

Non-consumptive predator effects intensify grazer–plant interactions by driving vertical habitat shifts

Andrew Davidson¹, John N. Griffin^{2,*}, Christine Angelini³, Felicia Coleman⁴,
Rebecca L. Atkins⁵, Brian R. Silliman⁶

¹Department of Biological Science, Florida State University, Tallahassee, Florida 32306, USA

²Department of Biosciences, Swansea University, Singleton Park, SA2 8PP, Wales, UK

³Environmental Engineering Science, Engineering School for Sustainable Infrastructure and Environment, University of Florida, Gainesville, Florida 32611, USA

⁴Coastal and Marine Laboratory, Florida State University, St. Teresa, Florida 32358, USA

⁵Odum School of Ecology, University of Georgia, Athens, Georgia 30602, USA

⁶Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, Beaufort, North Carolina 28516, USA

ABSTRACT: Predators non-consumptively induce prey habitat shifts, driving trait-mediated indirect interactions (TMII) with basal resources. Whether prey seek refuge within or avoid predator-containing patches determines the spatial re-distribution of prey and influences the nature of resulting TMII. In a southeastern US salt marsh, we tested how 2 species of sit-and-wait benthic predatory crab non-consumptively affect the habitat choices of grazing snails and how the resultant behavior affects cordgrass health. We first observed that snails climb higher on cordgrass around naturally occurring crab burrows and that this habitat shift corresponds with increased cordgrass leaf damage, suggesting a localized TMII. Then, by adding caged crabs to artificial burrows in the field, we found causative evidence that both crab species could drive snails upwards to the cordgrass canopy, thereby increasing leaf damage within a ~12 cm radius, but found no evidence that experimentally added crabs induce horizontal dispersal of snails. Next, in a marsh undergoing die-off, we added caged crabs to remnant cordgrass patches being rapidly colonized by snails. Crabs did not affect the rate of snail colonization of remnant patches, but did drive snails upwards once they had colonized a patch, suggesting snails do not preferentially avoid—but do alter how they locally utilize—patches of cordgrass in marsh die-off contexts. Our documentation of the spatial-scale and dimensionality of TMII in the field paves the way for spatially explicit models of this interaction. More generally, our results suggest that TMII may be consistent, predictable and tractable, lending themselves to incorporation into food-web models.

KEY WORDS: *Littoraria* · Marsh periwinkle · Non-consumptive effect · Salt marsh · *Spartina alterniflora* · Trait-mediated indirect effect · Trophic cascade

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INTRODUCTION

Predators can indirectly affect the biomass and persistence of plants by regulating the density and/or traits of intermediate consumers. Such 'trophic cas-

cases' have ecosystem-structuring effects across diverse systems, including kelp forests, rivers, grasslands, and rainforests (Pace et al. 1999, Schmitz et al. 2000, Terborgh & Estes 2010). Cascading effects of predators were traditionally attributed to their con-

sumptive effects on prey density (Hairston et al. 1960, Estes et al. 1978, Paine 1980, Oksanen et al. 1981). However, predators also non-consumptively induce shifts in prey traits (e.g. morphology, behaviour), which in turn affect prey interactions with their basal resources, driving 'trait-mediated indirect interactions' (TMIIs; Werner & Peacor 2003).

Prey commonly respond to the presence of predators—particularly sit-and-wait or sit-and-pursue predators—by shifting their location to limit predation risk (Schmitz et al. 2004). Prey can avoid a predator-containing area or patch (e.g. Fraser & Cerri 1982, Forrester 1994) by moving horizontally (across a landscape), which tends to reduce prey density and associated impacts within the vicinity of predators (e.g. Bertness & Coverdale 2013, Schmitz et al. 2004, Schmitz 2008). Alternatively, they can remain in predator-containing patches and seek refuge through small-scale (microhabitat) shifts, which often involve vertical movements such as climbing vegetation (Griffin et al. 2011), burrowing (Zhao et al. 2013), or sheltering under biogenic structures (Grabowski & Kimbro 2005). In this case, the broader landscape distribution of prey (from an aerial perspective) will remain relatively unaltered, although basal species may still be affected (positively or negatively) if impacts of prey are modified via TMIIs (Schmitz et al. 2004). Experimental studies that focus only on local effects without simultaneously evaluating the type and scale of prey dispersal decisions can bias estimates of TMIIs (Geraldi & Macreadie 2013). However, rarely are these broad-scale and localized dispersal patterns evaluated together.

In extensive salt marshes of the southeastern US coast, periwinkle snails *Littoraria irrorata* impose top-down control on the dominant grass *Spartina alterniflora*, cordgrass (Silliman & Zieman 2001, Atkins et al. 2015). Periodically, under drought conditions, these consumers trigger marsh die-offs, converting cordgrass stands to extensive mudflats. Subsequently, they form high-density grazing fronts along mudflat-cordgrass borders that further expand marsh die-offs (Silliman et al. 2005). Snails, in turn, are subject to predation risk from nektonic predators associated with the rising tide (Silliman & Bertness 2002) as well as from resident predatory crabs that remain on the marsh platform throughout the tidal cycle (Griffin et al. 2011, Soomdat et al. 2014). Snails climb higher on cordgrass to escape the rising tide and associated predation risk (Vaughn & Fisher 1992, Hovel et al. 2001, Kimbro 2012) and remain in elevated positions in the cordgrass canopy throughout

the tidal cycle in the presence of 2 species of resident predatory mud crab, *Panopeus obesus* and *Eurytium limosum* (Griffin et al. 2011). This localized microhabitat-shift from the benthos and heavily sheathed lower stems to the cordgrass canopy effectively reduces the predation risk of snails (Hovel et al. 2001). However, it also likely reduces snail access to nutritious benthic microalgae and detritus (Haines 1977, Sullivan & Moncreiff 1990, Moens et al. 2002) and has been shown to increase their grazing effects on the relatively vulnerable canopy leaves (Griffin et al. 2011, Kimbro 2012).

Previous experiments examining the behavioral responses of snails to predators and the consequences for cordgrass have restricted horizontal movement of snails by using enclosures (Griffin et al. 2011, Kimbro 2012). These studies also only evaluated these interactions in healthy marshes, overlooking that predator impacts on prey behavior may differ in marsh die-off conditions where snails are migrating horizontally across the marsh surface and reaching high densities in remnant cordgrass patches (Silliman et al. 2005). Further, despite the 2 resident predatory crabs, *Panopeus* and *Eurytium*, exhibiting seasonally dependent differences in predation rates (Griffin & Silliman 2011), previous experiments evaluated only the combined effects of these predators (Griffin et al. 2011) rather than species-specific effects on the TMII.

In this study, we demonstrate the intrinsic value of evaluating habitat shifts along multiple spatial dimensions simultaneously to clarify the extent of TMII effects. We used experiments in a southeastern US salt marsh to test how predatory mud crabs, and their species identity, influence snail vertical and horizontal habitat shifts and grazing impacts on cordgrass in both healthy and die-off contexts. We specifically hypothesized that snails would respond through spatial habitat shifts in 1 of 2 ways, with different consequences for plants: (1) by making vertical habitat shifts to the vulnerable canopy leaves, thereby increasing their impacts on cordgrass while leaving their density unchanged in the vicinity of predators; or (2) by making horizontal habitat shifts, thereby reducing their density and associated impacts on cordgrass in the vicinity of predators. We also hypothesized that these responses would depend on the species of mud crab predator. We evaluated the above hypotheses under 2 ecosystem-states: in healthy, cordgrass-dominated marshes with intermediate snail densities, and in cordgrass patches remaining within recently formed mudflats with high densities of snails.

MATERIALS AND METHODS

We worked at Airport marsh (31° 39' N, 81° 27' W) and Lighthouse marsh (31° 23' N, 81° 16' W) in the Sapelo Island National Estuarine Research Reserve, Georgia, USA. We focused on the short-form cordgrass zone, where snails occur at their highest densities within the marsh (Silliman et al. 2005). In this short zone, mud crabs concentrate on ribbed mussel *Geukensia demissa* mounds (Angelini et al. 2015), but they are not exclusively associated with mussels (Silliman et al. 2004).

Survey of natural crab burrows

We conducted field surveys across Airport and Lighthouse marshes to investigate whether there was any association between naturally occurring mud crabs (*Eurytium limosum* and *Panopeus obesus*), snail behavior, and cordgrass health. To locate mud crab burrows, we walked within the short zone and visually scanned the benthos. We located 10 (400 cm²; 20 × 20 cm) widely dispersed (separated by >25 m) plots in the open marsh, in the center of which was a single occupied mud crab burrow (~10 cm²) within a cordgrass monoculture. We also located 10 randomly chosen control plots without mud crabs within 2 to 3 m of each burrow within the short zone. We then measured snail climbing heights (random sub-sample of 3 snails per stem), the number of snails on the benthos, and the length of snail grazing scars (radulations; sensu Silliman & Zieman 2001) on 5 randomly selected cordgrass stems in each of the 20 plots. Within this survey, we did not distinguish between mud crab species or measure total snail density.

Experiment 1: effects of predatory mud crabs in healthy salt marsh

To isolate cause-and-effect relationships between mud crabs, snails, and cordgrass, test for predator identity effects, and describe the spatial extent of species interactions, we manipulated the presence/absence of each mud crab species using experimental cages in the field at Airport marsh. We marked twelve 1 m² plots in the short zone. In the center of each plot, we installed a wire mesh cylindrical cage (4 cm diameter × 20 cm height, 1 cm mesh; for photo, see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m537p049_supp.pdf). Each plot was

randomly assigned 1 of 3 treatments: cages with no crab, cages with *Panopeus* present, or cages with *Eurytium* present (n = 4 replicates per treatment). All crabs used measured between 30 and 36 mm carapace width.

To prevent desiccation stress to crabs and mimic natural burrow conditions, we sunk each cage 15 cm into the marsh substrate and surrounded each with oyster shells to provide shade. Crabs were fed 3 crushed snails every week throughout the duration of the experiment. Cues from crushed snails may contribute to non-consumptive effects of predatory crabs on snails; we therefore consider these snail cues as an indirect effect of crab presence and do not attempt to untangle effects of crab presence per se from these cues.

To facilitate measurement of snail climbing and density responses as well as the spatial extent of any responses, we created 40 cm long transects along the 4 cardinal directions from the cage using bamboo shoots (0.5 cm diameter × 30 cm height) to mimic cordgrass stems, positioning them upright at 2.5 cm intervals along each transect, for a total of 17 shoots in each direction (See Fig. S1 in the Supplement). Snails did not show a preference for climbing bamboo over cordgrass, or vice versa (for comparison, see Fig. S1 in the Supplement). We maintained these plots and took data over 6 wk during June and July 2012.

We measured the climbing height of every snail observed on each bamboo shoot during low tide twice weekly over the first 2 wk of the experiment (4 times in total). We then calculated an average snail height for each distance away from the cage (across the 4 cardinal directions and 4 sampling occasions) for each plot. To estimate horizontal shifts in snail distribution, we placed a 5 cm × 10 cm quadrat flat on the mud between successive pairs of bamboo shoots (i.e. 0 to 5 cm, 5 to 10 cm, etc) along each of the 4 transects in each plot and, in each quadrat, counted the number of snails on the mud, number of snails on the bamboo shoots, and total number of snails. These data were collected at the same time as the snail height data (4 times in total), and a single average was calculated for each distance. They were used to investigate 2 aspects of snail anti-predator response: habitat shift from the benthos to the cordgrass stems, and habitat shift horizontally across the substrate away from the crabs. Although we did not track movement of individuals, we assumed that a reduction in density relative to controls indicated a net horizontal shift (dispersal) of snails away from predators.

To estimate whether changes in snail distribution induced by the caged-predator treatments generated

spatial variation in grazing intensity on cordgrass, we measured the length of snail grazing scars (radulations) on a spatially explicit basis. We first established a baseline for each plot by measuring radulations on 5 haphazardly selected cordgrass stems per plot. Then, after 6 wk, we repeated measurements of radulations, accounting for distance by measuring damage on stems within 5 cm × 10 cm quadrats positioned between bamboo shoots (as with the snail distribution data). We then averaged radulation damage for each distance and subtracted from it the average initial damage for each plot to obtain an average net level of radulation damage across distance for each plot.

Experiment 2: effects of predatory mud crabs under salt marsh die-off conditions

At the time of this study, marshes at our study sites were still experiencing the effects of the extreme 2009–2011 regional drought (Georgia Coastal Ecosystems Long-Term Ecological Research Station meteorological data portal: www.gce-lter.marsci.uga.edu/portal) and were undergoing marsh die-off (see Silliman et al. 2005). We observed high densities of snails on isolated, remnant cordgrass stems toward the edges of expanding die-offs in our study sites. Within these die-offs, we performed 2 experiments simultaneously, which we describe below.

Experiment 2A

To assess the effects of mud crabs on snail vertical habitat shifts and resulting effects on cordgrass leaves (as in Experiment 1), we identified isolated cordgrass stems along the edge of a die-off in Airport marsh and randomly assigned each 1 of 3 treatments: no adjacent cage, an empty adjacent cage, or an adjacent caged crab ($n = 6$ per treatment). As in Experiment 1, we used wire-mesh cylindrical cages sunk ~15 cm into the marsh surface. The cages were placed directly adjacent to the isolated cordgrass stem (see Fig. S2 in the Supplement), and a mud crab predator (30 to 36 mm carapace width) was introduced to each cage. Note that we used *Panopeus* and *Eurytium* indiscriminately here because results from Experiment 1 indicated that snails responded similarly to both species (see 'Results'). As in Experiment 1, snails were left undisturbed at their naturally occurring density (i.e. none were added or removed). To assess treatment effects, we measured snail climbing heights twice weekly over the initial 2 wk

during low tide (then averaged by stem) and measured net grazing damage (relative to initial damage on each stem), as well as final snail density after 4 wk. This experiment ran mid-July to mid-August 2012.

Experiment 2B

We ran this shorter experiment (4 d) simultaneously at the same site using the same treatments to assess the rate at which snails accumulate on remnant cordgrass stems (patch-colonization decisions). In this case, after counting the naturally occurring number of snails on each stem, we removed all snails from all stems (relocating them >20 m from the die-off in a healthy marsh area) and monitored the subsequent accumulation of snails on each stem over 4 d.

Statistical analysis

All statistical analyses were performed using the statistical program R (R Development Core Team 2014). For all analyses, we checked for violations of model assumptions by plotting the standardized residuals and visually assessing homoscedasticity and normality.

Survey

We compared values of response variables in natural areas with predatory crabs vs. adjacent control areas (lacking predatory crabs). Specifically, we used *t*-tests to assess differences in snail climbing height and the amount of grazing damage on cordgrass plants; and we used a generalized linear model (GLM) with Poisson error distribution to assess differences in (total density of snails the benthos).

Experiment 1

To examine how predatory crabs influenced snail climbing height (vertical habitat shift), and the spatial extent of this effect, we used a linear mixed effects model (LMM), within the R package nlme (Pinheiro et al. 2015). Crab treatment was a fixed factor with 3 levels (no crab control, *Panopeus*, or *Eurytium*), distance (natural logarithm transformed to linearize effects) a continuous covariate, and plot a random factor (to account for multiple distance measures within same plot).

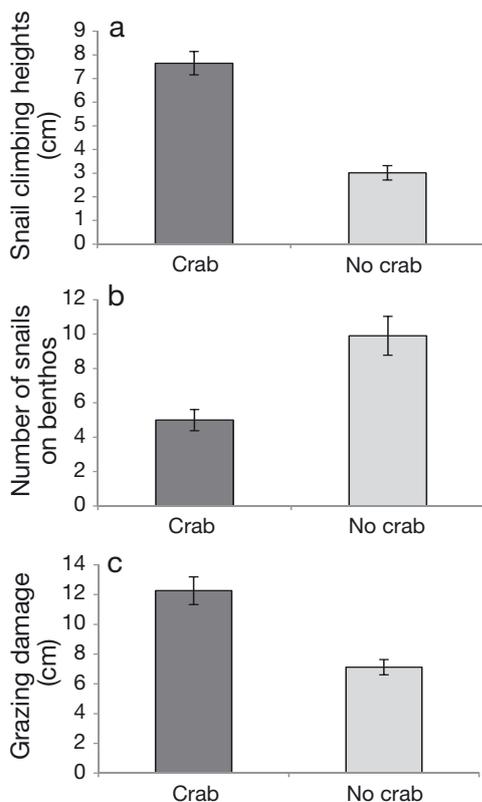


Fig. 1. Association between predatory crab presence, snail behaviour and cordgrass leaf damage as revealed by a survey in natural salt marshes. Shown are (a) snail climbing heights, (b) number of snails on the benthos and (c) snail grazing damage in the area immediately surrounding an occupied crab burrow as compared to adjacent control areas without crab burrows. Bars represent mean values \pm SE

To examine the effect of predatory crabs on (1) mean number of snails remaining on the benthos, (2) mean total snail density, and (3) net grazing damage at increasing distances from the center of the plots, we again used LMMs with a similar structure as above but with distance as a categorical variable (4 levels: 0–5, 5–10, 10–15, and 15–20 cm). On each LMM, we used analysis of variance (ANOVA) to examine the treatment effects. We further used multiple comparison tests via R's multcomp package (Hothorn et al. 2014) to evaluate differences between particular coefficients.

Experiment 2

To examine the effect of predatory crabs on (1) snail climbing heights and (2) net grazing damage on cordgrass, we used an ANOVA with treatment (control plots with no cage, control plots with empty

cages, or caged crabs) as a fixed factor (followed by a Tukey test). We used GLM with binomial error distribution to examine effects of predatory crabs on (3) proportion of initial snail density after 4 d of recovery in plots that had been subjected to snail removal and (4) proportion of initial snail density at the end of the experiment in plots not subjected to snail removal.

RESULTS

Survey of natural crab burrows

In the presence of predatory mud crab burrows, snails appeared to avoid the benthos ($\chi^2 = 19.343$, $p < 0.001$), climb higher on cordgrass plants (Treatment: $F_{1,18} = 63.451$, $p < 0.001$), and increase grazing activity on cordgrass leaves (Treatment: $F_{1,18} = 20.698$, $p < 0.001$) relative to the surrounding marsh area in which mud crab burrows did not occur (Fig. 1; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m537p049_supp.pdf).

Experiment 1

Snail climbing height on cordgrass varied with treatment and with distance from the center of the plot (the y-axis intercept on Fig. 2a, where the cage was located). Snails climbed significantly higher in treatments containing a predatory crab than in control plots (Treatment: $F_{2,9} = 11.832$, $p < 0.003$) regardless of species identity (*Eurytium* vs. control: $t_9 = 7.481$, $p < 0.0001$; *Panopeus* vs. control, $t_9 = 7.284$, $p < 0.0001$).

Snail climbing heights decreased with distance from the crab cage (overall: $\ln(\text{Distance} + 1)$: $F_{2,93} = 25.082$, $p < 0.0001$) but only if the cage contained a predatory crab (*Panopeus* \times $\ln(\text{Distance} + 1)$: $t_{93} = -5.986$, $p < 0.001$; *Eurytium* \times $\ln(\text{Distance} + 1)$: $t_{93} = -6.271$, $p < 0.001$). The decline in height with distance from caged predators varied little with the identity of the predatory crab (planned contrast: *Panopeus* vs. *Eurytium*: $Z = -0.285$, $p = 0.775$). Accordingly, by approximately 11 to 12 cm from the center of the plot (the point at which the 95% CIs overlap), snail heights in control plots containing no crabs were indistinguishable from those containing predatory crabs (Fig. 2a; see Table S2 in the Supplement).

We found significantly fewer snails on the benthos in plots containing predatory crabs (Treatment: $F_{2,9} = 8.858$, $p = 0.008$), regardless of species identity (*Eury-*

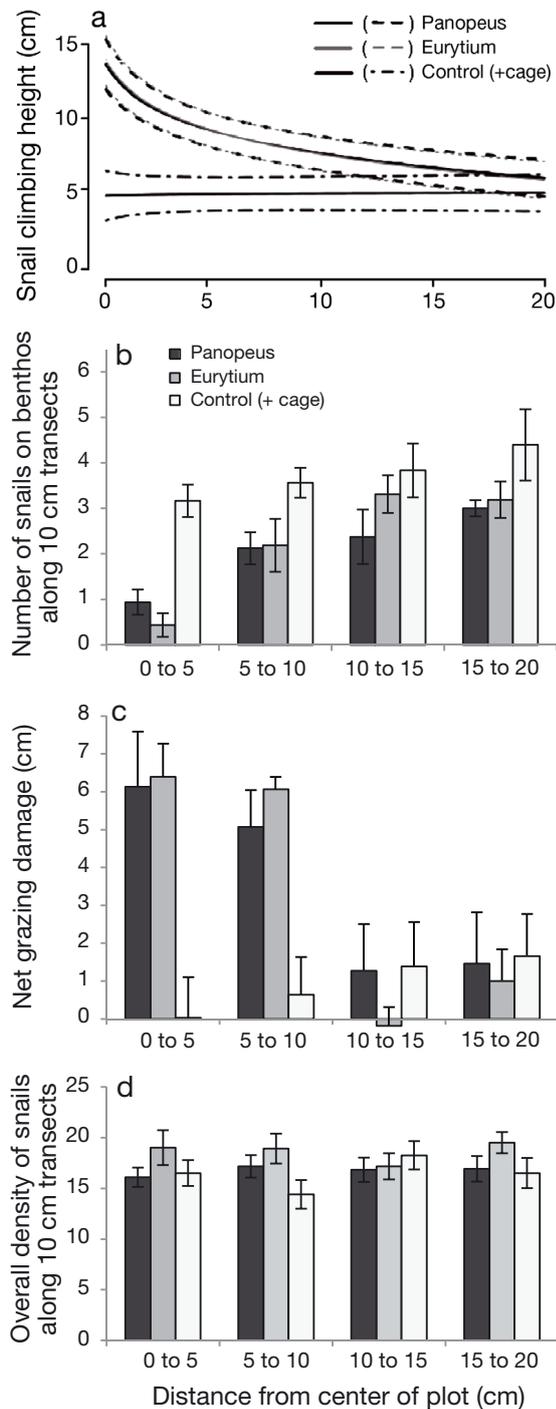


Fig. 2. Spatially explicit non-consumptive effects of predatory crabs on snails and resulting trait-mediated indirect interactions with cordgrass. Shown, with increasing distance from the center of an experimental plot (where the cage containing a predatory crab or an empty cage control was located), are (a) snail climbing heights, (b) number of snails on the benthos, (c) net change in snail grazing damage, and (d) snail density. Data in all panels are from Experiment 1. In panel a, model fits account for random effect of plot and include 95% confidence intervals (broken lines); in panels b–d, bars indicate means \pm SE

tium vs. control: $t_9 = -3.863$, $p = 0.004$, *Panopeus* vs. control: $t_9 = -3.406$, $p = 0.008$). Accordingly, we found no significant difference between species (planned contrast: *Panopeus* vs. *Eurytium*: $Z = 1.087$, $p = 0.277$). The number of snails on the benthos increased with distance from the crab cages (Distance: $F_{1,33} = 35.679$, $p < 0.001$). At 10 to 15 cm from the center of the plot, controls were indistinguishable from caged crab plots (Fig. 2b, Table S3 in the Supplement). However, the interaction between treatment and distance from the crab cage was not significant (Treatment \times Distance: $F_{2,33} = 2.013$, $p = 0.150$), implying that snails avoided the benthos to some extent in the area immediately surrounding the experimental cage, regardless of whether it contained a crab or not.

Snail grazing damage on cordgrass leaves increased in plots with predatory crabs (Treatment: $F_{2,9} = 4.312$, $p = 0.0486$), and declined with distance from the crab cage (Distance: $F_{1,33} = 33.565$, $p < 0.001$) but only if the cage contained a predatory crab (Treat \times Distance: $F_{2,33} = 19.020$, $p < 0.001$). As before, grazing damage did not differ with species of predatory crab (planned contrast: *Panopeus* vs. *Eurytium*: $Z = -0.947$, $p = 0.343$) and was only elevated relative to control values within the first 10 cm for plots containing either *Panopeus* or *Eurytium* (Fig. 2c, Table S3).

The density of snails did not vary with distance from the crab cage (Distance: $F_{1,33} = 0.406$, $p = 0.528$) irrespective of treatment (Distance \times Treatment: $F_{2,33} = 0.155$, $p = 0.857$) (Fig. 2d, Table S3), implying that snails do not move horizontally across the marsh surface to avoid predatory mud crabs.

Experiment 2

Within the active marsh die-off site, snails still responded to the presence of predatory crabs by climbing higher on cordgrass leaves (1-way ANOVA: $F_{2,15} = 24.42$, $p < 0.001$) than they did in control plots containing no cages (Tukey test: $p < 0.001$) or plots containing empty cages (Tukey test: $p < 0.001$), which were not significantly different from one another (Tukey test: $p = 0.925$; Fig. 3a; Table S4 in the Supplement). Consistent with the experiment in healthy marsh, the density of snails did not change in response to the presence or absence of mud crabs (Fig. 3b; $Z = 0.601$, $p = 0.5481$). However, there was an effect of cage presence on snail density. Plots containing empty cages had lower proportional (relative to initial) snail densities at the end of the experiment compared to cage-free control plots (Fig. 3b; $\chi^2 = 9.651$, $p = 0.008$; $Z = -2.285$, $p = 0.022$). Finally, unlike

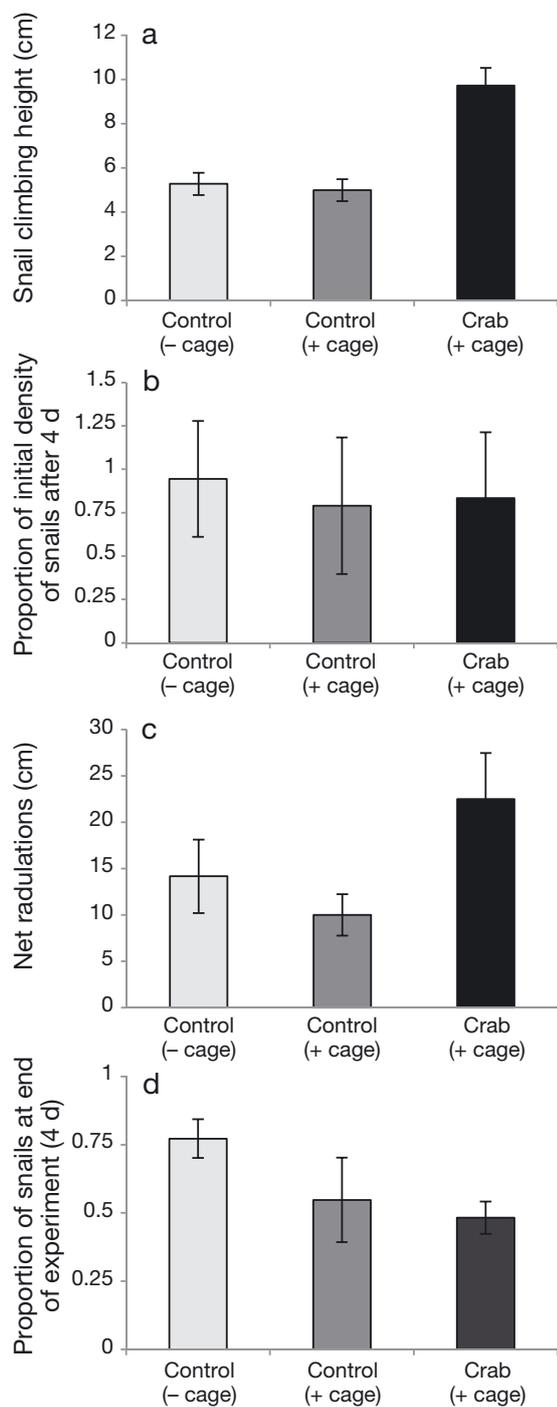


Fig. 3. Non-consumptive effects of predatory crabs on snails and resulting trait-mediated indirect interactions with cordgrass in an ongoing salt marsh die-off. Shown are (a) snail climbing heights, (b) proportion of initial density of snails present at the end of the experiment, (c) net snail grazing damage as evidenced by radulations, and (d) proportion of initial density of snails that recolonized removal plots after 4 d. Data in panels a, b, and c are from Experiment 2A; data in panel d are from Experiment 2B. Plots contained no cage and no crab (control [- cage]); an empty cage (control [+ cage]); or a caged mud crab (crab [+ cage]). Bars indicate means \pm SE

in the healthy marsh, there was no significant effect of treatment on snail grazing damage (1-way ANOVA: $F_{2,15} = 2.68$, $p = 0.101$; Fig. 3c, Table S4).

At the active die-off site, we also studied rates of snail arrival at cordgrass stems from which all pre-existing snails had been removed. In this case, the presence or absence of a crab did not affect the rate of snail arrival ($\chi^2 = 2.484$, $p = 0.289$; Fig. 3d, Table S4). This implies that snails still vertically migrate, but do not respond through horizontal shifts in habitat choice in response to crabs as they move within die-off fronts.

DISCUSSION

Our results from southeastern US salt marshes show that snails respond to 2 sit-and-wait predatory mud crabs in a similar fashion, that is, by undergoing a vertical habitat shift that ultimately increases their per capita grazing effect on cordgrass leaves. We also found that snails show no evidence of moving horizontally in response to the presence of predators, even when colonizing remnant stems under cordgrass die-off conditions.

The habitat shift of snails upwards toward the cordgrass canopy in response to mud crab presence may largely be explained by the relative habitat domains of predators and their prey (following Schmitz et al. 2004). While the mud crabs are restricted to the benthos and thus have a narrow vertical habitat domain, the snails have a broad vertical habitat domain, from the benthos to the upper cordgrass canopy. Thus, the snails are able to shift vertically to a microhabitat inaccessible to the mud crabs.

Given that snails responded to predation risk within a highly localized area (a ~ 12 cm radius; Fig. 2a), and mud crabs are sparse in the short zone, snails could hypothetically resume foraging on nutritious benthic algae and detritus by moving a relatively small distance horizontally (note that snails can move at up to 16 m h^{-1} ; Silliman et al. 2005). Nevertheless, even in the die-off where snails make the choice to move into (not out of) an area, we found no evidence of a horizontal shift associated with predator presence. Importantly, the nature of our experimental approach—measuring responses of naturally-occurring prey populations to predator addition in the field—ensured that prey would have been able to move horizontally unimpeded by experimental enclosures. We therefore have confidence that a vertical shift is the primary spatial response of snails to predation risk in this system. Notably, such a robust

assessment of the spatial dimensions of prey response has rarely been possible in past studies. Indeed, we found that 29 of 30 past experiments on TMIIIs (sampled from the literature) had used experimental enclosures that potentially constrained horizontal prey movement (see Table S5 in the Supplement at www.int-res.com/articles/suppl/m537p049_supp.pdf).

We acknowledge, however, that our experiment also had its limitations. By caging predators, we created a treatment with invariable crab presence and location. Under natural conditions, mud crab presence in burrows might be more temporally variable if they switch to a more active foraging mode during tidal immersion or at night. That said, mud crab burrow occupancy is relatively high at least during daytime tidal emersion (72% from 1100 burrows surveyed by Silliman et al. 2004), and our observational results suggest that snail impacts on cordgrass are locally intensified around natural mud crab burrows, mirroring and supporting our experimental result. Thus, while more work is required to elucidate the effects of predator movements, we suggest that our approach accurately captures the nature of the TMII.

The vertical habitat shift of snails in the presence of predators precipitated shifts in snail foraging behavior, from the benthos and lower cordgrass stems to the vulnerable canopy leaves. This, in turn, increased the leaf-damage (radulations) they inflicted on cordgrass, at least in healthy salt marsh. The similarity in spatial extent of climbing responses (~12 cm radius), reduced benthos use (~10 cm) and intensified leaf damage (~10 cm radius), and the match between our survey and experimental results provide strong support for this mechanistic interpretation and indicates that the TMII is an important factor explaining spatial variation in the intensity of grazing in natural marshes (see also Kimbro 2012). The cascading effects of predator-induced vertical habitat shifts have also been documented in Tibetan alpine meadows, where surface-dwelling predatory beetles cause earthworms to burrow more deeply, strengthening the positive per capita effects of these ecosystem engineers on soil conditions and plant biomass (Zhao et al. 2013). Collectively, these findings show that the sign of trait-mediated indirect interactions triggered by vertical habitat shifts can run counter to density-mediated indirect interactions predicted by theory.

In the die-off context, where snails also responded by climbing higher on cordgrass, the associated increase in leaf damage was less pronounced than in the healthy marsh and was not statistically significant. This lack of a TMII might be due to the shorter

duration of the experiment (4 wk instead of 6 wk) or due to density-dependent crowding on stems affecting snail response to predation risk. Thus, although the spatial dimensions of the interactions in healthy and die-off marsh contexts are consistent (exclusively vertical), we cannot yet confirm that the resulting TMII is invariable. Given the importance of interactions within active consumer fronts for the persistence of ecosystem-states (Silliman et al. 2013), further experiments investigating predator-prey interactions along consumer fronts are needed in this and in other systems.

The 2 species of mud crab elicited remarkably similar responses in snails and the resulting TMIIIs, which we attribute to their trait similarity. Specifically, the 2 species have the same foraging mode (sit-and-wait) and habitat domain (burrow-dwelling), which are traits that determine the ability of prey to detect and avoid them (Schmitz et al. 2004, Preisser et al. 2007, Miller et al. 2014). Moreover, because the species are similar in body size, one could infer that they elicit similar visual and olfactory cues to their prey, making them functionally equivalent. This supports the evidence that similarity in key predator traits may predict similarity in TMIIIs. However, we cannot rule out that the snails would respond differently to the mud crab species under seasonal conditions when their relative predation rate may differ (Griffin et al. 2011).

Our study represents a step towards integrating non-consumptive predator effects into our understanding of trophic cascades in southeastern US salt marshes. Here, trophic control of periwinkle snails prevents runaway consumption (Silliman & Bertness 2002) and likely reduces the probability of large-scale cordgrass die-off during droughts (Silliman et al. 2005). Previously, trophic control of snails has been attributed to a suite of predators including blue crabs, mud crabs and terrapins (Silliman & Bertness 2002). Although mud crabs are known to consume snails (Kneib 1990, Silliman et al. 2004, Griffin & Silliman 2011, Soomdat et al. 2014), our results suggest that by strengthening the negative per capita effects of snails on cordgrass, the role of mud crabs in preventing runaway consumption via trophic cascades may be weaker than would be predicted based on their effects on snail density alone. If mud crabs have net negative effects on cordgrass, by consuming mud crabs larger-bodied predators (e.g. blue crabs) may be more critical for marsh functioning than previously recognized. However, evaluation of the net long-term cascading effects of mud crabs in this system must consider that non-consumptive effects of

predators often entail a nutritional/energetic cost for prey, reducing their growth/reproductive rates and thus indirectly regulating their population densities (Preisser et al. 2007, Reynolds & Sotka 2011). This calls for development of a longer-term, population-level, perspective to fully understand the consumptive and non-consumptive pathways linking predators to snails and ultimately cordgrass in southeastern US salt marshes.

Our findings highlight consistency in the spatial scale and dimensionality of non-consumptive predator effects and resulting TMIs (at least within the healthy salt marsh) induced by sit-and-wait predators. These effects must now be integrated with consumptive effects of predators in this system and evaluated over larger spatiotemporal scales with the use of long-term experiments and simulation models. The effects of predators mediated by the exclusively vertical habitat shift we observed (i.e. intensification of local per capita impacts and no change in local density) have markedly different ecosystem consequences than the alternative horizontal redistribution of snails (i.e. no change in per capita effects, but a reduction in local density). This contrast highlights the importance of simultaneously assessing effects of prey movements in different dimensions and thus scales.

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