



# Predation patterns across states of landscape fragmentation can shift with seasonal transitions

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## Abstract

Nested scales of habitat heterogeneity may independently or synergistically influence faunal interactions. Fragmentation effects (i.e., the breaking apart of landscapes) and edge effects (i.e., ecological differences between edges and interiors of patches, nested within landscapes) are distinct yet related ecological concepts, linked mathematically by the habitat edge-to-area ratio. Our study quantified the separate and interactive effects of fragmentation and edge on predation using temperate seagrass. To assess how predation and generalized consumption were influenced by fragmentation state (i.e., continuous, fragmented), and proximity to edge (i.e., edges, interiors), we used tethering assays with two prey-items: juvenile crabs, *Callinectes sapidus*, and “squidpops” (dried squid mantle). We also investigated whether faunal densities (a proxy for consumption potential) and temperature (a proxy for a broad suite of seasonal changes) correlated with predation across landscapes. Results showed fragmentation state affected predation (i.e., crab) mortality, yet edge effects did not. Moreover, the directionality of fragmentation effects shifted across a temperature/seasonal gradient. Predation mortality more than doubled in continuous landscapes amidst temperature increases, surpassing initially higher mortality in fragmented landscapes, which did not systematically vary with temperature. This mortality magnitude “flip” matched spatiotemporal trends in faunal densities between continuous and fragmented meadows. Consumption rates of both prey-items increased alongside temperature and neither demonstrated edge effects. However, crabs showed fragmentation effects not seen with squidpops, suggesting differing foraging strategies used by consumers of these prey-items. We conclude that fragmentation and edge effects have dynamic influences on temperate predator–prey interactions, as faunal favorability of habitat heterogeneity can “flip” temporally.

**Keywords** Predation · Edge effects · Seasonality · *Callinectes sapidus* · Squidpops

## Introduction

Habitat amount and configuration are important drivers of ecological processes across landscape scales, patch scales, and habitat boundaries (MacArthur and Wilson 1967; Wiens 1989). Island biogeography theory has greatly influenced the

examination of effects of primary habitat amount and configuration within the context of low-quality matrix habitat(s), through the discussion of the species–area relationship and isolation effects, respectively. These concepts have been especially useful in the context of terrestrial reserve design to maintain faunal populations and ecosystem functionality (Pickett and Thompson 1978). This theory developed to further assess disturbances to habitat geometry (i.e., amount and/or configuration) of the primary habitat, matrix habitat, and their interface (Laurance 2008). Naturally or anthropogenically caused changes to habitat geometry can contribute to spatial variability in faunal biodiversity (Fahrig 2003; Yeager et al. 2016), density (Hovel and Lipcius 2002), and survival probabilities (Fahrig 1998; Hovel and Lipcius 2001) across ecosystems.

One such change in habitat geometry, fragmentation, is the process by which a landscape of continuous habitat

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breaks apart into more numerous and isolated patches, experiencing concomitant loss of total primary habitat area (Fahrig 2003, 2013). In terrestrial forest systems, fragmentation often leads to negative impacts on ecosystem function, reduced species richness, and increased species extinction proneness (Laurance 2008; Haddad et al. 2015). However, across coastal marine habitats, fragmentation effects are thought to be less consistent in response magnitude and direction due to a myriad of factors including hydrodynamic regimes and neutral or positive matrix effects (sensu Boström et al. 2006, 2011).

Habitat geometry can also be considered at scales nested within the landscape, such as patch-scale characteristics. Habitat patch edges are transition zones that can be physically, biologically, and ecologically different from patch interiors. Edge effects, broadly described as the enhancing or dampening of faunal response variables (e.g., density, mortality) near habitat boundaries or interfaces, have been well studied across ecosystems (Woodroffe and Ginsberg 1998; Bell et al. 2001; Ries et al. 2004). Although fragmentation and edge effects are distinct concepts within the subdiscipline of landscape ecology, they are fundamentally related in that fragmentation necessarily leads to an increase in the habitat edge-to-area ratio (i.e., perimeter-to-area ratio,  $P:A$ ; Farhig 2003). In terrestrial systems, where representative sampling across large landscapes is difficult, extrapolation of observed patch-scale edge effects to larger scales (i.e., landscape-scale fragmentation effects) has been deemed appropriate in several instances (Ries et al. 2004). However, the applicability of this extrapolation has yet to be widely examined in aquatic systems, including coastal marine habitats.

One potential explanation for the lack of a clear trend in faunal response to coastal marine habitat fragmentation effects is that ecological systems are dynamic and temperate systems may be particularly sensitive to external factors such as seasonality. Within temperate systems, seasonality constitutes a variety of commingling physical, biological, and ecological changes. Temperate estuaries experience strong seasonal shifts in water temperature, salinity regimes, turbidity, photoperiod, and dissolved oxygen saturation (Blanchard et al. 1997; Iriarte et al. 2010). Seasonality also accounts for complex intra-annual variation in aquatic faunal abundances, interactions, recruitment, and movement across multiple trophic levels, due to both top-down and bottom-up pathways (Sommer et al. 1986; Meise and Stehlik 2003; Baillie et al. 2015). Considering habitat landscape fragmentation, edge effects, and a broad suite of seasonal changes together may be particularly important to gain a more complete understanding of predator–prey interactions in dynamic temperate estuarine, marine, and terrestrial systems.

Our study aims to examine seasonal variability in the separate and interactive effects of fragmentation effects

and edge effects on predator–prey interactions in temperate estuarine seagrass systems. Landscape ecologists have often conflated seagrass fragmentation and edge effects on faunal communities, with little evidentiary support, perhaps as a result of suggestions that extrapolation of edge effects to fragmentation effects may be appropriate in some systems (Ries et al. 2004), the nested nature of patches within landscapes, the landscape perimeter-to-area ratio ( $P:A$ ), and similarity among hypotheses regarding seagrass habitat heterogeneity effects on predator–prey interactions. Predation mortality is enhanced at patch edges due to lower seagrass shoot densities (i.e., refugia reduction, Hovel and Fonseca 2005), higher prey densities (Bell and Westboy 1986; Virnstein and Curran 1986), and the tendency of predators to patrol edges in search of prey (Hovel and Lipcius 2002; Boström et al. 2006). Within fragmentated landscapes, the mosaic of habitat types provides unstructured corridors easing predator movement among patches (Hovel and Lipcius 2002), incidentally resulting in increased access to prey at patch edges. Despite the intersection of habitat fragmentation and edge increase, few coastal marine studies have looked at edge effects in landscapes of different configurations (i.e., continuous vs. fragmented) (but see Warry et al. 2009). We aimed to add to and clarify this field of inquiry by examining whether patch-scale edge effects can be extrapolated to landscapes-scale fragmentation effects in a non-terrestrial system. Seagrasses are a useful model system for this investigation due to their global distribution, and the wide variety of meadow sizes, shapes, orientations, and species compositions, often set upon relatively unstructured sandy/muddy matrix habitat.

Using tethering assays (live blue crabs and squidpops; Duffy et al. 2015), we investigated how predation/consumption was influenced by seagrass landscape fragmentation state (i.e., continuous or fragmented), proximity to seagrass patch edge (i.e., edges or interiors) and seasonality. In accordance with previous hypotheses, we expected that with some seasonal variability, fragmented landscapes would exhibit relatively higher predation/consumption rates than continuous landscapes. In addition, predation/consumption rates would be relatively higher in patch edges than interiors. We also expected the interactive effects of fragmentation and edge to amplify relative consumption in the patch edges of fragmented over continuous landscapes, yet not differ among patch interiors across fragmentation states. We also investigated whether relative densities of seagrass-associated fauna, which includes both potential predators and alternative prey (i.e., a proxy for community level consumptive potential, or hotspots of trophic transfer within our system), and which vary across landscapes and throughout the year, correlated with our observed relative predation rates.

## Methods

### Study site selection

We conducted our study across eight discrete seagrass meadows (hereafter referred to as landscapes) located in Back Sound, North Carolina (NC), USA ( $34^{\circ}42' N$  to  $34^{\circ}39' N$ ,  $76^{\circ}37' W$  to  $76^{\circ}31' W$ ) (Electronic Supplemental Material Fig. S1). All of our sampled landscapes were composed of a mixture of Back Sound's dominant seagrasses: eelgrass, *Zostera marina* (Linnaeus 1753), and shoal grass, *Halodule wrightii* (Ascherson 1868) (Yeager et al. 2016). Landscapes were chosen based upon available aerial imagery in Google Earth Pro as of 19-Feb-2017, and ground truthed for changes in seasonal seagrass growth/senescence using summer, 2017, drone photography and ImageJ 1.x (Schneider et al. 2012). No discernable differences in landscape fragmentation states (e.g., total area, number of patches) were found between the two aerial imagery sources. All landscapes were relatively shallow (1–1.5 m depth at high tide), reasonably isolated from other seagrass beds (distance to nearest seagrass meadow =  $112 \pm 17$  m [mean  $\pm$  standard error]) and were appropriately sized to encompass short-term (e.g., daily, monthly) movements of common seagrass-associated fauna in this system (Yeager et al. 2016). We identified similarly sized landscapes ( $25882 \pm 6592$  m<sup>2</sup>) available in Back Sound by defining the minimum convex polygon surrounding the seagrass meadow, regardless of the total seagrass cover within the polygon. Among eight candidate landscapes of similar size, we defined four continuous landscapes and four fragmented landscapes based on several alternative fragmentation metrics including the number of patches, the perimeter-to-area ratio (P:A), and the largest patch's percent cover of the total seagrass area (Yeager et al. 2016; Table 1). Seagrass fragmentation is often naturally coupled with habitat loss (Wilcove et al. 1986), resulting in our chosen fragmented and continuous landscapes covering a wide overlapping range of total seagrass areas. Although the mean seagrass area of our fragmented landscapes was nearly half that of our continuous landscapes (Table 1), we could account for this difference by examining the effects of seagrass area and P:A statistically as alternative metrics for fragmentation (see *Statistical Analysis* section). Due to inherent area differences among natural landscapes, our experiment was designed to examine the effects of fragmentation (i.e., the breaking apart of habitat concomitant with habitat loss) rather than fragmentation per se (i.e., the breaking apart of habitat without habitat loss; sensu Fahrig 2003). We acknowledge that repeated sampling of our eight landscapes may introduce statistical complications due to

**Table 1** Continuous (C) and fragmented (F) seagrass landscape characteristics obtained from aerial photography and analyzed in ImageJ 1.x

Parameter	C or F	Max	Min	Mean	SE
Number of patches	C	6	1	3.3	1.0
	F	82	13	44.8	16.0
Total area (m <sup>2</sup> )	C	29210	5995	13,284	5451
	F	18111	1320	6950	3921
Perimeter (m)	C	2229	519	1010	408
	F	4387	569	1982	831
Perimeter: area (m m <sup>-2</sup> )	C	0.10	0.05	0.08	0.01
	F	0.88	0.23	0.45	0.15
Largest patch area % of Total area	C	100.0	99.5	99.8	0.1
	F	86.9	28.6	58.2	12.2

non-independence, yet our study aimed to examine habitat heterogeneity effects on predation within a single system over time, therefore capture seasonal variation in ecological phenomena within the same landscapes.

### Predation assays

Relative predation mortality was measured using tethered juvenile blue crabs (*Callinectes sapidus* Rathbun) of carapace widths 10–40 mm. Tethering is commonly used to measure relative predation on juvenile blue crabs (Wilson et al. 1990; Hovel and Lipcius 2001). We note that tethering cannot be used to determine absolute predation rates, as tethered prey have restricted flee potential, generally raising the incidence of predation (Peterson and Black 1994). Still, when interpreted conservatively, tethering data can elucidate differences in the relative directionality of environmental factors affecting prey survival (i.e., positive or negative effects). Juvenile blue crabs were chosen for tethering due to their economic and ecological importance to coastal regions (McCann et al. 2017) and because they have served as a model prey organism in several previous studies of related design (e.g., Hovel and Lipcius 2001, 2002; Mahoney et al. 2018).

Crab predation assays were run from June to July as this was the period during which we could obtain sufficient numbers of appropriately sized crabs for our experiment. All juvenile blue crabs were captured in seine nets from Oyster Creek, NC ( $34^{\circ}49'19'' N$ ,  $76^{\circ}27'07'' W$ ). Crabs were glued (active ingredient cyanoacrylate) to 30-cm segments of 12-lbs test monofilament. We chose to use 30-cm segments of monofilament for tethers to allow crabs to exhibit natural burrowing behavior (Hovel and Fonseca 2005), mitigating some tethering artifacts of prey visibility (Peterson and Black 1994). Tethered crabs were attached to 60-cm long, 0.5-cm diameter, fiberglass stakes with attached floats for

easy relocation. Once tethered, crabs were held overnight as a check for attachment integrity, and then deployed across our landscapes on the following day.

Twenty tethered crabs were deployed (stakes pushed completely into the sediment) in each continuous and fragmented landscape per predation assay date. Within each landscape, ten tethered crabs were haphazardly placed within seagrass edges, defined as 30 cm (a tether length) from the seagrass–mudflat interface. The other ten tethered crabs were haphazardly placed in seagrass interiors, defined as  $\geq 1$  m from the seagrass–mudflat interface. Only patches with a radius of 1 m or larger were used for tethers classified as ‘interior’. However, patches with a radius of  $< 1$  m were used for a portion of our ‘edge’ tethers. All tethers were placed at least 1 m apart. We returned to landscapes at 1 h and 24 h to check crab status (i.e., live, eaten). All missing crabs were presumed eaten, as no crabs escaped tethers during the 24-h holding period. After 24 h, any remaining live crabs were removed from tethers and released. Crab tethering cycles were repeated four times in 2017 (9-Jun, 14-Jun, 5-Jul, and 13-Jul). On 13-Jul, only half of the continuous and fragmented landscapes were included in tethering assays due to a lack of crab availability. A total of 550 tethered juvenile blue crabs were deployed during our trials (see Table S1 for full sampling schedule and assay sample sizes).

Squidpops were also used to measure relative “depredation” across landscapes (acknowledging that a combination of predation and scavenging may account for observed loss patterns). Squidpops are 1-cm  $\times$  1-cm squares of dried squid mantle tied to 1-cm segments of monofilament (Duffy et al. 2015). We attached squidpops to 60-cm long, 0.5-cm diameter, fiberglass stakes. Twenty squidpops were deployed (stakes pushed 50 cm into the sediment to prevent squidpop tangling in seagrass or burial in sediment) within each of the eight landscapes per assay date during July and August in 2017 (5-Jul, 13-Jul, 26-Jul, 8-Aug, and 30-Aug), ten in the edge and ten in the interior of the seagrass patches as specified above for blue crab trials. A total of 720 squidpops were deployed (Table S1). Squidpop depredation assays did not occur in June due to lack of dried squid availability. During the first two squidpop deployment cycles, we checked squidpop status (present, absent/eaten) at 1 h and 24 h. We observed nearly 100% squidpop removal by 24 h, so for the remaining three deployment cycles we performed status checks at 1 h and 2 h.

### Seagrass-associated fauna sampling

Seagrass-associated fauna were sampled to explore relationships between our observed predation/depredation rates and seasonal faunal densities within each fragmentation state. We sampled seagrass-associated fauna during each crab tethering cycle with four baited (with  $\sim 8$  pieces of dried dog

food, Mahoney et al. 2018) Gee-style minnow traps (41-cm long, 22-cm wide, 0.3-cm galvanized mesh-wire cylinders, with 4-cm diameter funneled openings) haphazardly deployed in each landscape. We acknowledge that baiting traps increases catch rates in our system and could bias the captured community toward predators and scavengers (our target community), yet potential increase in catch rates with baiting seems to be uniform across positions within seagrass (i.e., edge effects, Mahoney et al. 2018). At 24 h, fauna were enumerated, identified to the lowest taxonomical level possible, and released. Since the last three cycles of squidpop depredation assays were not deployed for a full 24 h, minnow traps were not deployed on these dates.

We also sampled seagrass-associated fauna monthly (June, July, and August) by towing a small otter trawl in five continuous and eight fragmented seagrass landscapes according to the specifications and methods documented by Baillie et al. (2015), and Yeager et al. (2016) as part of an ongoing long-term survey. Trawl-caught fauna were enumerated, identified to the lowest taxonomical level possible, and released. Only three of our experimental landscapes overlapped with those randomly selected for the trawl survey during this period, so we classified each trawled landscape as continuous or fragmented for direct comparison to our targeted experimental trials. Previous studies in our system have shown that seagrass landscapes in Back Sound, NC are highly comparable as they experience similar environment conditions and ecological processes related to fragmentation state (Baillie et al. 2015; Yeager et al. 2016). Of our examined seagrass landscapes, five overlapped with those sampled by Baillie et al. (2015), five with those sampled by Yeager et al. (2016), and two landscapes were used in all three studies.

Point measurements of water temperature ( $^{\circ}\text{C}$ ) were taken in each landscape at the location and time of all tethering assays and faunal sampling using hand-held thermometers (Table S1). We chose temperature as our seasonality proxy (Fig. S2) because several other seasonally affected factors including faunal densities correlate with water temperature variability. In addition, the measurement of temperature is easy, cheap, reliable, and comparable to previous studies.

### Statistical analysis

To determine whether relative predation/depredation and (minnow trap) seagrass-associated fauna catch per unit effort (CPUE) varied with fragmentation, deployment position (edge or interior), and seasonality (proxied by water temperature,  $^{\circ}\text{C}$ ), we used generalized linear models (GLMs) with normal error distribution. We explored multiple alternative metrics for fragmentation including total seagrass area ( $\text{m}^2$ ), number of patches, perimeter-to-area ratio (P:A; i.e., edge-to-area ratio), and a categorical variable (i.e.,

continuous, fragmented). We chose to use the categorical variable (with levels, continuous and fragmentated) in our final model as total seagrass area and number of patches had no strong effects, while P:A led to similar results as the categorical variable (Table S2). Defining fragmentation state categorically has been widely used in studies similar to ours (e.g., Hovel and Lipcius 2001, 2002; Hovel and Fonseca 2005; Rielly-Carroll and Freestone 2017) and integrates many covarying landscape-scale metrics (e.g., patch number, P:A, total area, isolation, landscape heterogeneity), therefore better encompassing the processes cooccurring in landscape fragmentation than any single numerical metric. Individual GLMs included crab mortality, squidpop depredation, and minnow trap fauna (total fauna, blue crab, and pinfish) CPUE as response variables. For crab mortality and squidpop depredation GLMs, we used Akaike information criterion with a correction for small sample sizes (AICc) and weighted score to choose the best fitting models. For the minnow trap CPUE GLMs, we performed a two-way ANCOVA, excluding deployment position as a predictor, as minnow traps were haphazardly placed throughout meadows without specifying edge or interior. We also examined the correlation between crab mortality and squidpop depredation on overlapping assay dates, as well as the correlation between each of crab mortality and squidpop depredation with minnow trap (total fauna, blue crab, and pinfish) CPUE. Blue crab and pinfish CPUE were separated out from the total CPUE to elucidate relationships specifically between known major juvenile blue crab predators (i.e., other blue crabs, Moksnes et al. 1997; Meise and Stehlík 2003) and major squidpop consumers in our system (i.e., pinfish, Rodemann and Brandl 2017; Fodrie *unpublished data*) with the respective tethered prey-item.

Crab mortality and squidpop depredation data required arcsine square-root transformation to meet assumptions of normality (Shapiro–Wilk test). Consumption assays and faunal sampling replicates were binned according to edge/interior positions (for consumption assays only) within each landscape on a given assay date (i.e., ten tethered crabs, ten squidpops, four minnow traps). One minnow trap replicate caught a large aggregation of pinfish (*Lagodon rhomboides*,  $n=82$ ) which made its mean catch  $> 3$  SD from the mean CPUE. This minnow trap catch was treated as an outlier and excluded from further analysis (Howell 1998).

Initial analyses revealed that relative mortality rates of tethered crabs at 1 h were low ( $4.9 \pm 1\%$  overall) and relative depredation rates on squidpops after 2 h were similar to those at 1 h (paired Student's *t* test,  $t=0.485$ ,  $DF=45$ ,  $P=0.630$ ). Therefore, we focused our presentation and discussion of results on relative mortality of crabs at 24 h and relative depredation of squidpops at 1 h. Also, water level in this tidal system at the time of deployment expressed a positive linear relationship with squidpop depredation at 1 h

( $DF=1$ ,  $\chi^2=8.173$ ,  $P=0.004$ ) but no effect on crab mortality at 24 h (which experienced two full tidal cycles;  $DF=1$ ,  $\chi^2=0.343$ ,  $P=0.558$ ). Therefore, we detrended squidpop data after 1 h for the effect of tidal level at the onset of deployment.

For trawl CPUE of seagrass-associated fauna, we chose to use fragmentation state and month as predictor variables because water temperatures on trawling days were extremely similar [ $27.6 \pm 0.07$  °C], not covering the same  $\sim 10$  °C (21.7–31.8 °C) range seen during the tethering assays. This temperature discrepancy may be due to the vast difference in tidal state needed for each sampling method. Initial analyses of our trawled sites confirmed that controlling for the variation in seagrass percent cover between continuous ( $95 \pm 1.81\%$ ) and fragmentated ( $77 \pm 2.04\%$ ) landscapes did not significantly change the fauna CPUE between fragmentation states (Welch two sample *t* test;  $t=-0.76$ ,  $DF=61.9$ ,  $P=0.450$ ). Log( $x+1$ ) transformed trawl (total fauna, blue crab, and pinfish) CPUE were examined with a type II ANOVAs with unequal sample sizes and a post-hoc analysis was performed on significant results with Tukey's HSD test. Blue crab and pinfish CPUE were separated out of trawl data for the same reasons stated above for minnow trap data. All analyses were performed in R version 3.3.2 ( $\alpha < 0.05$ ; R Core Team 2016) using base R and the *car* package for ANOVAs/ANCOVAs (Fox and Weisberg 2011).

## Results

### Relative mortality and depredation rates

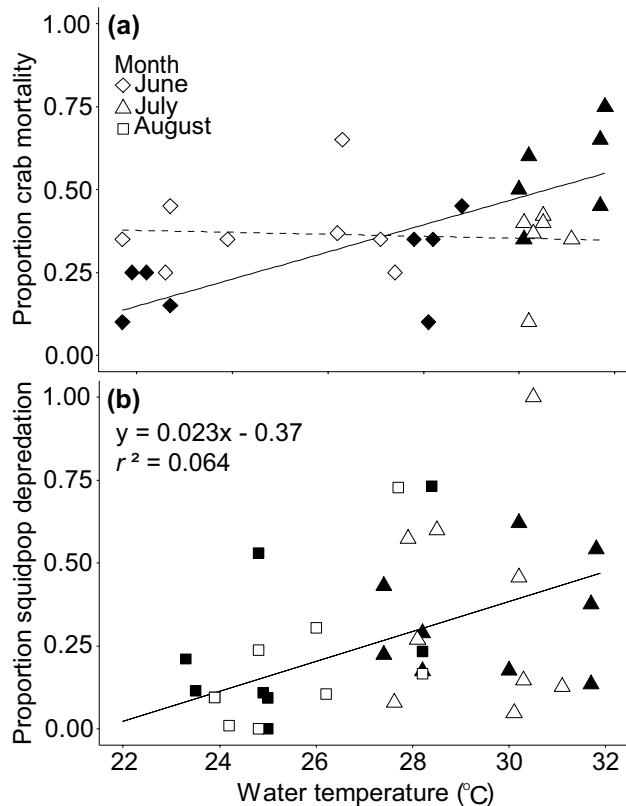
Overall,  $37.0 \pm 3.1\%$  ( $n=202$ ) of tethered crabs were consumed after 24 h deployments. In continuous landscapes  $37.9 \pm 5.4\%$  ( $n=106$ ) of crabs were consumed, while in fragmentated landscapes  $36.1 \pm 3.2\%$  ( $n=96$ ) were consumed. Despite these coarse similarities, there were important differences in relative mortality patterns across tethering cycles. The best fitting crab mortality model (chosen by  $\Delta$ AICc and weighted score) excluded deployment position (i.e., edge effects) as a predictor variable (Table 2). Crab mortality more than doubled in continuous landscapes with a water temperature increase of 10 °C ( $y=-0.75+0.041x$ ,  $r^2=0.609$ ), but mortality did not systematically vary with temperature in fragmentated landscapes ( $y=0.44-0.003x$ ,  $r^2=0.007$ ) (Fig. 1a). Crab mortality was initially relatively higher in fragmentated landscapes when water temperatures were lower in June but was outpaced by the increase in mortality in continuous landscapes by July, which exhibited higher water temperatures, producing an apparent “flip” in spatial mortality trends over time.

Overall,  $27.1 \pm 4.1\%$  ( $n=184$ ) of all squidpops were consumed after 1 h. In continuous landscapes,  $29.5 \pm 5.9\%$

**Table 2** Model selection by  $\Delta AIC_c$  and  $AIC_c$  weighted (wt) score for full (three-way) model and sequential variable exclusion

Variables included in model	Response variables			Squidpop depredation*		
	Crab mortality			Squidpop depredation*		
	DF	$\Delta AIC_c$	$AIC_c$ wt score	DF	$\Delta AIC_c$	$AIC_c$ wt score
Fragmentation state (F) $\times$ Position (P) $\times$ Temperature (T)	9	8.09	0.009	9	13.78	0.000
F $\times$ P	5	19.49	0.000	5	10.76	0.002
F $\times$ T	5	<b>0.00</b>	<b>0.526</b>	5	4.27	0.048
P $\times$ T	5	9.01	0.006	5	4.20	0.050
F	3	15.20	0.000	3	6.65	0.015
P	3	14.82	0.000	3	6.30	0.017
T	3	6.09	0.025	3	<b>0.00</b>	<b>0.409</b>
Intercept	2	12.96	0.001	2	4.47	0.044

The bolded 0 value  $\Delta AIC_c$  and highest wt score value indicate most parsimonious model. \*Tidally detrended



**Fig. 1** Relationship of a) crab (*Callinectes sapidus*) mortality water temperature in continuous (filled symbols) and fragmented (open symbols) landscapes ( $n=8$ ). Continuous landscapes (solid line): crab mortality =  $(0.041 \times \text{temperature}) - 0.75$ ;  $r^2=0.61$ . Fragmented landscapes (dashed line): crab mortality =  $(0.003 \times \text{temperature}) + 0.44$ ;  $r^2=0.007$ . Relationship of b) squidpop depredation to water temperature only (solid line). Note y-axes are back transformed proportions

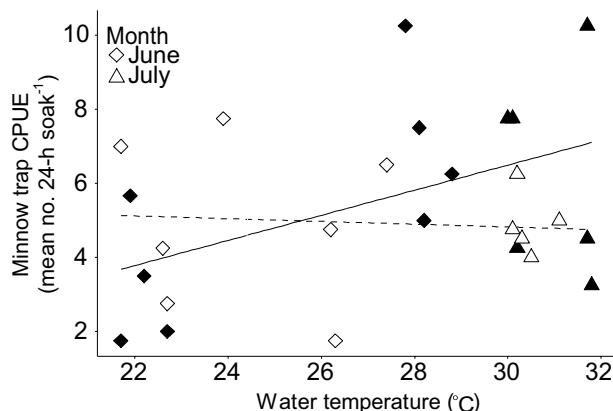
( $n=100$ ) were consumed, while in fragmented landscapes  $24.7 \pm 5.7\%$  ( $n=84$ ) were consumed. Unlike crab mortality,  $AIC_c$  revealed that the best squidpop model excluded

both fragmentation state and deployment position (Table 2). Squidpop depredation increased with water temperature ( $y = -0.37 + 0.023x$ ,  $r^2=0.064$ ; Fig. 1b). Crab mortality and squidpop depredation were only weakly positively correlated on overlapping tethering assay dates ( $30.76 \text{ }^{\circ}\text{C} \pm 0.23$ ) (Pearson correlation  $r=0.37$ ,  $P=0.28$ ).

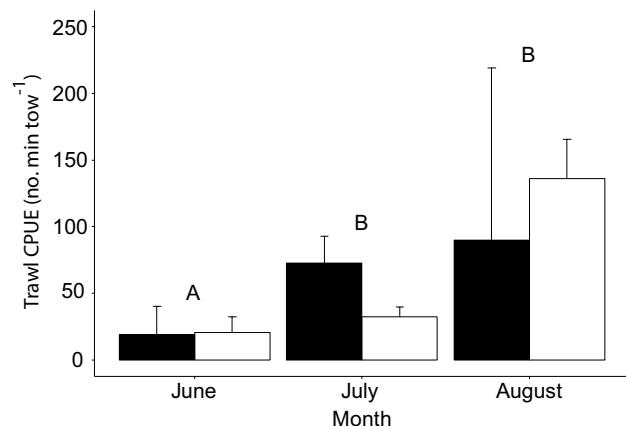
### CPUE of seagrass-associated fauna

A total of 801 seagrass-associated fauna individuals, representing 22 species, were captured in minnow traps. Neither crab mortality nor squidpop depredation were strongly correlated to minnow trap total fauna or pinfish CPUE (Table S3), yet crab mortality positively correlated to blue crab CPUE ( $r=0.401$ ,  $P=0.04$ , Table S3). In addition, minnow trap total fauna and pinfish CPUE were not affected by fragmentation state, water temperature, or their interaction, but blue crab CPUE was positively affected by temperature ( $DF=1$ ,  $\chi^2=8.503$ ,  $P=0.004$ , Table S4). While not statistically significant at  $\alpha=0.05$ , a striking similarity in the relationship between minnow trap total fauna CPUE and temperature (Fig. 2) to the relationship between crab mortality and temperature (Fig. 1a) was noted. Like crab mortality, minnow trap total fauna CPUE remained stable in fragmented landscapes from June to July ( $y=6.8 - 0.012x$ ,  $r^2=5.03e^{-05}$ ), yet approximately doubled in continuous landscapes over this same period ( $y=-3.7 + 0.34x$ ,  $r^2=0.227$ ). In both cases, there was a shift in the relatively higher response (i.e., minnow trap total fauna CPUE and crab mortality) from fragmented landscapes to continuous landscapes occurring at  $26-27 \text{ }^{\circ}\text{C}$ .

The otter trawl captured 4645 individuals, representing 41 species. Trawl catch rates of total fauna and pinfish increased with the month, while blue crab CPUE peaked in July, but no catch rate differed with fragmentation state



**Fig. 2** Relationship of minnow trap fauna CPUE and water temperature in continuous (filled symbols) and fragmented (open symbols) landscapes in June and July. Continuous landscapes: fauna CPUE =  $(0.34 \times \text{temperature}) - 3.7$ ;  $r^2 = 0.23$ . Fragmented landscapes: fauna CPUE =  $(-0.012 \times \text{temperature}) + 6.8$ ;  $r^2 = 5.03e^{-05}$



**Fig. 3** Trawl fauna catch (mean + SE) in continuous (filled bars) and fragmented (open bars) landscapes in Back Sound, NC ( $n=6$ ) per month. Letters indicate significant differences ( $P < 0.05$ ) between months using the Tukey HSD multiple comparison test

(Table S5). Trawl CPUEs for total fauna among fragmentation states were similar to blue crab CPUE trends in June and July (when crab mortality trails occurred, Fig. S3a) and similar to pinfish CPUE trends in July and August (when squidpop depredation trails occurred, Fig. S3b), so for simplicity we focused on trawl total fauna CPUE trends (Fig. 3) as with minnow trap CPUE. Although the interaction of fragmentation state and month was not statistically significant ( $DF = 2, F = 2.781, P = 0.102$ , Table S5), the pattern of relative catch rates between continuous and fragmented landscapes in June and July also matches the trends in minnow trap CPUE and crab mortality.

## Discussion

Our use of two tethered prey-items to assess relative predation/consumption rates across seagrass landscape fragmentation states, edge and interior positions, and a temperature gradient yielded results that varied with prey-item, fragmentation state, and temperature, but not edge-vs-interior transitions or the interaction of edge effects and fragmentation state. As we hypothesized, seasonality influenced both blue crab mortality and squidpop depredation. However, only blue crab mortality was influenced by fragmentation. The clear influence of fragmentation yet lack of observed edge effects on relative predation mortality within seagrass suggests to us that fragmentation and edge effects may be scale-dependent (i.e., landscape vs. patch scales) and should not be conflated across these nested scales due to the landscape P:A in this context. In addition, only blue crab mortality positively correlated with blue crab (their major potential predator) CPUE across landscapes, yet both minnow trap and trawl total fauna catch rates produced patterns that matched spatiotemporal patterns of crab mortality.

Unlike several long-term forest studies (reviewed within Haddad et al. 2015), with few exceptions, marine fragmentation effects are often studied over short time periods giving a “snapshot” of system conditions; in some instances, inadvertently leading to the presentation and interpretation of results as static rather than dynamic (Boström et al. 2011). From previous studies in both marine (Boström et al. 2006) and terrestrial habitats (Haddad et al. 2015), we knew fragmentation could easily have a positive, negative, or no strong effect on predation rates. Interestingly, our experimental investigation found that the effects of seagrass landscape fragmentation on relative predation rates are not consistent or unidirectional but vary seasonally. Juvenile blue crab mortality illustrated a seasonal shift from relatively higher mortality in fragmented to continuous landscapes correlating with increasing water temperatures from June to July (Fig. 1a). While crab mortality exhibited a clearer shift or “flip” in landscape-scale relative magnitude over time, squidpop depredation showed a marked increase in overall depredation rate positively correlated with temperature (Fig. 1b).

Although we used temperature as our proxy for seasonal change, we do not have data to suggest that temperature, or seasonality in general, is an underlying causal agent of variation in predation rates within seagrass systems. Seasonal cycles comprise a suite of physical and biological changes in temperate, shallow estuarine systems (Blanchard et al. 1997; Iriarte et al. 2010; Santos et al. 2017). It is likely that temperature in combination with other seasonal changes such as variations in predator and prey

densities and habitat selection (Cote et al. 2013), changing water clarity (Salini et al. 1998), or seagrass shoot density variability (Jankowska et al. 2014) have additive or synergistic effects on predation rates. Likewise, seasonality has also been shown to correlate with predation mortality in terrestrial systems potentially due to changes in predator and prey density as well as changes in habitat characteristics, such as vegetation complexity (Feierabend and Kiel-lan 2015). Furthermore, in a system like ours, Hovel and Lipcius (2001, 2002) saw variation in juvenile blue crab mortality response to patch connectivity and size (both components of fragmentation state), and among months (another proxy for seasonality).

The observed shift in relative total faunal density (i.e., consumption potential) in continuous and fragmented seagrass landscapes is a likely mechanism driving relative juvenile blue crab mortality rates. Blue crab mortality correlated with the CPUE of potentially cannibalistic blue crabs (Moksnes et al. 1997) across fragmentation states. In addition, regardless of whether the individual fauna captured in our total minnow trap samples are potential predators or alternative prey, a shift in overall habitat usage by seagrass-associated fauna is likely indicative of spatiotemporally variable hotspots for trophic transfer. Minnow trap fauna CPUE did not correlate with crab mortality or vary with fragmentation state or water temperature, and trawl fauna CPUE only differed among months. However, the similarity between the trends of crab mortality and total fauna CPUE in June and July is suggestive of a relationship between faunal densities and prey mortality (i.e., the ecological significance of the trends may outweigh statistical significance when considering ‘noisy’ catch data; Figs. 1a, 2, and 3). The relative density of seagrass-associated fauna (captured in both the minnow traps and trawl) matches the pattern of relative crab mortality over the same time period. A potential explanation for this match is potential blue crab predator densities responding to spatiotemporal variation in prey sources alternative to our tethered crabs leading to incidental consumption of our tethered prey. Therefore, we hypothesize that changes in overall faunal densities, proxying overall consumption potential (Reynolds et al. 2018), across landscapes and through time may be a driving factor behind the differences seen in relative blue crab mortality rates.

Indeed, previous studies provide corroborative evidence that overall faunal densities correlate with prey mortality rates in systems like ours. For instance, Reynolds et al. (2018) found that trap-based CPUEs of nekton in seagrass correlated remarkably well (Pearson’s  $r=0.42$ ) with predation rates on seagrass-associated mesograzers across broad biogeographic scales (i.e., 30° latitude and multiple ocean basins). Similarly, Duffy et al. (2015) found that faunal diversity was related to consumption pressure in seagrass habitats across global scales. Both Rielly-Carroll

and Freestone (2017) and Hovel and Lipcius (2001) found higher abundances of adult blue crabs in continuous than fragmented seagrass landscapes directly correlated with the mortality of and inversely correlated with the abundance of juvenile blue crabs. When taken together, ours and these studies indicate that predator foraging habitat selectivity varies geographically and/or between years but affects the mortality of juvenile blue crabs in the same manner. In our system, seasonal transitions may increase the number of mouths to feed within certain seagrass landscapes, potentially leading to higher predation rates in landscapes with higher overall faunal densities.

While squidpops are an accepted technique to assess feeding intensity from generalist consumers (Duffy et al. 2015; Rodemann and Brandl 2017), we observed notable differences between trends of crab and squidpop loss which should be considered in future experimental designs. Like crab mortality, squidpop depredation exhibited a positive correlation with water temperature, yet squidpop depredation did not differ among fragmentation states (yet see Table S2, indicating a P:A  $\times$  water temperature interaction). High squidpop depredation after 1 h, as compared to low crab mortality at 1 h, suggests squidpops and tethered crabs may test alternative mechanisms of foraging. Squidpops are inanimate, defenseless, dead prey-items, not only subject to active predation but also scavenging. These two foraging mechanisms combined may in part explain the extreme high squidpop depredation rates characteristic to North Carolina (Rodemann and Brandl 2017). Scavengers may be more readily attracted to highly visible food (Guaff et al. 2018) or opportunistically attack food that requires less handling time than would be necessary to prey upon live, defensive prey. In North Carolina, pinfish are known to be major consumers of squidpops (despite the lack of correlation in our study; Table S3) yet are not considered major predators of juvenile blue crabs (Rodemann and Brandl 2017; Fodrie *unpublished data*). Tethered crabs may be a more accurate assay for an aggressive predation mechanism in which defensive benthic prey are targeted and olfactory senses are used to locate cryptic burrowing crabs (Weissburg and Zimmer-Faust 1993). Future experimental designs should consider whether the use of squidpops accurately depicts the consumers in question. We agree that squidpops are an accurate assay for generalist consumer pressure (Duffy et al. 2015), but caution against language that suggests squidpops assess “predation pressure” or “predator activity”.

Preliminary analyses indicated squidpop depredation is strongly dependent upon tidal state. More squidpop depredation occurred at higher tide when water levels were higher over seagrass landscapes. Tidal water depth variation affects predation in tidal creeks (Rypel et al. 2007) and salt marshes (Banikas and Thompson 2012) but has yet to be studied in seagrass. However, tidal variation does affect the abundance

of fish taxa at seagrass edges (Becker et al. 2012), which could be a mechanism by which squidpop depredation varied with tidal state in our study. In addition, several of our seagrass landscapes were partially exposed at extreme low tide, perhaps preventing easy demersal scavenger detection of, or access to, squidpops.

Tidal state may also have played a role in the apparent spatiotemporal match of crab mortality, and lack of match of squidpop depredation, with observed total faunal densities. Tethered crabs, squidpops, and minnow traps were all deployed within 3 h of low tide, while trawling required tows be conducted within 3 h of high tide (Table S1). Crab tethers and minnow traps soaked for two full tidal cycles, therefore potentially experiencing the same communities sampled by the trawl at higher tides. However, high depredation rates on squidpops restricted analysis to 1 h data (often still within 3 h of low tide), potentially preventing the consumption assay from accurately representing the communities caught by the minnow traps and trawl. In addition, we note that squidpop assays did not entirely temporally overlap with crab tethering assays and minnow trap deployments (Table S1); therefore, a match of spatiotemporal trends among these samplings was not expected. Despite these limitations preventing inference of potential squidpop consumers in our study, a positive relationship with water temperature for both crab and squidpop consumption assays suggests seasonality may be an important correlate for relative consumption pressure regardless of tidal state, soak time, or assay dates.

Unlike numerous marine (sensu Mahoney et al. 2018) and terrestrial (e.g., Murcia 1995) studies which found strong increases in predation rates along habitat edges, our study did not find any clear effects of edge or interior deployment position on prey-item (i.e., crab or squidpop) loss. Although edge effects have been implicated in predation variation in seagrass (Boström et al. 2006), in the context of edge effect studies most similar to ours, specifically using tethered crustaceans to examine relative predation rates (i.e., Peterson et al. 2001; Hovel and Lipcius 2002; Mahoney et al. 2018), we see that trends in crustacean mortality as a response to seagrass edge are not firmly established. Peterson et al. (2001) tethered shrimp and crab species to find that in eelgrass beds, survival time (time to predation) and predation rates (the number of prey items removed per h) did not differ from edge to interior. Hovel and Lipcius (2002) found that blue crab survival decreased with increasing juvenile blue crab density from seagrass edges to interiors, suggesting that greater abundances of predators at edges depressed crab densities at edges. In contrast, Mahoney et al. (2018) found that blue crabs survived 2.5 times longer at edges than interiors of seagrass. The inconsistency of responses to edges between these and our study suggests that edge effects on crustacean

mortality are complex, variable, and may be confounded by unexamined predictor variables such as habitat patch characteristics, landscape-scale metrics, seasonality, or time of year. In addition to the lack of consistent edge effects on crustacean predation mortality, our study suggests edge effects may not be appropriate for extrapolation to landscape fragmentation effects in seagrass systems.

Our study results lead us to three main take-aways. (1) Seagrass landscape fragmentation effects on predation are not consistent but rather, are potentially dynamic over a suite of seasonal and other successional scales. In our study, we hypothesize that spatiotemporal variation in faunal densities, therefore moving loci of trophic transfer, where the primary mechanistic cause of the observed “flip” in relative mortality magnitude with fragmentation state. Therefore, assessment of responses such as prey mortality and potential predator densities should be conducted over longer time scales to encompass (monthly, seasonal, annual, etc.) changes in faunal abundances and habitat utilization. (2) Tethered blue crabs and squidpops may test alternative mechanisms of foraging, such as predation/cannibalism and consumption potential/scavenging, respectively. While both prey types showed increases in loss rates with temperature, landscape effects were only evident for juvenile blue crab mortality. Use of prey types with longer average time to predation may be more useful to tease apart variations between habitat types. (3) We caution against non-evidence-based extrapolation of patch-scale edge effects to landscape-scale fragmentation effects on faunal communities, as our study found no such connection in seagrass meadows. However, more simultaneous examination of both edge and fragmentation effects on faunal communities within coastal marine habitats is needed to determine the appropriateness of edge and fragmentation effect conflation in these systems.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflicts of interest.

**Ethical approval** All applicable institutional and/or national guidelines for care and use of animals were followed.

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