

## EXPOSING THE MECHANISM AND TIMING OF IMPACT OF NONINDIGENOUS SPECIES ON NATIVE SPECIES

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**Abstract.** The nonnative mudsnail *Batillaria attramentaria* was introduced to the west coast of North America in the early part of this century and has been displacing the native mudsnail *Cerithidea californica* on a marsh-by-marsh basis. We combined detailed, quantitative field data on this invader and its interactions with the native snail in an individual-based model that allowed us to address both general questions about the mechanism of displacement of native species and more specific concerns about detecting the trajectory and impact of the invasion. In empirically parameterized simulations the native snail was driven extinct within 55–70 yr after introduction of *Batillaria*, which closely matches direct field estimates. We then tested the relative importance of *Batillaria*'s demonstrated advantages in parasitism resistance (top-down effect), exploitative competition (bottom-up effect), and mortality rate (demographic advantage) in driving its displacement of *Cerithidea*. With its demographic advantage maintained, but without its advantages in competition and parasitism, *Batillaria* still drove *Cerithidea* extinct within 90 yr. Only when *Batillaria*'s mortality rate was set equal to that of *Cerithidea* could the native snail persist indefinitely, demonstrating this factor's overwhelming influence on the success of this invasion. The difference in mortality between the species was large relative to the other differences, but further simulations showed that the importance of this difference stems not just from its magnitude, but also from the sensitivity of this system to this demographic rate. Identification of the relative importance of mechanisms that contribute to an invader's success is one of the major benefits of such modeling efforts.

To identify empirically measurable quantities that provide the earliest warning of impact on the native species, we tracked many population- and individual-level responses of *Cerithidea* to *Batillaria*'s invasion, including population density, biomass, egg production, mean size, proportion of infected individuals, and individual growth rate, as well as availability of shared food resources. We used the empirically observed parameter values and an initial number of *Batillaria* invaders in these simulations that guaranteed extinction of *Cerithidea* within 90 yr. Despite a rapid initial increase in invader populations, all metrics for *Cerithidea* were slow to exhibit signs of impact. Most took at least 25 yr from invasion to exhibit detectable changes, by which time the nonnative species was established at high densities (>3000 snails/m<sup>2</sup>). *Cerithidea* egg production was the fastest, most consistent response metric exhibiting declines within 20–25 yr after invasion in ~90% of simulations. Difficulty in finding reliable, early warning metrics has crucial implications for how we should view and conduct monitoring programs and risk assessment analyses.

**Key words:** *Batillaria*; *Cerithidea*; coexistence; exotic species control; exploitative competition; extinction debt; individual-based models; invasion; local extinctions; stage-structured models; time lags; top-down and bottom-up effects.

### INTRODUCTION

As introductions of nonnative species continue in biological communities worldwide (e.g., Williamson 1996, Cohen and Carlton 1998), it is increasingly important for ecologists to understand the spread of invaders and for managers to be able to predict the impact

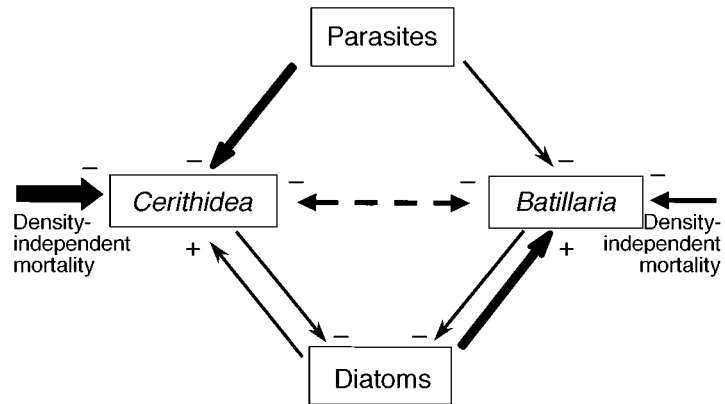
that a given invasion will have on native species (Parker et al. 1999). However, the complexity of multispecies communities and the novelty of each invader within them make it difficult to anticipate the course of any invasion, and quantitative predictions remain few. The paucity of detailed, mechanistic information about the interactions of nonnative species with native species has certainly also been a major limitation, though some workers have made predictions using correlative analyses of other successful invaders (Roy 1990, Perrins et al. 1992, Rejmánek 1995, 1996, Mack 1996, Reichard and Hamilton 1997, Lonsdale 1999). In the present study we combine detailed, quantitative field data on the life histories and interactions of a native and a nonindigenous marsh snail with an individual-based

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FIG. 1. Summary schematic of trophic interactions among *Cerithidea californica*, *Batillaria atramentaria*, their parasites, and their resources. The bold arrow to the upper left reflects *Cerithidea*'s higher infection rate by trematode parasites. The bold arrow to the bottom right reflects *Batillaria*'s superior resource conversion efficiency. The bold arrow to the left of *Cerithidea* represents its higher density-independent mortality rate. The dashed arrow between the two snails represents the negative indirect effects of each species upon the other via the effects of exploitative competition (the bottom half of the diamond-shaped schematic).



model to elucidate the relative importance of mechanisms responsible for native species displacement and to predict the trajectory and impact of an invasion. We show that mechanistic models may provide a useful means of incorporating and extending existing data to address both general and applied concerns and also show that detection of the impact of an exotic during the early stages of its invasion may be problematic.

The Asian salt marsh mud snail, *Batillaria atramentaria*, was introduced to marshes of northern California, USA ~70 yr ago when it was transported accidentally with Japanese oyster shipments for aquaculture (Barrett 1963). Since that time it has begun displacing the native snail *Cerithidea californica* from its common habitats (Byers 1999). Both species produce demersal egg sacs with directly developing larvae and exhibit limited movement as adults (J. E. Byers, unpublished data), so their populations within bays are essentially closed. Once mature ( $\geq 14$  mm), snails of both species are susceptible to infection by trophically transmitted trematode parasites that castrate the individuals that they infect, eliminating future reproduction; these parasites typically infect *Cerithidea* at a higher rate than they do *Batillaria* (Sousa 1983, Lafferty 1991, McDermott 1996, Byers 2000). Byers (2000) demonstrated that these snails also compete for shared, limited diatom food resources and that the introduced snail has an advantage in exploitative competition due to its higher resource conversion efficiency (Fig. 1). Predictions of interspecific effects of each species upon the other, based on quantification of consumer-resource interactions, were highly accurate at an individual level. In the present paper we expand these predictions to the population-level impact of the non-native species by constructing and parameterizing an individual-based model with these empirical data. We use this model not only to predict times of local extinction for the native snail, but also to focus on two areas of primary importance to invasion biology. First, we determine the relative importance of ecological mechanisms responsible for the exclusion of *Cerithidea* by *Batillaria*. Second, we identify empirically measurable quantities within a system that provide the ear-

liest detection of impact on the native species and signal the likely course of the invasion in a given location.

Understanding the mechanisms of successful invasion is important for predicting the impact of invaders and controlling their proliferation. To this end, our model allowed us to probe aspects of the snails' biology that are extremely difficult to manipulate in the field, such as parasitism rates and competitive strengths. Modeling variation in these parameters enabled us to test the relative importance of each mechanism that contributes to the success of *Batillaria* and consequent displacement of its native analogue. Identification of the most influential mechanisms to the invader's success also might help to expose a potential "Achilles heel" of the invasion, that is, a specific aspect of the invader's biology or interaction with native species that could be targeted for intervention to most effectively limit its success or impact.

The mechanisms for *Batillaria*'s success over *Cerithidea* can be considered in three nonexclusive groups: resource competition ("bottom-up"), parasitism ("top-down"), and demographic advantages. (The consequences of the first two may manifest themselves demographically, but nontrophically based differences in demography may also play a role.) Although the existence of all these mechanisms has been demonstrated empirically (Whitlatch and Obrebski 1980, McDermott 1996, Byers 2000), the relative influence of each advantage on the ultimate success of the invader has not previously been evaluated. Other factors, including freshwater runoff, habitat degradation, and other exotic species such as the green crab, *Carcinus maenas*, may also influence the success of *Batillaria*'s invasion, but seem to be rare and of only minor influence in our system. We view the present study as an early step in developing a full understanding of invaded systems.

In addition to clarifying mechanisms by which an invader affects native species, models such as ours help identify which individual- and population-level metrics should be monitored to enable the quickest and most efficient detection of invader impacts on the native species. Early control measures may allow resource managers to limit both ecological and economic losses and

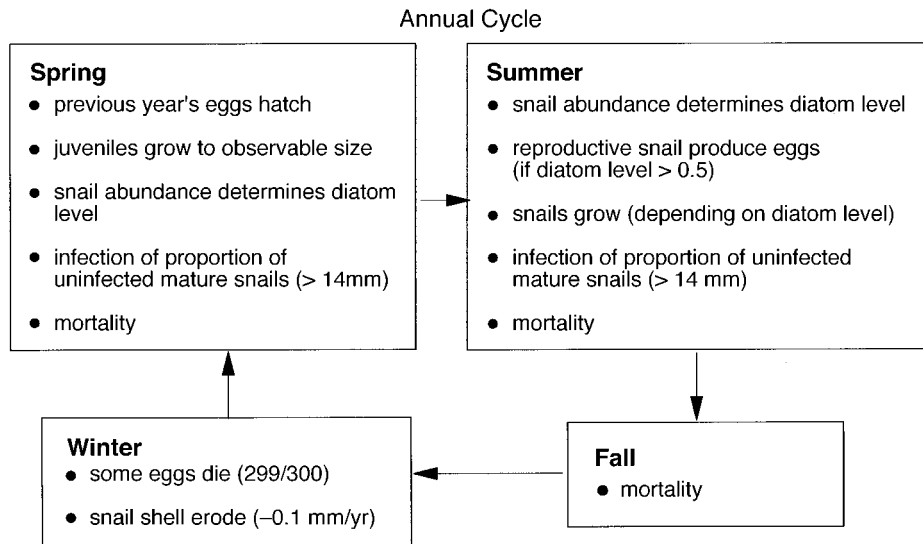


FIG. 2. Flow chart specifying major annual life history events of the snails as they were captured in the model.

are likely to be more cost- and energy-effective than later efforts. However, "false alarms," i.e., removals of nonimpacting invaders, may pose ancillary risks and cause damage to native species and systems (Leppla 1996, Rice and Toney 1998, Ussery and Krannitz 1998, Reeve-Morghan and Seastedt 1999), as well as desensitize the public to scientists' warnings. Ideal monitoring programs would not only help anticipate the course of impact, but would also enable distinctions between invasions that will displace or harm native species and those that will extinguish themselves or proceed with minor impact on native biota. Therefore it is crucial to identify metrics that can provide the earliest detection of invader impact. Clearly the areas of mechanism and monitoring are closely coupled: monitoring that detects changes in biological attributes of a native species may give insight into the means by which the invader proliferates.

#### METHODS

##### *Model structure and parameter estimation*

We constructed an individual-based, nonspatial model that tracked the species, sex, age, size, and infection status of each snail species through time. Fig. 2 depicts the annual life history and seasonal events that the model incorporated. We set most demographic rates and interaction coefficients with empirical data, either observational or experimental, derived from the populations in Bolinas Lagoon, California, USA (Byers 2000; J. E. Byers unpublished data). Most of the data were both size and species specific, and below we describe in detail how we used these data to set the parameters for individuals of all sizes. We used abundances that corresponded to an arena size of 0.1 m<sup>2</sup>. We set the initial populations to resemble the observed ones as closely as possible, using the observed mean and standard deviation in snail size ( $22.1 \pm 3.2$  mm for *Cerithidea* and  $18.4 \pm 3.9$  mm for *Batillaria*, re-

spectively) to establish the distribution from which we assigned the initial sizes to the snails. In all simulations in which *Batillaria* was introduced, we first ran *Cerithidea* alone for 11 yr to reduce any artifacts of the initialization.

The parameters of the model and the equations used to derive values for them are shown in Table 1. The Appendix presents pseudocode for the key routines of the computer program, giving a more detailed view of the simulations. Many of the parameter values were calculated by combining data across years or across snails of different sizes. Typically, data existed for snails of 10 and 20 mm in length and for the years 1995, 1996, and 1997, although not all quantities were measured in all three years. The values of many of the parameters differed markedly over the three years of data collection, and the small number of years of data made it unreasonable to try to quantify the degree of variability. Consequently, the variability in these simulations stems from demographic stochasticity and from the deterministically calculated probabilities associated with monthly mortality, parasitic infection, and assignment of sex, rather than from empirically derived probability distributions of observed parameter values.

Using an individual-based model (IBM) let us avoid many of the simplifying assumptions and artifacts that an aggregated model would have imposed. For instance, growth involves the accumulation of small changes that can differ from one snail to another. The binning of snails into size categories necessary for a size-structured model would have reduced these sums to probabilities of transitions from one size class to another, which would have both reduced precision and created a stochasticity that is not actually present. It also would have been difficult to impose a maximum age for snails (20 yr) without keeping track of the age of each snail. Some processes, such as density depen-

TABLE 1. (A) State variables and (B) parameters quantified in field experiments and used within the model.

A. State variables					
Model components	Units	Species and size class	<i>a</i>	<i>b</i>	Comments
Diatom level <sup>†‡</sup> = $a \times \exp(b \times \text{snail density})$	$\mu\text{m}^2$ diatom surface area/ $\mu\text{m}^2$ sediment surface area	C <sub>10</sub>	4.3	-0.0044	When snails of mixed species and sizes were present, the coefficients ( <i>a</i> and <i>b</i> ) were the means of their separate values.
		C <sub>20</sub>	4.02	-0.0067	
		B <sub>10</sub>	4.46	-0.0024	
		B <sub>20</sub>	4.22	-0.0061	
Resource-dependent individual growth <sup>†‡</sup> = $a \times \text{diatom level} + b$	mm	C <sub>10</sub>	0.36	1.73	Growth was constrained to be positive; a small decrease due to erosion or basic metabolism was applied separately. (In the field large <i>Cerithidea</i> at low resource levels exhibit negative tissue growth.)
		C <sub>20</sub>	0.40	-0.26	
		B <sub>10</sub>	0.03	2.85	
		B <sub>20</sub>	0.26	1.48	
Density independent mortality <sup>†</sup> = $a \times \text{length} + b$	% probability of death/mo	C	0.24	-2.07	For infected snails, the calculated value was increased 10%. The maximum age for all snails was 20 yr.
		B	0.0093	0.23	
Reproduction = $0.079 \times (\text{snail length})^{2.7}$	no. eggs/yr				None if snail infected, if <14 mm, or if diatom level <0.5.
B. Parameters					
Model components	Units	Relationship or Value		Comments	
Egg survival	probability of surviving·egg <sup>-1</sup> ·yr <sup>-1</sup>	1/300			
Parasitic infection rate <sup>†</sup>	probability per season	$p(\text{Batillaria}) = 0.3 \times p(\text{Cerithidea})$		Probability was applied once during spring and once during summer. Snails <14 mm are not susceptible to infection.	
Shell erosion	mm/yr	0.1			

Notes: For the first three state variables, empirical relationships were determined experimentally from plots with snails of single species (*Cerithidea* or *Batillaria*) and sizes (10 mm or 20 mm); hence, corresponding values are denoted by the first initial of each species with size class in millimeters as a subscript (except for mortality where snail length is explicitly part of the equation). For these first three state variables, values for snails of intermediate sizes were calculated by linear interpolation from the 10- and 20-mm snails. Snails below this range were treated as 10 mm, and snails above this range were treated as 20 mm. Parasitic infection rates were derived from field data; egg survival and shell erosion are informed estimates. See *Methods: Model structure and parameter estimation* for further explanation.

† For one or more of the state variables and parameters that differed between the species, some runs set the value for *Batillaria* equal to the value for *Cerithidea* to determine which differences may be most important in promoting the displacement of the latter by the former.

‡ Both a species' effect on the diatom resource and its growth response to diatom levels contribute to its exploitative competitive abilities. In simulations that removed *Batillaria*'s competitive advantage, both state variables were equalized to *Cerithidea*'s values. As empirical differences in the effects of each species on the resource were small (typically <10%), the majority of the effect of equalizing competition derives from changes in the efficiency of *Batillaria*'s conversion of resources to growth.

dence, influence some properties but not others, and an IBM allowed any associations between size, age, species, and parasite level develop in a relatively natural manner. Finally, to the degree that demographic stochasticity is important, an IBM incorporated it automatically.

Most of the field measurements were taken on snails of 10 or 20 mm in length (except reproduction, which was quantified for snails of all sizes) and showed that many rates vary strongly with size. The model included snails of all sizes, so it was necessary to estimate the rates for the other sizes. We used a continuous, piecewise linear function to estimate the values for other sizes: this function is linear between 10 and 20 mm and flat outside this interval (Table 1). Limiting the

rates to the observed range probably underestimates their full range slightly, but prevents biologically unreasonable extrapolations beyond measured values; this mathematically simple approximation also avoids the introduction of additional parameters and the resulting increased opportunity for error. For the fitted curves, when we had demographic data for several years, we did not average the values of the annual curves to calculate a rate for a snail of a given size. Instead, we averaged the parameters (such as slopes and intercepts) of all the separate annual curves to construct an average relationship over all years and then used this relationship to calculate the rate for any given size.

The model used a range of snail lengths from 8 to 33 mm; snails outside this range are rarely observed.

Shell length is easily measured in the field, but actual snail biomass is probably more meaningful biologically. However, snail biomass is tightly correlated with shell length in these species (Whitlatch 1974, Byers 2000), so that little is lost by building the model around the empirically more accessible quantity. The model included a small degree of shrinkage of the snails because of the observation that, particularly in times of low resource levels, snail growth can be slightly negative and erosion can reduce the size of shells. We incorporated shrinkage by subtracting a uniform amount from the size of every snail during the winter, thereby capturing the requirement that a snail have a positive nutrient intake to maintain a constant size. We then constrained the growth function to be positive in the absence of shrinkage.

The trematode parasites in this system progress through complex life history stages as they move trophically through the marsh system. Trematodes typically infect the gonads of snails, so immature snails (<14 mm) do not often become infected. Once a snail becomes infected it does not reproduce and cannot rid itself of infection. Although the rate of new infections of snails probably depends on the abundance of miracidia (the snail-infecting stage) in the water and marsh surface, which in turn may depend indirectly on the number of snails that are infected, this feedback loop was not included in the model. Because of their obligate trophic life cycle, trematodes are not transmissible from snail to snail and therefore are not directly influenced by changes in snail density. At present, too few data exist to allow us to incorporate the trophic transitions of the parasites' life cycle accurately; and the abundance of miracidia, which are spread in the feces of migratory birds, probably depends on spatial dynamics much larger than the spatial scale of a single marsh. Consequently, we simply used constant, species-specific probabilities of infection that were based on the observed infection rates. Lafferty (1991) found that infection in *Cerithidea* increased the chance of death; therefore, we applied a 10% increased probability of death to infected snails of both species. Due to the cumulative chance of infection over time, the percentage of snails infected increases with snail size and age in the model as in the marshes.

The reproductive output of *Cerithidea* was calculated with in situ field experiments to determine the relationship between snail size and egg sac production across the full adult range (J. E. Byers, unpublished data). Although similar experiments were also carried out on *Batillaria*, logistical problems resulted in too few sacs to produce a statistically valid size–fecundity regression. However, given the similarity of the few sacs obtained from *Batillaria* experiments to those of *Cerithidea*, identical absolute and relative gonad sizes in snails of each species (J. E. Byers, unpublished data), and the general similarity of the early life histories of the two species (Habe 1944 and Amio 1963, as cited in Whitlatch 1972), we conservatively assumed the relationship between snail size and egg production in *Batillaria* to be the same as that in *Cerithidea*.

Mortality rates of the two snails were determined by averaging three years of the rates measured by Byers (2000). These data had been collected from enclosure experiments that contained snails in intraspecific and intra-size class treatments at densities that ranged from 0.5 times to 4 times typical ambient levels. These data for each size class of each species were analyzed with logistic regression for each of the three years for density dependence. In only one case (20 mm *Cerithidea* in 1995) was there evidence for any density dependence in mortality rates; *Batillaria* did not exhibit density dependence in any year. Mortality was therefore treated as density independent across the densities in these simulations. Density independent factors that potentially influence mortality include freshwater shock, desiccation, and senescence. As a check on the sensitivity of the model to our treatment of mortality as density independent, we ran several simulations with density-dependent mortality for large *Cerithidea*; such alteration had no discernable qualitative effect on the outcomes.

The dynamics of the model required the inclusion of egg survival rates, but we lacked data to estimate this parameter, which might be difficult to measure empirically under any circumstances. We could do little more than use values that our field experience with this system and our general biological intuition suggested might be plausible. As we did with any parameter the value of which we were unsure, we experimented with a range of values to test the model's sensitivity to it. The differences in egg survival that we investigated had no discernable qualitative effect on the outcomes. Lacking any data to suggest otherwise, we conservatively set this value to be the same for *Batillaria* and *Cerithidea*.

We also varied the starting density of *Cerithidea* to determine both its effect on the course of an invasion and the sensitivity of monitoring to variability in population density. We started runs with either 60 or 200 individuals/0.1 m<sup>2</sup>; regardless of the starting density, populations in the model fairly consistently approached the higher density. It is not uncommon to observe the higher density in the field, although the lower density is observed more frequently. Most simulations were initiated with 60 *Cerithidea* because, as we show in *Results*, invasion impact was slightly easier to detect in populations of *Cerithidea* that started below carrying capacity. Therefore, by presenting the model runs where the native started with reduced density, we conservatively present the best case scenario for how quickly impact can be detected.

In summary, the model parameters and operations allow the number, sizes, and species of snails to determine the amount of resource available (Table 1). Snail growth rates vary with resource level; however, the two species differ more in their response to resource level (resource conversion efficiency) than in their consumption of the resource. Egg production also depends on resource level, since no reproduction occurs if the level falls too low. Egg mortality is constant and equal

between the species. Infected and immature snails (<14 mm) cannot reproduce; otherwise, reproductive output increases with snail size. Monthly mortality is density independent, and *Cerithidea* dies at a higher rate than does *Batillaria*. Maximum longevity for both species is 20 yr. Finally, parasitic infection rates are naturally lower in *Batillaria*, and infection increases the typical monthly mortality rate in both species by 10%.

#### Model validation

We examined three lines of evidence to determine how well this model captures the dynamics of this system. First, we analyzed the resulting densities and size distributions of *Cerithidea* and *Batillaria* in single-species runs to see how each matched observed size distributions of single-species populations. Although the initial size distribution in each run was chosen to match the observed distribution, that distribution could change markedly during the course of a run. Indeed, during the early phases of model building we found that the effects of some parameters on the population size distributions could be extremely complex, involving a nonintuitive interplay between size, age, reproduction, survival, and resource level. Second, we compared the prevalence of parasitic infection of both species with their observed prevalence of infection. Third, we compared the simulated times to extinction of *Cerithidea* to empirically estimated extinction times at a few sites in northern California for which data are available (from Byers 1999).

#### Mechanisms for exotic success

The simple fact of displacement of *Cerithidea* by *Batillaria* does not indicate which ecological differences between the two species play major roles and which are minor. In the model, *Cerithidea* and *Batillaria* differed in their rates of (1) exploitation, that is, in their effects on the resource level and growth in response to a given resource level, (2) parasitism, and (3) mortality. To test the relative importance of competitive and parasitic resistance on invasion success, we conducted simulation runs for each of five levels of invading *Batillaria* (see following paragraph) using four different parameter combinations. The first combination used all empirically derived parameter values for all three of the above parameters; the values for *Batillaria* thus differed from those of *Cerithidea*. Three other combinations set the rate of *Batillaria* equal to that of *Cerithidea* for exploitation alone, parasitism alone, or both together. Finally, to assess the importance of differences in mortality, we repeated exactly the same set of runs but with the mortality rates for *Batillaria* set equal to those of *Cerithidea*.

We ran 200 replicates of these simulations for 100 yr each: on longer time scales assumptions about density dependence and other nonlinearities tend to dominate the results, as do artifacts from even small errors in parameter estimation. Five different levels of *Batillaria* (1, 2, 4, 8, and 16 snails/0.1 m<sup>2</sup>) were introduced only once, in year 11. We recorded the percentage of runs that ended in extinction of either *Batillaria* or

*Cerithidea* and, when at least 50% of the runs resulted in the extinction of *Cerithidea* the median time to extinction.

A simple comparison of the effects of the observed differences between *Cerithidea* and *Batillaria* does not necessarily tell which kind of difference is most fundamental in driving the exclusion of *Cerithidea* by *Batillaria*. It is possible that some parameters have a large influence only because they are large relative to other differences. To control for the effect of the magnitude in assessing the importance of each parameter, we ran additional simulations in which the differences between *Cerithidea* and *Batillaria* were standardized to 50% for each parameter. For these runs, we first ran a series of simulations in which the values of *Batillaria* were identical to those of *Cerithidea* and then increased *Batillaria*'s exploitation rates 50% relative to those of *Cerithidea* (not relative to its own observed rates), decreased its parasitism rate 50%, or decreased its mortality rate 50%.

#### Monitoring

*Average aggregate impact.*—The above simulations examined the effects of *Batillaria* invasion on the probability of extinction of *Cerithidea* and the mechanisms by which those effects act, but they do not tell at what point the effects on *Cerithidea* might be detectable in practice. The simulations in this section compare several metrics over the course of invasions for which the outcome was certain. We used the above simulations to find parameters that would guarantee the extinction of *Cerithidea* within 90 yr of invasion (unequal [i.e., empirical] competition, parasitism, and mortality rates, and 16 *Batillaria* invaders per 0.1 m<sup>2</sup>). We calculated the metrics in the third and fifth years after the introduction of *Batillaria* and then at 5-yr intervals for the remainder of each run. Monitoring was ended 50 yr after invasion, because by this time *Cerithidea* density had dropped to zero or nearly zero, so the impact of the invasion was clearly detectable. At each monitoring interval, we recorded the average and standard deviation of each metric (indicated in Fig. 3) over all 200 replicates. Averaging across these 200 replicates was thus analogous in principle to sampling on a large scale over 200 identical replicate sites that had been invaded at the same time.

Because we assumed that higher initial population densities of the native would increase the length of time for any of the metrics to demonstrate impact, we started these simulations with a low density of *Cerithidea* (60 snails/0.1 m<sup>2</sup>). Simulations starting with 200 *Cerithidea*/0.1 m<sup>2</sup> confirmed that detection of impact was delayed with higher initial native densities. Initiating these simulations with a low density of *Cerithidea* therefore biased the results in favor of the most rapid detection of impact.

The use of growth rate (the change in snail size from one time step to the following year) as a monitoring metric requires an additional caution, because the growth rate of each snail depends on both its size and

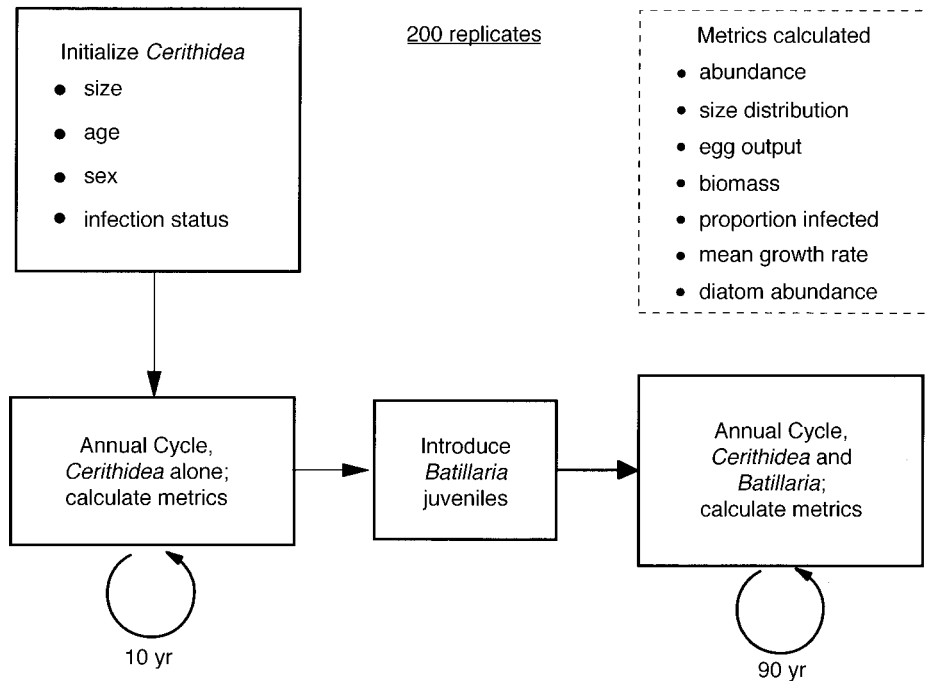


FIG. 3. Flow chart of the model.

the resource level. We wanted to monitor growth rate independently of the size distribution of *Cerithidea*; a separate metric tracked the latter. Consequently we standardized this metric as the calculated growth rate of a 16-mm snail, regardless of whether snails of that size were actually present.

*Within-site impact.*—The above simulations determined the value of each metric by averaging the 200 replicates. Averaging, however, may disregard useful information about the sequence of changes within each replicate, because correlations between responses of the native species within each site in consecutive time steps may aid in detecting the impact of an invasion both at a site and across sites. Accordingly, we ran a series of simulations to assess the ability of the metrics to detect impacts by tracking changes within each site. For these analyses we calculated metrics at the same

time steps as above but followed the metrics for each of 200 replicates separately. We tabulated the percentage of replicates for which a metric had decreased by at least 40%. This threshold seems to be conservative in identifying only changes that are large enough to be significant ecologically and outside the range of typical variation in uninvaded populations. Using a lower threshold would have decreased Type II errors at the expense of increasing Type I errors. We accounted for the effects of natural variability, occasionally apparent when *Cerithidea* was increasing from low population density, by comparing the percentages of replicates for each metric that changed at least 40% during invasion to the percentages from runs with *Cerithidea* alone. This comparison discounts the part of a metric's response that may be attributable to intraspecific dynamics of the native species and not directly to the invasion per se.

TABLE 2. Comparison of intraspecific snail simulations to equivalent field measurements in allopatric populations.

Species	Maximum density (no./m <sup>2</sup> )	Size (mm)	
		Mean	1 SD
<i>Cerithidea californica</i>			
Empirical	1900	19.7	5.2
Model	2500	16–19	4.8–5.2
<i>Batillaria attramentaria</i>			
Empirical	8000–10 000	20.6	5.4
Model	6500	16–19	5.2–7.1

Notes: Empirical data are from Whitlatch (1974), McCloy (1979), Whitlatch and Obrebski (1980), Lafferty (1991), Sousa (1993), McDermott (1996), and Byers (1999, 2000). Empirical mean size and standard deviation (SD) are medians of the mean values obtained.

## RESULTS

### Model validation

Populations of both species of snails in the simulations were self-sustaining and behaved realistically. When alone, *Cerithidea* persisted at least 100 yr in 100% of the runs. Snail densities, individual mean sizes, and size structure of the population all closely matched equivalent measurements of natural *Cerithidea* populations (Byers 2000). Likewise, for interspecific simulations in which *Batillaria* displaced *Cerithidea*, the remaining intraspecific *Batillaria* populations achieved densities, mean sizes, and size distributions typical of those observed in allopatric *Batillaria* populations (Table 2). There was a tendency for the model

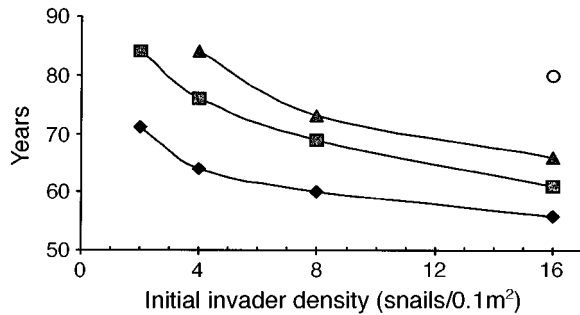


FIG. 4. The median years to *Cerithidea* extinction after initial introduction of *Batillaria* at different densities. The graph depicts model outcomes parameterized with all observed interspecific differences retained (♦), parasitism rates set equal and observed competition parameters (■), competition parameters set equal and observed parasitism rates (▲), and both parasitism and competition set equal (○). Medians were not calculable in several cases, particularly when both parameters were set equal (○), because extinction of *Cerithidea* occurred in <50% of the runs (see Fig. 5).

*Cerithidea* populations to approach population densities toward the high end of the observed range (200 snails/0.1 m<sup>2</sup>), but initial native snail density exhibited only small effects on nearly all of our results.

Also, the infection rates of the species were similar to those of natural populations. Typical model rates of infection were: *Cerithidea* 13.4 ± 8.2% (mean ± 1 SD) and *Batillaria* 5.7 ± 2.9%; and observed rates were: *Cerithidea* 14.2 ± 7.8% and *Batillaria* 4.6 ± 3.3% (from McDermott 1996, Byers 2000).

Finally, predictions of the number of years that the two species coexist before local extinction of *Cerithidea* corresponded well to empirical estimates. The times of coexistence in the four northern California marshes in which both snails did or do co-occur (Byers 1999) range from 35 to 68 yr, with a best estimate of 55–68 yr before the exclusion of *Cerithidea* by *Batillaria*. (The estimated time before the extinction of *Cerithidea* is a range because of uncertainty about the exact year of *Batillaria*'s introduction.) These species have now coexisted in Bolinas Lagoon for 45 yr (Byers 1999). In our simulations with empirically derived parameter values, the median time to extinction of *Cerithidea* was 56–71 yr, depending on the number of invading *Batillaria* (Fig. 4).

*Mechanisms of exotic success*

For all combinations of parameter values, the percentage of simulations that resulted in the extinction of *Cerithidea* within 90 yr of *Batillaria*'s introduction increased with increasing numbers of invading *Batillaria*, usually reaching 100% with 16 invading *Batillaria* per 0.1 m<sup>2</sup> (Fig. 5). The relative ranking of extinction occurrence for different parameter combinations remained consistent over all initial numbers of invaders.

For a given number of invading *Batillaria*, runs that retained all empirically observed differences between the species resulted in the largest number of extinctions

of *Cerithidea*. Removing the differences in parasitism rates reduced extinctions slightly, and removing the differences in competition but retaining the differences in parasitism rates had a similar effect. When both competition and parasitism were equalized between the two species, removing the advantages of top-down and bottom-up pathways, there were markedly fewer extinctions of *Cerithidea*. However, even with these two of the three differences between the species removed, *Batillaria* continued to displace *Cerithidea* a large proportion of the time (e.g., 76.5% of runs with 16 invaders). In contrast, equalizing the only remaining difference between the snails in the model at this point, mortality, reduced the level of *Cerithidea* extinction to near 0%, regardless of the presence of *Batillaria*'s parasitism and competition advantages (Fig. 5).

The four combinations of species' differences had similar effects on the median times to extinction of *Cerithidea*, again exhibiting nonadditive effects of parasitism and competition (Fig. 4). At low initial invader density, and even up to 8 invaders/0.1 m<sup>2</sup> for simulations in which all species differences were equalized, the median time to extinction could not be calculated because <50% of the runs resulted in the extinction of *Cerithidea* within 90 yr of the introduction of *Batillaria* (Fig. 5). For the same reason, the median extinction time could not be calculated when the mortality rates were equalized, regardless of the number of invading *Batillaria*, which again demonstrates the importance of the interspecific difference in mortality.

While *Cerithidea*'s fate depended on *Batillaria*'s competition and parasitism rates, *Batillaria*'s estab-

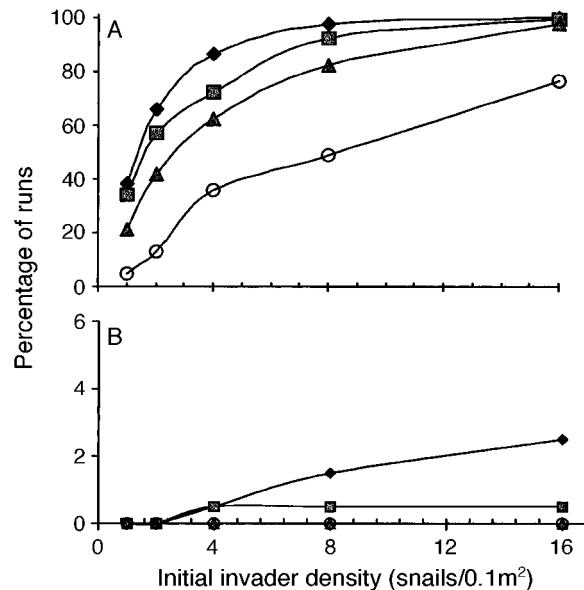


FIG. 5. Percentage of model runs that resulted in extinction of *Cerithidea* within 90 yr for different densities of invading *Batillaria*. Symbols are as in Fig. 4. (A) Extinction percentages when species-specific differences in mortality are maintained; (B) extinction percentages when the mortality rate of *Batillaria* has been set equal to that of *Cerithidea*.



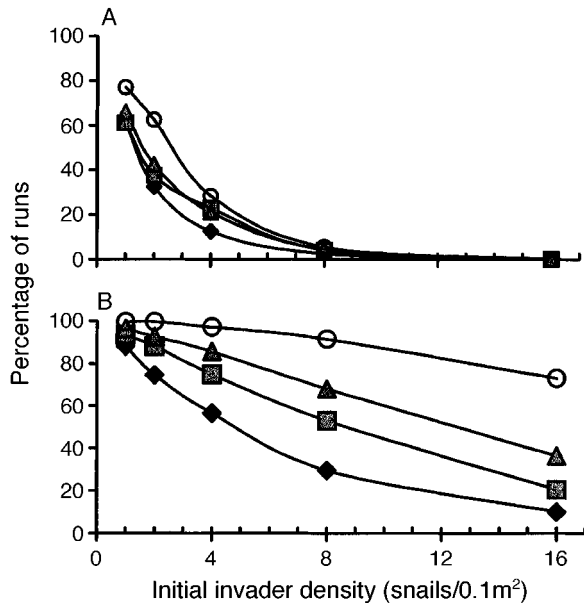


FIG. 6. Percentage of model runs that result in the extinction of *Batillaria* (i.e., lack of permanent establishment) within 90 yr for different densities of invading *Batillaria* (A) when the species-specific differences in mortality are maintained and (B) when the mortality rate of *Batillaria* has been set equal to that of *Cerithidea*. See Fig. 4 for combinations of competition and parasitism parameters (and their associated symbols).

ishment success depended little on these factors (Fig. 6A). Only the initial number of invading snails had a strong effect on the success of *Batillaria*, and this effect was driven largely by the probability that the invaders would include only males. These species are dioecious, and we considered each replicate (site) in the model in isolation of neighboring sites, so some invasions were doomed to fail due to lack of females. (We assumed that females would always be inseminated every year, so if only females invaded in the first year they were assumed to arrive inseminated.) For instance, an invasion with a single *Batillaria* invader had a 50% probability of failure for lack of females; with 16 invaders the probability of failure for this reason dropped to  $1.53 \times 10^{-5}$ , and *Batillaria* went extinct in none of these runs.

As with *Cerithidea*, the interaction of mortality, competition, and parasitism in determining the persistence of *Batillaria* was nonadditive. Given its natural advantage in mortality, *Batillaria* always persisted with 16 invaders regardless of whether it retained its advantages in competition and parasitism (Fig. 6A). When *Batillaria* had an advantage in competition and parasitism but not mortality, its probability of persistence remained high, at 90%. However, without the difference in mortality, competition, or parasitism, *Batillaria* persisted in at most 27% of the runs (Fig. 6B).

The runs with standardized, 50% differences between the species underscore the primary role of mortality in determining the outcome of the invasion. Even

when *Batillaria*'s advantages were standardized to 50% those of *Cerithidea*'s values, the difference in mortality favors the establishment of *Batillaria* and the extinction of *Cerithidea* much more strongly than do changes to the other interspecific differences (Table 3). Thus, for a given proportional difference, the system is more sensitive to differences in mortality than to differences in the other parameters.

#### Monitoring: earliest detection of exotic impact

**Average aggregate impact.**—Marked increases in *Batillaria* populations are clearly visible 10 yr after its introduction (Fig. 7); within 15–20 yr *Batillaria* populations that had started with 16 invaders averaged 300 snails/0.1 m<sup>2</sup>. *Cerithidea* populations, however, did not decrease markedly until at least year 25 after the invasion (Fig. 7). Changes in *Cerithidea* population biomass were similarly small for at least 25 yr (Fig. 8). Another population-level metric, parasitic infection rate, remained essentially constant for *Cerithidea* throughout the invasion and became highly variable only toward the end (Fig. 8). The mean size of *Cerithidea* individuals showed no consistent trend, although there was high variability throughout the invasion (Fig. 8). A substantial decrease in total egg production provided one of the earliest signs of impact, but it did not occur until almost 17 yr after the invasion began (Fig. 9). Finally, declines in both per capita growth of *Cerithidea* and diatom availability were evident 10 yr after the invasion (Fig. 9); however, a sizable decline in both metrics occurred in the absence of *Batillaria* as the density of the native species increased from the low initial value of 60 individuals/0.1 m<sup>2</sup>. High initial densities of *Cerithidea* eliminated the confounding influence of an increasing *Cerithidea* population on these declines, but they also delayed detection of impact until at least year 20–25. Thus, the first reliable detection of impact from *Batillaria*'s invasion was between years 15 and 20.

**Within-site impact.**—The performance of the metrics

TABLE 3. Percentage of model runs resulting in extinction of either snail species within 90 yr.

Parameter values of <i>Batillaria</i> , relative to those of <i>Cerithidea</i>	Percentage of simulations resulting in extinction of:	
	<i>Cerithidea</i>	<i>Batillaria</i>
Same	0.5	73.5
Parasitism -50%	0	46.5
Competition +50%	1.5	31.5
Mortality -50%	11.5	7.5

**Notes:** For each analysis, 200 runs were initialized with 16 invading *Batillaria*. For the first runs, parameter values for *Batillaria* were equalized to *Cerithidea*'s values. Then, one at a time, each parameter for *Batillaria* was adjusted by 50% to give it an advantage over *Cerithidea*. These results are for 60 initial *Cerithidea*; simulations starting with 200 *Cerithidea* gave a very similar pattern with overall lower rates of extinction for *Cerithidea* and higher rates for *Batillaria*. Especially in the second through fourth cases, the runs in which *Batillaria* persisted would have resulted in the extinction of *Cerithidea* if they had been extended for longer time periods.

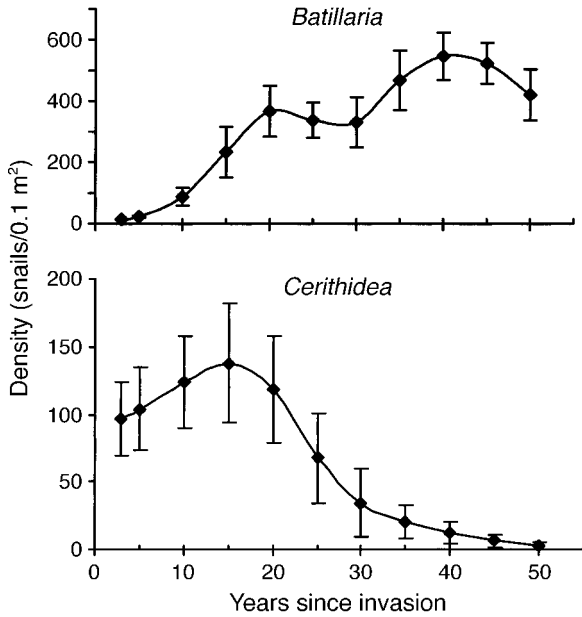


FIG. 7. Density of *Batillaria* and *Cerithidea* across 200 simulation replicates as a function of time since introduction (means  $\pm$  1 SD). The density of invading *Batillaria* was 16 snails/0.1 m<sup>2</sup>.

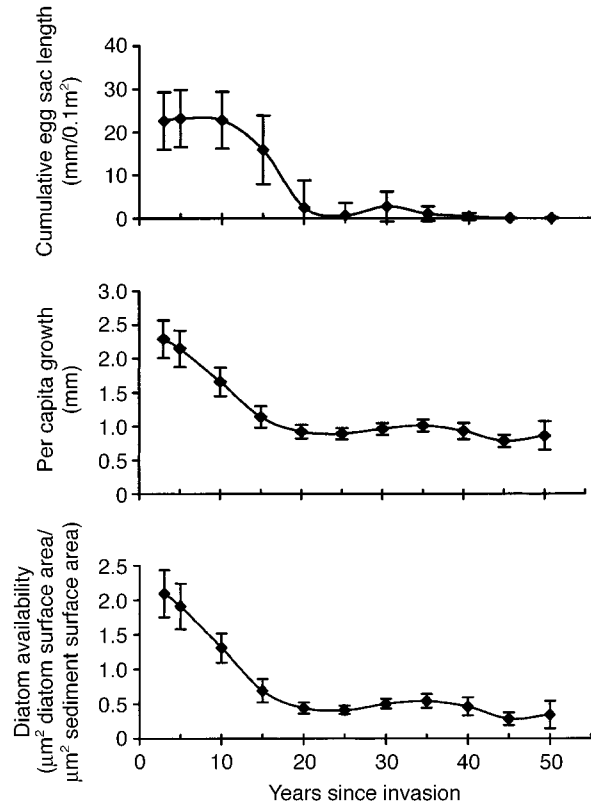


FIG. 9. Cumulative length of *Cerithidea* egg sacs, individual growth of a 16-mm *Cerithidea*, and diatom availability as a function of time since the introduction of *Batillaria* (means  $\pm$  1 SD). The density of invading *Batillaria* was 16 snails/0.1 m<sup>2</sup>.

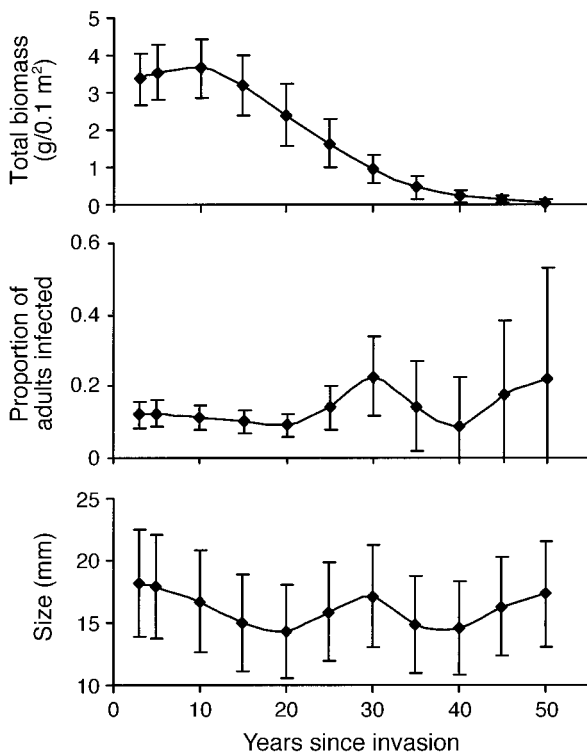


FIG. 8. Population biomass, parasitic infection, and per capita size of *Cerithidea* across 200 replicates as a function of time since the introduction of *Batillaria* (means  $\pm$  1 SD). The density of invading *Batillaria* was 16 snails/0.1 m<sup>2</sup>.

that tracked individual plot changes was similar to that of the aggregate measures. Changes that indicate a negative impact of the invader on the native were not detectable with accuracy ( $\geq 90\%$ ) until at least year 15 and commonly not until 20–30 yr after the invasion (Figs. 10 and 11). When *Cerithidea*'s initial density was low, individual snail growth again showed promise of providing early detection, with impact signaled by year 15 in 94% of cases. However, much of the decline would have occurred anyway due to *Cerithidea*'s response to its own increasing density: 25% of runs with no invasion exhibited impact-level ( $\geq 40\%$ ) reductions in growth by year 25, and 50% did so by year 45. Likewise, diatom availability quickly exhibited declines (by year 15 in 99% of simulations); however, as with growth, pronounced declines also occurred in intraspecific *Cerithidea* simulations. For instance, 50% of runs with no invasion showed the same degree of reduced diatom availability by year 25 as did invaded runs (Fig. 11). High initial *Cerithidea* densities again tended to reduce the ability of the monitoring metrics, especially changes in individual growth rate, to detect the effects of the invasion (Fig. 11). With high initial *Cerithidea* densities, only 40% of invasions were deemed impacting by year 50.

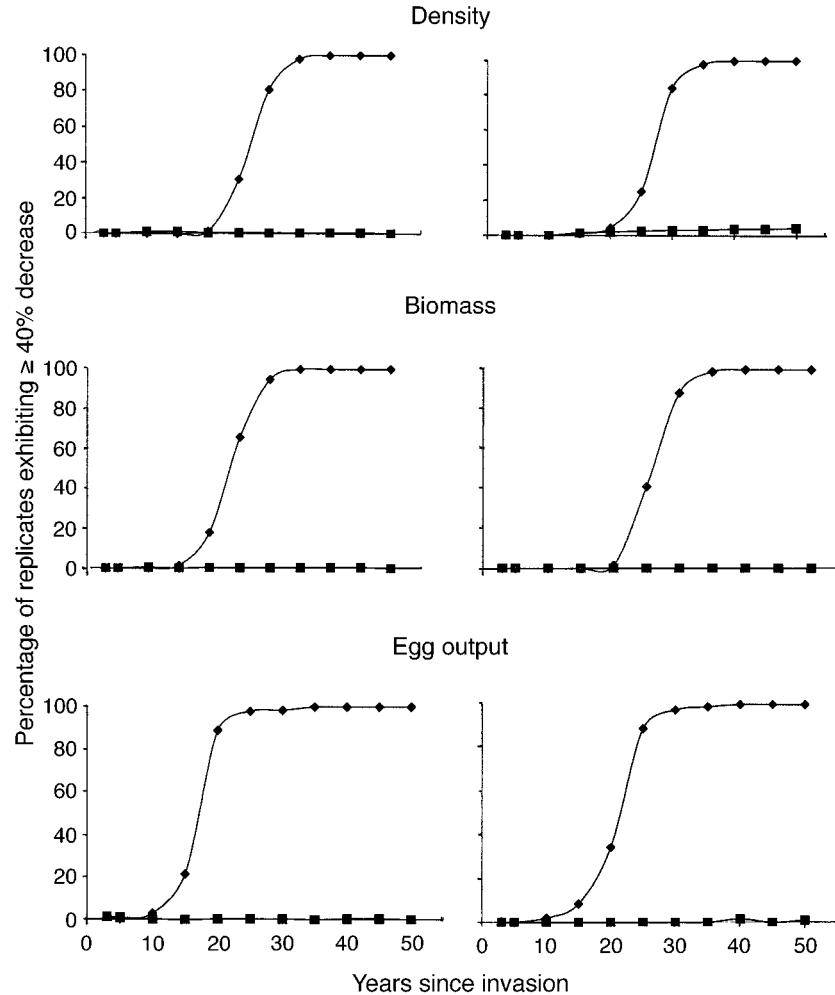


FIG. 10. Percentage of replicates that exhibited a decrease of at least 40% in *Cerithidea* density, biomass, and egg output after 16 *Batillaria* were introduced (♦) with initial densities of *Cerithidea* at 60 and 200 snails/0.1 m<sup>2</sup> (left and right columns, respectively). *Cerithidea* went extinct in 100% and 99% of runs, respectively, within 90 yr. Results from simulations with *Cerithidea* alone (■) help distinguish between impacts caused by *Batillaria* and changes due to natural fluctuations or intraspecific effects within *Cerithidea* populations.

#### DISCUSSION

Modeling has been a useful tool in the identification of critical stages in the conservation of threatened and endangered species (Crouse et al. 1987, Doak et al. 1994, Middleton and Nisbet 1997, Letcher et al. 1998, Root 1998). Similarly, as we demonstrate here, modeling the interactions between invading species and native biota can identify the critical factors that govern success and impact of an invader. The model presented here has highlighted the synergistic effect of both competition (bottom-up) and parasitism (top-down) acting in concert, as well as the overwhelming importance of differences in mortality between these snail species on the demise of *Cerithidea*. Equalizing *Batillaria*'s advantages in both parasitic resistance and competition decreased *Cerithidea*'s extinction more than would be predicted if top-down and bottom-up forces acted independently (Figs. 4 and 5A). It is also noteworthy that

every one of the observed differences between *Cerithidea* and *Batillaria* favors the invader.

The distribution of snail sizes appears to link the strong influence of mortality on invasion outcome and the relative sensitivity of reproductive output as a metric of impact. Snail fecundity increases markedly with size (a 20% increase in size results in a 64% increase in egg output), so, barring parasitic infection, large snails contribute disproportionately more to population growth than do small ones. A smaller mortality rate for *Batillaria* means that a larger proportion of *Batillaria* survive to reach larger, more fecund sizes. This advantage means that *Batillaria* can eventually outproduce *Cerithidea* even without its additional efficiency in resource use. Further, regardless of any difference in resource use, the competition for resources exacerbates the higher mortality in *Cerithidea* by slowing individual growth rates, reducing the opportunities for

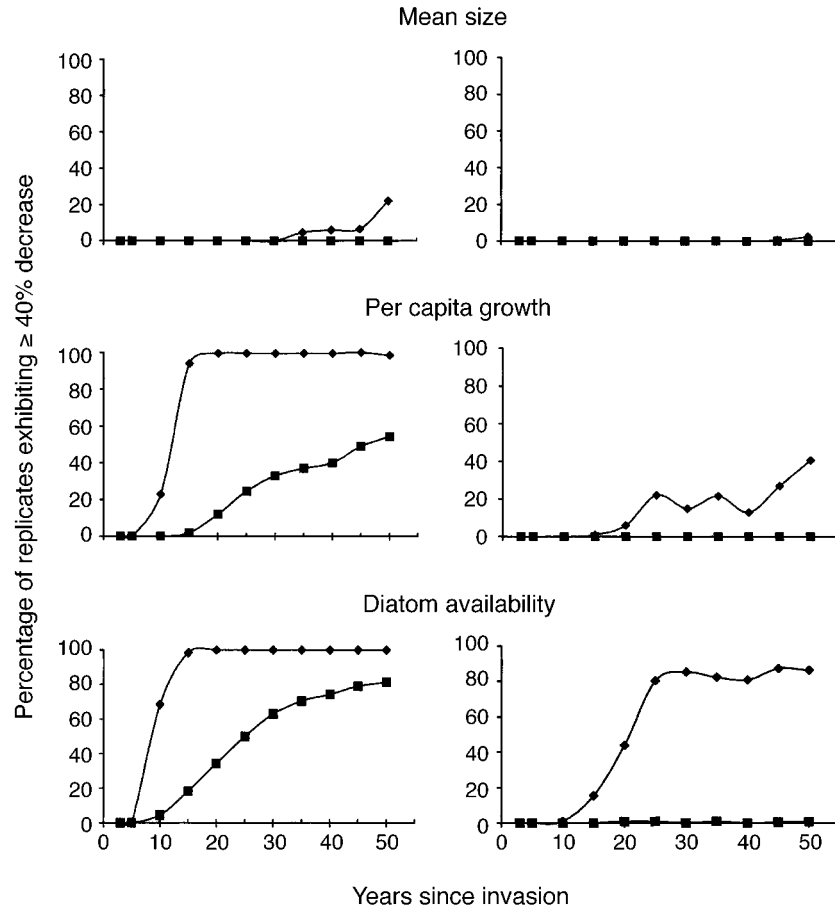


FIG. 11. Percentage of replicates that exhibited a decrease of at least 40% in *Cerithidea* mean size, per capita growth of a 16-mm *Cerithidea*, and diatom availability after *Batillaria* was introduced (◆) with initial densities of *Cerithidea* at 60 and 200 snails/0.1 m<sup>2</sup> (left and right columns, respectively). All other information is as in Fig. 10.

snails to grow to large sizes, increasing the probability of becoming parasitically castrated before reaching large size, and limiting their average lifetime reproductive output. In the simulations, 40 yr after *Batillaria* invades there are no *Cerithidea* longer than 26 mm, in contrast to the 4 or 5 per 0.1 m<sup>2</sup> that are typically present at that time when *Batillaria* does not invade. This chain of influences also explains the time lag in *Batillaria*'s effect on *Cerithidea*. The invader takes time not simply to increase in density, but also to generate the large individuals that boost its ability to out-produce *Cerithidea*.

Interestingly, the course of the invasion does not depend strongly on the population size of *Cerithidea* at the time of *Batillaria*'s invasion. A more than three-fold increase in the initial *Cerithidea* population increased the median time to extinction only from 56 to 65 yr. It may be that *Batillaria*'s consistent advantage across a variety of parameters reduces the circumstances under which initial conditions might influence ultimate outcomes. The sensitivity of some of the metrics to impact, however, did depend on the initial conditions, because those conditions determined the baseline values to which the postinvasion conditions were com-

pared. High initial numbers of *Cerithidea* affected all metrics, especially growth, in much the same way that *Batillaria* did, so the observed changes following the invasion were correspondingly smaller. Even with low initial numbers of *Cerithidea*, the responses of per capita growth and diatom level were limited in their sensitivity to the effects of *Batillaria*. Most response metrics did not decrease in the absence of *Batillaria*, but both of these metrics did (Fig. 11). Their decreases with *Cerithidea* alone reflected increased intraspecific competition for the resource as the density of *Cerithidea* increased. Thus, the apparent early changes of these metrics under low initial *Cerithidea* density does not provide unequivocal evidence of impact. The good performance of diatom level at higher initial *Cerithidea* density, however, suggests that, in some cases, monitoring other species within the community may provide an earlier warning of impact than does directly monitoring the species of interest.

This model provides information that may be useful for intervention, although it does not automatically reveal any easy means of ameliorating invader impact. The synergy between competition and parasitism suggests that simultaneous efforts to influence the top-

down and bottom-up forces in this system might be more effective than the sum of either alone, but they still may be swamped by the overriding importance of mortality (Figs. 5 and 6). Similarly, Lampo and De Leo (1998) found that adult survivorship was the most important factor to manipulate to reduce the extremely high densities of nonnative cane toads in Australia. Further work on the present system might focus on learning more about the determinants of mortality in *Batillaria* and what might be done to manipulate them. Physically removing the invader would be a simple way to increase the effective mortality of *Batillaria*; however, in many invaded systems such removal programs are logistically difficult, not cost effective, or too damaging to the native species (Townes et al. 1997, Arnold et al. 1998, Choi and Pavlovic 1998, Pickart et al. 1998).

The time lag between *Batillaria*'s establishment and its impact is both unexpected and sobering. Even with a wide range of metrics, 200 replicates, and no measurement error, monitoring was unable to detect the impact of *Batillaria* until the invasion had proceeded for about two decades. Delays in detection can make management efforts both more costly and less likely to succeed. Such time lags are similar to the extinction debt of Tilman et al. (1994), whereby species extinctions occurred generations after the triggering event of habitat destruction. Similarly, in simulations of grizzly bear populations, Doak (1995) found that population declines caused by habitat degradation were often not detected for at least 10 yr after degradation began. Despite the difference in the causative agent, our study suggests that nonnative species may also create an extinction debt because their exclusion of native species may be delayed but nonetheless inevitable.

Notably, the density of the native species was one of the slower metrics to respond to the invader (30 yr for >80% detection). Even in the absence of any formal monitoring program, this metric is surely the one most commonly used to assess impact of nonnative species. Our simulations suggest that significant decreases in the density of the native species may occur only far along into an invasion, after considerable damage is already inevitable. The long life span of *Cerithidea* exacerbates this slow response because individuals can linger on even though the invader has created conditions in which reproduction fails. In contrast, egg production, which in practice is likely to require more measurement effort, was relatively fast (sensitive) and somewhat robust to initial conditions. However, with its delay of at least 20 yr, its utility is still limited.

Our model results emphasize two aspects of invasion processes that are not widely appreciated. First, even small per capita differences between native and exotic species can be very important to the overall impact of an invasion. Although large differences may receive the most attention, small differences can be just as effective at producing impact over time and may be more insidious for ecologists because they increase the difficulties in estimating the parameters that determine

the risk of extinction (Ludwig 1999). Second, detrimental impacts can be achieved through "nonnovel" means, that is, an invader need not be a novel predator or disease or need not exploit a new niche to be detrimental. An invader need only do exactly what the native species does, just slightly better. The more similar the native and the invading species, the more difficult it may be to assess the danger to the native.

The good match between our simulations and the observed interactions between *Cerithidea* and *Batillaria* suggests that, even with limited data available, this kind of model can capture the dynamics of multispecies systems well enough to help in understanding and predicting the course of invasions. Such models might be constructed early enough following the introduction of nonnative species to be able to anticipate which invaders have the potential to be most problematic and how fast native species are likely to go extinct. Also, in this case at least, the key demographic rates could be usefully measured in isolation rather than waiting for the invasion to proceed. Because monitoring with even the best metrics may alert us too late to the dangers of an invader, one value of models such as this one lies in elucidating the relative importance of the mechanisms that govern the success of nonnative species. With a better understanding of these mechanisms, resource managers can direct their responses to the most effective means of intervention and may be able to anticipate, rather than simply respond to, the effects of invaders on native species.

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## APPENDIX

Pseudocode for key routines in the individual-based model used in this paper is available in ESA's Electronic Data Archive: *Ecological Archives* E082-017. The Appendix is divided into four subsections that cover the main body of the program, seasonal routines, demographic routines, and additional routines.