COMPETITION BETWEEN TWO ESTUARINE SNAILS: IMPLICATIONS FOR INVASIONS OF EXOTIC SPECIES

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Abstract. An introduced snail, *Batillaria attramentaria,* has successfully invaded several salt marshes and mud flats in northern California. In these areas populations of the native mud snail, *Cerithidea californica,* have declined precipitously. Since both species feed on epipelic diatoms, I hypothesized that the decline in *Cerithidea* was a result of exploitative competition with *Batillaria.* To test this hypothesis I manipulated snail densities in Bolinas Lagoon, California, to estimate their effects on, and responses to, food resources. For two size classes of each snail species I quantified (1) the effect of intraspecific density on food availability, and (2) the growth response of each size class to different food levels. These relationships were used to generate predictions of the exploitative competitive effect of each snail on the other species. These predictions were tested against direct measurements of the effect of interspecific competition on snail tissue growth using field experiments. The observed values of snail growth matched well the predicted relationships, suggesting that exploitative competition does occur. Although the two snails did not differ in their effect on resource levels at any experimental snail density, the introduced snail was always more efficient at converting limited resources to tissue growth. Similar results were obtained in three different experimental periods. *Batillaria*'s enhanced resource conversion efficiency provides a sufficient explanation for its successful invasion and subsequent exclusion of *Cerithidea.* Theoretically, conversion efficiency of resources should be just as important as resource suppression and uptake to exploitative competitive ability, but it is rarely examined experimentally. By separating exploitative competition into its component parts, the protocol used here allowed identification of a seldom implicated mechanism that can affect invasion success.

Key words: Batillaria; Cerithidea; competitive exclusion; consumer–resource interactions; diatoms; exploitative competition; indirect effects; interspecific competition; introduced species; mud snails; nonindigenous species; resource conversion efficiency; salt marshes.

INTRODUCTION

Invasions of ecosystems by exotic species are increasing, especially in aquatic environments (Drake et al. 1989, Carlton 1992, Carlton and Geller 1993, Lodge 1993, Mills et al. 1993, Ruesink et al. 1995, Lafferty and Kuris 1996, Cohen and Carlton 1998). Understanding the mechanisms that lead to the success of exotic species will provide predictive power for future invasions and insight for the management of presently invaded systems. Several authors have stressed the importance of a mechanistic understanding of invasions, calling for experiments delineating the interactions between native and exotic species (Wootton 1994*a*, Grosholz and Ruiz 1996, Petren and Case 1996). Such information would enhance our understanding of traits of successful invaders, and the conditions under which these traits promote invasion.

Most studies of invasion have emphasized the instrumental role that freedom from natural predators plays in enabling the establishment of exotic species

(e.g., Huffaker 1971, Lawton and Brown 1986, Crawley 1987, Wilson 1989, Wells and Henderson 1993, Trowbridge 1995). The ''predator-free space'' provided by a novel environment may indeed be important to successful invasions, but a basic requirement for any species, including exotics, is resources. An alternative determinant of invasion success may thus be the nature of competitive interactions with native ecological analogs (Herbold and Moyle 1986). Therefore, competitive superiority could be an essential trait leading to successful invasion. Superior competitive ability could manifest itself through interference and/or exploitation, neither of which has been explored as intensively in the context of invasion ecology as the role of ''predator-free space.'' The development and influence of Elton's (1958) concept of empty niches and island biogeography theory (MacArthur and Wilson 1967), which both largely attribute successful invasion to a lack of competition, may explain partly why competitive ability has been undervalued as a viable explanation for invasion success. To investigate the role of competitive ability in invasions, I have examined interactions between a native salt marsh mud snail and an invading, non-indigenous mud snail.

The common mud snail, *Cerithidea californica,* is

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TABLE 1. Mortality rates over the duration of experiments and incidence of parasitic infection. Missing snails were not included in these computations.

Year	Species	Mortality (%)	Parasitism (%)
1995	Large *Batillaria*	0	2.6
	Large *Cerithidea*	6.5	20.5
	Small *Batillaria*	0	0
	Small *Cerithidea*	0.16	1.97
1996	Large *Batillaria*	0.26	1.83
	Large *Cerithidea*	2.9	5.54
	Small *Batillaria*	0.85	0
	Small *Cerithidea*	1.4	1.3
1997	Large *Batillaria*	3.1	3.7
	Large *Cerithidea*	2.9	16.2

an abundant epifaunal grazer that inhabits salt marshes from San Ignacio Bay, Mexico to Tomales Bay, California, USA. The exotic mud snail, *Batillaria attramentaria,* is common in a few bays and estuaries at the northern extent of *C. californica*'s range. *B. attramentaria* is one of several species introduced to a few bays in northern California in the early part of this century with plantings of the Japanese oyster, *Crassostrea gigas* (Bonnot 1935). Because it is a direct developer, *B. attramentaria* has stayed confined within these bays. In these bays, the native snail has declined and, in a few areas where *B. attramentaria* has attained high abundances, it may have disappeared entirely (Carlton 1975, McDermott 1996). For example, in parts of Tomales Bay (50 km north of San Francisco Bay) *Cerithidea* used to be ''seen by the thousands'' along the west bank (Dickson 1936). Since the arrival of *Batillaria* ~50–70 years ago (Bonnot 1935, Carlton 1992) only one small, isolated marsh in Tomales Bay now contains *Cerithidea* (Byers, *in press*). In isolated sections of Bolinas Lagoon (Marin County, California), *Cerithidea* populations have disappeared and densities of *Batillaria* up to 5000 snails/m² have been measured (McDermott 1996; Byers, *in press*). In Elkhorn Slough (Monterey County, California) *Cerithidea* is completely absent, and *Batillaria* achieves densities up to 10 000 snails/m², nearly an order of magnitude greater than *Cerithidea* has been observed to attain anywhere (Byers, *in press*).

The principal natural enemy of the snails, parasitic trematodes, may play a role in *Batillaria*'s success (McDermott 1996), as *Batillaria* exhibits lower prevalence of infection by parasitic trematodes than does *Cerithidea* (Table 1). These parasites do not typically kill their snail host, but rather castrate it, thereby cutting off all future reproduction of the snail. Competition, however, may also play a major role in this species invasion. The two species are practically identical in many life history attributes. They grow to about the same maximum size, live for the same length of time, enter winter dormancy at the same time for the same duration (November–March), become mature at the same age, reproduce at the same time of year, and share the same preferred food resource: epipelic diatoms (diatoms that grow on mud surfaces) (McLean 1960, Driscoll 1972, Whitlatch 1972, Yamada and Sankurathri 1977, Morris et al. 1980, Whitlatch and Obrebski 1980, Yamada 1982, Race 1982). Whitlatch and Obrebski (1980) demonstrated that epipelic diatoms numerically comprise 70–80% of both snails' diets. Additionally, snails and other soft sediment feeders are capable of limiting diatom or detritus resources (Fenchel 1975, Curtis and Hurd 1981, Bertness 1984, Levinton 1985, Olafsson 1986, Lopez and Levinton 1987). Given the high overlap of resource use, the two snails in this system may compete exploitatively. Exploitative competition has been demonstrated in several aquatic snails (e.g., Fenchel and Kofoed 1976, Schmitt 1985, 1996, Osenberg 1989, Skilleter and Underwood 1993). Further, intraspecific competition has been documented among *C. californica* (Lafferty 1993*a*).

The simplest model of exploitative competition illustrates the key characteristics involved. The dynamics of a resident species and its resources can be determined by the Lotka-Volterra equations:

$$dR/dt = rR - \alpha_1 N_1 R \tag{1}$$

$$dN_1/dt = \alpha_1 \varepsilon_1 R N_1 - m_1 N_1 \tag{2}$$

where r is the intrinsic rate of increase of the biological resource, R is the density of the resource, N_1 is the population density of consumer species 1, α_1 is the per capita consumer consumption rate, ε_1 is the per capita efficiency of converting resource into new consumers, and m_1 is the density-independent death rate of consumer 1. At equilibrium:

$$R_1^* = m_1/\alpha_1 \varepsilon_1 \tag{3}$$

where R_1^* is the equilibrium value of the resource when only species 1 is present. A second species, N_2, can invade only if it can increase from small numbers when the resource density is R_1^*, i.e.,

$$dN_2/dt = \alpha_2 \varepsilon_2 R_1^* N_2 - m N_2 > 0 \tag{4}$$

or, after rearranging,

$$R_1^* > m_2/\alpha_2 \varepsilon_2. \tag{5}$$

Invasion therefore requires:

$$m_1/\alpha_1 \varepsilon_1 > m_2/\alpha_2 \varepsilon_2. \tag{6}$$

The invasion criterion (Eq. 6) emphasizes that species 2 can win by having a lower death rate (m_2) or a higher conversion efficiency (ε_2), even if the per capita feeding rates (α) are the same. The study described here indicates that in fact *Batillaria* has advantages in both parameters over *Cerithidea.*

Although exploitative competition has been studied for decades (e.g., Gause 1932, Lack 1945, MacArthur 1958, Cody 1968, Brown and Davidson 1977, Peterson 1982, Holt et al. 1994), the two components of ex-

ploitative competition—the consumer's per capita consumption rate (α) and its conversion efficiency (ε)—are nearly always combined into a single, density-dependent relationship (Eisenberg 1966, Brown 1982, Kerfoot et al. 1985, Schmitt 1985). Separation of the two components, however, allows for a more thorough, mechanistic understanding of competitive relationships, helping us to better understand species interactions and allowing us to make more robust predictions (Tilman 1987, Osenberg 1989, Murdoch et al. 1996, Schmitt 1996).

This study examines the role of exploitative competition in the outcome of *Cerithidea–Batillaria* interactions by (a) quantifying for each snail species its effects on and responses to the food resource, (b) generating predictions of the outcome of competitive interactions by combining these relationships into mathematical functions, and (c) comparing the predictions with experimental measurements of species' responses to interspecific densities. If the direct measurements from step c accurately match the predictions of step b, then exploitative competition between the snails is corroborated. Partitioning exploitative competition into its component parts—consumer effects on, and responses to resource levels—should provide insight into which species and size classes are competitively dominant, how superiority is achieved (i.e., via a higher feeding rate or higher efficiency in resource use), and whether trade-offs exist that may allow coexistence.

METHODS

Along the California coast, several embayments exist where either *Batillaria* or *Cerithidea* dominates, but few sites exist where both species are in high abundance. The experiments reported here were performed in Bolinas Lagoon, California, 20 km north of San Francisco Bay in the summers of 1995–1997. I chose this site because the salt marsh area at its southern end contains similar densities of *Batillaria attramentaria* and *Cerithidea californica* (McDermott 1996), suggesting that this bay would be ideal for quantifying the invasion of *Batillaria* and testing the role of competition in invasion success. I measured densities and sizes of the snails from mean high tide level to mean low tide level along five transects that ran perpendicular to a primary channel (the principal passage through which water enters the marsh from the lagoon). In order to create an array of enclosure areas in which to manipulate snail density, I arranged a row of pens parallel to the channel on the gently sloping, unvegetated channel bank. The pens were sited along a height contour that had roughly equal densities of both species of snail (*Cerithidea*: 19 $\pm$ 0.85 snails/0.1 m^2 (mean $\pm$ SE); *Batillaria*: 24.4 $\pm$ 5.62 snails/0.1 m^2) and similar mean sizes (*Cerithidea*: 21.2 $\pm$ 0.8 mm (mean $\pm$ SE); *Batillaria*: 17.2 $\pm$ 0.59 mm). Pens were constructed of 2-mm clear Vexar mesh (Nalle Plastics, Austin, Texas) formed into cylinders 35 cm in diameter, which I in-

serted 8 cm into the mud substrate of the marsh. Each pen enclosed ~0.1 m^2 of natural marsh bottom and protruded 0.42 m above the mud surface. The pens had open tops to reduce effects of shading on diatom growth. I removed snails from the pens and rubbed each mud bottom by hand to ensure that all snails had been removed and to homogenize any potential initial spatial variability in epipelic diatom abundance between pens. The pens were left undisturbed for three days before initiating the experiment.

During this time, I collected snails and sorted them 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 1993b). I measured length from apex to anterior tip of aperture, width at aperture, and wet mass of a large subset of the snails used in the experiment. Each of the measured snails was also marked with Testor's enamel. All snails were kept in containers with marsh water until the start of the experiment, and snails were not kept out of the marsh more than two days. Although parasitized snails were present in typically low numbers in the experiment (Table 1), they should not have affected the performance of the other snails or the response of the microalgal resource since (1) the trematode parasites are not transmissible from snail to snail and (2) infected snails have been shown to have the same effect on the resource as uninfected snails (Lafferty 1993a).

To examine intraspecific effects on resources and the corresponding growth responses of the snails to various diatom densities, I created treatments of 0, 12, 23, 35, 46, 69, or 92 individuals from a single size class of either *B. attramentaria* or *C. californica* in 1995. These levels represented 0, 0.5$\times$ ambient, 1.0$\times$ ambient, 1.5$\times$ ambient, 2$\times$ ambient, 3$\times$ ambient, and 4$\times$ ambient intraspecific densities, respectively. In 1997, treatment densities were 0, 0.5$\times$ ambient, 1.0$\times$ ambient, 2$\times$ ambient, and 4$\times$ ambient with large snails only (Table 2). To measure the growth of snails in the experiments, each group of snails added to the pens included 10 measured and marked snails. During the experiments I monitored the pens every day, particularly during and immediately after high tides, to keep snails off the sides of the enclosures. (Snails are only capable of climbing vertical surfaces during high tides.)

I ran similar experiments in 1996 to examine temporal variation in resource use and growth responses, with the exception that I modified the design to include tests of interspecific interactions. Field densities and sizes in 1996 were very similar to 1995 (*Cerithidea*: 18.4 $\pm$ 2.9 snails/0.1 m^2, 21.9 $\pm$ 0.45 mm; *Batillaria*: 28.8 $\pm$ 5.51 snails/0.1 m^2, 20.4 $\pm$ 0.73 mm). Therefore, I used the same total snail density as in 1995. I placed 0, 10, 20, 40, or 80 individuals of either *B. attramentaria* or *C. californica* from the large size class into each pen. To quantify interspecific interactions, I also added 0, 2, 3, 6, or 12 measured and marked large snails

TABLE 2. Experimental design for each species; in 1995 the design was repeated for each size class as well.

Year	Treatment variable (snails/replications)	Treatments						
		0×	0.5×	1×	1.5×	2×	3×	4×
Intraspecific experiments								
1995 (37 d)	No. snails	0	12	23	35	46	69	92
	No. *Batillaria* reps.†	4	4	3	3	3	3	3
	No. *Cerithidea* reps.‡	4	4	3	3	3	3	3
1997 (60 d)	No. *Batillaria* reps.	3	4	4	...	4	...	4
	No. *Cerithidea* reps.	3	4	4	...	4	...	4
Interspecific experiment								
1996 (39 d)	Total snails	0	12	23		46		92
	(No. primary)/(no. secondary)	...	(10/2)	(20/3)		(40/6)		(80/12)
	Secondary snails as percentage of total density	...	16.7%	13%		13%		13%
	No. *Batillaria* reps w/secondary *Cerithidea*	4	9	6		3		2
	Extra intraspecific *Batillaria* pens	...	8	6		4		4
	Cerithidea reps w/secondary *Batillaria*	4	9	6		3		2
	Extra intraspecific *Cerithidea* pens		8	6		4		4

Notes: "Treatments" category relates experimental density levels to mean ambient intraspecific densities found in the marsh. For 1996, "primary" refers to the individuals of the species chosen to be numerically dominant in each pen and for which consumer–resource information was measured. "Secondary" refers to the number of snails of the species different from the primary species added to the enclosure pen. In 1996, the extra intraspecific pens listed are the replicates that were part of a separate experiment to test effects of large snails on small secondary snails, utilized in the present study to help quantify consumer–resource interactions of large snails.

† Number of replications with *Batillaria.*

‡ Number of replications with *Cerithidea.*

of the second species to the five respective intraspecific density treatments (Table 2). The number of heterospecifics in a cage was thus between 13% and 16.7% of the total snails in each pen. The more abundant species in each pen was termed the "primary" species, while the less abundant species was termed the "secondary" species. I intentionally kept the number of secondary snails added to each pen low so that their presence would have minimal impact on the consumer–resource interactions of the primary snail species and its resource (Mittelbach 1988). The design therefore focused on quantifying the impact of the abundant snail on the rarer one. Replication was unbalanced to keep the total number of secondary snails similar at each density treatment level (Table 2). In parallel, as part of a separate experiment I initiated treatments that used large snails as the primary snails and small snails as the secondary snail additions to explore size specific interspecific interactions. These treatments were used in the present study as additional replicates for quantifying the intraspecific consumer–resource interactions of large snails (see following sections).

Effects of snails on resource

While I purposely limited the duration of the experiments so that snail mortality would not significantly influence results, effects of snails on food abundance might vary through the experiment as a consequence of changes in snail densities; therefore, I replaced any

dead snails in the pens. Mortality levels, however, were quite low (Table 1).

To measure the final density of diatoms in pens after exposure to snail grazing, I took sediment cores from the bottoms of all pens on the day before the end of the experiment. Using modified plastic syringes (diameter = 1 cm) I extracted four sediment cores to a depth of 6 mm from the same relative position in the bottom of each pen. I pooled all cores from each pen in a single scintillation vial, and immediately preserved the samples in 6% Lugol's solution in sterilized seawater. In the laboratory, I shook sediment samples on a Vortex mixer (Fisher Scientific, Pittsburg, Pennsylvania) for 1 min to suspend uniformly all sediment particles and immediately pipetted 250 μL of the mixture. I diluted this subsample in deionized water and shook it on the mixer again, then immediately extracted a 350-μL subsample and plated it onto an 18 mm diameter cover slip. Slips were covered with a box and allowed to dry overnight. The following day I stained the slides with a drop of Lugol's solution, which turns chloroplasts green (and thus distinguishes live cells from dead at the time of collection), and viewed them under a light microscope at 400×. I counted all live diatoms along a haphazardly selected transect across the diameter of each cover slip, using a digitizing pad to tally every species of diatom encountered and to measure the heights and widths of all diatoms. Using data on the height, width, and geometry of each species,

I calculated total surface area of all diatom cells for each of 2–3 replicate cover slips. I used the average of these replicates to estimate the total surface area of diatom cells per area of sediment surface sampled. For the 1996 analyses, five pens of each species were chosen at random at each density level (including pens from the experiment designed to measure effects of large snails on small secondary snail additions) in order to keep regression analyses balanced. In 1995, with the exception of the 1.5 ambient density pens for small snails and the few pens that were lost, all pens were cored, as replicates were balanced at each density. I log-transformed diatom abundance and used two-way ANOVA to test for statistical differences in the effects of species and snail density on diatom abundance.

To determine if microalgal density stabilized early in the experiment, in 1997 I sampled diatoms every 5 d from six pens (three from each snail species) of the highest (4× ambient) and lowest (0.5× ambient) snail density levels used during the three experimental years. These extremes of grazing pressure should represent the shortest and longest times needed for the resource to stabilize. I ran this experiment 3 wk longer (for a total of 60 d) than in the two previous years in order to increase the likelihood that stable levels of the resource were reached.

To measure potential cage effects on diatoms I haphazardly took 12 cores of 1 cm diameter (pooled into three vials of four cores each) of ambient marsh sediment at the end of the experiment in 1996 at the same tidal height as the experimental cages. I used ANOVA to compare these samples to cores taken from cages of 2× ambient density treatment. (Since density treatment levels were determined based on intraspecific densities, the 2× level most closely matched ambient *total* snail density). The test showed no significant differences in diatom abundance inside vs. outside 2× cages (μm^2 diatom surface area/μm^2 sediment surface area, with 95% confidence interval; Inside = 2.81 ± 0.35; Outside = 2.34 ± 0.65; $F_{1, 14}$ = 1.78, P > 0.204). However, power was low (1 − β < 0.3). Thus, despite no detectable statistical effect of the pens, they cannot conclusively be dismissed as having no effect on final diatom abundance. However, even if the cages had an effect, their influence trended toward increasing diatom levels, a tendency that would lead to an underestimation of the intensity of competition compared to ambient conditions.

Effects of food resource on snails

At the end of the experiments, snails were sieved from the pen bottoms and frozen for later dissection. I measured the focal snails' final shell dimensions and dissected them to determine their sex and prevalence of parasitic infection. I then extracted the tissue and dried it for 4 h at 70°C to obtain a dry tissue mass. At the beginning of the experiments, I had estimated initial dry tissue mass of each marked snail using empirically

determined relationships between basal shell diameter and dry tissue mass. These relationships were calculated by haphazardly selecting snails of both species over a range of sizes, measuring their external shell dimensions, removing the tissue from the shells, drying the tissue, and weighing it. For each species I regressed dry tissue mass against shell width (both R^2 > 0.97). I calculated the relative growth of each snail species using the formula: (final dry tissue mass − estimated initial dry tissue mass)/(estimated initial dry tissue mass). While change in dry tissue mass is a highly sensitive measure of growth and potentially most important for fitness considerations, I also examined changes in other growth metrics—length, width, total body wet mass—to ensure that species-specific differences in growth form or differential allocation between shell and tissue did not lead to any discrepancies in results that could alter conclusions about relative growth rates. I excluded parasitized snails (typically a low percentage of total numbers, see Table 1) from final analyses because the trematode parasites infecting these snails have been shown to substantially alter growth rates (Sousa 1983, Lafferty 1993*a*).

To determine the relative growth of each size and species of snail as a function of the final density of diatoms, I regressed the average relative growth rate for all marked snails within a pen against final diatom abundance using data from the same pens used in the previous analyses. I expected growth to have the same shape as a Type II functional response, minus maintenance. Therefore, to express the growth increment of a specified size class of species i, ΔG_i, as a function of the final diatom level, F, I fit the saturating function:

$$\Delta G_i = (a_i F)/(b_i + F) - c_i. \qquad (7)$$

The parameters a_i and b_i, and the constant c_i, which was constrained to a minimum value of 0 (since snail growth rate should not be positive in the absence of food), were calculated by fitting the equation to empirical data. Data were fit using a nonlinear general model fitting function of Systat (Systat 1992). I also log-transformed diatom abundance and tested differences between the snails' growth responses to resource levels via ANCOVA using species as the independent variable and resource level as the covariate.

To test for potential effects of caging on snail growth, I marked and took wet masses of several hundred snails of both species and size classes in 1995 and 1996. I placed these snails in the marsh in the immediate area surrounding the experimental pens. At the end of the experiment I collected all marked snails that I could find (approximately one-third were recovered) and air dried and weighed them. The change in the average per capita wet masses of these snails was well within the variation of wet mass growth seen in enclosure pens of equivalent snail densities (Fig. 1). Therefore, pens
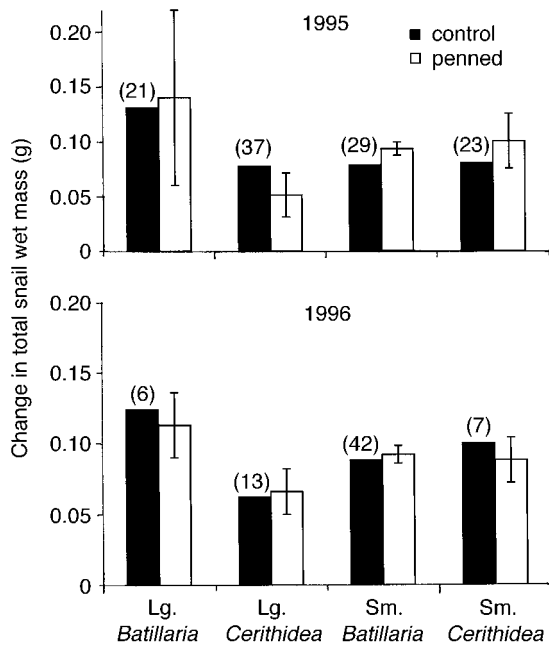
FIG. 1. Average change in per capita total wet mass (shell and tissue) for free-ranging control snails and snails in enclosure pens with densities equivalent to ambient marsh densities. Because experimental treatment levels were determined based on density measurements in the marsh of each species irrespective of the other, the 2× intraspecific treatment level most closely matched ambient *total* snail density. The number above the control snail columns indicates the snails in that category at the end of experiment. Variance calculations for control snails were not possible as snails were measured collectively and were not individually identifiable. For penned snails, the figure presents the mean of average snail growth in each pen (±95% confidence intervals). For small snails in 1995, the penned-snail responses are reported from enclosures of 92 small individuals/0.1 m², a biomass roughly equivalent to ambient snail biomass in the marsh. For small snails in 1996 the penned-snail responses are reported from density enclosures ($N = 8$ for each species) of 54 small individuals/0.1 m², the highest enclosure density of small snails available for comparison; the total biomass of these cages was, therefore, somewhat less than ambient levels.

appeared to have had little influence on snail growth rates.

Intraspecific effects on growth

To evaluate the effects of intraspecific competition on the relative growth rates of both species in all three years, I expressed snail tissue growth (examined above) as a function of intraspecific density. In addition, I examined species-specific differences in the effect of density on growth rates with two-way ANOVA using species and snail density as the independent variables. Some relationships of the effect of snail density on growth were nonlinear. Linear models fit these relationships well when the reciprocal of density was regressed against growth rates. For consistency, all relationships of snail density on growth were transformed

using the reciprocal of snail density. All enclosure pens were included in these analyses.

Testing predictions of competition's effect on snail growth

Quantification of snail effects on, and responses to, resources obtained from the single-species experiments allowed me to predict how interspecific exploitative competition affected the growth rate of large snails. I predicted the effect of species 1 on the relative growth of dry tissue mass of species 2, and vice versa, by substituting the equation describing the effect of the density of species 1 on food availability into the equation describing the response of species 2 to food density. Specifically, the predicted effect of a given density of snail species j, D_j, on the growth increment of species i, ΔG_i, via the effect of D_j on diatom density, F, was calculated by substituting into Eq. 7 values for F derived from:

$$F = g_j \exp(h_j D_j) \tag{8}$$

where coefficients g and h were calculated by fitting the equation to empirical data. After generating the two predicted relationships for each snail's effect upon the other, I then compared the predictions to the growth of the secondary heterospecific individuals in the 1996 experiments, which provided direct measurements of the effect of each species on the growth rate of the other. To ascertain the accuracy of the predictions to the empirical results I calculated coefficients of determination (R^2) for the relationships of the observed values to the prediction lines.

RESULTS

Effects of snails on resource

Examination of the time series data on diatom densities in the 1997 intraspecific enclosure experiment confirmed that food resources rapidly achieved abundances roughly equal to final values within 3–4 d of the initiation of the experiment (Fig. 2). The initial increase in diatom abundance during the 3 d before the start of the experiment reflects the recovery of the diatoms from the initial homogenization of the mud surface by hand in the absence of snail grazing. After a 15–20 d overshoot of what became the final density, which reached a maximum of 30% above final values in the high grazer treatments and 40% in the low grazer treatments, the diatom abundance came to within 10% (high grazer treatment) and 15% (low grazer treatment) of the final diatom abundance for the remainder of the experiment. Overall, the resource levels were within 20% of the final value for >70% of the experiment duration at both high and low grazing intensities. Thus, final diatom abundance measured in these experiments can be viewed as the density of resource to which the snails responded throughout most of the experiment.

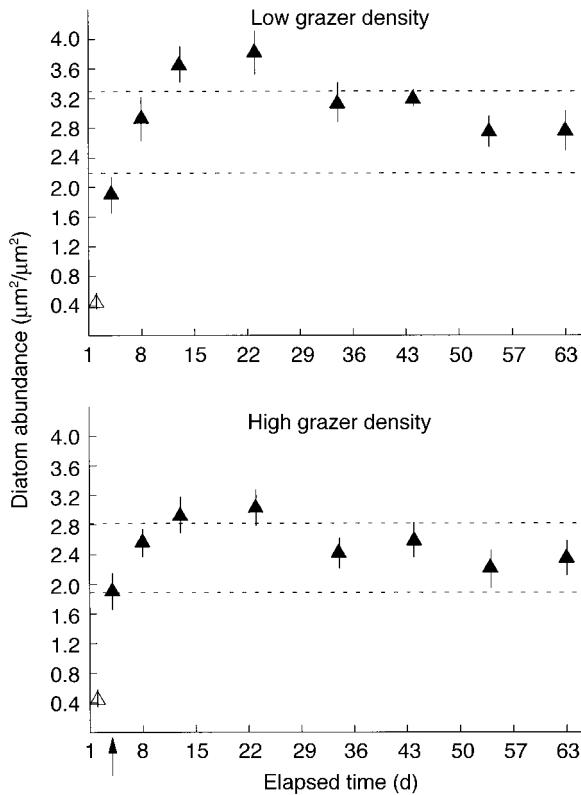The snail species were basically interchangeable in

FIG. 2. Mean diatom abundance (with 95% confidence intervals) in intraspecific snail enclosure experiments through time in 1997. Diatom abundance is expressed as diatom surface area (μm^2)/sediment surface area (μm^2). Because analyses of snails on food resources showed little or no difference between species, I pooled data from both species treatments for a given density level. The top graph depicts values for the lowest grazer density treatment (12 snails/0.1 m²). The bottom graph shows values for the highest grazer density treatment (92 snails/0.1 m²). Dashed lines represent the bounds for values within 20% of final diatom abundance. The arrow represents the date the experiment was initiated, i.e., the snails were added. Data on day 1 ($\triangle$) represent the diatom abundance immediately after the substrate was rubbed by hand in order to indicate the effectiveness of this technique at removing and homogenizing diatom abundances.

their effect on food density. Rates of resource depletion, i.e., species $\times$ density interaction, were not different in either year or size class (Table 3). In 1995, the effect of species of both size classes on diatom abundance was statistically significant (Fig. 3, Table 3); however, the differences in overall diatom abundance were small (intercepts of log linearized data: large *Batillaria* = 1.46, large *Cerithidea* = 1.36; small *Batillaria* = 1.50, small *Cerithidea* = 1.46). In 1996, the snail species did not differ in their effect on the absolute diatom abundance (Table 3, Fig. 4).

Effects of food resource on snails

Relative growth rates of the two size classes of both species increased with increasing food densities (Figs. 5 and 6). For both years and both size classes, *B. attramentaria* grew significantly more than *C. californica* at any given diatom density (ANCOVA: small snails 1995: $F_{1, 26}$ = 19.62, $P < 0.00018$; large snails 1995: $F_{1, 33}$ = 17.4, $P < 0.00022$, large snails 1996: $F_{1, 39}$ = 22.5, $P < 0.00003$). This higher efficiency in converting resources to tissue growth was not merely a result of differential allocation between shell vs. tissue, as *B. attramentaria*'s growth surpassed that of *C. californica* for nearly all growth measurements taken (shell length, shell width, and wet mass) (Appendix).

Large *C. californica* lost tissue mass at very low diatom abundance values. The density of resource that exactly balanced basal metabolic demands for large *C. californica* was 3.0 μm^2 diatom surface area/μm^2 sediment surface area in 1995 (Fig. 5) and 1.4 μm^2 diatom surface area/μm^2 sediment surface area in 1996 (Fig. 6). Resource densities were never low enough in either year for *B. attramentaria* to exhibit zero or negative growth.

Intraspecific effects on growth

Intraspecific density had a significant effect on the relative growth of both snails in all three years (Table 4). Growth of both species declined exponentially as a function of snail density in the pens (Figs. 7, 8, and 9), indicating both intraspecific and intra-size class

TABLE 3. Two-way ANOVA results for effect of intraspecific density and species on log-normalized diatom abundances.

Year	Snail size	Source	df	MS	F	P
1995	Small	Species	1	0.14	8.26	0.011
		Density	4	0.064	3.80	0.022
		Species $\times$ density	4	0.038	2.26	0.11
		Error	24	0.017		
1995	Large	Species	1	0.068	5.64	0.027
		Density	5	0.104	8.63	0.00012
		Species $\times$ density	5	0.010	0.84	0.54
		Error	22	0.012		
1996	Large	Species	1	0.028	0.64	0.43
		Density	3	0.90	20.5	<0.00001
		Species $\times$ density	3	0.046	1.04	0.39
		Error	32	0.044		

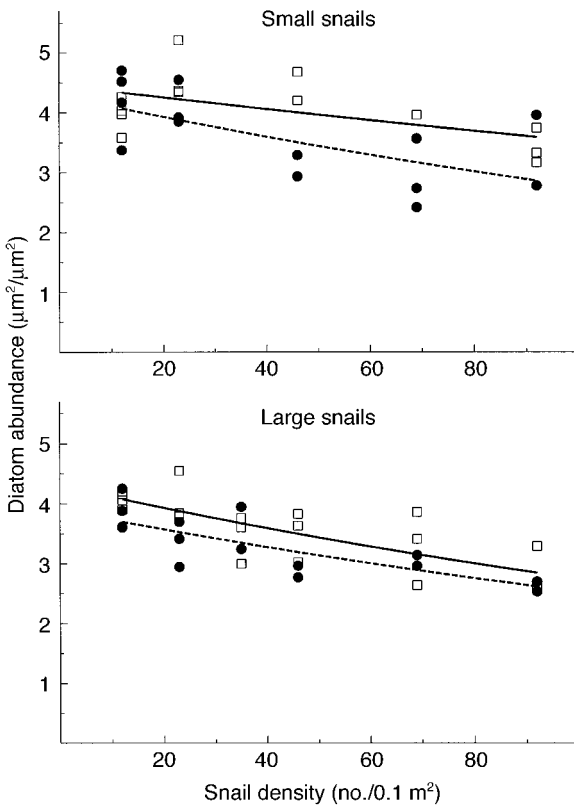FIG. 3. Effects of density of large and small *B. attramentaria* (□, solid lines) and *C. californica* (●, dashed lines) on the final density of diatoms after 37 d in 1995. Diatom abundance is expressed as diatom surface area (μm²)/sediment surface area (μm²). Negative exponential models were fit to the data. Relationships were significant; equations (with final diatom abundance = F) are as follows: small *B. attramentaria* ($R^2 = 0.33$), $F = 4.46e^{-0.0024 \times \text{snail density}}$; small *C. californica* ($R^2 = 0.40$), $F = 4.29e^{-0.0044 \times \text{snail density}}$; large *B. attramentaria* ($R^2 = 0.57$), $F = 4.30e^{-0.0045 \times \text{snail density}}$; large *C. californica* ($R^2 = 0.63$), $F = 3.9e^{-0.0043 \times \text{snail density}}$.

competition. The species-specific growth response to density differed significantly (Table 4). Because each snail species depressed the resources to similar levels (Figs. 3 and 4), but *Batillaria* grew more at any given resource level than *Cerithidea* (Figs. 5 and 6), *B. attramentaria* consequently grew more at any given snail density (Table 4, Figs. 7 and 8). At high densities *C. californica*'s tissue mass shrank during the course of the experiment.

Predictions of the effect of competition on snail growth

The field experiments described above quantified the species- and size-specific effects of snails on food density, as well as snail growth responses to particular food levels. Because relationships of snail effects on food and snail responses to food varied between the two years examined, presumably due to differences in diatom quality or productivity, predictions and tests of

predictions needed to come from within the same year. Data from 1996 experiments, therefore, were used to generate and test predictions, because in this year I directly quantified inter- as well as intraspecific competitive effects. Data from 1995, however, demonstrate the consistency of the qualitative relationships between each species/size class and its resources.

Predictions of interspecific competitive effects on growth generated from the equations describing the effects of each species on resource levels and their growth responses to resource levels corresponded well to empirical measures of competitive effects (Fig. 10). These curves were generated by substituting the effect of *Cerithidea* density on food levels (diatom abundance = $4.191e^{-0.0092 \times \text{density}}$) into *Batillaria's* response to different food densities [Growth = $(1.17 \times$ diatom abundance)/$(4.33 +$ diatom abundance)] (Fig. 10A), as well as substituting the effect of *Batillaria* density on food density (diatom abundance = $4.131e^{-0.0077 \times \text{density}}$) into *Cerithidea's* response to food density [Growth = $(1.54 \times$ diatom abundance)/$(2.51 +$ diatom abundance) $- 0.55$] (Fig. 10B). Empirically quantified growth measurements are compared with the predicted lines in Fig. 10. The predicted relationships accounted for 64% of the variation in *Cerithidea*'s effect on *Batillaria,* and 75% of the variation in *Batillaria*'s effect on *Cerithidea.*

DISCUSSION

Combining the independently measured components of exploitative competition, consumer effects on and responses to resource levels, correctly predicted the directly measured outcomes of individual-level effects of interspecific interactions between the snails. The
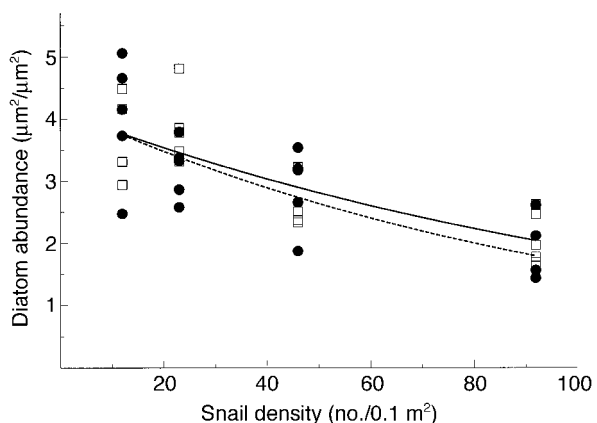

FIG. 4. Effects of large *B. attramentaria* (□, solid line) and *C. californica* (●, dashed line) densities on the abundance of diatoms after 39 d in 1996. Diatom abundance is expressed as diatom surface area (μm²)/sediment surface area (μm²). Negative exponential models were fit to the curves. Regression lines for the snails are significant. Equations (with final diatom abundance = F) are as follows: *B. attramentaria* ($R^2 = 0.67$), $F = 4.13e^{-0.0077 \times \text{snail density}}$; *C. californica* ($R^2 = 0.62$), $F = 4.19e^{-0.0092 \times \text{snail density}}$.
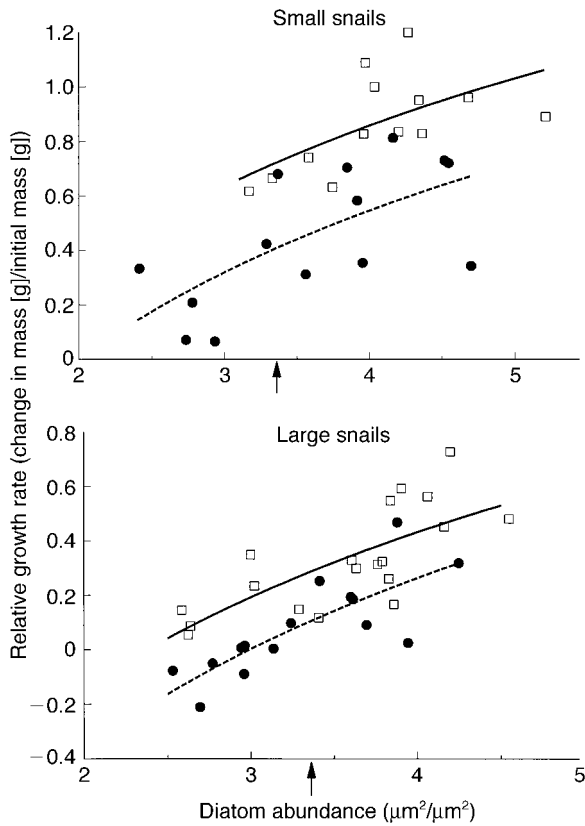
FIG. 5. Relative change in tissue dry mass of *B. attramentaria* (□, solid lines) and *C. californica* (●, dashed lines) of both size classes in 1995 at different diatom abundance levels over 37 d. Diatom abundance is expressed as diatom surface area (μm^2)/sediment surface area (μm^2); relative growth rate is expressed as change in tissue dry mass (g)/initial tissue dry mass (g). Saturating functions [relative growth = ($a \times$ diatom abundance)/(b + diatom abundance) − c] were fit to the data. Equations for the lines (with ΔG = relative tissue growth and F = final diatom abundance) are as follows: small *B. attramentaria* (R^2 = 0.33), ΔG_{BS} = (4.06 $\times F$)/(14.97 + F); small *C. californica* (R^2 = 0.44), ΔG_{CS} = (3.67 $\times F$)/(1.6 + F) − 2.07; large *B. attramentaria* (R^2 = 0.55), ΔG_{BL} = (4.92 $\times F$)/(12.0 + F) − 0.80; large *C. californica* (R^2 = 0.77), ΔG_{CL} = (4.43 $\times F$)/(1.33 + F) − 3.064. The arrows on the *x*-axes mark the average ambient diatom abundance at the end of the experiment.

predicted competitive effects in this community were not only qualitatively correct in terms of trends and rank order of snail growth between species, but also highly accurate quantitatively. I was able to predict 65–75% of the variance in growth over a substantial range of density of each snail species from data on the growth rate of each species in relation to food density plus data on the effect of each species on food density. This accuracy was obtained while predicting the outcome of exploitative competition, which is an inherently indirect effect because it involves the effect of one species on a second mediated through a third (the resource). Previous attempts to quantify predictions of biotic responses to indirect interactions have been rare (Tilman

1976, Rothhaupt 1988, Wootton 1994*b*), and such accuracy in the quantitative prediction of indirect effects on individuals has seldom, if ever, been obtained.

The results of the analyses of the component parts of exploitative competition illuminate the specific mechanism responsible for the superior competitive ability of the exotic snail. In the experiments, the snails differed little (1995) or not at all (1996) in their feeding, and hence in the level to which a *fixed* density of snails suppressed the resource. The marked difference between the snails was a superior growth response by *Batillaria* at any given level of resource. This higher conversion efficiency was apparent in both years that consumer-resource relationships were measured and at all resource levels by both size classes of these snails. Moreover, larger body size should translate into higher fecundity (Levitan 1989, Forbes and Lopez 1990, France 1992, Carroll and Quiring 1993). Thus, the population-level consequence of *Batillaria's* higher conversion efficiency should be that the invading *Batillaria* population eventually achieves a higher density than *Cerithidea*. As a result the *Batillaria* population should drive the resource below the equilibrium density set by *Cerithidea* (R_1*), thereby causing *Cerithidea* to decline and be replaced by *Batillaria*. The exclusion process should be accelerated by the higher mortality rate of *Cerithidea*. In sum, using the invasion criterion (Eq. 6):

$$\underline{m_1}/\alpha_1\varepsilon_1 > m_2/\alpha_2\underline{\varepsilon_2}$$

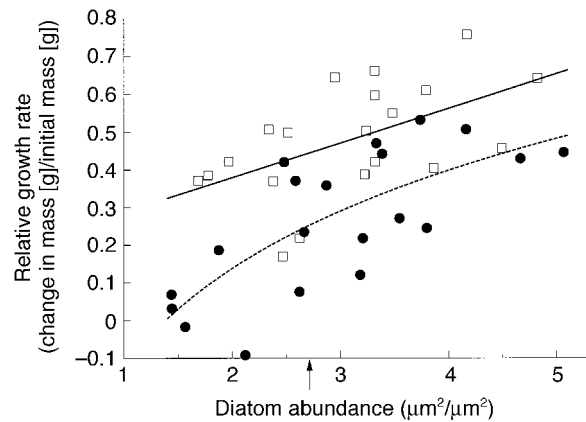where *Cerithidea* = species 1, *Batillaria* = species 2,

FIG. 6. Relative change in tissue dry mass of the large size class of *B. attramentaria* (□, solid line) and *C. californica* (●, dashed line) in 1996 at different diatom abundance levels over 39 d. Diatom abundance is expressed as diatom surface area (μm^2)/sediment surface area (μm^2); relative growth rate is expressed as change in tissue dry mass (g)/initial tissue dry mass (g). Again, the saturating functions [relative growth = ($a \times$ diatom abundance)/(b + diatom abundance) − c] were fit to the data. Equations for the lines are *B. attramentaria* (R^2 = 0.29), ΔG_{BL} = (1.17 $\times F$)/(4.33 + F); *C. californica* (R^2 = 0.54), ΔG_{CL} = (1.54 $\times F$)/(2.51 + F) − 0.55. The arrow on the *x*-axis marks the average ambient diatom abundance at the end of the experiment.

TABLE 4. Two-way ANOVA results for effect of intraspecific density and species on relative growth rates.

| Year	Snail size	Source	df	MS	F	P
1995	Small	Species	1	1.26	52.8	<0.00001
		Density	5	0.12	5.18	0.003
		Species × density	5	0.03	1.22	0.33
		Error	20	0.024		
1995	Large	Species	1	0.57	70.7	<0.00001
		Density	5	0.17	21.3	<0.00001
		Species × density	5	0.004	0.50	0.77
		Error	22	0.008		
1996	Large	Species	1	0.85	106.3	<0.00001
		Density	3	0.40	50.7	<0.00001
		Species × density	3	0.013	1.62	0.19
		Error	75	0.008		
1997	Large	Species	1	2.78	123.7	<0.00001
		Density	3	0.093	4.13	0.017
		Species × density	3	0.003	0.14	0.93
		Error	24	0.022		
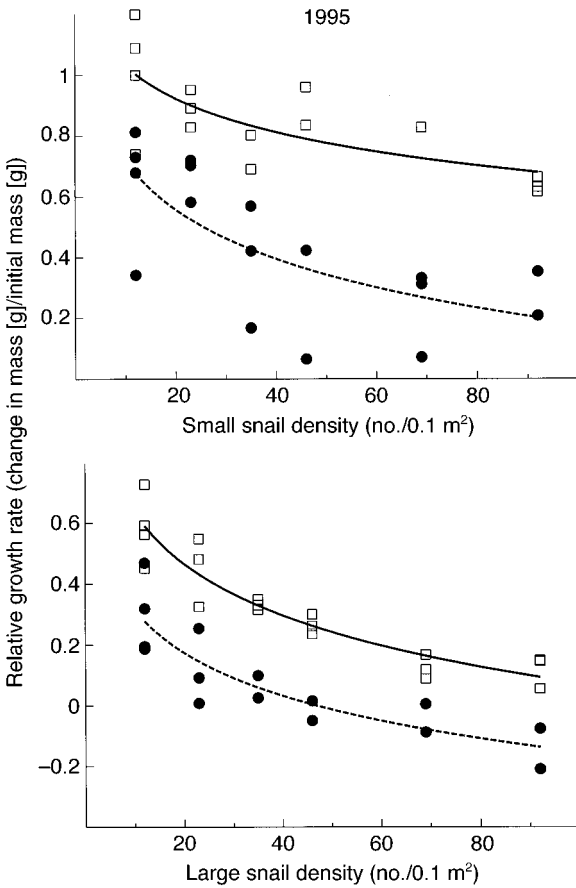
FIG. 7. Density-dependent growth responses over 37 d for the two size classes of *B. attramentaria* (□, solid lines) and *C. californica* (●, dashed lines) in 1995. Relative growth rate is expressed as change in tissue dry mass (g)/initial tissue dry mass (g). Data represent pen averages of relative changes in tissue dry mass for principal focal individuals. Linear transformation using the reciprocal of snail density was used to compare the species' responses to density. For both the small and large size classes, the species differed significantly in their growth responses to intraspecific density (Table 4).

m = death rate, ε = resource conversion efficiency, and underlining designates the larger of the two parameters represented by the same symbol. The findings that: (1) an increase in *Batillaria* density to just 4× ambient was typically enough to cause shrinkage of tissue in *Cerithidea* while *Batillaria* grew, and (2) *Batillaria* achieves population densities sometimes up to an order of magnitude larger than *Cerithidea* (McDermott 1996; J. E. Byers, *unpublished data*) corroborate this process of exclusion via exploitative competition.

Although superior exploitative competitive ability achieved by an enhanced resource conversion efficiency provides a sufficient explanation for the exclusion of *Cerithidea* by *Batillaria,* the higher parasitism rate of *Cerithidea* may also contribute. By cutting off reproduction without usually killing their hosts (and therefore allowing them to continue consuming re-
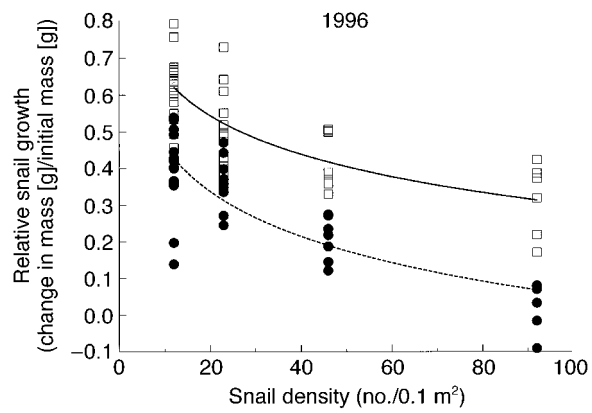

FIG. 8. Density-dependent growth responses over 39 d for the large size class of *Cerithidea* (●, dashed line) and *B. attramentaria* (□, solid line) in 1996. Relative snail growth is expressed as change in tissue dry mass (g)/initial tissue dry mass (g). The species differed significantly in their growth response to intraspecific density (Table 4). See Fig. 7 for more explanation.
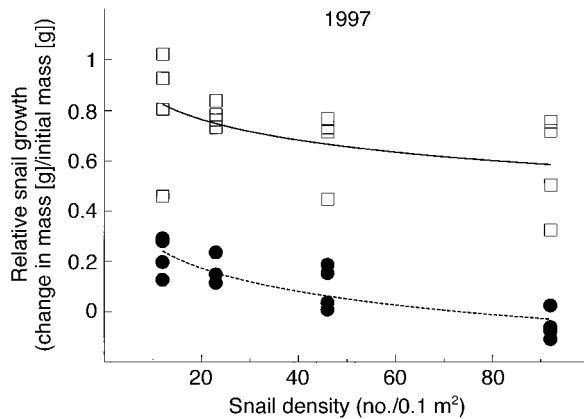
FIG. 9. Density-dependent growth responses over 60 d for the large size class of *Cerithidea* (●, dashed line) and *B. attramentaria* (□, solid line) in 1997. Relative snail growth is expressed as change in tissue dry mass (g)/initial tissue dry mass (g). The species differed significantly in their growth response to intraspecific density (Table 4). See Fig. 7 for more explanation.

sources), parasitic castrators reduce the average ε in a population. The larger reduction of ε in *Cerithidea* than *Batillaria* should increase *Batillaria*'s relative advantage and further foster its successful invasion.

Two principal factors that might prevent exclusion, trade-offs in competitive ability and immigration, appear absent in this system. No trade-offs in the snails' competitive ability were apparent as *Batillaria* grew more than *Cerithidea* at all resource levels in all years. Trade-offs have been demonstrated to be an essential factor in species persistence in the classic work on species coexistence (Hutchinson 1961, MacArthur and Levins 1967, Wilbur 1972, Armstrong and McGehee 1976, Tilman 1982, 1990, Warner and Chesson 1985). Recent theoretical and empirical work on *Tegula* spp. (marine benthic grazing snails) revealed that trade-offs in the snails' ability to affect and respond to the algal resource at different levels (area intensive vs. area extensive grazing *sensu* Schmitt 1996) is a key factor promoting coexistence between these otherwise highly similar species (Schmitt 1996, Wilson et al. 1999).

Immigration provides a second potential reason that empirical studies of exploitative competition between marine organisms in the field have not always confirmed the expectation of local exclusion of inferior competitors (e.g., Peterson 1982, Branch 1984, Underwood 1992, Schmitt 1996). Unlike most marine organisms, both of these mud snails produce nonplanktonic, dispersal-limited young (Whitlatch and Obrebski 1980, Race 1981, McDermott 1996), such that localized differences in body growth directly translate into differences in local input of newborns. Within a closed system where progeny are predominantly offspring of the local population, the influences of local, density-dependent processes, such as the effect of competition on individual growth, are directly related to local re-

cruitment/fecundity. Thus, in closed systems competitive effects have quicker and more direct impacts on local populations than typically found in open systems. As the *Cerithidea–Batillaria* system examined here is both closed and lacking in competitive trade-offs, exclusion of the inferior native competitor is unlikely to be prevented.

While the experiments described here quantify rates of resource use and conversion of resource and snail density for only 5 ½–8 ½ weeks at a time, the findings from these time periods are relevant to annualized rates for three primary reasons. First, the snail species are dormant for all of late fall through winter months (November–March) (Whitlatch 1974, McCloy 1979, Race 1981, Sousa 1983). Secondly, McDermott (1996) con-
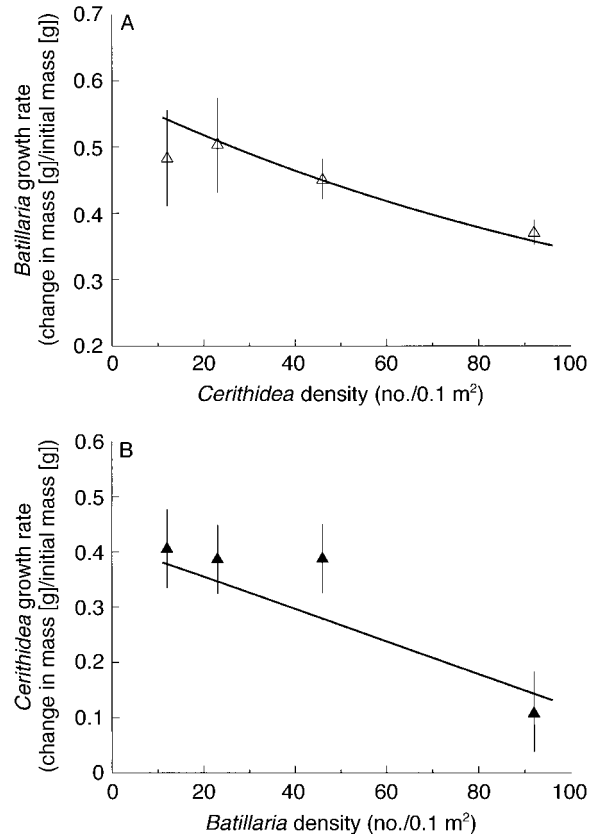

FIG. 10. Predicted relative growth of each snail species across a density gradient of heterospecific competitors (solid lines). Relative growth rate is expressed as change in tissue dry mass (g)/initial tissue dry mass (g). Functions were derived for large snails in 1996 from mathematical relationships describing the effect of each snail on the resource (Fig. 4) and the growth response of each snail to various resource densities (Fig. 6). Symbols ($\triangle$, ▲) represent direct measurements of relative snail growth at each density of heterospecific competitor ($\pm$ 1 SE). (A) Effects of *C. californica* density on *B. attramentaria* growth rates. The R^2 value of the fit of the observed points to the prediction line is 0.64. (B) Effects of *B. attramentaria* density on *C. californica* growth rates. The R^2 value of the fit of the observed points to the prediction line is 0.75.

ducted similar studies on snail density effects on growth in 21–25 mm *Batillaria* and *Cerithidea* in Bolinas Lagoon. His experiment spanned 71 d (22 July– 30 Sept 1995) and provide measurements of competitive effects on snail growth 55–60 d later in the year than my experiments. Using ambient and 2× ambient densities he found the difference in absolute growth of *Batillaria* to be ~2× greater than *Cerithidea.* Likewise, his results indicate a substantial advantage to *Batillaria* through a mortality rate nearly eight times less that of *Cerithidea* (*Cerithidea* 12.1% vs. *Batillaria* 1.6%). Finally, the results presented here incorporate three years of interannual variation. In all years, (1) *Cerithidea* and *Batillaria* affected their food resource to an almost identical degree, (2) *Batillaria* responded to food levels with a higher resource conversion efficiency, (3) *Batillaria's* superior resource conversion held for all levels of resource, i.e., trade-offs in the ability of *Batillaria* to exploit the resource as resource levels varied were not apparent, and (4) intraspecific density had a much greater effect on growth rates of *Cerithidea* than *Batillaria.* The consistency of the results despite variable conditions that undoubtedly existed between these years underscores their robustness in describing interactions applicable to a time period longer than each individual experiment.

Role of competition in species invasion

Many studies that have attempted to document the mechanisms responsible for the success of introduced species have emphasized the role of ''predator-free space'' (e.g., Debach 1974, Goeden and Louda 1976, Kuris and Norton 1985, Pimm 1987, Meng and Orsi 1991). The role of competitive ability enabling invasions has received much less attention. Certainly, the well-developed body of theory on competitive exclusion has not, for the most part, been incorporated into empirical studies of nonindigenous species invasion. Elton (1958) suggested that empty niches, i.e., the lack of competition, within some communities facilitated establishment of invading species. Several years later, this hypothesis shaped a large part of island biogeography theory, and the ease of insular invasions was often attributed to the lack of competition (MacArthur and Wilson 1967, Simberloff and Wilson 1970, Diamond 1975). Additionally, nonequilibrium theory emphasized the role that disturbances played in keeping populations from attaining equilibrium levels, thereby reducing the role of competition in community interactions, which aided the invasion/establishment of competitively inferior species (Paine 1966, Wiens 1977, Connell 1978, Huston 1979, Sousa 1979). Recent work has suggested that not all unsaturated communities are more invasible than saturated communities (Herbolde and Moyle 1986, Crawley 1987), and controversy over the vulnerability of islands to invasions has grown (Lake and O'Dowd 1991, Simberloff 1995).

Ambiguity regarding the role of competition in in-

vasions may result from difficulties in demonstrating competition unequivocally. Lodge (1993) concludes from his review of biological invasions that the two leading causes of failed exotic establishment are inappropriate climate and predation. He also states, however, that the effects of competition, disease, and other factors are likely underestimated since they are more difficult to measure. If superior competitive abilities are responsible for successful species invasions, it may be very difficult to catch exotic–native interactions before complete exclusion has occurred (Murdoch et al. 1996). Studies of animal invasions that have attributed the success of an exotic species to superior competitive abilities often exhibit shortcomings. Many of these studies are frequently supported by observational rather than experimentally derived evidence (Nevo et al. 1972, Crowell 1973, Porter et al. 1988, Doncaster 1992, Douglas et al. 1994, Caron et al. 1996). For example, overlap in resource use between an exotic and a native species is often considered ample evidence that competitive ability is important to the establishment of the exotic species.

In conclusion, the approach applied here confirms a potentially important pathway of interaction between a native and an introduced species that has seldom been examined experimentally. In this system, although other mechanisms may have important roles, exploitative competition appears to provide a substantial, and certainly sufficient, explanation of the exotic species' success at invasion. The specific mechanism of *Batillaria*'s success is not through superior exploitation of the resource, as is often the mechanism assumed or examined in competitive displacement studies (Human and Gordon 1996, Petren and Case 1996, De Biseau et al. 1997, Ducobu et al. 1998), but rather through superior conversion of the resource (as in Murdoch et al. 1996). Future studies of exotic invasions should not automatically assume the primacy of ''predator-free space'' as the driving force behind exotic species' success, but consider other potentially important mechanisms, such as superior competitive ability, as important forces as well.

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APPENDIX

A table reporting average relative changes of different per capita metrics of growth of both sizes and both species of snail for all years is available in ESA's Electronic Data Archive: *Ecological Archives* E081-013.

Average relative changes [(final − initial)/initial] of different per capita metrics of growth (means, with 1 SD in parentheses) of both sizes and species of snail for all years. C = *Cerithidea californica*; B = *Batillaria attramentaria.*

Year	Size class	Species	Density	Length (mm)	Width (mm)	Wet mass (g)	N
1995	Small	C	12	0.33 (0.048)	0.27 (0.042)	1.28 (0.21)	4
		B	12	0.31 (0.038)	0.30 (0.021)	0.99 (0.13)	4
		C	23	0.31 (0.052)	0.26 (0.05)	1.03 (0.035)	3
		B	23	0.28 (0.33)	0.23 (0.034)	0.87 (0.10)	3
		C	35	0.25 (0.024)	0.21 (0.015)	0.84 (0.068)	3
		B	35	0.28 (0.048)	0.22 (0.011)	0.93 (0.014)	2
		C	46	0.26 (0.0062)	0.19 (0.039)	1.16 (0.23)	2
		B	46	0.28 (0.024)	0.28 (0.0111)	0.95 (0.049)	2
		C	69	0.26 (0.037)	0.21 (0.034)	0.95 (0.15)	3
		B	69	0.29 (N/A)	0.26 (N/A)	0.93 (N/A)	1
		C	92	0.21 (0.021)	0.19 (0.031)	0.79 (0.04)	2
		B	92	0.27 (0.027)	0.27 (0.032)	0.89 (0.11)	3
	Large	C	12	0.050 (0.019)	0.080 (0.025)	0.21 (0.054)	4
		B	12	0.13 (0.025)**	0.11 (0.023)	0.29 (0.046)	4
		C	23	0.040 (0.026)	0.083 (0.056)	0.11 (0.068)	3
		B	23	0.12 (0.035)*	0.12 (0.031)	0.30 (0.019)**	3
		C	35	0.015 (0.0059)	0.047 (0.017)	0.064 (0.0063)	2
		B	35	0.12 (0.0087)**	0.11 (0.13)**	0.25 (0.28)**	3
		C	46	0.027 (0.014)	0.050 (0.0015)	0.079 (0.012)	2
		B	46	0.097 (0.026)*	0.10 (0.019)*	0.25 (0.060)*	3
		C	69	0.011 (0.032)	0.034 (0.0093)	0.055 (0.039)	2
		B	69	0.083 (0.011)*	0.085 (0.0077)**	0.20 (0.019)**	3
		C	92	0.0066 (0.0007)	0.039 (0.023)	0.035 (0.017)	2
		B	92	0.078 (0.0067)**	0.083 (0.027)	0.18 (0.012)**	3
1996	Small	C	54	0.23 (0.042)	0.21 (0.41)	0.95 (0.16)*	7
		B	54	0.23 (0.024)	0.21 (0.025)	0.78 (0.071)	8
	Large	C	12	0.045 (0.015)	0.040 (0.038)	0.24 (0.049)	17
		B	12	0.096 (0.026)**	0.091 (0.014)**	0.30 (0.080)**	17
		C	23	0.029 (0.012)	0.040 (0.016)	0.18 (0.051)	11
		B	23	0.088 (0.023)**	0.081 (0.017)**	0.27 (0.053)**	12
		C	46	0.011 (0.0050)	0.017 (0.010)	0.12 (0.032)	7
		B	46	0.081 (0.015)**	0.076 (0.017)**	0.22 (0.062)**	7
		C	92	0.0057 (0.0059)	0.016 (0.011)	0.11 (0.036)	6
		B	92	0.074 (0.017)**	0.064 (0.021)**	0.23 (0.048)**	6
1997	Large	C	12	0.073 (0.018)	0.067 (0.017)		4
		B	12	0.14 (0.061)	0.077 (0.046)		4
		C	23	0.052 (0.023)	0.038 (0.026)		4
		B	23	0.14 (0.019)**	0.089 (0.012)*		4
		C	46	0.045 (0.024)	0.032 (0.020)		4
		B	46	0.13 (0.024)**	0.077 (0.018)*		4
		C	92	0.025 (0.010)	0.024 (0.015)		4
		B	92	0.12 (0.019)**	0.066 (0.013)**		4

Notes: Density is the number of snails in each enclosure pen (0.1 m²). Length was measured from apex to anterior tip of aperture, and width was measured at largest whorl at mouth. Wet mass represents the entire body mass (shell + tissue) of the snail. Pairwise *t* tests were performed to compare the two species at each density level for each of the three metrics.

* $P \leq 0.05$; ** $P \leq 0.01$ (significant differences).