for successful settlers is the same; by living near other smaller mussels rather than larger individuals, smaller mussels most likely minimize the growth depression cost of association, while maintaining the survivorship advantages of an aggregated distribution.

Mussel dominance in intertidal habitats

Why are mussels so successful in intertidal habitats? Mussel dominated zones in intertidal habitats are a conspicuous feature of both hard-bottom (Seed 1969a, b; Paine 1971, 1974; Paine and Levin 1981; Suchanek 1978) and some soft-bottom habitats (Teal 1962). In rocky habitats, where space is often limiting to sessile populations (Connell 1961; Jackson 1977), mussels are often the competitive dominants for primary space (Paine 1971, 1974; Menge 1976). In soft-bottom habitats, where substratum stability often limits populations (Orth 1977; Woodin 1978), mussels have been shown to stabilize substratum (Bertness 1984). In each of these habitats, then, mussels directly affect the most critical variable limiting populations in these dissimilar situations. We suggest that the aggregated distribution of mussels is the key to their success on both hard and soft substrata.

If *Geukensia* did not live in a clumped matrix of individuals, a variety of mortality agents would severely limit their distribution and abundance. If we extrapolate the results of our six-week juvenile survivorship experiment and estimate summer (12 week) survivorship of smaller mussels (<40 mm in length) for the ~ two years that it takes *Geu-*

kensia to grow >40 mm, our results predict that no juveniles would survive on the marsh edge and only 65% of the few juveniles that settle on the marsh flat would survive without adults present. Considering the effect of winter physical disturbance, our annual winter mortality estimate of 35% when mussels on the marsh edge are not in a dense, aggregated distribution, suggests that the mussel population on the marsh edge would be reduced to 11.5% of its current size in only five years. Similarly, on the marsh flat, an unaggregated mussel population would be reduced to 24.0% of its current size in five years. Since the mean age of *Geukensia* in our population is ~5.5 years, these projections suggest that if *Geukensia* did not exhibit a clumped distribution it would not dominate the habitat both due to the reduced success of juvenile and adult mussels. These extrapolations indicate that the success of *Geukensia* in dominating certain marsh habitats is contingent on its propensity to form dense aggregations.

As with *Geukensia*, the success of matrix forming mussels that live on hard substrata is also most likely the product of their aggregated distribution. Because of the mobility of mussels within the matrix of *Mytilus californianus*, newly created free space can be occupied by mussels moving or being pushed into free space (Paine and Levin 1981). Mussel aggregations on hard substratum also provide refuges from predators to organisms within the mussel matrix (Witman 1983). We suggest that the dominance of intertidal mussels in both hard- and soft-bottom habitats is a consequence of their ability to form dense aggregations. These aggregations confer many of the ecological advantages of a clonal life style (Jackson 1977) to an organism that is phylogenetically constrained to a solitary design.

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