Habitat use patterns and edge effects across a seagrass–unvegetated ecotone depend on species-specific behaviors and sampling methods

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ABSTRACT: Although habitat edges can be areas of elevated richness and intense ecological interactions, results from studies of mesopredators in seagrass ecosystems are equivocal, with some communities sensitive to the mere presence of seagrass, while others respond specifically to edges and landscape structure. We attempted to address these discrepancies through a species-specific lens, investigating patterns in aggregate and per-taxon mesopredator densities and behaviors across a seagrass–unvegetated ecotone at 3 sites in Washington State, USA, with special focus on patterns apparent on edges. Aggregate abundance was enhanced inside eelgrass (in seines) and on edges (in videos) relative to unvegetated habitats, a difference attributed to the abilities of the 2 methods to sample dominant taxa in different habitats. Both methods concurred that structure-association primarily occurred for pelagic, not benthic taxa. Videos suggested that shiner perch and stickleback moved more slowly in eelgrass interiors relative to unvegetated habitat, that stickleback fed more frequently in interior habitat, and that habitat use did not differ between low and high water. Eelgrass appears to disproportionately benefit small pelagic taxa rather than benthic species, but no distinct responses to edges were detected for the distribution or behavior of dominant taxa. Overall, responses to structure were taxon-specific, and for most taxa, shoot structure seemed more important than landscape structure for distribution and behavior. Our results suggest that the wide variation in community responses to landscape structure found in the literature may result from differences in local species pools, and the ability of sampling gear to detect specific taxa in different habitats.

KEY WORDS: Edge effect · Seagrass · Mesopredators · Method comparison · Species-specific responses · Landscape ecology

INTRODUCTION

Seagrasses are marine angiosperms that provide biogenic habitat structure in shallow coastal environments. Consistently, nekton abundance tends to be enhanced in the presence of seagrass relative to unvegetated areas (Heck et al. 1989, Jackson et al. 2001, Hughes et al. 2002, Lazzari & Tupper 2002).

The effects of the configuration of seagrass habitat on nekton abundance and performance, however, are equivocal (Connolly & Hindell 2006, Smith et al. 2008, Boström et al. 2011, Farina et al. 2016), and the effects of edge or interior, patch size, or within-patch ranges of structural complexity may be species-specific (Horinouchi 2007, Pfeifer et al. 2017). Discrepancies between past studies showing that nek-

ton abundance may be affected by local- and land-scape-scale structure, or shows no responses to structure (Connolly & Hindell 2006, Smith et al. 2008, Macreadie et al. 2010, Boström et al. 2011), may be attributed to focus on aggregate response or broader community structure, and less focus on species-specific reponses to habitat or landscape structure. Because species pools differ within and among seagrass-vegetated sites and regions, species-specific responses could be key to understanding why edge and broader landscape effects are so variable across seagrass systems. Additionally, these results may be sensitive to interactions between the sampling gear, habitat type, and species present at particular sites (Kimball & Able 2012, Peters et al. 2015).

Seagrass has been subject to many tests of theory developed in terrestrial landscape ecology literature, particularly because it tends to form distinct patches or 'islands' with distinct edges in an otherwise unvegetated sediment matrix (Robbins & Bell 1994, Boström et al. 2006). Despite over 20 yr of work on these systems, some definitions of basic seagrass landscape features, including 'edges,' remain unclear. A review by Boström et al. (2006) defined the edge of a seagrass patch in 3 ways: (1) a region of change from one habitat to another as perceived by a focal organism, (2) the portion of a discrete habitat near its perimeter where the conditions of the surrounding habitat dominate over conditions present in the patch center, or (3) the junction between 2 habitat types in a seascape mosaic of multiple habitats. Edges and their effects on seagrass fauna have not often been measured directly, with studies of perimeter-to-area ratio, fragmentation, patch size, and other variables standing in for direct measurements of edge effects on abundance or community composition. Additionally, the sampling of seagrass edges may be conducted to include just vegetated habitat against a seagrass–sand interface (e.g. Macreadie et al. 2010), both the unvegetated and vegetated habitat along the edge together in one sample (Becker et al. 2012), or both unvegetated and vegetated habitat along edges separately (e.g. Smith et al. 2008, 2011). Here we defined edges as the region of the seascape where vegetated and unvegetated habitats connect, and sampled edges as both the outer parts of vegetated patches together with the unvegetated sediment that abuts them.

For many species, seagrass edges are places where food–risk tradeoffs occur. These tradeoffs may be linear, meaning that predation risk and food availability increase across edges from vegetated to unvegetated habitat. For example, unstructured habitats may expose organisms to predators, but are also areas of greater food availability or allow uninhibited movement between discrete patches (Carroll et al. 2012, Shinomiya et al. 2017). Seagrass beds and other structured habitats may develop 'halos' of lowered infaunal abundance in adjacent unvegetated substrate, as zoobenthivorous predators using structure as shelter preferentially feed in these areas but stay relatively close to the structure because of elevated predation risk in distant unstructured areas (Posey & Ambrose 1994).

Tradeoffs between food and predation risk can also be non-linear across patch edges. Generally, edges can be an ideal foraging habitat because they are areas of high prey concentration (Brooks & Bell 2001, Smith et al. 2008, Macreadie et al. 2010) or because they present access to prey uniformly distributed throughout the patch via an easy-to-navigate unstructured corridor (Macreadie et al. 2012). However, edges are often risky locations for small animals (Gorman et al. 2009, Macreadie et al. 2012), particularly when cruising predators disproportionately patrol edges (Peterson et al. 2001). The magnitude of an edge effect may depend on habitat fragmentation; continuous patches may show a stronger edge effect than fragmented patches because they present a distinct interior refuge from predation (Macreadie et al. 2012) absent from fragmented patches or because the concentration gradient of prey is less pronounced when the perimeter-to-area ratio of patches is greater (Macreadie et al. 2010).

In this study we examined mesopredator (fish and decapod crustacean) habitat use across the seagrass–unvegetated ecotone. We asked (1) How does aggregate mesopredator abundance and community structure differ across this ecotone, and (2) Are there significant community-level and species-specific patterns of abundance, foraging, and movement behavior across the ecotone? In keeping with most studies globally (e.g. Heck et al. 2003, McDevitt-Irwin et al. 2016), we expected that seagrass and unvegetated habitats would differ in abundance and community structure, while abundance at edges could either be greater than interior and unvegetated habitat or intermediate. We conducted univariate and multivariate analyses that focused on whether edges were intermediate or distinct habitats from the vegetated and unvegetated endpoints in terms of abundance and community structure in video and seine samples. For major taxa within the mesopredator assemblage, we examined abundance and behavior across interior vegetated, edge, and unvegetated habitats. We expected that edges could generate enhanced move-

ment or foraging due to the contrast between open and structured environment, whether or not densities were elevated there, although we were unsure of species-specific responses to this level of structure, as these kinds of data are limited locally.

MATERIALS AND METHODS

Study sites

Sampling for mesopredators was done at 3 sites spanning 186 km in Washington State, USA (Fig. 1A), where soft-sediment habitats near mean lower low water (MLLW) are characterized by a mosaic of seagrass (eelgrass *Zostera marina*) and unvegetated patches (ranging from roughly 3 to 1500 m^2). These 3 sites (Port Gamble Bay, 47.84° N, 122.58° W; Skokomish River Delta, 47.36° N, 123.13° W; and Willapa Bay, 46.52° N, 123.99° W) differed in mesopredator species richness as sampled by seine (Gross et al. 2017). These 3 sites were considered representative of habitat mosaics near MLLW in estuaries of Washington State; therefore, site was a random effect in the analyses.

Each site contained 3 subsites. Each subsite comprised 3 intertidal habitat types: eelgrass bed interior, edge, and unvegetated tideflat. Sediment at our sites did not include any coarse gravel and contained less than 2% organic content. Aboveground biomass of eelgrass was similar across sites (63 g dry wt m^{-2}), and interior shoot density averaged 168 m^{-2} across all sites, with edges about half as dense, at 92 m^{-2} (Gross et al. 2017). In Washington State, eelgrass habitats have been grouped into 2 general categories based on shoreline geomorphology: narrow fringing beds on steep, linear shorelines, or broad, extensive meadows where shorelines form shallow-sloped embayments (Dowty 2005). At 2 of our study sites (Port Gamble Bay and Willapa Bay), subsites contained fringing beds (ca. 10–30 m width), while at the Skokomish Delta, subsites included sections of a meadow spanning 100s of meters. Nevertheless, sampling was identical across all estuaries in that edges were natural features due to desiccation or sloughs, and the interior and unvegetated samples were each collected >2 m from any edge.

Capture and camera sampling of fishes and decapods

Two methods were employed to sample mesopredators: beach seines and submerged video cam-

eras. The beach seine (3 mm mesh) sampled a circular area of 11 m^2 when water was below 1 m in depth. The seine was pursed manually, chasing mesopredators into the cod end, where they were counted, identified to the lowest possible taxonomic level (typically species), and released. Two seines were carried out in each replicate of each habitat type, for a total of 18 seines site^{-1}. The sampling period spanned no more than 4 d over the several hours around low tide. The edge was encircled with the border near the center of the seine (rather than sampling from the border into eelgrass). This allowed capture of species potentially foraging from the edge out onto unvegetated habitat or cruising unimpeded along the ecotone (Peterson et al. 2001, Macreadie et al. 2012). Edge
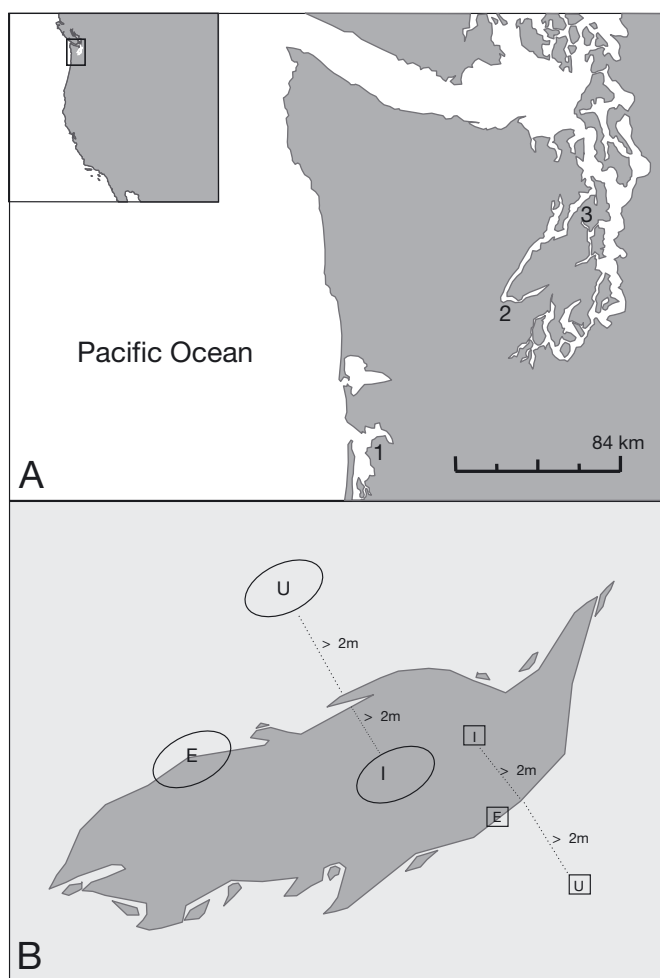

Fig. 1. (A) Field sites in Washington State, USA (48° N, 123° W). Inset map shows the context of the region in the Northeast Pacific. 1: Willapa Bay; 2: Skokomish River delta; 3: Port Gamble Bay. (B) Sampling scheme for seines (ellipses) and video cameras (squares). I: seagrass bed interior; E: bed edge; U: unvegetated substrate. Interior and unvegetated samples were collected at a distance >2 m from the patch edge. Drawing not to scale

seines contained approximately 50% each interior and unvegetated habitat, or about 1.5 m each into the patch interior and unvegetated substrate, including the border of the eelgrass patch (Fig. 1B). The 3 sites were sampled during separate spring tide periods from early July to mid-August 2015.

Two-minute segments of video were recorded every 10 min during daylight over the course of 3 d, including days when beach seining occurred, using submerged cameras (Go-Pro Hero 3+) and programmable time-lapse intervalometers (CamDo Solutions) in waterproof housing. Cameras were attached to the top of a PVC pipe pyramid mount 70 cm above the substrate and pointed obliquely at a 1 m^2 quadrat on the bottom. Cameras in interior and unvegetated habitat were placed on mounts at least 2 m from an edge; edge cameras were placed to cover and record activity along 1 m^2 of the vegetated–unvegetated ecotone, the view encapsulating 0.5 m^2 of where the eelgrass patch ended and 0.5 m^2 of where the unvegetated substrate began (Fig. 1B). Data were extracted only for the day with best visibility, corresponding to about 2 d of seine sampling at each site. The first 10 videos following submersion of each camera were examined, spanning 90 min, followed by 10 videos recorded 3 h after the first set of 10 and therefore near high water, spanning another 90 min. We prioritized visibility over this precise timing, such that the low-to-high water gap was shorter in 38% of cases, but always at least 1.5 h. Each habitat type per sub-site consequently had a low-water and high-water sample of mesopredators. For each of these video samples, mesopredators observed within the 1 m^2 pyramid base, but not seemingly attracted to the structure of the PVC base (hereafter 'free' mesopredators) were tallied separately from those associated directly with the PVC structure (within 10 cm, hereafter 'PVC' mesopredators; for a comparison of free and PVC mesopredators, see the Supplement at www.int-res.com/articles/suppl/m598p021_supp.pdf). We were unable to recover some video sets, resulting in 18 samples for the Skokomish delta and 16 each for Willapa Bay and Port Gamble Bay sites (50 total video samples). Taxonomic resolution was coarser for videos than for seines; we were unable to distinguish species of gunnels or small flatfish.

Behavior of free individual mesopredators was assessed in videos based on time in view (TiV) and feeding events. For all but 1 subsite at Willapa Bay (videos were lost following count data collection at this subsite), TiV was recorded for individuals in each 2 min video segment, for up to 10 sets of observations for species in each habitat type (interior, edge, and unvegetated) at high or low water. If a mesopredator was absent from view and did not reappear within 10 s, it was deemed to have left the sampling area (Smith et al. 2011, Jenkins et al. 2015). Instances of feeding (lunging and buccal expansion for fishes, movement of chelipeds to mouth for crabs) were tallied for each individual observed in each group of 10 segments, and converted to individual feeding rates by dividing by TiV.

Multivariate analyses of mesopredators

In seines, 1 sample consisted of the sum of individuals caught in the 11 m^2 seines (n = 2) in the same patch. For videos, a sample was the sum of individuals seen in the 1 m^2 quadrat across 10 segments of video, distinguishing low and high water and including only free individuals. Each seine sample was re-coded to the lowest taxonomic resolution available in videos. This clustering did not affect seine-only significance of habitat effects. Finally, assemblages were calculated in terms of the fraction of each taxon per sample, in order to facilitate comparison across seine and video methods, which differed in sampling area and time sampled. Overall community structure was compared visually among habitat types and between seine and video methods in non-metric multidimensional scaling (NMDS) plots, using Bray-Curtis dissimilarities. A permutational multivariate ANOVA (PERMANOVA, maximum permutations = 9999) was carried out on the sample-by-species abundance matrix to test whether mesopredator communities differed according to 'sampling method' (3 levels: seines, high-water videos, and low-water videos), habitat, and their interaction, with permutations within subsites as strata (random variable). Additional PER-MANOVAs used pairwise comparisons of 'sampling methods' and habitats to determine which levels within groups differed significantly from each other. When assemblages varied statistically, we applied a similarity percentage (SIMPER) analysis to determine which taxa contributed to this variation. Analyses were conducted using the 'vegan' package in R (Oksanen et al. 2015, R Core Team 2015).

Univariate analyses of mesopredators

We compared mesopredator individuals per sample across the 3 habitat types in aggregate (total abundance) and for the 6 most frequently encountered taxa: shiner perch *Cymatogaster aggregata*, three-

spined stickleback *Gasterosteus aculeatus*, staghorn sculpin *Leptocottus armatus*, small flatfishes, gunnels (Pholidae), and crabs in the genus *Metacarcinus* (*M. magister* and *M. gracilis*). Because we were interested in the patterns detected by the 2 methods, we analyzed data from seines and from videos separately. Site and subsite were considered nested random effects in linear mixed-effects models. Seine models tested a single fixed effect (habitat) against abundance (log-transformed to conform to a normal distribution) using a Gaussian error structure, and video models tested for effects of habitat, water level, and their interaction on untransformed abundances with a Poisson error structure. We used likelihood ratio tests to compare models with and without each fixed effect. If they did not differ significantly, we selected the simpler model as the best-fitting one. Post hoc tests of habitat effects were carried out on data subsets containing all 3 pairwise combinations of habitat type. Specifically, we were interested in an interior–unvegetated comparison, used to determine the effect of structured habitat on abundance, and an interior–edge comparison, used to determine if any effects of habitat structure differed across an eelgrass patch. We used the Bonferroni α level correction to account for multiple comparisons in post hoc tests (α = 0.017).

Detectability in seines and videos could differ by taxon. As in multivariate analyses, taxon-specific comparisons across methods had to be carried out on proportional contributions to each method because seines sampled a wider area than videos over a single time point. We used non-parametric paired tests (Wilcoxon signed-rank tests) to individually examine how the fractional contribution of the 6 major taxa to sampled assemblages varied by sampling method; specifically, we paired video and seine samples collected in each patch (N = 27 pairs). Because we found no significant influence of water height in videos on densities of these taxa, we averaged the relative densities in low and high water pairs of video samples to facilitate comparison with seine samples.

Behavioral analyses

Because the error structure of TiV did not conform to any straightforward statistical distribution, we used nonparametric Kruskal-Wallis tests to examine the effects of habitat on TiVs of our 6 focal taxa. Fish or crabs that remained in view for the entire 2 min segment were accordingly ranked as the longest TiV. As in abundance analyses, site and subsite were nested random effects. For taxa showing a significant habitat difference for TiV, post hoc tests were carried out comparing each pair of habitats (Bonferroni α = 0.017). Individual feeding rates also showed data distributions unsuitable for generalized linear models. We instead used a PERMANOVA on Euclidian distances (9999 permutations) to determine the effect of habitat on feeding rates across video samples, both for the total assemblage and for our 6 focal taxa. For taxa showing specific habitat patterns in feeding rate, post hoc PERMANOVAs were carried out for each of the 3 pairwise habitat combinations (α = 0.017). Analyses were conducted using the 'lme4' and 'vegan' packages in R (Bates et al. 2015, Oksanen et al. 2015, R Core Team 2015).

RESULTS

Multivariate analyses of mesopredator assemblages by seine and video

Low intertidal mesopredators in 3 estuaries of Washington State consisted primarily of shiner perch, stickleback, shrimps, gunnels, sculpins, flatfishes, pipefish *Syngnathus leptorhynchus*, and cancrid crabs, together accounting for >98% of individuals in seines and >90% of individuals in videos (Table 1). Based on multivariate analyses, taxonomic composition differed significantly by method (pseudo-$F_{2,68}$ = 5.2, p < 0.001), and by habitat (pseudo-$F_{2,68}$ = 3.2, p < 0.001, Fig. 2), but showed no method × habitat interaction (pseudo-$F_{4,68}$ = 0.93, p = 0.14). This method-based distinction emerged from mesopredators in seines differing from those seen in videos. Community structure did not differ significantly between low and high water assemblages (pseudo-$F_{1,44}$ = 0.87, p = 0.15), and there was no habitat × water level interaction (pseudo-$F_{2,44}$ = 0.22, p = 0.92). PVC-associated communities were significantly different from free communities (Table S1, Fig. S2 in the Supplement), supporting our decision to exclude PVC-associated individuals from our analysis. The taxa with the largest contribution to habitat differences were shiner perch, staghorn sculpin, sticklebacks, gunnels, and flatfishes (Table 2). These species, along with hippolytid shrimps, also contributed to dissimilarity in methods (Table 3). Community analyses were carried out on the fractional representation of each taxon, which was necessary for combining capture and camera data, but could result in specific taxa contributing statistically to habitat differences without differing in density across habitat types, only because other taxa had strong habitat associations.

Table 1. Mesopredator taxa in Washington State estuaries, in order of abundance found during this study. Abundances for videos include both high-water and low-water videos. Taxon: F: fish; S: shrimp; C: crab; HC: hermit crab

Taxon	Species	Common name	Willapa Bay Seine	Willapa Bay Video	Skokomish Delta Seine	Skokomish Delta Video	Port Gamble Seine	Port Gamble Video	Total Seine	Total Video
F	*Cymatogaster aggregata*	Shiner perch	3781	142	286	239	71	62	4138	443
F	*Gasterosteus aculeatus*	Three-spined stickleback	729	9	1679	23	574	54	2982	86
S	Hippolytidae spp.	Grass shrimp	2	0	25	0	899	1	926	1
F	Pholidae spp.	Gunnels	29	0	24	22	584	88	637	110
F	*Leptocottus armatus*	Pacific staghorn sculpin	52	24	156	325	60	88	268	437
F	*Porichthys notatus*	Plainfin midshipman	0	0	156	1	130	1	286	2
F	Pleuronectidae spp.	Flatfishes	87	7	38	44	45	63	170	114
S	*Crangon* sp.	Sand shrimp	36	0	49	1	67	0	152	1
F	*Syngnathus leptorhynchus*	Bay pipefish	9	1	53	0	73	4	135	5
C	*Metacarcinus gracilis*	Graceful crab	0	0	4	9	30	69	34	78
C	*Metacarcinus magister*	Dungeness crab	69	19	0	0	3	0	72	19
F	*Lumpenus sagitta*	Snake prickleback	0	0	1	0	12	58	13	58
C	*Hemigrapsus* sp.	Shore crab	0	0	10	46	2	0	12	46
F	*Clevelandia ios*	Arrow goby	0	0	0	0	52	1	52	1
C	*Pugettia producta*	Northern kelp crab	0	0	1	3	3	12	4	15
F	Unidentified sculpin	–	0	0	1	0	9	3	10	3
F	*Amphistichus rhodoterus*	Red-tailed surfperch	8	0	0	0	0	0	8	0
F	*Lepidogobius lepidus*	Bay goby	1	0	1	0	3	0	5	0
HC	Paguridae sp.	Hermit crab	0	0	0	2	0	2	0	4
F	*Oncorhynchus tshawytscha*	Chinook salmon	3	0	0	0	0	0	3	0
S	*Pandalus hypsinotus*	Coonstripe shrimp	0	0	0	0	3	0	3	0
S	*Pandalus danae*	Dock shrimp	0	0	0	0	2	0	2	0
C	*Cancer productus*	Red rock crab	0	0	0	0	1	0	1	0
C	*Oregonia gracilis*	Decorator crab	0	0	0	0	1	0	1	0
C	*Telmessus cheiragonus*	Helmet crab	0	0	0	0	1	0	1	0
F	*Hypomesus pretiosus*	Surf smelt	0	0	0	0	1	0	1	0
F	*Aulorhynchus flavidus*	Tubesnout	0	0	0	1	0	0	0	1

Habitat associations of major mesopredator taxa

Total mesopredator abundance varied significantly across habitats in seines ($\chi^2_2 = 29.3$, p < 0.001) and in videos ($\chi^2_2 = 46.5$, p < 0.001). In seines, abundance was highest on average in interior habitat (interior–unvegetated p < 0.001, interior–edge p = 0.006), while in videos, abundance was highest on edges (edge–unvegetated p < 0.001, edge–interior p < 0.001; Fig. 3). Two dominant taxa showed habitat associations in both seines and videos, although with slightly different habitat associations for one of these taxa by method: shiner perch and stickleback abundance varied significantly by habitat in seines (shiner perch: $\chi^2_2 = 21.7$, p < 0.001; stickleback: $\chi^2_2 = 26.3$, p < 0.001, Fig. 4A,B) and in videos (shiner perch: $\chi^2_2 = 16.9$, p < 0.001; stickleback: $\chi^2_2 = 9.53$, p = 0.009, Fig. 4A,B). Shiner perch were associated with interior habitat in seines, but with both interiors and edges in videos. Sticklebacks were densest in interior habitat and on edges in both videos and seines (Tables S3 & S4). Flatfishes showed no significant habitat associations in seines, but did in videos ($\chi^2_2 = 16.7$, p < 0.001, Fig. 4D),

where they provided a single case of higher densities in unvegetated habitat and edge than interiors. Gunnels showed a significant habitat association in seines ($\chi^2_2 = 6.96$, p = 0.031, Fig. 4E), with abundance greatest in interiors and edges, but not in videos. For staghorn sculpins and *Metacarcinus* spp., abundance did not vary significantly between habitats in videos or seines (Fig. 4C,F).

The outcome of 3 of 6 major taxa showing different habitat associations between sampling methods suggests a difference in how well they were detected in seines and videos. This detectability difference was corroborated by comparisons between methods of the fractional representation of each taxon in each patch. Sticklebacks were relatively more abundant in seines than videos (stickleback p = 0.003; Table S2), whereas staghorn sculpins, shiner perch, and *Metacarcinus* spp. were relatively more abundant in videos than in seines (staghorn p < 0.001, shiner p < 0.001, *Metacarcinus* p = 0.014; Table S2). Flatfishes and gunnels did not differ significantly in their relative contributions to videos vs. seines (Table S2).

Fig. 2. Mesopredator assemblages, as a fraction of total individuals, visualized by non-metric multidimensional scaling (NMDS). Mesopredators in 3 habitats at each of 3 sites were sampled by (A) seines and (B) high- and low-water videos. Global stress = 0.15. Shiner perch, staghorn sculpin, sticklebacks, gunnels, and flatfishes contributed the most to pairwise differences in assemblages among habitats. These species, along with hippolytid shrimps, also contributed the most to dissimilarity in methods. Data were analyzed as an ensemble, but distinguished in plots to more easily show dispersion of data from each sampling method; assemblages in high- and low-water videos were not statistically different

Behavior of mesopredators across habitats

Shiner perch and stickleback showed different TiVs across habitats (stickleback $\chi^2_2 = 10.71$, p = 0.006, n = 81, Fig. 5A; shiner perch $\chi^2_2 = 16.17$, p < 0.001, n = 370, Fig. 5B), but other mesopredators did not. Post hoc tests revealed that sticklebacks had significantly longer TiV in interior than unvegetated habitat, with edge intermediate (p < 0.001, Tables S5 & S7), and shiner perch had significantly longer TiV in both interior and edge than in unvegetated habitat (Tables S5 & S7). Gunnels, staghorn sculpin, *Metacarcinus* spp., and flatfishes showed no significant
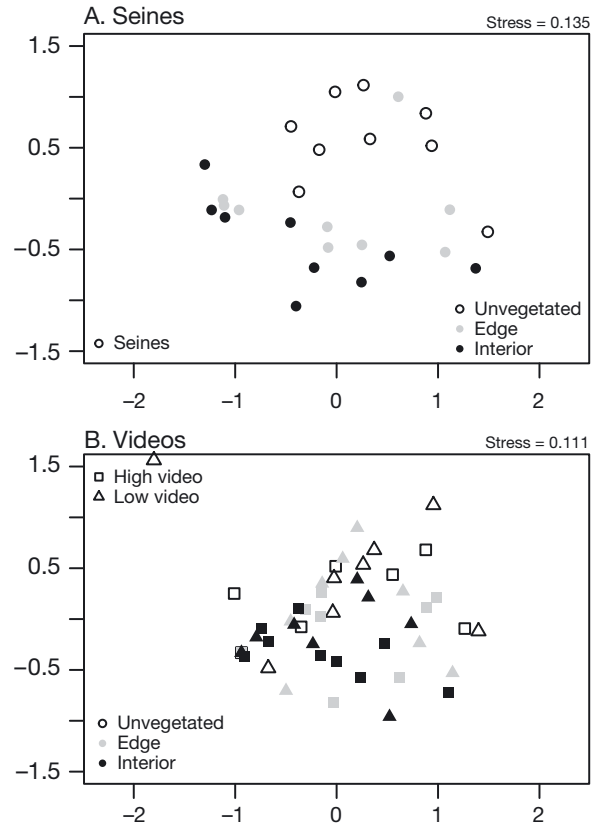
Table 2. Similarity percentage (SIMPER) analyses, showing percent contribution to pairwise differences in assemblage structure for the 5 most influential taxa among habitats, and their average relative density in each habitat. Average relative density (mean ± SE) was calculated from the proportional contribution of each taxon to sampled assemblages across videos and seines

| Taxon | Average relative density | | Contribution |
	Unvegetated	Edge	%
Shiner perch	0.26 ± 0.060	0.33 ± 0.60	26.69
Three-spined stickleback	0.053 ± 0.020	0.13 ± 0.039	17.54
Staghorn sculpin	0.24 ± 0.045	0.18 ± 0.039	15.05
Dungeness crab	0.082 ± 0.045	0.015 ± 0.012	7.14
Gunnels	0.062 ± 0.021	0.075 ± 0.020	6.69
	Edge	Interior	
Shiner perch	0.33 ± 0.60	0.46 ± 0.067	26.60
Staghorn sculpin	0.18 ± 0.039	0.11 ± 0.026	15.20
Three-spined stickleback	0.13 ± 0.039	0.20 ± 0.046	14.83
Flatfishes	0.058 ± 0.015	0.017 ± 0.008	9.12
Gunnels	0.075 ± 0.020	0.067 ± 0.020	7.29
	Unvegetated	Interior	
Shiner perch	0.26 ± 0.060	0.46 ± 0.067	27.58
Staghorn sculpin	0.24 ± 0.045	0.11 ± 0.026	15.92
Three-spined stickleback	0.053 ± 0.020	0.20 ± 0.046	11.50
Gunnels	0.062 ± 0.021	0.067 ± 0.020	8.08
Flatfishes	0.13 ± 0.036	0.017 ± 0.008	7.15

patterns in TiV (Table S5). Individual feeding rates of stickleback and staghorn sculpin did vary significantly by habitat (stickleback pseudo-$F_{2,78}$ = 3.84, p = 0.027, Fig. 5C; staghorn sculpin pseudo-$F_{2,333}$ = 3.20, p = 0.026, Fig. 5D; Table S6). Although post hoc PERMANOVAs revealed no significant pairwise differences at a Bonferroni-corrected α level of 0.017, some trends emerged. Sticklebacks were not observed feeding in unvegetated habitat and appeared to have greater feeding rates inside eelgrass than on edges, while staghorn sculpins tended towards elevated feeding rates on edges and had similar feeding rates in unvegetated and interior habitats (Table S8).

DISCUSSION

Mesopredators typically distribute themselves by habitat, often generating patterns of increased abundance

Table 3. Similarity percentage (SIMPER) analyses, showing percent contribution to pairwise differences in assemblage structure for the 5 most influential taxa between videos taken at high and low water and seine samples, and their average relative density in each sample type. Average relative density was calculated from the proportional contribution of each taxon to sampled assemblages across all habitats

Taxon	Average relative density		Contribution %
	High-water video	Seine	
Shiner perch	0.36 ± 0.062	0.25 ± 0.060	23.83
Three-spined stickleback	0.079 ± 0.027	0.25 ± 0.049	16.42
Staghorn sculpin	0.25 ± 0.045	0.10 ± 0.029	16.28
Gunnels	0.058 ± 0.020	0.081 ± 0.024	7.16
Flatfishes	0.090 ± 0.035	0.041 ± 0.010	6.89
	Low-water video	Seine	
Shiner perch	0.46 ± 0.065	0.25 ± 0.060	27.89
Three-spined stickleback	0.054 ± 0.020	0.25 ± 0.049	16.59
Staghorn sculpin	0.18 ± 0.034	0.10 ± 0.029	12.40
Gunnels	0.064 ± 0.017	0.081 ± 0.024	7.10
Hippolytid shrimps	0.00 ± 0.00	0.091 ± 0.034	6.36

with structural complexity (Perez-Matus & Shima 2010), and these distribution patterns may be highly species- or functional group-specific (Hori et al. 2009, Gross et al. 2017). Aggregate abundances in seines and videos appeared to be driven by small pelagic species like shiner perches and sticklebacks (Figs. 3
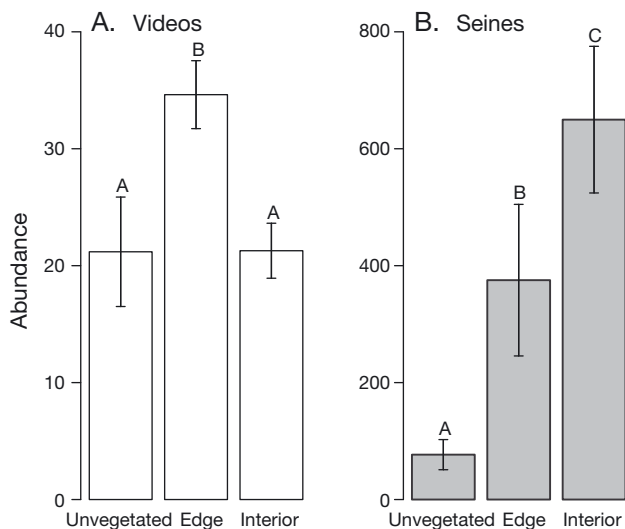

Fig. 3. Mean total abundance observed in each habitat type per sampling method: (A) video and (B) seine samples. High- and low-water videos were grouped together and therefore represent fish seen in a total of 20 min; for seines, samples covered a total area of 22 m². Error bars represent SE (3 replicate patches at each of 3 sites). Bars with the same letters represent means for which no significant difference was found in post hoc tests; separate post hoc tests were conducted to compare habitats among video and seine samples

& 4). For both methods, abundance of these fishes was greater in interior samples relative to unvegetated samples (Fig. 4A,B), consistent with other studies showing that small schooling fishes inhabiting the water column occur at higher densities inside than outside of seagrass (Heck et al. 1989, Hughes et al. 2002, Hori et al. 2009, Gross et al. 2017). Shiner perch and sticklebacks traveled slowly through patch interiors (extended TiV; Fig. 5A,B) and fed more frequently there (sticklebacks, Fig. 5C), which could explain the higher abundance in interior habitat for these taxonomic groups in seines. In seines, gunnels showed a similar abundance pattern to sticklebacks and shiner perch across the habitats sampled, but showed low densities across all habitats in videos (Fig. 4E), which may be because their small size and cryptic coloration limit their detectability. In contrast, other benthic taxa like staghorn sculpins, flatfishes, and *Metacarcinus* spp. exhibited uniform densities across all habitat types. These taxa are generally thought to exhibit negative or neutral responses to seagrass density (Hori et al. 2009, Gross et al. 2017), because their body shapes make movement through dense vegetation difficult, or because they are cryptically colored to match unvegetated substrates. Overall, a diversity of reactions to habitat complexity among taxa was a key result, with eelgrass habitat association stronger for pelagic than benthic mesopredator taxa.

Capture and camera techniques provided different results regarding the magnitude of habitat association with eelgrass and whether abundance was enhanced in edge samples relative to interior and unvegetated samples. Differences between sampling methods in the overall abundance trends across the habitat mosaic reflect the distribution patterns and behaviors of the most abundant taxa, which may bias peak abundances towards one habitat or another. For example, pelagic fishes like shiner perch and stickleback, which were among the most abundant taxa overall, moved more slowly through eelgrass patch interiors (Fig. 5A,B), reducing their rate of appearance in this habitat within the video frame and shifting observed total abundance towards edge samples in videos (Fig. 3A). In contrast, seines appeared to undersample benthic taxa (Table S2). Given that crabs and sculpins were over-represented in videos,
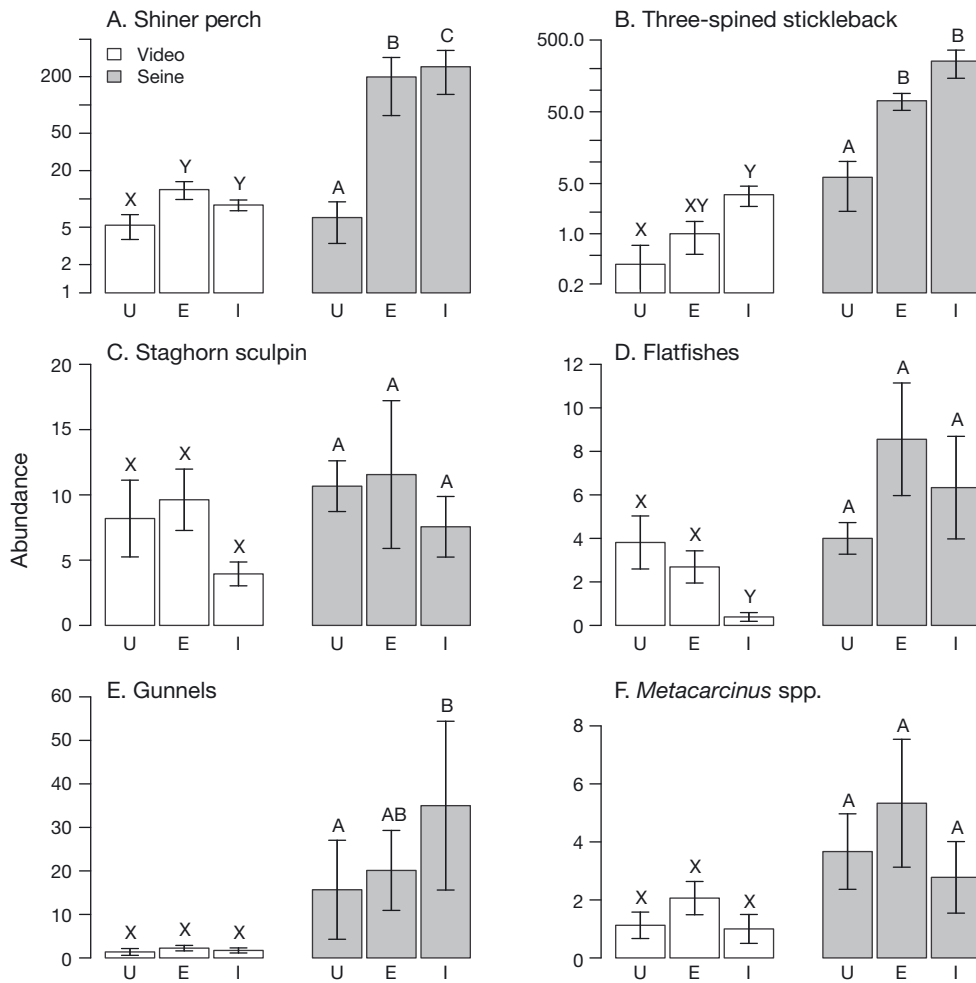
Fig. 4. Densities of major taxa at 3 estuarine sites in Washington State, each of which was sampled in 3 replicate patches of unvegetated, edge, and interior habitat. Note the logarithmic scale in A and B. Error bars represent SE of mean abundances; bars with the same letters represent those for which no significant difference was found in post hoc tests (separately for videos and seines) on log-transformed densities. Seines had 9 samples per habitat; videos consisted of 16 samples in unvegetated habitat and edge and 18 in interior, including videos at high and low water levels

these may be taxa that can avoid the seine, e.g. by slipping underneath as it was pursed. The act of sampling may also shift apparent community structure and habitat associations by altering mesopredator behavior. For instance, the number of individuals present in edge seine samples may have been artificially reduced as mesopredators normally present on edges were driven into the center of the eelgrass bed away from the net. Likewise, the PVC structure of the camera mount was associated with significant changes in community composition and abundance relative to areas of the field of view away from the PVC (Figs. S1 & S2). Responses to the PVC structure were also taxon-specific (Fig. S3). Eelgrass blades also obscure parts of the image in videos and may reduce detection of all mesopredators in vegetated

habitats relative to seines, although this effect may have been lessened on edges because of the lower density of eelgrass in this habitat (Gross et al. 2017). Overall a strong case was made that video data should be used with caution in defining community composition due to its sensitivity to habitat structure and swimming speed, which vary across taxa and habitats.

Of the 6 most abundant mesopredator groups, most exhibited equal densities, TiVs, and feeding rates in edge and interior samples (Tables S5 & S6), suggesting no difference in use between these habitats in our sites. Moreover, crabs and sculpins did not differentiate even between interior and unvegetated in terms of abundance (Fig. 3). In many cases, the edge of a structurally complex habitat like seagrass may
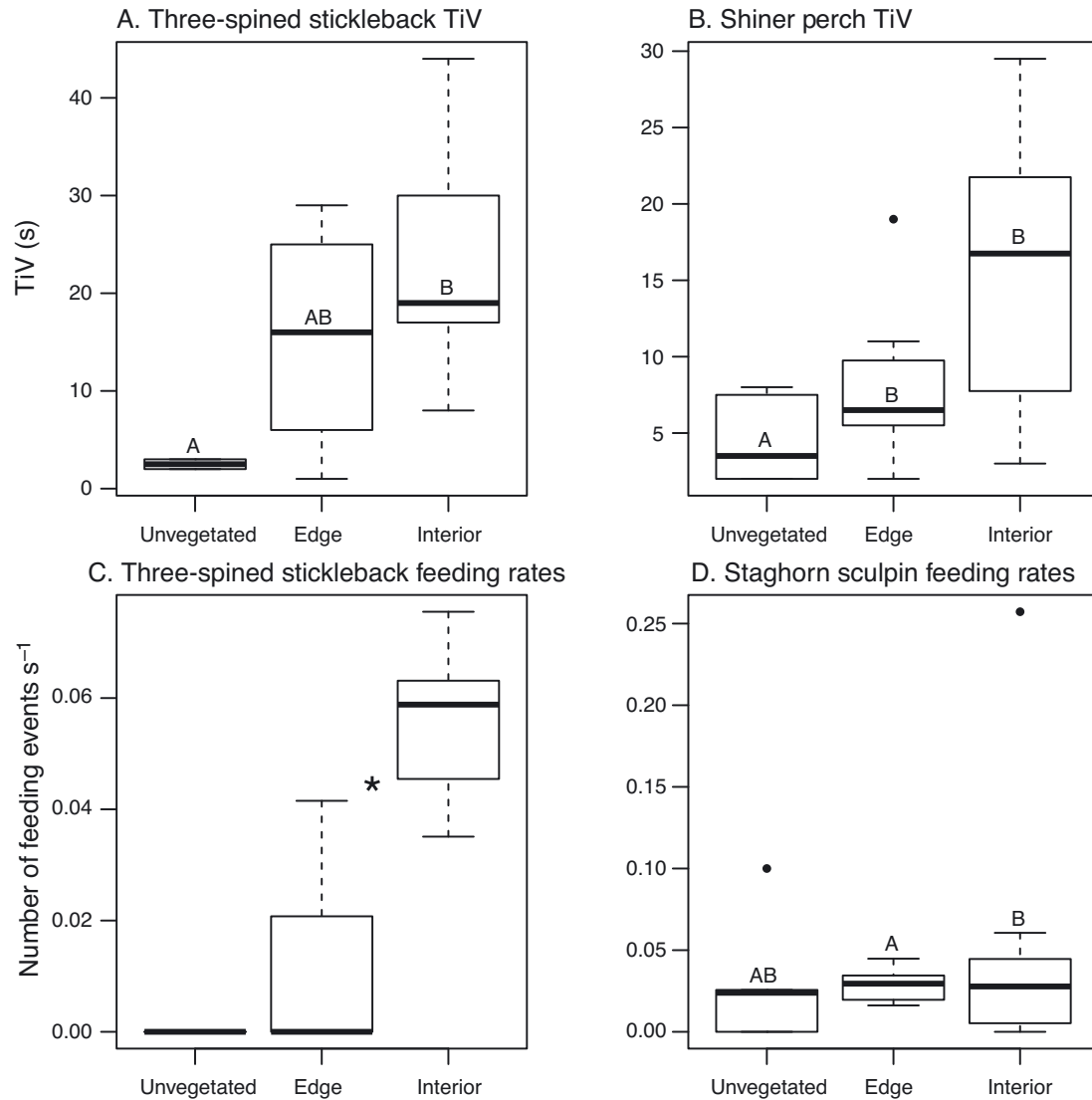
Fig. 5. Movement (time in view, TiV) of (A) sticklebacks and (B) shiner perch, and feeding rates of (C) sticklebacks and (D) staghorn sculpins observed in videos. Sticklebacks were observed in 2 sets of 10 unvegetated videos (not feeding), 5 edge sets (feeding in 1), and 9 interior sets (feeding in 8), while shiner perch were observed in 11 sets of 10 unvegetated videos, 14 edge sets, and 15 interior sets. Staghorn sculpin were observed feeding in 6 sets of 10 unvegetated videos, 9 edge video sets, and 7 interior video sets, including videos at high and low water levels, which were combined in this visualization. Boxes with the same letters represent those for which no significant difference was found in post hoc analyses. Midline: median; box limits: upper and lower quartiles; whiskers: extreme values; points: ouliers. * Significant difference based on a Bonferroni $\alpha = 0.017$

provide a unique habitat in that it allows mesopredators to easily access and visually survey unvegetated areas where food may be more abundant (Brooks & Bell 2001, Barberá-Cebrián et al. 2002, Bologna & Heck 2002) while at the same time providing an easily accessible refuge from visual predators like birds that may also forage in unvegetated areas (Semmens 2008, Thistle et al. 2010). Edges themselves may act as filters, accumulating organisms by inhibiting their entry into interior habitat and elevating concentrations of food, promoting abundance at higher trophic levels (Brooks & Bell 2001, Bologna & Heck 2002,

Arponen & Boström 2012, Macreadie et al. 2012). However, only 1 of our 6 most abundant taxa showed elevated feeding on edges (staghorn sculpins, main effects of habitat but no pairwise differences in post hoc tests). In keeping with other seagrass studies (e.g. Connolly & Hindell 2006, Boström et al. 2011), we saw no consistent abundance patterns on edges, which grouped with unvegetated or interior habitat, or were intermediate between the two. While edge effects on nekton in seagrass are plausible and identified, they may be obscured in patchy landscape configurations (Macreadie et al. 2010, 2012). In our

system, while we observed a difference in structural complexity between edge and eelgrass interior (shoot density, Gross et al. 2017) that may have affected habitat use, any true edge effects on nekton in our system were highly variable and may have been masked by the high perimeter-to-area ratio of fringing eelgrass beds.

Mesopredator assemblages differed between interior and unstructured habitats across sampling methods, with edges intermediate (Fig. 2). This view is consistent with a number of studies showing different species assemblages associated with seagrass-vegetated and unvegetated habitats (Nagelkerken & van der Velde 2004, Ferraro & Cole 2010). Surprisingly, we found no significant difference between assemblages in videos at high and low tide. Our multivariate results for habitat contrast with studies in Willapa Bay by Hosack et al. (2006) and Dumbauld et al. (2015), which showed that assemblage structure did not differ significantly between interior and unvegetated habitats. The distinctions among habitats were evident despite the close proximity of eelgrass and unvegetated tideflat in the mosaic where we focused our sampling. That is, assemblages differed by habitat even though the samples were just a few meters apart, clearly within the range of access for these mobile mesopredators.

A practical outcome emerges from the comparison of assemblages close to and away from the PVC frame used to demarcate a consistent area in the view of each camera. Excluding PVC-associated individuals was important prior to statistical analysis as the use of area near PVC was species- and habitat-specific (Figs. S1 & S3). In particular, crabs and sculpin were likely to associate with the PVC frame, and PVC-association was more likely when the general structural complexity of the habitat was low (i.e. in unvegetated habitat; Figs. S1 & S3). These results also point towards the importance of explicitly testing mesopredator behavior and abundance in areas where humans add structural complexity to tideflats, for instance stakes and racks for shellfish aquaculture.

Overall, our results indicate the importance of considering multiple species' responses to both the presence of seagrass and its configuration in a broader landscape context. These responses vary across habitat types and species pools, and species-by-habitat interactions affect how the impacts of edges or other landscape features on community structure appear across different sampling methods. Thus, differing species pools among sites and regions are a likely driver behind discrepancies in aggregate community responses to landscape structure observed in the literature. For instance, in Washington State estuarine systems, where small pelagic schooling fishes dominate in seagrass habitats, the behavior and habitat selectivity of these fishes strongly influence our ability to detect edge effects in the aggregate assembly of mesopredators in both seines and videos. Additionally, different habitats, landscape features, or patch morphologies may be used differently by a given species. Sticklebacks, for instance, showed no significant difference in abundance between seine samples in interiors and on edges (Fig. 4), but had significantly higher feeding rates in interiors than on edges (Fig. 5). As seagrass populations decline worldwide (Short & Wyllie-Echeverria 1996, Orth et al. 2006, Waycott et al. 2009, Short et al. 2011, Sweatman et al. 2017), the responses of individual species or functional groups, especially those that comprise the majority of an assemblage or may have the greatest impacts (via predation, ecosystem engineering, etc.) become increasingly relevant to restoration and management efforts focused on seagrass communities.

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