

## ORIGINAL PAPER

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## Crab: snail size-structured interactions and salt marsh predation gradients

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**Abstract** We studied size-structured predator-prey interactions between blue crabs (*Callinectes sapidus*) and marsh periwinkles (*Littoraria irrorata*) with a combination of field studies, laboratory experiments and individual-based modeling. Size distributions of *Littoraria* differed among years at the same sites in a salt marsh and could largely be explained by dominance of strong cohorts in the population. At a given site, abundance increased with elevation above tidal datum. Size-selective predation by blue crabs does not appear to be an important regulator of snail size distributions but may have a major effect on local abundance. Laboratory studies indicated that predator-prey interactions between *Callinectes* and *Littoraria* are strongly size-dependent. Crabs were generally effective at feeding on periwinkles at size ratios greater than approximately 6 (crab width: snail length). At lower size ratios crabs were far less effective at manipulating the snails, which often survived but with damaged shells. An individual-based model which incorporated information about incidence of snail shell scarring (resulting from non-lethal interactions) and snail density, predicted reduced predation rates and smaller average crab size with distance from the low tide refugium for crabs.

**Key words** Size-structure · Predation · *Callinectes Littoraria* · Salt marsh

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### Introduction

Salt marsh ecosystems are characterized by complex physical and hydrological features that are primarily determined by tidal dynamics. The structuring forces of tides have important effects on the ecology of salt marsh communities. Tidal action produces distinct horizontal zonation of vegetation (Pomeroy and Wiegert 1981; Frey and Basan 1985) and affects the extent and duration of predator-prey interactions among natant (temporary) and permanent marsh residents (Montague et al. 1981; Kneib 1984; Frey and Basan 1985). The ecological consequences of tidal forcing is not as clear for soft-substrate salt marsh systems as it is for rocky intertidal systems (Kneib 1984; Peterson 1991) where biotic interactions are well-defined along the tidal gradient (e.g., Connell 1970; Paine 1974; Menge and Sutherland 1976).

Tides, by determining water height, directly control the extent of biotic interactions among natant and permanent marsh residents by limiting interaction time between predators and prey (Kneib 1984). Blue crabs are an important predator in salt marshes and their spatial distributions are limited to inundated areas which change as tides flood and ebb. Therefore, it is reasonable to expect that crab predation intensity varies along elevation gradients within salt marshes (Kneib 1984; West and Williams 1986).

Here we examine the predator-prey interactions between two abundant salt marsh species, the blue crab (*Callinectes sapidus*) and the marsh periwinkle (*Littoraria irrorata*) along a presumed predation gradient created by tidal dynamics. Blue crabs invade the marsh with flood tides and prey heavily on periwinkles (Hamilton 1976; Stiven and Hunter 1976; Stanhope et al. 1982) and other prey like small oysters, mussels and clams, then retreat to the refugia of tidal creeks or the adjacent sound with ebb flow. We examined the field evidence for predation gradients and assessed prey population size structure and density as the basis for inferring predation rates along the tidal gradient.

Evidence of predation attempts is available from scars on snail shells. Blue crabs must damage the shells of their gastropod prey in order to consume them. Unsuccessful predation attempts often result in a permanent scar in the animal's shell (Vermeij 1972). Scarring patterns in populations of periwinkles offer a valuable, temporally integrated basis for inferring both predation intensity and size structure of the crab population (Vermeij 1982a, b).

We used results from laboratory experiments to develop an individual-based model (Huston et al. 1988) designed to evaluate how crab size may interact with snail populations to produce scarring and distribution patterns observed in the field. The model relates predation rates, crab size and snail scarring rates within a simulation framework in such a way that characteristics of any two of these features may be used to predict the third. We implemented the model to test the hypothesis that spatial patterns in scarring frequency of *Littoraria* may be used to infer predation rates and size distributions of crabs throughout a salt marsh. We expected that decreased inundation time with increased elevation should cause both decreased predation rates and decreased mean size of crab predators with distance from the tidal datum.

## Methods and materials

### Study site

We conducted this study at Sapelo Island (31°N, 81°W), a barrier island in the mid-coastal region of Georgia. It is the site of the University of Georgia Marine Institute and has been the focus of extensive research work (Pomeroy and Weigert 1981). This region has low elevation gradients, strong diurnal tides, and a tidal amplitude of approximately three metres. The extensive salt marshes on Sapelo Island are dominated by the smooth cordgrass *Spartina alterniflora* (Loisel).

Field sampling of *Littoraria* was conducted at three sites selected on the basis of expected level of crab predation (Fig. 1). Lighthouse Marsh (LH) is located at the south end of Sapelo Island on Doboy Sound near the mouth of tidal Dean Creek. This site was expected to have maximal predation intensity due to its proximity to Doboy Sound, the source of blue crabs to the system. The Dean Creek Marsh (DC) site is located approximately 1 km inland from Doboy Sound. Dean Creek Marsh was expected to have lower crab predation intensity than the LH site. A third site, North End Marsh (NE) is located at the headwaters of Dean Creek about 3 km from Doboy Sound. We expected crab predation intensity to be lowest at this site due to its distance from Doboy Sound and relatively brief tidal inundation time.

### Field observations

We collected live *Littoraria* at the three sites along Dean Creek in late October in both 1989 and 1991. Because an elevation gradient also exists within sites at Lighthouse Marsh and Dean Creek Marsh, we sampled three subsites (30 m, 70 m and 100 m from the creek bank) along transects perpendicular to Doboy Sound (LH) or from the Dean Creek channel (DC) (Fig. 2). Within each subsite we sampled *Littoraria* from at least three (1 m<sup>2</sup>) quadrats. Quadrats were selected haphazardly. Because small *Littoraria* (<10 mm) are easily obscured in folds of *Spartina* leaves and may

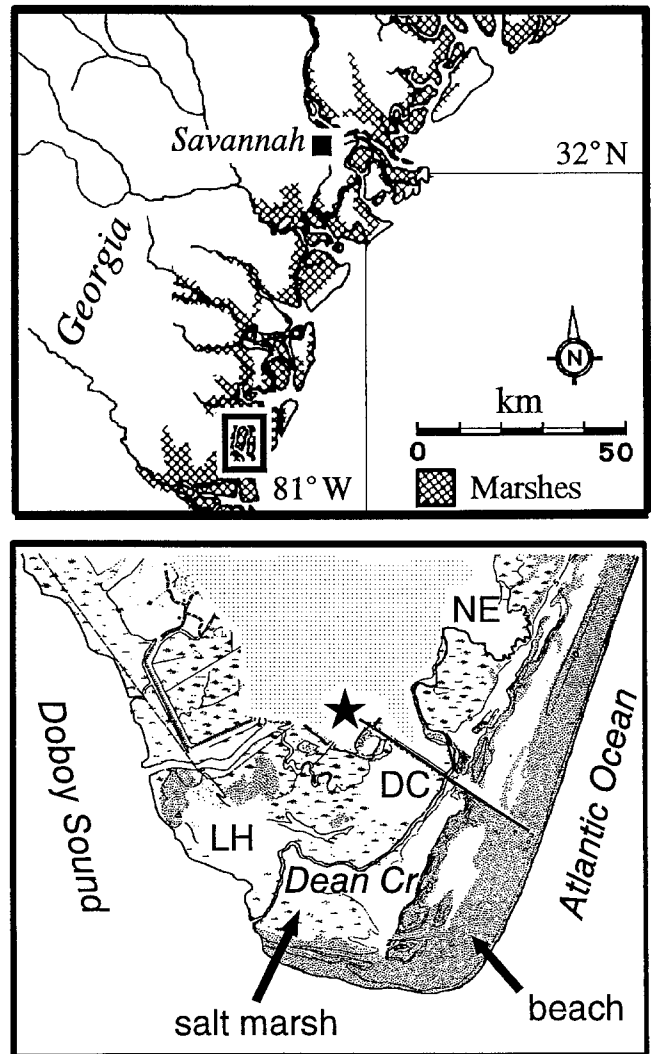
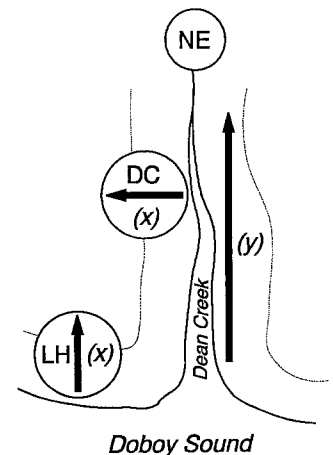


Fig. 1 Location of Sapelo Island off the coast of Georgia (inside rectangle-top panel, modified from Pomeroy and Wiegert (1981) with permission of Springer-Verlag) and the sampling sites located along the length of Dean Creek near the University of Georgia Marine Institute (denoted by star in bottom panel, modified from USGS map 4647 IV NE). At Lighthouse Marsh (LH) and Dean Creek Marsh (DC) sampling sites were located 30 m, 70 m and 100 m from the sound and creek respectively. Only one site was sampled at North End Marsh (NE)

Fig. 2 Schematic diagram of two tidal inundation gradients considered in this study. One gradient is associated with distance from Doboy Sound along Dean Creek ( $y$ ), and the second ( $x$ ) is associated with the perpendicular distance from the shoreline of Doboy Sound at LH or from the creek bank at DC. Only one area was sampled at the NE site at the headwaters of Dean Creek



**Table 1** Morphological regressions ( $Y = mX + b$ ) among commonly used body size measures for *Littoraria* and *Callinectes*. Shell length is length of the shell along its main axis. Shell height is the distance from the tip of the spire to the top of the aperture. Shell width is the maximum width measured perpendicular to the main axis, from the back of the body whorl to the edge of the aperture. We measured snails in a size range from 10 mm to 23 mm in shell length. Carapace length is the anterior-posterior carapace length. Base-to-base width is the width of the carapace between the base of the lateral spines. Tip-to-tip is the carapace width from lateral spine tip to lateral spine tip. We measured crabs in a size range from 56 mm to 135 mm base-to-base width. All measurements were made with dial calipers in mm. All regressions are significant at  $p < 0.001$

| Dependent variable (Y) | Independent variable (X) | Slope (m) | Intercept (b) | r <sup>2</sup> | N   |
|------------------------|--------------------------|-----------|---------------|----------------|-----|
| <i>Littoraria</i>      |                          |           |               |                |     |
| Shell length           | Shell height             | 1.717     | 1.224         | 98.3           | 100 |
| Shell length           | Shell width              | 1.421     | -0.366        | 95.9           | 79  |
| <i>Callinectes</i>     |                          |           |               |                |     |
| Carapace length        | Base-to-base width       | 0.584     | 0.262         | 91.1           | 97  |
| Carapace length        | Tip-to-tip width         | 0.446     | 4.481         | 90.8           | 51  |
| Base-to-base width     | Tip-to-tip width         | 0.775     | 4.928         | 95.3           | 62  |

be insufficiently sampled (Hamilton 1978), we excluded snails < 10 mm from the analysis.

We measured *Littoraria* shell length (apex of spire to tip of aperture, the longest dimension) using dial calipers. All snails were scored as either intact or as scarred from previous encounters with predators. We calculated scarring rate of *Littoraria* as the percentage of snails  $\geq 10$  mm that had at least one shell scar. Although information about the size of snails when they were scarred can also be extracted from the snail shells, we did not consider that data in this study to simplify analysis.

*Littoraria* growth rates were inferred from length-frequency analysis and von Bertalanffy growth equations developed for *Littorina* (shell width as a function of time) in three North Carolina salt marshes (Stiven and Hunter 1976). The models of Stiven and Hunter (1976) show that growth rates of snails vary between different marshes. We used their intermediate growth rate model that predicts size-at-age within  $\pm 15\%$  of both their fastest and slowest growth rate models. We derived a shell width-length relationship to express growth in length (Table 1).

Because *Littoraria* density (number/m<sup>2</sup>) and scarring rates were similar at 70 m and 100 m sites (medium and high elevation), we averaged the values to simplify the presentation. We averaged scarring rates and densities computed for 1989 and 1991 at each location to obtain a time-integrated depiction of scarring and density patterns across the marsh.

We encountered a variety of measures of *Littoraria* and *Callinectes* body size in the literature. To allow for comparison with other studies, we calculated regressions to describe the isometric relationships (Table 1) among these various measures. We used *Littoraria* shell length and *Callinectes* carapace width (at base of lateral spines) as our standard body size measures.

#### Laboratory experiments

Crabs were collected from baited traps set at South End Creek and Dean Creek, then held in large flow-through tanks for 48–72 h before they were used in laboratory experiments. Crabs that had recently molted or had damaged or missing chelae were not used in any of the experiments. Experiments were done with crabs held

in individual 20 gallon glass aquaria provided with continuous flow seawater exchange (tank flushing rate of approximately once per hour). Only those crabs that fed vigorously prior to the experiments (i.e. would consume a small snail within 1 minute of introduction) in the aquaria were used for laboratory studies. Snails were collected by hand from the Dean Creek (70 m) study site (what we predicted as the site of intermediate predation intensity) and held in glass containers with continuous seawater flow.

#### Manipulation time experiments

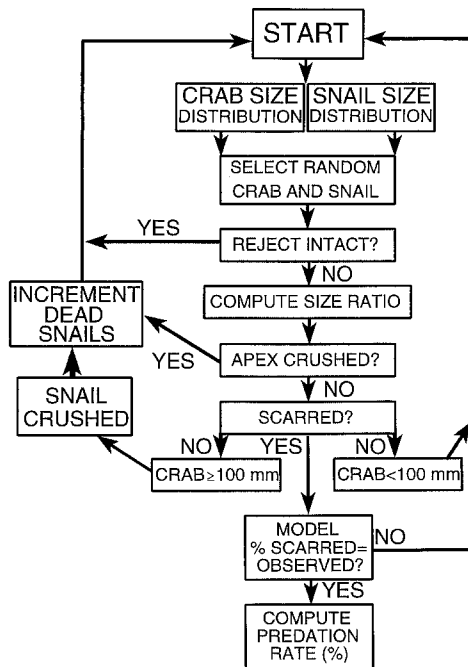
We measured manipulation times for crabs preying on snails from nine crabs that represented the size range we were able to capture throughout the salt marsh (56–130 mm) in baited crab traps. Each crab was offered individual snails representing the range of sizes (except snails smaller than 8 mm) also observed throughout the salt marsh. Crab: snail size ratios (crab base-to-base carapace width: snail shell total length) ranged from 3.5 to 12. A total of 54 separate trials was performed. We defined manipulation time as the length of the time interval between when the crab picked up a snail to the point it either rejected it or made contact between its mouthparts and edible snail tissue. A linear least squares curve fit procedure (Wilkinson 1989) was used to determine an appropriate model for manipulation time data.

#### Size selection experiments

Selectivity was determined by allowing six individual crabs (starved for 24 hours prior to experiment) to prey on uniform size distributions of snails. We used two crabs from each of three general size classes (small: carapace width =  $59.5 \pm 3.5$  mm (mean  $\pm$  half-range), medium =  $102.5 \pm 1.5$  mm, large =  $126.0 \pm 4.0$  mm). Each crab was placed in an aquarium with snails that were equally distributed among eight (nine for the large crabs) 1 mm size classes (five snails per size class). Snail size ranges offered to small, medium and large crabs were 8–15, 14–21 and 14–22 mm respectively. All snails were measured and marked with permanent ink so that we could identify individuals which were killed or damaged. Wire screens were placed over the aquaria to prevent the snails from escaping the enclosures. Crabs were allowed to feed for 4 h and then all live snails and shell remnants were removed for examination. Live snails were scored as either intact or chipped (aperture damage that would have eventually produced a shell scar). Identifiable shell remnants were scored as either killed due to aperture chipping or to shell apex damage. All snails that could not be accounted for by these criteria were assumed to have been killed and the shells completely crushed.

#### Preference experiments

An assumption important to the evaluation of prey choice is that any size selection by crabs occurs only after the crab has handled the prey item (i.e., that crabs show no active selection by visual or chemosensory cues for certain sizes of snails before they handle them). To test this assumption we presented crabs with a medium sized snail (13 mm) and a large snail (20 mm) simultaneously (but at haphazard locations within the aquaria), and then observed which snail the crab attacked first. After each such choice both snails were removed from the aquarium. The next preference trial was conducted after a 15 minute recovery period. Five such trials were run with each of seven crabs. Chi-square was used to test whether the pattern of snail selections by the crabs was random or size-selective.



**Fig. 3** Flow diagram of the iteration sequence of the individual-based model for *Callinectes* predation on *Littoraria*

#### Simulation model

##### Model description

As a more general analytical tool, we developed a simple individual-based model (Huston et al. 1988) for the blue crab – marsh periwinkle predator – prey system (Figure 3). The model incorporated results of our laboratory experiments in a framework that captured some of the complexities of size-based predator – prey interactions throughout the salt marsh. We used this framework to infer crab predation rates and size structure of the crab population from observed scarring rates and densities of snails. This method represents an alternative to direct sampling of crabs throughout the salt marsh, whose densities are often difficult and tedious to assess largely due to crab mobility (Kneib 1984).

The model allowed for random encounters of individual crabs with individual snails. Each interaction resulted in periwinkle death, shell damage, or rejection of the undamaged snail. The outcome of each interaction was determined by a series of size-based binomial probabilities. All of the functions used in this model were derived and parameterized from the results of our laboratory experiments (see Results section and Table 2).

**Table 2** Values of all model parameters derived from the experimental portion of this study. Standard errors are given to indicate variance associated with parameters. Source refers to the portion of this study the parameters were derived from. *nv* no variance to estimate errors; 1 scarring rates observed in snails from the field; 2 manipulation time experiments; 3 size-selectivity experiments

| Parameter           | Description                                  | Value      | Standard Error | Source |
|---------------------|--|------------|----------------|--------|
| FIELDSCAR           | percentage scarred                           | (variable) | ...            | 1      |
| $P_{\text{INTACT}}$ | probability of rejection intact              | 0.037      | 0.029          | 2      |
| MAXTIME             | maximum handling time (s)                    | 800        | nv             | 2      |
| APICALC             | apical crushing coefficient <sup>a</sup>     | 1.043      | 0.057          | 2, 3   |
| APICALS             | apical crushing slope <sup>a</sup>           | 0.147      | 0.009          | 2, 3   |
| SCARC               | large crab scarring intercept <sup>a</sup>   | 3.477      | 0.249          | 2      |
| SCARS               | large crab scarring slope <sup>a</sup>       | 347.9      | 93.4           | 2      |
| SMSCARC             | small crab scarring coefficient <sup>a</sup> | -6.369     | nv             | 2      |
| SMSCARS             | small crab scarring slope <sup>a</sup>       | 2.718      | nv             | 2      |

<sup>a</sup> dimensionless parameter

In order to account for different feeding modes of different size classes of crabs, we defined two general size classes of crabs in the model. We define ‘large crabs’ in the model as any crab greater than or equal to 100 mm while ‘small’ crabs are less than 100 mm in carapace width. We defined these size distinctions based on different foraging strategies observed for these two sizes of crabs in the laboratory experiments (see Results).

The input data required by the model were 1) an initial size distribution of snails 2) an initial size distribution of crabs, and 3) the percentage of scarred individuals (FIELDSCAR) observed in the population of live snails in the field. Each iteration of the model randomly picked one crab from the predator population and one snail from the prey population. Because we observed that crabs sometimes rejected prey in the lab without apparently trying to consume them, the model allowed for a small initial probability ( $P_{\text{INTACT}}$ ) that the snail was rejected by the crab intact after a predator – prey encounter. If the snail was rejected, it was returned to the available prey population intact and the next iteration was started. If the prey was retained by the crab (with probability  $1 - P_{\text{INTACT}}$ ) the model calculated the size ratio (RATIO):

$$\text{RATIO} = \text{crab size (mm)} / \text{snail size (mm)} \quad (1)$$

If the predator – prey encounter involved a ‘large’ crab there was a chance for the snail to be killed by crushing the apex of the snail shell (as described later). The model calculated a size ratio-specific apical crushing probability ( $P_{\text{APICAL}}$ ) as:

$$P_{\text{APICAL}} = \text{APICALC} - (\text{APICALS} * \text{RATIO}) \quad (2)$$

where APICALS is the slope and APICALC the intercept of a regression describing the relationship between the probability of apical crushing and the size ratio of the crab and snail. This function is illustrated as line ‘b’ in Fig. 4.

If  $P_{\text{APICAL}}$  was greater than a randomly chosen probability, the snail was killed, removed from the population of available prey, and the number of dead snails was incremented. If the snail was not killed by apical crushing (with probability  $1 - P_{\text{APICAL}}$ ) the model calculated the probability of scarring ( $P_{\text{SCAR}}$ ) as:

$$\ln(P_{\text{SCAR}}) = \text{SCARC} + \text{SCARS} * \exp^{-\text{RATIO}} + \ln(\text{MAXTIME}^{-1}) \quad (3)$$

where SCARS is the slope and SCARC the intercept of a regression describing the relationship observed in the lab between manipulation time and the predator: prey size ratio. MAXTIME is the maximum manipulation time we observed in the laboratory. This function is illustrated as line ‘a’ in Figure 4. The ratio of 4.7 represents the point where the predicted manipulation time function equalled the maximum manipulation time observed in the laboratory.

If the ‘large’ crab did not scar the snail (with probability  $1 - P_{\text{SCAR}}$ ) it killed it and the snail was removed from the prey population. Otherwise the snail was returned to the prey distribution as scarred, and if it had not been scarred in a previous encounter, the number of scarred snails was incremented.

Results of our laboratory experiments show that small crabs appear to be more constrained by snail size than large crabs and

therefore scar more snails in the process of predation. Accordingly, we incorporated an additional manipulation time curve that allowed 'small' crabs extra opportunity to scar snails. If the particular model encounter involved a small crab (<100 mm) at a size ratio less than 4.7 a different scarring probability ( $P_{SMSCAR}$ ) was calculated as:

$$P_{SMSCAR} = \exp(SMSCARC + SMSCARS * \text{RATIO}) \quad (4)$$

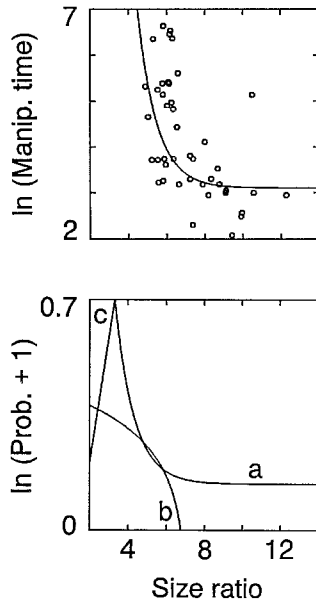
where SMSCARC is the intercept and SMSCARS the slope of a regression describing a relationship between scarring probability and crab: snail size ratio, illustrated as line 'c' in Figure 4. The snail was retained (intact) in the prey population if it was not scarred (with probability  $1 - P_{SMSCAR}$ ).

At the end of every sequence of decisions that determined the outcome of each individual crab: snail interaction, the model scarring rate (MODSCAR) was calculated as the number of scarred, living prey divided by the number of living prey remaining in the simulation. If MODSCAR was less than FIELDSCAR (scarring rate observed in field) the model started with a new encounter between another randomly chosen snail and crab pair. If MODSCAR was greater than or equal to the field scarring rate the simulation stopped and the predation rate (PRED) was calculated as the proportion of snails in the initial population that were killed during the simulation.

## Results

### Field observations

Size distributions of *Littoraria* collected at a given site differed dramatically between 1989 and 1991 (Fig. 5).



**Fig. 4** The  $\ln$  of manipulation time versus the crab: snail size ratio for lab experiments (*top panel*). Circles represent actual data points and solid line represents curve fitted to the data by linear least squares regression ( $F = 13.87$ ,  $p = 0.0006$ ,  $r^2 = 0.26$ ). Schematic illustrating the shape of the three main model probability functions (*bottom panel*). Function 'a' represents the shape of the scarring probability curve for interactions at ratios  $\geq 4.7$ . If the snail was not scarred based on this curve, it was crushed and eaten. Function 'b' describes the probability of an adult crab killing a snail by the apical crushing method ( $F = 249.1$ ,  $p = 0.04$ ,  $r^2 = 0.96$ ). Function 'c' represents the shape of the scarring probability curve for small crabs at ratios  $< 4.7$ . If the snail was not scarred based on this curve, it was rejected intact

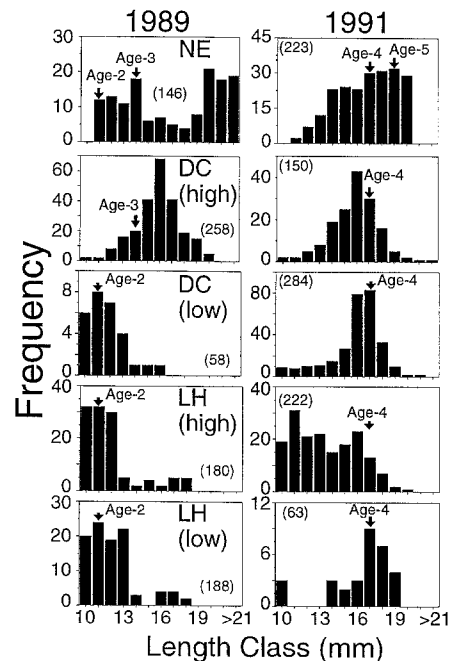
These differences held for sampling areas throughout the marsh, without regard to elevation or distance from Doboy Sound.

Interannual differences observed in the snail size distributions could be explained by the progression of age-class cohorts through time. There was excellent correspondence between the modes in length-frequency histograms and the mean size of various age-classes of *Littoraria* estimated from the growth function (Fig. 5) suggesting that our use of the empirical growth function (Stiven and Hunter 1976) was justified.

Comparison of size distributions across sampling areas within a year showed considerable variability in cohort strength that did not appear to be associated with position in the marsh (Fig. 5). Based on the range of the size distributions, it appears that recruitment may be slightly less variable at the NE site than lower in the marsh. Progression through time of strong cohorts (supported by predictions of growth function) was evident at 4 of 5 sampling sites (Fig. 5). We did not detect such a cohort phenomenon at the DCH site.

Snail abundance generally increased with elevation and distance from tidal creeks. Abundance was lowest at LH (21.5 snails  $m^{-2}$ ) closest to Doboy Sound and was highest at the high elevation DC site (65.9  $m^{-2}$ , Table 3). Densities were in general, significantly different between the extremes of the predicted predation gradients in the salt marsh (Table 4).

Snail scarring rates were inversely related to both distance from Doboy Sound (along Dean Creek) and local distance (elevation) from the shore of the sound or



**Fig. 5** Length-frequency histograms of *Littoraria irrorata* collected in 1989 and 1991 at four sites along Dean Creek, Sapelo Island, Georgia. Ages were derived from von Bertalanffy growth functions reported in Stiven and Hunter (1976)

**Table 3** Mean, standard deviations and sample sizes of snail densities and scarring rates at sampling locations in a salt marsh on Sapelo Island, Georgia in 1989 and 1991. Density and rates were estimated for *Littoraria*  $\geq 10$  mm. See text for derivation of hypothetical crab predation rates. Lighthouse marsh is closest to Doboy Sound, and North End marsh is furthest from the Sound. Low elevation sites were 30 m from the Dean Creek, high sites were 70–100 m from the creek

| elevation:<br>abbreviation:     | Lighthouse |             | Dean Creek |             | North<br>End) |
|---------------------------------|------------|-------------|------------|-------------|---------------|
|                                 | low<br>LHL | high<br>LHH | low<br>DCL | high<br>DCH |               |
| Density (# m <sup>-2</sup> )    |            |             |            |             |               |
| mean                            | 21.5       | 43.5        | 51.5       | 65.9        | 52.0          |
| std. dev.                       | 14.6       | 33.1        | 48.3       | 13.0        | 8.2           |
| n                               | 6          | 11          | 6          | 12          | 7             |
| Scarring Rate (%)               |            |             |            |             |               |
| mean                            | 66.5       | 61.3        | 45.7       | 25.7        | 20.1          |
| std. dev.                       | 14.9       | 27.1        | 29.3       | 17.0        | 3.0           |
| n                               | 6          | 11          | 6          | 12          | 7             |
| Hypothetical Predation Rate (%) |            |             |            |             |               |
| A                               | 40.0       | 95.7        | 40.0       | 83.0        | –             |
| B                               | 50.0       | 96.4        | 50.0       | 86.0        | –             |

**Table 4** Results from multiple comparison test (Fisher PLSD) of densities and scarring rates of snails at sampling sites throughout the marsh for 1989 and 1991 data combined. Pairwise comparisons are significantly different with 95% confidence (\*\*) and 90% confidence (\*). Non-significant differences are denoted 'ns'. ANOVA detected significant differences among sites for both density ( $F=2.992$ ,  $p<0.05$ ) and scarring rate ( $F=8.283$ ,  $p<0.001$ ). Site names are listed in hypothesized order of increasing predation intensity, abbreviations are as in Table 3

| Density       | LHL | LHH | DCL | DCH |
|---------------|-----|-----|-----|-----|
| LHH           | ns  |     |     |     |
| DCL           | *   | ns  |     |     |
| DCH           | **  | *   | ns  |     |
| NE            | **  | ns  | ns  | ns  |
| Scarring Rate | LHL | LHH | DCL | DCH |
| LHH           | ns  |     |     |     |
| DCL           | *   | ns  |     |     |
| DCH           | **  | **  | *   |     |
| NE            | **  | **  | **  | ns  |

creek bank (Table 3). At LH, scarring rates were relatively high for both the low and high marsh sites. Scarring rate was much lower at DC. At NE, the site which is most distant from Doboy Sound, scarring rates were the lowest observed in the study but not significantly different from the high elevation DC site (Table 4). Scarring rates were significantly different between sites located at the extremes of the predicted predation gradients (Table 4).

## Laboratory experiments

### General feeding patterns

Crabs exhibited three general feeding patterns. The most common pattern observed at crab: snail size ratios  $>6$  was a crushing method where the crab fit the entire snail in its chela and quickly crushed the shell (63% of all trials). Alternatively, at size ratios  $<6$ , the crab chipped the aperture of the shell with its crushing chela, thereby exposing and allowing extraction of the edible tissue. Many such attempts involved relatively long manipulation times (mean: 305 s; standard deviation: 237) and often (88%) resulted in rejection of the live snail with a damaged shell.

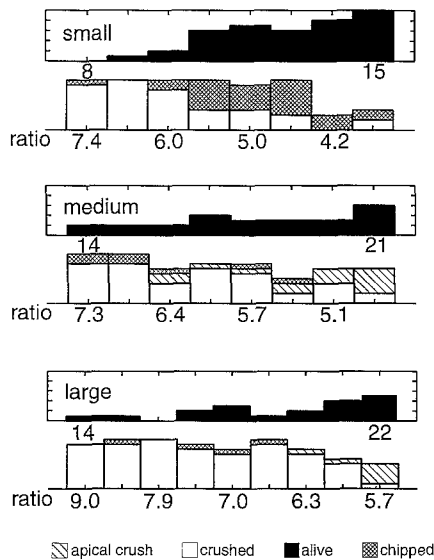
Crabs  $>100$  mm exhibited a third method when handling relatively large snails (size ratios  $<6$ ). These crabs would insert one chela into the aperture of the snail while crushing the apex of the shell with the other. We observed this phenomenon in 16% of trials with ratios  $<6$ . We refer to this method as “apical crushing”.

Manipulation times were relatively short and similar at crab: snail size ratios greater than approximately 8 (Fig. 4). Manipulation time increased rapidly for most interactions at size ratios near 6. The few interactions that resulted in short manipulation times at low size ratios ( $<6$ ) were caused by immediate rejection of the snail or the crab quickly killing the snail using the apical crushing method.

### Size selectivity

Three different size categories of crabs showed significantly different overall predation rates (ANOVA,  $F=22.8$ ,  $p<0.02$ ) and effects on shell damage (scarring) of living snails (ANOVA,  $F=15.9$ ,  $p<0.03$ ). Small crabs foraged most size selectively (Fig. 6). All of the 8 mm snails were killed and predation rate declined steadily with increasing snail sizes. Small crabs produced an overall predation rate of 50% which was significantly different from overall predation rates caused by medium and large crabs (Fisher PLSD,  $p<0.05$ ). Small crabs damaged the aperture (scarred) of 33% of all snails offered as prey. This result is significantly different from overall scarring rates caused by large and medium crabs (Fisher PLSD,  $p<0.05$ ). Aperture damage by small crabs was most common at size ratios between 4.6 and 5.4.

Total mortality caused by the medium (69%) and large (84%) crabs was relatively uniform across snail sizes (Fig. 6). Mortality rates of medium and large crabs were marginally significantly different from each other (Fisher PLSD,  $p<0.10$ ). Using the crushing method, both of these groups of crabs were able to kill snails in all size categories but were only able to use the apical crushing method on snails at size ratios  $\leq 6.4$  for medium crabs and  $\leq 6.3$  for large crabs (Fig. 6). Frequency



**Fig. 6** Outcome of the six, size selectivity experiments. Each set of paired panels represents the sum of the data collected for each size group of crabs. A total of 10 snails from each 1 mm size category is represented. The shaded region of the top panel of each pair represents the distribution of snails that remained alive at the end of the experiment – all others were killed. The second panel of each pair depicts the fate of the snails in each size category that did not survive intact. These snails were either killed by apical crushing or entire shell crushing, or were rejected alive with damaged shells. Numbers of alive snails are plotted against snail size, while the distribution of feeding methods is plotted against the corresponding crab: snail size ratio

of chipped apertures (scarred) of surviving snails was 25% from medium crabs and 26% from large crabs which were not significantly different from each other (Fisher PLSD,  $p > 0.10$ ).

### Preference experiments

When presented two different sizes of snails, crabs showed no significant size preference in attack behaviors. The observed results for 35 trials ( $n = 7$  crabs) were not different from random binomial probabilities ( $\chi^2 = 4.7$ ,  $p = 0.58$ ). Therefore, we assumed that attacks commence with each encounter and that size selectivity takes place after the crab has begun to manipulate the prey.

### Simulation model

#### Model parameters

All model parameters (Table 2) were estimated from the results of the laboratory experiments. The probability that a snail was rejected intact ( $P_{\text{INTACT}}$ ) was calculated as the proportion of all manipulation time trials where the snail was rejected without observable damage to its shell.

Crabs from the ‘large’ and ‘medium’ size categories of the experimental portion of this study showed different feeding modes and scarring rates than crabs from the ‘small’ size group. We therefore combined the ‘medium’ and ‘large’ experimental size classes and simply refer to them as ‘large’ crabs (i.e. crabs  $\geq 100$  mm) in the individual-based model.

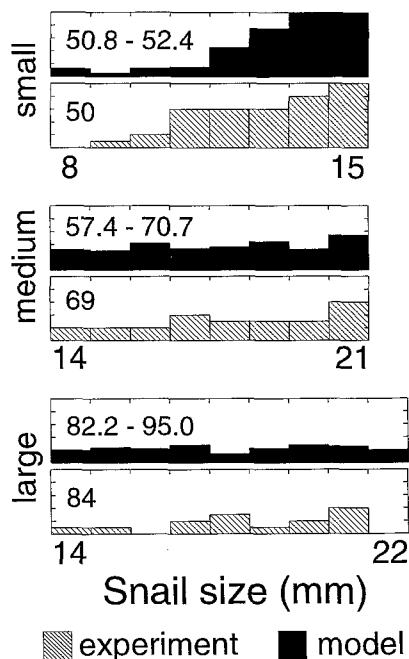
The probability that a ‘large’ crab can kill a snail by apical crushing ( $P_{\text{APICAL}}$  – equation 2) was calculated from the results of the manipulation time and size selectivity experiments. A linear model (least squares fit) of the proportion of snails suffering apical crushing relative to crab size was calculated to provide estimates of APICALC and APICALS.

The probability of scarring ( $P_{\text{SCAR}}$ ) by all ‘large’ and ‘small’ crabs at size ratios  $\geq 4.7$  (the ratio where the predicted manipulation time equalled the maximum manipulation time observed in the laboratory) was determined from the manipulation time experiments. A linear least squares fit of manipulation time to size ratio produced parameters SCARC and SCARS. Equation 4 was derived to allow for nominal scarring by ‘small’ crabs at a size ratio of 3.7 (the lowest ratio where aperture chipping was observed) but that would allow increased probability of scarring as the size ratio increased to 4.7. We arbitrarily determined the scarring probability to be low at a ratio of 3.7 and then fit an exponential function between this point and the point intersecting the adult scarring probability curve at a ratio of 4.7. The probability of scarring by small crabs at a ratio of 3.7 was determined (0.05) by adjusting this parameter value until the model predicted snail scarring rates that corresponded to the scarring rates we observed for small crabs in the lab.

### Model corroboration and sensitivity analysis

We simulated the size selection experiments using the crab-snail individual-based model. For each of the three size categories of crabs a simulation was run with the same initial uniform distribution of snails used in the lab experiments. We used 10 times more snails in each of the size categories to allow for more precise estimates of the model prediction. Crab sizes were those used in each of the experiments. We ran each simulation until the model scarring rate (MODSCAR) equalled the ratio of chipped snails that remained in each of the size selection experiments.

Model predation rates agreed well with the predation rates observed in the size selectivity experiments (Fig. 7). Confidence intervals (95%) determined from 10 repeated simulations bounded predation rates observed in the laboratory for large and medium sizes of crabs (Fig. 7). The model predicted marginally higher predation rates for small crabs than was observed in the laboratory. The model also accurately predicted the size selectivity observed for small crabs in the laboratory experiments,



**Fig. 7** Comparisons of size selection experiments ( $n=2$  experiments per size class) with parallel model simulations. Shaded regions represent snails still living at the end of each of the experiments. Experimental results are for 10 snails per 1 mm size class, and model results are for 100 snails per 1 mm size class. The mean value of predation rate for the experiments is shown with the 95% confidence interval of predation rate determined by model simulation ( $n=10$ )

**Table 5** Sensitivity of model estimates of predation rate in response to 5% perturbations in individual parameters and input scarring rate. Responses are expressed as percent change of the mean predation rate ( $n=10$  simulations) from its value at the nominal parameter value (NV)

| parameter           | description                         | Deviation in predation rate (%) |         |
|---------------------|-------------------------------------|---------------------------------|---------|
|                     |                                     | 95% NV                          | 105% NV |
| FIELDSCAR           | scarring rate observed in field (%) | -19.5                           | 15.5    |
| $P_{\text{INTACT}}$ | initial prob. of rejection          | 0.5                             | 0.4     |
| MAXTIME             | maximum handling time (s)           | -1.9                            | 1.5     |
| APICALC             | apical crush. coefficient           | -1.7                            | -2.9    |
| APICALS             | apical crush. slope                 | -0.6                            | -1.1    |
| SCARC               | 'large' scar intercept              | 12.6                            | -9.7    |
| SCARS               | 'large' scar slope                  | 0.6                             | -4.4    |
| SMSCARC             | 'small' scar coefficient            | -2.7                            | -1.1    |
| SMSCARS             | 'small' scar slope                  | 2.1                             | -3.6    |

and the uniformity of medium and large crab predation across all snail sizes. We were therefore confident that the individual-based model captured much of the underlying size-structured interactions between *Callinectes* and *Littoraria* and could be used to infer predation gradients in the salt marsh.

We performed an individual parameter perturbation (IPP) sensitivity analysis (Byrlynsky 1972) on the crab-

snail model. Sensitivity of each model parameter was determined as the percent change in predicted predation rate as a result of  $\pm 5\%$  parameter perturbation to its nominal value. We performed 10 independent simulations with each individual perturbation to determine the mean change in the response variable.

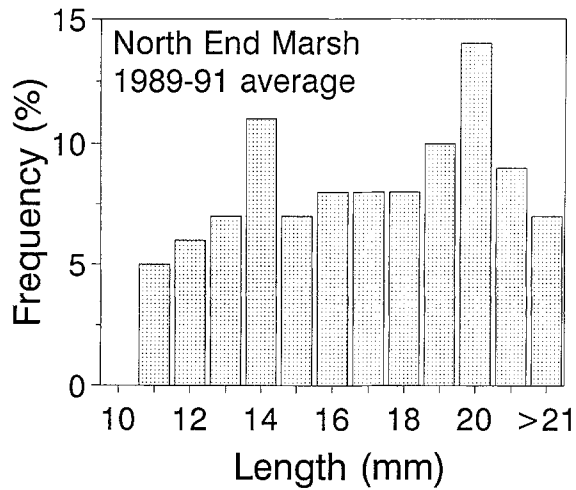
Model predictions were robust ( $\leq 5\%$ ) to variation in all but one parameter. The response variable changed 9.7 to 12.6% in response to  $\pm 5\%$  changes in the intercept of the manipulation time curve (SCARC, curve 'a' of Fig. 4) (Table 5). Variation in the input variable (FIELDSCAR) had a much greater impact on model output (predation rate) than any of the parameters (15.5 to 19.5%).

#### Model application

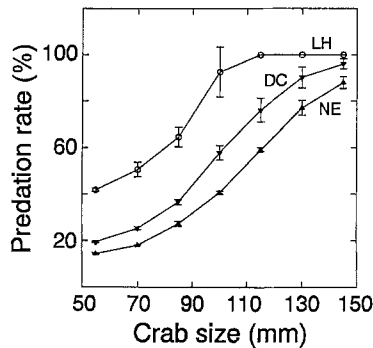
We addressed two general questions with the crab-snail model. First, we determined how predation rates might vary along the tidal gradient in response to crab size and observed patterns of snail scarring. To do this we ran simulations with a range of crab sizes (all normally distributed with variance equal to twice the mean – the shape of the size distribution we observed in the salt marsh) between 55 mm and 145 mm, and with a uniform snail size distribution with a range of 10 mm to 22 mm. Field snail size distributions were highly variable among sites and from year to year. However, the average (between years) snail size distribution at NE, where we assume that the size selective effects of crab predation should be lowest (because we propose that crab predation intensity is lowest there), was close to uniformly distributed (Fig. 8). We did not include snails  $< 10$  mm in size in the model analyses for two reasons. Firstly, Hamilton (1978) suggested that small snails are difficult to sample effectively and therefore we did not attempt to quantitatively sample them in the salt marsh. Secondly, these individuals represent the youngest snails in the population who recruit with unscarred shells. Therefore, scarring frequencies on young snails do not represent a time-integrated record of predation intensity for the entire population.

We also used the crab-snail model to predict average crab size at two elevations at LH and DC. These simulations are not entirely independent of the simulations described above but utilize a different subset of field data and assumptions. In order to do this we ran different model scenarios that included a range of differences in predation rates between high and low elevations. For the most extreme predation gradient scenario, we assumed that relative differences in snail density (average of 3–6 quadrats in both years) at different elevations within a site were entirely attributable to differences in predation rates. The model scenario that represented the opposite end of the range of predation differences was where we assumed that predation rates were equal at high and low elevation sites. The combination of predation rates and observed field scarring rates could then be used to predict average crab sizes at each location.

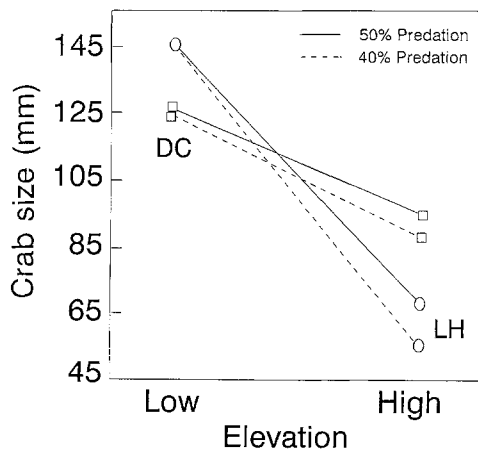




**Fig. 8** Mean size distribution of snails at NE for two years to illustrate how progressions of strong cohorts through the population makes the overall snail distribution approximate a uniform distribution over an infinite time horizon



**Fig. 9** Predicted mean crab predation rates and 95% confidence intervals ( $n=10$ ) as a function of mean crab size at three study sites using observed field scarring rates at different sites as the input variable



**Fig. 10** Predicted mean crab size at high and low elevations at DC and LH derived from differences in scarring rates between sites. For the predictions presented here, we assumed that relative differences in densities of snail between the two elevations were entirely due to differences in predation rates. Solid and dashed lines represent predictions based on assumptions of 50% and 40% predation rates at the high elevation sites

### Model predictions

Model simulations predicted that increases in both average crab size and proximity to Doboy Sound would increase predation rates in support of our *a priori* hypothesis (Fig. 9).

Mean crab size was predicted to decrease with increasing marsh elevation for all model scenarios that included increased predation rates with decreased elevation (perpendicular distance from Doboy Sound or Dean Creek). The largest difference in crab size between low and high elevation sites was predicted to occur when we assumed that snail density differences between low and high elevation sites were due entirely to differences in predation rates (i.e. when predation rate differences between high and low sites was the greatest, Fig. 10). The model also suggested that the crab size gradient at LH is steeper than the size gradient further up Dean Creek at DC. This result did not change qualitatively based on our assumption of predation rates at high elevations.

### Discussion

Inter-year variability in size distributions implied that snail recruitment was variable across years within sites, and across the marsh within a year. *Littoraria irrorata* produce meroplanktonic larvae (Bingham 1972) that settle widely over the marsh and disperse little from the settlement site over their lifetime (Newell 1958; Hamilton 1978). Apparently small scale variation in site characteristics contribute to heterogeneous settlement and post-settling survival, and hence age/size structure of the population at the site. Growth of occasional strong cohorts can have large effects on size distributions of *Littorina irrorata* (Hamilton 1978) much as they do for *Littorina littorea* (Moore 1937). Such cohort phenomena may obscure the effects of size-selective predation by crabs and, therefore, snail size distributions do not appear to be a suitable indicator of crab predation intensity at a site. If predation rates are to be inferred from characteristics of snail populations, alternative measures are required.

Snail density varied in accordance with expected patterns of predation intensity along a tidal gradient. The confounding effects of differential growth rates and recruitment dynamics prevent direct explanation of density gradients through predation. Faster growth rates of snails at high elevation sites may account for higher densities there because fast growing snails would be present at predation-vulnerable (small) sizes for shorter periods of time. However, our field data of snail size distributions through time suggests that growth rates may not vary substantially throughout the salt marsh. Higher settling rates of *Littoraria* larvae at high elevations could also account for the observed pattern. However, higher settlement of snails at lower elevations might be expected on the basis of inundation time or

particle deposition arguments (Peterson 1991), assuming that larval settling is not an active process in response to other cues that vary with elevation (but see Grosberg 1981). Thus, snail density at any particular site offers only weak corroboration of predation intensity.

The ability to reconstruct predation regimes from the snail scarring record offers an additional type of evidence not available in many other predator-prey studies. We observed that the process of predation and shell scarring in crab-snail interactions is highly size-dependent. Therefore, field scarring rates may offer insight into probable size distributions and predation rates of crabs along the tidal gradient. The model we have presented here incorporates this paleoecological evidence of predator-prey interactions, an approach that is relatively rare in ecological studies (but see Kitchell et al. 1981; Vermeij 1982b; Kitchell and Carpenter 1987; for examples). This approach allowed us to reconstruct characteristics of the predator population – information that otherwise can only be obtained by often difficult, intensive sampling of a highly mobile predator (Kneib 1984). Analysis of snail shell scars also allowed us to examine a long-term predation record that is an integration of short-term (inter-seasonal and inter-annual) fluctuations that may have occurred in predator and prey populations. Direct sampling of predators and prey would only offer analogous evidence if they were sampled across seasons and years. We think that this approach offers a more efficient means of making time-integrated inferences about predation gradients in salt marshes.

Whether the size constraints of individual crab: snail interactions are extended to processes that affect community level organization (e.g. Paine 1966) is not obvious. Integration of specific foraging characteristics into large scale analyses of predator-prey systems has been advocated as an important step towards understanding the regulatory processes of ecological systems (Peterson 1990). The ability to retain important individual-level processes (which are easily quantifiable) and address broad scale questions is a powerful feature of individual-based modeling approaches that is not possible with state variable models (Huston et al. 1988; DeAngelis and Gross 1992).

This modeling approach allowed us to integrate snail scarring patterns within a simple foraging model to assess crab predation gradients in the heterogeneous marsh environment. We suggest that the size-regulated processes in our model make predictions that are consistent with patterns that occur in salt marshes. A combination of the physical forcing of tides and size-structured predation interactions are possibly driving mechanisms that govern predation gradients. Although model performance was excellent in verifying the results of laboratory experiments, the predictions we make have yet to be directly tested in the field.

Model results indicate that predation intensity decreases away from the low tide refugium for crabs. Such

a predation gradient is expected because tidal inundation, and hence the foraging time available to crabs and other natant predators, is shortest high in the marsh (Kneib 1984). Although predator mobility may overcome restrictions caused by limited inundation time (Peterson 1991), alternative evidence also exists. For example, crab densities have been shown to vary with tidal level in other systems (Willason 1981). Sousa (1993) showed that local variation in predation intensity on cerithid snails by grapsid crabs is largely a function of local crab densities. We know that tidal inundation time does vary throughout the marsh and this variation is likely to have direct effects on predation rates (Kneib 1984; Peterson 1991). However, the relative importance of variation in crab densities along tidal gradients in determining predation rates remains unknown.

Because we were unable to obtain reliable abundance estimates of crabs throughout the salt marsh we cannot determine the primary cause of the predation gradients we predict. To obtain direct measures of crab densities and size distributions along the hypothesized predation gradients would require intensive sampling that spanned both inter-seasonal and inter-annual time periods. Shell scars accumulate in populations of snails and represent an integrated record of predation attempts over a time scale equivalent to their life span. Therefore, scarring frequencies in snails may be poorly correlated with predation pressure in any particular year or at any given time of year. Short-term temporal variations in crab population characteristics may obscure the underlying predation gradients that we argue are better represented in the snail paleoecological record.

Cordgrass (*Spartina*) is a dominant feature of Sapelo Island salt marshes. Its high densities and growth form may also account for the gradients in predation intensity we have inferred. *Spartina* density generally increases with distance from mean low water height (West and Williams 1986), a pattern that is not well understood but may be determined by salinity gradients (Adams 1963). *Spartina* may provide a refuge for *Littoraria* from swimming predators such as *Callinectes* by acting as a physical barrier impeding crab movements or by providing substrate above water, not accessible to predators (Hamilton 1976; Warren 1985). *Spartina* could also act as a filter for crab size and may account for the crab size differences that we predict with distance from tidal creeks. Crab movements must follow water movements with incoming and outgoing tides. Smaller crabs would probably be able to move more efficiently through dense vegetation than large crabs and therefore would be more likely to reach sites at higher elevations in the marsh (Arnold and Kneib 1983). Therefore, the predation gradients associated with tidal inundation gradients are probably determined by a combination of 1) crab density, 2) inundation time and 3) average crab size, all of which are predicted to decrease away from tidal creeks and the low tide refugium.

Model results suggested that the gradient in crab

sizes between high and low elevation at LH was greater than at the DC site (Figure 10). Several mechanisms may account for this. Differences in elevation gradients at these two sites would create differences in inundation time and therefore differences in the time available for crabs to disperse into the marsh. Higher densities of *Spartina* at the LH site would also serve as a stronger filter of crab size than at DC. Unfortunately, we do not know whether either of these possibilities is correct. Our predictions of crab size at a given location were also dependent on our assumptions of predation rates between high and low sites. If the reasons for snail density differences between high and low elevations varied greatly between the LH and DC sites, our prediction of greater differences in crab size at LH than at DC may be invalidated.

Model simulations also tested how observed snail scarring rates and crab size might be used to predict predation rates. Large crabs were more successful predators and produced lower scarring rates than small crabs. This result suggests that the combination of snail density and scarring rate can be used to infer size structure of the local predator population, assuming that snail recruitment patterns are broadly similar with respect to time and space throughout the marsh. If high scarring rates are observed with high snail density in the field, large crabs probably do not dominate the predator population. Predation by large crabs is least constrained by snail size and therefore produces high scarring rates only as a consequence of high predation rates. This result is supported by the observed combination of low snail densities and high scarring rates nearest Doby Sound (LH). Co-occurrence of relatively high scarring rates with high snail densities is indicative of greater relative abundance of small crabs because small crabs are not effective at killing snails and scar many individuals in the process of predation attempts.

Although we have concentrated on *Callinectes*, other predators co-exist with *Littoraria* in these salt marshes. Their effects may also be expressed in local snail densities and scarring rates. For instance, xanthid (mud) crabs (*Panopeus obesus* and *Eurytium limosum*) are common in these salt marshes (Kneib and Weeks 1990). Both are capable of feeding on *Littoraria*. Although mud crabs may select for smaller snails than blue crabs, there is substantial overlap in the range of sizes that each is capable of consuming (B. M. Johnson, unpublished data). Without knowledge of blue crab predation rates in comparison with mud crabs, we cannot assess the relative impacts of each on *Littoraria* populations. However, mud crab predation on *Littoraria* appears to reflect similar size-structured interactions as those for blue crabs and other decapod crustaceans (Juanes 1992).

Predictions derived from the individual-based model appear to be generally robust to model parameters. Only the intercept of the handling time curve (SCARC) was significantly sensitive to parameter perturbation. The fact that SCARC was sensitive to perturbation does not make our modeling predictions invalid. The model out-

put was most sensitive to input data (scarring rates of snails – FIELDSCAR). Therefore, the qualitative nature of our model predictions should not be affected by small variability in SCARC because predictions were largely determined by snail scarring rates observed in the field.

Several assumptions were needed to implement this model. We have assumed that size-selectivity occurs only after a crab has begun to manipulate its prey. Although crabs have relatively well developed visual and olfactory systems and may use these systems to select prey, the results of our size-preference experiments offer evidence that this assumption of our model is valid.

We assumed that the long-term averages of snail densities were indicative of predation intensity across the elevation gradient. Inherent inter-annual heterogeneity in local recruitment will produce patchy spatial distributions of snails. This suggests that multi-year data sets may provide a better indicator of long-term trends along tidal gradients. Accordingly, differences in densities and scarring rates from our aggregated data set offered a more temporally integrated record of predation gradients.

We also assumed that morphological characteristics and growth rates of snails did not vary with respect to location in the salt marsh. Local differences in shell thickness could bias the probability of scarring or predation success. Although it is possible that the physical – chemical characteristics which vary with elevation may affect snail growth and shell characteristics, evidence from the progression of snail cohorts suggests that growth rates are similar throughout the marsh. Therefore, it is reasonable to assume that shell morphology is also comparable throughout the marsh.

We have taken a relatively general approach to describing the interactions between blue crabs and marsh periwinkles. It is possible that we have not included important details of snail responses to predation intensity that may have caused biases in our predictions. For example, the shell morphology of other gastropods has been shown to vary due to characteristics of their predators (Appleton and Palmer 1988). If such a phenomenon occurs in the *Littoraria* – *Callinectes* system it would not invalidate the qualitative nature of our predictions. It is possible that predation gradients may induce local variations in snail shell morphology that may provide increased protection from crab predators. However, increased durability of snail shells would only cause increases in scarring rates of small snails. Because we incorporate scarring rates within the crab–snail model, we may already account for such variation in our predictions.

*Littoraria* also exhibit vertically oriented movements associated with tides along vegetation within salt marshes. These movements may be an escape response of snails to crab predation (Hamilton 1976). Size-specific differences in migration rates and therefore predation vulnerability may bias our predictions of predation rates. Such specifics of snail responses to predators are

beyond the scope of this study but may add important detail to the understanding of the system in general. If vertical migration were wholly effective, then it is difficult to reconcile the high scarring rates observed in the field. Other selection pressures must be operating in concert with predator avoidance.

We have not explicitly incorporated time in the crab-snail model. We assumed that the patterns it predicts span an infinite time horizon. Therefore, we have also assumed that at the time scale the snail scarring record represents (i.e. the life span of the snails), prey selection by crabs has not changed and the behavior we observed in the laboratory experiments accurately depicts these prey selection processes. Evidence for the generality of strong mechanical constraints on crabs feeding on molluscan prey supports this assumption (Juanes 1992).

Because we do not know crab densities we are unable to predict absolute predation rates on *Littoraria*. Predation rates by crabs will certainly be affected by thermal regimes associated with seasonality (West and Williams 1986; Eggleston 1990), variability in tidal amplitude, and phenomena such as progressions of strong cohorts through snail and crab populations. However, as others have argued (Vermeij 1982a, b) the information preserved in scarring patterns of molluscs offers a temporally integrated record of predator – prey interactions. Our model utilizes the information expressed in snail scarring patterns which provides evidence of long-term (greater than annual) predation regimes. We have not explicitly incorporated the information available from snail shells that indicates their size when scarred in our analyses. Doing so may allow further refinements of the predictive power of this model.

The common currency of these effects is time. Distance and vegetation density combine to influence the time required for crabs to invade with the flood tide, progress through the habitat in search of snails and engage in the predation process. Logically, differences in local selection pressures should be evident in snail behaviors, abundance and scarring characteristics. For example, snails nearest the source of crabs should exhibit the most pronounced anti-predator vertical migration behaviors because negative selection pressures on non-migrating individuals would be strongest at these locations. All of these factors probably play important roles in determining the predation gradients we observe which in turn may cause a cascade of direct and indirect effects expressed in community and system level processes within salt marshes (Paine 1966; Kneib 1991; Posey and Hines 1991).

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