Distribution and relative predation risk of nekton reveal complex edge effects within temperate seagrass habitat

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ABSTRACT

Edge effects may be important drivers of community dynamics across marine habitat mosaics. Past research has consistently suggested that within temperate and sub-tropical seagrass habitats, organisms inhabiting meadow edges experience lower survivorship, presumably correlated with increased predation. However, these survivorship trends have not consistently translated to differences in faunal densities between edge and interior regions of seagrass meadows. We evaluated the evidence of edge effects on predation upon two dominant mesopredators within temperate eelgrass (*Zostera marina*) communities of the U.S. East Coast: blue crabs (*Callinectes sapidus*) and pinfish (*Lagodon rhomboides*). We considered three lines of data to arbitrate the null hypothesis that edge has no impact on distribution or predation on blue crabs or pinfish: (1) relative density as measured by catch-per-unit-effort (CPUE) of blue crabs and pinfish within edge (< 1 m from unstructured sandflat boundaries) versus interior (> 3 m from unstructured sandflat boundaries) regions of eelgrass meadows; (2) distribution of acoustically tagged red drum (*Sciaenops ocellatus*), a recognized predator of both blue crabs and pinfish, within eelgrass meadows (at 1-m bin resolution); and (3) relative mortality of tethered blue crabs and pinfish within edge versus interior regions of eelgrass meadows. Additionally, we manipulated seagrass shoot density to evaluate potential interactions between local habitat complexity and edge effects. We found no statistically detectable difference in catch rates of blue crabs or pinfish in edge versus interior habitats, and red drum detection frequencies were statistically indistinguishable moving from the seagrass-sandflat boundary toward the meadow interior. Despite these findings, we did record statistically and ecologically significant edge effects on predation rates of tethered blue crabs and pinfish. Counter to previous work, we found that blue crabs survived > 2.5× longer, and pinfish survived > 2× longer, along the meadow edge relative to interior. Furthermore, the strength of these predation-related edge effects was most notable for blue crabs within plots with higher shoot density, while the opposite pattern was true for pinfish. These findings are, in part, consistent with the dichotomy apparent in the seagrass literature with respect to edge effects on faunal density and survivorship. Additionally, our work provides new detail on how habitat edges may affect the population ecology of larger bodied, more mobile mesopredator species that have not received as much attention in previous studies (i.e., higher survivorship possible along edges).

1. Introduction

Estuarine landscapes are comprised of mosaics of interconnected habitats such as mudflats, salt marshes, shellfish reefs, mangrove forests, and seagrass meadows. Along the boundaries between these habitats, edge effects may manifest as differences in the density, biomass, settlement, growth, or survivorship of flora and fauna between the interior versus outer margin (i.e., edge) of a habitat patch (Jelbart et al., 2006; Johnson and Heck, 2006; Murcia, 1995; Ries et al., 2004). In marine habitats, these differences may arise following from gradients in

flow (e.g., food or larval supply; Carroll et al., 2012) or predator accessibility (Smith et al., 2011) along an axis moving from the habitat boundary into the interior. Still, evidence regarding the direction (i.e., negative, positive) of impact of edges on resident organisms is equivocal, with many examples of fitness being depressed (Shulman, 1985; Amortegui-Torres et al., 2013), enhanced (Baltz et al., 1993; Peterson and Turner, 1994), or insensitive (Hindell and Jenkins, 2005 [Biomass]) with regard to proximity to habitat boundaries.

When focusing within individual estuarine habitats, however, more consistent edge effects may emerge. Seagrass, for example, is one of the

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Table 1
Summary table of studies examining potential edge effects on the density and survival of seagrass-associated fauna.

| Study	Seagrass	Location	Taxa	Edge distance	Response variable	Conclusion
Hovel and Lipcius, 2002	Z. marina	Virgina (USA)	Crustaceans	< 1 m	Density	Edge < Interior
Bell et al., 2001	H. wrightii, T. testudinum	Florida (USA)	Polychaetes	< 1 m	Density	Edge < Interior
Johnson and Heck, 2006	H. wrightii, T. testudinum	Florida, Alabama (USA)	Crustaceans	< 1 m	Density	Edge < Interior
Hovel et al., 2002	H. wrightii, T. testudinum	North Carolina (USA)	Fishes	Undefined	Density	Edge < Interior
Carroll et al., 2012	ASU	New York (USA)	Bivales	< 1 m	Density	Edge > Interior
Macreadie et al., 2010	ASU	South Australia (AUS)	Fishes	< 0.5 m	Density	Edge > Interior
Macreadie et al., 2010	ASU	South Australia (AUS)	Crustaceans	< 0.5 m	Density	Edge > Interior
Moore and Hovel, 2010	Z. marina	California (USA)	Epifauna	< 1 m	Density	Edge > Interior
Moore and Hovel, 2010	ASU Caging	California (USA)	Epifauna	< 0.5 m	Density	Edge > Interior
Smith et al., 2008	H. nigricaulis	South Australia (AUS)	Fishes	< 1 m	Density	Edge > Interior
Warry et al., 2009	H. nigricaulis	Port Phillip Bay (AUS)	Many taxa	0 m	Density	Edge > Interior
Bologna and Heck, 1999	T. testudinum	Florida (USA)	Bivales	< 1 m	Density	Edge > Interior
Eggleston et al. 1998	Z. marina, H. wrightii	North Carolina (USA)	Crustaceans	Undefined	Density	Edge > Interior
Eggleston et al. 1998	ASU	North Carolina (USA)	Crustaceans	Undefined	Density	Edge > Interior
Moore and Hovel, 2010	Z. marina	California (USA)	Fishes	< 2 m	Density	Edge = Interior
Bologna and Heck, 2002	T. testudinum	Florida (USA)	Multiple invert Taxa	< 0.5 m	Density	Edge > < = Interior
Jelbart et al., 2006	Z. capricorni	Sydney (AUS)	Fishes	< 4 m	Density	Edge ≤ Interior
Boström et al., 2006	Multiple species	Global	Multiple invert taxa	Undefined	Density	Edge ≥ Interior
Tanner, 2005	Zostera	South Austrailia (AUS)	Multiple invert taxa	< 1 m	Density	Edge ≥ Interior
Smith et al., 2011	H. nigricaulis	South Australia (AUS)	Fish	< 1 m	Density	Edge > < Interior
Carroll et al., 2012	ASU	New York (USA)	Bivales	< 1 m	Survivorship	Edge < Interior
Peterson et al., 2001a, 2001b	Z. marina	Maine, Florida (USA)	Crustaceans	< 2 m	Survivorship	Edge < Interior
Gorman et al., 2009	Z. marina	Newfoundland (CAN)	Fish	0 m	Survivorship	Edge < Interior
Hovel and Lipcius, 2002	Z. marina	Virgina (USA)	Crustaceans	< 1 m	Survivorship	Edge < Interior
Smith et al., 2011	H. nigricaulis	South Australia (AUS)	Fish	< 1 m	Survivorship	Edge < Interior
Bologna and Heck, 1999	T. testudinum	Florida (USA)	Bivales	< 1 m	Survivorship	Edge < Interior

Artificial sea grass (ASU).

major structurally complex, biogenic habitats in estuarine environments, and has received considerable attention in studies assessing edge effects (Boström et al., 2006). Seagrass serves as a useful model system in this context due to the diverse patch orientations observed among meadows (Boström et al., 2006; Yeager et al., 2016), clear boundaries between seagrass and unstructured sandflat habitats, as well as the presence of abundant and species-rich faunal communities (Thayer et al., 1984). In particular, the dynamics of predator-prey interactions along habitat edges, with subsequent effects on faunal density, have been scrutinized across a number of seagrass species and predator-prey combinations (Table 1). Six previous studies explicitly compared survivorship of small prey species (bivalves, crustaceans, and small fishes) in edge versus interior regions of seagrass meadows (Bologna and Heck, 1999; Carroll et al., 2012; Gorman et al., 2009; Hovel and Lipcius, 2002; Peterson et al., 2001a, 2001b; Smith et al., 2011). In every case, survivorship of these taxa was depressed along seagrass edges, presumably due to elevated predation threats (Table 1). Notably, these differences in survivorship between seagrass edge versus interior did not appear to translate reliably in to elevated bivalve, crustacean, or fish densities in interior regions of seagrass habitat relative to seagrass edges (e.g., Bell et al., 2001 versus Warry et al., 2009). Approximately two-thirds of the 20 published comparisons (allowing for taxon specific comparisons within publication) documented higher densities along seagrass edges relative to seagrass interiors (Table 1).

Several factors may contribute to this disconnect. Elevated settlement (Carroll et al., 2012) or growth rates (Bologna and Heck, 2002) within edge regions of seagrass habitat may offset relationships between survivorship and density. Indeed, the tradeoffs between resource availability and risk along edge-to-interior transects is well documented in the literature (Table 1 and references therein). However, the fitness consequences of survival generally outweigh those related to resource acquisition (sensu Heck Jr et al., 2003), and thus this dynamic is unlikely to completely explain the differences between density and survivorship patterns within seagrass meadows. Additionally, movement of seagrass-associated species between edge and interior regions within habitat patches may swamp gradients in predation pressure, attenuating the effects of spatially structured survivorship on resultant prey

density patterns. Furthermore, most previous studies within seagrass have examined survivorship of small epifauna (bivalves, mesograzer crustaceans) preyed upon by crabs and fishes that range in size between 5 and 15 cm (carapace width or total length). Notably, these mesopredatory crabs and fishes are also subject to predation by even larger fishes, birds, reptiles, and mammals that may forage differently between edge and interior regions of habitat patches. For instance, tiger shark tracking has shown that these large mobile predators prefer seagrass edge microhabitats (Heithaus et al., 2006). Indeed, large (> 50 cm) mobile predators are often conceptualized as putative edge specialists within estuarine habitat mosaics (sensu, Wirsing et al., 2007), although quantitative data on the distribution of these animals are markedly rare at landscape scales. Thus, understanding how these higher-order predators affect the survivorship and distribution of mesopredators (5–15-cm crabs and fishes) could explain why previous research has documented an obvious disconnect between the survivorship and abundance of even smaller (1–5 cm bivalves, crustaceans, and fishes) seagrass-associated fauna along edge-to-interior gradients (sensu Table 1).

Within temperate U.S. East Coast and Gulf of Mexico estuaries, red drum (Sciaenops ocellatus) are often anecdotally depicted - as are other large mobile fishes - as edge predators along seagrass, oyster reef, and saltmarsh habitats (Dance and Rooker, 2015). Red drum are also major predators on blue crabs (Callinectes sapidus) and pinfish (Lagodon rhomboides) (Scharf and Schlicht, 2000), which themselves function as dominant mesopredators within seagrass communities (Nifong and Silliman, 2013). Notably, blue crabs (Hovel and Lipcius, 2002) and pinfish (Hovel et al., 2002) densities have been reported as depressed along seagrass meadow edges, relative to interior regions, potentially corroborating the hypotheses that higher-order predators such as red drum exert elevated mortality of mesopredators along seagrass edges. Therefore, we examined the potential for differences in predator-prey interactions among these species between edge and interior regions of seagrass meadows to expand the functional groups (e.g., larger body size, greater mobility) represented in tests of edge effects, and potentially contribute toward the reconciliation of an existing paradox evident in previous edge studies regarding seagrass-associated faunal
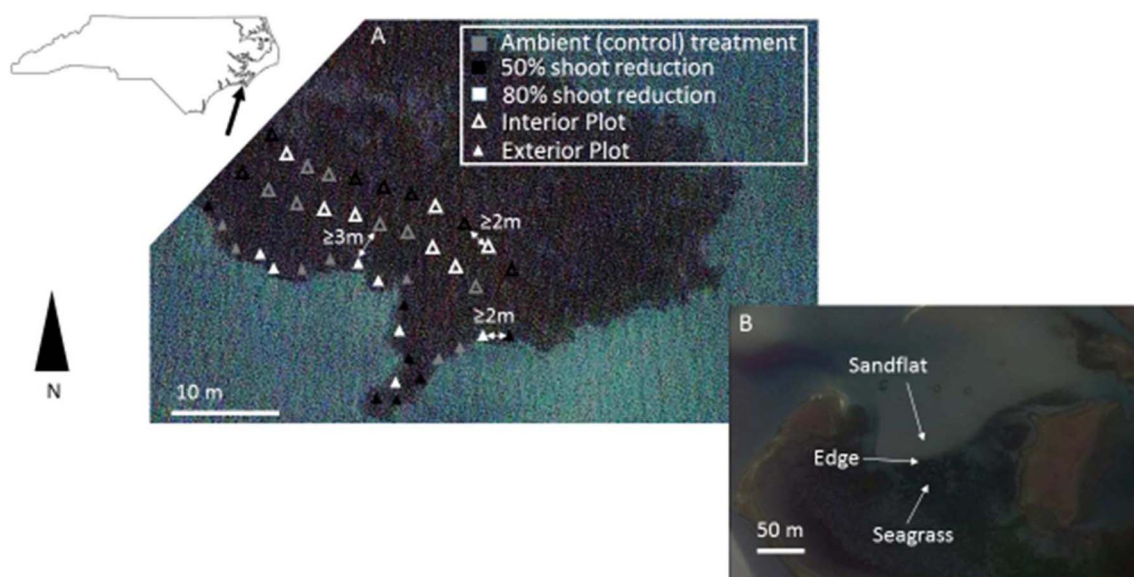
Fig. 1. Aerial imagery of Jack's Island (A) and Middle Marsh (B) seagrass study sites in Back Sound, North Carolina. Included in the Jack's Island imagery is the spatial orientation of tethering plots to assess the effects of location with meadow and seagrass shoot density on predation on juvenile blue crabs and pinfish. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

survivorship and density patterns. We evaluated evidence for edge effects in this model system using three complimentary lines of data: relative density of blue crabs and pinfish between edge and interior regions of seagrass meadows; distribution of red drum between edge and interior regions of seagrass meadows; and relative mortality of blue crabs and pinfish between edge and interior regions of seagrass meadows.

2. Methods

2.1. Study sites

Our investigation of seagrass edge effects on mesopredators and larger predators took place in Back Sound, North Carolina. We utilized two existing research initiatives, comprising two study sites, to complete our experiments. First, relative density (catch rates) and predation-driven relative mortality (loss rates of tethered individuals) of blue crabs and pinfish were monitored within a 5600 m^2 seagrass meadow at Jack's Island (N34°40′21″, W76°34′30″) along the southern rim of Back Sound (Fig. 1). These density and predation measurements were collected during June–July 2015, in connection with the global-scale Zostera Experimental Network study (sensu, Reynolds et al., 2017). Second, the distribution of acoustically tagged red drum was evaluated in July–August 2011, across a 31,000 m^2 seagrass meadow and adjacent sandflat in Middle Marsh (N34°41′28″, W76°37′17″), along the western end of Back Sound (Fodrie et al., 2015) (Fig. 1). We chose Middle Marsh for the tracking component of our study due to its semi-enclosed nature (useful in maximizing the detection range/frequency of fish). Although we were not able to conduct all aspects of our study within the same seagrass meadow, and Jack's Island is 4.5 km to the east-southeast of Middle Marsh, the two sites are of similar depth (~0.25 m at mean low tide), tidal regime (~1.5 m average range), salinity (> 30 psu), seagrass shoot density/height (577 ± 36 shoots m^{-2} vs. 575 ± 36 shoots m^{-2} (mean ± SE), respectively, based on the average of forty 0.02-m^2 quadrats collected at each site), and nekton composition (Baillie et al., 2015; Yeager et al., 2016). Additionally, both sites are contiguous meadows (i.e., one connected unit) as detailed in Fodrie et al. (2015), Yeager et al. (2016), and Livernois et al. (2017). Therefore, we expect results from each site to be representative of the other in the broader context of how edges might influence density and predator-prey dynamics of mobile nekton within these seagrass meadows.

2.2. Blue crabs and pinfish relative densities between seagrass edge and interior

To quantify relative densities of both blue crabs and pinfish, we deployed 12 Gee-style minnow traps (41-cm long, 22-cm wide, 0.3-cm galvanized mesh-wire cylinders, with funneled openings standardized to 4-cm diameter) 0–1 m from the seagrass-sandflat boundary (i.e., "edge"), and 12 minnow traps > 3 m from the seagrass-sandflat boundary (i.e., "interior") during five separate trials (June 10–June 24, 2015). These distances correspond with edge/interior classifications in previous seagrass studies (Table 1), but otherwise the deployment of traps was haphazard within the meadow. We used a combination of baited (N = 6; using ~10 pieces of dried dog food; Able et al., 2015) and unbaited (N = 6) traps during each deployment in both edge and interior regions of the seagrass meadow to sample individuals that may be attracted to food + structure (baited trap), or structure alone (trap only). Minnow traps were deployed between 11 am and 3 pm and soaked for 24 h, after which we identified, enumerated, and released all captured crustaceans and fishes. Catch-per-unit-effort (CPUE; individuals trap^{-1}) was determined for both blue crabs and pinfish across the 120 total trap deployments.

2.3. Red drum distribution between seagrass edge and interior

We used a combination of high-resolution aerial imagery and acoustic tagging to chart the movement activity of red drum in relation to distance from a sandflat-seagrass boundary in Middle Marsh as part of a broader red drum tracking study (e.g., Fodrie et al., 2015 and methods therein). We considered these data as one proxy of predation potential on blue crabs and pinfish across a local seagrass meadow, acknowledging that we were not able to monitor the entire predator field. We obtained satellite images (< 1-m resolution) of Middle Marsh taken on July 15, 2011, through National Oceanic and Atmospheric Administration databases (Geo-Eye; https://www.satimagingcorp.com/gallery/geoeye-1/). Using these images, we characterized and mapped seagrass and sandflat habitats as distinct polygon features in ArcMap 10.0.

Beginning on July 15, 2011, we collected eight red drum (47.1 ± 2.7 cm total length) via hook-and-line from in-and-around Middle Marsh. Coded acoustic tags (LOTEK Wireless MM-MR-11-28) were surgically implanted following Dresser and Kneib (2007), and

these fish were released 24-h post-implant surgery at the center of our acoustic detection arena in Middle Marsh (described below), where they were then allowed to move freely. The LOTEK tags emitted a pulsed chirp, unique to each fish, every 5 s that we used to chart each individual's position with respect to the seagrass-sandflat boundary from the time of release (variable among fish) through August 31, 2011.

We used a LOTEK MAP 600 Acoustic Telemetry System to detect the signals emitted from the tagged red drum. Our system consisted of eight georeferenced hydrophones, each cabled to a central processing unit. Hydrophones were positioned to allow acoustic "line of sight" for at least three of the listening stations along the entire seagrass-sandflat boundary (375 m in length), and to a distance of > 40 m into the interior of both the seagrass meadow and the adjacent sandflat. When signals from a LOTEK transmitter were detected by ≥ 3 of the hydrophones, we triangulated that fish's position with sub-meter accuracy. Detection accuracy was checked daily using beacon tags placed at known, georeferenced positions within the array (Fodrie et al., 2015). All detection locations were mapped in ArcMap 10.0 to determine the position of fish throughout the entire study period in relation to distance from the seagrass-sandflat boundary. We treated individual red drum as the unit of replication. For each fish, we binned position data with breaks at every meter from 0 to 40 m, both within the seagrass and the sandflat habitats, separately. We determined the spatial coverage (m^2) of each of those 1-m wide bins moving from the seagrass-sandflat boundary toward the habitat interior by creating new polygon features in ArcMap 10.0. We then calculated the detection density (detections m^{-2}) at each distance (e.g., 0–1 m, 1–2 m, 2–3 m, etc.) for each fish within seagrass and sandflat habitats, separately.

2.4. Relative predation on blue crabs and pinfish between seagrass edge and interior

We utilized tethering trials as a proxy of relative predator-driven mortality of blue crabs and pinfish within edge and interior regions of the seagrass meadow at Jack's Island. Our design consisted of 21 "edge" (0–1 m from seagrass-sandflat boundary) and 21 'interior' (> 3 m from seagrass-sandflat boundary) plots, with each plot defined by two 1×1-m subplots separated from each other by 0.5 m (but with the entirety of each plot being at the suitable distance for edge/interior designations). Each of the 42 total plots were separated from one another by > 2 m (Fig. 1). For both the edge and interior treatments, seagrass shoot density was reduced by 50% in a third of the plots, seagrass shoot density was reduced by 80% in another third of the plots, and seagrass shoot density was left at ambient in the final third of plots (all randomly assigned). This resulted in a 2×3 experimental design in which meadow location and shoot density were fully crossed. Reduction of shoot densities was achieved by deploying a 1×1-m quadrat with a 10×10 grid (each grid cell = $0.01\ m^2$). We then removed all seagrass in 50 or 80 of the cells (randomly selected) for the 50% and 80% reduction treatments, respectively. The resultant shoot densities were as follows: ambient treatments had a mean of 575 ± 36 shoots m^{-2}, 50% reduction treatments had a mean of 283 ± 18 shoots m^{-2}, and 80% reduction treatments had a mean of 124 ± 7 shoots m^{-2} (without noticeable differences in edge versus interior plots at this site, and no overlap in shoot counts among ambient, 50% reduced, and 80% reduced treatments).

We deployed 126 tethered blue crabs (5.2 ± 0.1 cm carapace width) and 168 tethered pinfish (5.1 ± 0.1 cm total length) in plots over three and four trials, respectively. We ran one less trial with blue crabs due to the availability of specimens within our preferred size range during our experimental window. All crabs and pinfish were collected via small trawl on the day before deployment. During each trial, a tethered blue crab was randomly assigned to one of the subplots within each plot, while a tethered pinfish was placed in the remaining subplot (i.e., 42 juvenile blue crabs and 42 pinfish were deployed in a trial). Each tethering device consisted of a lawn staple anchor placed in

the center of a subplot, connected to a 30-cm long section of 3.6-kg clear monofilament fishing line. For blue crabs, the free end of the monofilament was glued to the center of the crab's carapace after making a lasso around the crab's body. Blue crabs had each of their claws lightly glued shut using Loctite super glue gel to prevent them from cutting the tether. Pinfish were tethered through the soft tissue immediately behind their lower jaw bone by piercing this tissue, threading the line through the piercing, and the tying an overhand knot in the line. As a method check, we tethered > 40 blue crabs and > 20 pinfish in laboratory tanks outfitted with artificial seagrass. Over a 4-day period, none of the tethered animals became free, tethered animals did not behave noticeably different than untethered animals also in the tank (aside from restricted movement), and tethered animals did not become entangled in artificial seagrass blades. In our previous experiments, the loss of tethered organisms in field cages (controls) was also essentially zero (e.g., Peterson et al., 2001a), although we acknowledge that the relative predation rates we report could represent some overestimate if unaccounted-for tether loss in the field did occur.

Tethered blue crabs and pinfish were deployed in our field experiment ~3 h before daytime high tides. Following deployment, each tethered animal was checked after 1 h, 2 h, 3 h, and 24 h to assess loss rates (presumably via predation). Individual blue crabs or pinfish missing at the 1-, 2-, 3-, and 24-hour checks were randomly assigned a survival time ranging between 0–1, 1–2, 2–3, and 3–24 h, respectively, to acknowledge that we could not be sure within check intervals when predation occurred. Furthermore, this approach insured that we did not artificially reduce variances among replicates, and was thus considered a conservative approach. Any animal remaining on its tether after 24 h was assigned a survival time of 24 h, and then released after removing the monofilament tether (both species) and separating the claws by severing the glue bond (blue crabs).

2.5. Statistical approaches

To assess whether catch rates of blue crabs and pinfish varied across edge versus interior portions of the seagrass meadow, we ran two-way ANOVAs, separately for each species, with location (edge v interior) and trap presentation (unbaited v baited) as factors on CPUE data from minnow traps (individuals trap^{-1}). CPUE data passed tests of normality and homoscedasticity (F-max test) for each main effect for both species. To assess the distribution of red drum across a seagrass-sandflat ecotone, we ran one-way ANOVAs, separately for acoustic positioning data from seagrass and sandflat habitat types. We used distance from the seagrass-sandflat boundary (in 1-m bins) as the experimental factor, and detection density within each distance bin, averaged among fish, as the response variable (detections m^{-2} fish^{-1}). For both seagrass and sandflat, the red drum position data appeared normally distributed and passed the parametric assumption of homoscedasticity (Levene's test). Finally, two-way ANOVAs were performed to assess the main and interactive effects of meadow location (edge v interior) and local shoot density (ambient v 50% reduced v 80% reduced) on predation rates of tethered blue crabs. We used time to consumption (removal from tether) of each blue crabs among treatment combinations as the response variable. Time-to-consumption data passed tests of normality and homoscedasticity (F-max test) for blue crabs, but only the normality assumption for pinfish. Log $(x + 1)$ transformations failed to homogenize variance levels between treatments (edge v interior) for pinfish data. Therefore, we proceeded with non-parametric analogues to assess the effects of meadow location (Mann-Whitney U) and shoot density (Kruskal-Wallis) on time to consumption for tethered pinfish. Statistical significance was set at $\alpha = 0.05$ for all analyses. We conducted all analyses in StatView 5.0.1.
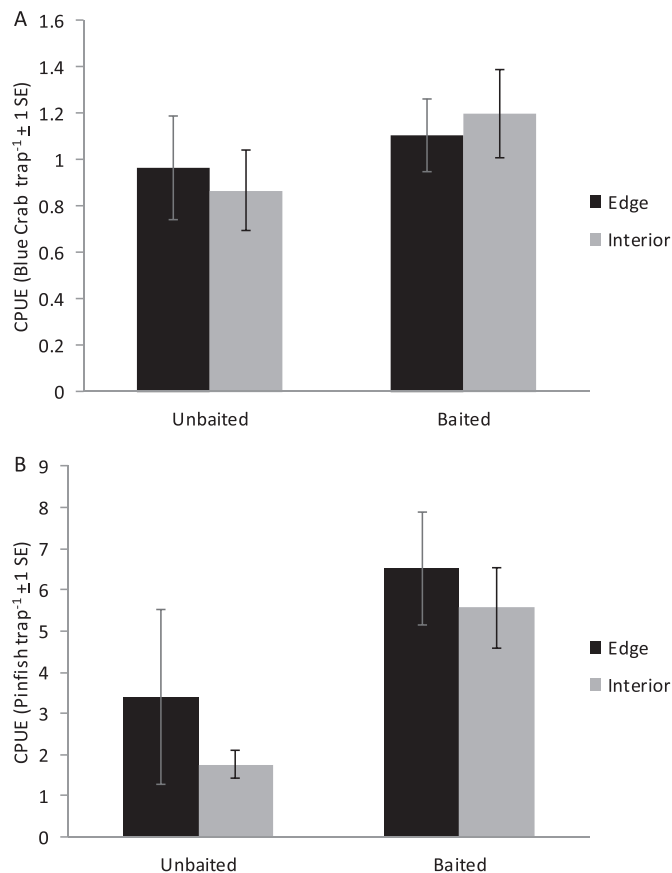
Fig. 2. Catch Per Unit Effort (CPUE; mean + 1SE) of Blue Crabs (A) and Pinfish (B) in baited and unbaited minnow traps. Catch rates of both species were recorded along the seagrass edge (< 1 m from seagrass-sandflat boundary) and within the meadow interior (> 3 m inside the seagrass-sandflat boundary). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Blue crabs and pinfish relative densities between seagrass edge and interior

Pinfish (493 individuals, 61.8% of total catch) and blue crabs (125 individuals, 15.7%) dominated our catches, in which we captured 798 individual animals in total, representing 20 species. Pigfish (*Orthopristis chrysoptera*, 83 individuals, 10.4%), oyster toadfish (*Opsanus tau*, 29 individuals, 3.6%), mud crabs (*Panopeus herbstii*, 21 individuals, 2.6%), grass shrimp (*Palaemonetes pugio*, 9 individuals, 1.1%), and penaeid shrimp (*Penaeus* spp., 8 individuals, 1.0%) were other taxa that comprised > 1% of the total catch, and all these taxa exhibited statistically indistinguishable catch rates between seagrass edge and interior. For blue crabs CPUEs, we found no statistically significant interaction between (F = 0.262, df = 1, P = 0.610), or main effects of, location within the seagrass meadow (F < 0.001, df = 1, P = 0.993) and trap presentation (F = 1.501, df = 1, P = 0.223). Indeed, we uniformly captured ~1.0–1.25 blue crabs trap^{-1} across all treatment combinations (Fig. 2A). Similarly, we found no statistically significant interaction between meadow location and trap presentation on the CPUEs of pinfish (F = 0.010, df = 1, P = 0.921), and there was no statistically reliable main effect of meadow location on pinfish CPUEs (F = 0.273, df = 1, P = 0.602). We do acknowledge, however, that in both baited and unbaited traps, there were statistically non-significant trends of higher mean pinfish CPUEs along the seagrass meadow edge (~3–6 pinfish trap^{-1}) relative to the interior (~2–5 pinfish trap^{-1}) (Fig. 2B). Unlike blue crabs, we did document a statistically significant effect of trap presentation on pinfish CPUEs (F = 20.179, df = 1, P < 0.001). Along both the meadow edge, as well as in the meadow interior, we caught ~25–50% more pinfish in baited traps than in unbaited traps (Fig. 2B).

3.2. Red drum distribution between seagrass edge and interior

For both the seagrass meadow (F = 0.126, df = 39, P = 0.999) and sandflat (F = 0.445, df = 39, P = 0.994), red drum detection densities were statistically indistinguishable moving across transects from the seagrass-sandflat boundary toward the interior of each habitat, separately. Broadly, we recorded 0.02–0.09 detections m^{-2} fish^{-1} across the entire seagrass meadow (Fig. 3). Although the data suggested a modest peak in detection densities at 10–15 m inside the seagrass meadow, our study was characterized by high individual variability among red drum, indicating no clear gradient in the use of edge versus interior regions of seagrass meadows of this predator at the population level. Compared to seagrass habitat, detection densities were uniformly low across the sandflat (Fig. 3; < 0.02 detections m^{-2} fish^{-1}). We do note that within 4 m of the seagrass-sandflat boundary, the mean detection density of red drum on the sandflat roughly doubled to ~0.04 detections m^{-2} fish^{-1}, although this trend was also characterized by high inter-individual variability (Fig. 3). We also considered if red drum habitat use differed between night and day, but found no evidence that distribution patterns shifted over diel cycles.
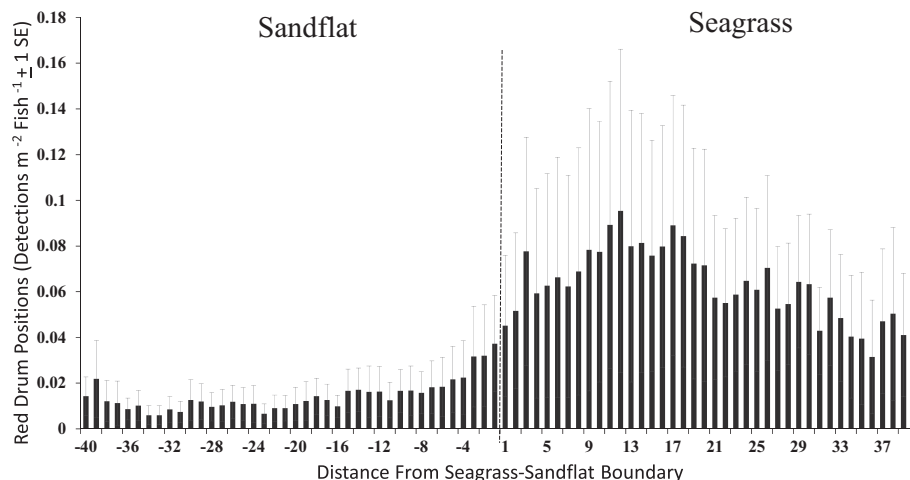
Fig. 3. Density of red drum detections, averaged across eight acoustically tagged individuals (detections m^{-2} fish^{-1}), at 1-m intervals, from the seagrass-sandflat boundary (centered along the x-axis) to 40 m inside each of these two habitats. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
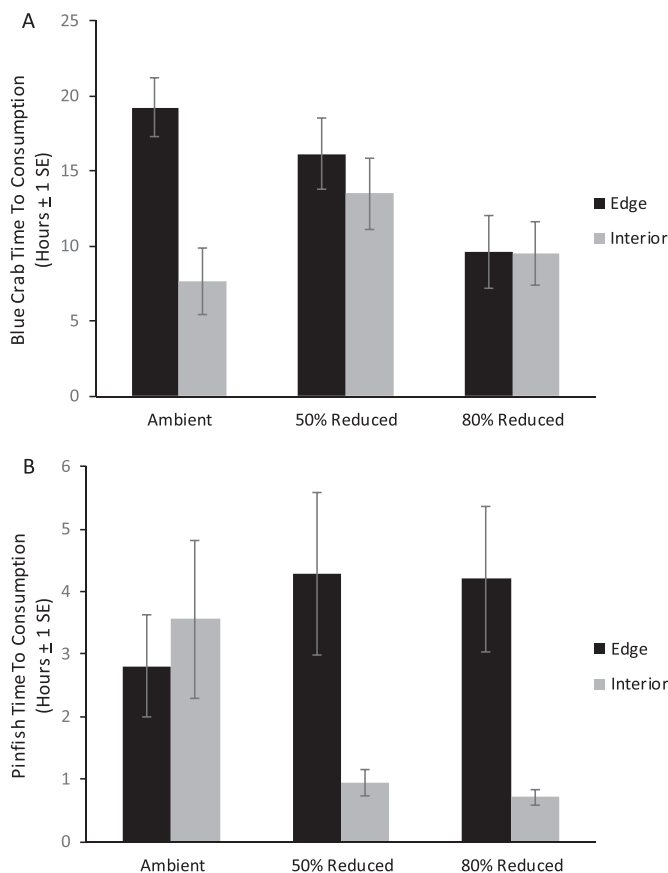
Fig. 4. Time to consumption of tethered blue crabs (A) and pinfish (B) as a function of location with a seagrass meadow and seagrass shoot density. Tethered animals were deployed along the seagrass edge (< 1 m from seagrass-sandflat boundary) and within the meadow interior (> 3 m inside the seagrass-sandflat boundary). Within these two meadow locations, tethers were placed in plots that either remained at ambient shoot densities, or in which shoot densities were reduced by 50% or 80%. We determined time to consumption via serial checks of tethered individuals at 1, 2, 3, and 24 h. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Relative predation on blue crabs and pinfish between seagrass edge and interior

For relative predation rates on blue crabs (time to consumption), we found a statistically significant interaction between location within the seagrass meadow and shoot density ($F = 3.448$, df = 2, $P = 0.036$). While time to consumption of blue crabs generally decreased with reductions in shoot density, there was little difference in time to consumption between edge and interior treatments when seagrass shoot density had been reduced by 50% (time to consumption was ~14 h regardless of meadow location) or 80% (time to consumption was ~10 h regardless of meadow location) (Fig. 4A). Conversely, mean time to consumption of tethered blue crabs was > 2.5× longer in edge plots (~20 h) relative to interior plots (~7.5 h) where seagrass shoot density remained at ambient levels (Fig. 4A). Overall, only 12% of blue crabs tethered along the meadow edge were consumed within 3 h, while 40% of the blue crabs tethered within the seagrass interior were consumed during that period.

Time to consumption of pinfish was statistically different between edge and interior treatments ($Z = -2.243$, $P = 0.024$), but not consistently affected by our experimental manipulation (removal) of patch-level biogenic structure ($H = 5.533$, df = 2, $P = 0.063$). Across all individuals, 70% of pinfish tethered along the seagrass edge were consumed within 3 h, while 94% of pinfish tethered in the seagrass interior were consumed over that interval. Although our non-parametric

approaches did not allow us to evaluate the statistical support of interactive effects among location (edge v interior) and shoot density, patterns within our dataset strongly suggest that an interaction was likely present. Whereas location within the seagrass bed appeared to have the largest effect on blue crabs survival at ambient shoot densities, the opposite was true for pinfish. Time to consumption for pinfish was roughly equivalent between meadow locations at ambient shoot densities (~3 h), but was > 4× longer in edge versus interior plots in both the 50% and 80% shoot reduction treatments (i.e., > 4 h compared to < 1 h) (Fig. 4B).

4. Discussion

Our experiments demonstrated that both blue crabs and pinfish may experience lower predation risk along the edge of the seagrass meadow at our study site. Interestingly, these edge effects for blue crabs and pinfish were apparently modulated by patch-level seagrass shoot density, suggesting multiscale interactions in predator-prey dynamics within this system. While our results differ from the literature that has consistently reported increased predation risk along seagrass edges (Table 1), our work targeting mesopredators may also help explain these earlier findings that focused primarily on smaller bivalves, crustaceans, and fishes. Consistent with the literature, however, the differences we observed in predation risk between seagrass edges and interiors did not manifest as clear differences in blue crabs or pinfish catch rates in edge versus interior seagrass habitats. Nor did we observe obvious differences in habitat use across an edge-to-interior transect by red drum - a known predator of both blue crabs and pinfish (e.g., Scharf and Schlicht, 2000; although certainly not the only predator). Below, we place these results in greater context regarding the landscape ecology of marine habitat mosaics.

Inclusion of interactions at multiple trophic levels will support a more complete understanding of how edge effects govern predator-prey interactions and overall community dynamics. This is particularly evident as we learn more regarding density and behaviorally mediated trophic cascades that play out across marine landscapes. For instance, dolphins, dugongs, and turtles have all been shown to occupy deeper-water edges of tropical seagrass in response to the foraging behaviors of tiger sharks (e.g., Wirsing et al., 2007), with consequences for nutrient cycling and lower trophic levels across meadow landscapes (Burkholder et al., 2013). To our knowledge, our work is among the first to demonstrate evidence of reduced mortality on larger mesopredator species (> 5 cm in carapace or total length) along the edges of temperate seagrass meadows. Therefore, we speculate that this could serve as a mechanism for why previous studies have consistently documented greater danger for smaller-bodied fauna along seagrass edges (Table 1). Specifically, our results suggest that mesopredators along the edges of seagrass may, in some contexts, experience less threat from larger predators, allowing them to impose greater foraging pressure on their own prey resources such as smaller bivalves, crustaceans, and fishes (even if mesopredator densities are not measurably different between edge and interior habitats). This is particularly important in the context of behaviorally mediated, rather than density mediated, top-down effects that may be important in seagrass ecosystems (e.g., Toscano et al., 2010).

Our examination of edge effects on faunal density, distribution, and relative survival complements previous studies linking these variables to other landscape attributes such as patch size, patchiness, and connectivity. Patchy habitats and small patches contain a high proportion of edge habitat, and effects of patchiness and patch size on density and survival may largely be due to edge effects (Carroll and Peterson, 2013). Our results correspond to some previous studies on smaller mesopredators (juvenile crabs smaller than the ones used in our study) that found higher survival rates in small patches and in patchy seascape configurations (e.g., Hovel and Lipcius, 2001; Hovel and Fonseca, 2005), but are opposite to some studies on bivalves (scallops and hard

clams) for which survival was higher in larger patches and in continuous seascapes (e.g., Irlandi et al., 1995; Carroll and Peterson, 2013).

Notably, we also observed an interaction between landscape-scale (edge-interior) and patch-scale (shoot density) factors that determined relative predation risk for blue crabs and also, potentially, pinfish (although for pinfish we relied on visual interpretation of the data). Blue crabs only exhibited lower predation risk along edges in patches defined by relatively high (ambient) shoot densities. Conversely, pinfish experienced lower predation along edges in patches characterized by low (reduced) shoot densities. Although a predictive framework to explain differences in predation patterns for these two mesopredators is beyond the scope of our current data, several hypotheses based on the natural history of these species are worth considering. For instance, we suspect that at ambient shoot densities, cannibalistic adult blue crabs were a major source of tethered blue crabs mortality (Hines and Ruiz, 1995). Indeed, on multiple occasions we observed larger blue crabs attacking our tethered blue crabs, while other predators are not as effective in foraging for juvenile blue crabs in dense seagrass (Hovel and Lipcius, 2001). Adult blue crabs may have concentrated in the seagrass meadow interior, as well as avoided plots with reduced seagrass cover, as they themselves generally prefer dense seagrass for protection and movement corridors (sensu Micheli and Peterson, 1999). As a result, we saw the largest difference in blue crabs survival at ambient shoot densities as this is where larger, adult blue crabs may have concentrated (although this remains a question for further testing). Conversely, in reduced seagrass plots, we suspect other predators capitalized on the exposure of tethered blue crabs. Potentially, these other predatory species did not forage differentially between edge and interior plots (e.g., red drum).

Whereas blue crabs rely heavily on concealment, which is effective except against larger conspecifics, pinfish are more conspicuous and rely on a combination of refuge use and mobility to avoid predation. At high shoot densities, pinfish have substantial cover to conceal themselves from their predators, regardless of broader landscape-level conditions. At lower shoot densities, however, the inability of pinfish to hide in the surrounding habitat could have increased their visibility and susceptibility to either roving or ambush predators occupying seagrass (sensu Martin et al., 2010). The limits of our data preclude any conclusive determination regarding the identity of predators, although we hypothesize that ambush predators may have played a key role given the edge-interior patterns we observed, and we do note that one tether was recovered with a lizardfish (*Synodus foetens*) still holding on to the swallowed pinfish. Despite these limitations, we documented cursory evidence of a relative predation refuge for pinfish along the edge of seagrass (versus interior) when seagrass density is low.

A remaining question is why survival differences between edge and interior regions of seagrass meadows do not translate to differences in blue crabs and pinfish densities. Notably, since our data do not follow the pattern of higher relative survivorship in meadow interiors, the resource-risk tradeoffs invoked in previous studies (sensu Table 1 and references therein) to explain why densities are uniform across edge-to-interior transects are unlikely to account for our findings. We propose two other mechanisms: first, given the relative small distances between edge and interior treatments that define nearly all existing studies (Table 1), mobility within a single seagrass meadow may swamp the ability of mortality to generate spatial gradients in densities; and second, our findings highlight that patch-level features such as shoot density may interact with landscape-level features such as distance to seagrass boundaries (see also: Smith et al., 2011). Often, as in our study, this is not accounted for in sampling mobile fauna densities. We conducted both minnow trapping and acoustic tagging without accounting for patch-scale gradients in seagrass characteristics, which may have obscured the ability to observe edge-interior differences in catch rates. However, we do note that differences in epifaunal (Tanner, 2005; Moore and Hovel, 2010) and juvenile blue crabs (Hovel and Lipcius, 2002) densities between seagrass patch edges and patch interiors did

not depend on edge-interior differences in structural complexity in previous work.

Despite widespread appreciation for the potential importance of edge effects on population fitness or community dynamics, the width of functional edges within habitat patches are notoriously hard to define and are likely taxon and habitat specific. The edges of seagrass habitats have been described as critical foraging areas for a variety of marine predators (Boström et al., 2006). Though edge effects on epifaunal survival and density often occur only at very small distances from the seagrass-unvegetated sediment interface (e.g., Tanner, 2005; Moore and Hovel, 2010), fine-scale analyses of predator association with edges are extremely limited. Red drum in particular have been suggested to display close associations with habitat edges (Dance and Rooker, 2015). Rather than presuming that red drum were edge specialists, or arbitrarily defining edge and interior habitat a priori, we allowed high-resolution tracking data to define habitat use in-and-around seagrass. This is an approach/framework that we consider to have broad merit for studying edge effects going forward. In our study system, the data call in to question the presumption that large mobile predators such as red drum are typically "edge predators" (although conclusive evidence would require knowing where feeding occurs). In the broader context of blue crab and pinfish predation, we certainly acknowledge that other predators should be considered to understand our observed predation patterns. For instance, juvenile blue crabs are common prey for bonnethead sharks (*Sphyrna tiburo*) and the aforementioned adult blue crabs. Pinfish are preyed upon by flounders (*Paralichthys* spp.), oyster toadfish (*Opsanus tau*), juvenile gag grouper (*Mycteroperca microlepis*), etc. While it was not possible to track all potential predators in this study, multi-species tracking does represent an exciting potential avenue to evaluate edge effects at the community level. In the interim, red drum represent an important model that highlight the complexity of seagrass edge effects.

This study contributes to a growing literature on dynamic interactions along habitat edges in marine systems. In particular, our results highlight that mesopredators (nekton > 5 cm in carapace width or total length) may not always experience increased risk along seagrass edges, and this could have a cascading influence on smaller-bodied bivalves, crustaceans, and fishes. Moreover, we have highlighted that edge effects are likely context dependent – being influenced by patch-level features such as shoot density. Both of these findings are worthy of future investigation, along with expanded use of increasingly available high-resolution tracking technologies that will allow size- and species-specific animal behavior to help further our understanding of edge effects.

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