Effects of body size and resource availability on dispersal in a native and a non-native estuarine snail

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Abstract

I manipulated snail densities of two coexisting species of salt marsh snail, *Cerithidea californica* Haldeman (native) and *Batillaria attramentaria* Sowerby (non-indigenous) to investigate how resource levels set by intraspecific competition may influence dispersal rates. I used two distinct size classes of the snails (mature and immature) to determine if the effects of competition on dispersal differed between developmental stages of a consumer. Dispersal attempts were measured within enclosure pens by counting snails climbing the sides of the enclosure. The influence of snail density per se and resource levels (which were set by snail densities) on dispersal rates were separated by comparing responses of snails to density before and after resources became depleted. For large snails of both species, dispersal increased as resource levels decreased, supporting the hypothesis that competition influences dispersal rates. Small snails of both species, in contrast, always dispersed at relatively higher rates than larger individuals, but were not influenced by variation in resource levels. This result corroborates other studies that have shown reduced competition in these species at smaller size, and suggests that another mechanism, such as genetically coded behavior to disperse when young, influences their behavior. Previous experiments demonstrated *Batillaria's* superior resource conversion efficiency; therefore, I had hypothesized that for any given resource level, *Cerithidea* would disperse more, because it was more affected by resource availability. Adult *Batillaria*, however, responded more sensitively to resource levels (i.e., dispersed more at any given resource level) than *Cerithidea*. This counterintuitive result illustrates the potential importance of genetic limitations on behavioral responses available to a species. Constraints on behavioral responses may have been accentuated since *Batillaria* is a non-indigenous species whose evolved behavioral responses are not necessarily adapted to its present, non-native environment.   © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Dispersal is a commonly observed short-term response to competition among mobile species (Holbrook and Schmitt, 1989; Korona, 1991; Naslund et al., 1993; Weins et al., 1993; Iribarne et al., 1994; Crowe and Underwood, 1999). Increases in competitor density may intensify resource depletion or interference behaviors that create unfavorable conditions and stimulate departure (Underwood, 1977; Levinton, 1979; Branch and Branch, 1981). By necessity however, experiments used to quantify competitive effects on vital rates typically rely on enclosures (e.g., cages, pens) to ensure that a constant density of competitor is maintained throughout the experimental period, and secondarily to ensure initially measured organisms are retrievable at termination. Because dispersal is prohibited, competitive effects measured inside enclosures may be artificially intensified because containment disallows a natural "pressure release valve" of dispersal. Nonetheless, in the majority of enclosure experiments the ability of dispersal to potentially mitigate measured competitive effects is often ignored, or only occasionally speculated (e.g., Lee, 1996). Creative attempts to capture both responses have been rare (see Denno and Roderick, 1992; Fenske, 1997).

To investigate intraspecific competitive interactions of a native and a non-indigenous salt marsh snail, I enclosed snails using a range of intraspecific densities. Byers (in press) presents quantification of the intraspecific competitive effects of snail density on resource availability and snail growth rates. Here I present my effort to simultaneously quantify levels of (attempted) dispersal due to competition while still allowing accurate quantification of the aforementioned intraspecific competitive effects of snail density. To quantify snail responses to constant density and snail dispersal attempts concurrently, I capitalized on an aspect of these snails' biology – that they readily climb vertical substrates. To measure the number of snails trying to disperse from enclosure pens, I counted daily the number of snails climbing the sides of the enclosures before placing them back onto the mud bottom of the enclosures.

As the influence of competition on dispersal may be influenced by the developmental stage of an organism, I also examined competition's effect on dispersal as a size-structured process. Behavioral and life-history differences between developmental stages of organisms result from ontogenetic shifts in exposure to, and impacts from, predators (Mittlebach, 1988; Werner and Hall, 1988; Sousa, 1993; Arsenault and Himmelman, 1996; Mol, 1996; MacPherson, 1998), parasites (Lafferty, 1993a; Murdoch et al., 1995; Kollar, 1996; Calvo-Ugarteburu and McQuaid, 1998), environmental stress (Anger, 1995; Dabrowski et al., 1996), and competition (Bergman and Greenberg, 1994; Loreau and Ebenhoen, 1994; Arendt and Wilson, 1997). Thus, juveniles and adults are likely to be differentially stimulated by any given influence. Incorporating size as a variable in analyses may help account for some otherwise unexplained variation in dispersal rate and allows for the testing of whether the influence of competition on dispersal differs between life stages of the study organism. That is, the amount small individuals disperse in comparison to large conspecifics may indicate something about the relative environmental pressures acting on the study species and how the influences of these processes vary with the development of the organism.

1.1. The study system

Cerithidea californica Haldeman is an epifaunal grazing snail whose habitat in northern California has been invaded by *Batillaria attramentaria* Sowerby, an ecologically similar species (Byers, in press). Both snails share the same limited food resource, epipelic diatoms (Whitlatch and Obrebski, 1980), and have been shown to interact almost exclusively through exploitative competition (Byers, in press). From an enclosure experiment I determined that while both species' per capita effect on resource levels is virtually identical, *Batillaria* achieves a marked advantage over *Cerithidea* through its superior resource conversion efficiency (Byers, in press). For a given level of resource *Batillaria* adds on average 20–30% more tissue mass than *Cerithidea* during the growing season – an advantage that translates into faster population growth and is a sufficient mechanism to account for displacement of the native snail (Byers, in press). Heightened metabolic efficiency in general has been demonstrated to decrease a species' sensitivity to competition for shared resources (Clarke, 1996; Murdoch et al., 1996; Baruch and Goldstein, 1999; Bystrom and Garcia-Berthou, 1999). The species appear to have similar capacities for movement, as large snails of both species have been observed to move similar net distances of 9–10 cm per day over the marsh surface (J.E. Byers, unpublished data). Both snails are frequently observed clinging to vertical surfaces such as vegetation (*Salicornia virginica* and *Distichlis spicata*), rocks, and woody debris in the marsh (McDermott, 1996, J. Byers, personal observations). During a cumulative 2-h search over two tidal series I found 324 snails of both species climbing vertical surfaces.

Because I use climbing as a measure of snail dispersal it is important to know whether the snails may be climbing for reasons other than attempted dispersal. Dispersal in at least one snail, *Hydrobia ventrosa*, has been demonstrated due to food limitation (Levinton, 1979). Climbing in aquatic molluscs, however, has often been explained as an escape from subtidal predators (Warren, 1985; Main, 1987; Vaughn and Fisher, 1988; McKillup and McKillup, 1993; Duncan and Szelistowski, 1998), behavioral modification due to infections of trophically-transmitted parasites (Levri and Lively, 1996; McCoy and Nudds, 1997), and alleviation of harsh physical factors such as substrate temperature (McBride et al., 1989; Williams and Appel, 1989; McGuinness, 1994). In the *Cerithidea–Batillaria* system however, these typically implicated stimuli are unlikely to be of much influence. Both species are the primary host for a suite of trematode parasites (Sousa, 1983; Lafferty, 1993a; McDermott, 1996), however these parasites do not likely influence climbing behavior because the increased height of climbing snails would not facilitate their successful transmission to the secondary fish and crab hosts (K. Lafferty, personal communication). Regardless, the obligatory multi-trophic life cycle of these parasites ensures that the snails cannot transmit the parasites directly to one another; therefore, even if parasites incidentally affect climbing rates, as snail density increases parasites should not cause an increase in the proportion of snails climbing. In addition, the small (immature) size class used in this experiment is virtually uninfected by these trematodes that only inhabit mature gonads (Byers, in press; Sousa, 1983; Lafferty, 1993a; McDermott, 1996). Finally, predation by macro predators on the snails is uncommon (Stenzel et al., 1976; Sousa, 1993; McDermott, 1996) and the two largest

potential environmental stressors for these snails, freshwater run-off and sedimentation, are virtually absent in the summer months when this study was conducted (McDermott, 1996, J. Byers personal observation). In any event, demonstration of climbing as a density and resource dependent process supports competition as the predominant stimulus for dispersal.

As the role of exploitative competition in this system (Byers, in press) and among other gastropods is strong (Underwood, 1978; Branch and Branch, 1980; Levinton, 1985; Skilleter and Underwood, 1993), I hypothesized that resources would decrease with increasing snail density, causing snails to disperse more. If dispersal is motivated primarily by low levels of resources, when resources are high the relationship between dispersal and snail density should be weak regardless of snail density. At a later sampling time however, I expected density would exert a strong effect on snail dispersal since resources were likely to become depressed in high-density treatments and remain high in low density treatments. This differential effect of snail density through time would manifest itself as significant effect of density on the difference in snail dispersal rates after and before resource depression. Additionally, from my previous studies on these snails I hypothesized that because *Cerithidea* is impacted more heavily than *Batillaria* by low resource availability, *Cerithidea* should disperse at a higher rate than *Batillaria* as a means to seek areas with less exploited resources. Conversely, because *Batillaria* converts resource more efficiently than its competitor I expected it would tolerate lower resource levels and disperse less than *Cerithidea* for any given level of resource. Since small snails experience reduced effects of competition due to lower quantities of resource needed, i.e., resources are not as limiting (Byers, in press), I expected a weakened density dependent dispersal response to resource levels in small snails relative to large snails. For the same reason, the absolute proportion of small snails that disperse in comparison to large snails should be less if the behavior is motivated entirely by competition. Alternatively, heightened predation or general dispersal tendencies may induce small snails to disperse more frequently than large snails.

2. Methods

To measure both short-term (dispersal) and long-term (growth, resource equilibrium) responses of each snail species at two distinct size classes to variations in intraspecific densities, I conducted experiments in Bolinas Lagoon, California, 20 km north of San Francisco Bay, from 29 June to 8 August, 1995. Details and results of long-term responses are presented in Byers (in press). I measured densities and sizes of snails from mean high tide level to mean low tide level along transects that ran perpendicular to a primary channel feeding the salt marsh at the southern end of the lagoon. As manipulating snail density has been shown to be an effective method to manipulate resource levels (Byers, in press), I created an array of enclosure pens in which to maintain experimental snail densities. I arranged a row of pens parallel to the channel along a height contour which the density measurements had shown to contain approximately equal numbers of both species of snail [*Cerithidea*, 19.0 ± 0.80 (S.E.);

Batillaria 24.4 mm±5.26 per 0.1 m²] and similar mean sizes [*Cerithidea*: 21.2 mm±0.80 (S.E.); *Batillaria*: 17.2 mm±0.59]. Pens were constructed of 2 mm clear Vexar mesh formed into cylinders 35 cm in diameter which I inserted 8 cm into the mud substrate of the marsh; each pen thus enclosed ~0.1 m² of natural marsh bottom and protruded 0.42 m above the mud surface. The pens had open tops to minimize effects of shading on diatom growth. I removed all snails from the pens and rubbed each mud bottom by hand to ensure that all snails had been removed and to homogenize any initial spatial variability in epipelic diatom densities. Analysis of this technique indicated that this rubbing is effective at reducing diatom levels to near zero and results in a rapid recovery, even in the presence of grazers, peaking 17–18 days after rubbing and settling to stable levels about 27–28 days after rubbing (Fig. 1). After rubbing the pens were left undisturbed for three days before initiating the experiment.

During these three days I collected snails and sorted them in the laboratory by species into two size classes: 8–10 mm (immature) and 18–20 mm (mature). Both species typically reach maturity at 13–15 mm (Whitlatch, 1974; Lafferty, 1993a). I placed 12, 23, 35, 46, 69 or 92 individuals of either *B. attramentaria* or *C. californica* from a single
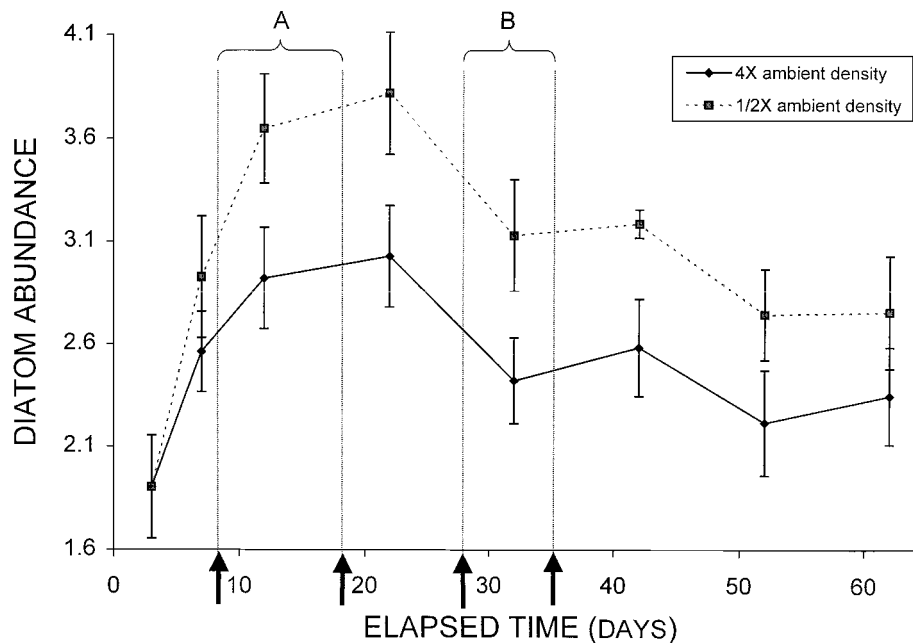

Fig. 1. Diatom abundance (μm² diatom surface area/μm² sediment surface area) at highest density (4× ambient density, ♦, –) and lowest density (1/2 ambient density, ■, - - -) of large snail grazers (±1 standard error) through time in 1997. Because analyses of snails on food resources showed little or no difference between species, I pooled data from both species at the same density level (for a total $n = 6$ for each data point). The marsh surface was homogenized, i.e., rubbed, on day 0 and the experiment was initiated, i.e., the snails were added, on day 5. Arrows and dashed vertical lines represent periods during which counts of climbing snails for peak and low resource abundance blocks were made [A = high resource sampling period, B = low resource (steady state) sampling period]. Data are from Byers, in press.

size class into each pen. Respectively, these treatment levels represented 1/2 ambient, ambient, 1.5× ambient, 2× ambient, 3× ambient and 4× ambient intraspecific densities. Because similar sized snails of each species affect their food resource identically, and because the snails' interact almost exclusively through their impacts on the shared resource (Byers, in press), the response of each snail in these intraspecific treatments should reflect its response to interspecific conditions as well. I used three replicates for each density level except for the 1/2 ambient treatment, for which I used four. During each morning low tide after addition of the snails to the pens I brushed snails off the sides of the enclosure pens to prevent their escape, to prevent snails from being able to feed on diatoms colonizing the pen walls, and to maintain the snails on the mud bottom of the pen at the proper density. I began recording counts of these climbing snails found on the sides of enclosures only after the experiment had been running for three days so that the snails could fully recover from any potential effects of handling during set-up.

In order to tease apart the effects of density per se and resource levels (which were set by varying snail densities) on climbing behavior, I performed low tide counts in two blocks – one while resources were reaching a peak (days 8–17) and one after resources reached their lowest stable levels (days 28–35). I define the resource stable state as the lowest level of resource given a constant density of consumers. Comparison of sampling times to diatom responses through time at highest and lowest grazer densities confirmed that these sampling blocks were squarely within time periods that should have corresponded to the highest and lowest resources available during the experiments (Fig. 1). To determine if snails exhibited density-dependent dispersal behavior before resources became limiting, I regressed the proportion of climbing snails against snail density during peak resource availability. To compare the effect of snail density on the change in dispersal after resources had declined to steady state levels I regressed the difference in the proportion of snails dispersing between peak and steady state sampling blocks against snail density for each size class of each species of snail. The intercept was examined for significant differences from zero that would indicate an overall increase (or decrease) in dispersal at lower resource availability. A significant effect of density on the difference in the proportion of snails climbing post and pre resource depression would indicate a differential effect of density during the period of lower resource availability. Since the same snails were used in high and low resource measurement periods, analyses on the difference in climbing rates between the two time periods for each enclosure pen also should correct for any within cage correlation between the two sample periods. To normalize the distribution data on proportion of snails climbing I analyzed the data after arcsine squareroot transformation.

To determine the effect tidal level had on the dispersal of the snails, I floated alongside the array of pens on an inner tube and systematically rubbed along the inner circumference from top to bottom while tallying the number of snails bumped off the pen wall. I performed these counts after resource levels were declining over a 10-day series of high tides when the water was approximately 0.3 m over the tops of the enclosure pens. During the high tide sampling dates (days 18–27) I advanced my time of sampling as the time of the tide advanced in order to maintain my counts from the same relative point of each tide. In order to ensure independence in high and low tide

sampling, low tide counts were not recorded during the block of days that high tide counts were performed.

Dispersal and effects of snails on the food levels might vary through the experiment as a consequence of changes in snail densities; therefore, I replaced dead snails in the pens every five days. Mortality, however, was quite low ($< 3\%$). The mean number of snails ($\pm$S.E.) that escaped daily, i.e., climbed or floated out of the enclosure pens, was low (0.14 ± 0.03), with a slight trend of increasing escapees in both species as the density of large snails increased. These missing snails were replaced within 24 h when their absence was detected during the following low tide counts. The level of parasitized snails in the experiment (determined after termination of the experiment by dissecting snail gonads) of both species combined was also low ($< 6.5\%$). In any event, parasites should not have influenced the response of the microalgal resource to snail grazing since infected snails have been shown to have the same effect on the resource as uninfected snails (Lafferty, 1993b).

To measure the final density of diatoms in pens after exposure to snail grazing, I cored the bottoms of all pens at the end of the experiment. I extracted three or four sediment cores from each pen with modified plastic syringes (diameter $= 1$ cm) to a depth of 6 mm, pooled all cores from each pen in a single scintillation vial, and immediately preserved the samples in 6% Lugol's solution in sterilized seawater. Samples were processed in the lab where I both counted and measured the surface area of diatoms cells in subsamples with a digitizing pad under a light microscope at $400 \times$ to calculate the total surface area of resource available to the snails (for exact protocol, see Byers, in press). With the exception of the $1.5 \times$ ambient density treatment (35 snails/0.1 m^2) for small snails and the few pens that were lost during the experiment, total surface area of diatom cells per area of sediment surface sampled was quantified for all pens. I used ANCOVA to test for effects of snail density and resource levels for differences in the dispersal rates between the two size classes of each species and between the two species at the same size class at high tide. To meet the assumption of linearity necessary for ANCOVA I log transformed snail densities to analyze the effect of snail density on dispersal of large snails. As for previous low tide analyses, the proportion of snails climbing was arcsine squareroot transformed.

3. Results

3.1. Low tide

During low tide both species in the small size class were found on the pen walls at low frequencies (Fig. 2). In fact, *Batillaria* was seldom found on the sides at all. For each species at the small size class, climbing responses were not significantly density dependent during peak resource availability (*Cerithidea* $r^2 = 0.001$, $P > 0.96$; *Batillaria* $r^2 = 0.028$, $P > 0.52$) (Fig. 2). Small *Cerithidea* were not found on pen walls significantly more at low steady state resource levels than peak resource levels, and density had no differential effect on dispersal between the two sampling periods (Table 1). The proportion of small *Batillaria* also was not significantly different at high versus
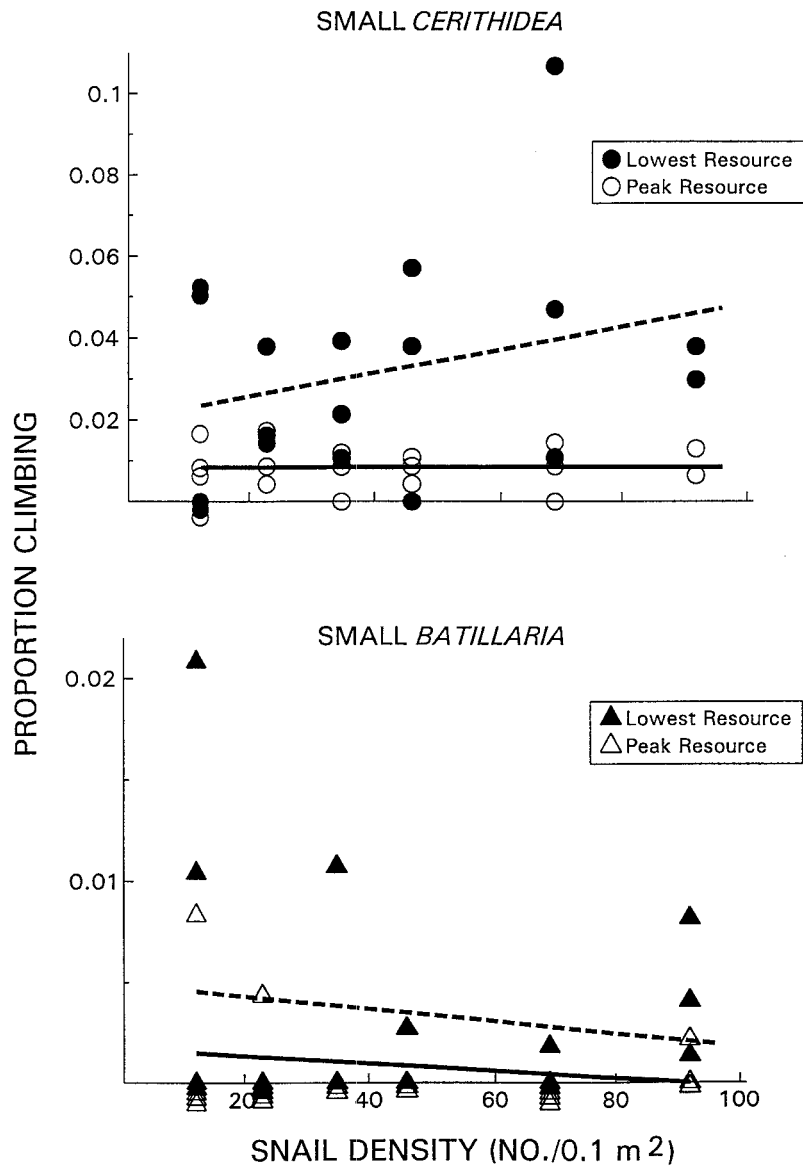
Fig. 2. The effect of density of small *C. californica* (○, ●) and *B. attramentaria* (△, ▲) on the proportion of snails found on enclosure walls at **low tide** both at peak resource abundance (open symbols, –) and at lowest (steady state) resource abundance (darkened symbols, - - -). To enable all data points to be seen (some of which were obscured due to overlap of points at dispersal values of zero), symbols were spread and thus sometimes appear slightly below the *x*-axis.

Table 1
Results of linear regressions for each size class of each snail species examining the effect of density on the difference in the proportion of snails climbing after resource depression versus before resource depression[a]

Size class and species	Variable	T	P	R^2
Small *Cerithidea*	Intercept	1.01	0.33	
	Density	1.62	0.12	0.14
Small *Batillaria*	Intercept	0.70	0.49	
	Density	0.55	0.59	0.019
Large *Cerithidea*	Intercept	− 1.53	0.15	
	Density	2.40	0.032	0.31
Large *Batillaria*	Intercept	− 0.35	0.73	
	Density	2.51	0.022	0.27

[a] Corresponding T and P values are reported for each variable in the model along with the overall fit of the model to the data (R^2). The proportions of climbing snails were arcsine squareroot transformed.

low resource availability and exhibited no differential effect of density in the different sampling periods (Table 1).

Large *Cerithidea* and *Batillaria* climbed significantly more during steady state resource availability than at peak abundance, but only at higher snail densities (Table 1). For large *Batillaria*, dispersal rates were not dependent on snail density at peak resource availability ($r^2 = 0.016$, $P > 0.6$) (Fig. 3). Large *Cerithidea*, however, had a significant climbing response to density both at peak resource availability ($r^2 = 0.68$, $P < 0.0002$) and at steady state ($r^2 = 0.77$, $P < 0.0001$). However, *Cerithidea's* density dependent response was twice as strong after resources were scarcer (compare *Cerithidea* slopes Fig. 3).

3.2. High tide

At high tide a higher proportion of all size classes and species of snails were found on the pen walls than had been found at low tide (Fig. 4). Small *Batillaria* did not exhibit a significant change in dispersal with increasing density ($r^2 = 0.15$, $P > 0.13$), while small *Cerithidea* dispersed significantly less with increasing density ($r^2 = 0.28$, $P < 0.025$). Mean proportions of small climbing *Batillaria* and *Cerithidea* differed significantly (ANCOVA $F_{1,34} = 27.6$, $P < 0.00001$). The species at the large size class responded at significantly different rates with increases in density (ANCOVA log linearized data $F_{1,33} = 8.77$, $P < 0.006$). Both species at the large size class exhibited significant increases in the proportion climbing with increasing density (log linearized data *Cerithidea*: $r^2 = 0.63$, $P < 0.0004$; *Batillaria* $r^2 = 0.77$, $P < 0.000001$).

In addition to snail density, resource levels also significant affected dispersal rates of large snails (*Cerithidea* $r^2 = 0.60$, $P < 0.0007$; *Batillaria* $r^2 = 0.32$, $P < 0.01$) (Fig. 5). Specifically, large snails dispersed less when resources were more abundant. Small snails, however, did not exhibit significant changes in dispersal with variation in resource levels (*Cerithidea* $r^2 = 0.088$, $P > 0.28$; *Batillaria* $r^2 = 0.05$, $P > 0.42$) (Fig.
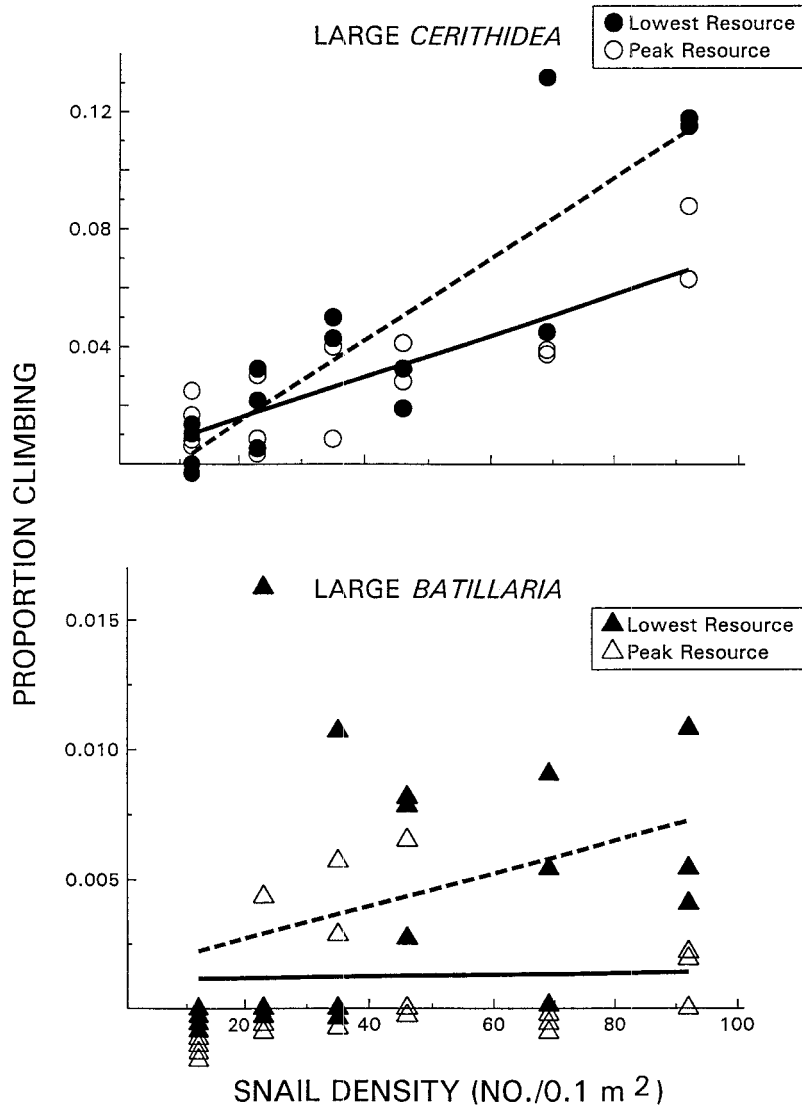
Fig. 3. The effect of density of large *C. californica* ($\bigcirc$, $\bullet$) and *B. attramentaria* ($\triangle$, $\blacktriangle$) on the proportion of snails found on enclosure walls at **low tide** at peak resource abundance (open symbols, –) and at lowest resource abundance (darkened symbols, - - -). The slopes of the climbing responses of *Cerithidea* at peak (0.002) and steady state (0.004) levels of resource abundance differed significantly (timing $\times$ density effect $F_{1, 29} = 6.0$, $P < 0.02$). For *Batillaria*, its climbing responses at peak and steady state resource levels also differed significantly ($F_{1, 37} = 4.7$, $P < 0.037$).

5). When comparing between species within a size class, large *Batillaria* climbed significantly more than large *Cerithidea* at any given density of resource ($F_{1, 33} = 6.7$, $P < 0.015$) (Fig. 5). Although their responses to resource levels were independent of
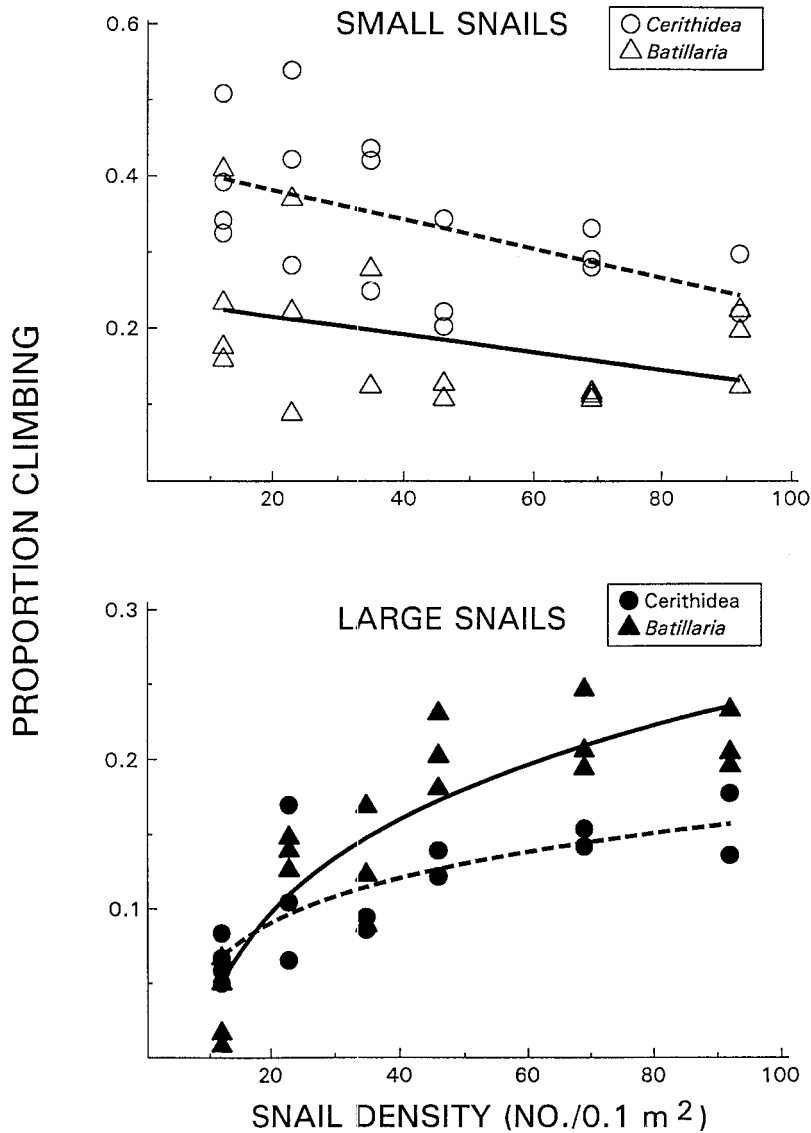
Fig. 4. The effect of density of small and large *B. attramentaria* (△, ▲, –) and *C. californica* (○, ●, - - -) on the number of snails found on enclosure walls at **high tide**.

density, small snails of both species differed significantly in the absolute magnitude of their dispersal responses with *Cerithidea* climbing more than *Batillaria* ($F_{1, 29} = 16.6$, $P < 0.0004$) (Fig. 5). When comparing within a species, large and small *Cerithidea* responded at significantly different rates to changes in resource levels (ANCOVA resource × size effect $F_{1, 29} = 8.29$, $P < 0.008$) with small snails climbing more often
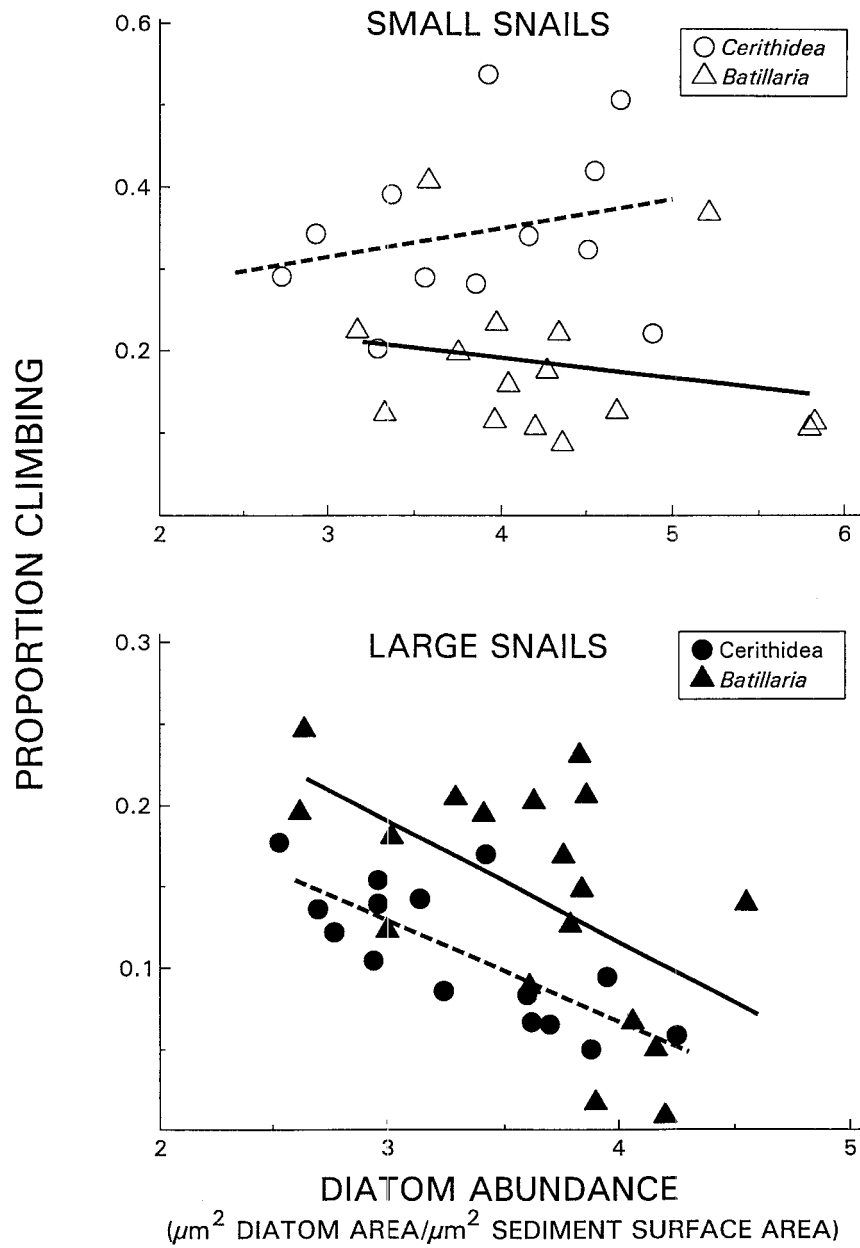
Fig. 5. The effect of resource abundance on proportion of snails climbing at **high tide** in the small size class (*Batillaria* △, –; *Cerithidea* ○, - - -) and large size class (*Batillaria* ▲, –; *Cerithidea* ●, - - -). Within a given size class the two species differed significantly from each other.
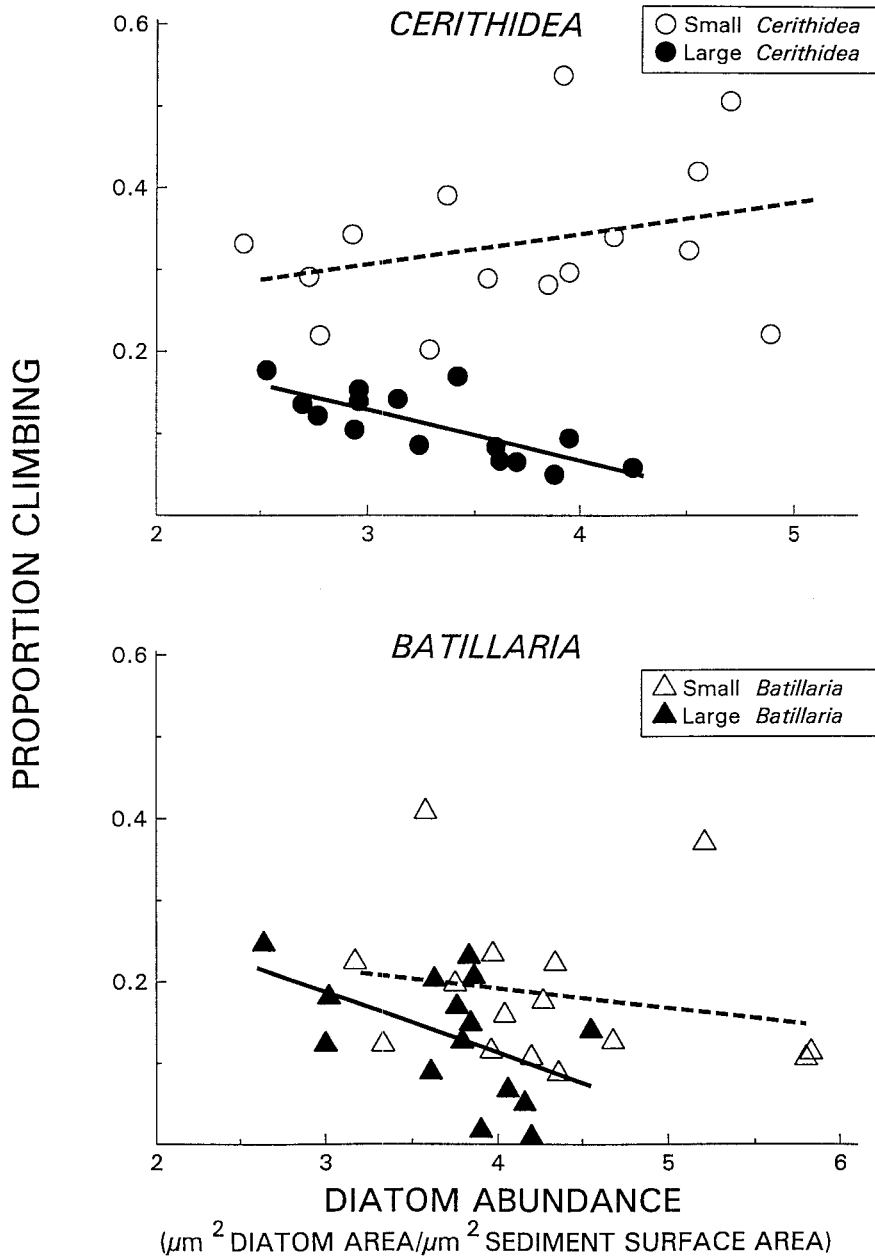
Fig. 6. The effect of resource abundance on climbing incidence at **high tide** of both size classes of *Cerithidea* (small ○, - - -; large ●, –) and *Batillaria* (small △, - - -; large ▲, –). Data are the same as in Fig. 5 but grouped differently for purposes of intraspecific comparison between size classes discussed in text. The two size classes compared within species differed significantly from one another in their response to the resource.

(Fig. 6). Compared to large *Batillaria*, small *Batillaria* climbed significantly more for a given resource level ($F_{1, 33} = 5.43$, $P < 0.027$) (Fig. 6).

4. Discussion

Density and resource dependent dispersal by adult *Cerithidea* and *Batillaria* indicate that competition for a shared resource can induce dispersal; as resources became scarce, particularly within high density treatments, snails climbed more. Since resource levels in this experiment were set by snail density, the pre- versus post-resource depression comparisons help to separate the effect of density per se (interference competition) from the effects of resource levels (exploitative competition) on dispersal. Large *Batillaria* did not demonstrate a significant dispersal response to density when resources were high, but did once resources became depressed. This switch implicates exploitative competition as a predominant agent affecting its dispersal response. Large *Cerithidea* exhibited a significant response to density while resources were high, indicating either an effect of interference competition or exploitative competition due to an unusually high demand for resources. In either case, *Cerithidea*'s dispersal rate after definitive resource depression doubles in magnitude. Dispersal thus appears to play a sizable role in attempting to alleviate short-term effects of exploitative competition, particularly among the larger, more metabolically sensitive snails.

A striking result from this study, however, is the order of magnitude difference in the numbers of snails on the pen walls between high and low tide. For the large snails, the relative ranking of climbing rates of the two species was reversed between the sample times. Furthermore, since resource levels were not fully depressed to steady state during some of the high tide sampling, the climbing estimates are likely to underestimate the occurrence of this behavior. The discrepancy in estimates of climbing incidence from the two observational time periods accentuates the importance of timing in measuring response variables in behavioral and ecological studies. The snail species in this study actively climb only when the substrate is wet, i.e., at high tide or immediately after (Lafferty, 1993b, McDermott, 1996, J. Byers, personal observations). As the pen wall and the snail's foot dry out from desiccation during low tide, the loss of moisture causes the snail to fall; therefore, low tide counts reflect the ability of snails to cling, not climb. Thus, studies that use exclusively low tide counts of climbing snails, particularly species related to those in this study (e.g., McGuinness, 1994) should be interpreted cautiously. McGuinness (1994) found that *Cerithidea anticipata* increased its height on vertical surfaces during neap tides as opposed to spring tides, concluding that this behavior may be driven by increased marsh surface temperatures associated with neap tides. Due to logistical constraints (salt-water crocodiles) he was not able to sample at high tide. During low tide counts he often observed the snails predominantly on the shaded sides of trees or hanging by dried mucous with only a small part of the lip in contact with the surface (as opposed to being in an active climbing position with the foot attached to the surface). These observations suggest that, as in the present study, snails fell from vertical substrates when exposed and consequently desiccated at low tide. Trends drawn from relative comparisons within low tide samples may correctly identify motivating

mechanisms by holding confounding factors such as desiccation relatively constant, however, the absolute rates of behavior McGuinness reports may be underestimated since data were not gathered from high tide also.

This problem of inappropriate sample time is, of course, not limited to studies on snail dispersal, or even high versus low tide sampling problems, but applies to other ecological studies where sampling times are chosen primarily due to logistical constraints or convenience to the researcher. Some researchers have exposed prominent examples of such sampling, where intervening forces to operate between the initiation of a process or behavior and measurement by the researcher, and include the use of counts of recruits of planktonic organisms as a proxy for their initial settlement (Keough and Downes, 1982; Schmitt and Holbrook, 1996) and diurnal samples of predominantly nocturnal processes (Holbrook and Schmitt, in press; Robles, 1996).

Despite superior resource conversion efficiency, *Batillaria* at high tide appeared less tolerant of changes in resource levels, as it dispersed more than *Cerithidea* for a given level of resource. I had based my initial hypothesis that the non-native *Batillaria* would disperse less frequently on my knowledge of its decreased sensitivity to resource availability relative to *Cerithidea* (Byers, in press). However, I failed to consider that differences in dispersal behavior might not have evolved in ways expected by the snails' current selection regime. Alternative explanations for higher dispersal rates include *Batillaria* having evolved the ability to (1) forage farther or faster to locate food more efficiently in a heterogeneous environment, (2) resist desiccation better and therefore be less inhibited about exposing itself by climbing upward, or (3) simply climb vertical surfaces better. Regardless, *Batillaria's* higher resource-dependent dispersal rates are not what one might initially expect given its superior resource conversion efficiency; however, the discrepancy highlights that its behavioral response to the resource is a product of genetic as well as environmental influences.

Many studies, however, have sought to make similar inferences about relative competitive abilities from observed behavioral differences between species without fully considering phylogenetic constraints (e.g., Iwasaki, 1994; Viitala et al., 1994; Gilbert, 1995; Gabor et al., 1997). Garland and Adolph (1994) in a five-year (1989–1993) review of the *Journal of Physiological Zoology* found that 37% (18/49) of two-species comparisons neglected the contribution of genetic influences on behavior when inferring relative competitive abilities of species by comparing their intraspecific responses to environmental stimuli. While all multi-species behavioral comparisons are potentially confounded by differences in species' evolutionary history, such comparisons involving a non-indigenous species seem more likely to confront accentuated differences since the non-indigenous species evolved, by definition, in a separate environment.

Within-species comparisons between sizes of individuals, however, are still useful as they remove the confounding factor of differences in phylogenetic history, and therefore should underscore environmental variables that motivate dispersal and may change with development of the organism. In this study small snails disperse at high rates at high tide, but their response is not strongly influenced by density or resource levels, suggesting that this behavior may be a programmed mechanism for dispersal, affected little by immediate environmental conditions. Large snails, on the other hand, exhibited resource dependent dispersal, with increased levels of dispersal at low resource levels.

Such sensitivity to resource levels perhaps indicates higher metabolic demands for snails of this size. Ultimately, competition appears to be an important driving force for dispersal by adult snails of these species, but may be easily overlooked or under-estimated if a smaller size class or an inappropriate sample time is used.

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