

Propagule risk in a marine foundation species: Seascape effects on *Zostera marina* seed predation

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Abstract

- Both biotic and abiotic factors can affect whether seagrass meadows establish as large, continuous features or as a mosaic of smaller patches, and these processes act across multiple spatial scales. Of these processes, sexual recruitment is considered vital for the recovery and resilience of seagrass meadows. Because numerous estuarine fauna can impact sexual recruitment by consuming seeds, it is important to understand variation in seed consumption throughout the seascape.
- We sought to determine how cross-scale processes affected seed consumption of *Zostera marina*, a widely distributed seagrass species. We deployed seed predation units (SPU) within patches ranging in size from 0.28 to 28.48 m², and on unvegetated, sandy bottom. Seed consumption was analysed across patch sizes, at patch centres and edges and within the context of total seagrass cover within buffer zones surrounding SPU locations.
- Using structural equation modelling, we found that measured seascape parameters explained 34% of the observed variation in seed consumption. Specifically, we found that seagrass presence had the strongest effect on seed predation followed by a negative effect of patch size on seed consumption. Although there was no direct effect of percent seagrass cover (within a 4-m buffer of the SPU) on seed predation, percent seagrass cover had a negative indirect effect through its positive correlation with patch size. However, we found that once variation due to patch size and areal cover were accounted for, seeds placed at patch interiors actually experienced greater consumption rates. We did not find similar relationships with our potential seed consumers, although our snapshot sampling likely obscured transient effects.
- We argue that seagrass recruitment could be affected by seed predation, which is influenced by multiple processes, including predator dispersal, behaviour and aggregation. Since seed-based restoration is becoming more common, and the role of sexual recruitment in meadow maintenance appears to be increasingly important for seagrass resilience, our results demonstrate that for current management strategies to be successful, there is a need to better understand seed predation in seagrass-dominated seascapes.

5. *Synthesis.* Factors that influence propagule supply and recruitment success of seagrass operate and interact across multiple spatial scales, which can have implications for management.

KEYWORDS

buffer analysis, escape hypothesis, granivore, landscape ecology, propagule, seagrass, seed predation, *Zostera marina*

1 | INTRODUCTION

Understanding the factors that affect successful recruitment of new individuals to populations requires consideration across multiple spatial scales. For coastal habitats dominated by marine angiosperms, patterns and processes that manifest at the patch scale (1–10 m) can only be understood when placed in the context of seascape composition and configuration (10–1,000 m). Although scaling issues are a major concern in ecology (Boström, Jackson, & Simenstad, 2006; Levin, 1992), the nascent field of seascape ecology has only begun to investigate context of patch composition and configuration (the seascape; 10–1,000 m). Seagrasses, ecosystem engineers that support highly abundant and diverse communities (Heck & Orth, 1980; Jackson, Rowden, Atrill, Bossey, & Jones, 2001), are particularly well suited for exploring how hierarchical spatial patterns affect community processes (Boström et al., 2006; Irlandi, Ambrose, & Orlando, 1995; Robbins & Bell, 1994). Issues of patch size and shape, amount of edge habitat, existence of corridors and degrees of isolation have all been investigated as drivers of patterns within seagrass meadows, particularly with respect to economically and ecologically important fauna (Carroll, Furman, Tettelbach, & Peterson, 2012; Hovel & Lipcius, 2001; Irlandi et al., 1995). Few studies, however, have examined the impacts of local- and seascape-scale processes in the recruitment of seagrass propagules (but see Manley, Orth, & Ruiz-Montoya, 2015).

Seagrasses can form extensive meadows, with up to thousands of hectares of continuous cover (Zieman, Fourqurean, & Iverson, 1989), or they can exist as patch mosaics, varied in size, shape and number of patches (Robbins & Bell, 1994). Both biotic factors, such as patterns in clonal growth and grazer-mediated disturbance, and abiotic factors, including wind-wave energy, light attenuation and eutrophication can affect meadow stability and growth. While asexual reproduction has been considered most important for meadow maintenance and expansion, sexual reproduction is known to be critical for gene flow, patch development and recruitment, especially following disturbance (Jarvis, Brush, & Moore, 2014; Jarvis, Moore, & Judson Kenworthy, 2014; Livernois et al., 2017; Orth, Moore, Marion, Wilcox, & Parrish, 2012). Seed production, therefore, establishes the annual seed banks that fuel changes across a broad range of spatial scales (Furman & Peterson, 2015; Jarvis, Moore et al., 2014). Flowering shoots appear unaffected by habitat fragmentation (Livernois et al., 2017) or patch size (Stubler, Jackson, Furman, & Peterson, 2017), but the overall relationship between seed density and patch size and cover is unclear (Livernois et al., 2017; Stubler et

al., 2017). Thus, the roles patch and seascape level processes play in seed production remain poorly understood.

For some seagrass species, seed banks can be quite dense, with up to 3,000 seeds m^{-2} (Manley et al., 2015). Despite this, sexual recruitment, in terms of seedling success, is generally thought to be low (Marion & Orth, 2009). Establishment from seed is a complex process wrought with substantial eco-physiological pitfalls (Orth, Fishman, Harwell, & Marion, 2003), including dispersal to unfavourable habitats (Harper, 1977), burial below a critical depth (Howe & Smallwood, 1982) and physiological dormancy (Jarvis, Moore et al., 2014). Seed predation is another potential process driving the loss of seeds and low seedling establishment (Orth, Kendrick, & Marion, 2006; Wassenberg, 1990). In terrestrial habitats, seed predation can be as high as 100% (Crawley, 1992; Wenny, 2000), but for marine angiosperms, the impacts of predation vary across species and locations. For example, seed predation is probably an important bottleneck for *Posidonia australis* (Orth et al., 2006; Orth, Kendrick, & Marion, 2007), as seeds are a major component of tiger prawn diets (Wassenberg, 1990; Wassenberg & Hill, 1987). For *Zostera* spp., however, impacts of predation on recruitment are unclear. Predation rates have been shown to be either relatively unimportant (Manley et al., 2015; Orth et al., 2003) or high enough to reduce seedling recruitment (Fishman & Orth, 1996; Nakaoka, 2002).

Generally, predation within seagrass meadows is thought to be influenced by patterns and processes operating at multiple spatial scales (Boström et al., 2006). Seed predation pressure is likely related to faunal abundance, which varies at within-patch scales (i.e. centre vs. edge habitat; Bologna & Heck, 1999; Healey & Hovel, 2004; Carroll et al., 2012; shoot density; Irlandi, 1994), patch scales (i.e., size and shape; Bowden, Rowden, & Atrill, 2001; Hovel & Lipcius, 2002; Laurel, Gregory, & Brown., 2016) and seascape scales (i.e., configuration and connectivity; Eggleston, Etherington, & Elis, 1998; Hovel & Lipcius, 2001). Therefore, seed consumption patterns are likely to be similarly impacted. For example, since small seagrass fauna often concentrate at patch edges or on small patches (Eggleston et al., 1998), seed predation pressure is likely to be higher in these areas. Similarly, small fauna may be more abundant on more isolated seagrass patches, so seeds in those areas may experience different mortality than those embedded in continuous meadows.

Unlike studies on faunal survival (Carroll & Peterson, 2013), seagrass seeds appear to be preferentially consumed within seagrass meadows rather than on adjacent, unvegetated sandy bottoms (Darnell & Dunton, 2015; Orth et al., 2006). This supports the 'escape hypothesis' that seeds experience higher survival when they

escape the vicinity of their parents (Howe & Smallwood, 1982; Janzen, 1970; Manley et al., 2015). Since seed predators are residents in the seagrass patches (Carroll et al., 2012; Hovel & Lipcius, 2002), they are unlikely to travel often or far beyond the seagrass structure, potentially creating a spatial refuge from predation for seeds outside of patches. Thus, patterns and processes of seed density, within-patch location and faunal abundance observed at the patch scale interact with seascape-scale patterns of connectivity, recruitment and faunal distribution to control seed predation rates and the ecological impact of sexual recruitment. Understanding how cross-scale processes modulate seagrass seed predation, therefore, is vital for understanding meadow maintenance and expansion.

Since sexual recruitment is important for both recovery and restoration (Marion & Orth, 2009), it is important to understand how seed predation varies across spatial scales. In the current study, we explored how cross-scale processes affected seed predation of eelgrass, *Zostera marina*, seeds. Specifically, we investigated rates of seed predation across seagrass patches ranging in size, between the edge and interior of seagrass patches, and across a range of areal seagrass cover. We hypothesized that seed predation would vary with coverage patterns at both patch and seascape scales. To test this, we used a hierarchical approach to quantifying seed consumption, while also exploring faunal abundance throughout our seascape. We found a negative relationship between patch and seed predation that was modulated by percent cover in the surrounding area, and that sand habitat provided a clear spatial refuge from predation. This study thereby contributes

to the growing knowledge of how multi-scale processes influence meadow maintenance and recovery.

2 | MATERIALS AND METHODS

2.1 | Study site

All fieldwork was conducted in Shinnecock Bay, Long Island, New York. Shinnecock Bay is a back-barrier lagoonal estuary along the southeast coast of Long Island, with an average depth of 2 m (MLLW) and semi-diurnal tides of 0.8 m (USACE, 2004). The study area encompassed a patchily distributed *Zostera marina* meadow in the southeastern portion of the bay, approximately 2.5 km east of the Shinnecock Inlet (40.842278°N, 72.476484°W) and 400 m from shore (Figure 1). Depths at this site ranged from 0.25 to 1.25 m MLLW. Surficial sediments consisted of siliceous sands low in organic and nutrient content (Carroll, Gobler, & Peterson, 2008). Seagrass was mapped using available aerial imagery beginning in 2001, and then balloon-mounted camera bi-monthly since 2011 (Furman & Peterson, 2015). Using maps from 2012, a 250 m (parallel to shore) × 225 m (perpendicular to shore; total area 56,250 m²) site was mapped, and over 2,200 patches ranging in size from 0.01 to 20,000 m² were delineated with ArcGIS. The meadow was characterized by variable floral densities, with up to 40 reproductive shoots m⁻² (Jackson, Furman, & Peterson, 2017). Seed densities were highest in small (2.5 m²) patches and negatively correlated ($r = -0.39$) to total seagrass cover (Stubler et al., 2017).

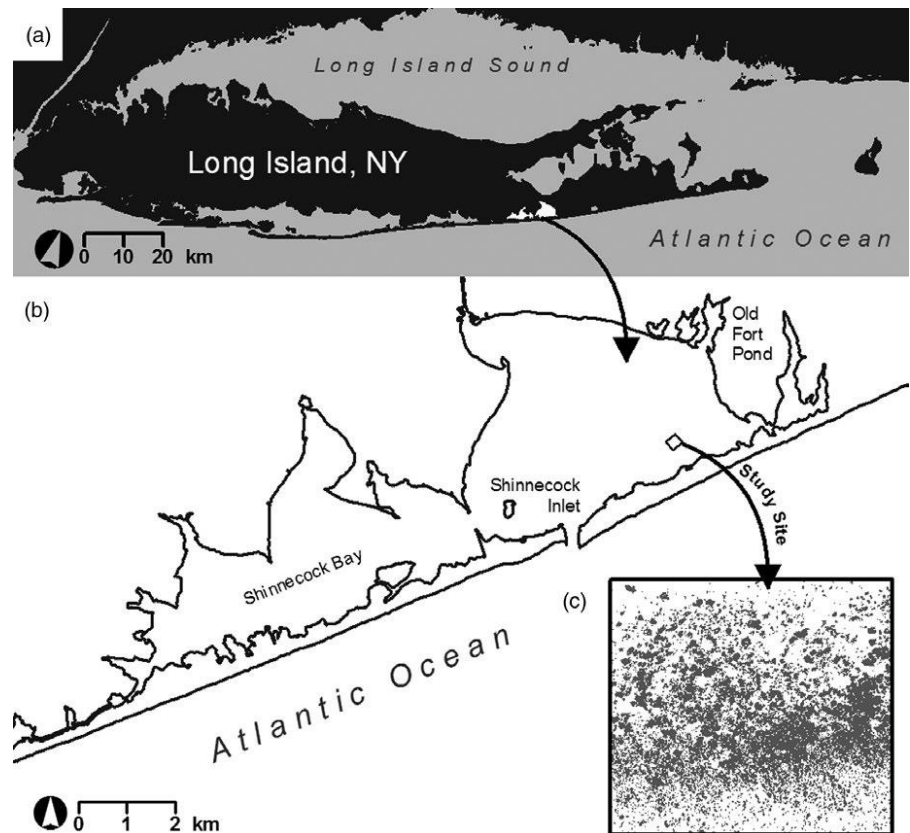


FIGURE 1 Long Island, NY (a) where the basin highlighted in white is Shinnecock Bay (b). Study location is denoted by the small box and blown up to illustrate the patchy nature of the seagrass meadow (c) examined in this study

2.2 | Seed predation experiments

During the summer of 2012, seed predation was measured using seed predation units (SPU; Manley et al., 2015). Briefly, 10 seeds were fastened to a small 10 × 3 cm wood board using pins (Figure S1). The predation units were then secured in the field with large staples and marked with flagging tape. We used the aerial maps to deploy SPU into 158 seagrass patches across five size categories: <2.5, 2.5, 5, 10 and 20 m², although actual patch sizes (0.28 to 28.48 m²) were used for subsequent analysis. For the 40 largest patches, we placed SPU at both at the edge (within 1 m of the edge of the patch) and at the interior (>1 m from the edge of the patch; Peterson, Luettich, Micheli, & Skilleter, 2004). In addition, we also placed 53 SPU in adjacent (~1 m) unvegetated sandy habitats. SPUs were deployed ~11 days; they were all deployed for at least 7 days but for some deployed units, weather and underwater visibility prevented recovery for up to 15 days. Consumption was standardized to seeds eaten per day. Any seed not recovered was considered consumed, as SPUs placed in laboratory mesocosms (95-L Rubbermaid tubs) with a flow rate of ~5L/min—did not lose seeds over a 2-week period.

2.3 | Mesocosms

To ensure that potential predators could access seeds on the SPU, we ran a mesocosm experiment using three potential granivores from Shinnecock Bay, including the mud crab *Dyspanopeus sayi* and the long-claw hermit crab *Pagurus longicarpus*, both of which are common in seagrass meadows around Long Island (Carroll et al., 2010) and have been demonstrated to consume *Zostera marina* seeds (Wigand & Churchill, 1988). In addition, we also used the invasive green crab *Carcinus maenas*, which negatively impacts eelgrass habitats along the western Atlantic (Davis, Short, & Burdick, 1998; Garbary, Miller, Williams, & Seymour, 2014; Malyshev & Quijon, 2011) and has recently been identified as a seed predator (Infantes, Crouzy, & Moksnes, 2016).

Mesocosm experiments were conducted at the Stony Brook University's Southampton Marine Station using 5-gallon buckets placed within 95-L Rubbermaid® tubs. The approximate bottom area of each mesocosm was 530 cm². Buckets were lined with a layer of sand. Half of the buckets received seagrass mimics, constructed using 5 mm curling ribbon (Virnstein & Curran, 1986). Mesocosms were plumbed with constantly flowing raw seawater from Old Fort Pond (40.8845°N, 72.4419°W), Southampton, NY, to allow conditions among the mesocosms to remain at ambient for the duration of the experiment. Air diffusers were placed within each mesocosm to ensure adequate dissolved oxygen. Within each mesocosm, we placed one SPU and one individual crab. Crabs were randomly assigned to buckets. Ten green crabs (CW = 32.6 ± 4.6 mm, mean ± SE), 20 mud crabs (CW = 22.8 ± 1.8 mm) and 20 long-claw hermit crabs (CW = 6.0 ± 2.1 mm) were used in the experiment, with half of the individuals in tubs with seagrass mimics and half in tubs with bare sand. Crabs were starved for 24 hr in the mesocosms before SPUs

were added, and were allowed to feed for a period of 5 days. Crabs and SPU were then removed, remaining seeds on each SPU were counted, and sand was sieved for any seeds that might have become dislodged but not consumed.

2.4 | Potential granivore and alternative prey abundance

We surveyed for potential predator abundance at three patches of each size category by suction dredging, an effective in situ method for sampling decapod crustaceans (Johnson & Heck, 2006a; Orth & van Montfrans, 1987). A 1-m² metal frame with a 1-m high, 1-mm mesh curtain was used as a throw-trap prior to dredging. We targeted the centre of the two smallest patch sizes and the centre and edge of the two largest patch sizes. Dredged fauna were retained on a 750-µm mesh bag, placed on ice and returned to the laboratory for processing. Individuals were identified to the lowest possible taxon and counted. We considered most decapod crustaceans we encountered to be potential seed predators, along with small fish (Table 1). We were also able to count clams and mussels, potential alternative prey items, since most seed predators prefer to eat other prey items (Wigand & Churchill, 1988). We treated isopods separately since they could be both potential seed consumers, but also alternative prey for other predators.

2.5 | Analysis

We developed a structural equation model (SEM) to estimate the effects of seascape properties on seed predation rates in an integrated way (Grace et al., 2012). The SEM was based on a conceptual model of pathways of influence between covariates and the response variables (Figure 2). We built the SEM in a Bayesian framework using JAGS (Plummer, 2003), run in the R environment (R Development Core Team, 2017).

All covariates were standardized so that estimated effects could be directly compared for relative importance. We assigned uninformative uniform prior probability distributions to binomially distributed variables and uninformative normal priors to all other variables (Table S1). We ran three independent Markov chain Monte Carlo (MCMC) simulations, discarding the first 100,000 MCMC samples as a burn-in and storing every fifth sample of the remaining 200,000 MCMC iterations for further analysis. We tested for Markov chain convergence to a stationary posterior distribution with the Gelman–Rubin diagnostic (Bolker, 2008). We summarized posterior distributions for all parameters with the mean of all MCMC samples as a point estimate and the 2.5 and 97.5 percentiles of the MCMC samples as a 95% credible interval (Bolker, 2008). We estimated the amount of variance explained by predictor variables by creating prediction equations of mean effects and computing R² values using linear regressions (Grace et al., 2012).

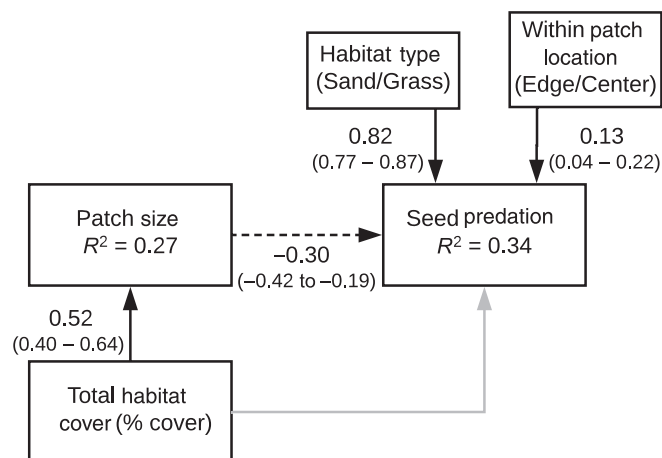
Observed seed predation from each SPU were binomially distributed, so that for the *j*th SPU:

$$y_i \sim \text{Bin}(p_i, \tau_i) \quad (1)$$

TABLE 1 Summary of species that are potential seagrass seed consumers

Crustaceans	
Anomuran Decapods	
<i>Calcinus dapsiles</i>	Orth et al., 2006
<i>Pagurus bernhardus</i>	Infantes et al., 2016
<i>Pagurus longicarpus</i>	Wigand & Churchill, 1988, this study
<i>Paguristes purpureantennatus</i>	Orth et al., 2006
<i>Pagurus</i> spp.	Darnell & Dunton, 2015
Brachyuran Decapods	
<i>Callinectes sapidus</i>	Fishman & Orth, 1996; Darnell & Dunton, 2015
<i>Carnicas maenas</i>	Infantes et al., 2016, this study
<i>Libinia</i> spp	Darnell & Dunton, 2015
<i>Nectocarcinus integrifrons</i>	Orth et al., 2006
<i>Naxia aurita</i>	Orth et al., 2006
<i>Ovalipes ocellatus</i>	Wigand & Churchill, 1988
<i>Pachygrapsus crassipes</i>	Holbrook, Reed, Hansen, & Blanchette, 2000
<i>Panopeus herbstii</i>	Wigand & Churchill, 1988
<i>Pugettoa product</i>	Holbrook et al., 2000
Unidentified portunid	Orth et al., 2006
Penaeid Decapods	
<i>Penaeus esculentus</i>	Wassenberg & Hill, 1987, Wassenberg, 1990, O'Brien, 1994
Pericarids	
Gammaridae amphipods	Orth et al., 2007
<i>Idotea resicata</i>	Holbrook et al., 2000
<i>Cymodoce</i> sp.	Orth et al., 2006
<i>Zeuxo</i> sp.	Nakaoka, 2002
Echinoderms	
Echinoids	
<i>Strongylocentrotus droebachiensis</i>	Infantes et al., 2016
Fishes	
Batrachoidiforms	
<i>Opsanus tau</i>	Wigand & Churchill, 1988
Cyprinodontiforms	
<i>Fundulus heteroclitus</i>	Wigand & Churchill, 1988
<i>Fundulus majalis</i>	Wigand & Churchill, 1988
Perciformes	
<i>Lagodon rhomboides</i>	Sumoski & Orth, 2012
Tetradontiforms	
<i>Sphoeroides maculatus</i>	Sumoski & Orth, 2012

where y_i is the observed number of eaten seeds for the i^{th} SPU, p_i is the seed predation rate for the i^{th} SPU and τ_i is the number of trials for the i^{th} SPU (trials = number of seeds \times number of days). We

**FIGURE 2** Structural equation model of seascape effects on seed predation rates. Solid black arrows are estimated positive effects, dashed arrows are estimated negative effects and grey arrows are estimated zero effects. Estimates are means (95% credible intervals)

modelled effects of habitat cover, patch size, habitat type (sand or grass) and within-patch location (centre or edge) on p_i as logit-linear effects. We also modelled patch size as a normally distributed variable with a linear effect of habitat cover. Sand samples were classified as having zero patch size. Sand samples were excluded from estimation of the within-patch location effect as they could not be classified as being centre or edge.

We conducted buffer analysis using the 2-, 4- and 8-m buffers for habitat cover values (Figure S2). Briefly, we conducted a buffer analysis using ESRI ArcGIS software to explore the percent cover of seagrass within a number of buffer zones surrounding the point of the SPU. We opted to use seagrass cover as a proxy for configuration as the amount of seagrass cover in an area surrounding often covaries with patchiness and distance between patches (Hovel, 2003). We used multiple buffer zones for our exploratory analysis, including buffer zones with a 2-m, 4-m, 8-m, 16-m, 32-m and 64-m radii surrounding the point of each individual SPU, resulting in buffer areas of $\sim 13 \text{ m}^2$, 50 m^2 , 201 m^2 , 804 m^2 , $3,217 \text{ m}^2$ and $12,868 \text{ m}^2$ respectively. Unfortunately, our ability to detect seagrass cover was bounded by the area surveyed, and so any buffers that extended beyond the boundaries of the mapped area were excluded from analysis. This resulted in losing 0, 6, 11, 20, 53 and 129 of the 212 total SPUs deployed across the different buffers from the analysis respectively. Furthermore, a Pearson correlation matrix showed strong positive correlations between the percent cover of the 8 m buffer and all subsequent buffers (Figure 3), suggesting 8 m is a good proxy for larger scales used in this study. Thus, we chose to use the three lowest buffers (2-, 4- and 8-m radius) for all subsequent analysis, since previous studies at this location suggest the 4-m buffer was demonstrated to be the scale of action for seed production (Stubler et al., 2017) and since many of the potential granivores are relatively small and thus exhibit limited post-settlement (i.e., post water column) dispersal (Eggleston et al., 1998). We present the 4-m buffer results here.

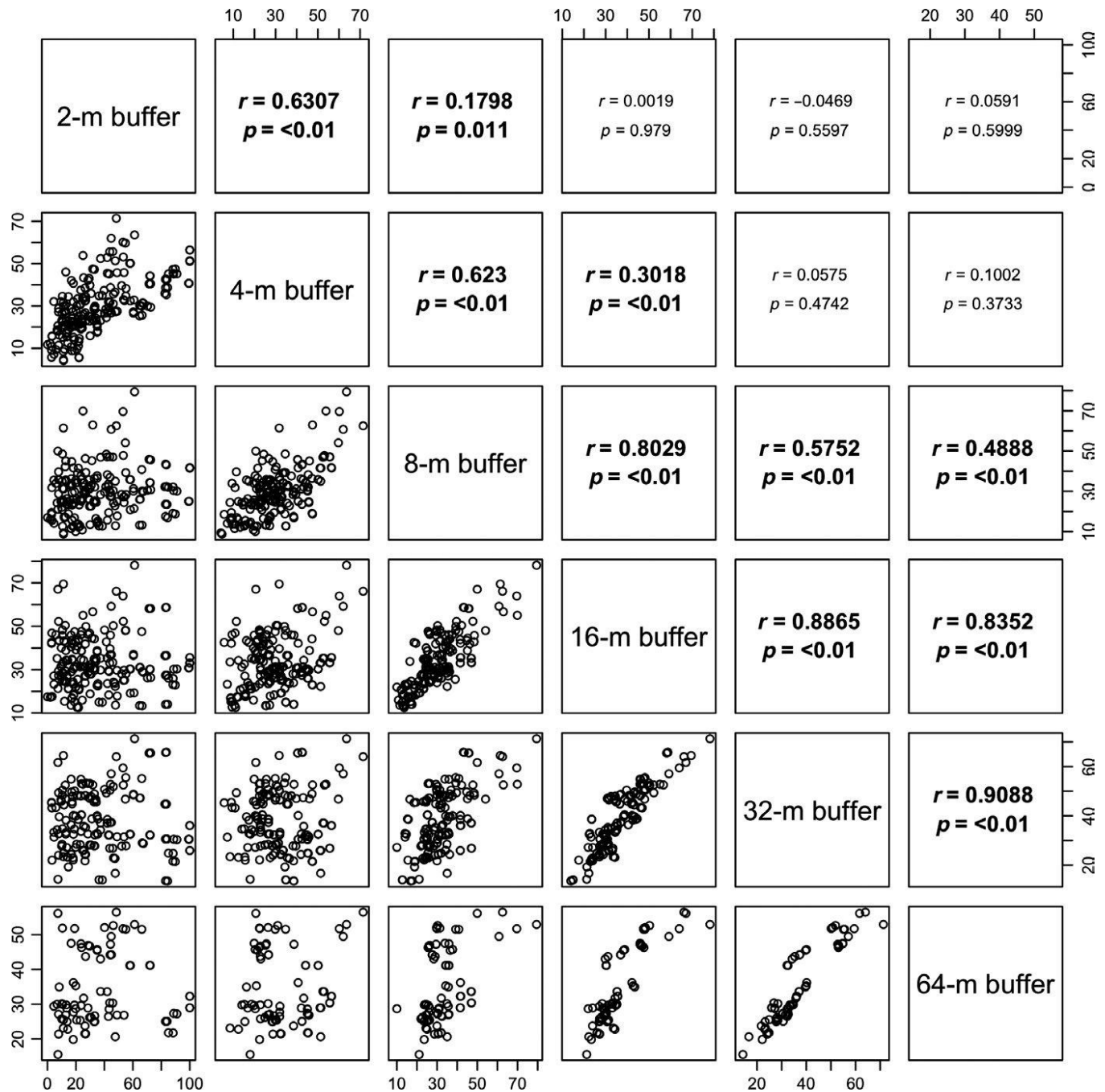


FIGURE 3 Scatter plots and correlation coefficients (significant correlations in bold) illustrating the relationship between seagrass cover at each of the different buffer sizes

We tested structural treatment or predator identity effects on seed consumption from the mesocosm experiments using a two-factor logistic generalized linear model (GLM) with quasi-binomial error distribution using R statistical software (R Development Core Team, 2017), where granivore species and seagrass presence/absence were the treatments and proportion of seeds consumed as the dependent variable.

The predator-prey analysis was run separately from the seed predation SEM because SPUs and suction samples were collected from different patches. Due to the small number of suction samples ($n = 12$), we did not create an SEM and instead analysed separate multiple linear regressions for each response variable. We

considered most crustaceans and fish to be potential predators. Specifically, we counted mud crabs, green crabs, long-claw hermit crabs, blue crabs *Callinectes sapidus*, rock crabs *Cancer irrorata*, spider crabs *Libinia* sp. and lady crabs *Ovalipes ocellatus*. We also identified mummichogs *Fundulus heterochaelis* as potential predators. We did not count caridean shrimp (i.e. grass shrimps *Palaemonetes pugio* and *Palaemonetes vulgaris* and the sand shrimp *Crangon septemspinosa*) as potential granivores since there is no evidence from the literature that they or other caridean shrimp consume seeds. Alternative prey included small bivalves and seagrass seeds. While isopods (*Idotea* spp.) may consume seeds (Holbrook et al., 2000),

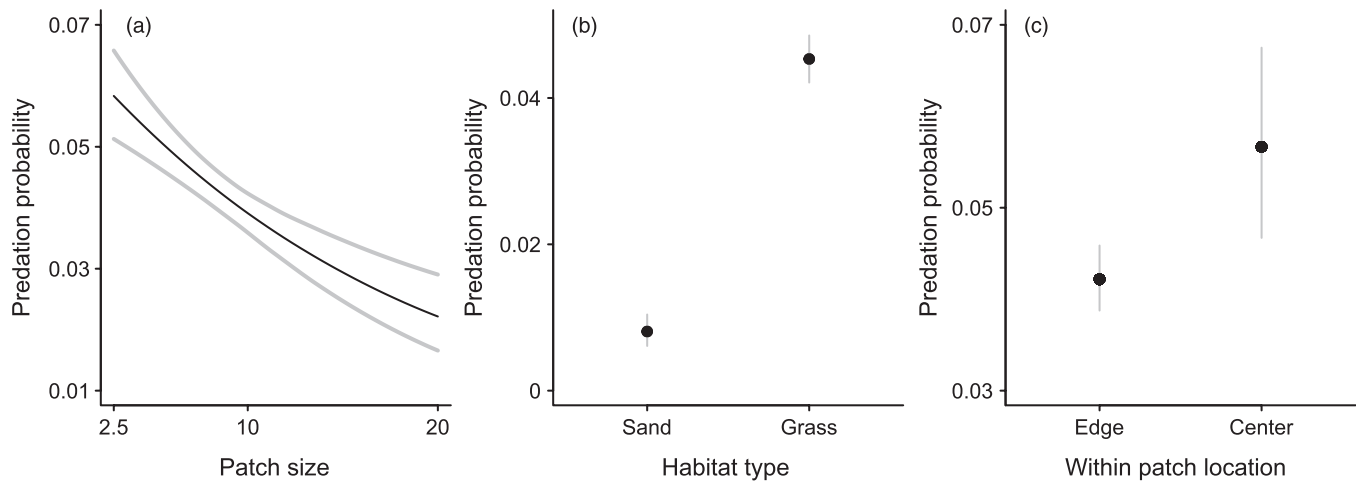


FIGURE 4 Effects on seed predation probability (estimated using a structural equation model) of (a) patch size, (b) habitat type and (c) within-patch location. Represented effects are means (black line, points) and 95% Bayesian prediction intervals (grey lines), with non-represented effects held at their mean value

we could not clearly categorize them as either seed predators or alternative prey, so we analysed them separately. Thus, there were three response variables: seed predator density, alternative prey density and isopod density. Each response variable was modelled as a normally distributed variable with linear effects of habitat cover, patch size and within-patch location (centre or edge). Models were run in a Bayesian framework using the same procedures as above (Table S2).

3 | RESULTS

3.1 | Seed predation

The strongest effect on seed predation rates was whether the SPU was in sand or grass habitat (Figure 2), with predation rates being much higher in grass habitats (Figure 4b). Patch size also had a negative effect on seed predation rates (Figures 2 and 4a). Total habitat cover of grass within a 4-m buffer had no direct effect on seed predation (the 95% credible interval of the effect included zero); however, there was a strong effect of habitat cover on patch size (Figure 2). Therefore, habitat cover had an effect on seed predation, but it was modulated through the effect of patch size. Within-patch location (centre or edge) also had a small effect on seed predation after accounting for patch size effects (Figure 2), with patch centres experiencing higher seed predation rates (Figure 4c). These combined effects explained a substantial amount of the variance in the seed predation rate ($R^2 = 0.34$).

3.2 | Mesocosms

Mesocosm experiments demonstrated that all three predators could consume seagrass seeds from the SPUs; however, consumption was variable. Mud crabs were the most consistent seed predators. After

removing two mesocosms where crabs died, 13 of the remaining 18 mud crabs consumed at least 1 seagrass seed, and 5 consumed all 10 seeds over the 5-day period. Only half of the green crabs consumed seeds, but when they did, they consumed between 8–10 seeds, and while only 4 of 20 hermit crabs consumed seeds—three of them consumed all 10 seagrass seeds during the observation period. There was no significant difference across structure treatments ($F_{2,39} = 1.618$, $p = 0.211$) and only a marginal effect of species ($F_{2,39} = 2.970$, $p = 0.063$), likely due to the high variability (Figure S3). Regardless, the mesocosm experiments indicated that common granivores in the field were able to consume seeds pinned to SPUs and that instances of multiple seed consumption were not uncommon. Furthermore, we did not recover any dislodged, non-consumed seeds while sieving sand, suggesting that dislodgement without consumption is not common.

3.3 | Potential granivore and alternative prey abundance

We assumed that most crustaceans could potentially prey on seagrass seeds in our field surveys (Table 1). For both seed predator density and alternative prey density, there were no non-zero effects of patch size, total habitat cover or within-patch location (Figure 5). For isopods, patch size had a positive effect and total habitat cover had a negative effect on isopod density (Figure 5). There was no effect of within-patch location on isopod density. These effects explained a large proportion of the variance in isopod density ($R^2 = 0.56$).

4 | DISCUSSION

Seedbank dynamics within a given seascape is the product of a complex suite of interacting processes, including plant reproduction, seed dispersal, predation, granivory and a number of indirect

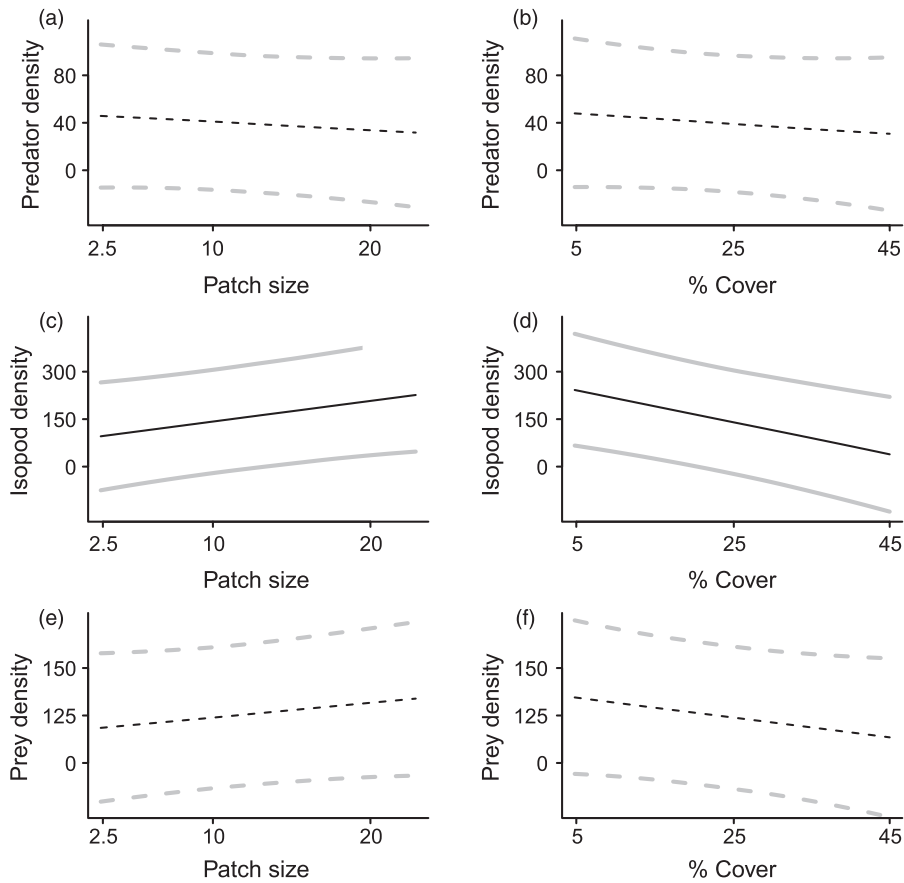


FIGURE 5 Effects of patch size (a, c, e) and total habitat cover (b, d, f) on predator (a, b), isopod (c, d), and prey (e, f) densities. Represented effects are means (black line, points) and 95% Bayesian prediction intervals (gray lines), with non-represented effects held at their mean value. Solid lines represent non-zero effects; whereas dashed lines have effects that overlap with zero.

interactions therein. Understanding processes operating across spatial scales has proven a central challenge to seascape ecology (Bell & Furman, 2017; Boström, Pittman, Simenstad, & Kneib, 2011), but using a hierarchical approach may help disentangle observed patterns (Didham, Kapos, & Ewers, 2012). As expected, whether the seeds were placed in sand versus seagrass locations had a strong effect on seed predation, with sand acting as a spatial refuge for seeds. Additionally, we found that seed predation decreased with increasing patch size. The observed patch size effect was modulated by total seagrass cover in the area surrounding the SPU and patch, suggesting that seascape configuration plays a role in both patch size and subsequently seed predation. When patch size and percent cover were accounted for, there was a within-patch (i.e. centre vs. edge) effect, although predation was higher within the centres of patches. These results demonstrate that interactions between processes operating at different spatial scales are important to predicting patch scale seed predation and seed bank densities. This study, therefore, highlights the importance of testing ecological processes at multiple scales while exploring seed bank dynamics.

For seed predation, the strongest effect on seed survival was whether the seeds were tethered in seagrass habitat or on unvegetated, sandy bottom >1 m away from a seagrass patch, where survival was highest. Typically, seagrasses are thought to serve as a predation refuge, and, at least for fauna, survival can be higher within seagrass than in the surrounding unvegetated sand (Heck & Orth, 2007). Similarly, we expected that seeds without the

protection of complex, structured habitat would have experienced high mortality. However, it has been posited that seed and seedling survival increases with distance from the parent plants due to 'distance responsive' seed predators that concentrate around the adult plants and do not venture into the unstructured/low-structured areas (Janzen, 1970). In some terrestrial examples, seeds and seedlings located close to parent plants experience higher mortality due to a variety of invertebrate and vertebrate consumers (Howe, 1977; Janzen et al., 1976; Vandermeer, 1977). Because our most common granivores are likely to function as distance responsive predators, they are unlikely to venture far into unstructured areas—leading to a pattern of seed predation consistent with the escape hypothesis (Howe & Smallwood, 1982).

Similar patterns have been documented in other studies with higher seed consumption within seagrass meadows as compared to adjacent sandy matrix (Darnell & Dunton, 2015; Orth, Heck, & Tunbridge, 2002; Orth et al., 2007). As parental sources of seeds (Furman, Jackson, Bricker, & Peterson, 2015; Jarvis & Moore, 2010; Orth, Luckenbach, & Moore, 1984), seed banks are routinely higher within patches, decreasing with distance from patch edges (Livernois et al., 2017; Manley et al., 2015). Seed predators also aggregate in seagrass patches, around parent plants (Eggleston et al., 1998; Hovel & Lipcius, 2002). The net effect of these patterns is difficult to forecast for any given estuary, but should lead to higher survival of seagrass seeds dispersed more than 1 m from patch edges into unstructured bottom.

At the patch scale, we observed the highest consumption rates on the smallest patches, and patch size had a strong, negative effect on seed consumption. The amount of seagrass in the area surrounding the locations of the SPU also indirectly affected seed predation through its influence on patch size. Generally, as seagrass cover decreases, patch size also tends to decrease (Fonseca & Bell, 1998), which may be problematic for seed bank dynamics in fragmenting habitats. Numerous fauna, including isopods and grass shrimps (Eggleston, Elisa, Etherington, Dahlgren, & Posey, 1999), hermit and mud crabs (Lefcheck et al., 2016), juvenile blue crabs (Hovel & Lipcius, 2002), and numerous fishes (Jelbart, Ross, & Connolly, 2007; McNeill & Fairweather, 1993) are all likely to be more abundant in small, isolated seagrass patches than contiguous meadows. Furthermore, mobile seed predators are also more likely to encounter and utilize smaller seagrass patches while navigating similar seascapes (Eggleston et al., 1999; Healey & Hovel, 2004; McNeill & Fairweather, 1993; Sogard, 1989). In addition, small, isolated patches might be more risky for seeds because they are less risky for seed predators. For example, large blue crabs avoid small seagrass patches to reduce predation risk, thus releasing their prey (small granivores) in those patches from predation pressure (Hovel & Lipcius, 2001, 2002). Therefore, granivores might be responding to both structure and local predators at different spatial scales resulting in higher abundances on more isolated patches and at the smallest patch sizes. Unexpectedly, total granivore densities did not vary as a product of patch size or area cover in our surveys. We interpret the lack of a clear signal in our granivore surveys as an artefact of natural variability and the limitations of snapshot sampling.

Independent of patch size and seagrass cover, seagrass seeds affixed to SPUs experienced enhanced risk when placed at patch centres, suggesting a continuum of decreasing survival from unvegetated bottom to patch centres. This was an unexpected since numerous studies have demonstrated enhanced predatory mortality along seagrass patch edges (Carroll & Peterson, 2013; Gorman, Gregory, & Scheider, 2009; Peterson, Thompson, Cowan, & Heck, 2001; Smith, Hindell, Jenkins, Connolly, & Keough, 2011), including for seagrass seeds (Manley et al., 2015). Seed density may also be higher at meadow edges (Livernois et al., 2017), so enhanced mortality there might suggest either numerical or functional-type response of granivores to seed resources in meadow edges. However, seeds in this study experienced the highest predation rates in the smallest patches, which are almost exclusively edge habitat (i.e. all points of the patch were <1 m from the patch edge; Peterson et al., 2004), and patch-level effects are often considered up-scaled edge effects (Carroll et al., 2012). Therefore, where previous studies found a patch edge effect, we found a strong effect of patch size, and disentangling the two effects is complex as they are inherently correlated.

The drivers of discordance between our expectations and observations is unclear. One interpretation is that unlike larger, continuous meadows, more fragmented meadows, such as the one examined here, do not appear to enhance seed production (Stubler et al., 2017) or abundance (Livernois et al., 2017) at patch edges. Therefore, there might not be a functional response of predators to seeds at patch

edges in patch mosaics. Additionally, there could be a behavioural component that our sampling regime was not designed to test. For example, large predators may indirectly affect seed consumption by altering granivore behaviour, such as reduced feeding effort or efficacy (Peckarsky et al., 2008; Trussel, Ewanchuk, & Matassa, 2006). Based on the available literature, we would also expect that a behavioural response would also lead to more consumption at patch edges, since large fishes tend to forage in larger, more contiguous patches and patch interiors than small isolated patches (Johnson & Heck, 2006b; Laurel, Gregory, & Brown, 2003; Mahoney, Kenworthy, Geyer, Hovel, & Fodrie, 2018). However, the major predators in our system are fluke *Paralichthys dentatus*, which actively forage in sand and along sand-seagrass ecotones, and oyster toadfish *Opsanus tau*, who are sit-and-wait predators (Nuttall, Jordaan, Cerrato, & Frisk, 2011). It is possible that independent of patch size and cover, risk alters granivore feeding behaviour such that consumption is increased at patch interiors, although more detailed studies are required. Regardless, these results also demonstrate the importance of separating interactive and potentially confounding effects of patch size and seascape scale effects operating within patch edges.

Within seagrass meadows, a confluence of scale-dependent processes result in seed consumption patterns at odds with the escape hypothesis, and suggesting that seed predation can be context dependent when examined at multiple spatial scales. Seed predator densities (Manson, Ostfeld, & Canham, 1998), the concentration of alternative food resources (LoGiudice & Ostfeld, 2002), the plant species and geographic location (Hyatt et al., 2003) all effect survival and can be impacted by spatial configuration. As previously mentioned, we did not see consistent patterns of predator or alternative prey densities at any of the spatial scales we examined. Despite this, we argue that seed predator densities and alternative food resources likely play a role in the seed predation patterns we recorded. There was an overall negative, albeit zero-inclusive, trend in predator density across patch scales and seagrass cover in the buffer zone, matching the trend observed in consumption. Independent of patch size and isolation, the similar trends in seed consumption and predator density suggest that support for the escape hypothesis may be modulated by predator density. In addition, isopods showed a positive relationship with patch size and a negative relationship with overall cover. Isopods may be considered as potential granivores (Holbrook et al., 2000), although they are also likely alternative prey for many of the other, larger granivores in our system. We unfortunately did not identify isopods to the species level or attempt to categorize isopods by size, and so we cannot be certain what effect this faunal distribution pattern might have had on the seagrass seed survival. The apparent drivers of spatial patterns in seed survival were confounded by countervailing faunal patterns, and possibly even behaviour, within the same seascape, therefore, our results do not support any of the previously listed context-dependent variables that might affect whether seed predation patterns fit the escape hypothesis. We argue that landscape/seascape patterns should also be considered as context-dependent variables in future escape hypothesis studies.

Our model incorporated empirical estimates and literature-derived delineations of habitat type, within-patch location, patch size and total habitat cover. Despite obvious limitations in variable estimation, it was capable of explaining 34% of the observed variation in seed predation. Three sources of error likely contributed to model performance: (a) measurement error, (b) the presence of missing exogenous or endogenous variables and (c) temporal variation in strength of one or more causal relationships. Habitat type (sand/seagrass) was highly correlated with seed predation, and given the granivore composition, distribution and behaviour, we are confident in this variable estimate. However, the within-patch location showed a weaker correlation with seed predation, likely because it was unclear what constituted centre or edge from the seed predator perspective (i.e. its species-specific perspective; Weins & Milne, 1989). We opted for the commonly cited 1-m distance to delineate edge versus interior habitat (Carroll et al., 2012; Peterson et al., 2004), but selecting the appropriate scale for edge effects remains challenging in seascape ecology generally and seagrass ecology specifically (Boström, Pittman, & Simenstad, 2018). In particular, separating edge from interior habitats is dependent upon the processes being examined, the habitat perception of the species examined and behaviour and movements of organisms. Improving our understanding of the scale of edge effects for granivores could greatly improve our model results if the 'within-patch location' variable could be broken down into multiple species-specific variables in the SEM. For patch scale effects, which were modulated by total habitat cover, a number of features may have influenced our seed predation results, including unmeasured alternative food resources (epiphyte loads, infauna; Bologna & Heck, 1999, 2002), shoot density (Carroll et al., 2015) and macroalgal cover (Bell, Hall, & Robbins, 1995), all of which could be included in the SEM to improve overall model fit. Finally, the importance of all of the factors we did examine could themselves be temporally variable depending on a suite unexamined variables, including wave energy, tidal cycle, daylight, time of year, temperature and so forth. Despite limitations, our model represents a strong foundation from which to form hypotheses regarding causal relationships among oft-measured parameters in seagrass landscapes and rarely considered predation of seagrass seeds.

In conclusion, our estimates of seed consumption in our system were relatively low, similar to other studies of *Zostera marina* (Manley et al., 2015; Wigand & Churchill, 1988), as well as of other seagrass species (Darnell & Dunton, 2015; Nakaoka, 2002) and predation events outside patches were almost nonexistent. Thus, seeds that arrive in unstructured bottom likely have a higher probability of surviving to germination than those that settle within patches, a pattern critical for the persistence and resilience of seagrass patches and meadows, which rely on seed production and seed banks for meadow formation, expansion (Furman et al., 2015; Kaldy & Dunton, 1999) and recovery from loss (Jarvis, Brush et al., 2014; Orth et al., 2012). Anthropogenic activities have caused dramatic declines in seagrass coverage world-wide (Burdick & Short, 1999; Waycott et al., 2009). Extant meadows are experiencing both

loss and fragmentation, leading to patch mosaics with a range of patch sizes, shapes and degrees of connectivity (Bell, Hall, Soffian, & Madley, 2002; Bishop, Peterson, Summerson, & Gaskill, 2005; Robbins & Bell, 1994), and there is the potential for seed predation to have important consequences for seagrass resilience, recovery and restoration. For example, seed predation in small (newly established) patches shifts importance to asexual recruitment during the first few years until multiple patches coalesce or lateral expansion is great enough to allow edge-centre differences to reduce predation in patch interiors. We are just now beginning to appreciate how these seascape configurations can interact with sexual recruitment patterns, controlling meadow maintenance and trajectories of recovery and expansion. Seagrasses are foundation species in shallow, coastal ecosystems, and the factors that influence propagule supply and successful recruitment appear to operate and interact across a range of spatial scales; therefore, to successfully manage and restore these critical habitat types, it is important to consider both patch- and seascape-scale drivers of seed survival.

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AUTHORS' CONTRIBUTIONS

B.J.P. and L.J.J. conceived the ideas and designed the methodology. L.J.J. and B.T.F. conducted field work and collected the data, and performed the buffer analysis. J.M.C., E.A.H., L.J.J. and B.T.F. analysed the data, and J.M.C. and B.J.P. led the writing of the manuscript. All authors made significant contributions to the drafts and have given final approval for publication.

DATA ACCESSIBILITY

Data available through Digital Commons @ Georgia Southern repository <https://doi.org/10.20429/data.2019.01> (Carroll et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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