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RECRUITMENT AND POSTRECRUITMENT INTERACTIONS IN A COLONIAL HYDROID

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Abstract. The colonial athecate hydroid Hydractinia echinata encrusts gastropod shells inhabited by hermit crabs of the genus Pagurus. In field samples recruits were found clustered in specific locations on the undersurface of Urosalpinx cinerea shells. Assays of the behavior of larvae indicated that the bacteria that induce metamorphosis coat the entire shell. A series of laboratory experiments demonstrated that site-specific recruitment reflected the interplay between initial sites of contact with the shell, movement prior to metamorphosis, and differential mortality after metamorphosis. In situ experiments demonstrated that growth rates were high in the areas most frequently occupied by recruits. Recruitment sites determined the ontogenetic timing of subsequent intraspecific encounters between colonies, and thus influenced both the cost and outcome of competition. These results show that bacterial induction of metamorphosis is associated with extensive juvenile mortality, that field distribution of recruitment represents differential mortality rather than adaptive patterns of habitat choice, and suggest that environmental variation in recruitment position acts to maintain genetic variation in competitive ability.

Key words: competition; differential mortality; dispersion; hermit crab; Hydractinia; hydroid; larval movement; microhabitat; Pagurus; recruitment; settlement; Urosalpinx.

INTRODUCTION

Sessile organisms are dependent on a choice of habitat made by the dispersal stage of their life cycle. A number of remarkably sophisticated devices have evolved to insure the selection of an adequate habitat. For example, plants often display elaborate relationships with seed pollinators (see Gilbert and Raven 1973) and sessile marine invertebrates often utilize subtle chemical and/or biological cues (see Meadows and Campbell 1972, Scheltema 1974, Buss 1979). While mechanisms of habitat selection are often effective in the localization of an adequate habitat on a gross spatial scale, the fidelity of pollinators and/or cues to metamorphosis to favorable sites for growth and development remains largely unknown (Keough and Downes 1982, Louda 1983, Weathere 1986).

The relative effectiveness of many mechanisms of habitat selection may be expected to be scale dependent. The mechanism may act to locate a site with high probability of survivorship relative to other sites on a gross spatial scale, but provide little resolution of appropriate microsites within the selected areas. In marine invertebrates, bacterial induction of metamorphosis is widespread and serves as a useful model in which to address the spatial scale over which habitat selection is effective. The small size and often quite specialized habitat distribution of bacteria offer the potential for quite precise location of appropriate sites of settlement. However, if bacterial distributions also map to unfavorable sites, this mechanism of habitat selection may induce recruitment to sites that are either inappropriate for further growth or that predispose adults to particular postsettlement interactions (a "cost of dispersal" sensu Strathmann et al. 1981).

Hydractinia echinata, a colonial athecate hydroid typically found encrusting hermit crab shells, displays several traits that make it suitable for the study of recruitment. Hydractinia echinata is induced to metamorphose in the presence of bacteria of the genus Alteromonas, and this requirement appears absolute, as larvae fail to metamorphose in their absence (Müller 1969, 1973, Spindler and Müller 1972; P. O. Yund, personal observation). The ultrastructure of both the planula larva and the process of bacterially induced metamorphosis have been described in detail (Weis et al. 1985, Weis and Buss 1987). In addition, the mechanism and phenomenology of competitive interactions between colonies of H. echinata have been investigated (Ivker 1972, Buss et al. 1984; L. W. Buss and R. K. Grosberg, personal communication) allowing assessment of the effects of recruitment patterns on subsequent postsettlement interactions. Finally, gastropod shells are an easily manipulated substrata whose approximate shape and dimensions are replicated in great numbers, facilitating experimental analysis of settlement.

We have explored the relationship between induction of metamorphosis by bacteria, subsequent juvenile mortality, and postsettlement interactions by (a) documenting the distribution of H. echinata recruits on Urosalpinx cinerea shells in the field, (b) assaying...
the distribution of inducing bacterial species on these shells, (c) quantifying the contribution of larval settlement, movement, and differential mortality in producing natural patterns of recruitment, (d) exploring the consequences of recruitment position on subsequent growth and survivorship, and (e) determining the effects of recruitment position on the duration, cost, and outcome of intraspecific competitive encounters between adult colonies. These data prompt us to suggest that bacterial induction of metamorphosis is associated with substantial juvenile mortality, that correlations between sites of recruitment and enhanced survivorship need not be the result of adaptive habitat choice, and that genetically based variation in competitive ability may be maintained by variation in recruitment sites.

Materials and Methods

Study species

*Hydractinia echinata* colonies are dioecious, gametes are released at dawn (Bunting 1894, Ballard 1942), eggs drop unprotected to the substratum, and zygotes develop directly into crawling larvae. Planulae adhere to sand grains by their anterior pole and extend their posterior pole, rich in nematocysts and neurosensory cells, into the water column, where they encounter passing hermit crabs (Weis et al. 1985). The disturbance produced by a moving shell, presumably sensed by neurosensory cells and/or cnidocils, results in the discharge of nematocysts (Schijfsm 1935, Cazaux 1958, Müller 1969, Chia and Bickell 1978, Weis and Buss 1987). Once on a shell, larvae crawl over the surface until they encounter any of four different species of the bacterial genus *Alteromonas* (Müller 1969, 1973, Spindler and Müller 1972). Contact with inducing bacteria results in the cessation of larval movement (Müller 1969), secretion of the contents of mucus cells, loss of neurosensory cells, and initiation of metamorphosis (Weis and Buss 1987).

Experimental overview

This paper is composed of a number of different experiments that explore the process of settlement and recruitment in *H. echinata*. Larvae make contact with a shell, move, contact bacteria, and metamorphose. After settlement, they either start to grow or die. If they grow they may engage in competition, in which they either win or die. In order to facilitate an understanding of how each experiment relates to the process as a whole, we have provided a flow chart (Fig. 1). The experiments reported below test the effects and relative importance of these processes.

Larvae used in these experiments were produced by mating newly collected colonies. Pairs of male and female colonies were isolated in the dark overnight, morning light triggered the release of eggs and sperm, and fertilized eggs were transferred to fresh seawater, where they developed into competent planulae in 2–4 d. All shells used as settlement surfaces were used within 7 d of collection and all planulae within 3 d after fertilization. Larvae retained for longer periods are lethargic and shells begin to lose their potential to induce metamorphosis.

All field work and collections for mating purposes were done at the Yale Peabody Museum Field Station in Old Quarry Harbor, Connecticut, on Long Island Sound (41°16’ N, 72°44’ W). Two different sites, Harrison Point and Baines Island, were used at various times in this study. These two locations are at the mouth of Old Quarry Harbor, <200 m apart.

**In situ patterns of recruitment**

The positioning of *H. echinata* recruits on *U. cinerea* shells was documented from shells collected along a transect line at Harrison Point, during the summer settlement season (May to September) in 1982 and 1983 (Observation 1 in Fig. 1). Each shell was examined with a dissecting microscope, and the location of recruits marked on a standardized camera lucida drawing of a *U. cinerea* shell. The majority of our sample consisted of very young colonies (<10 polyps, hence <1 wk old). Thus, recruitment patterns represent the end product of larval movement, settlement preferences, and site-specific pre- and early postmetamorphic mortality.

![Flowchart of the recruitment process from initial contact between larva and shell through adulthood](image-url)
Distribution of inducing bacteria

To insure that larval metamorphosis on shells accurately assays the distribution of inducing bacteria, we compared the rate of larval metamorphosis on autoclaved shells and shells collected from the field. Ten hermit crabs were removed from their shells by briefly heating the apex with a flame, shells were autoclaved, and autoclaved shells were re-tenanted with crabs. Autoclaved and control shells were then placed in dishes of sterile seawater in the dark with 100 larvae. The number of larvae metamorphosing on each shell was recorded after 24 h.

To test the hypothesis that the observed distribution of *H. echinata* recruitment mirrors an underlying distribution of the bacteria that induce metamorphosis, we assayed the distribution of inducing bacteria from observations of the behavior of larvae (Experiment 2, Fig. 1). A single larva was placed in one of nine different positions on the surface of a crab-inhabited *U. cinerea* shell. Shells were held motionless for 30 s to insure initial adherence of the larva to the shell. The shells were examined after 2 h and scored as to whether the larva had initiated metamorphosis at the site of contact. This procedure was replicated with 20 shells for each position. The outer surface of the *U. cinerea* shell consists of alternating ridges and grooves running longitudinally. Larvae were also scored for location within grooves or upon ridges before and after metamorphosis.

Initial patterns of contact

To determine the locations at which larvae initially adhere to the surface of a shell, we recorded the locations of contact between larvae and shells (Experiment 3, Fig. 1). Five hundred larvae were placed in a container filled with sand and seawater. The container was wrapped in aluminum foil with a single hole at the top so that the positively phototactic planulae positioned themselves atop sand grains. A crab-occupied *U. cinerea* shell was then introduced to the container and the crab and shell were allowed to move about for 1 min. The shell was removed, examined under a dissecting microscope, the location of any larvae adhering to the shell recorded, larvae were removed, and the shell returned to the container. This procedure was repeated until 10–15 contact points had been recorded for each shell, and was replicated with 11 shells.

Each shell used in this experiment was scored for the fit of the hermit crab to the shell by the method of Blackstone (1985). Crabs were teased with a probe until they retreated as far into the shell as they could go. Crabs that could retreat out of sight, or very nearly so, were scored as small for their shell. Crabs whose main claws formed a tight operculum in the aperture of the shell, without protruding, were scored as medium. Crabs whose main claw protruded from the aperture were scored as large for their shell. Of the 11 crabs used in this experiment, 6 were classified as small, 2 as medium, and 3 as large.

Larval movement

Four experiments were performed in order to elucidate the contribution of larval movement to the observed juvenile recruitment pattern (Experiment 4, Fig. 1). First, an experiment was designed to test the hypothesis that larval movement varies as a function of larval density. Larval movement was recorded for two density conditions. In the dense treatment six sibling larvae were placed adjacent to one another in a groove on the underside of the shell at a location where planulae frequently contact the shell. After 1 h, at which point virtually all of the planulae had begun metamorphosis, the distance of the planula from its initial position was measured by an ocular micrometer. In the solitary treatment, a single larva was placed in the same position and shells were agitated with forceps for 1 min to simulate the handling time required to establish the dense treatment. Six replicate shells were established for the density treatment and 36 for the solitary treatment, totaling 36 larvae for each treatment. The curvature of the shell introduced some error in distance measurements, but no systematic bias was present and the error was minimized by the short distances moved by larvae (<6 mm).

Recent observations of a bryozoan (Keough 1984) and an ascidian (Grosberg and Quinn 1986) have demonstrated that larval behavior relative to conspecifics can be influenced by their relatedness and/or histocompatibility determinants. *Hydractinia echinata* adults are known to express a genetically based historecognition system (Hauenschild 1954, 1956, Ivker 1972, Buss et al. 1984). Two experiments were performed to determine if larvae utilize a recognition system to respond to conspecific larvae or adults. To test the ability of larvae to respond to adults, *F₁* larvae known to fuse to both parents were produced. Larvae were then placed in a Petri dish with two related, histocompatible colonies (the parents) and two unrelated, histoincompatible colonies. Ten replicates were established, larvae were allowed to choose sites for metamorphosis, and the location of each recruit was marked on a camera lucida drawing. The distance of each larva to all four adults was then measured. To test the ability of larvae to move in relation to conspecific larvae, two groups of sibling larvae were produced from incompatible parents, each known to produce *F₁* offspring that would fuse with their own sibs, but reject *F₁* offspring of the other cross. Larvae from one cross were stained in a toluidine blue solution (0.5%) for 20 min. The stained and unstained larvae were allowed to settle in five Petri dishes, and their settlement sites recorded as above. In both of these experiments water used in the Petri dishes was taken from containers previously inhabited by hermit crabs, insuring the presence of the appropriate bacteria to induce metamorphosis.
The final experiment on the effect of larval movement examined movement on shells prior to settling combined with early differential mortality. Five of the shells classified as occupied by small crabs in the experiment designed to determine the initial pattern of contact between larvae and shells (described in the previous section, Experiment 3 in Fig. 1) were kept in their containers for 36 h, at which point the positions of newly settled polyps were recorded.

**Differential mortality**

Postmetamorphic survivorship was determined at four locations on *U. cinerea* shells: in the siphon of the shell (labeled and hereafter known as “siphon,” Fig. 2), on the back of the shell where the first whorl joins the spire (labeled and hereafter referred to as “back,” Fig. 2), the aperture where the first whorl joins the spire (labeled and hereafter known as “aperture,” Fig. 2), and the “rub spot” (i.e., an area of the shell which is chafed as the crab walks) (Fig. 2). Two sets of survivorship data were collected. (1) These four locations are a subset of the nine used in the experiment on the distribution of the inducing agent. Primary polyps in that experiment were examined 22 h after metamorphosis, generating survivorship data for *H. echinata* on the shells of isolated crabs. (2) In an effort to approximate field conditions more closely, a similar experiment was performed in an aquarium with a sand substrate and higher hermit crab densities. Larvae were allowed to settle in these four locations. Shells harboring primary polyps at these locations were released into the aquarium, and the number of larvae surviving was scored after 24 h.

**In situ survivorship and growth**

To determine whether sites of recruitment in the field correspond to sites suitable for the development and persistence of adults, the growth rates and survivorship of three different strains were determined in situ during the summer of 1983 (Experiment 6, Fig. 1). Each strain was established in three different positions on *U. cinerea* shells, simulating recruitment in that location. Two of the three positions used were the locations where we most often found recruits in the field: the siphon and the aperture. The third location, on the back of the shell, was chosen as a location where recruits were more rarely found in nature.

Genotypic replicates were established by explanting tissue from laboratory stock colonies onto shells. Stock colonies had originally been collected from Harrison Point, Long Island Sound, or were first-generation offspring of colonies collected from this site. All strains had been maintained in laboratory culture for up to 1 yr prior to use in the experiment. Three polyp explants were removed from stock colonies and held in the desired position on the shell with quilting thread until they attached (1–3 d) and began to grow onto the shell. The strings were removed and *P. longicarpus* that had been removed from their shells by the method of Blackstone and Joslyn (1984) were allowed to occupy the shells. Crabs, shells, and colonies were maintained in a running seawater system for 5–10 d; the colonies were trimmed with a scalpel to a uniform size of five polyps and placed into field enclosures.

Enclosures were 19-L (five-gallon) buckets with the bottoms removed and the lids replaced with 0.6-cm Vexar screen. Buckets were pushed halfway into the mud–gravel bottom 7 m below the water surface adjacent to Baines Island, Long Island Sound. Using SCUBA, crabs were placed in these cages, one crab to a bucket. Crabs were retrieved from the field enclosures once a week, the number of feeding and reproductive polyps on each shell was counted under 12× magnification, and shells were returned to the field the same day. Crabs in transit were kept isolated in plastic scintillation vials to prevent colony damage.

This caging procedure produced an environment that differed from naturally occurring conditions in two important ways. First, the buckets acted as sediment traps, thus potentially trapping suspended infauna and leading to artificially inflated food levels. Second, since crabs were isolated in each bucket, the potentially detrimental effect of aggression between crabs on the hydroids was removed. Nevertheless, this experiment provides a valuable relative measure of the performance of colonies recruiting to various positions.

**Recruitment sites and intraspecific competition**

When more than one larva metamorphoses on a given shell, the relative settlement locations of the larvae will ultimately determine the size at which colonies encounter one another. To determine the effect of intercolony spacing on the cost and outcome of subse-
Results

In situ recruitment

Does *H. echinata* recruit to specific sites on a shell? Recruitment on *U. cinerea* shells is concentrated on the undersurface of the shell, particularly at the shell’s aperture and siphon (Fig. 2). Recruitment also tends to occur in crevices on the shell, as where two whorls meet. The number of recruits per shell ranged from 1 to 7, with 42% of the shells occupied by >1 recruit. There were no obvious variations in the spatial distribution of recruits as a function of recruitment density. Field samples may underestimate the actual frequency of shells occupied by >1 recruit, since shells might have encountered further recruitment had they remained in the field.

Distribution of inducing bacteria

Do assays of larval behavior and metamorphosis faithfully reflect the distribution of inducing bacteria? The mean number of larvae that metamorphosed on control shells was 7.40 (standard deviation 3.21, *n* = 5 shells), while only one larva metamorphosed on an autoclaved shell (*n* = 10 shells). Clearly, metamorphosis on control shells far exceeded that observed on autoclaved shells (*t*-test, *P* < .05). These results confirm that larval metamorphosis observed in our experiments was induced by some heat-labile agent on the shell’s surface. As stated earlier, previous work (Müller 1969, 1973) has shown this agent to be bacteria of the genus *Alteromonas*.

Does the distribution of recruits seen on field-collected shells mirror the distribution of the inducing bacteria? Larvae metamorphosed at appreciable frequencies (>50%) in all nine positions tested (Fig. 3) and there was no significant effect of position (*G*-test, *P* > .25). Larvae were as apt to metamorphose in locations where they are rarely found in the field as in locations where they are commonly found.

Shell microtopography had an effect on larval settlement. Larvae initially placed on ridges moved at higher frequencies than larvae placed in grooves (*G*-test, *P* < .025), and metamorphosis occurred in grooves at a higher frequency than on ridges (*G*-test, *P* < .05, sample size of 124). This pattern may well reflect an underlying microdistribution of the inducing agent.

Initial patterns of contact

Is the field recruitment pattern a function of the sites of initial contact between the larva and the shell? Laboratory experiments indicate that larvae contact the shell most frequently in the “rub spot” (Fig. 4), but recruits are rarely found in this location in the field (Fig. 2). Though most larvae contact the rub spot, there is a clear effect of crab shell fit. As the crab gets smaller in proportion to its shell, the larval distribution is more dispersed and more of the larvae contact other areas (Fig. 4). Crabs that are too small for their shells are...
often hindered in walking, tending to wobble and consequently bringing more of the shell into contact with the substrate. Although crab shell fit influences the initial distribution of larvae on shells, this effect must be interpreted with caution. Larvae frequently move prior to metamorphosis, and movement may swamp the effect of the pattern of initial contact.

**Larval movement**

Is larval movement a function of the density of larvae? The mean distance moved by larvae was calculated for each shell in the density treatment, and these means were compared to the distances moved in the solitary treatment with a $t$ test. Larval density did not have a significant effect on movement ($P > .05$). The majority of larvae move only a short distance from initial sites of contact with the shell (Fig. 5). The distance moved by larva was bimodal in both treatments. A possible explanation for this bimodality can be found in the microtopography of the *U. cinerea* shell. On 15 shells of a similar size, we measured the intergroove distance and found that it averaged 1.93 mm, with a standard deviation of 0.13 mm. This value closely corresponds to the distance between the two peaks in Fig. 5, suggesting that this movement pattern reflects the tendency of larvae to settle in grooves.

Can larvae distinguish between histocompatible and incompatible conspecifics? The distances of each larva from the two compatible and the two incompatible adults were compared with $t$ tests. There were no significant differences in any of the 10 replicates ($P > .45$). The spatial patterns of larval settlement relative to compatible and incompatible larvae were quantified by the method of Hopkins and Skellam (1954). Aggregation indices were calculated for all larvae as a group and for both kin groups separately. In no case did the aggregation index significantly differ from 0.5 ($P > .05$), indicating that larvae were randomly dispersed. *H. echinata* larvae are either unable to determine kin relationships, or are unable to exploit this information at the time of settlement. Thus larvae are unable to avoid future intraspecific competitors at the time of settlement.

Is the field recruitment pattern a function of larval movement and differential mortality prior to settlement? Larvae dispersed from their initial points of contact with the shell (Fig. 6A) to reflect more closely field recruitment patterns (Fig. 6B, C). Larvae were nevertheless found in locations rarely observed as field recruitment sites (e.g., the rub spot and the back of the shell).

**Differential mortality**

Does early postmetamorphic survivorship generate the distribution of naturally occurring recruits? There was no significant difference in survivorship between the data sets generated in experiments on distribution of inducing bacteria and on differential mortality (test for equality of percentages, $P > .15$, Sokal and Rohlf
RECRUITMENT AND COMPETITION

location, since the time span of the experiment was only 22–24 h, and newly metamorphosed colonies in the field are vulnerable for several days (see in situ experiment below). Higher postmetamorphosis mor-

1969:608). Therefore, data from these two experiments were combined for the analysis of differences between positions. Survivorship at the aperture, siphon, rub spot, and back positions was 89, 95, 60, and 82%, respectively ($N = 26, 18, 26, \text{and } 25$, respectively). $G$ tests were performed on all six pairwise combinations of positions. Only differences between the rub spot and the siphon ($P < .025$) and the rub spot and the aperture ($P < .05$) were significant. Positions on the back of the shell displayed greater mortality than aperture or siphon sites, but these differences were not significant. This experiment underestimates total mortality in each

FIG. 6. Larval movement. (A) Initial sites of larval contact (identical to Fig. 4A). (B) Settlement sites on the same shells after 36 h. Note that these metamorphosed larvae are not the same individuals as in A. (C) Recruitment sites in the field, after movement and differential mortality. Note that this figure (identical to Fig. 2) does not constitute a third observation on the same set of shells. Fig. 6A and C are repeated to facilitate comparison between sites of original contact, larval movement from these sites, and field distributions.

FIG. 7. In situ growth and survivorship. (A) Survivorship curves for each recruitment position. Each point represents the percentage of the initial cohort surviving at that time. (B) Growth curves as a function of time for each recruitment position. Points represent the mean number of feeding and reproductive polyps combined. (C) The mean number of reproductive polyps as a function of time for each settlement position.
tality at the rub spot, and also on the back of the shell (see in situ experiment below), contributes to the siteselective recruitment pattern.

In situ survivorship and growth

Do colonies that metamorphose in naturally occurring recruitment sites realize advantages in situ in increased juvenile survivorship, growth rate, and reproductive output relative to those recruiting to less favored sites? Survivorship curves for colonies established at three different sites (Fig. 7A) were calculated by determining the percentage of the initial cohort that was still alive each week. Only colonies known to have died while on a crab-occupied shell were counted as dead; colonies on crabs that escaped from enclosures, were lost during the collection process, or that died, were excluded from this analysis. Survivorship in the back position, the site least commonly occupied in the field, was lower than in the other two positions, due mainly to heavier mortality at a small size (during 1st wk, chi squared, \( P < .25 \)). Colonies that recruited outside of the two commonly occupied areas suffered higher juvenile mortality.

Two further tests were performed to determine the effects of recruitment position on growth and reproduction of surviving colonies. Colony growth over time was approximately logistic, with the logarithmic growth phase lasting through week 7 (Fig. 7B). The total number of polyps in each colony at each point in time through week 7 was log-transformed to linearize the data. A linear regression was then calculated for each position, with the intercept forced through zero, and the slopes of the equations compared in all three pairwise combinations with \( F \) tests (Program P1R, BMDP). The results are shown in Table 1A. Colonies on the back had a significantly smaller slope, indicating a lower growth rate, than colonies in the siphon or near the aperture, which were not significantly different from one another. Mortality throughout the experiment resulted in unequal sample sizes and made these statistical techniques preferable to a repeated-measures ANOVA.

The number of reproductive polyps at each week through week 7 was analyzed in a similar fashion. The data were log-transformed and linear regressions calculated, but the slopes were not forced through zero, as the onset of reproduction was highly variable. The data were grouped by starting position and strain, and the equations were compared with pairwise \( F \) tests, which test for differences between both the slopes and the intercepts (Program P1R, BMDP). No significant differences were found between coefficients (Table 1B).

These results indicate that colonies that recruit to the aperture and siphon positions have higher survivorship and growth rates than colonies that recruit to an area outside of these positions (the back). The pattern by which colonies cover shells in situ (Fig. 8) offers a simple explanation for these results. Colonies that recruit to the commonly occupied sites in the siphon and by the aperture inevitably direct their initial growth around the aperture until they surround it (Fig. 8A, B). Colonies that recruit to the back of the shell first direct
their growth down one or both sides toward the aperture. Upon reaching the aperture, these colonies also expand to surround it (Fig. 8C). A large fraction of the food consumed by the colony is captured from the feeding currents of the hermit crab (Christensen 1967). Newly metamorphosed polyps in the siphon or by the aperture find themselves bathed in the crab’s feeding currents, whereas young colonies on the back of the shell are distant from this food source. Hence colonies in the siphon or by the aperture would be expected to enjoy higher growth rates and survivorship at small size than colonies on the back, as was observed. Furthermore, this position effect should disappear once those colonies surviving on the back increase in size and reach the zone of high food levels, as observed in the lack of clear differences in reproductive output.

**Recruitment and intraspecific competition**

Do differences in recruitment location result in differences in the outcome or the cost of competition? Combats between two colonies initiated in the same location all resulted in the death of one combatant (strain 3) within 9½ wk (Fig. 9C, D). The same genotype (strain 2) won all of these encounters, and its growth dropped only slightly below that of the controls (Fig. 9D). In contrast, in none of the combats in which the two colonies were initiated at different recruitment positions had the contest been resolved by the end of the 9½ wk experimental period (Fig. 9A, B). During this period, colonies involved in competition suffered a marked reduction in polyp number relative to their control groups (Fig. 9A, B). The outcomes of these interactions were checked after 18 wk, and only four of the interactions had led to exclusion by this time. The outcomes were not strictly determinate; of the four interactions that went to exclusion, three were won by the same genotype that won all of the smaller fights, but there was also one reversal. Thus, recruitment site strongly influences both the outcome and cost of competition.

**DISCUSSION**

*Spatial scale, bacterial induction, and juvenile survivorship*

The larvae of *H. echinata* occur at the sediment-water interface and gain access to hermit crabs via nematocyst discharge (Schijfsma 1935, Cazaux 1958, Müller 1969, Chia and Bickell 1978, Weis and Buss 1987). Once on the shell, settlement is dependent upon the presence of appropriate bacterial species. While colonies are, on rare occasions, found on immobile substrata (Karlson 1978) and while one of us (C. W. Cunningham) has observed metamorphosis, indicating bacterial presence, on algae, the two-step mechanism appears to insure that the larvae will locate hermit crab shells with high fidelity.

Yet the efficacy of this mechanism of habitat selection appears to be scale dependent. The coupled system of habitat selection of moving objects populated by appropriate bacteria insures that the overwhelming majority of larvae contact the undersurface of the shell (Fig. 4). Locations on the back of the shell, shown to be less amenable to larvae in terms of both growth and survivorship (Fig. 7), are avoided by most larvae as a consequence of the tendency for larvae to contact the shell’s undersurface and to move only short distances from the site of contact with the shell (Figs. 5, 6). At the scale of the shell itself, the *H. echinata* system appears moderately effective at locating the best side of the shell. However, the precise site of settlement on the shell surface is apparently not assured. Unless the larva is capable of recognizing and avoiding bacterial cues at inappropriate sites, settlement will be com-
Fig. 9. Competition as a function of recruitment position. Points represent the mean number of polyps (±1 sd) in colonies as a function of time. Shell sketches to the right indicate the recruitment scenario for the competitors in the two graphs on that line; one colony by the aperture and the second colony in the siphon for (A) and (B), vs. both colonies by the aperture in (C) and (D). Strains were paired in combats with the strain in the graph next to them, so that the competitor in (A) was fighting the competitor in (B) and the competitor in (C) was fighting the competitor in (D).

pelled at these sites. *Hydractinia echinata* larvae are apparently unable to avoid settlement in sites occupied by the bacteria. Larvae cease movement upon contact with the bacteria (Müller 1969). Bacterial induction is associated with the loss of neurosensory cells and the release of the contents of mucus cells (Weis and Buss 1987). The former presumably limits the larva’s capacity for further sensation, and the latter acts to adhere the larva to the substratum. Since the inducing bacteria occur over the entire surface of the shell (Fig. 3), and certain regions of the shell are more amenable to the development and persistence of adults than other regions (Fig. 7), substantial juvenile mortality occurs.

These results are of potentially broad significance. Many marine invertebrates respond to bacterial cues for metamorphosis, and our results suggest that microfloral induction of metazoan metamorphosis would be expected, a priori, to insure high juvenile mortality. Substantial juvenile mortality can be avoided only if (1) there is a one-to-one association of sites appropriate for bacterial growth and for metazoan growth, (2) all inappropriate sites occupied by bacteria are inaccessible to larvae, and/or (3) larvae have the capacity to avoid settlement in an inappropriate site harboring the inducing bacteria.

**Adaptive patterns of habitat choice**

Larval settlement is usually inferred from observations of field recruitment, and frequently interpreted as representing adaptive patterns of habitat choice. Patterns of field recruitment, however, are confounded by the process of postmetamorphic mortality (Keough and Downes 1982). Recruitment patterns may reflect the differential mortality of individuals that have settled in inappropriate sites, rather than adaptive patterns of habitat choice. This appears to be the case in *H. echinata*. Recruits observed in the field are clustered in sites that both laboratory and field experiments show to be amenable to development and persistence of adults (Figs. 2, 7), inviting an adaptationist interpretation.
However, observations of larval settlement show that metamorphosis can occur at high frequencies at several sites on the surface of the shell (Fig. 3). Young colonies occur in sites amenable to further development only as a product of undirected larval movement and extensive differential mortality (Figs. 6, 7). These observations strongly suggest that apparently adaptive field recruitment patterns should be interpreted with caution.

**Recruitment and intraspecific competition**

The mismatch between favorable sites for colony survivorship and sites that induce metamorphosis has potentially profound significance in determining the course of postsettlement interactions and, in turn, in shaping organismal adaptation to postsettlement sources of mortality. Unless a species is capable of assessing the presence, density, and/or size of other recruits, variation in recruitment generated by the mismatch will insure asymmetries in subsequent competitive encounters. Variation in competitive ability among colonial marine invertebrates has been documented in detail (reviewed by Jackson 1983, Buss 1985), and is known to vary as a function of encounter angle (Jackson 1979, Buss 1981a. Rubin 1982), size (Connell 1961, Day 1977, Buss 1980, Russ 1982), and density (Buss 1981b). Each of these parameters is highly sensitive to variation in recruitment, suggesting that variation in recruitment site may be responsible for maintaining variation in competitive ability in sessile marine invertebrates (Buss 1985).

Larvae of *H. echinata* are apparently unable to sense the presence of conspecifics and hence avoid occupied substrates and subsequent intraspecific competition. Recruitment occurs at high frequencies at several locations on the shell, generating considerable variation in the distances separating recruits on a given shell (Fig. 2). Recruitment to different sites on the shell insures that colonies will encounter one another at different stages in their ontogeny, with different outcomes and vastly different costs of competition (Fig. 9). Variation in sites of recruitment results in variation in the ontogenetic stages in which colonies engage in competition.

Competitive ability in *H. echinata* varies as a function of colony ontogeny. The relative rate of production of stolonal tissues through ontogeny is highly variable (Schijfsma 1939, Hauenschild 1954, McFadden et al. 1984), such that colonies range from highly stoloniferous to completely stolonless. This variation is genetically based (McFadden et al. 1984) and is responsible for ontogenetic variation in competitive ability (Buss et al. 1984). Stolons that contact allogenic tissue are induced to differentiate a specialized hyperplastic stolon (Müller 1964, Ivker 1972, Buss et al. 1984). Hyperplastic stolons are formed by the widespread movement of multipotent interstitial cells and cnidoblasts into the stolon tip, where they mature into nematocysts. Nematocysts discharge into a competitor’s tissues, causing considerable local destruction. The cumulative effect of several such stolon encounters frequently leads to the demise of competing colonies (Fig. 9). Since colonies differ in their ontogenetic rates of stolonal production, competitive ability varies with ontogeny.

The competitive mechanism of *H. echinata* appears to allow colonies to exploit differentially the various habitats produced by environmental variation in recruitment. Variation in recruitment produces some shells occupied by only one colony, some by two or more colonies. Since stolonless colonies display higher fecundity (P. O. Yund, personal observation) and poorer competitive ability than stoloniferous forms, stolonless colonies are favored on shells lacking other recruits. Conversely, stoloniferous colonies, which display a greater competitive ability, are favored on shells occupied by more than one recruit. These considerations can be expanded to account for intermediate morphologies. Growth phenotypes which are stolonless early in ontogeny and stoloniferous late in ontogeny would be favored on shells on which recruits had become established at distant locations. Conversely, growth phenotypes which are stoloniferous early in ontogeny and stolonless late in ontogeny would be favored on shells on which recruits had become established near one another. Associated with each growth phenotype is a recruitment habitat in which its fitness would be expected to exceed that of rival phenotypes. Thus the available evidence is consistent with the hypothesis that variation in recruitment position acts to maintain the variation in competitive ability seen in *H. echinata* (Buss 1985).

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**Literature Cited**


