

## ACES Final Technical Report

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**Title:** Determinants of Small-Scale Variation in the Abundance of the Blue Crab *Callinectes sapidus*  
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### Background and Objectives:

Estuarine ecosystems support a variety of commercially important fish and invertebrate species. Understanding what controls the abundance of these species has immediate practical value in enabling us better to estimate the levels of exploitation that constitute sustainable harvests. Taking a longer view, if we can determine the manner in which trophic transfer occurs in estuarine food webs, then we will be better able to predict how natural and anthropogenic perturbations will affect ecosystem function and, hence, the stock sizes of commercially important species.

There is considerable debate over whether “top-down” predatory effects or “bottom-up” productivity effects control the population densities of species in estuaries (e.g., Seitz and Lipcius 2001; Seitz et al. 2001; and references therein). In reality, of course, the issue is far more complex than this simple dichotomy suggests. Population density at a particular time and place may be determined by larval supply, post-settlement mortality, emigration and immigration, and other density-dependent and density-independent factors affecting multiple life stages. Furthermore, different factors can be expected to become more or less important at different scales of time and space. The challenge is to understand the factors that control the overall, or “mean” abundance of a target species in an estuarine ecosystem, and then to dissect that system and identify the determinants of smaller-scale variation, which is to say those factors responsible for the variance within the ecosystem.

Our long-term goal, of which this preliminary study is a part, is to determine if local variations in the population densities and predatory activities of the blue crab *Callinectes sapidus* in the Mobile Bay Estuary can be explained by local prey abundance. The abundance of blue crabs on larger scales is influenced in different situations by such factors as larval supply, post-settlement mortality, predation, competition, cannibalism and food supply, separately and in combination (Hines and Ruiz 1995; Lipcius et al. 1995; Pile et al. 1996; Heck et al. 2001; Seitz et al. 2003; Spitzer et al. 2003). Is it nevertheless possible that on a scale of tens to hundreds of meters variations in population density are determined simply by prey abundance? On this small scale, the movements of the crabs and other behaviors such as agonistic interactions are likely to be important in determining their distribution (Clark et al. 1999). Since the predatory fishes that eat blue crabs range over larger spatial scales, one simple a priori hypothesis to

explain differences in abundance *at this small scale* is that abundance is related to the availability of food; at this scale, bottom-up effects should be more important than top-down effects (see also Seitz et al. 2003). The prediction can be refined to state that blue crabs within the Mobile Bay Estuary should be concentrated in habitats with abundant prey and should forage more actively in those habitats, a hypothesis supported by observations of density-dependent predation by blue crabs on bivalve prey (Fouke and Lawton 1988; Eggleston et al. 1992; Seitz et al. 2001) and on the marsh periwinkle *Littoraria irrorata* (Schindler et al. 1994) in other locations.

The specific objectives of this study were to: (1) test whether densities of *Callinectes* are positively related to densities of *Littoraria*, (2) test whether predation by *Callinectes* on *Littoraria* is density-dependent, and (3) evaluate two simple, indirect methods of population estimation for blue crabs, which are based on the effects of the crabs on *Littoraria* populations.

In order to articulate formally the hypotheses to be tested in this study, it is necessary to define two aspects of predator-prey relationships: predation potential and predation pressure (Aronson 1987, 1989). Predation potential is defined as the rate at which the prey of interest—*Littoraria* in this case—would be consumed were they readily available to predators. Predation pressure is defined as the natural frequency of attacks by predators on their prey. Predatory attacks can be further categorized as lethal or sublethal, a point that will become important when it comes to assessing predation pressure. If predation by blue crabs on *Littoraria* is density-dependent, then dense populations of periwinkles should, *on a per capita basis*, experience greater predation potential and greater predation pressure than sparser populations. Predator abundance, predation potential and predation pressure should, therefore, be correlated with each other. This would mean that predation potential and predation pressure, which are relatively simple to measure, should predict the abundance of *Callinectes*, which is more difficult to assess accurately (e.g., with baited traps that can attract crabs from outside the habitat).

The following hypotheses were tested in this study:

I. Abundances of blue crabs and marsh periwinkles.

Hypothesis: Population densities of *Callinectes* are positively related to population densities of *Littoraria*.

Null Hypothesis: Population densities of *Callinectes* and *Littoraria* are not positively related.

II. Predation potential and predation pressure.

Hypothesis: Per capita predation potential and predation pressure on *Littoraria* are greater in habitats with higher population densities of *Callinectes*.

Null Hypothesis: Predation potential and predation pressure are not positively related to predator abundance.

III. Density dependence.

Hypothesis: Predation pressure is positively or negatively related to the prey density:predator density ratio.

Null Hypothesis: Predation pressure is not related to the prey density:predator density ratio.

To test these hypotheses, we measured four parameters: population densities of *Callinectes*; population densities of *Littoraria*; predation potential, which was assessed by tethering experiments with *Littoraria*; and predation pressure, which was estimated from sublethal injuries (repaired shell cracks) in *Littoraria* populations. We conducted bimonthly assessments of sublethal damage and biweekly tethering experiments and crab abundance assessments in two salt marshes along the coast of Alabama for six months (May to November 2003). During this time, crab activity was highest in the shallow intertidal salt marshes of coastal Alabama.

## Materials and Methods

### Study Sites

Two salt marsh locations dominated by *Spartina alterniflora* were chosen for surveys and experimental work: Airport Marsh, Dauphin Island and Point-Aux-Pines, Bayou La Batre. Individual sites were identified within each location as probable high- and low-predation microhabitats based on accessibility to *Callinectes* and a preliminary assessment of sublethal damage in the local *Littoraria* populations. Since *Callinectes* generally enters the marsh only during periods of inundation, sites adjacent to open bodies of water, such as sounds, tidal pools, creeks, and channels, gives the crabs access. Higher incidences of sublethal shell repair in these areas imply greater predation pressure.

Two sites at Airport Marsh were separated by a road and differed in their accessibility to open water. The north side of the marsh bordered Mississippi Sound and was bounded to the south by a road and to the west by a seawall. This site consisted of a band of *Juncus* bordering open water and a large depression inhabited exclusively by *Spartina* that was isolated from open water by a low sand berm. Crabs accessed the depression via a tidal creek. This site will be referred to as APM1. An area on the south side of the marsh, which was blocked from Mississippi Sound by the road, lacked many of the small creeks and pools found on the north side. This site will be referred to as APM2. The north side of the marsh was more accessible to *Callinectes* and preliminary observations indicated that the frequency of sublethal shell repair in *Littoraria* was significantly higher on that side: the proportion of individuals of shell length  $\geq 18.00$  mm bearing one or more repaired shell cracks was 0.76 on the north side, and 0.16 on the south side ( $n=200$  in both cases; chi-square test,  $P<0.001$ ).

The salt marsh at Point-Aux-Pines also consisted of a putatively high-predation site and a putatively low-predation site (see fig. 2). An area bordering Mississippi Sound was accessible to *Callinectes* and the *Littoraria* population showed a high frequency of sublethal shell repair. This site will be referred to as PAP1. A second site, PAP3, which was set back approximately 5 m from the end of a tidal channel, bordered a small tidal creek, and was less accessible to blue crabs. The frequency of shell repair was considerably lower (frequencies of repaired shells: 0.75 versus 0.40;  $n=122$  and 108 respectively;  $P<0.001$ ).

### Predation Potential

Predation potential was measured with tethering experiments. Despite objections that have been raised against tethering (Peterson and Black 1994; Kneib and Scheele 2000),

the approach remains a viable method for comparing predation potential among sites (Aronson and Heck 1995; Aronson et al. 2001). *Littoraria* of 14.50-16.50 mm shell length (the smallest size range consistently available throughout the year) were affixed to 7-cm lengths of spectrum line (the lines were super-glued to the shells) and tethered individually to shoots of *Spartina* at the study sites. The short length of the tethers prevented the snails from exiting the water during high periods of high water.

Fifteen tethers were randomly tied to shoots of *Spartina* within an 80-m<sup>2</sup> plot at each site. Due to seasonal differences in snail population size-structure, sets of tethered snails were occasionally limited to ten. The same plot was used for each experimental replicate. After 24 h, the tethers were collected and the proportion of attacked snails was assessed for each site. A predation event was counted if the tether and/or snail met one or more of the following criteria: 1) the entire shell was crushed, 2) the shell was intact but the lip was damaged, 3) the shell was absent or undamaged with a crimped or frayed tether and/or 4) the shell was empty. Controls consisted of ten individually caged snails (the cages measured 18 x 18 cm) tethered to individual *Spartina* shoots. Control cages were set at PAPI for every other tethering trial. The hydrodynamic stresses experienced by caged snails were not significantly different from those snails not placed in cages (based on caged and non-caged plaster block dissolution rates; R. Moody personal observations).

#### Predation Pressure

The proportion of *Littoraria* at each site with one or more repaired shell cracks was used as an estimate of natural predation pressure by *Callinectes*. Blue crabs are responsible for virtually all the sublethal damage to *Littoraria* in the salt marshes of Alabama, judging from the morphologies of the repaired cracks (Hamilton 1976; Stanhope et al. 1982; R. Moody, aquarium observations, 2001). Vermeij (1982a) argued that the frequency of sublethal shell damage—repaired cracks—in a gastropod population should be positively related to the antipredatory value of that population's morphological defenses: higher frequencies of sublethal damage should imply lower frequencies of lethal predation. Interpreting the frequency of shell repair can be problematic, however, because if only a few shells in a population display sublethal damage, then either the attack rate is high and most attacks are lethal, or both the lethal and sublethal attack rates are extremely low (Schoener 1979). Implicit in the design of this study is the hypothesis that rates of lethal and sublethal predation are positively related.

Fifty snails from three size classes (small: 5.00-11.99 mm; medium: 12.00-16.99 mm; large:  $\geq 17.00$  mm) were collected from each site once per time interval (see Statistical Analysis for sampling design). Due to seasonal variability in recruitment and differences in the size structure of snail populations among sites, it was not always possible to collect fifty snails for each size class. In this case, the largest sample possible was obtained. Because of size-related behavioral differences in climbing behavior (Stanhope et al. 1982) and the tendency for large snails to inhabit lower elevations in the marsh than smaller snails (Schindler et al. 1994), all snails were collected during low tide. Empty shells and those inhabited by hermit crabs were rejected.

Prior to scar identification, all shells were cleaned with a rotary tool fitted with a wire brush. This method of cleaning removed all epibionts and debris, which might have obscure small scars on the spire, without scratching or marring the shell. Scars were counted on all whorls of the shell with the aid of a dissecting microscope. Scars were

identified as raised or depressed, jagged discontinuities in the shell surface, generally running across growth sutures. Scar frequency was calculated as the proportion of individuals bearing one or more scars. The distribution of scars on snail shells was also analyzed within each site, season and size class to determine if scars were randomly distributed (i.e., if sublethal attacks are independent events; see Statistical Analysis) in each population or if individuals bearing one or more scars are disposed to more or fewer future scars.

### Predator Abundance

Population densities of *Callinectes* were measured by placing modified recreational crab traps at each site. Traps were covered in 0.5-cm Vexar<sup>®</sup> mesh and cable ties were fitted across the trap openings in a configuration that allowed crabs to enter the trap but not escape. All traps were baited with chicken. Traps were placed along the shore of sites that bordered open water (APM1 and PAP1) and at the mouth of the creek that served as the nearest aquatic point of entry to PAP3. Permanent trap locations were chosen for APM2 because the nearest tidal creek was approximately 25 m away from the midpoint of the site. A trap was placed in an area adjacent to the site and at an equal distance from the tidal creek as the site's midpoint. Each trap deployment period was 24 hours (essentially one full tidal cycle). The carapace width of all crabs caught was measured to track changes in the mean carapace width of *Callinectes* throughout the year. Carapace width was measured from the base of the lateral spines to prevent error associated with damage and erosion to the spines. Traps were set concurrently at all sites upon retrieval of the tethered snails.

### Prey and Cordgrass Densities

Snail and cordgrass densities were measured using a 0.5-m<sup>2</sup> PVC quadrat. Five random samples were taken per site per time interval (see Statistical Analysis for sampling design) for both snail and cordgrass density assessments. The collecting constraints used for collecting snails for damage assessments were used for snail density collections.

### Sampling Design and Schedule

The study was conducted from the late spring through the early fall (April to November 2003), during which the activity of *Callinectes* was maximal in the salt marshes of Alabama (there is little activity in winter because the crabs migrate offshore; West and Williams 1986). This time frame was divided into three contiguous intervals of equal time, defined as spring, summer and fall, to test for seasonal effects of predation by blue crabs. Densities of *Littorina* and *Spartina* were measured once at each site during each interval. Snails used for damage assessments were collected on the same day as those collected for density assessments. *Callinectes* abundance was measured at each site during each time interval for a 24-hr period immediately following the retrieval of tethered snails. Tethers were set concomitantly at all sites, as were crab traps during the following 24-hr period. Tethered snails were set on five random days for each time interval (approximately biweekly). Even though crab traps were set after each tethering trial, traps were occasionally damaged or washed ashore because of heavy seas. These

data were removed from analysis and resulted in trap data for four random days at each site per season.

### Statistical Analysis

#### *Predation Potential*

The proportions of tethered snails attacked were analyzed via a three-way analysis of variance (ANOVA), with site (APM1, APM2, PAP1 and PAP3) and season (spring, summer and fall) defined as fixed factors and the day of the tethering experiment nested within season. Predator abundance and crab size, described below, were analyzed using the same design as that used for predation potential. Tukey multiple comparison tests were performed where appropriate. No data transformations were necessary.

#### *Predation Pressure*

Mutual and partial tests of independence for proportions of scarred snails were performed between site, scars and season using  $R \times C \times L \chi^2$  contingency tables (Zar 1993). Mutual and partial tests of independence between site, scars and season were performed for each size class. For size classes in which both site and season were significant, heterogeneity was present and pair-wise tests of independence were required for each season and size class using  $2 \times 2 \chi^2$  contingency tables. When no seasonal effect was detected, the data were pooled within each site across season and site differences were tested using  $2 \times 2 \chi^2$  contingency tables. We also tested whether scars were randomly distributed within populations (i.e., whether attacks were random events) by testing the fit of the data to a Poisson distribution using the  $\chi^2$  goodness-of-fit test. A Bonferroni correction was applied to the prescribed value of  $\alpha=0.05$  to control the experimentwise error rate (i.e., to correct for multiple independent tests).

#### *Predator Abundance*

Crab counts were analyzed using a three-way ANOVA. Crabs with a carapace width  $<30$  mm were removed from the analysis because they are not likely sources of damage or mortality for the size range of snails used in the tethering experiments. Tukey multiple comparison tests were performed where appropriate. A  $[\log(Y+1)]$  transformation was used to meet the assumptions of parametric statistics.

#### *Crab Size*

Crab size was analyzed using a three-way ANOVA. Crabs of all sizes were included in the analysis. Tukey multiple comparison tests were performed where appropriate. No data transformations were necessary.

#### *Correlation Analyses*

Pearson product-moment correlation analysis was used to explore relationships among the densities of *Spartina* shoots, prey and predators; between predator density and predation potential; between predation pressure and prey density; and between predation pressure and the prey density:predator density ratio. Data transformations were applied as necessary.

## Results and Discussion

### Predation Potential

The mean proportion of attacked snails and their corresponding standard errors are presented in Table 1. A significant site effect was detected; PAP1 and PAP3 exhibited the highest proportion of attacks and APM2 exhibited the lowest. Proportions of attacks at APM1 did not significantly differ from PAP3. No losses were observed among caged snails.

Both PAP1 and PAP3 bordered open water (Mississippi Sound and a tidal creek, respectively), giving crabs access to both sites at any time during high water. PAP1 was located in a low-marsh area with tall-form, relatively sparse density of *Spartina* and rarely drained during the course of the experiment. APM1 also bordered Mississippi Sound but was only accessible to crabs if the water level reached a critical depth of approximately 0.33 m. Tides were highly variable and only varied about 1.0 m between high and low water. Despite these differences, all of the sites significantly differed from APM2, which was located in a high marsh zone consisting of dense, short-form *Spartina*. The closest tidal creek or channel to the APM2 tethering area was located approximately 20 m away and the site required a critical tidal height of approximately 0.33 m before the site became inundated. Dense grass, combined with the long distance necessary for the crabs to travel in order to reach the tethering zone, likely reduced crab foraging time. This is supported by the relatively high abundance of crabs in the site (see Predator Abundance) despite the low rates of attack.

*C. sapidus* migrates offshore to deeper water from late fall to early spring and is not present in appreciable numbers in the marsh during that time (Warren 1985; West and Williams 1986). Recruitment in *Callinectes sapidus* occurs twice a year in the northern Gulf of Mexico: during the spring months of April and May, and during the fall months of September and October (Rabalais et al. 1995; Heck et al. 2001). This means that two pulses of predation were expected, with the larger one occurring in late summer and early fall (K. L. Heck, personal communication). Seasonal differences in predation potential were not detected, however. Given the large size of the snails tethered, 14.5-16.5 mm, small crabs (less than ~30 mm) were either too small to contribute significantly to attacks on tethered snails or were not abundant enough to produce a significant seasonal effect. More work is needed to determine if a developmental response in blue crabs significantly affects *Littoraria* population size-structure.

### Predation Pressure

Results of the R x C x L  $\chi^2$ -contingency tables used to test for independence among the factors site, scar and season are presented in Table 2. Due to the significant dependence of both site and season on other factors for medium and small snails, it was necessary to compare sites separately among seasons (i.e., the R x C x L  $\chi^2$ -contingency tests for season and site exhibited heterogeneity and were therefore not comparable). Therefore, it was not possible to conduct comparisons of seasonal proportions of scarring. No seasonal effect was detected for large snails and multiple comparisons among sites were conducted for pooled proportions of scarring across season. Results of all pairwise

site comparisons and the results of individual significant pairwise tests among size classes and season are presented in Table 3.

The proportion of snails exhibiting one or more scars significantly differed among sites for all size classes and a seasonal effect was detected for medium (12.00-16.99 mm) and small (5.00-11.99 mm) snails. The shells of large snails ( $\geq 17.00$  mm) represent a highly integrated, multi-year record of predation, so seasonal differences were not expected. Snails within the medium and small size classes represent the zero to three-year age classes and, due to their small size and thin shells, are prone to higher levels of damage and mortality when attacked. Therefore, they are more sensitive to potential seasonal differences in the number and size of predators. Results were variable in the medium and small size classes; no site differences were detected in the summer and fall for medium-sized snails nor were differences detected in the fall for small snails. Only one size class of snails was tested for predation potential (snails with a shell height of 14.50-16.50 mm), so were are unable to speculate as to whether differences in crab abundance and size actually drive the distribution of scars in small snails.

Within large snails, PAP1 and PAP3 exhibited the highest frequency of shell repair. APM1 did not significantly differ from PAP3 but all sites exhibited significantly higher proportions of repair compared to APM2. These groupings are consistent with the results of the tethering experiments. Therefore, large, multi-year old snails accurately reflect predation at the small scale of predation examined in this study. In seasons within medium and small size-classes that exhibited significant differences among sites, PAP1 consistently reflected the highest level of predation pressure. No significant differences were detected among the remaining three sites. Medium and small snails are therefore not consistent indicators of predation pressure due to their smaller shells and more fragile shells relative to large snails.

Repaired shell cracks were randomly distributed in *Littoraria*, indicating that the snails are randomly attacked by crabs and that an attack does not predispose a snail to more or fewer attacks in the future ( $\alpha = 0.05 / 35$  tests =  $\alpha_{\text{adj}} 0.0015$ ;  $p < 0.001$  for all sites within their respective seasons and size classes). This means that shell-structure is not weakened by the presence of one or more scars (this has been experimentally supported by Blundon and Vermeij 1983) and that no behavioral changes take place because of attacks (i.e., increased climbing, hiding, etc.). In addition, if attacks are naturally random, than the use of tethers to measure predation potential should artificially inflate the attack rate (the tethers prevent the snails from climbing during high tide) yet accurately reflect relative differences in predation among sites.

#### Predator Abundance and Size

A significant site and seasonal effect was detected for blue crab abundance. Crabs with a carapace width  $< 30$  mm were removed from the analysis because they are too small to prey upon the size class of snails used in the tethering experiments (14.50-16.50 mm). The mean numbers of blue crabs caught at each site are presented in Table 4. PAP1 and APM2 exhibited the highest number of crabs but no significant differences were detected between APM2 and the remaining three sites. The high abundance of crabs at PAP1 is consistent with the high level of predation pressure on, and the proportion of scarring exhibited by, large snails. The high abundance of crabs at APM2 is surprising

given the consistently low levels of predation (based on tethers and scars) and likely reflects limited foraging times (see Predation Potential).

Crab abundance was significantly higher in the summer than in the spring (fall was not significantly different from either spring or summer). This was not reflected in the tethering experiments, indicating that either predation pressure is independent of crab abundance or that the power of the analysis was limited by the small number of trap deployments. A significant correlation was found between predator abundance and predation potential, however ( $R^2=0.198$ ;  $p<0.001$ ).

Crabs caught at APM2 were significantly smaller than those caught at the remaining three sites (see Table 5). The difference between APM2 and PAP3 was marginally significant ( $p=0.058$ ). APM2 is dominated by adult snails and we are unable to determine whether the age-structure of the population is attributable to intrinsic factors or predation by small crabs on small snails. No seasonal effect was detected for crab size; that is, we were unable to identify crab recruitment pulses.

#### Predator, Prey and *Spartina* Abundance

A significant positive correlation was detected between mean *Littoraria* and *Spartina* densities (on  $[\log(Y+1)]$ -transformed densities;  $R^2=0.42$ ;  $p=0.024$ ;  $n=12$ ). The density of snails therefore increased with *Spartina* density. Mean crab density was *negatively* correlated with *Spartina* density (on square-root-transformed data;  $R^2=-0.38$ ;  $p=0.031$ ;  $n=12$ ); this provides further evidence for a filtering effect imposed by grass (discussed above). Consistent with these findings, mean crab density was negatively correlated with mean snail density (on square root-transformed data;  $R^2=-0.52$ ;  $p=0.008$ ;  $n=12$ ). Interestingly, a significant, negative relationship was still detected when snail densities were corrected for structure (i.e., *Spartina* density) by dividing mean snail densities by their respective mean grass densities ( $R^2=0.36$ ;  $p=0.038$ ;  $n=12$ ). The mean proportion of large, scarred snails was not related to prey:predator density ratios, however. Given that attacks are random, we interpret these results to indicate that *Spartina* density controls the access of crabs into the marsh and their foraging rates, and that encounter rates are therefore not dependent on snail density.

*Littoraria* exhibits circatidal, vertical migration and crabs primarily catch prey by climbing shoots of *Spartina* and knocking snails into the water (Hamilton 1976; R. Moody pers. obs. 2003). The random distribution of scars indicates that crabs do not show a size-preference in this stage of prey acquisition. The size of both the snail and crab will determine whether the attack results in a lethal or sublethal encounter, however. Furthermore, this indicates that tethering integrates all aspects of prey availability (despite contentions that habitat-structure must remain identical for tethering to accurately reflect relative rates of predation) and provides an accurate measure of relative predation potential between sites varying in predator, prey and grass density.

#### **Conclusions**

We detected a strong positive relationship between the proportion of large *Littoraria* with sublethal injuries and the proportion of tethered snails attacked. Although this relationship was not strictly correlative, both methods reflected the relative per capita predation intensity experienced by snails at each site. Predator abundance was not as accurate in predicting predation intensity, although it did reflect extremes among the

highest- and lowest-predation sites. *Spartina* density significantly affected crab activity in the marsh and, in the case of APM2, imposed a filter on crab size. Proportions of scarred adult snails and mortality in tethering experiments incorporated these differences in predation and habitat structure, and provided an accurate relative indicator of crab activity. We found no evidence of density-dependent predation by *Callinectes* on *Littoraria*.

Blue crabs are ubiquitous in salt marshes along the Gulf and Atlantic coasts and are an important commercial species in both regions. Although blue crabs are the primary predators of *Littoraria*, *Littoraria* is not the only prey of blue crabs. Nevertheless, measures of predation potential and predation pressure on *Littoraria* can be used as independent estimators of marsh utilization by *Callinectes*.

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Table 1. Results of a three-way ANOVA on untransformed proportions of tethered *Littoraria irrorata* attacked among sites and seasons.

Source of Variation	df	F	P	Level	Mean ( $\pm$ SE)
Site	3	17.61	<0.001	PAP1	0.536 $\pm$ 0.0563 <sup>a</sup>
				PAP3	0.444 $\pm$ 0.0484 <sup>ab</sup>
				APM1	0.334 $\pm$ 0.0652 <sup>b</sup>
				APM2	0.100 $\pm$ 0.0350 <sup>c</sup>
Season	2	1.68	0.201		
Day(Season)	12	2.67	0.011		
Season x Site	6	0.87	0.530		
Error	36				
Total	59				

Notes: Means with the same superscript are not significantly different at a overall (family) error rate of  $p < 0.05$  (Tukey). Factors consisted of season (spring, summer, fall) and site (APM1, APM2, PAP1 and PAP3).

Table 2. R x C x L  $\chi^2$  contingency table results for three size classes of snails: Large (17.00+ mm), medium (12.00-16.99 mm) and small (5-11.99 mm). Tests were considered significant at  $\alpha_{adj} = 0.05 / 12 \text{ tests} = 0.0042$ .

Test	$\chi^2$	df	critical $\chi^2$	P
<u>Large</u>				
Mutual	130.14	17	27.59	<0.001
Site	125.94	14	23.69	<0.001
Scar	125.15	11	19.67	<0.001
Season	9.82	15	25.00	0.831
<u>Medium</u>				
Mutual	92.67	17	27.59	<0.001
Site	82.59	14	23.69	<0.001
Scar	44.29	11	19.67	<0.001
Season	49.76	15	25.00	<0.001
<u>Small</u>				
Mutual	144.26	12	21.03	<0.001
Site	99.67	10	18.31	<0.001
Scar	96.63	8	15.51	<0.001
Season	59.27	8	15.51	<0.001

Notes: "Mutual" denotes test of independence among site, scar and season. Results for Site, Scar and Season are tests of partial independence. APM2 is not included in the analysis of small snails due to a lack of consistent availability throughout the year.

Table 3. Significant pair-wise tests of independence for sites among season and size class via  $2 \times 2 \chi^2$ -contingency tables. Tests were considered significant at  $\alpha_{\text{adj}} = 0.05/33$  tests = 0.0015.

Size Class/Season	$\chi^2$	P	Site	Proportion Scarred
<b>Large<sup>†</sup></b>				
APM1 vs. APM2	39.124	<0.001	PAP1 <sup>a</sup>	0.81
APM1 vs. PAP1	19.400	<0.001	PAP3 <sup>ab</sup>	0.70
APM2 vs. PAP1	104.142	<0.001	APM1 <sup>b</sup>	0.57
			APM2 <sup>c</sup>	0.22
<b>Medium</b>				
<u>Spring</u>				
APM1 vs. PAP1	25.011	<0.001	PAP1 <sup>a</sup>	0.84
APM2 vs. PAP1	19.872	<0.001	PAP3 <sup>b</sup>	0.43
PAP1 vs. PAP3	17.502	<0.001	APM1 <sup>b</sup>	0.40
			APM2 <sup>b</sup>	0.37
<u>Summer<sup>††</sup></u>	-----	-----		
<u>Fall<sup>††</sup></u>	-----	-----		
<b>Small</b>				
<u>Spring</u>				
PAP1 vs. PAP3	19.186	<0.001	PAP1 <sup>a</sup>	0.75
			APM1 <sup>b</sup>	0.55
			PAP3 <sup>b</sup>	0.30
<u>Summer</u>				
APM1 vs. PAP1	21.869	<0.001	PAP1 <sup>a</sup>	0.64
PAP1 vs. PAP3	14.586	<0.001	PAP3 <sup>b</sup>	0.26
			APM1 <sup>b</sup>	0.18
<u>Fall<sup>††</sup></u>	-----	-----		

<sup>†</sup> : Proportion of damaged snails pooled within sites across seasons.

<sup>††</sup>: No significant differences detected.

Notes: All pair-wise comparisons were carried out between sites (APM1, APM2, PAP1, PAP3); those comparisons not listed were not significant at  $\alpha_{\text{adj}} = 0.0015$ . APM2 was not included in the analysis of small snails due to a lack of consistent availability. Means with the same superscript are not significantly different at a overall (family) error rate of  $p < 0.05$  (Tukey).

Table 4. Three-way ANOVA on  $[\log(Y+1)]$ -transformed crab counts among sites and seasons.

Source of Variation	df	F	P	Level	Mean ( $\pm$ SE)
Site	3	11.65	<0.001	PAP1	$0.961 \pm 0.055^a$
				APM2	$0.608 \pm 0.105^{ab}$
				PAP3	$0.597 \pm 0.104^b$
				APM1	$0.386 \pm 0.080^b$
Season	2	6.12	0.006	Summer	$0.793 \pm 0.093^a$
				Fall	$0.627 \pm 0.084^{ab}$
				Spring	$0.494 \pm 0.095^b$
Day(Season)	9	3.46	0.006		
Season x Site	6	0.81	0.572		
Error	27				
Total	47				

Notes: Means with the same superscript are not significantly different at a overall (family) error rate of  $p < 0.05$  (Tukey). Factors consisted of season (spring, summer, fall) and site (APM1, APM2, PAP1 and PAP3). Crabs with a carapace width  $< 30$  mm were removed from the analysis.

Table 5. Three-way ANOVA on raw carapace width of crabs among site and season.

Source of Variation	df	F	P	Level	Mean ( $\pm$ SE)
Site	3	8.72	<0.001	APM1	81.45 $\pm$ 4.36 <sup>a</sup>
				PAP1	74.97 $\pm$ 1.68 <sup>a</sup>
				PAP3	70.30 $\pm$ 2.22 <sup>ab†</sup>
				APM2	57.35 $\pm$ 2.10 <sup>b†</sup>
Season	2	2.43	0.105		
Day(Season)	10	0.78	0.643		
Season $\times$ Site	6	1.70	0.155		
Error	30				
Total	51				

†: p-value = 0.058

Notes: Means with the same superscript are not significantly different at a overall (family) error rate of  $p < 0.05$  (Tukey). Factors consisted of season (spring, summer, fall) and site (APM1, APM2, PAP1 and PAP3). Design is unbalanced. Sample sizes: APM1: n=32; PAP1: n=108; PAP3: n=68; APM2: n=64.