

Tidal regime dictates the cascading consumptive and nonconsumptive effects of multiple predators on a marsh plant

DAVID L. KIMBRO¹

Florida State University Coastal and Marine Laboratory, 3618 Highway 98, Saint Teresa, Florida 32358 USA

Abstract. Prey perception of predators can dictate how prey behaviorally balance the need to avoid being eaten with the need to consume resources, and this perception and consequent behavior can be strongly influenced by physical processes. Physical factors, however, can also alter the density and diversity of predators that pursue prey. Thus, it remains uncertain to what extent variable risk perception and antipredator behavior vs. variation in predator consumption of prey underlie prey–resource dynamics and give rise to large-scale patterns in natural systems. In an experimental food web where tidal inundation of marsh controls which predators access prey, crab and conch (predators) influenced the survivorship and antipredator behavior of snails (prey) irrespective of whether tidal inundation occurred on a diurnal or mixed semidiurnal schedule. Specifically, cues of either predator caused snails to ascend marsh leaves; snail survivorship was reduced more by unrestrained crabs than by unrestrained conchs; and snail survivorship was lowest with multiple predators than with any single predator despite interference. In contrast to these tidally consistent direct consumptive and nonconsumptive effects, indirect predator effects differed with tidal regime: snail grazing of marsh leaves in the presence of predators increased in the diurnal tide but decreased in the mixed semidiurnal tidal schedule, overwhelming the differences in snail density that resulted from direct predation. In addition, results suggest that snails may increase their foraging to compensate for stress-induced metabolic demand in the presence of predator cues. Patterns from natural marshes spanning a tidal inundation gradient (from diurnal to mixed semidiurnal tides) across 400 km of coastline were consistent with experimental results: despite minimal spatial variation in densities of predators, snails, abiotic stressors, and marsh productivity, snail grazing on marsh plants increased and plant biomass decreased on shorelines exposed to a diurnal tide. Because both the field and experimental results can be explained by tidal-induced variation in risk perception and snail behavior rather than by changes in snail density, this study reinforces the importance of nonconsumptive predator effects in complex natural systems and at large spatial scales.

Key words: antipredator behavior; blue crab; consumptive and nonconsumptive effects; density-mediated indirect interactions; multiple-predator effect; periwinkle; risk perception; *Spartina alterniflora*; tidal forcing; top-down control; trait-mediated indirect interactions; trophic cascade.

INTRODUCTION

How predators influence ecological communities continues to be an important topic in ecology (Connell 1961, Lima and Dill 1990, Hawlena and Schmitz 2010). In addition to increasing prey diversity by preferentially consuming competitively dominant species (Paine 1966), predators can indirectly influence basal resources (e.g., plants) by consuming their prey (consumptive effect, CE; Estes and Palmisano 1974, Carpenter et al. 1985) and by altering the foraging behavior of their prey (nonconsumptive effect, NCE; Abrams 1995, Werner and Peacor 2003). The distinction between these direct effects of predators on prey and how they indirectly cascade two or more trophic levels away from the

predator (i.e., density- vs. trait-mediated indirect interactions; DMII vs. TMII) is not trivial. Recent research clearly demonstrates that DMII and TMII can have substantial but different consequences for basal community composition and thus for important ecosystem functions including primary production, nutrient cycling, and the trophic transfer of energy (Schmitz 2008, Trussell et al. 2008).

While researchers are actively developing a framework to predict how CEs and NCEs structure natural systems (Schmitz et al. 2004, Preisser et al. 2009), a long history of research already illustrates that physical gradients can be used to improve our understanding of community dynamics. For example, until Whittaker (1956) empirically demonstrated that plant communities are likely organized by the interplay of competition and individual plant responses to gradients in temperature and moisture, adjacent vegetation types were long believed to represent predetermined plant associations

Manuscript received 31 March 2011; revised 21 September 2011; accepted 7 October 2011. Corresponding Editor: S. A. Navarrete.

¹ E-mail: dkimbro@bio.fsu.edu

along a succession trajectory (Clements 1936). This mechanistic understanding was improved when Connell (1961) experimentally showed that a marine shoreline gradient in sessile invertebrate species is maintained by predation, competition, and then individual physiological tolerances as desiccation stress increases from low intertidal to high intertidal. Experimental reexamination of this desiccation gradient, however, refined this paradigm by illustrating that the upper intertidal distribution of invertebrates exceeds that predicted from physiological tolerances alone because algal canopies ameliorate the desiccation experienced by groups of associated invertebrates (Bertness et al. 1999). Given that physical gradients have a long history of improving our knowledge about community dynamics, it is reasonable to consider whether such gradients also create predictable patterns in the direct (i.e., CEs and NCEs) and indirect effects (i.e., DMIs and TMIs) of predators.

For physical gradients to create patterns in predator effects, they must consistently affect how prey perceive risk (Trussell et al. 2008) and/or how prey are hunted by predators (Schmitz et al. 2004). With respect to risk perception, increasing physical factors such as water flow (Smee and Weissburg 2006), habitat complexity (Trussell et al. 2008), and wind (Carr and Lima 2010) have been shown to decrease the risk perceived by prey. If prey respond to this reduced perception of risk by consuming more basal resources, then CEs and subsequent DMIs will benefit basal resources more in environments where risk perception is inhibited (e.g., high habitat complexity), whereas NCEs and TMIs will be more influential in environments where risk perception is facilitated (e.g., low habitat complexity; Trussell et al. 2008). Thus, a basal resource distributed along a physical and risk-perception gradient may experience a corresponding gradient as to whether it is indirectly influenced more by CEs or NCEs.

Risk perception is also affected by predator hunting mode. Predators that sit-and-wait for prey are predicted to generate concentrated levels of risk cues while predators that actively roam for prey are predicted to generate diffuse risk cues (Schmitz et al. 2004). Because these hunting modes elicit different risk levels for prey and because hunting mode depends on predator identity, predator identity also determines whether basal resources are indirectly controlled more by CEs than NCEs (Schmitz 2008). Like prey risk assessment, predator identity may also be affected by physical gradients. For example, patterns of precipitation on islands and flow in rivers (via dams) often dictate which islands have different species of predatory rodents (Stapp and Polis 2003) or which portions of a river contain predatory fish that are native vs. invasive species (Moyle and Mount 2007). Along these physical gradients with segregated predator types, patterns in CEs vs. NCEs and their indirect propagation throughout food webs would therefore depend on how the gradient

simultaneously affects predator identity as well as prey perception of risk (Smee et al. 2008).

Prey in natural systems, however, are often exposed to multiple predators (Sih et al. 1998). Although predators may avoid overlapping with each other by partitioning resources over space and/or time (MacArthur 1958), in most cases many predators do overlap amply in their diets (Berlow et al. 2009) and often interact to inhibit or facilitate their CEs and NCEs on prey beyond what would be predicted solely from their individual effects (Navarrete and Menge 1996, Sih et al. 1998, Bourdeau 2009). Given that physical gradients may often produce different combinations of prey perception and predator hunting mode of individual or multiple predators, physical gradients might cause spatial patterns in basal resources by consistently influencing the strengths and indirect consequences of CEs and NCEs.

Here, I used an experiment and surveys of natural populations to test the following hypotheses. (1) Variation in the frequency and duration of tidal inundation modulates how multiple predators individually and interactively affect the survivorship (CE) as well as the antipredator behavior (NCE) of snail prey. (2) Tidal-induced variation in the consumptive and non-consumptive effects of predators on grazing snails cascades to the lower trophic level, cordgrass, so that the relative importance of DMIs and TMIs changes predictably with tidal regime. (3) Large-scale spatial variation in snail grazing and cordgrass productivity can be explained by the effects of tidal regime on the predator avoidance/foraging behavior of snails.

METHODS

Study system

I focused on a three-level food web in the northeastern Gulf of Mexico that resembles one in southeastern Atlantic marshes where blue crabs (top predator, *Callinectes sapidus*) indirectly maintain smooth cordgrass by consumptively preventing high densities of snails (Silliman and Bertness 2002). At high densities (i.e., absence of blue crabs), snails can switch from consuming benthic algae (Peterson and Howarth 1987, Sullivan and Moncreiff 1990) and stands of dead cordgrass (Barlocher and Newell 1994) to grazing live cordgrass (via fungal farming; Silliman and Newell 2003) and thereby cause the loss of cordgrass habitat. The northeastern Gulf system, however, has several unique features. (1) There is a second predator (crown conch, *Melongena corona*) that strongly influences snail density and behavior (Wilber and Herrnkind 1982, Hamilton 1996; see Plate 1). Unlike the actively roaming blue crab, which enters and leaves the marsh with each flood and ebb tide, the crown conch is relatively slow and often remains in the marsh throughout ebb tide. (2) There is a gradient in tidal inundation, with shorelines west of the Apalachicola River (29°33'27.89" N, 84°57'25.72" W; Appendix A) being inundated and then exposed for 12 h (i.e., diurnal tide), and shorelines east

of the Apalachicola being inundated and exposed at 6-h intervals for part of the month but inundated for 18 h and exposed for 6 h for another portion of the month (i.e., mixed semidiurnal tide, hereafter mixed tide). (3) There appears to be spatial variation in snail grazing on live cordgrass without corresponding variation in snail density.

Given these three characteristics of the northeastern Gulf, I addressed the overall hypothesis that spatial variation in snail grazing is due to an interaction between tidal inundation and the predator avoidance/foraging behavior of snails. As demonstrated by Dix and Hamilton (1993) and Hovel et al. (2001), snails have a highly plastic strategy for avoiding marine predators that involves ascending cordgrass leaves during flood tide (predators present) and descending cordgrass leaves during low tide (predators absent) to resume feeding on benthic algae and detritus. Because cordgrass leaves are susceptible to grazing, differences in tidal inundation, in addition to generating variation in the risk perceived by snails, may affect the severity of snail grazing on cordgrass leaves. Tidal variation may also interact with the different hunting modes of individual and multiple predators to alter the strength and outcome of CEs and NCEs on snails, and the overall snail effect on cordgrass (via DMII and TMII).

Tidal regime and predator experiment

In July 2009, I conducted a factorial experiment to examine how tidal regimes (main plot) interact with the direct effects of individual and multiple predators (subplot) to indirectly influence snail grazing on cordgrass. This experiment used 64 outdoor tanks (68 L) at the Florida State University Coastal and Marine Laboratory (FSUCML). Tanks were grouped into four blocks, each consisting of two adjacent rows of eight tanks. Arrangement of tanks in blocks was necessary to efficiently manipulate tidal regimes. Within each block, each row of eight tanks was randomly assigned one level of the main-plot factor (i.e., diurnal or mixed tide).

Within each block, tidal regime was manipulated using automatic sprinkler valves wired to mechanical timers that controlled the inflow:outflow rate of seawater, generating high and low tide conditions. For the first five days of the experiment, both tidal patterns had 10.5 h of low and 13.5 h of high tide. But because mixed tides along the Gulf coast oscillate every five days between having two and one low tide per day sufficient to expose cordgrass, I altered the mixed-tide timers to generate only one low tide per day (6-h duration) after the fifth day of the experiment. During the final five days of the experiment, this alteration generated daily low tides that were 4.5 h longer in the diurnal than in the mixed-tide schedule.

Within each level of the main plot, I randomly assigned the eight tanks to receive different predator treatments: (1) cordgrass; (2) snails and cordgrass; (3) conch, snails, and cordgrass; (4) crab, snails, and

cordgrass; (5) conch, crab, snails, and cordgrass; (6) nonlethal conch, snails, and cordgrass; (7) nonlethal crab, snails, and cordgrass; and (8) nonlethal conch, nonlethal crab, snails, and cordgrass. While treatments (3) to (5) assessed how individual and multiple predators indirectly structure cordgrass biomass (DMII and TMII) by varying both snail density (CE) and snail behavior (NCE), treatments (6) to (8) only assessed how predators nonconsumptively (NCE and TMII) structure this food web.

All tanks were planted with five 10 cm diameter plastic pots containing three cordgrass plants each. I used sieved (1-mm mesh) sediment from the local marsh to fill in spaces between pots (depth 9 cm). Based on preliminary survey results concerning snail density per unit area, I then added 60 snails to all tanks except those in treatment 1. To prevent prey depletion in this experiment, I added snails to tanks so that snail density did not remain below 15 individuals for more than 24 hours. This minimum density threshold was justified by monitoring the immigration of snails (over 24 h) into vacant, natural marsh plots of equivalent size (D. L. Kimbro, *unpublished data*). Nonlethal predator treatments were created by placing each predator in a modified plastic container that allowed inflow of water and outflow of predator cues but prevented predators from feeding on the 60 focal prey. To promote alarming predator cues consisting of both predators and crushed conspecifics (Trussell and Nicklin 2002), I fed predators in containers 10 snails each day. This feeding schedule equalized the strength of predator cues between corresponding lethal and nonlethal predator treatments (Appendix B). Finally, because blue crabs are uncommon in the marsh during low tide, they were only added to the tanks at high tide. In contrast, crown conchs were left in experimental tanks at all times.

This experiment ran for 10 days and generated four types of data: snail behavior, snail survivorship, snail herbivory on cordgrass, and change in cordgrass biomass. To circumvent behavioral differences between tidal treatments due to time of day, temperature, or humidity, I only collected behavioral data 30 min before each morning high tide. Data collection involved counting the snails that were on cordgrass but were also >10 cm above the ground. Snails on cordgrass but <10 cm above the ground were assumed to be more susceptible to predators compared to snails on the more distal leaves. Because snails often climb tank walls rather than cordgrass, I attached copper tape (snail deterrent) around the inner bottom of tanks. Proportional snail survivorship was quantified by sieving all tanks at the end of the experiment and dividing final snail density by initial snail density. For predator tanks that received supplemental snails to prevent prey depletion, supplemental snails were factored into this calculation. To assess snail herbivory, I quantified the total length of snail grazing scars on living plant tissue (green) before and after the experiment. Snail scars are distinguished

by longitudinal wounds on the leaf surface that snails create with their radulae to farm fungus and/or consume senescent leaf material (Silliman and Newell 2003). I also measured the cumulative length of green leaves in each tank at the beginning and end of the experiment. Using a length:biomass index developed with 60 plants from the same site ($y = 0.018x + 0.08$, $R^2 = 0.81$), I then converted these length data into biomass estimates.

Data analysis for the experiment.—Because snail scars could not be quantified on the brown-shredded leaves that dominated tanks with significant cordgrass loss, snail herbivory appeared to be greater in treatments with minimal loss of cordgrass biomass. As a result of this artifact, the herbivory data were not analyzed. Data analysis of snail behavior, snail survivorship, and change in cordgrass biomass involved fitting a series of mixed models that encompassed a range of parameter combinations. In the models, fixed effects included tidal regime, specific identity of predator (e.g., conch and conch cue), general identity of predator (e.g., no predator, predator, or predator cue), day of experiment, and first (days 1–5) or second portions (days 6–10) of the experiment. These last two fixed effects were applicable only for the behavioral models. While models of daily snail behavior included a random effect of tank nested within block, the models of snail survivorship and change in cordgrass biomass included only block as a random effect. After model fitting, I then performed model selection using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 1998). This procedure identified the most parsimonious explanatory model for each response variable.

After model selection, analyses of snail survivorship and cordgrass biomass required additional steps. First, in addition to analyzing treatments for differences in snail survivorship, I used a multiplicative risk model to test for an emergent multiple-predator effect (MPE) of crab and conch on snail survivorship (e.g., facilitation or inhibition; Sih et al. 1998). To create an expected MPE with error, I used the fixed-effect estimates from the most parsimonious model on snail survivorship and this model's variance-covariance matrix to generate 10 000 additional fixed-effect estimates from a multivariate normal distribution. For each of the 10 000 iterations, I reconstructed estimated treatment means as well as an expected multiplicative predator effect ($1 - \text{conch effect} - \text{crab effect} + \text{conch} \times \text{crab effect}$). To detect differences among treatments, I used the 10 000 values associated with each treatment to generate a treatment mean and its 85% confidence interval (CI) so that the hypothesis of interest could be evaluated with an approximate 5% significance level (see Payton et al. 2003). Because of equal variances, nonoverlapping CIs were declared significant (Payton et al. 2003).

To compare the strength of indirect pathways (DMII and TMII) by which predators changed cordgrass biomass, I repeated this simulation process. Specifically,

estimates from the best model on change in cordgrass biomass and its variance-covariance matrix were used to generate 10 000 parameter estimates from a multivariate normal distribution. From each iteration, I obtained fixed-effect estimates and calculated the size of TMII for predator cue treatments and TMII \times DMII for lethal predator treatments using the following index: $1 - ([\text{predator effect} - \text{plant effect}] / [\text{snail effect} - \text{plant effect}])$. For instance, an index value of 1.0 means that the gain in cordgrass biomass was 100% greater in communities with predators than without predators. This index differs from that used in Trussell et al. (2008) by accounting for plant autogenic error as well as error associated with the effect of snails (denominator). To detect differences among treatments, I used the 10 000 index values associated with each treatment to generate a treatment mean and its 85% CI. These CIs permit an overall hypothesis testing with approximate 5% significance (Payton et al. 2003).

Because the modified indirect effect index used estimates from a model with treatments lacking predators, I was unable to analyze whether variation in the indirect effects was better explained by alternative models such as the main effect of tidal regime across all predator treatments. As a result, I also calculated index values in accordance with Trussell et al. (2008) by averaging (separately for each tidal regime) the change in cordgrass biomass across all replicates with only cordgrass and snails (i.e., treatment 2) and the change in cordgrass biomass across all replicates with only cordgrass (i.e., treatment 1). For each tidal regime, I then subtracted these two means and divided the resultant value (denominator) into a tank-specific numerator as described before. These resulting quotients were then subtracted from one ($1 - \{[\text{predator effect} - \text{plant effect}] / [\text{snail effect} - \text{plant effect}]\}$) before being analyzed with model selection. All data were analyzed with R 2.10.1 (R Development Core Team 2008).

Survey of cordgrass, snails, sediment properties, and predator distributions

To determine whether the experimental results were consistent with natural marsh patterns, I surveyed seven sites along a tidal inundation gradient (400 km) in the northeastern Gulf of Mexico. Of these seven sites (Appendix A), three experience diurnal tides, and four experience mixed tides. In August 2010, I created a nested sampling design by demarcating two 50×20 m (long edge parallel to shoreline) areas of marsh at each site that were separated by at least 100 m. Within each marsh area, I then permanently established 20 nested plots (0.5×0.5 m) by haphazardly tossing a 0.5×0.5 m quadrat and inserting PVC posts into the ground at the corners of each plot.

Within each plot, I quantified the percentage of cordgrass cover as well as the maximum height of six randomly selected cordgrass plants. Using the average of these lengths and the length:biomass index, I

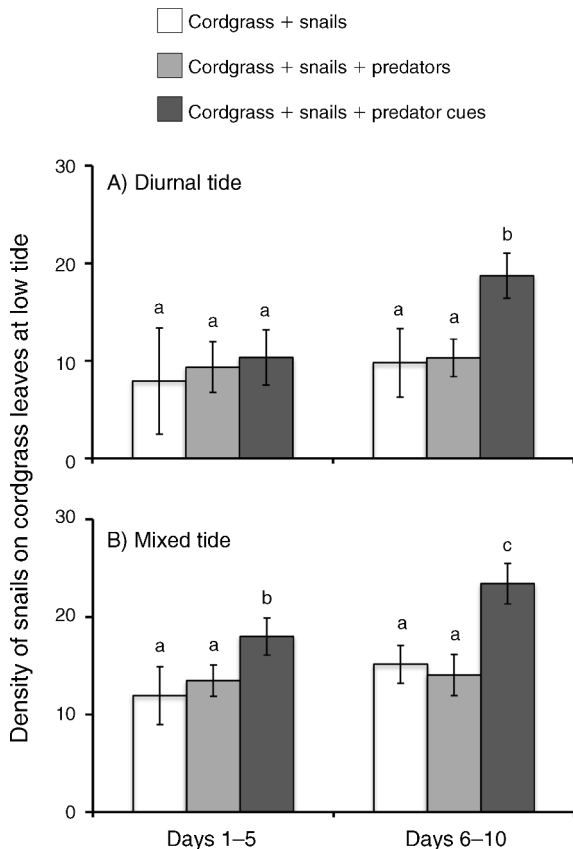


FIG. 1. In experimental tanks during ebb tide, in the northeastern Gulf of Mexico, the abundance of snails (mean with 95% CI) observed on *Spartina alternifolia* (cordgrass) leaves in (A) a diurnal tide and (B) a mixed semidiurnal tide for the first (days 1–5) and second (days 6–10) portions of the experiment. Different treatments include: cordgrass and snails (open bars); cordgrass, snails, and predators (gray bars); and cordgrass, snails, and predator cues (dark gray bars). Different lowercase letters above bars indicate significant difference between means (\pm 95% CI) at $P < 0.05$.

converted average length into a biomass estimate. I then multiplied this value by the percentage of cordgrass cover to estimate biomass for the larger plot. These six plants were tagged to prevent their remeasurement during subsequent sampling and were also measured for total length of snail scars (Silliman and Newell 2003). To standardize scar length data in each quadrat, I divided total scar length by the average height of the six plants. While snail scar length may not directly equate to herbivory, use of this metric has precedent in salt marsh systems (Silliman and Newell 2003) and my quantification of it on individual plants over time should strengthen its ability to represent herbivory. For tagged plants lacking scars, their change in length from March to July 2011 was used to examine plant growth independent of snail grazing. Snail density within a smaller quadrat (0.25×0.25 m) centered in each 0.5×0.5 m plot was also quantified.

Three additional variables sampled from each quadrat included: redox potential (5 cm depth), pore water salinity (5 cm depth), and C:N ratio of the second youngest leaf from one tagged plant. These data were collected because high pore water salinity can exacerbate the effects of snail grazing on cordgrass (Silliman et al. 2005) and low redox potential is a proxy for soil anoxia, which is associated with high H_2S concentrations and which negatively affects plants lacking compensatory mechanisms such as aerenchyma (Devai and Delaune 1995). Low C:N ratios in cordgrass leaves can enhance snail grazing (Silliman and Zieman 2001).

To estimate predator abundances, I deployed 10 baited crab traps along the long edge of each marsh area at the beginning of each marsh survey. The density of adult blue crabs captured in each trap was divided by deployment time (9–24 h) to correct for differences in sampling effort. Following the marsh surveys, crown conchs were quantified at each site by searching for them within 2 m of each marsh area's long edge (50 m).

All sampling was conducted in August 2010, October 2010, March 2011, and July 2011. Deviations from this sampling design included: (1) C:N samples were collected only in October; (2) redox and pore water salinity data from October were collected from only 10 quadrats per marsh area; (3) predators were not sampled in March 2011; (4) data from sites 2 and 3 in the mixed tidal regime were collected only in July 2011.

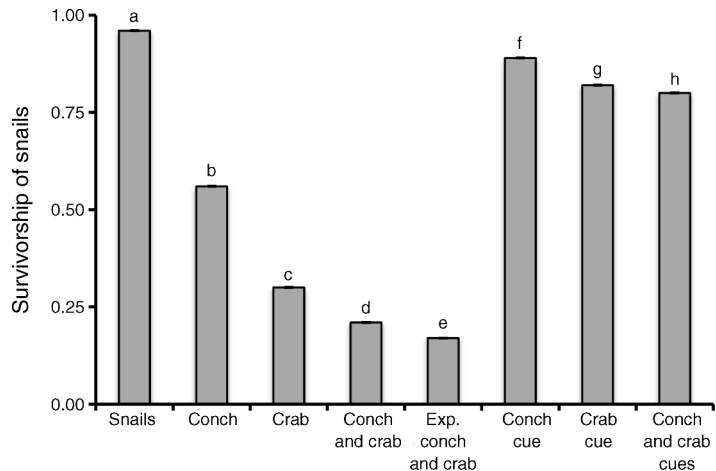
Data analysis for the survey.—The survey data on predators, snails, cordgrass, and abiotic conditions were individually analyzed by collapsing all data to the level of tidal regime (diurnal, $n = 3$; mixed, $n = 4$) and by averaging across time. Using univariate t tests, I then utilized these collapsed means to test whether the two tide regions differ in each of the response variables. To meet parametric assumptions, data concerning the abundance of conchs and snails were log-transformed while data on the abundance of snail scars were square-root transformed.

RESULTS

Tidal regime and predator experiment

Snail antipredator behavior.—Variation in snail antipredator behavior was best explained by a model with a three-way interaction among tidal regime, general status of predator, and portion of experiment (see Appendix C for results and plot of raw data). According to this model, in the diurnal tide, snails observed on plant leaves did not differ across the three types of predator treatments until the second portion of the experiment (AIC weight = 1.0; Fig. 1). At this time, more snails were observed on cordgrass leaves only when snails were exposed to predator cues. In the mixed tide, however, this effect of predator cue was observed in both the first and second portions of the experiment. In addition, predator cues and a mixed tide in the second portion of the experiment led to slightly more snails on cordgrass leaves. Finally, the presence and absence of a predator

FIG. 2. Survivorship of snails (mean with 85% CI) in predator treatments averaged over the diurnal and mixed semidiurnal tide. The expected multiplicative risk effect of a crab and conch on snail survivorship ("Exp. conch and crab") is also presented. Different lowercase letters above bars indicate significant differences between means at $P < 0.05$.



led to similar snail distributions on cordgrass leaves at low tide regardless of tidal regime and portion of the experiment.

Snail survivorship.—In this experiment, snail survivorship was best explained by a model distinguishing among predator treatments irrespective of tidal regime (AIC weight = 0.87; Appendix D; Fig. 2). Specifically, treatments with a conch and a crab reduced snail survivorship when compared to the no-predator and the predator-cue treatments, which were all >80%. The multiple-predator treatment reduced snail survivorship further, but to a lesser extent than expected based on snail survivorship with individual predators and the multiplicative risk model.

Cordgrass biomass.—Although the direct predator effects on snail behavior and survivorship were similar for each tidal regime, effects on cordgrass biomass were best described by a model with an interaction between tidal regime and predator treatment (AIC weight = 0.99; Appendix E, Fig. 3A). In both tidal regimes, the absence of predators did not cause snails to reduce the biomass of cordgrass to a level differing from zero (i.e., no change). But five of the six predator treatments in the diurnal tide caused a loss of cordgrass biomass (i.e., mean \pm error below zero), while five of the six predator treatments in the mixed tide caused a small gain or no change in cordgrass biomass. Because biomass changes in the cordgrass-only treatments were not statistically different, tank or tidal regime effects alone cannot explain the observed treatment differences. Instead of tank effects, an indirect effect index based on the model's fixed effects suggests that the influence of predators and their cues on snails in a mixed tide indirectly created either a positive or no effect on cordgrass (Fig. 3B). In contrast, the influence of predators and their cues on snails in a diurnal tide predominately (two-thirds of the treatments) created negative effects on cordgrass. When the same index was calculated with the observed data from predator treatments, model selection suggests that all predator treatments in a mixed tide caused a gain of

cordgrass biomass (mean \pm error above zero) while all predator treatments in a diurnal tide caused a loss of biomass (mean \pm error below zero; AIC weight = 0.54; Appendix E; Fig. 3B).

Field survey

Diurnal and mixed tide regions did not differ in the abundance of crown conchs, blue crabs, snails, and proportional growth of cordgrass (conch, $F_{1,5} = 3.24$, $P = 0.13$; crab, $F_{1,5} = 0.53$, $P = 0.50$; snail, $F_{1,5} = 0.48$, $P = 0.52$; plant growth, $F_{1,3} = 0.98$, $P = 0.40$; Fig. 4). These regions also did not differ in C:N ratio of cordgrass, pore water salinity, or redox potential of the sediment (C:N ratio, $F_{1,4} = 1.02$, $P = 0.37$; salinity, $F_{1,5} = 0.04$, $P = 0.85$; redox, $F_{1,5} = 0.04$, $P = 0.85$). These sites, however, did differ in snail grazing scars on cordgrass (scar, $F_{1,5} = 11.41$, $P = 0.02$) and estimated cordgrass biomass per quadrat (biomass, $F_{1,5} = 15.57$, $P = 0.01$), with lower grazing and higher biomass in the mixed tidal regime.

DISCUSSION

This study suggests that indirect predator effects on salt marshes can be beneficial or detrimental depending on the nature of tides. In the northeastern Gulf of Mexico, USA, I found that cordgrass inundated by a diurnal tide had more snail grazing scars and had less aboveground biomass than cordgrass inundated by a mixed tide (Fig. 4). This pattern was not related to variation in conspicuous top-down (predator and snail abundance), bottom-up (plant growth and C:N), or abiotic stress (salinity and redox) factors; rather, it appears to result from the foraging behavior of snails in response to predation risk. In an experiment with manipulated tidal regimes, predator cues induced snails to ascend cordgrass during high tide and to remain on cordgrass throughout low tide whether the tidal schedule was diurnal or mixed semidiurnal. In this predation refuge, however, snails subjected to predator cues and a diurnal tide increased their grazing of cordgrass, while snails subjected to predator cues and a mixed tide decreased their grazing of

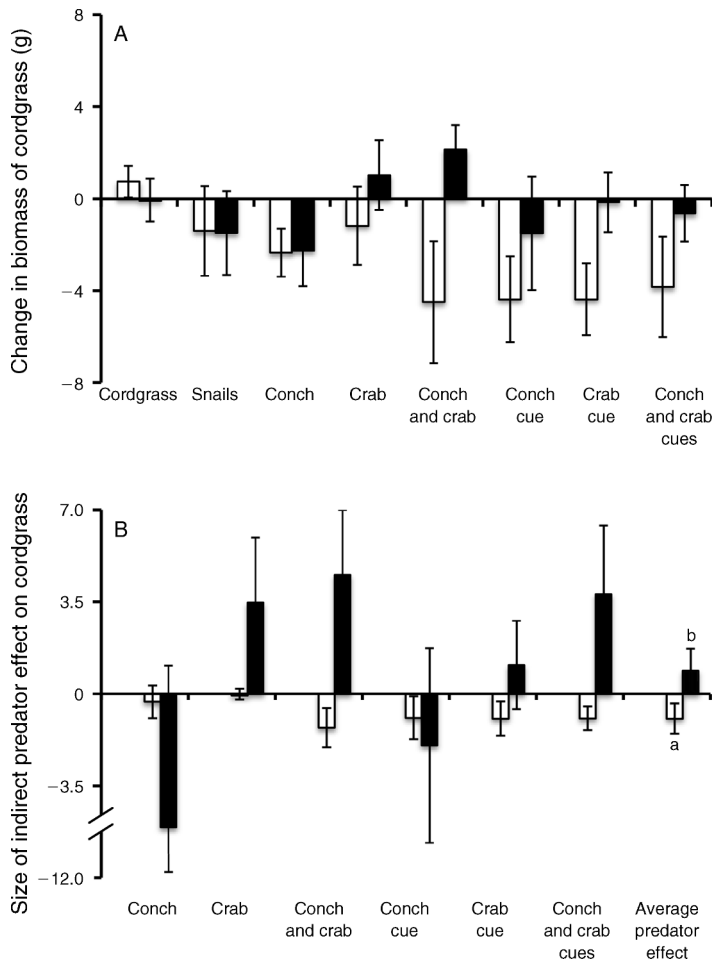


FIG. 3. (A) Change in cordgrass biomass (mean with 95% CI) for all combinations of the predator and tidal regime treatments for diurnal (open bars) and mixed (solid bars) tidal regimes in an outdoor laboratory experiment. (B) Indirect effect size (mean with 95% CI) of each predator treatment on cordgrass biomass (diurnal tide, open bars; mixed tide, solid bars) and indirect effect size averaged across predator treatments within each tidal regime (diurnal, open bar; mixed tide, solid bar). Different lowercase letters above bars indicate significant difference between means at $P < 0.05$.

cordgrass. Because these contrasting nonconsumptive effects (NCEs) were not altered by weak or strong reductions in snail survivorship (i.e., CEs), predator cues and tidal signals appear sufficient to create the divergent snail grazing patterns. Furthermore, the consistency of these NCEs at low snail survivorship levels indicates that snails may increase their foraging to compensate for stress-induced metabolic demand. Collectively, these data suggest that a large-scale cordgrass pattern is caused by a physical gradient (tidal regimes) reversing the outcome in how predatory NCEs cascade to cordgrass.

Given that snail density has been implicated in cordgrass losses throughout the southeast Atlantic coast (Silliman and Bertness 2002), it is worth considering why predatory CEs and resultant changes in snail density failed to influence cordgrass in my study. But before doing so, I first acknowledge that my surveys did not detect the high densities of snails (e.g., 400–700 snails/m²) that have been implicated in cordgrass losses of southeast Atlantic marshes (Silliman et al. 2005), nor did I experiment with high snail densities. At high densities, crowding on cordgrass may inhibit the antipredator behavior of snails in which they ascend and descend cordgrass with each

high and low tide, respectively (Dix and Hamilton 1993). If crowding causes many snails to remain on cordgrass leaves throughout low tide and thereby inhibits their foraging on benthic algae and/or detritus, then crowding may cause snails to overgraze cordgrass. Thus, at high snail densities, predatory CEs should alleviate overgrazing (as originally proposed by Silliman and Bertness [2002]) by reducing crowding and allowing snails to balance the risk of predation with the benefit of consuming benthic resources via their tidal migration behavior.

While predators may help maintain snail migration behavior at high snail densities and with the semidiurnal tide of the Atlantic coast, this predator-avoidance strategy was evidently disrupted by predatory NCEs when snail densities were moderate in the current study: Snails remained on cordgrass leaves throughout low tide (Fig. 1). The disruption of snail behavior, however, created diverging indirect effects in that it stimulated snail grazing in the diurnal tide but suppressed snail grazing in the mixed tide (Fig. 3B). Interestingly, these opposing indirect effects were unmodified by a weak CE due to conch predation or a strong CE due to an emergent MPE between the crab and conch that was slightly weaker than

expected (i.e., risk reduction; Sih et al. 1998). A partial explanation of why CEs failed to influence how predators indirectly affected cordgrass may come from a recent experiment demonstrating that the fear of predators metabolically increases energy needs and feeding rates of prey (Hawlena and Schmitz 2010).

Because fear of predators could have increased snail feeding rates in the current study and because predators positively benefited cordgrass along the southeast Atlantic coast in another study (Silliman and Bertness 2002), I hypothesize that predator cues in the diurnal tide of my experiment were present for sufficient time to both increase snail metabolic rates and restrict snails to cordgrass leaves throughout low tide. I also hypothesize that predator cues were sufficiently absent each day in the diurnal tide so that the restricted snails had enough time and leaf space (relative to water level) to respond to the fear of predation and the ensuing need of additional energy by grazing more cordgrass. Although predator cues in the mixed tide were also sufficiently present to restrict snails to cordgrass leaves throughout low tide, the short duration of the low tide and corresponding absence of predator cues may have provided insufficient time and leaf space for snails to graze more cordgrass. Overall, my results suggest that linkages among fear, metabolic rates, and compensatory feeding rates of prey depend on how often and how long the environment exposes prey to predation threats.

The experiment in this study contains several limitations. First, I manipulated predators so that snails were exposed to a predation threat with each high tide. But because blue crabs are highly mobile (Lenihan et al. 2001), blue crabs and their cues may not affect snails of a given marsh location with every high tide. Although I minimized this artifact by removing blue crabs at low tide, I likely created “press” effects in which snails were overexposed to predator cues (Bender et al. 1984, Lima and Bednekoff 1999). While undoubtedly present, this press effect should not alter the interpretation of results given that cues of both predators equally affected snail behavior and snail grazing on cordgrass. Because crown conchs are consistently abundant in Gulf coast marshes and even remain in the marsh at low tide, snails in natural marshes are probably exposed to the threat of predation (whether by crab or conch) with each high tide.

The second limitation of the experiment concerns the manner in which tidal regimes were manipulated each day. Unlike the experimental inundations, natural tidal inundations along this coast exhibit substantial spatial and temporal variation in frequency, duration, and depth. These three tidal components may interact to change snail exposure to predators and subsequently the relative strength of CEs and NCEs on cordgrass. Recently, a similar interaction between the components of water flow (i.e., velocity and turbulence) was shown to have complex effects on how the European green crab (predator) nonconsumptively affected snails (prey;

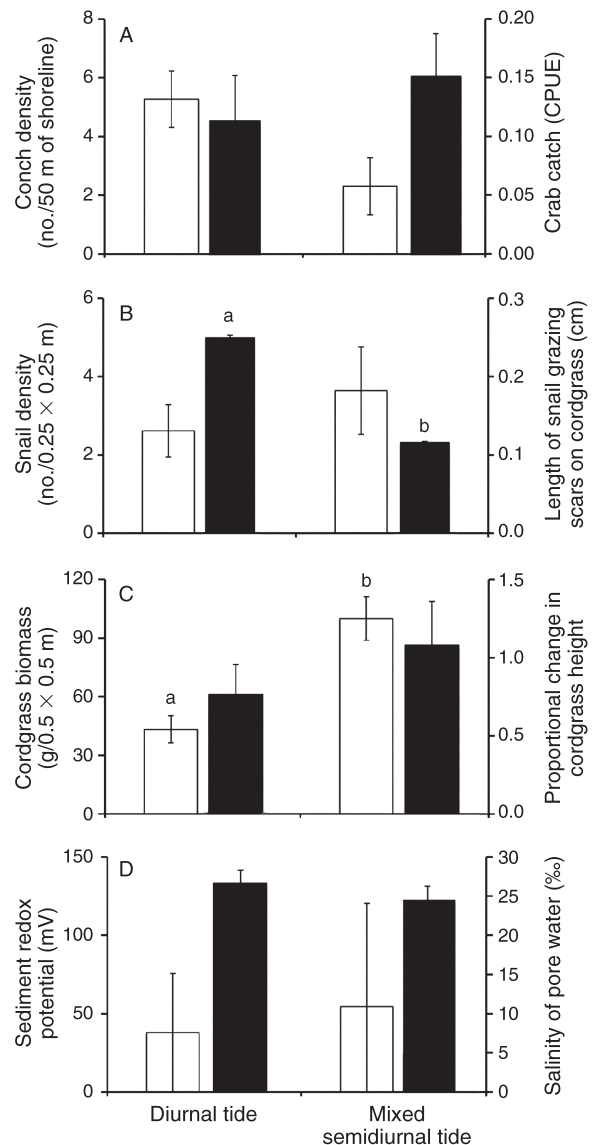


FIG. 4. For sites with diurnal and mixed semidiurnal tides, (A) the density of crown conchs (open) and blue crabs (solid); (B) the density of snails (open) and the length of grazing scars on cordgrass (solid); (C) estimated cordgrass biomass (open) and proportional change in height, which was originally measured in cm (solid); (D) the redox potential of sediment (open) and salinity of pore water (solid). Crab catch per unit effort (CPUE), measured as crab density per hour, corrects for the different duration of deployment among the traps. All values are shown as mean \pm SE; lowercase letters above bars indicate significant difference between means at $P < 0.05$.

Large et al. 2011). Thus, in the presence of predator cues, future experiments should test how combinations of tidal components affect snail grazing on cordgrass.

A third limitation concerns the linkage between the experimental and survey results because a field experiment in Virginia demonstrated that modest snail



PLATE 1. Snail (*Littoraria irrorata*) climbing a marsh plant to avoid the predatory crown conch (*Melongena corona*) in the northeast Gulf of Mexico, USA. Photo credit: Tanya Rogers.

densities impact cordgrass by suppressing growth over several months rather than by reducing biomass over a few weeks (Silliman and Zieman 2001). This result suggests that my laboratory experiment promoted short-term impacts on cordgrass biomass over longer-term impacts on growth. It is reasonable, however, to expect that the predator mechanisms in my experiment could have helped produce the striking field pattern of cordgrass by causing spatial variation in cordgrass growth over time. But at the same time, interannual variation and long-term anomalies in sea level (independent of snail grazing) can account for annual variation in primary production of marshes along the Atlantic coastline (Morris et al. 2002). Thus, variation in tidal inundation may solely explain why growth of plants lacking snail scars was 30% less in the diurnal regime than in the mixed-tidal regime (Fig. 4C). Still, this differential growth does not account for the larger discrepancy (60%) in aboveground biomass between the two tidal regimes. As a result, future field experiments are needed not only to test the falsifiable hypothesis that snails help cause the field pattern of cordgrass, but also to determine whether snails create this pattern through the loss of cordgrass biomass and/or suppression of cordgrass growth.

In addition to limitations, my study has two strengths. First, CE/NCE-predator experiments have been criticized for creating “pressed” results by constantly exposing prey to predators (Bender et al. 1984, Lima and Bednekoff 1999). By simulating tidal regimes and removing predators according to their natural history, I minimized this artifact. Second, ecological communities contain multiple-predatory species with unique foraging strategies that may interactively determine how predatory CEs and NCEs impact prey. While I did not consider a diversity of larger predators such as alligators (Keddy et al. 2009) and birds (Ellis et al. 2007) that likely consume and alter the behavior of blue crabs and conchs, I did consider a community of the most conspicuous species in Gulf marshes that provides a useful compromise between the study of oversimplified predator–prey communities, which facilitate analysis, and whole communities, which can defy mechanistic analysis (Paine 1963). By considering the complex yet tractable details of this salt marsh community, I devised manipulative experiments that tested for CEs vs. NCEs across a dominant environmental gradient, revealing in this manner unanticipated and far-reaching aspects of community dynamics associated with predator–prey interactions and their effects on basal trophic levels.

In conclusion, multiple predators have various effects on prey that can indirectly propagate throughout food webs to differentially influence important ecosystem functions (Schmitz 2008, Trussell et al. 2008). The effect of the environment on these indirect predator effects has seldom been related to spatial patterns in natural systems. This paucity of examples is understandable given the numerous factors that have been shown to determine the nature of indirect predator effects in controlled systems. But just as seminal experiments were conducted to disentangle how predation, competition, and facilitation create patterns in rocky intertidal systems, complex predator effects in diverse and multitrophic systems will be understood better through further experimentation across environmental stress gradients.

ACKNOWLEDGMENTS

I thank M. Bertness, E. Grosholz, J. Grabowski, D. Grubbs, W. Herrnkind, R. Hughes, B. Inouye, B. Jaffee, B. Silliman, C. Stallings, G. Trussell, W. White, and anonymous reviewers for comments that improved this manuscript. N. Calhoun, M. Daniels, H. Garland, B. Henderson, C. Martinez, E. Pettis, T. Rogers, S. Seip, L. Sheldon, D. Tinsley, and R. Zerebecki generously provided field and laboratory assistance. Funding for this study was provided by the Northern Gulf Institute (award no. 069200-540-02885).

LITERATURE CITED

Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *American Naturalist* 146:112–134.

- Barlocher, F., and S. Y. Newell. 1994. Phenolics and proteins affecting palatability of *Spartina* leaves to the gastropod *Littoraria irrorata*. *Marine Ecology* 15:65–75.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65:1–13.
- Berlow, E. L., J. A. Dunne, N. D. Martinez, P. B. Stark, R. J. Williams, and U. Brose. 2009. Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences USA* 106:187–191.
- Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80:2711–2726.
- Bourdeau, P. E. 2009. Prioritized phenotypic responses to combined predators in a marine snail. *Ecology* 90:1659–1669.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–639.
- Carr, J. M., and S. L. Lima. 2010. High wind speeds decrease the responsiveness of birds to potentially threatening moving stimuli. *Animal Behaviour* 80:215–220.
- Clements, F. E. 1936. Nature and structure of the climax. *Journal of Ecology* 24:252–284.
- Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of barnacle *Balanus balanoides*. *Ecological Monographs* 31:61–71.
- Devai, I., and R. D. Delaune. 1995. Formation of volatile sulfur compounds in salt marsh sediment as influenced by soil redox condition. *Organic Geochemistry* 23:283–287.
- Dix, T. L., and P. V. Hamilton. 1993. Chemically mediated escape behavior in the marsh periwinkle *Littoraria irrorata* Say. *Journal of Experimental Marine Biology and Ecology* 166:135–149.
- Ellis, J. C., M. J. Shulman, M. Wood, J. D. Witman, and S. Lozyniak. 2007. Regulation of intertidal food webs by avian predators on New England rocky shores. *Ecology* 88:853–863.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185:1058–1060.
- Hamilton, P. V. 1996. Tidal movement pattern of crown conchs, *Melongenella corona* Gmelin. *Journal of Molluscan Studies* 62:129–133.
- Hawlena, D., and O. J. Schmitz. 2010. Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences USA* 107:15503–15507.
- Hovel, K. A., A. Bartholomew, and R. N. Lipcius. 2001. Rapidly entrainable tidal vertical migrations in the salt marsh snail *Littoraria irrorata*. *Estuaries* 24:808–816.
- Keddy, P. A., L. Gough, J. A. Nyman, T. McFalls, J. Carter, and J. Siegrist. 2009. Alligator hunters, pelt traders, and runaway consumption of Gulf coast marshes: a trophic cascade perspective on coastal wetland losses. Pages 115–136 in B. Silliman, E. Grosholz, and M. Bertness, editors. *Human impacts on salt marshes: a global perspective*. University of California Press, Berkeley and Los Angeles, California, USA.
- Large, S. I., D. L. Smee, and G. C. Trussell. 2011. Environmental conditions influence the frequency of prey responses to predation risk. *Marine Ecology Progress Series* 422:41–49.
- Lenihan, H. S., C. H. Peterson, J. E. Byers, J. H. Grabowski, G. W. Thayer, and D. R. Colby. 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecological Applications* 11:764–782.
- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* 153:649–659.
- Lima, S. L., and L. M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599–619.
- Morris, J. T., P. V. Sundareshwar, C. T. Nietch, B. Kjerfve, and D. R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83:2869–2877.
- Moyle, P. B., and J. F. Mount. 2007. Homogenous rivers, homogenous faunas. *Proceedings of the National Academy of Sciences USA* 104:5711–5712.
- Navarrete, S. A., and B. A. Menge. 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecological Monographs* 66:409–429.
- Paine, R. T. 1963. Trophic relationships of eight sympatric predatory gastropods. *Ecology* 44:63–72.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–73.
- Payton, M. E., M. H. Greenstone, and N. Schenker. 2003. Overlapping confidence intervals or standard error intervals: What do they mean in terms of statistical significance? *Journal of Insect Science* 3:34.
- Peterson, B. J., and R. W. Howarth. 1987. Sulfur, carbon, and nitrogen isotopes used to trace organic matter flow in the salt-marsh estuaries of Sapelo Island, Georgia. *Limnology and Oceanography* 32:1195–1213.
- Preisser, E. L., D. I. Bolnick, and J. H. Grabowski. 2009. Resource dynamics influence the strength of non-consumptive predator effects on prey. *Ecology Letters* 12:315–323.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>
- Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* 319:952–954.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7:153–163.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* 13:350–355.
- Silliman, B. R., and M. D. Bertness. 2002. Atrophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences USA* 99:10500–10505.
- Silliman, B. R., and S. Y. Newell. 2003. Fungal farming in a snail. *Proceedings of the National Academy of Sciences USA* 100:15643–15648.
- Silliman, B. R., J. van de Koppel, M. D. Bertness, L. Stanton, and I. Mendelsohn. 2005. Drought, snails, and a large-scale die-off of southern U.S. salt marshes. *Science* 310:1803–1806.
- Silliman, B. R., and J. C. Zieman. 2001. Top-down control of *Spartina alterniflora* production by snail grazing in a Virginia salt marsh. *Ecology* 82:2830–2845.
- Smee, D. L., M. C. Ferner, and M. J. Weissburg. 2008. Alteration of sensory abilities regulates the spatial scale of nonlethal predator effects. *Oecologia* 156:399–409.
- Smee, D. L., and M. J. Weissburg. 2006. Clamming up: environmental forces diminish the perceptive ability of bivalve prey. *Ecology* 87:1587–1598.
- Stapp, P., and G. A. Polis. 2003. Influence of pulsed resources and marine subsidies on insular rodent populations. *Oikos* 102:111–123.
- Sullivan, M. J., and C. A. Moncreiff. 1990. Edaphic algae are an important component of salt marsh food-webs: evidence

- from multiple stable isotope analyses. *Marine Ecology Progress Series* 62:149–159.
- Trussell, G. C., P. J. Ewanchuk, and C. M. Matassa. 2008. Resource identity modifies the influence of predation risk on ecosystem function. *Ecology* 89:2798–2807.
- Trussell, G. C., and M. O. Nicklin. 2002. Cue sensitivity, inducible defense, and trade-offs in a marine snail. *Ecology* 83:1635–1647.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100.
- Whittaker, R. 1956. Vegetation of the great Smoky Mountains. *Ecological Monographs* 26:1–69.
- Wilber, T. P., and W. Herrnkind. 1982. Rate of new shell acquisition by hermit crabs in a salt-marsh habitat. *Journal of Crustacean Biology* 2:588–592.

SUPPLEMENTAL MATERIAL

Appendix A

Map of survey sites along the northeastern Gulf of Mexico, USA (*Ecological Archives* E093-032-A1).

Appendix B

A summary of experimental data concerning predator cue strength and snail behavior across all treatments (*Ecological Archives* E093-032-A2).

Appendix C

Model selection summary for analysis of snail behavior (*Ecological Archives* E093-032-A3).

Appendix D

Model selection summary for analysis of snail survivorship (*Ecological Archives* E093-032-A4).

Appendix E

Model selection summary for analysis of indirect predator effects on cordgrass (*Ecological Archives* E093-032-A5).