

# Habitat area more consistently affects seagrass faunal communities than fragmentation per se

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## Abstract

Seminal ecological theories, island biogeography and the single large or several small (SLOSS) reserve debate, examine whether large contiguous habitats conserve biodiversity better than multiple smaller patches. Today, delineating the ecological effects of habitat area versus configuration in a fragmentation context remains difficult, and often confounds efforts to understand proximate and ultimate drivers of community change in response to habitat alteration. We examined how the major components of fragmentation, habitat division versus area loss, independently influence faunal communities using landscapes constructed from artificial seagrass at scales relevant for juvenile estuarine nekton. We deployed 25 unique, 234-m<sup>2</sup> landscapes designed along orthogonal axes: habitat percent cover (i.e., area) and fragmentation per se (i.e., patchiness) to examine their effects on faunal density, community composition, and probability of bait-assay consumption. Faunal sampling occurred in both artificial seagrass and interspaced sandflat matrix. We also examined whether larval-settler density drove faunal density patterns across landscapes. Further, we assessed the relative importance of landscape-scale parameters versus fine-scale complexity—canopy height and epiphyte biomass—in determining faunal densities. We most consistently observed increasing epibenthic fish and macroinvertebrate density with increasing seagrass percent cover. Fragmentation per se only negatively affected epibenthic faunal density within the matrix at low seagrass coverage. Bait consumption increased with seagrass cover, suggesting larger habitats are relative foraging hotspots. Alternatively, benthopelagic fish density was unaffected by habitat parameters, reflecting lower seagrass reliance, or increased matrix tolerance. Community compositions did not vary across landscapes, suggesting that abundant species used landscapes indiscriminately. Finally, the relative importance of habitat parameters shifted across faunal guilds and life stages. Landscape percent cover most affected epibenthic faunal density, but not benthopelagic fish density, and neither pattern was related to settler density. Further, only fine-scale complexity influenced settler densities. Collectively, our results indicate habitat area is a primary, positive driver of faunal densities and generalist consumption,

and therefore should be prioritized in seagrass conservation. However, sampling across spatial scales and habitat types revealed nuances in habitat use patterns among faunal guilds and life stages that were not solely area-dependent, illustrating that a variety of landscape configurations support essential nursery functions.

#### KEY WORDS

acoustic imaging, artificial habitat, catch per unit effort, contiguous versus patchy, DIDSON, habitat degradation, percolation probability, recruitment, squidpop, storm effects, structural complexity

## INTRODUCTION

Globally intensifying habitat degradation and loss are primary modern threats to biodiversity across taxa and ecosystems (Dirzo & Raven, 2003; McCauley et al., 2015). At local scales, habitat degradation alters a range of landscape structural components to which biotic communities respond, including habitat area, mean patch size, patch isolation, and perimeter-to-area ratio. Further, the extent of less structured matrix habitat interspersed among more structured habitat patches can change. Because these landscape parameters are often tightly correlated, their independent influences on community structure and dynamics are difficult to delineate. Early efforts to describe these habitat configuration influences examined the independent and interactive effects of habitat area and patchiness. These efforts included island biogeography theory (MacArthur & Wilson, 1967) and the single large or several small (SLOSS) reserve debate (Diamond, 1975), which both investigated whether larger, more contiguous habitat would recruit and maintain biodiversity better than smaller and more isolated patches. As these theories continued to develop, further study highlighted additional habitat components, such as edge and matrix effects, which can alter dispersal abilities, survival rates, and species interactions (Fischer & Lindenmayer, 2007; Laurance, 2008). Improved understanding of these interrelated habitat structural components ultimately led to the advent of fragmentation theory. Fragmentation theory provides a framework to explore the mechanisms by which biotic communities respond to the conversion of more structured habitat to matrix habitat, which is often less structurally complex and potentially inhospitable for certain species (Laurance, 2008).

Habitats naturally occur in both contiguous and patchy configurations, yet habitat degradation often shifts more contiguous landscapes to patchier configurations through fragmentation. Landscape fragmentation is a process by which a habitat breaks apart into more

numerous patches, often concomitant with overall habitat loss (Fahrig, 2003). The simultaneous increase in habitat patchiness with decreasing area makes the delineation of their individual effects difficult, often confounding the main drivers of community change in both pristine and human-impacted natural systems. In all major biomes, ecological theories and empirical evidence such as island biogeography theory and species-area curves, respectively, generally agree that habitat loss leads to biodiversity loss (Dirzo & Raven, 2003; McCauley et al., 2015; Preston, 1962). However, biodiversity responses to fragmentation per se, or increasing habitat patchiness independent of area loss, are often weak (Fahrig, 2003). When detected, the overall directionality of fragmentation per se effects appear context-dependent relative to whether fragmentation is defined and examined from the perspective of patch-scale habitat loss or landscape-scale heterogeneity increase (Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018).

Examining habitat fragmentation at appropriate relative and absolute spatial scales is particularly important for interpreting fragmentation effects (Fahrig, 2013). Unfortunately, ecological studies typically operate at logically feasible scales, which are usually smaller than the scales at which ecological processes occur, and effects often do not translate across scales easily (Levin, 1992). For example, fragmentation effects should be studied across multiple landscapes rather than multiple patches to accurately assess impacts on communities (Fahrig, 2013, 2017). Further, sampling across both the primary and matrix habitats within a landscape is desired because the direction and strength of fragmentation effects can be directly related to the suitability of the matrix habitat to the organisms of interest (Dixo & Metzger, 2010; Prevedello & Vieira, 2010). Organism responses should also be observed at absolute spatial scales (e.g., millimeters, meters, kilometers) relevant to their body sizes and movements. As such, manipulative fragmentation studies, which often require habitat alteration or creation, tend to be limited to small spatial scales and, thus,

small-sized or low mobility organisms (McGarigal & Cushman, 2002).

While virtually all aspects of fragmentation theory have been exhaustively studied in terrestrial systems, fragmentation per se has yet to be extensively studied in manipulative settings within coastal marine habitats, particularly at scales relevant to juvenile estuarine nekton. The examination of ecological responses to the effects of habitat area and fragmentation per se independently and interactively is a necessary next step to better understand the consequences of marine habitat degradation. Seagrass landscapes are a useful model coastal marine system for examining habitat degradation effects, as they are particularly vulnerable to fragmentation through water quality changes, disturbance events like hurricanes, and local physical damage due to boating, fishing, or dredging activities (Cabaço et al., 2008; Orth et al., 2006; Waycott et al., 2009). As such, seagrass meadows exist across a range of fragmentation states, thereby allowing for a space-for-time substitution in which fragmentation state can be used as a proxy to understand the effects of fragmentation as a process. In this system, simple binary comparisons of primary habitat to matrix habitat are possible, as seagrass landscapes often exist embedded within sandflat surroundings. Further, a single seagrass landscape can match the spatial extent of the short-term movements (i.e., over days, weeks, or months) of various common estuarine fauna (Yeager et al., 2016).

There is an emerging body of literature examining seagrass fragmentation effects on associated faunal communities that has revealed complex, variable responses (reviewed by Boström et al., 2006; Yarnall et al., 2022). Numerous—sometimes competing—mechanisms stemming from both larval settlement patterns and post-settlement processes are hypothesized to drive faunal responses to seagrass fragmentation, including responses to habitat area, patchiness, mean patch size, and perimeter-to-area ratios. In addition, while fragmentation effects are most accurately assessed at the landscape scale, patch- and fine-scale mechanisms are often proposed as contributing influences (Yarnall et al., 2022). For instance, marine larval settlement patterns depend upon multiple abiotic and biotic factors that operate at different scales, like wind, currents, and habitat complexity (Jackson, 1986). Within seagrass, these factors can manifest higher larval densities in small versus large patches (Boström et al., 2010) or higher settlement in patches with relatively more perimeter (Bologna & Heck, 2000). These patterns can be interpreted at the patch scale (i.e., as patch area or perimeter effects), but may also suggest that settlement is highest where larvae being transported in currents first meet fine-scale complex habitat (Bologna &

Heck, 2000). Settlement then gradually lessens farther into seagrass due to incremental reductions in both currents and larval concentration (i.e., settlement shadows; Orth, 1992). By extension, at the landscape scale more larvae per unit seagrass area may settle in landscapes composed of small patches with relatively higher perimeter-to-area ratios (Arponen & Boström, 2012; Warry et al., 2009).

Beyond initial settlement patterns, additional opposing mechanisms have been suggested to drive post-settlement faunal responses to seagrass fragmentation. Because many settling species are mobile, larval distributions may not reliably predict faunal densities across landscapes. Juvenile and adult faunal densities can be elevated in large contiguous landscapes relative to patchy meadows, due to relatively higher survival away from patch edges (Yarnall et al., 2022) and positive abundance-area relationships (Boström et al., 2006). However, other evidence suggests that fragmented landscapes may support similar or higher faunal densities than contiguous landscapes of similar area (Arponen & Boström, 2012). This perhaps suggests that fragmentation per se influences are context-dependent, such that when averaged across studies, effects on seagrass community structure are weak (Boström et al., 2006; Fahrig, 2003). One instance of this context dependence is demonstrated by the “fragmentation threshold hypothesis”, which describes how fragmentation per se only negatively influences communities when the primary habitat area is <20% of the landscape footprint area (Trzcinski et al., 1999). Supporting evidence for this hypothesis has been observed within seagrass systems, where landscape fragmentation per se did not alter fish communities until seagrass cover was below 25% within 16,000 m<sup>2</sup> study domains (Yeager et al., 2016).

Further aspects of community composition, such as diversity, species richness, and relative abundance, are also negatively affected by decreases in seagrass cover yet can be neutrally or positively influenced by fragmentation per se (Arponen & Boström, 2012; Yeager et al., 2016). Mosaics of structured habitat and unstructured matrix may increase diversity by supporting both habitat- and matrix-associated species (Dixo & Metzger, 2010; Laurance, 2008). For example, while faunal density and species richness are generally higher in seagrass than adjacent mudflat (Baillie et al., 2015), fragmented seagrass landscapes may better support numerous trophic levels, as predator species use sandflat matrix as search corridors among patches (Hovel & Lipcius, 2002) and restrict prey to vegetated refugia (Bishop & Byers, 2015; Virnstein & Curran, 1986). As such, predator-prey interactions may also increase at patch edges (reviewed by Mahoney et al., 2018) and in

landscapes with relatively more edge habitat (Hovel & Lipcius, 2002; Irlandi et al., 1995). However, predation rates may not be uniformly elevated across fragmented landscapes, as patch isolation can reduce predator movement among distant patches (Fodrie et al., 2015; Micheli & Peterson, 1999) or increase the effort needed for a predator to search among patches for prey (Hovel & Lipcius, 2001).

Faunal responses to habitat area and configuration are also influenced by covariates such as fine-scale structural complexity (Hovel & Lipcius, 2001; Jackson et al., 2006). Fine-scale complexity attributes, such as seagrass shoot density, canopy height, and epiphyte growth on seagrass leaves, may influence faunal communities through the provision of predation refugia in interstitial spaces (Guidetti & Bussotti, 2002), camouflage for cryptic and low mobility species (Yeager et al., 2016, 2019), food for mesograzers (Ebrahim et al., 2014), or water flow attenuation (Hansen & Reidenbach, 2013) and larval catchment (Bologna & Heck, 2000). Fine-scale structure can also alter the function of seagrass patch edges, which are proximate drivers of shifts in faunal abundances and interactions at patch and landscape scales (Hovel et al., 2021; Yarnall et al., 2022). These covariates may impact fauna as much or more than seagrass fragmentation in some cases (Yeager et al., 2019).

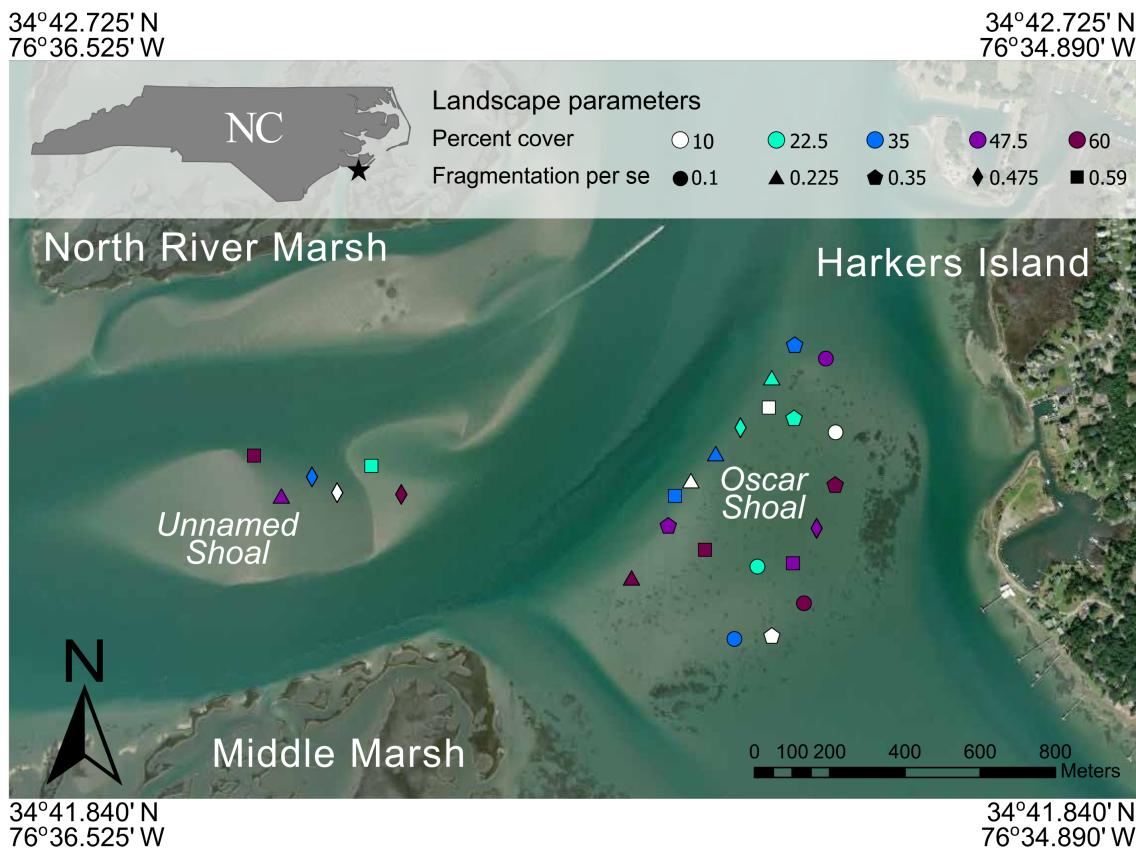
The covariation of—and indeed, dynamic feedbacks between—landscape configuration and fine-scale habitat characteristics challenge efforts to isolate the mechanisms underpinning fragmentation effects on faunal communities in natural seagrass systems (Yarnall et al., 2022). Within natural systems, it is difficult to achieve adequate sample size for replicating treatment effects across a broad range of both habitat area and patch number (Yeager et al., 2016). Alternatively, constructing landscapes from artificial seagrass is labor-intensive, which often restricts studies employing artificial seagrass units (ASUs) to a few square meters in footprint area. Accordingly, ASU studies often examine faunal communities of restricted size distributions and mobilities (Arponen & Boström, 2012; Warry et al., 2009). However, ASUs have become an important tool for controlling covarying and confounding habitat characteristics intrinsic to natural seagrass, allowing for more direct investigations of faunal responses to specific habitat structure and configuration components. In the context of fragmentation effect studies, artificial seagrass landscapes can be designed to separately test habitat area and patchiness effects (Ljungberg et al., 2013; Warry et al., 2009).

To parse the ecological effects of habitat area and fragmentation per se on the community structure and dynamics of juvenile estuarine fauna, we employed ASU landscapes at a scale relevant to the habitat fidelity of common fishes and macroinvertebrates in a temperate study system (Johnson & Eggleston, 2010; Potthoff & Allen, 2003; Yeager et al., 2016). We deployed 25 unique ASU landscapes, designed along orthogonal axes of artificial seagrass percent cover of each landscape and fragmentation per se. Using multiple regression, we delineated their independent and interactive effects on seagrass-associated fish and macroinvertebrate communities within both artificial seagrass and the sandflat matrix. We examined how landscape parameters influenced seagrass faunal density, species richness, Pielou's evenness, community composition, and bait consumption probability by generalists. Based on consistent trends across habitat fragmentation studies (Fahrig, 2003), we hypothesized that seagrass percent cover would be positively related to faunal community metrics, such as destiny, species richness, and evenness. Further, based on the fragmentation threshold hypothesis (Trzcinski et al., 1999), we expected that negative influences of fragmentation per se on faunal communities would only manifest within landscapes of less than 20%–30% seagrass cover (Yeager et al., 2016). We also investigated whether fish and macroinvertebrate settler density drove post-settler faunal density patterns across landscape configurations. Finally, we examined the relative importance of landscape parameters versus fine-scale complexity metrics, artificial seagrass canopy height and epiphyte biomass, in influencing faunal density patterns within structured seagrass.

## METHODS

### Study location

We conducted this study on Oscar Shoal and an adjacent unnamed shoal in Back Sound, NC, USA ( $34^{\circ}42'20''$  N to  $34^{\circ}41'60''$  N,  $76^{\circ}36'15''$  W to  $76^{\circ}35'17''$  W) from June to November of 2018 (Figure 1). Both shoals are shallow, with depths  $<0.5$  m at low tide, and historically supported expansive, ephemeral seagrass meadows (Peterson et al., 2001) that have been absent over the previous decade. During 2018, these shoals had large expanses of sandy area speckled with small patches of seagrass, which were avoided during experimental landscape siting. These natural patches were composed of a mixture of eelgrass, *Zostera marina* (Linnaeus 1753), and shoal grass, *Halodule wrightii* (Ascherson 1868) (Yeager et al., 2016).



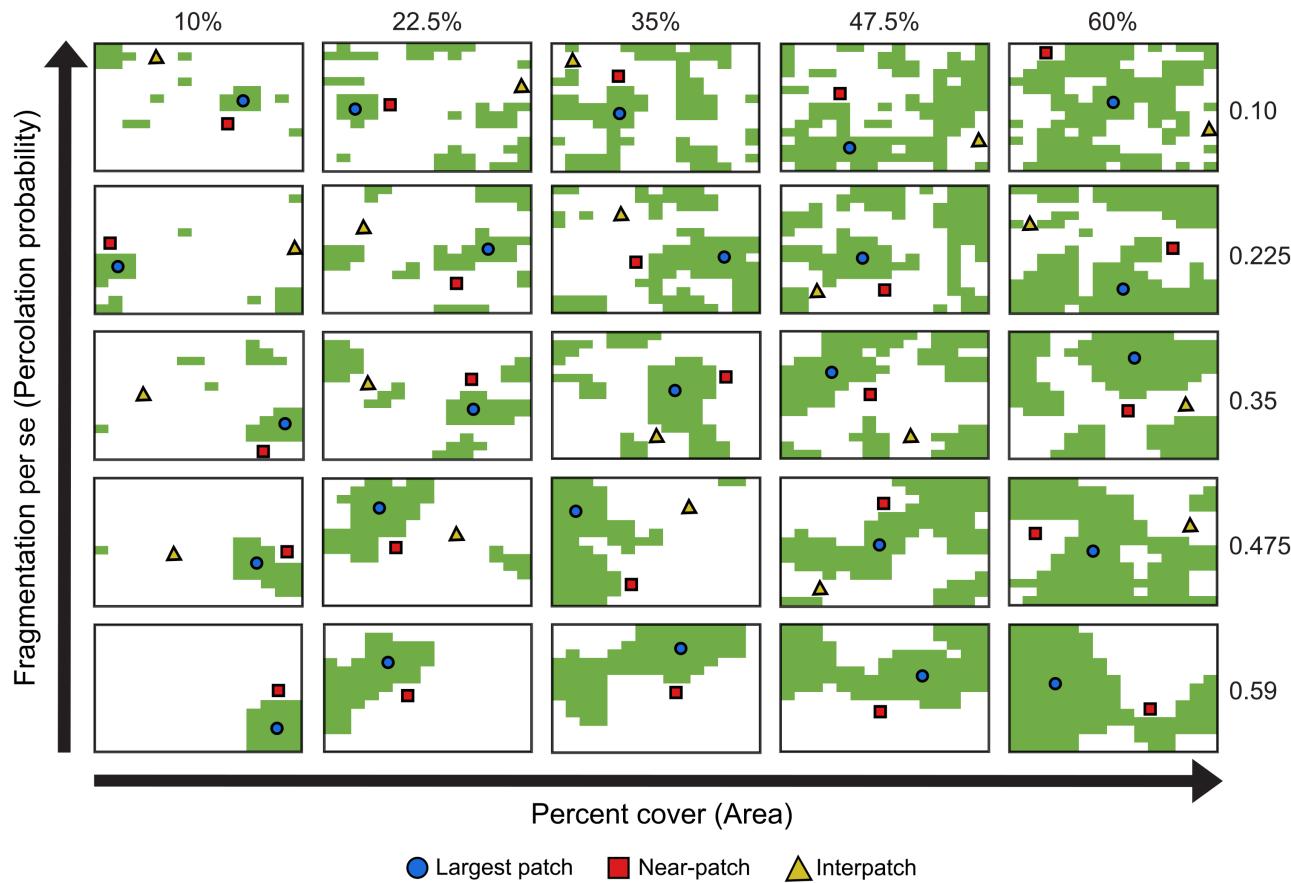
**FIGURE 1** Map showing the location of 26 artificial seagrass landscapes in Back Sound, NC. One landscape design with 60% cover and 0.59 percolation probability was replicated on both the unnamed and Oscar shoals. All other landscapes are unique.

Both shoals were adjacent to boating channels between two large saltmarsh complexes to the north (North River Marsh) and south (Middle Marsh).

### ASU landscape construction

To examine fragmentation components independently and interactively, we generated 25 unique landscape grids of  $15 \times 15$  cells. Each cell was a  $\sim 1\text{-m}^2$  rectangle ( $0.86\text{-m} \times 1.2\text{-m}$ ), the size of a single ASU, making the full landscape grid area =  $234\text{ m}^2$  ( $18\text{-m} \times 13\text{-m}$ ). The 25 unique landscapes were designed such that grid arrangements of ASUs were treatments along orthogonal axes of percent cover of seagrass within the landscape footprint (10%, 22.5%, 35%, 47.5%, 60%) and fragmentation per se, which was indexed by percolation probability (0.1, 0.225, 0.35, 0.475, 0.59) (Figure 2). To generate our 25 landscape grids which were then constructed in the field, our percent cover and percolation probability values were used as input parameters in the modified random cluster (MRC) method (Saura & Martinez-Millan, 2000) using the *randomHabitat* function in the *secr* package in R (Efford, 2016). Percolation probability initially

determined the probability that a cell was occupied by a given habitat type, either an ASU or sandflat matrix. The MRC method then identified clusters of cells within a given neighborhood and assigned a habitat type, ASU or sandflat, based on the percent cover parameter. The remainder of the grid was then filled in based on the existing clusters and the percent cover parameter, to create the final landscape grid (Saura & Martinez-Millan, 2000). For each landscape, the percent of total ASU area held within the largest ASU patch was a function of percolation probability. Therefore, landscapes of low percolation probability were composed of numerous smaller ASU patches and were more fragmented. Using the MRC method, the lower limit of realistic landscape fragmentation is typically approached at percolation probability = 0.1. Further, generated landscapes are typically most contiguous when both percent cover approaches ~60% and percolation probability approaches ~0.59 (Saura & Martinez-Millan, 2000). Therefore, we chose 60% cover and percolation probability = 0.59 as the upper limits of our landscape parameters, and 10% cover and percolation probability = 0.1 as the lower limits. We also note that the generated landscapes exhibited a range of patch numbers (1–15 patches)



**FIGURE 2** Twenty-five unique 18-m × 13-m (234 m<sup>2</sup> footprint area) landscapes generated along orthogonal axes of habitat percent cover treatment (area) and fragmentation per se treatment (percolation probability). Each landscape is marked with two to three symbols indicating faunal sampling locations: The rough center of the largest patch (“largest patch”), 1 m away from the largest patch within the matrix (“near-patch”), and bisecting an interpatch distance within the matrix (“interpatch”). Landscapes of 0.59 percolation probability did not receive interpatch samples because they consisted of a single patch.

observed within natural, low seagrass area landscapes (250–375 m<sup>2</sup>) in our system (Appendix S1: Figure S1) (Yeager et al., 2016). For simplicity, landscape parameters will be hereafter described in the context of percent cover and fragmentation per se (low percolation probability is high fragmentation per se). Landscapes were constrained to fall within 2% of the percent cover input parameter (relative to the 234 m<sup>2</sup> footprint area) and maintain consistent perimeter-to-area ratios within individual fragmentation per se treatment levels (*secr* package in R; Efford, 2016). Within an individual landscape defined by >1 seagrass patch, discrete patches of artificial seagrass were separated from one another by ≥0.86 m (the short-side length of an ASU) of sandflat matrix in all directions.

Each landscape contained 22 to 135 ASUs designed to mimic shoot density, shoot width, and canopy height of *Z. marina* meadows in this system (Yeager et al., 2016). For each ASU, 30-cm lengths of 0.5-cm width green curling ribbon were tied to ~1-m<sup>2</sup> bases of rigid black plastic VEXAR (0.86-m × 1.2-m, 2.5-cm mesh) so that each ASU

had uniformly spaced “shoots” (450 m<sup>-2</sup>) with two ~15-cm length “leaves.” A total of 2059 ASUs were constructed, with each ASU requiring ~3 h to create. The entire manufacturing effort, with work divided among several technicians and community volunteers, required the equivalent of three full-time person work years.

Twenty-five ASU landscapes were deployed over the course of 10 days, from 21 May to 31 May 2018, in hap-hazard order and placement. Individual ASUs were secured to the sediment surface and each other with 16 lawn staples and 0–4 cable ties (based on presence/absence of adjacent ASUs), respectively. All ASU landscapes were ≥50 m apart from each other and ≥30 m from natural seagrass patches to improve landscape independence. These minimum distance constraints, combined with our avoidance of strong currents and increasing depths along shoal edges, necessitated that only 19 landscapes could be co-located on Oscar Shoal, while the remaining 6 were co-located on the adjacent, unnamed shoal. Due to these constraints, we allocated

extra ASUs toward replicating the landscape with 60% cover and 0.59 percolation probability (i.e., “60%-0.59”; hereafter individual landscapes will be named by this convention), on 8 June 2018. As this replication of 60%-0.59 had a sample size of two, this 26th landscape was used only to gauge for potential qualitative and logistical differences between the two shoal environments. No clear qualitative differences (e.g., sediment movement, water current differences) were observed between the two shoal environments throughout the experiment. Further, statistical differences in faunal responses between the replicate 60%-0.59 landscapes were ruled out (Wilcoxon rank sum tests; Appendix S1: Table S1). Therefore, all variables sampled in the two replicate 60%-0.59 landscapes were averaged for further analyses, and the shoal were considered functionally equivalent settings.

## Faunal sampling locations and regimes

To examine potential differences among juvenile estuarine fish and macroinvertebrate responses to habitat configuration within artificial seagrass habitat versus sandflat matrix, faunal densities were sampled at three locations within each landscape (Figure 2). Samples of seagrass-associated fauna were taken within the largest ASU patch of each landscape, as well as two locations within the matrix, which we termed “near-patch” and “interpatch.” The largest ASU patch was sampled because it represented landscape treatments; the area increased with landscape percent cover and decreased with landscape fragmentation per se. Linear models (LMs) were used to check that neither the area nor perimeter of the largest ASU patch had significant relationships with sampled faunal densities across landscapes, such that sampling the largest patch would confound landscape parameter effects (Appendix S1: Table S2). The two matrix locations were chosen to assess faunal responses at a constant distance from the seagrass habitat and among various interpatch distances, respectively. The near-patch location was selected within the landscape border such that the largest patch in the landscape was 1-m away in a single direction (i.e., not 1 m away from the largest patch in multiple directions), while all other patches were >1 m away. The interpatch location was selected to bisect the linear distance between two patches, and was judged to be the most distinguishable from other nearby interpatch distances. As such, interpatch distances generally scaled inversely with landscape parameters; the distance increased with decreasing landscape percent cover, and the distance increased with decreasing fragmentation per

se (i.e., increasing percolation probability) (Appendix S1: Table S3). However, given the irregular configuration of each patch and landscape, there were some exceptions to this pattern. Interpatch samples were not taken in landscapes with 0.59 percolation probability, as they only had one patch.

To survey faunal responses across landscapes of varying percent cover and fragmentation per se, three primary sampling regimes were used. Two sampling regimes, minnow traps, and Dual frequency IDentification SONar (DIDSON), were used to sample relatively low-mobility epibenthic fishes and macroinvertebrates and high-mobility benthopelagic fishes, respectively. These samples were taken in all three sample locations within the landscape: the largest ASU patch, near-patch matrix, and interpatch matrix. The third sampling regime deployed one Standardized Monitoring Unit for the Recruitment of Fishes (SMURF; Ammann, 2004) per landscape, only in the largest ASU patch, to assess whether settler density patterns drove post-settler faunal density patterns across landscapes.

## Minnow trap sampling of epibenthic fishes and macroinvertebrates

From June to September 2018 (Table 1; note, additional October samples were excluded from analyses, see *Hurricane Florence*), primarily juvenile epibenthic fishes and macroinvertebrates (hereafter collectively referred to as “epibenthic fauna”) were sampled with Gee-style minnow traps (41-cm × 22-cm cylinders, 0.3-cm galvanized wire-mesh, with 4-cm diameter funneled openings) baited with ~8 pieces of dry dog food (Able et al., 2015). Minnow trap (hereafter “trap”) sampling was completed on an alternating weekly basis in the ASU versus matrix locations of all 26 landscapes, due to gear availability. One trap was deployed within the largest patch of each landscape on nine occasions and at each of the two matrix locations simultaneously on four occasions (Table 1). Trap sampling was conducted the most frequently of the three sampling regimes to best characterize faunal communities, in terms of species composition and catch per unit effort (CPUE; a common proxy for density). Each trap deployment lasted 24 h, at which time all fauna were enumerated, identified to the lowest taxonomical level possible, and released.

## DIDSON sampling of benthopelagic fishes

A full set of DIDSON samples across the three sampling locations within all landscapes was completed once during July and once during September (Table 1; note,

**TABLE 1** Schedule, sample size (excluding lost samples), and sampling location of gear deployments in 2018.

Month	SMURF		Minnow trap		DIDSON		Squidpop
	ASU	ASU	ASU	Matrix	ASU	Matrix	ASU edges
Jun	77	51	46		...	...	...
Jul	26	52	46		25	46	...
Aug	50	52	46		...	...	...
Sept	...	...	46		25	44	...
Oct	...	(60)		...	(26)	...	203
Nov	...	...	...		...	...	203

Note: Minnow trap samples in ASU locations were not taken in September due to the arrival of Hurricane Florence. Values in parentheses indicate post-Florence samples which were excluded from statistical analysis.

Abbreviations: ASU, artificial seagrass unit; DIDSON, Dual Frequency Identification Sonar; SMURF, standardized monitoring unit for the recruitment of fishes.

additional October samples were excluded from analyses; see *Hurricane Florence*). DIDSON allowed us to reliably detect fishes regardless of water visibility, sample an order-of-magnitude higher number of fishes than traps, and expand the size range of organisms we were able to sample versus traps alone. While there was likely some overlap in the fish species sampled by DIDSON and traps, the two sampled assemblages appeared to be distinct. However, DIDSON imagery generally does not allow for species identification. Therefore, we refer to the communities sampled by each method using their general habitat use patterns as observed from the species composition in traps, and movement behaviors and body shapes in DIDSON recordings. In general, epibenthic fishes (and macroinvertebrates) were better sampled by traps, while benthopelagic fishes were better sampled by DIDSON. We acknowledge that both guilds use the benthos to some degree and some species can fall in either category.

DIDSON sample recordings, each 1 min in length, had a field of view that ranged from 2 to 6.5-m from the DIDSON. DIDSON samples were standardized by positioning the sampling location (i.e., the symbols in Figure 2) at a range of 4.5-m in the center of the viewing field. We acknowledge that more than one habitat type (i.e., artificial seagrass, sandflat matrix) may have been in view depending on sampling location and landscape configuration, yet we still included all fishes in view to keep the recording area around the sampling location consistent. The DIDSON was mounted to a kayak, held stationary by a person on the opposite side of the sampling field, and was operated at a consistent depth below the surface (~10 cm) and oriented to include most of the water column and also the substrate (Appendix S1: Figure S2). DIDSON sampling was completed the least frequently of three faunal sampling regimes as it has strict weather requirements for data collection and the ability to observe

high numbers of fish in a single recording frame, leading to high data processing time demands.

Using DIDSON software (V5.26.06), recordings were first watched from beginning to end to assess quality. Then fish were counted and measured on ten randomly selected frames from each 1-min sample. Random frame selection was constrained such that all frames were spaced a minimum of 25 frames apart to improve sub-sample independence. Fish counts for all 10 frames per sample were summed for further statistical analysis. This method does not differentiate between fish that are maintaining position within the area versus transiting through, but theoretically represents a cumulative total of fish presences (Boswell et al., 2019; Smith et al., 2021). To account for potential reader bias in fish counts and length measurements (in centimeters), ~15% of samples were randomly selected to be analyzed by two ( $n = 13$ ) or three ( $n = 15$ ) readers, reading identical sample frames. Readers counted statistically similar numbers of fishes per sample (pairwise comparisons across readers using Wilcoxon sign-ranked tests,  $p > 0.05$ ), ruling out significant reader bias on fish counts. We further determined that the SD in fish counts across readers did not increase for samples with higher mean fish counts (linear regression,  $p > 0.05$ ). To examine potential reader bias in fish length measurements, we subset the data to only include frames on which all readers agreed on fish count. We then used a linear mixed model with fish length as the response variable, reader identity as the fixed effect, and frame number as a random intercept. In this case, significant bias in fish measurement was observed among readers ( $\chi^2 = 101.1$ ,  $df = 2$ ,  $p < 0.001$ ), where some readers consistently measured fishes at smaller or larger sizes than other readers. Therefore, we converted fish lengths to  $z$ -scores and divided them into 0.5 SD bins for further supplemental statistical analysis (included in Appendix S1). For frames with

multiple readers, mean length  $z$ -scores per fish were calculated.

DIDSON samples in landscape 47%-0.225 during July were major outliers due to a large aggregation of small fish sampled across all three positions (i.e., largest patch,  $n = 91$ ; near-patch,  $n = 186$ ; interpatch,  $n = 735$ ). This aggregation appeared, by body shape, to be forage fishes, which are pelagic bait fish and have no strong association with seagrass or sandflat. At each of the three positions, these samples had the highest fish counts and were  $>3$  SD higher than the mean of all other sample counts. Preliminary analysis revealed these to be influential outliers (Cook's distance  $>0.5$ ) preventing resolution of fish densities in all other landscapes. Therefore, these outliers were excluded from analysis (Howell, 2011; Rawlings et al., 1998) (models excluding influential outliers are listed in Appendix S1: Table S4).

## SMURF sampling of larval fish and crab megalopae settler densities

To assess whether faunal density patterns across landscapes were driven by settlement patterns, larval fishes and crab megalopae (hereafter collectively referred to as "settlers") were sampled using SMURFs (Ammann, 2004). SMURFs were created from 2.5-cm mesh VEXAR, zip-tied to create a 1-m long, 0.2-m diameter cylinder with folded-end closures. To facilitate settlement and accommodate various settler sizes, each cylinder was stuffed with two sizes of plastic mesh: 3 m<sup>2</sup> of 5-cm × 7.5-cm and 5 m<sup>2</sup> of 1-cm × 1-cm mesh. Each SMURF was positioned at the estimated "center" of the largest ASU patch in each landscape (Figure 2). SMURFs were then secured to each landscape by a 20-cm sand screw and 25-cm paracord line attached to the underside of the sampling unit. Floats were attached to cylinder ends for added buoyancy and to suspend the SMURFs up to 25 cm above the seafloor. However, we note that currents typically gently pressed SMURFs to the ground in the direction of water flow. SMURFs were deployed for 48 h to maximize larval collection (Ammann, 2004) while minimizing biofouling (Tavernetti et al., 2009). Deployments occurred seven times from June to August 2018 (Table 1) to bracket the seasonal timing of settlement by the majority of species that occupy local seagrass as nursery habitat (Baillie et al., 2015). After the first deployment cycle it was noted that SMURFs retrieved closer to sunrise had higher settler abundances. Subsequent deployments were therefore timed to coincide with a 4-h collection window surrounding sunrise. Upon retrieval, 5-gal buckets of seawater were poured over each SMURF into a collection bin while

the SMURF was shaken and rotated. This process was repeated a minimum of three times or until no additional fauna were observed being washed into the collection bin. Samples were sieved (0.5-mm mesh) and collected fauna were frozen for later identification and enumeration in the lab. All SMURFs were rinsed with freshwater and dried by sunlight before redeployment.

One SMURF, in landscape 60%-0.225 on 11 July, collected a large number of brachyuran megalopae ( $n = 49$ ), which was the highest settler density observed in any SMURF and was  $>3$  SD higher than the mean of all other settler densities. Upon preliminary analysis, this SMURF catch was shown to be an influential outlier (Cook's distance  $>0.5$ ) that prevented resolution of settler densities in all other landscapes, therefore this outlier was excluded from analysis (Howell, 2011; Rawlings et al., 1998) (models excluding influential outliers are listed in Appendix S1: Table S4).

## Community-level generalist consumption

To measure generalist consumption probabilities across landscapes, we conducted two bait consumption assays on 19 October and 1 November 2018 (Table 1). Consumption assays were conducted after all faunal sampling was completed, in order to avoid attracting additional fauna to landscapes during sampling, but also prior to the seasonal egress of nekton from local seagrass meadows (Baillie et al., 2015). Bait assays were conducted with squidpops, which are 1-cm × 1-cm squares of dried squid mantle tied to 1-cm segments of monofilament (Duffy et al., 2015). Squidpops were secured to 60-cm long, 0.5-cm diameter, fiberglass stakes with attached floats for relocation. On each assay date, up to 10 squidpops were deployed within ASUs in each landscape, 1 m apart and  $\leq 0.5$  m from the ASU–matrix interface, to control for potentially different consumption probabilities between seagrass patch edges and interiors (Mahoney et al., 2018). Most landscapes received all 10 squidpops (mean of  $9.2 \pm 1.8$  SD), however for six landscapes the number of squidpops deployed was reduced due to the length of available edge (see Hurricane Florence). Squidpop presence/absence was checked after 1, 2, and 3 h to retrospectively assess the timeframe in which overall consumption probabilities were between one- and two-thirds of all bait consumed, allowing for resolution of differences in consumption rates among sites. This threshold was met after 1 h, therefore we focus our results on these data. All absent squidpops were presumed eaten based on previous efforts that have demonstrated negligible spurious bait loss (Lefcheck et al., 2021). Preliminary analyses of these data, including

and excluding landscapes with <10 squidpops deployed, determined that uneven sampling across landscapes did not influence the overall pattern of generalist consumption probabilities observed.

## Artificial seagrass fine-scale complexity

Although not intentionally manipulated, the habitat features of our ASU landscapes had the potential to be modified by sediment burial or scour and by epiphyte growth after installation. Therefore, in July and September 2018, fine-scale habitat complexity metrics, including ASU canopy height and epiphyte biomass, were sampled along a transect from the edge to the center of the largest patch in each landscape. Along each transect, five ribbon clippings were taken per ASU and an additional five clippings were taken on the edge ASU, within 0.5 m of the ASU-matrix interface. The number of ASUs sampled per landscape (mean of  $6.81 \pm 3.24$  SD) differed based on percent cover and configuration. Each ASU ribbon was haphazardly selected and clipped at the sediment surface, then measured to approximate above-sediment landscape canopy height. In the lab, epiphytes were scraped off each side of the ribbon, dried for 12 h at 60°C, then burned for 4 h at 500°C to determine ash content (Peterson & Heck, 2001). Ash-free dry epiphyte biomass (hereafter “epiphyte biomass”) was calculated as dry weight minus ash weight, then divided by the surface area of the ribbon to obtain standardized epiphyte biomass (in milligrams per square centimeter). Preliminary analysis revealed that artificial seagrass blade height and epiphyte biomass were positively correlated (Pearson pairwise correlation,  $r = 0.19$ ,  $df = 1075$ ,  $p < 0.001$ ); however, we still examined faunal density relationships with both fine-scale variables, as they represent different forms of complexity. Mean epiphyte biomass per landscape ranged from 0.02 to 6.89 mg cm<sup>-2</sup> while artificial seagrass canopy height ranged between 65 and 126 mm. No significant relationships between landscape parameters and mean canopy height or mean epiphyte biomass were observed (LMs; Appendix S1: Table S5, Figure S3).

## Statistical analyses

To determine how landscape parameters influenced seagrass faunal communities, we used generalized linear models (GLMs) with negative binomial error distributions (using R v3.6.2; R Core Team, 2019; Venables & Ripley, 2002; Zeileis & Hothorn, 2002). Predictor variables for all analyses, unless otherwise stated, were landscape percent cover, fragmentation per se, and their

interaction (percent cover × fragmentation per se), all coded as continuous variables. To enable simple GLM interpretation, percent cover and fragmentation per se (i.e., percolation probability) were analyzed on matching scales as proportions and probabilities from 0 to 1. Response variables included epibenthic fauna CPUE from traps and benthopelagic fish CPUE in DIDSON samples, examined at each sample position (i.e., largest patch, interpatch, near-patch) separately. Settler CPUE in SMURFs was also examined as a response variable to determine if landscape influences on settlers were comparable to their influences on epibenthic faunal densities from traps. Epibenthic fauna and benthopelagic fish CPUEs in the interpatch locations were also regressed directly with interpatch distance (in meters). We further examined the influence of landscape percent cover only (see *Hurricane Florence*) on generalist consumption of squidpops after 1 h using binomial logistic regression.

To assess whether settlement patterns predicted juvenile faunal densities across landscapes, we used pairwise correlation analysis for monthly CPUE of taxa in SMURFs and traps. Three genera were captured sufficiently frequently in both SMURFs and traps for this analysis: *Callinectes*, *Lutjanus*, and *Stephanolepis* (Appendix S1: Table S6). Based on growth rates for early life stages of these genera (Denit & Sponaugle, 2004; Rogers et al., 2001; Zmora et al., 2005) and our monthly sampling frequencies for both SMURFs and traps, a 2-month time lag was used to attempt to capture the interval by which these genera grow from settler (millimeters in length) to juvenile (centimeters in length) stages, therefore correlating catch rates of the same cohort. For example, we correlated the SMURF CPUE of June settlers to the trap CPUE of August juveniles of the same species.

We further explored landscape parameter influences on faunal community composition with both univariate and multivariate analyses. First, landscape parameter effects on species richness per se (i.e., identified to the lowest taxonomic level possible) and Pielou’s evenness ( $J$ ) of epibenthic fauna caught in traps and settlers caught in SMURFs were examined with LMs, separately. Due to uneven SMURF sampling across months (Table 1) and uneven trap sampling across landscapes (i.e., single vs. multi-patch landscapes, Figure 2), raw individual counts per species would not be representative of landscape communities. Therefore, the monthly CPUE per species collected per SMURF or trap in each landscape was used to indicate species’ relative abundances. Monthly species counts per landscape were summed to calculate total species richness per se and Pielou’s evenness per landscape over the course of the study. Second, the community compositions of epibenthic fauna and settlers across landscapes were explored,

separately, by PERMANOVAs (permutations = 999) of Hellinger-transformed species counts (i.e., square-root relative species abundances; Legendre & Gallagher, 2001). Communities were then displayed graphically using non-metric multi-dimensional scaling (NMDS) based on Bray-Curtis dissimilarities (*vegan* package in R; Oksanen et al., 2020). Because fish species were not identifiable from DIDSON samples, benthopelagic fish length *z*-score 0.5 SD bins were used as an analogue for species to calculate fish-length richness and evenness in each landscape. Their relationships to the landscape parameters were then examined with LMs. To examine fish-length community compositions in each landscape, we used PERMANOVA displayed by NMDS for *z*-score bins. Fish length *z*-score patterns were explored as supplemental analyses (see Appendix S1).

To determine whether landscape or fine-scale complexity parameters, canopy height or epiphyte biomass, had relatively more predictive influences on epibenthic fauna, benthopelagic fish, or settler densities, we examined July faunal samples taken within the largest patch of each landscape, because this was the month and location where all faunal sampling methods overlapped with ribbon sampling. We first subset each of epibenthic fauna CPUE (from traps), benthopelagic fish CPUE (from DIDSON), and settler CPUE (from SMURFs) to only include the sampling date closest to the July ribbon sampling date. We then fit negative binomial distributed GLMs for each response variable. Predictor variables for each model were landscape percent cover, fragmentation per se, the interaction term (percent cover  $\times$  fragmentation per se), mean canopy height, and mean epiphyte biomass. For these July subset models, we did not generally reconsider the partial effects of the landscape parameters, as this was already done for the full sampling period. However, we did consider whether parameters from one or both spatial scales (i.e., landscape-scale vs. fine-scale) were statistically important and the direction of the fine-scale parameter partial effects. Finally, we examined whether canopy height and epiphyte biomass had independent influences on each faunal density response variable using one-way negative binomial GLMs.

## Hurricane Florence

The study area and artificial landscapes were directly impacted by Hurricane Florence from 13 to 16 September 2018. Despite additional lawn staple and cable tie reinforcements made to ASUs prior to Florence's landfall, our landscapes experienced disturbance, in many cases completely removing or burying ASUs (Appendix S1:

Figure S4). Therefore, we recalculated landscape parameters based on ASU-by-ASU checks made after Hurricane Florence. Holding the original landscape 234-m<sup>2</sup> footprint constant, the percent cover of each landscape was recalculated from the remaining number of ASUs, excluding buried ASUs, as they were not expected to influence above-ground faunal responses. Percolation probability is a fragmentation per se input parameter for landscape generation (Saura & Martínez-Millan, 2000) but is not generally used to describe existing or natural landscapes. Therefore, to determine how landscape fragmentation per se was altered, we first determined the linear relationship between the initial number of seagrass patches and our percolation probability treatments ( $y = 0.63 - 0.06x$ ,  $r^2 = 0.96$ ; Appendix S1: Figure S5). We then used this relationship to predict post-Florence landscape percolation probabilities from the remaining number of patches in each landscape, excluding buried ASUs (Appendix S1: Figure S6).

Trap and DIDSON samples were taken both before and after Florence. Due to considerable landscape parameter alterations over this timeframe and potentially confounding disturbance influences, we excluded post-Florence faunal densities from analyses (Table 1). By contrast, squidpop consumption assays were only conducted after Florence. Only the influence of post-Florence landscape percent cover was examined for the squidpop consumption analysis because post-Florence landscape percent cover and percolation probability were highly negatively correlated ( $r = -0.54$ ,  $df = 21$ ,  $p = 0.007$ ) (i.e., percent cover was positively correlated to fragmentation per se).

## RESULTS

### Habitat percent cover and fragmentation per se effects on faunal densities and consumption

Trap-based epibenthic fauna CPUE was 2.5-times and 3-times higher within the largest patch of artificial seagrass than in the interpatch and near-patch matrix positions, respectively (Wilcoxon rank sum tests,  $W = 1154$ ,  $p < 0.0001$ ;  $W = 2322$ ,  $p < 0.0001$ ). Examination of epibenthic faunal responses to landscape parameters across each of these three landscape sampling locations revealed additional density patterns. Epibenthic fauna CPUE within the largest patch of each landscape was only significantly influenced by landscape percent cover (Table 2), with CPUE increasing by 54% as landscape percent cover increased from 10% to 60% (Figure 3a). Among the two matrix positions, epibenthic fauna CPUE

**TABLE 2** Negative binomial generalized linear model results for catch per unit effort (CPUE) of epibenthic fauna and benthopelagic fish within the largest patch, near-patch, and interpatch locations of each landscape, as well as settlers within the largest patch of each landscape only.

Response	Location	Parameter	df	Estimate	SE	p
Epibenthic fauna CPUE	Largest patch	Intercept		0.68	0.32	0.04
		P	1	1.85	0.79	0.02
		F	1	0.36	0.84	0.67
		P × F	1	-2.83	2.08	0.17
		Residual	146			
	Near-patch	Intercept		0.52	0.49	0.29
		P	1	-1.92	1.33	0.15
		F	1	-1.72	1.32	0.19
		P × F	1	5.54	3.36	0.10
		Residual	96			
Benthopelagic fish CPUE	Interpatch	Intercept		-2.06	0.81	0.01
		P	1	4.33	1.77	0.01
		F	1	4.60	2.25	0.04
		P × F	1	-9.70	5.18	0.06
		Residual	76			
	Near-patch	Intercept		2.04	0.60	<0.001
		P	1	-0.66	1.60	0.68
		F	1	-1.02	1.53	0.50
		P × F	1	4.23	3.99	0.29
		Residual	44			
	Interpatch	Intercept		1.70	0.97	0.08
		P	1	0.62	2.61	0.81
		F	1	2.62	2.47	0.29
		P × F	1	-3.24	6.53	0.62
		Residual	44			
Settler CPUE	Largest patch	Intercept		1.97	0.91	0.03
		P	1	0.46	2.44	0.85
		F	1	0.03	2.80	0.99
		P × F	1	1.06	7.40	0.89
		Residual	34			
		Intercept		0.77	0.59	0.20
		P	1	-0.75	1.53	0.62
		F	1	1.90	1.48	0.20
		P × F	1	-1.65	3.87	0.67
		Residual	166			

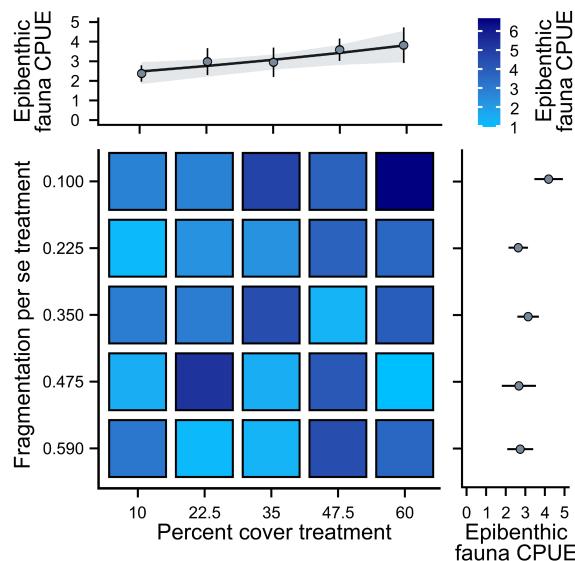
Note: Predictor variables for each are landscape percent cover, fragmentation per se, and their interaction.

Abbreviations: F, fragmentation per se; P, percent cover.

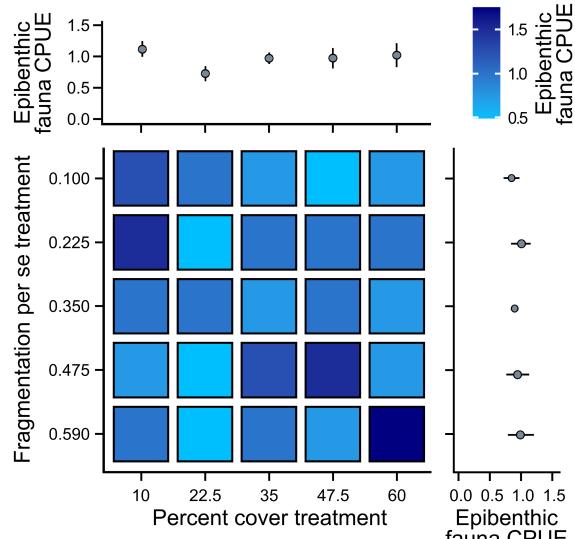
was not affected by landscape parameters in the near-patch location (Figure 3b, Table 2), but within the interpatch location CPUE significantly increased with increasing percent cover and decreasing fragmentation

per se (i.e., increasing percolation probability, increasing contiguity) (Figure 3c, Table 2). There was also some evidence of an interaction between the two landscape parameters (Est. = -9.70, SE = 5.18, p = 0.06).

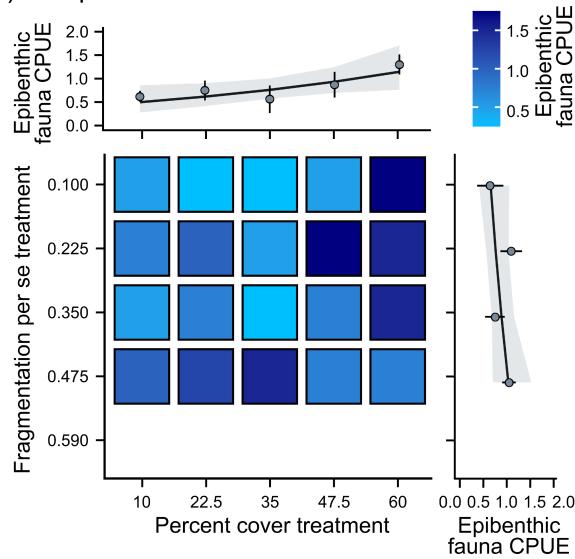
## (a) Largest patch



## (b) Near-patch



## (c) Interpatch



Average epibenthic fauna CPUE increased with percent cover when landscapes were relatively patchier (i.e., fragmentation per se treatments = 0.1, 0.225, 0.35). However, for the most contiguous landscapes with more than one patch (i.e., fragmentation per se treatment = 0.475) CPUE slightly decreased with increasing percent cover (Figure 3c). Notably, epibenthic fauna CPUE was not directly related to interpatch distance (Est. = -0.01, SE = 0.05,  $p = 0.75$ ).

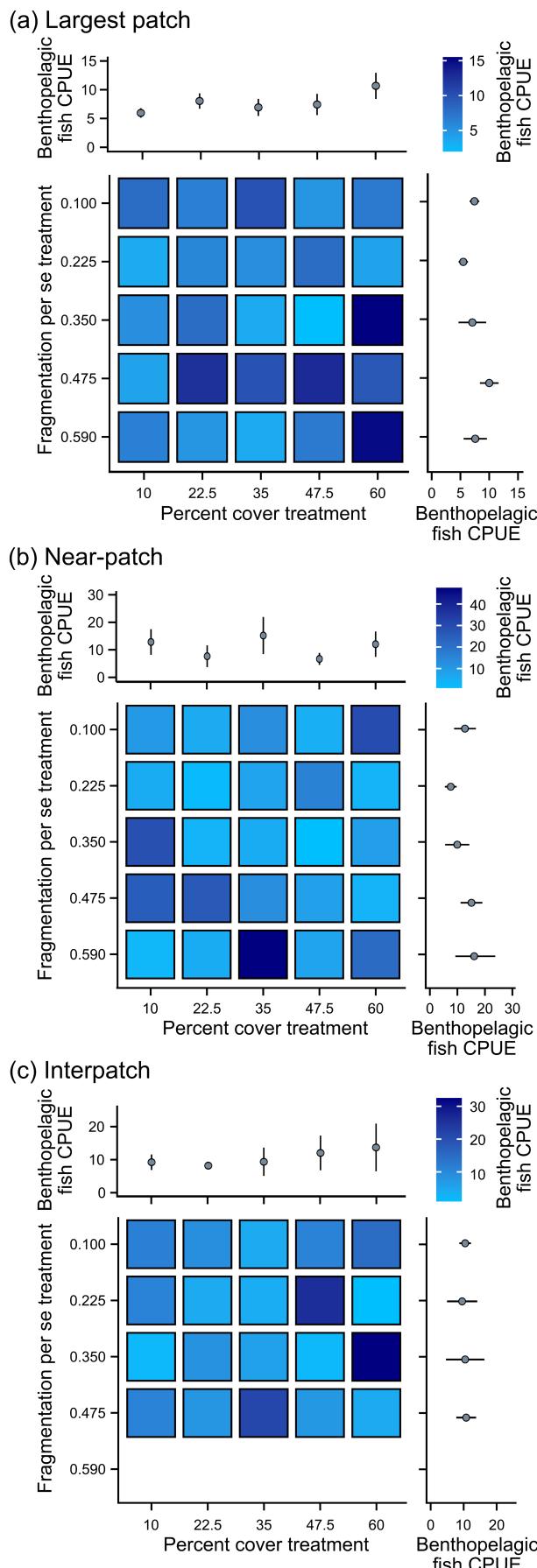
In contrast to trap-based epibenthic faunal sampling, DIDSON sampling of benthopelagic fishes did not capture statistically different numbers of fishes within the largest artificial seagrass patch versus near-patch or interpatch matrix locations, respectively (Wilcoxon rank sum tests,  $W = 408$ ,  $p = 0.22$ ;  $W = 257$ ,  $p = 0.49$ ). Further, neither landscape percent cover, fragmentation per se, nor their interaction, influenced benthopelagic fish CPUE within any of the three sampling locations (Table 2; Figure 4). Benthopelagic fish CPUE was also not directly related to interpatch distance (Est. = -0.004, SE = 0.06,  $p = 0.94$ ).

Community-level generalist consumption probabilities, indexed by squidpop consumption along artificial seagrass landscape edges, exhibited a positive relationship with landscape percent cover (Est. = 3.25, SE = 0.69,  $p < 0.001$ ) (Figure 5). The probability of squidpop consumption at 1 h more than tripled across landscapes ranging from 1% to 60% cover (note, assays were conducted post-Hurricane Florence therefore landscape percent covers no longer matched original treatments).

### Settler density as a driver of post-settler epibenthic faunal density across landscapes

Settler CPUE in SMURFs was not influenced by either landscape parameter or their interaction (Table 2). Further, settler density patterns across each of the landscape percent cover and fragmentation per se treatments

**FIGURE 3** Epibenthic fauna catch per unit effort (CPUE, indiv. per trap) (mean  $\pm$  SE) in the (a) largest patch, (b) near-patch, and (c) interpatch locations of each landscape. Each panel shows CPUE relationships with the percent cover treatment (top), and fragmentation per se treatment (right) and their interaction (percent cover  $\times$  fragmentation per se; center). Trendlines and shaded ribbons are significant model-predicted responses and 95% CI, respectively.



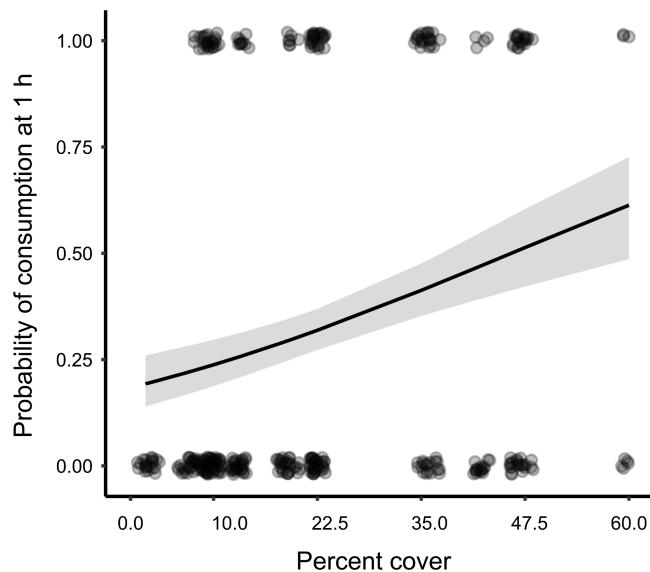
(Figure 6) did not appear to be related to the patterns observed for trap-based epibenthic fauna or benthopelagic fish CPUEs (Figures 3a and 4a). In fact, the relationship of settler CPUE to each landscape parameter, while not significant, showed opposite directional trends as compared to trap-based epibenthic fauna CPUE patterns.

Three genera were caught sufficiently frequently as both settlers in SMURFs and as juveniles in traps (Appendix S1: Table S6) to assess whether taxa-specific settlement correlated with juvenile faunal densities within the same cohort (i.e., across a 2-month time lag). Settler and juvenile CPUE of *Callinectes* spp. showed no correlation ( $r = -0.05$ ,  $df = 74$ ,  $p = 0.66$ ). Likewise, *Lutjanus* spp. settlement was not correlated to juvenile CPUE ( $r = 0.16$ ,  $df = 76$ ,  $p = 0.15$ ). In contrast, *Stephanolepis* spp. settlement showed a significant positive correlation to juvenile CPUE over the 2-month time lag ( $r = 0.31$ ,  $df = 74$ ,  $p = 0.006$ ).

## Faunal community composition

Across landscapes, total epibenthic faunal species richness per se ranged from 3 to 14 and Pielou's evenness ranged from 0.64 to 0.97 (Appendix S1: Figure S7a,b). The total settler species richness per se ranged from 1 to 7, while evenness ranged from 0.10 to 1.00 (Appendix S1: Figure S7c,d). Species richness per se and evenness of each of epibenthic faunal and settler communities were not significantly influenced by either landscape parameter or their interaction (Table 3). Similarly, neither epibenthic fauna nor settler community compositions were clearly related to percent cover, fragmentation per se, or their interaction (Appendix S1: Table S7, Figure S8). Finally, analogous univariate and multivariate analyses on the distribution and community of benthopelagic fish length z-scores (i.e., 0.5 SD bins used as a proxy for species identity) showed no significant relationships with landscape parameters (Appendix S1: Table S8, Figure S9).

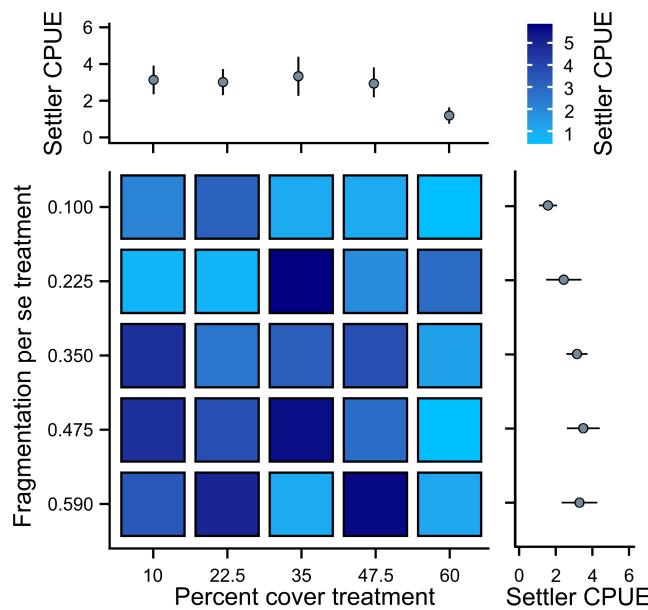
**FIGURE 4** Benthopelagic fish catch per unit effort (CPUE) (individual per dual frequency identification sonar sample) (mean  $\pm$  SE) in the (a) largest patch, (b) near-patch, and (c) interpatch locations of each landscape. Each panel shows CPUE relationships with the percent cover treatment (top), fragmentation per se treatment (right), and their interaction (percent cover  $\times$  fragmentation per se; center).



**FIGURE 5** Binomial logistic regression of squidpop consumption along artificial seagrass landscape edges at 1 h in relation to post-Hurricane Florence landscape percent cover (Estimate = 3.25, SE = 0.69,  $p < 0.001$ ) in October and November. Datapoints are transparent and staggered for visibility. Trendline and shaded ribbon are the model-predicted probabilities of consumption and 95% CI, respectively.

### Landscape parameter versus fine-scale complexity influences on faunal communities

The partial influences of fine-scale complexity parameters when combined with landscape parameters differed in some cases from their independent effects on faunal density patterns. July epibenthic fauna CPUE in the largest patch of each landscape was significantly influenced by the independent and interactive effects of the landscape parameters as well as epiphyte biomass (Table 4). In this case, along with landscape parameter partial effects, July epibenthic fauna CPUE increased by a factor of 2.7 across the range of epiphyte biomasses from 0 to 7 mg cm<sup>-2</sup> (Est. = 0.14, SE = 0.06,  $p = 0.03$ ). However, when examined as a bivariate relationship, epiphyte biomass did not affect epibenthic faunal densities in July (Est. = 0.09, SE = 0.06,  $p = 0.14$ ) (Table 5, Figure 7b). Alternatively, there was a significant direct positive bivariate relationship between canopy height and July epibenthic faunal density in which CPUE increased by a factor of 3.6 across the range of canopy heights from 65 to 130 mm (Est. = 0.02, SE = 0.01,  $p = 0.03$ ) (Table 5, Figure 7a). In contrast, July benthopelagic fish CPUE in the largest patch, was not influenced by any landscape or fine-scale complexity parameter partial effects (Table 4). Further, neither canopy height nor epiphyte biomass had apparent direct relationships with July benthopelagic fish



**FIGURE 6** Settler catch per unit effort (CPUE, individual per Standardized Monitoring Unit for the Recruitment of Fishes) (mean  $\pm$  SE) in the largest patch of each landscape. Panel shows CPUE relationships with the percent cover treatment (top), and fragmentation per se treatment (right) and their interaction (percent cover  $\times$  fragmentation per se; center).

densities (Table 5, Figure 7c,d). When all landscape and fine-scale complexity parameter effects were examined, July settler CPUE was only significantly negatively related to the partial influence of canopy height (Est. = -0.02, SE = 0.01,  $p = 0.01$ ). July settler CPUE exhibited a 4.4-fold decline as canopy height increased. July settler CPUE may have also been influenced by the landscape parameter interaction term and fragmentation per se (Table 4). When fine-scale complexity parameter influences were examined independently, canopy height and epiphyte biomass each had a significant negative bivariate relationship with July settler density (Table 5). July settler CPUE showed a 5.7-fold decrease across the range of canopy heights (Est. = -0.03, SE = 0.01,  $p = 0.001$ ) (Figure 7e), as well as a 2.7-fold decline as epiphyte biomass increased (Est. = -0.14, SE = 0.07,  $p = 0.05$ ) (Figure 7f).

### DISCUSSION

We conducted a manipulative habitat experiment with artificial seagrass at spatial scales relevant to the seasonal habitat fidelity of juvenile estuarine fishes and macroinvertebrates. We measured and synthesized habitat use patterns across landscapes ranging in habitat percent cover and fragmentation per se at three locations within each landscape: the largest patch, near-patch

**TABLE 3** Linear model (LM) results for species richness per se and Pielou's evenness of settler and epibenthic fauna (from standardized monitoring unit for the recruitment of fishes and traps, respectively) predicted by landscape percent cover, fragmentation per se, and their interaction.

Response	Parameter	df	Estimate	SE	p
Epibenthic fauna species richness per se	Intercept		8.83	2.15	<0.001
	P	1	-3.52	5.47	0.53
	F	1	-8.40	5.51	0.14
	P × F	1	19.76	14.06	0.17
	Residual	21			
Epibenthic fauna evenness	Intercept		0.91	0.08	<0.001
	P	1	-0.38	0.21	0.08
	F	1	-0.22	0.21	0.31
	P × F	1	0.86	0.53	0.12
	Residual	21			
Settler species richness per se	Intercept		3.68	1.62	0.03
	P	1	-3.15	4.13	0.45
	F	1	0.007	4.16	0.99
	P × F	1	9.04	10.61	0.40
	Residual	21			
Settler evenness	Intercept		0.92	0.27	0.002
	P	1	-0.90	0.67	0.20
	F	1	-1.31	0.68	0.07
	P × F	1	2.78	1.72	0.12
	Residual	20 <sup>a</sup>			

Abbreviations: F, fragmentation per se; P, percent cover.

<sup>a</sup>In one landscape, a single settler species was captured, therefore that landscape was excluded from the evenness LM.

matrix, and interpatch matrix. Our landscape-scale field experiments suggested that habitat percent cover was a more influential driver of epibenthic fish and macro-invertebrate densities (sampled by traps) than fragmentation per se. Landscapes of higher percent cover also supported higher generalist consumption probabilities, suggesting that landscapes with more seagrass habitat area may serve as foraging habitats, therefore attracting higher consumer densities. However, differences between observed density patterns of epibenthic fauna (in traps) and benthopelagic fishes (from DIDSON) suggest the magnitude of the influence of landscape percent cover may depend upon the degree to which the target community relies on seagrass habitat structure versus unstructured sandflat matrix within the landscape context (Dixo & Metzger, 2010; Yeager et al., 2019). In addition, despite positive effects of landscape percent cover on epibenthic faunal density, the species composition, richness per se, and evenness of epibenthic fauna and larval settler communities appeared similar across our experimental landscapes. Further, while total settlement

density did not appear to predict total epibenthic faunal density across landscapes for most species, certain species traits (e.g., mobility) may drive correlations between densities of larval and juvenile cohorts of the same species regardless of landscape configuration. Finally, our findings also suggest that the spatial scale of meaningful habitat influence on fauna may vary by life stage. Although landscape-scale influences on larval settlement patterns are not straightforward in this study, our results demonstrate that fine-scale complexity generated by seagrass canopies and epiphyte biomass can modulate settlement densities.

### Habitat area loss had more consistent negative influences than fragmentation per se on epibenthic faunal density and generalist consumption probability

Our landscape-scale experiment showed that seagrass percent cover was a more consistent driver of epibenthic faunal densities than fragmentation per se. Across

**TABLE 4** Negative binomial generalized linear model results for epibenthic fauna catch per unit effort (CPUE, in traps), benthopelagic fish CPUE (in Dual Frequency Identification Sonar samples), settler CPUE (in standardized monitoring unit for the recruitment of fishes) within the largest patch of each landscape during July.

Response	Parameter	df	Estimate	SE	p
Epibenthic fauna CPUE	Intercept		-2.33	1.17	0.05
	P	1	5.85	1.69	<0.001
	F	1	4.13	1.90	0.03
	P × F	1	-10.07	4.16	0.02
	CH	1	0.01	0.01	0.48
	EB	1	0.14	0.06	0.03
	Residual	19			
Benthopelagic fish CPUE	Intercept		-0.64	1.33	0.63
	P	1	0.24	2.23	0.91
	F	1	-1.37	2.35	0.56
	P × F	1	4.69	5.49	0.39
	CH	1	0.02	0.01	0.09
	EB	1	-0.03	0.11	0.81
	Residual	18			
Settler CPUE	Intercept		3.94	0.91	<0.001
	P	1	1.74	1.85	0.35
	F	1	3.21	1.72	0.06
	P × F	1	-8.14	4.43	0.07
	CH	1	-0.02	0.01	0.01
	EB	1	-0.06	0.08	0.44
	Residual	18			

Note: Predictor variables were landscape-scale percent cover, fragmentation per se, percent cover × fragmentation per se, mean canopy height and mean epiphyte biomass.

Abbreviations: CH, canopy height; EB, epiphyte biomass; F, fragmentation per se; P, percent cover.

landscapes, positive relationships between seagrass percent cover and epibenthic fauna CPUE were evident in both the largest seagrass patch and interpatch matrix locations. Therefore, the positive faunal density-area relationships appeared to only occur within the two sampling positions that were directly related to the landscape percent cover parameter. That is, the area of the largest seagrass patch increased and the linear interpatch distance generally decreased with increasing landscape percent cover. Alternatively, the near-patch matrix location was held at a constant distance of 1 m from seagrass regardless of the landscape parameters. This perhaps explains why epibenthic fauna sampled at this location exhibited no density-area (i.e., percent cover) relationship.

Direct, positive relationships between faunal density and habitat area regardless of configuration (Table 2; Figure 3a) are often observed across ecosystems. For instance, in both terrestrial and marine vegetated habitats, habitat area loss generally has measurable negative

effects on biodiversity metrics, including total abundances, per-unit-area densities, and species richness across taxa (e.g., arthropods, fishes, birds), independent of habitat patchiness (Boström et al., 2006, 2011; Fahrig, 2013; Haddad et al., 2015; With & Pavuk, 2012). Further, our observed epibenthic faunal density responses to habitat area show agreement with a previous study within natural seagrass, despite differences in the ranges of absolute spatial scales examined. Within our study system, Back Sound, NC, Yeager et al. (2016) found that fish densities, sampled by trawl tows over seagrass and sandflat matrix, were positively related to seagrass area, which ranged from 250 to 12,250 m<sup>2</sup> across natural landscapes. As such, both the current large-scale manipulative study and the previous more expansive mensurative study (Yeager et al., 2016) suggest that landscapes with relatively more seagrass area support more fauna per unit area regardless of configuration.

Further evidence suggests that seagrass loss may have negative influences on habitat use for foraging specifically,

**TABLE 5** Bivariate negative binomial generalized linear model results for each of epibenthic fauna catch per unit effort (CPUE), benthopelagic fish CPUE, and settler CPUE with each of mean artificial seagrass canopy height (in millimeters) and mean epiphyte biomass (in milligrams per square centimeter) within the largest patch of each landscape.

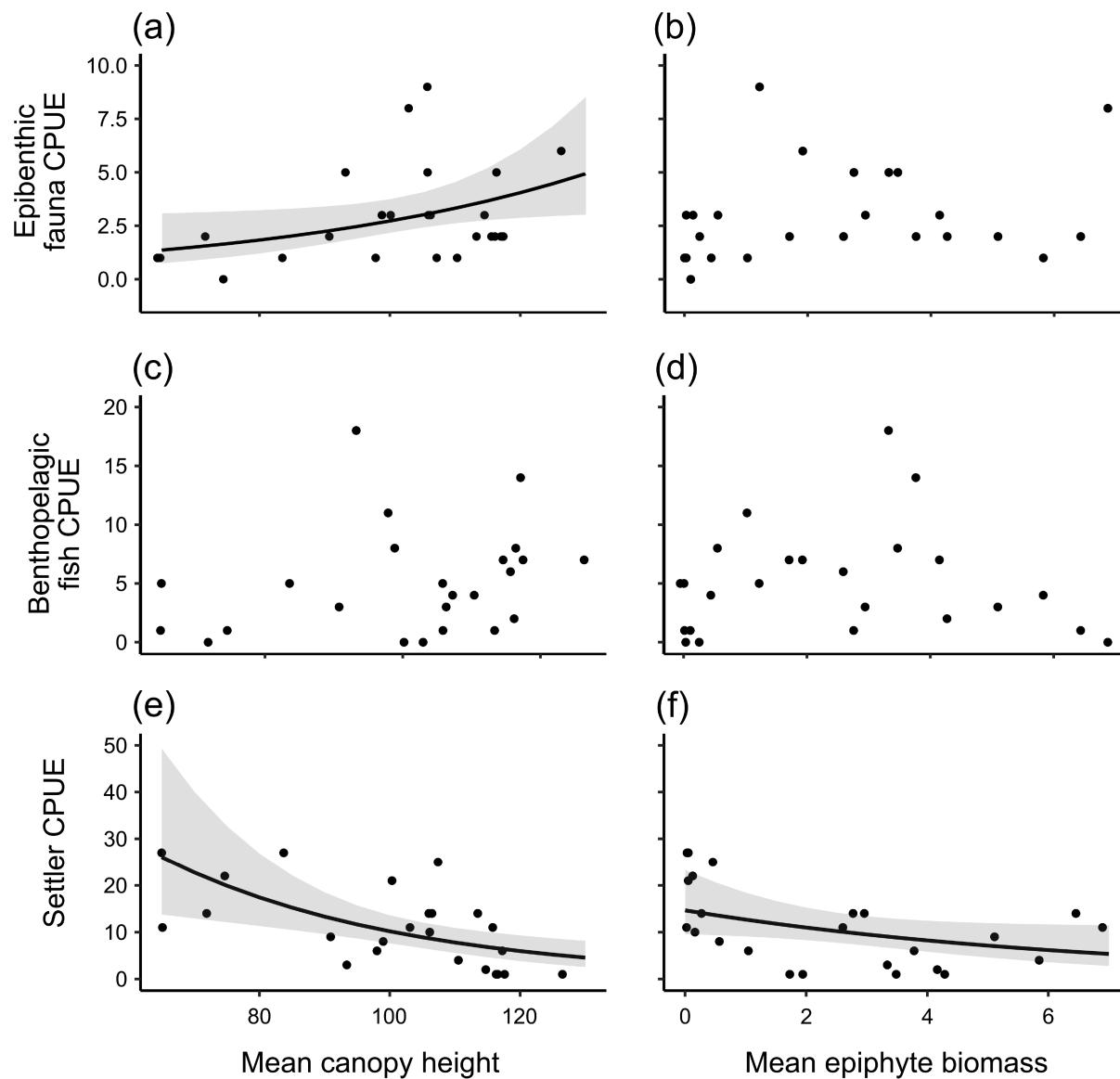
Response	Parameter	df	Estimate	SE	p
Epibenthic fauna CPUE	Intercept		-0.98	0.98	0.32
	Canopy height	1	0.02	0.01	0.03
	Residual	23			
	Intercept		0.83	0.22	0.0002
	Epiphyte biomass	1	0.09	0.06	0.14
	Residual	23			
Benthopelagic fish CPUE	Intercept		0.02	1.16	0.99
	Canopy height	1	0.02	0.01	0.17
	Residual	22			
	Intercept		1.60	0.29	<0.0001
	Epiphyte biomass	1	0.01	0.09	0.93
	Residual	22			
Settler CPUE	Intercept		5.01	0.85	<0.0001
	Canopy height	1	-0.03	0.01	0.001
	Residual	22			
	Intercept		2.68	0.23	<0.0001
	Epiphyte biomass	1	-0.14	0.07	0.05
	Residual	22			

as shown by probabilities of generalist consumption of squidpops. Likely because higher percent cover landscapes supported higher epibenthic faunal densities, they also exhibited relatively higher generalist consumption probabilities (Figure 5). Considering that predator densities, prey densities, and predation rates are all often spatiotemporally correlated, this suggests that landscapes with increased seagrass area support higher consumer-resource encounter rates and therefore are hotspots for trophic transfer (Yarnall & Fodrie, 2020). Alternatively, low-seagrass-area landscapes may not provide the same opportunities for foraging as their higher-area counterparts. As such, low-area or degraded habitats are more rarely visited by opportunistic predators, such as squidpop consumers (Rodemann & Brandl, 2017). However, despite supporting lower faunal densities overall, low-seagrass-area landscapes may still serve as important predation refugia to occupants (Hovel & Lipcius, 2001).

Our study showed no relationships between the densities of epibenthic fauna or benthopelagic fish and fragmentation per se within the largest patch of artificial seagrass (Figures 3a and 4a). However, in the interpatch matrix location, epibenthic fauna CPUE had a significant negative relationship with fragmentation per se (i.e., positive relationship to percolation probability). Yet,

the lack of direct relationship between CPUE and linear interpatch distance may indicate that isolation from seagrass was not at all, or was only a partial, controlling factor for epibenthic faunal density in the matrix. Rather, access to one or more relatively large seagrass patches in a landscape, as fragmentation per se decreased (i.e., percolation probability increases), correlated to an increase in epibenthic faunal density (Fahrig, 2013). These findings also suggest that studies of fragmentation effects should sample across both primary and matrix habitats to gain a complete understanding of how landscape configuration influences faunal communities.

The present study agrees with a previous natural seagrass study in our system that showed evidence of an interactive influence of seagrass percent cover (or area) and fragmentation per se (or patch number) on faunal communities, though in different contexts. Specifically, Yeager et al. (2016) observed that high fish species richness was maintained in all landscape configurations until seagrass cover was <25%. In our study, epibenthic faunal densities at interpatch matrix locations were consistently the lowest in landscapes of both relatively low percent cover ( $\leq 35\%$ ) and relatively high fragmentation per se (percolation probability  $\leq 0.35$ ) (Figure 3c). The patterns observed in both of these studies provide evidence of fragmentation threshold effects (Flather & Bevers, 2002;



**FIGURE 7** Bivariate negative binomial generalized linear model results for each of (a, b) epibenthic fauna catch per unit effort (CPUE), (c, d) benthopelagic fish CPUE, and (e, f) settler CPUE with each of (a, c, e) mean artificial seagrass canopy height (in millimeters) and (b, d, f) mean epiphyte biomass (in milligrams per square centimeter) within the largest patch of each landscape. Trendlines and shaded ribbons are the model-predicted responses and 95% CI, respectively.

Trzcinski et al., 1999). In both cases, seagrass faunal community responses were most negatively influenced by fragmentation per se when habitat area was low. However, in our study, this fragmentation threshold effect was evident only within the matrix, not the primary habitat. Epibenthic fauna appeared to more readily occupy the interpatch sandflat matrix in landscapes where contiguous seagrass or sufficiently large patches were nearby (Figures 2 and 3c). However, landscapes of low seagrass percent cover and high fragmentation per se contained more expansive sandflat matrix dotted with smaller seagrass patches (Figure 2). It is possible that interpatch locations in these landscapes supported

consistently lower epibenthic faunal densities because dispersed small seagrass patches were relatively less accessible or less suitable for protection or foraging. This potential mechanism underlying the observed fragmentation threshold effect may therefore be explained by the “habitat amount hypothesis” (Fahrig, 2013). This hypothesis suggests that faunal communities can be negatively influenced by decreased access to sufficient habitat amounts, or the interaction of increasing patch isolation and decreasing patch size. We reiterate that in our study this relationship would not have been observed if only the primary habitat had been sampled (Radford et al., 2005). The different context in which the present

study versus Yeager et al. (2016) observed fragmentation threshold effects is not surprising given that even independent fragmentation per se effects are often complex, variable, or may have little influence on faunal communities, as compared to the more consistent negative effects of habitat area loss (Fahrig, 2003).

## Guild-specific matrix tolerance and habitat use patterns may determine sensitivity to habitat area loss

Sampling faunal communities within both primary and matrix habitats across a heterogeneous landscape, as opposed to only within patches of the primary habitat, can improve understanding of density responses across habitat mosaics stemming from guild-based differences in habitat utilization (Jambhekar & Isvaran, 2022; Laurance, 2008). Fauna that disproportionately utilize one habitat type over another may be more impacted by loss of their primary habitat than fauna that readily use both the primary and matrix habitat. In this context, fauna that are adaptable to increased use of the matrix habitat are considered to be more “matrix-tolerant” (Dixo & Metzger, 2010; Evans et al., 2017). In seagrass systems, faunal functional traits including microhabitat specialization, body size, dispersal ability, and mobility have important influences on species sensitivity to habitat fragmentation (Yeager et al., 2019). Highly mobile benthopelagic fishes use seagrass and sandflat matrix more interchangeably, suggesting a high degree of matrix tolerance (Williams et al., 2016; Yeager et al., 2016). By contrast, epibenthic fishes and macroinvertebrates more often rely upon structured seagrass habitat for predation refuge or foraging habitat, therefore, may be less matrix-tolerant (Hovel & Lipcius, 2001; Ljungberg et al., 2013).

Observed differences in faunal density responses to landscape parameters between trap-based and DIDSON-based sampling methods are suggestive of differences in relative matrix tolerance and habitat use patterns between the two communities sampled (Table 2). During the initial viewings of DIDSON recordings, benthopelagic fishes were seen swimming across visible seagrass and matrix habitats quickly, exhibiting real-time observable matrix tolerance. In addition, benthopelagic fish densities were similar among artificial seagrass and matrix sampling locations and were not influenced by landscape parameters. This suggests that fish sampled by DIDSON may have been exhibiting transient behavior, moving between seagrass patches and beyond. Further, we suspect that DIDSON more effectively sampled pelagic bait fishes, as observed by body shape, such as

Atlantic silversides (*Menidia menidia*), which were not captured by traps, suggesting these species were not using seagrass for foraging or that they use seagrass habitat at a broader scale. Alternatively, trap-based epibenthic fauna were less abundant in matrix than artificial seagrass samples, and captured a wider range of seagrass resident taxa, including juvenile fishes, crabs, shrimp, and gastropods. In addition, epibenthic faunal density positively related to landscape seagrass percent cover within the largest patch and exhibited a negative fragmentation threshold within the interpatch matrix. Both relationships suggest that at the landscape scale, traps were inherently more effective at sampling fauna that preferred structured over unstructured habitat for foraging or refuge purposes (Yeager et al., 2016) as compared to DIDSON. These differences illustrate that matrix tolerance and habitat use patterns may considerably change faunal sensitivity to habitat configuration and potentially degradation (Dixo & Metzger, 2010) within marine systems.

In addition to the influence of landscape effects on certain faunal abundance metrics, we also found that finer scale habitat features explained some variation in catch data. Specifically, July epibenthic faunal density, in combination with landscape parameter partial effects, was positively related to epiphyte biomass (Table 4). This may indicate that along with the landscape-scale parameter influences described above, increased vegetative structure and biomass may further support certain epibenthic faunal community uses of seagrass. For example, increased epiphyte biomass in seagrass not only provides ideal habitat for epiphyte grazers (Ebrahim et al., 2014), but can also simultaneously facilitate cryptic species by providing more fine-scale habitat structure for predation refuge (Guidetti & Bussotti, 2002; Yeager et al., 2019) within high seagrass cover landscapes. In fact, as both seagrass area and epiphyte biomass increased, the density of epibenthic fauna in July also increased. While it appears landscapes of greater seagrass area may be hotspots for opportunistic predation, increased fine-scale complexity may also help to maintain higher abundances of cryptic prey species through the addition of camouflage and structural refuge (Hovel & Lipcius, 2001). However, at least for the range of epiphyte biomasses observed, it still appeared that seagrass area was the relatively more important factor controlling faunal densities, as landscape percent cover increased CPUE 3.2-fold, while epiphyte biomass increased CPUE 2.7-fold (Table 4). Notably, when landscape parameters are ignored and direct relationships to fine-scale complexity parameters were examined, canopy height, but not epiphyte biomass, was positively related to July epibenthic fauna CPUE (Table 5, Figure 7a,b). Therefore, independent of all other

habitat parameter effects, the influence of increased habitat structure alone from artificial canopy height had a more important positive effect on epibenthic faunal density than increased grazing opportunities from epiphyte biomass. In contrast to epibenthic fauna, July benthopelagic fish CPUE was not consistently affected by fine-scale structural complexity in conjunction with or independently of potential landscape parameter effects (Tables 4, 5). This provides further evidence that DIDSON sampling better targeted matrix-tolerant or habitat generalist fishes that were not strictly reliant on seagrass habitat or epiphyte biomass structural complexity.

### Settler densities were not influenced by seagrass landscape parameters

Larval settlement in marine systems is highly variable and dependent on numerous physical and biological factors in addition to habitat configuration (Jackson, 1986; Morton & Anderson, 2013). The current study found that the density of larval fish and crab megalopa exhibited no relationship to landscape percent cover or fragmentation per se (Figure 6). It is possible that settlers responded to settlement cues on much larger spatial scales than our landscapes, preventing the resolution of those patterns in our experiment (Jackson, 1986). Although the underlying mechanism of landscape-scale variation in settlement was unclear in this study, we observed a strong positive correlation between settler and juvenile CPUEs of *Stephanolepis* spp., suggesting that settlement may drive juvenile density for some epibenthic low-mobility fish species. By contrast, settler CPUE of a highly mobile benthopelagic fish species, *Lutjanus* spp., was not an important driver of juvenile density. This may indicate that settlement influences on juvenile densities are species trait-dependent. Likewise, Yeager et al. (2016) observed that cryptic epibenthic fish species, including *Stephanolepis hispidus*, move between seagrass patches nearly five times less frequently than benthopelagic fish species. As such, settlement patterns of taxa with inferior swimming abilities and heavy reliance on seagrass canopy microhabitat refugia can drive juvenile densities across seagrass landscapes (Yeager et al., 2016, 2019). Alternatively, the settlement and post-settlement abundances of more mobile species may be decoupled due to increased dispersal abilities, post-larval movements, and predation vulnerability during movements between structured habitats (Hixon & Carr, 1997; van der Veer & Bergman, 1987).

The direct negative relationships between settler CPUE and each of canopy height and epiphyte biomass

(Table 5; Figure 7e,f) suggest that fine-scale seagrass complexity effects outweigh landscape configuration influences on settlement patterns. Further, although SMURFs were only positioned at the center of the largest ASU patch, preliminary analyses (Appendix S1: Table S2) revealed that the size and perimeter of the largest patch did not influence settler densities. Previous work has shown that planktonic larvae settlement incrementally decreases as water flows across structurally complex habitats (Boström et al., 2010). This study suggests that increased fine-scale complexity, regardless of patch or landscape configuration, was the primary obstruction to settlers reaching SMURFs. That is, the increased structure of relatively unburied ASUs with taller canopies, as well as ASUs with greater epiphyte biomass, may have been better larval catchment devices than the SMURFs (Barcelona et al., 2023; Bologna & Heck, 2000). Further study to sample settlers before concentrations are reduced by flowing across ASU fine-scale structure—such as by directly sampling ASUs or placing SMURFs closer to seagrass edges—may be needed to better discern patterns of faunal settlement across landscape configurations.

### Community composition remained consistent across landscape parameters

Faunal density is an aspect of community structure often influenced by habitat area loss, yet further examination of the faunal communities at settlement and post-settlement life stages indicated that landscape parameters did not influence the species richness per se, evenness (Table 3), or community composition (Appendix S1: Table S6) of epibenthic fauna or settlers. Therefore, although higher percent cover landscapes may support higher epibenthic faunal densities, it seems that species compositions are not altered at varying densities or by habitat area, at least at these artificial landscape scales. Commonly sampled species appeared in all ASU landscapes of varying sizes and configurations during our study. However, this does not mean that all seagrass landscapes provided identical ecosystem services to all species (Yeager et al., 2019). As described by the SLOSS debate, large contiguous habitats can recruit and support high biodiversity through species-area relationships (Connor & McCoy, 1979; Diamond, 1975), while habitat mosaics composed of patches of varied sizes can provide assorted ecological niche spaces (Hortal et al., 2009; Resasco et al., 2018; Tscharntke et al., 2002) and facilitate the persistence of competing species (Fahrig, 2003; Klapwijk & Lewis, 2011; Youngentob et al., 2012). One or both mechanisms may be at play in our experimental landscapes, therefore we

do not suggest that simply because higher percent cover landscapes support higher faunal densities, they have more ecological value than low percent cover landscapes.

## Drivers of seagrass fragmentation effects on faunal communities

This study provides a useful framework for parsing the proximate and ultimate mechanistic drivers of fragmentation effects on communities. Overall, our findings agree with previous work that indicates that habitat area loss most often negatively influences marine faunal densities (McCauley et al., 2015). However, the spatial scale of habitat influence differed according to faunal life stage (Carroll et al., 2012; Eggleston et al., 1998; Williams et al., 2016). While only fine-scale complexity influences were relevant to larval and megalopal densities, landscape area was the more important driver of juvenile and adult epibenthic faunal density. This manipulative field study also lends support to the fragmentation threshold hypothesis that fragmentation per se effects only appear to negatively influence epibenthic faunal communities in low-habitat-cover landscapes (Flather & Bevers, 2002; Trzcinski et al., 1999). Notably, this faunal density pattern was also consistent with the “habitat amount hypothesis”, which suggests that landscape configuration effects (i.e., patch isolation effects, patch size effects) on faunal communities can often be explained by accessibility to sufficient habitat amounts (Fahrig, 2013). This observation required sampling across the habitat mosaic and would have been overlooked if matrix sampling had not occurred (Radford et al., 2005). Surveying both seagrass and sandflat also revealed different habitat use patterns across guilds, showing that apparent matrix tolerance versus reliance on seagrass structure can have important implications for density responses to habitat area and configuration. Further, although guild-specific patterns of density were observed, within-guild community compositions were not altered across landscape parameters. This understanding is particularly important for seagrass systems, as meadows will likely continue to experience fragmentation and habitat loss from climate change (Micheli et al., 2008; Waycott et al., 2009) and anthropogenic disturbances (Orth et al., 2002). Although habitat restoration and recovery efforts often give primary focus to increasing seagrass landscape area (Orth et al., 2006), landscapes of different sizes may perform distinct ecosystem services. While high-cover seagrass landscapes that maintain high faunal densities may serve as foraging hotspots for opportunistic predators (Yarnall & Fodrie, 2020) and generalist consumers (Figure 5), their smaller area counterparts may better provide refuge for

fauna maintained at low densities (Hovel & Lipcius, 2001). Further, conservation efforts should not discount the utility of protecting and restoring patchy landscapes, as they support similar community densities and compositions to contiguous landscapes of the same size (Fahrig, 2003). Therefore, although seagrass area is a primary driver of total faunal abundance, nuances in guild- and life-stage-specific habitat usage of seagrass-sandflat mosaics indicate that a variety of landscape configurations perform essential estuarine nursery functions.

## AUTHOR CONTRIBUTIONS

Lauren A. Yeager and F. Joel Fodrie led study design, approach, and oversaw landscape construction. Amy H. Yarnall led landscape construction efforts, data collection, statistical analysis, and wrote the manuscript. Cori Lopazanski and Abigail K. Poray led and oversaw ASU construction, assisted with data collection and analysis. James W. Morley led DIDSON data collection and analysis efforts. Allen H. Hurlbert contributed to species richness, evenness, and community analyses. All authors contributed comments and edits to the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data are publicly available through the Biological and Chemical Oceanography Data Management Office in seven datasets as follows: landscape parameters (Yarnall, Fodrie, Lopazanski, et al., 2023c), <https://doi.org/10.26008/1912/bco-dmo.891670.1>; landscape fine-scale complexity (Yarnall, Fodrie, Lopazanski, et al., 2023b), <https://doi.org/10.26008/1912/bco-dmo.891652.1>; trap epibenthic fauna CPUE (Yarnall, Fodrie, Lopazanski,

et al., 2023a), <https://doi.org/10.26008/1912/bco-dmo.891859.1>; DIDSON benthopelagic fish CPUE (Yarnall, Fodrie, Morley, et al., 2023f), <https://doi.org/10.26008/1912/bco-dmo.891779.1>; DIDSON benthopelagic fish length Z-Score (Yarnall, Fodrie, Morley, et al., 2023g), <https://doi.org/10.26008/1912/bco-dmo.891686.1>; SMURF settler CPUE (Yarnall, Fodrie, Lopazanski, et al., 2023d), <https://doi.org/10.26008/1912/bco-dmo.891835.1>; Squidpop consumption probability (Yarnall, Fodrie, Lopazanski, et al., 2023e), <https://doi.org/10.26008/1912/bco-dmo.891794.1>. Code (Yarnall, 2024) is available in Zenodo at <https://doi.org/10.5281/zenodo.13362916>.

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## SUPPORTING INFORMATION

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

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