



Abiotic Cycles Mediate the Strength of Cross-Boundary Consumption Within Coastal Food Webs

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Abstract

Understanding the effect of habitat edges on species interactions (e.g. predation) is critical for determining landscape-scale patterns in productivity and the structuring of communities in an ever-changing environment. Both abiotic cycles and habitat structure can mediate faunal movements across habitat edges and determine predators' ability to access prey across both space and time. To quantify the effects of cyclical abiotic factors and habitat structure on consumer-resource dynamics across habitat boundaries at the land-sea interface, four complementary studies were conducted. Marsh periwinkles *Littoraria irrorata* were tethered within salt marshes of varying tidal amplitude, at 3 distances from the marsh edge, and assessed for predation after 24 h. Nekton catch rate was assessed with fyke net sampling as a proxy for predator utilization of the marsh platform. Consumption rates were positively correlated with tidal amplitude and proximity to the seaward marsh edge, and there was also a slight positive relationship between tidal amplitude and nekton access to the marsh. Tidal amplitude was positively correlated with *Spartina alterniflora* shoot density and negatively correlated with shoot height. Therefore, to separate the effects of habitat structure from tidal forcing, independent manipulations of shoot density and shoot height were conducted. We found that the signal of local habitat structure on consumption rates appears to be secondary to the effects of abiotic cycles on consumption. Disentangling the interactions between abiotic cycles and biotic structure of ecosystems across ecological boundaries is key to understanding both the strengths of species interactions and the mediation of cross-boundary energy flow.

Keywords Consumer-resource interactions · Salt marsh · Tidal inundation · Habitat structure · Edge

Introduction

Within heterogeneous landscape mosaics, habitat boundaries can alter the connectivity and dynamics between adjacent habitat types. Previous studies have investigated a variety of ecological phenomena in both terrestrial and aquatic systems to understand changes in diversity, reproduction, and mortality across natural and fragmented habitat boundaries (Fagan et al.

1999). In many instances, species interactions at or across these ecological boundaries have been shown to drive community structure (Menge and Sutherland 1987) and ecosystem functioning via changes in the flow of energy from one system to another (Polis and Strong 1996). The magnitude or direction of species interactions across habitat edges can be mediated by the underlying environmental gradients, abiotic cycles, and other biotic interactions that occur along the habitat interface (Yahner 1988; Grover and Wilbur 2002).

Abiotic cycles and biotic habitat structure can impact the rate of key species interactions such as predator-prey dynamics. For instance, predation by owls on gerbils at night is highest on illuminated (e.g. nights with a full moon) sand dunes with no shrub cover. However, on nonilluminated (e.g. nights with a new moon) sand dunes with small amounts of shrub cover (~10%), predation is significantly dampened (Kotler et al. 1991). As predators or prey move across habitat boundaries to forage, changes in the periodicity or intensity of abiotic cycles and habitat structure may also mediate the rate and mode of consumption. Therefore, to better understand overall ecosystem structure (community composition) and

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functioning (secondary production), it is important to understand how differences in cyclical abiotic forcing (e.g. lunar cycle, photoperiod, and tidal cycle) and changes in habitat structure within and across habitat boundaries may alter cross-boundary movements of species, predator-prey interactions, and subsequent energy flows.

The loss of connectivity (ability to move freely) between habitats due to abiotic or biotic factors may also have profound effects on food web dynamics and energy flow across ecotones. For instance, when physical barriers prevent the input of terrestrial insects into forest streams, fish feeding preferences shift from terrestrial arthropods to relying solely on aquatic insects, decreasing overall production during summer months (Nakano and Murakami 2001). At the land-water interface, the flow of energy may be driven by a combination of abiotic and biotic forces that can vary across large geographic scales. Predator access to terrestrial habitats or prey moving from land into the water can offer increased feeding opportunities for aquatic species, which promotes production (Deegan et al. 2000). For example, arboreal mangrove crabs shift habitat preference from the dry mangrove canopy to the water in the presence of avian predators and subsidize the diets of gray snapper (Yeager et al. 2016). When connectivity is limited across the land and sea interface, however, there may be decreases in fish and crustacean (nekton) growth and overall marine secondary production (Kneib 2000).

Salt marshes are an ideal ecosystem to study the drivers of cross-boundary species interactions and edge dynamics because they occupy distinct interfaces along the land-sea margin. Salt marshes are found across broad latitudinal gradients with varying geomorphologies, plant structures/composition, and astronomical and meteorological tidal regimes (Rozas 1995). Regardless of whether tidal marsh production is transferred up marine food webs by direct foraging on the marsh surface or through intermediate consumers off the marsh or outwelling of energy via detritus, hydrology plays a key role in trophic transfer from the marsh to estuarine or coastal systems. Previous work has shown that the level of tidal inundation (water) over the surface of the marsh can greatly affect the ability of nekton to access the marsh platform (Minello et al. 2012; Baker et al. 2013) affecting gut fullness of fishes (e.g. pinfish *Lagodon rhomboides*; Potthoff and Allen 2003) and growth of nekton (Shervette and Gelwick 2008). Specifically, mobile crustaceans (e.g. crabs and shrimps) need at least 5 cm of water above the marsh surface to move freely (Minello and Rozas 2002). Across geographic scales, tides range from a few centimeter amplitudes (meteorologically/wind driven) to several meter amplitudes (astronomically driven) with inundation periodicity ranging from several weeks intermittently to a predictable ~6 h, respectively. Due to the variation in tidal amplitude and duration of marsh flooding, the function of marshes as an energy source varies across regional and biogeographic scales. Additionally, free-swimming crustacean

(i.e. brown shrimp *Farfantepenaeus aztecus* and blue crab *Callinectes sapidus*) densities greatly decrease landward from the marsh edge (Minello and Rozas 2002), and predation by blue crabs tends to decrease landward from the edge as well (Lewis and Eby 2002). However, if the marsh habitat structure is completely removed, predation rates increase farther onto the marsh platform indicating that habitat structure may mediate these interactions (Lewis and Eby 2002).

In this study, we experimentally investigated the role of inundation (tidal amplitude and flooding duration), distance from the edge, and habitat structure in mediating edge predator-prey interactions and marsh utilization by nekton across a biogenic habitat boundary. We conducted four complementary studies to tease apart the interactive effects that drive predator-prey interactions across the marsh-estuarine interface. We investigated how predation on marsh periwinkles *Littoraria irrorata* varied across a tidal amplitude gradient. We explored nekton abundance as a proxy for predator utilization of the marsh along a tidal amplitude gradient. To experimentally separate the effects of tidal inundation and habitat structure (which naturally vary together) on consumption, we conducted two manipulative field experiments to assess the importance of shoot density and subsequently shoot height on predator-prey interactions across the marsh-tidal creek interface at an intermediate inundation site.

Methods

Predation Assays

We conducted predation assays at 5 salt marshes with varying tidal amplitudes and structural habitat characteristics. Four sites were located along the coast of North Carolina (NC), USA: Wilmington (34.17537, -77.84147), Hoop Pole Creek (34.70669, -75.75191), North River (34.78915, -76.61668), and Hatteras (35.22487, -75.68533), and one site was located near Port Sulfur, Louisiana (LA), USA (29.44861, -89.74944; Fig. 1). Minello et al. (2012) found that flooding metrics varied greatly over a relatively small geographic range along the NC coast, and therefore, sites across coastal NC may be especially useful in understanding marsh utilization and predator-prey interactions across the marsh-estuarine boundary. We included a site in LA to determine whether salt marshes with meteorological/wind-driven tidal regimes have similar rates of predation along both the South Atlantic and Gulf Coasts of the USA. The marshes were all *Spartina alterniflora* dominated, but other common plant species included *Juncus roemerianus*, *Spartina patens*, *Distichlis spicata*, and *Salicornia virginica*. Tidal amplitudes were approximately 1.00–1.50 m in Wilmington, 0.50–1.00 m in Atlantic Beach, and 0.50–1.00 m in Beaufort, with all three sites dominated by astronomical components. Tidal

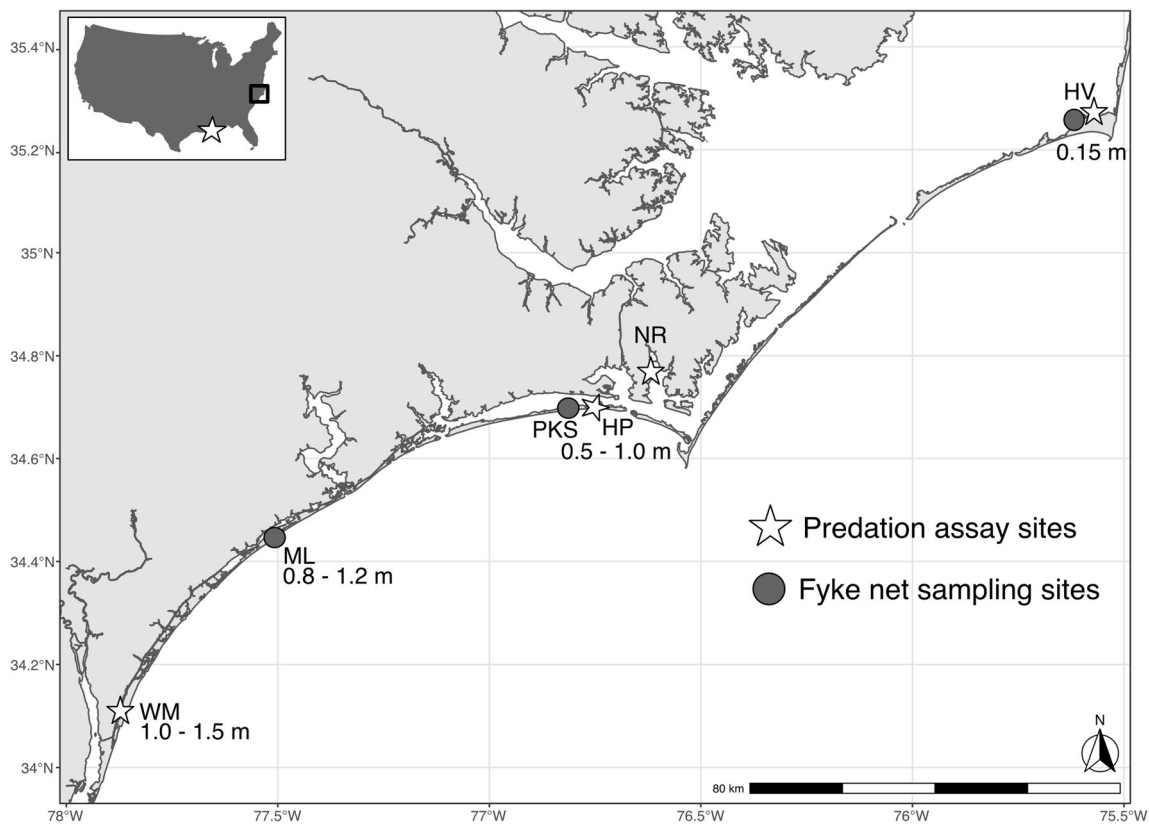


Fig. 1 Map of sampling sites zoomed in along the coast of North Carolina, USA. Stars indicate sites where snail predation assays were conducted (both Louisiana and North Carolina; WM Wilmington, HP Hoop Pole Creek, NR North River, and HV Hatteras Village). Circles

designate the location of fyke net sampling sites (HV Hatteras Village, PKS Pine Knoll Shores, and ML Morris Landing). Values are the average tidal amplitude range for a given area

amplitudes in both Hatteras and LA were ~ 0.15 m and driven by meteorological forces (i.e. wind driven). We conducted our study in the low-to-intermediate zone of the marsh because we expected consumption to be highest in this area due to proximity to subtidal estuarine habitats and access for predators.

At each site, 12–5 m transects were placed parallel to the marsh edge at 4 distances: 5 m seaward in unvegetated (subtidal) habitat, in vegetation within 1 m of the seaward marsh edge, 5 m into the marsh platform, and 10 m into the marsh platform ($n = 3$ transects for each distance). Predation assays were conducted monthly from June through September 2016. Marsh periwinkles (17.0–21.0 mm at largest width; $\mu = 19.02 \pm 0.04$ mm) were glued to monofilament fishing line (Stren Original 0.27-mm diameter, 0.25 m in length) and tethered to plastic stakes. The length of the tether allowed for natural snail behavior related to movement up and down *S. alterniflora* shoots with tidal inundation (S. Ziegler, personal observation). At each site, 8 (LA) or 10 (NC) tethered snails were placed approximately 0.5 m apart along each transect (for a total of 96 or 120 snails per site). Snails were left for 24 h and then inspected for predation. Predation was assumed when the snail was absent, the shell was crushed, or the line was snapped.

Habitat Characteristics

To determine the structure of the *S. alterniflora* marsh stand at each site in NC, we examined vegetation characteristics along the established transects described above ($n = 3$ quadrats per transect) in June 2016. Along each transect, we counted *S. alterniflora* shoots and measured maximum shoot heights within haphazardly placed quadrats (0.0625 m²), standardized counts to 1 m², and averaged these samples for analyses.

Tidal Amplitude and Duration

HOBO water-level loggers (Onset HOBO U20L) were submerged at each site in NC from June through September 2016 to calculate water-level values. HOBO pressure records were adjusted for ambient air pressure (obtained from the nearest NOAA weather station, 8656483) to determine the amount of water above the sensor throughout our study. Elevation (NAVD88) of marsh sites was obtained from NOAA LIDAR images in ArcMap (NC OneMap; <https://www.nconemap.gov/>). LIDAR cannot penetrate through the marsh canopy, and therefore elevation reported is to the top of the marsh grass instead of the marsh platform surface. We then calculated the

water height over the marsh canopy and inundation time (i.e. marsh flooding duration) with respect to flooding over the marsh canopy. Water height above the marsh grass (hereafter water height) was calculated by subtracting LIDAR elevations from all water-level values (m). Inundation time (hours of marsh flooding) was extrapolated by determining the amount of time during a given predation assay that water height was greater than 0 indicating water was above the marsh canopy (error range = 1.56–0.48 m; Aguilar et al. 2010).

Nekton Sampling

We conducted monthly nekton (fish and crustacean) sampling from June–September 2016 at 3 sites across the coast of North Carolina of varying tidal amplitudes. Fyke net sites were located at Hatteras Village (~0.15 m tidal amplitude, 0.8 km from predation site), Pine Knoll Shores (~0.5–1.0 m; ~7 km from Hoop Pole Creek) and Morris Landing, and Holly Ridge (~0.8–1.2 m; ~40 km from Wilmington, NC; Fig. 1). At each site, two fyke nets were placed in the water along the vegetated edge of a natural marsh (i.e. facing the marsh to collect fauna emerging from the marsh; $n = 2$). Nets were set at nighttime high tide and left to soak through one tidal cycle (~6 h) during spring tides for maximum tidal difference. The fyke nets were comprised of a $0.9 \times 0.9 \times 5.1$ -m central mesh bag (3.175 mm mesh), with two 0.9×5.1 -m wings extending from either side. All nekton caught were identified to the lowest taxonomic level possible, counted and weighed wet. Fyke net catch rates were standardized by fyke net wing width to account for differences in the amount of marsh edge drained into the net.

Shoot Density Experiment

We conducted our manipulative field experiments focused on shoot density in Hoop Pole Creek, Atlantic Beach, NC, a site with median tidal height, to minimize variability and reduce confounding effects of tidal flooding and plant structure, across two seasons: summer and fall. Nine transects ~20 m in length were placed parallel to the marsh edge at 3 distances relative to the seaward marsh edge in vegetation: within 1 m of the marsh edge, 5 m into the marsh platform, and 10 m into the marsh platform. Along each transect, 15 replicate 0.25-m^2 plots were established 1–2 m apart. Each plot was randomly assigned 1 of 3 density treatments: reduced, ambient, or increased. Reduced plots had 50% of ambient shoots physically removed from the plot via haphazard thinning (7.22 shoots \pm 0.11 SE), ambient plots remained unaltered (15.06 shoots \pm 0.19 SE), and increased plots had shoot density increased by 50% utilizing 1.25-cm diameter wooden dowels as *S. alterniflora* mimics haphazardly placed in the plot (22.22 shoots \pm 0.29 SE). During each sampling event ($n = 8$), 1 squidpop (described by Duffy et al. 2015) was placed into each plot at high tide. Squidpops were chosen over snails due to higher rates of consumption in

NC on squidpops (Duffy et al. 2015), allowing for an understanding of consumption across shoot density treatments at shorter time scales (2 h vs. 24 h). In addition, the use of squidpops prevented bias in tethered snails becoming tangled in high-density plots. Squidpops were checked for predation every 30 min as the tide receded until the marsh was no longer inundated (between 2 and 3 h) and assessed with a binary response of eaten or uneaten.

Shoot Height Experiment

At Hoop Pole Creek, Atlantic Beach, NC, one experimental transect was placed 2 m from the seaward edge of the marsh. Along the transect, we set up $30\text{--}0.25\text{-m}^2$ plots placed 2 m apart. Plots were randomly assigned 1 of 5 shoot height treatments: 10 cm, 25 cm, 50 cm, 75 cm, and ambient shoot heights (~75–100 cm; replicates = 6). Each shoot height treatment indicates the tallest shoot height within a given plot, and all *S. alterniflora* shoots within a plot were clipped to the assigned shoot height. During each predation trial ($n = 4$), we placed one tethered marsh periwinkle snail in each plot. In order to assess predation while allowing the natural behavior of marsh periwinkles, tethers were measured up to 1 m in length and shortened to the tallest shoot height within the plot to allow snails to move up and down *S. alterniflora* shoots but not move outside of the manipulated plots. After 24 h, snails were checked for predation. Predation was assumed when the snail was absent, the shell was crushed, or the line was snapped.

Statistical Analyses

Predation Assays

To assess the relative predation rate on snails across sites varying in tidal amplitude, we first converted presence-absence data for each tether to proportion of snails eaten by dividing the total number of snails eaten by the total number of snails placed along each transect ($n = 8$ per transect in LA, $n = 10$ per transect in NC). All proportion data (across all experiments) were non-normal, and therefore arcsine transformations were employed. Despite the fact that data were non-normal after arcsine transformations, we continued to employ ANOVAs for 2- and 3-way interactions due to the robustness of the statistical test. All analyses were conducted in R statistical software (R version 4.0.0).

To investigate broadly how predation of snails varied across tidal amplitude regime and with distance into the marsh, we employed a two-way ANOVA. To determine the effect of both habitat structure and site-specific tidal factors (water height and inundation time) on predation upon snails at different distances into the marsh (for sites in NC), we ran generalized linear models with the following parameters:

distance into the marsh, maximum water height (cm), inundation time (hr), shoot density (m^{-2}), and shoot height (mm). Louisiana predation data were not included in the models due to lack of tide and habitat characteristics data. A drop-one jackknife approach was systematically employed to serially drop the least important factor from each model until the most simplistic model was found (Wolter 2007). Akaike information criterion was then used to identify the model with the best fit.

Nekton Sampling

To investigate differences in catch of total nekton (potential predators) from fyke nets across 3 sites with varying tidal amplitude in NC, we ran a repeated measures ANOVA with tidal amplitude as a factor and month of sampling as an error term to account for the repeated sampling of the same sites.

Shoot Density Experiments

To assess the rates of consumption on squidpops in varying shoot density treatments, we converted presence-absence data for each plot into proportion of squidpops consumed per treatment along a given transect for both fall 2016 and summer 2017 experiments ($n = 8$). To identify the effects of shoot density, season, and distance into the marsh on consumption rates, we ran a 3-way interactive ANOVA.

Shoot Height Experiments

To determine if shoot height alone influenced predation of marsh periwinkle snails, we converted presence-absence data into the proportion of snails eaten for each shoot height treatment and compared across sampling days ($n = 4$). To assess the effect of shoot height on predation rates, we ran a repeated measures ANOVA with an error term of sampling date.

Results

Predation Assays

Snail predation was statistically distinct among tidal amplitude regime ($F_{1,158} = 116.58$, $p < 0.001$) and distance into the marsh ($F_{1,158} = 11.48$, $p < 0.001$), with no interaction between the two ($F_{1,158} = 0.64$, $p = 0.43$; Fig. 2). Overall, the proportion of snails eaten was highest at the Wilmington, NC, site (0.45 ± 0.02) and lowest at Hatteras Village, NC, (0.05 ± 0.04). Predation was the lowest at the two meteorological tide (wind driven) sites compared with sites with larger astronomically driven tides; however, predation rates were

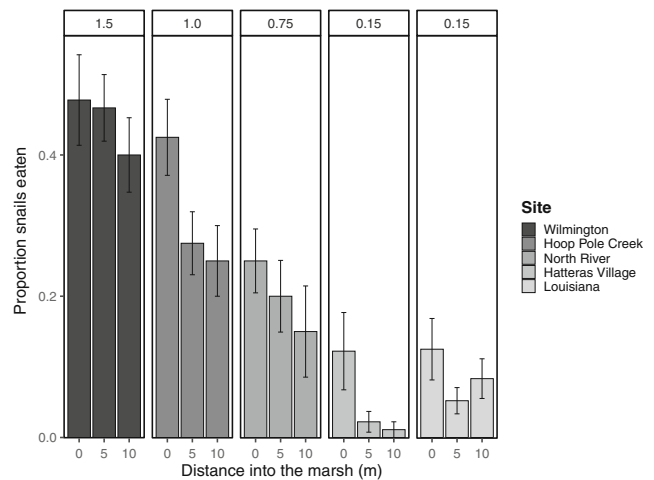


Fig. 2 Proportion of snails eaten across sites with increasing distance into the marsh from the seaward edge. Numbers at the top of the plots indicate average tidal amplitude (m). All values are means \pm SE

slightly higher in Louisiana (0.09 ± 0.02) than in Hatteras Village (0.05 ± 0.04). For site-specific trends across North Carolina, the model that best explained the proportion of snails eaten was an additive model with independent variables of distance into the marsh ($t = -0.874$, $p = 0.384$), inundation time over marsh grass ($t = 2.082$, $p = 0.039$), *S. alterniflora* shoot density ($t = -1.958$, $p = 0.053$), and *S. alterniflora* shoot height ($t = 2.552$, $p = 0.012$; Table 1; Fig. 3).

Nekton Sampling

Catch rates of nekton were not statistically distinct across the tidal amplitude gradient ($F_{2,6} = 0.675$, $p = 0.54$). Across all sites, fyke net catches were dominated by small nekton (< 20 cm) such as penaeid shrimp (*Penaeidae*), blue crabs, pinfish, and pigfish (*Orthopristis chrysoptera*). Potential predators captured in fyke nets were rare but included flounders (*Paralichthys spp.*), red drum (*Sciaenops ocellatus*), and sheepshead (*Archosargus probatocephalus*). There was a tendency for catch rates of nekton in fyke nets to be lowest at Hatteras Village, our wind-driven site with tidal amplitude of ~ 0.15 m, compared with sites with higher tidal amplitude, Pine Knoll Shores (0.5–1.0 m site) and Morris Landing (0.8–1.2 m site; Fig. 4).

Shoot Density Experiment

There was no detectable effect of shoot density ($F_{3,252} = 1.09$, $p = 0.35$) on the proportion of squidpops eaten at any distance into the marsh or across seasons (Fig. 5). While there was no effect of shoot density on consumption, we did find an interaction between season and distance into the marsh ($F_{2,252} = 18.88$, $p < 0.001$) on proportion of squidpops eaten. In the fall, consumption of squidpops decreased by approximately 1/3 with increasing distance from the marsh-estuarine edge

Table 1 Summary of AIC and degrees of freedom (df) for all additive model combinations to explain predation on marsh periwinkle snails. The model in italics is the final model selected

Model	AIC	df
distance into marsh + maximum water height + inundation time + shoot height + shoot density	-56.7175	7
<i>distance into marsh + inundation time + shoot height + shoot density</i>	-58.5529	6
distance into marsh + maximum water height + shoot height + shoot density	-54.8274	6
distance into marsh + inundation time + shoot height	-56.6066	5
distance into marsh + maximum water height + shoot height	-52.3896	5
distance into marsh + inundation time + shoot density	-53.9317	5
distance into marsh + maximum water height + shoot density	-51.6150	5
distance into marsh + inundation time	-51.3762	4
distance into marsh + maximum water height	-51.0009	4
distance into marsh	-17.3874	3

regardless of shoot density (Fig. 5). In the summer, there appeared to be slightly higher consumption at the marsh-estuarine edge (0 m) for plots with shoot densities between 10 and 30 shoots/0.25 m²; however, there was no statistically clear trend across distance into the marsh or with shoot density (Fig. 5).

Shoot Height Experiment

Shoot height treatments did not have any statistical effect on predation rates ($F_{4,12} = 0.636$, $p = 0.65$; Fig. 6) along the marsh-tidal creek interface. However, there was a trend of slightly higher rates of predation in the 10 cm treatment

compared with all other shoot height treatments (Fig. 6). The increase in predation rate was almost 3-fold in the 10 cm compared with ambient (~75–100 cm) treatment and may be ecologically relevant for marsh systems.

Discussion

Understanding the movement of species and inter- and intra-specific interactions between adjacent habitats is a vital step in understanding landscape-scale community structure and ecosystem function. Our results suggest that abiotic cycles (e.g. tides) at the land-sea interface are key in mediating the

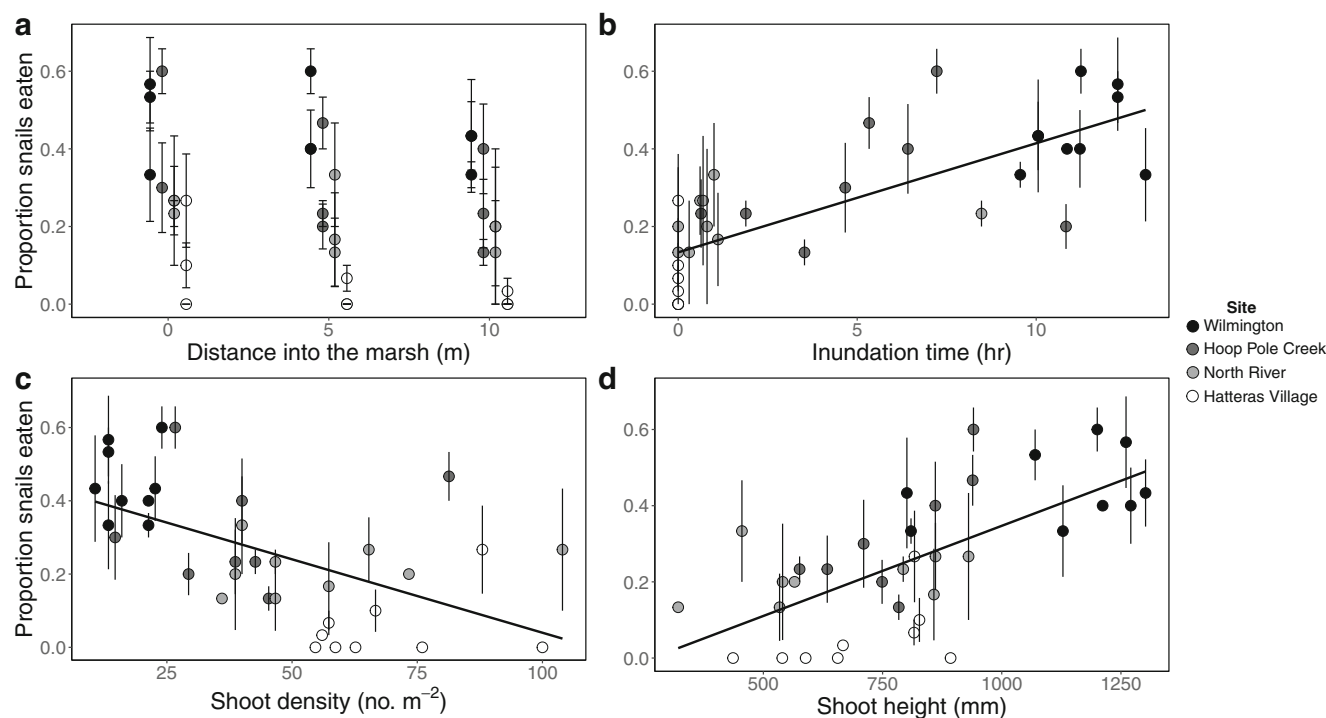


Fig. 3 Proportion of snails eaten with respect to **a** distance into the marsh, **b** inundation time over marsh grass in hours during 24-h predation assay, **c** *S. alterniflora* shoot density, and **d** shoot height. All values are means ± SE

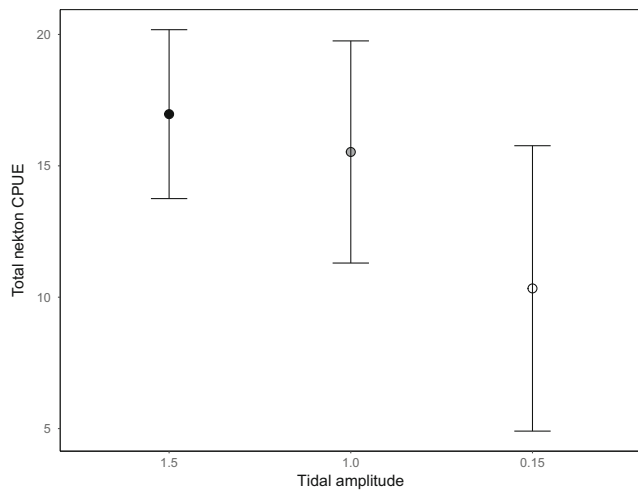


Fig. 4 The catch per unit effort (CPUE, catch rate/net soak time) of all nekton captured in fyke nets along a tidal gradient in NC. All values are means ± SE

strength of species interactions across habitat edges and potentially overall energy flows across this ecological boundary. When species move across ecosystem boundaries, they necessarily encounter habitat edges which can have mediating effects that alter ecosystem function and dynamics. Habitat edges can increase predation, allowing predators to more easily spot their prey (Gorman and Connell 2009), creating an ecological trap where mortality increases for prey species. In these instances, access to adjacent habitats across edges increases foraging success for predatory species and may amplify the flow of energy across ecological boundaries enhancing overall production in the adjacent system (Polis and Hurd

1996). In contrast, the movement of prey species across habitat boundaries from relatively unstructured to highly complex habitats may increase survival by providing refuge and ultimately decrease the flow of energy to higher trophic levels. For sedentary or low mobility prey species (e.g. marsh periwinkles) increased habitat structure along ecotones or habitat edges may also provide increased refuge by obscuring predator visibility or limiting access increasing overall prey abundance; however, this benefit to prey may be mediated by abiotic forces such as tidal amplitude.

We found that the highest rates of predation and predator utilization of the marsh platform occurred at sites with the highest tidal amplitude, suggesting that increased water levels may mediate the ability of predators to move across the land-sea interface to access their prey. In meteorological or wind-driven systems, there was overall low predation on the marsh platform most likely a result of inconsistent access for predators to the marsh platform. During our study, there was little to no detectable water over the marsh grass during predation assays at either wind-driven site. Potential fish predators (e.g. flounders and red drum) cannot access the marsh platform under low water levels. However, crustacean predators such as blue crabs are able to use the marsh platform at shallow depths of ~ 5 cm (Minello et al. 2012) and therefore may still have access to the marsh in areas with wind-driven flooding. We recognize that marsh-resident species (mud crabs *Panopeidae*), terrestrial species (e.g. raccoons), and wading birds can forage on the marsh during low or no tidal inundation; however, we do not expect that these predators had a large influence on consumption rates as there was low

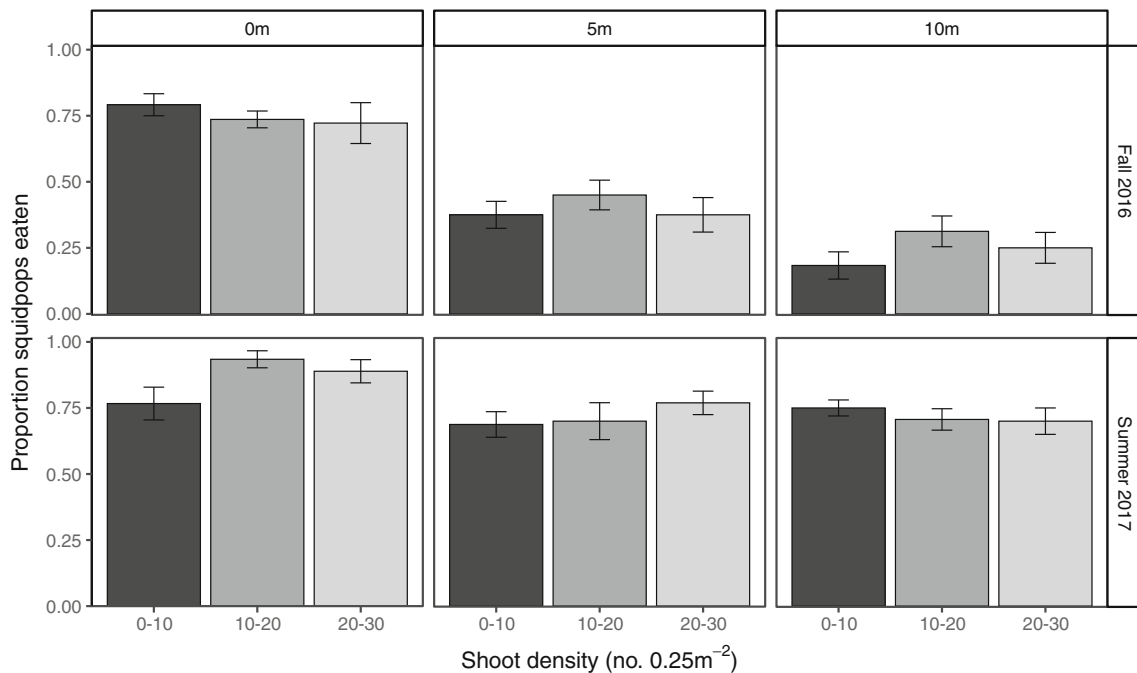
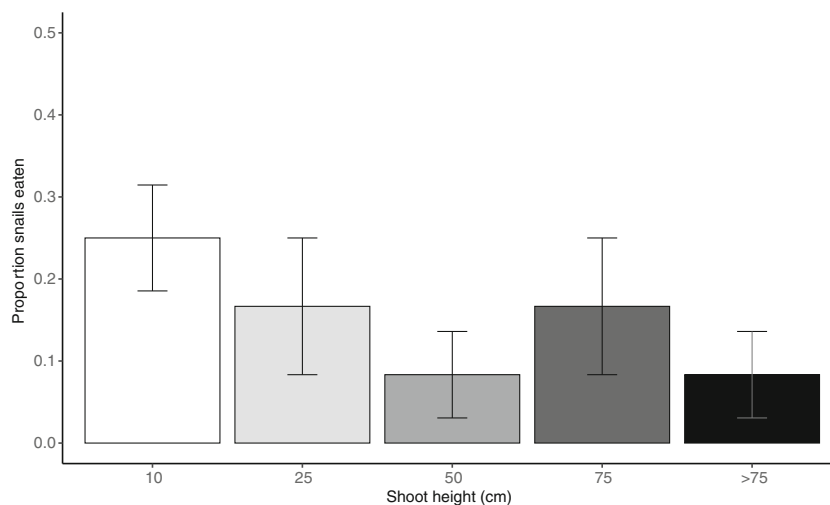


Fig. 5 The proportion of squidpops eaten with increasing shoot density (binned 0–10 shoots, 10–20 shoots, and 20–30 shoots) in both **a** fall 2016 and **b** summer 2017. All values are means ± SE

Fig. 6 The proportion of snails eaten with respect to *S. alterniflora* shoot height. All values are means \pm SE



predation across both our sites with meteorologically driven tides. Since duration of marsh flooding was positively correlated with predation rates, we may have observed higher predation rates at sites with predominantly wind-driven tides if we had sampled during times of sustained marsh flooding. It has been observed that small marsh-associated fauna such as shrimps and killifish in areas with greater flooding duration (i.e. the Gulf of Mexico) have a higher contribution of *S. alterniflora* primary production in their tissues (Baker et al. 2013) than in areas with astronomically driven tides. Yet, the dynamics of the connection between marsh production and larger predatory species is not well explained in areas with low tidal amplitude and high flooding duration or in regard to habitat structure.

Our predation assays along a tidal inundation gradient indicate that habitat structure (shoot density and shoot height) may be an additional factor influencing consumption across the land-sea interface. Specifically, our results show that areas with the tallest shoots and lowest shoot density have the highest predation. First, this could be due to increased tidal amplitude at sites with low shoot density and tall shoot heights allowing for greater predator access at these sites. Secondly, low shoot density may provide increased interstitial space between shoots for predators to move through and visualize their prey when foraging (Carroll et al. 2015), and tall shoots may allow snails to move up the grass out of an area of potential consumption. However, along our tidal inundation gradient, shoot height and shoot density were inversely correlated. Therefore, to tease apart the interactive effects of tide and habitat structure, we separately manipulated shoot density and shoot height at a site with median tidal amplitude.

Experimental manipulations indicated that plant density had little to no influence on consumption rates and shoot height only displayed a small effect on consumption rates. Although there appeared to be minimal or secondary impacts of plant structure on consumption rates at the shoot densities,

shoot heights, and tidal regime tested, this is not to say that plant structure does not matter; a total lack of plant material would alter the system greatly in terms of refuge and nursery habitat value. In addition, *S. alterniflora* shoots are on average tall enough to remain partially out of the water when the marsh platform is inundated allowing snails to escape consumption. Similarly, our results suggest that *S. alterniflora* stem density does not get dense enough to impede the mobility of small crabs and fish. Therefore, there would need to be a major shift in plant height or extreme change in shoot density (e.g. shift from *S. alterniflora* to *J. roemerianus* or *Phragmites australis* dominance) for plant characteristics to alter trophic dynamics. There may also be nonintuitive interactions between habitat structure, predators, and prey in structured coastal habitats (Mattila et al. 2008), mediated by local abiotic factors. While not statistically distinct, our manipulative shoot height experiment revealed a 3-fold difference in predation of snails in our 10 cm treatment compared with our ambient plots. These results suggest there may be an interaction between shoot height and tidal height such that predation will be high in areas where the water level completely covers the shoots. Along our tidal amplitude gradient, we observed high rates of predation at our Wilmington site where both shoot height and tidal amplitude are high. However, at Hatteras Village, the water height over the marsh platform may have been too low for most nekton to move freely, resulting in low predation rates overall. While the tether lengths used for the shoot height experiment (up to 1 m) were different from the maximum length of 0.25 m used in the predation assays across a tidal inundation gradient, these two experiments were not intended to be directly comparable. We do recognize that consumption rates may have differed if longer tethers were used for the predation assay across a tidal amplitude gradient; however, we still hypothesize that abiotic cycles (e.g. tide, seasonality) on predation may mediate the influence of local habitat structure alone along the marsh-estuarine habitat boundary.

The support of nekton and the transfer of secondary production (i.e. energy flows) from tidal marshes to coastal systems can occur directly or indirectly via ontogenetic shifts or trophic transfers (“relays”; Deegan et al. 2000; Kneib 2000) and appear to be mediated by tidal dynamics of a given area. For example, in the northern GoM (where flooding duration is high and tidal amplitude is low), penaeid shrimp use marsh habitats and obtain resources before migrating offshore (Zimmerman et al. 2000), linking marsh-derived production to coastal systems (Turner 1977). Marsh production is also exported through direct predator-prey interactions and trophic transfers (Kneib 1997). These “relays” occur when intermediate consumers (e.g. pinfish) directly access the marsh surface or adjacent creek channels during flood tides, accumulate marsh production, and move into estuarine or coastal waters where they are consumed. Trophic transfers also occur in areas with higher tidal amplitudes, when large mobile predators (e.g. red drum, flounders) cross into the marsh to consume resident (e.g. mummichog) and more transient prey species (e.g. blue crabs; Nelson et al. 2012; Baker et al. 2016).

With changing climate, there may be shifts in abiotic cycles across terrestrial and aquatic ecosystems that alter trophic interactions across local and regional scales. For instance, changes in temperature in relation to photoperiod (day length) has resulted in phenological mismatches between predators and prey species across many taxa (Renner and Zohner 2018). This mismatch in the life cycle of predators and prey has caused booms in prey abundance and declines for predatory species, altering overall community structure (Edwards and Richardson 2004). Changes in sea level, increasing tidal amplitude and inundation time, may have the opposite effect in coastal systems. Our results show that as the water levels over coastal biogenic habitats increase, predators may have increased foraging opportunities, with concomitant impacts on prey populations. Immediate rises in water levels may benefit predators by increasing access across the edge and potentially increasing the flow of energy from marshes to estuarine habitats. However, if salt marsh grasses cannot outpace the rise in water levels over time, there could be a decline in habitat and nursery function (Kirwan et al. 2010). With continued changes in climate, untangling the interactions between abiotic cycles and biotic components of ecosystems across ecological boundaries is key to understanding both species interaction strengths and the mediation of cross-boundary energy flows.

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Data Availability Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at <https://data.gulfresearchinitiative.org> (doi: <https://doi.org/10.7266/n7-k3ey-ez49>).

Compliance with Ethical Standards

Disclaimer All applicable institutional and/or national guidelines for the care and use of animals were followed (IACUC 15-194.0).

Conflict of interest The authors declare that they have no conflict of interest.

References

- Aguilar, F.J., J.P. Mills, J. Delgado, M.A. Aguilar, J.G. Negreiros, and J.L. Pérez. 2010. Modelling vertical error in LiDAR-derived digital elevation models. *ISPRS Journal of Photogrammetry and Remote Sensing* 65 (1): 103–110.
- Baker, R., B. Fry, L.P. Rozas, and T.J. Minello. 2013. Hydrodynamic regulation of salt marsh contributions to aquatic food webs. *Marine Ecology Progress Series* 490: 37–52.
- Baker, H.K., J.A. Nelson, and H.M. Leslie. 2016. Quantifying striped bass (*Morone saxatilis*) dependence on saltmarsh-derived productivity using stable isotope analysis. *Estuaries and Coasts* 39 (5): 1537–1542.
- Carroll, J.M., L.J. Jackson, and B.J. Peterson. 2015. The effect of increasing habitat complexity on bay scallop survival in the presence of different decapod crustacean predators. *Estuaries and Coasts* 38 (5): 1569–1579.
- Deegan, L.A., J.E. Hughes, and R.A. Rountree. 2000. Salt marsh ecosystem support of marine transient species. In *Concepts and controversies in tidal marsh ecology*, ed. M.P. Weinstein and D.A. Kreeger, 333–365. Dordrecht: Springer.
- Duffy, J.E., S.L. Ziegler, J.E. Campbell, P.M. Bippus, and J.S. Lefcheck. 2015. Squidpops: a simple tool to crowdsourcing a global map of marine predation intensity. *PLoS One* 10 (11): e0142994.
- Edwards, M., and A.J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430 (7002): 881–884.
- Fagan, W.F., R.S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. *The American Naturalist* 153 (2): 165–182.
- Gorman, D., and S.D. Connell. 2009. Recovering subtidal forests in human-dominated landscapes. *Journal of Applied Ecology* 46 (6): 1258–1265.
- Grover, M.C., and H.M. Wilbur. 2002. Ecology of ecotones: interactions between salamanders on a complex environmental gradient. *Ecology* 83 (8): 2112–2123.
- Kirwan, M.L., G.R. Guntenspergen, A. D’Alpaos, J.T. Morris, S.M. Mudd, and S. Temmerman. 2010. Limits on the adaptability of coastal marshes to rising sea level. *Geophysical Research Letters* 37 (23): L23401.
- Kneib, R.T. 1997. Early life stages of resident nekton in intertidal marshes. *Estuaries* 20 (1): 214–230.
- Kneib, R.T. 2000. Salt marsh ecosystems and production transfers by estuarine nekton in the southeastern United States. In *Concepts and controversies in tidal marsh ecology*, ed. M.P. Weinstein and D.A. Kreeger, 267–291. Dordrecht: Springer.

- Kotler, Burt P., Joel S. Brown, and Hasson Oren. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72 (6): 2249–2260.
- Lewis, D.B., and L.A. Eby. 2002. Spatially heterogeneous refugia and predation risk in intertidal salt marshes. *Oikos* 96 (1): 119–129.
- Mattila, J., K. Heck, E. Millstein, E. Miller, C. Gustafsson, S. Williams, and D. Byron. 2008. Increased habitat structure does not always provide increased refuge from predation. *Marine Ecology Progress Series* 361: 15–20.
- Menge, B.A., and J.P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* 130 (5): 730–757.
- Minello, T.J., and L.P. Rozas. 2002. Nekton in gulf coast wetlands: fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications* 12 (2): 441–455.
- Minello, T.J., L.P. Rozas, and R. Baker. 2012. Geographic variability in salt marsh flooding patterns may affect nursery value for fishery species. *Estuaries and Coasts* 35 (2): 501–514.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences* 98 (1): 166–170.
- Nelson, J., R. Wilson, F. Coleman, C. Koenig, D. DeVries, C. Gardner, and J. Chanton. 2012. Flux by fin: fish-mediated carbon and nutrient flux in the northeastern Gulf of Mexico. *Marine Biology* 159 (2): 365–372.
- Polis, G.A., and S.D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist* 147 (3): 396–423.
- Polis, G.A., and D.R. Strong. 1996. Food web complexity and community dynamics. *The American Naturalist* 147 (5): 813–846.
- Potthoff, M.T., and D.M. Allen. 2003. Site fidelity, home range, and tidal migrations of juvenile pinfish, *Lagodon rhomboides*, in salt marsh creeks. *Environmental Biology of Fishes* 67 (3): 231–240.
- Renner, S.S., and C.M. Zohner. 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics* 49 (1): 165–182.
- Rozas, L.P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries* 18 (4): 579–590.
- Shervette, V.R., and F. Gelwick. 2008. Relative nursery function of oyster, vegetated marsh edge, and nonvegetated bottom habitats for juvenile white shrimp *Litopenaeus setiferus*. *Wetlands Ecology and Management* 16 (5): 405–419.
- Turner, R.E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. *Transactions of the American Fisheries Society* 106: 411–416 Taylor & Francis.
- Wolter, K.M. 2007. The jackknife method. *Statistics for Social and Behavioral Sciences*. In *Introduction to variance estimation*, ed. K.M. Wolter, 151–193. New York: Springer.
- Yahner, R.H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2 (4): 333–339.
- Yeager, L.A., E.W. Stoner, J.R. Peters, and C.A. Layman. 2016. A terrestrial-aquatic food web subsidy is potentially mediated by multiple predator effects on an arboreal crab. *Journal of Experimental Marine Biology and Ecology* 475: 73–79.
- Zimmerman, R.J., T.J. Minello, and L.P. Rozas. 2000. Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the northern Gulf of Mexico. In *Concepts and controversies in tidal marsh ecology*, ed. M.P. Weinstein and D.A. Kreeger, 293–314. Dordrecht: Springer.