



Nekton Community Responses to Seagrass Differ with Shoreline Slope

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Abstract

Seagrass beds vary in patch size and shoot density, which can influence the distribution and abundance of nekton responding to habitat structure. In Washington State, USA, eelgrass (*Zostera marina*) occurs under two distinct shoreline slope conditions: shallow tidal flats where eelgrass forms extensive meadows, and steep slopes near channels where it forms narrow, often patchy, fringes adjacent to unvegetated sediment. We sampled nekton in these naturally occurring habitat mosaics with a crossed design: unvegetated, edge, and interior eelgrass (habitat) in flats and fringes. Multivariate community structure showed additive effects of habitat and slope, while aggregate body size did not vary across habitat, shoot density, or slopes. Total nekton abundance responded to structure on fringes (interior > unvegetated; edge = unvegetated; and interior > edge) but not on flats, while half of the most common taxa showed a significant habitat-by-slope interaction in abundance. Diversity and species richness were greater in fringes than flats, irrespective of habitat type. Since canopy height and shoot density did not differ significantly between fringes and flats, it is unlikely that fine-scale aspects of vegetation structure explain why fauna responded differently to eelgrass fringes and flats. We instead attribute these different responses to underlying differences between fringes and flats in within-habitat heterogeneity and connectivity to deeper habitats, as well as species-specific responses to greater edge/interior ratios in fringing beds. Our study shows that topographic and seascape heterogeneity as well as habitat connectivity may play key roles in the value of nearshore estuarine habitats for nekton in the Northeast Pacific.

Keywords Habitat heterogeneity · Structural complexity · Habitat connectivity · Community structure · Seagrass · Nekton

Introduction

Seagrass provides habitat that increases the abundance and diversity of fauna relative to unvegetated areas, regardless of patch size, interpatch connectivity, or fragmentation (in most cases; Connolly and Hindell 2006; Bostrom et al. 2011;

Lefcheck et al. 2016). However, studies in seagrass seascape ecology have infrequently addressed the effects of broader physical characteristics of the seascape on faunal assemblages, both directly and indirectly by affecting seagrass patch morphology. For instance, fragmentation may result from human disturbance but may also vary with the physics of light and water motion interacting with bottom topography and depth (Dowty et al. 2005; Stevens and Lacy 2012). Differences in underlying physical structure can have complex effects on seagrass structure at multiple spatial scales, and determining the scale of greatest import to nekton can inform our understanding of seagrass habitat use by these animals.

Shoreline slope has three potential mechanisms by which to influence nekton interaction with seagrass habitat: (1) proximity to deeper (channel) habitats (De Angelo et al. 2014); (2) amount of seagrass habitat that is close to edge (Smith et al. 2008); and (3) density or size of seagrass shoots, which could covary with patchiness (Hyndes et al. 2003). Where seagrass extends across a depth gradient, zonation often occurs in the associated nekton communities. Across a depth gradient in the English Channel, deeper seagrass beds harbored more

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abundant and species-rich fish and decapod communities than shallow (Jackson et al. 2006), while in a study in the northwest Mediterranean Sea, the pattern was reversed, with elevated abundance and diversity in shallow beds (Francour 1997). Because of distinct assemblages in deep and shallow beds, seagrass beds on steeply sloping seafloors where shallow and deep sections of the bed are in close proximity can be expected to have greater abundance and richness (Heithaus 2004; De Angelo et al. 2014), or be influenced by species interactions such as predators foraging from deeper areas (Peterson 1991).

Because the slope of the seabed can directly determine how much area is available with suitable conditions for seagrass (i.e., light, immersion time), differences in slope create seascapes with patches differing in perimeter-to-area ratios as well as distances from edge. Steeply sloping bottoms are often associated with channel edges, coarser sediments, and patchy, fringing bands of seagrass, while broad, gently sloping bottoms are associated with finer sediments and extensive, continuous seagrass flats. In the case of flats and fringes in Washington State, flats are vegetated by eelgrass (*Zostera marina*) that generally extends several 100 m, whereas fringes typically span 10s of meters perpendicular to the shoreline (Dowty et al. 2005). The effects of increased edge habitat on overall nekton diversity and abundance are inconsistent across studies, with some showing increasing edge habitat positively affects abundance and diversity (e.g., Macreadie et al. 2010), others showing negative effects (e.g., Gorman et al. 2009), and others showing no effects (e.g., Lefcheck et al. 2016). These inconsistencies may reflect threshold effects of fragmentation or species-specific responses (Connolly and Hindell 2006; Horinouchi 2007; Bostrom et al. 2011; Hensgen et al. 2014; Lefcheck et al. 2016; Yeager et al. 2016).

The structural complexity provided by seagrass provides a third potential mechanism by which shoreline slope could influence nekton assemblages. Patchy seagrass may contain smaller or sparser shoots, relative to continuous meadows, since phenotypic traits vary with light, water motion, and sediment type (Keller and Harris 1966; Holmer et al. 2009; Yang et al. 2013). Abundance and richness often respond positively to increasing habitat structural complexity (MacArthur and MacArthur 1961; Tews et al. 2004; Stein et al. 2014). Seagrass can disproportionately benefit certain functional groups of nekton, such as pelagic schooling fishes and cryptic shoot-associated species (Horinouchi 2007; Gross et al. 2017), and the density of shoots may also constrain the body size distribution of associated taxa (Hyndes et al. 2003). Vegetation can facilitate survival of smaller animals relative to unvegetated habitats by impeding the movement or vision of larger predators (Irlandi 1994; Horinouchi 2007; Canion and Heck 2009; Jaxion-Harm and Speight 2012). Thus, parameters of structural complexity at the shoot level, such as shoot density or canopy height, are often important to small

nekton (Horinouchi 2007), and may limit body sizes of nekton living and foraging in vegetated habitats (MacArthur and Hyndes 2001; Nanjo et al. 2014).

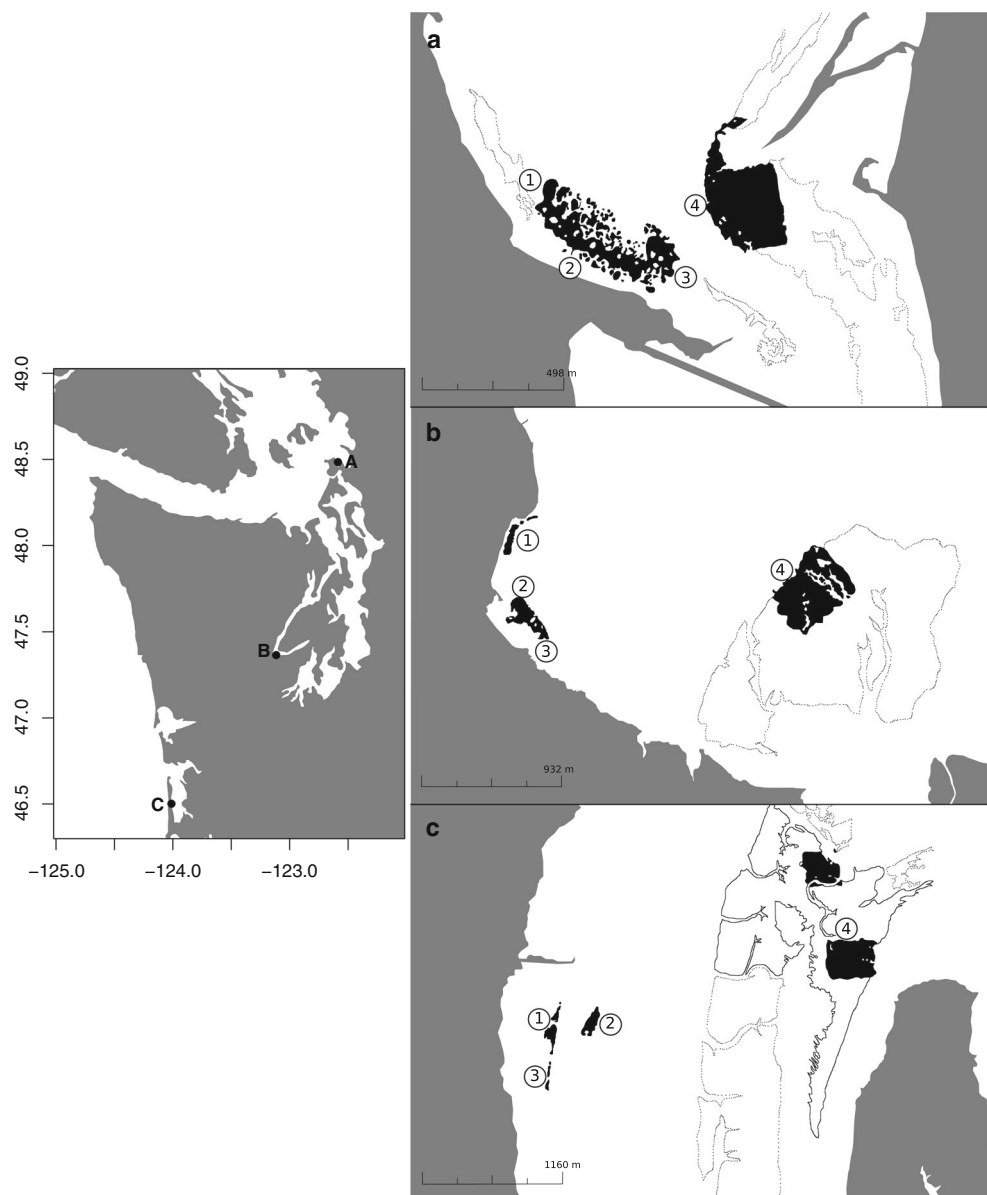
The main objective of our study was to compare nekton assemblages in eelgrass flats and fringes at a common low intertidal elevation, testing the indirect role of shoreline slope in shaping community structure by modifying eelgrass bed structure. In both flats and fringes, we sampled across unvegetated, edge, and interior habitats to measure how nekton response to the vegetated-unvegetated ecotone varied between the two shoreline slope types. We also measured eelgrass size and density to evaluate how nekton responded to the fine-scale structural complexity of habitat on flats and fringes. We expected that (1) eelgrass would elevate nekton density above that observed in unvegetated habitats, particularly via pelagic or shoot-associated taxa, regardless of slope or distance to edge; (2) nekton body size and structural complexity of eelgrass would be inversely related (i.e., smaller body size in more structurally complex habitats); and (3) nekton assemblages would be less distinguishable across habitat types (unvegetated, edge, interior) in fringes than in flats, due to mobility of organisms relative to patch size. We examined these expectations through a crossed study design (slope \times habitat) with response variables of total abundance, abundance of dominant taxa, diversity, body size, and multivariate community structure.

Methods

Sites and Sampling Methods Three sites were selected along the coastline of Washington State, USA: Fidalgo Bay, the Skokomish River delta, and Willapa Bay. These sites share a mesotidal regime (mean diurnal range 2.8 to 3.5 m) and encompass nearby areas of low-angle (flats) and steep slopes (fringes; Fig. 1, Fig. 2). Eelgrass (*Zostera marina*) occurred just below mean lower low water at all three sites. Nekton were sampled from 2 July to 18 August 2016, when water levels were < 1 m over the target depth just below mean lower low water in both vegetated and unvegetated habitats, which were available at the same tidal elevation due to naturally patchy eelgrass beds. Eelgrass shoots were sampled at low water during spring tides when the sites were briefly immersed.

At each site, we chose four subsites: three near fringing eelgrass and one flat. This unbalanced design was constrained by the low frequency of independent flat eelgrass subsites at each site (Fig. 1) but was accommodated statistically by appropriate nesting such that the flat/fringe comparisons were based on a sample size of three sites. In each subsite, we sampled three habitat types: interior eelgrass, edge, and unvegetated. Nekton samples in interior eelgrass were collected closer to the edge in fringes than on flats due to differences in perimeter-to-area ratios but were collected at least 2 m from

Fig. 1 Map of study sites showing eelgrass (*Zostera marina*) fringes and flats in Washington State (USA). Dark areas are those in which eelgrass was measured during acoustic surveys (supplemental methods), while outlines indicate the full extent of eelgrass shown in Google satellite images (see Supplementary Material for further details). Numbers at each site indicate the position of eelgrass patches used to define subsites; 1–3 represent fringe subsites, and 4 is the flat subsite. **a** Fidalgo Bay (48.49°N, 122.59°W), **b** Skokomish River delta (47.36°N, 123.13°W), **c** Willapa Bay (46.52°N, 123.99°W)



the edge in both slope types (Smith et al. 2008). Fringing eelgrass had an average width of 98.67 ± 6.83 m perpendicular to the shoreline and perimeter-to-area ratio of 0.085 ± 0.024 (Table S1, S2). Flats had eelgrass across an average width of 556.67 ± 56.58 m, with a perimeter-to-area ratio of 0.020 ± 0.002 (Table S1, S2). The distribution and morphology of eelgrass fringes and flats were surveyed with a Biosonics DT-X single beam sonar. The biosonics transducer head was set to emit 10 pings per second, and a biosonics surface unit integrated this sonar data with post-processed position data acquired with a Trimble Pro 6H GPS, accurate to 1 m. Visual Acquisition software used to acquire the sonar data was exported into a post-processing software (Visual Habitat), where seagrass was easily identified, and beds were delineated. Bed morphology for all sites was surveyed in

2017, with the exception of the Skokomish delta flat subsite, which was surveyed in 2015. Seafloor maps (Fig. 2) are largely consistent with our summer 2016 sampling design, although some discrepancies exist in areas where patches that appeared to be discrete in sampling were actually connected at lower tidal elevations (see supplemental material).

Attributes of eelgrass were sampled at the edge and interior (in close proximity to nekton sampling) of each subsite patch in ten 0.25 m^2 quadrats, sampled every 5 m along 50-m transects. In each quadrat, shoots were counted, of which the first five were measured for maximum length. Prior to analysis, shoot density measurements were converted to shoots per square meter and log-transformed to conform to a normal distribution; shoot length was averaged per quadrat as an index of canopy height.

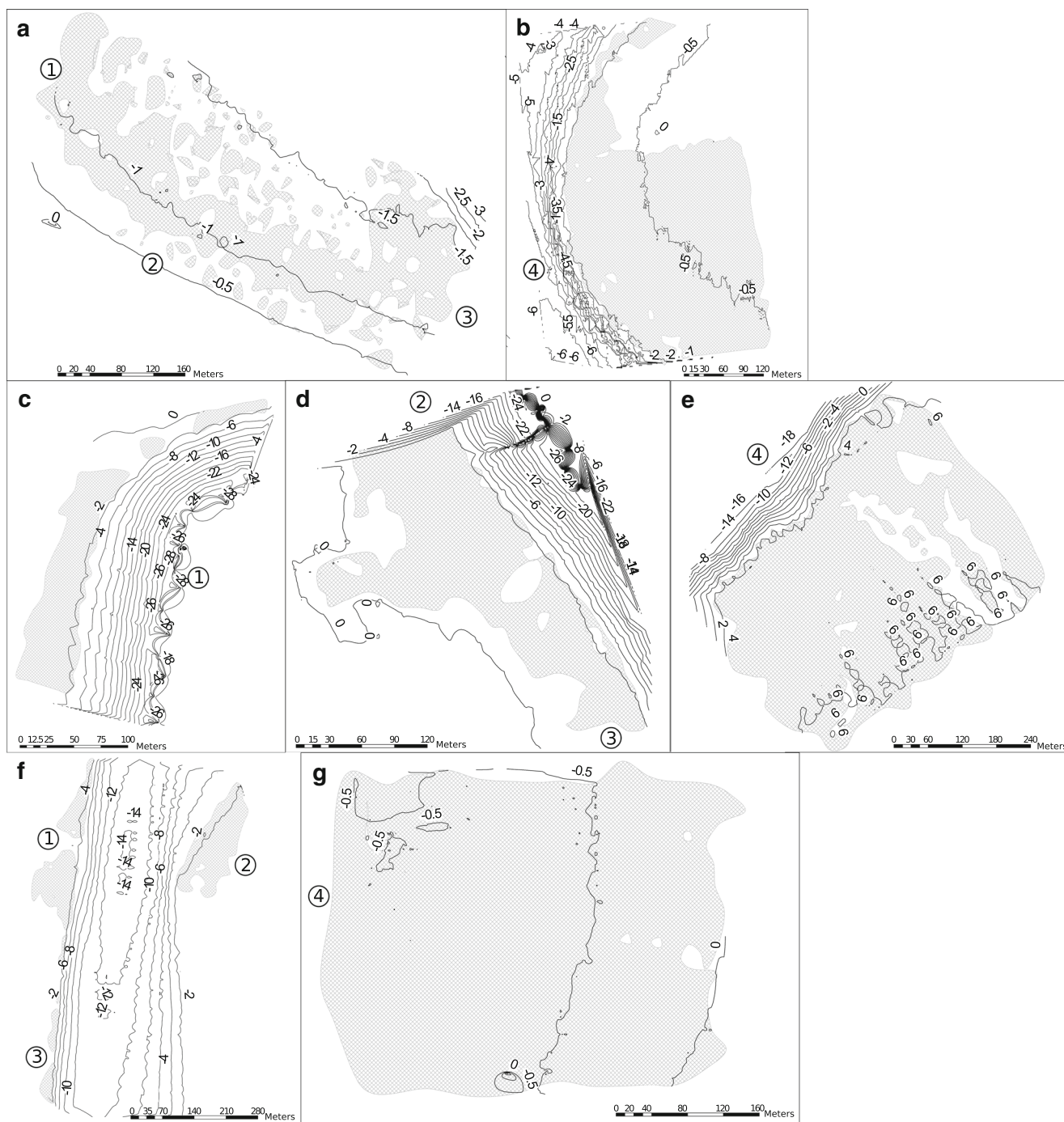


Fig. 2 Map of eelgrass beds surveyed in this study. Hatched areas represent the extent of eelgrass-vegetated habitat as measured by camera transects (supplemental methods), while lines represent isobaths in feet below mean lower low water. Where possible, fringing eelgrass

beds at a given site are shown together in one panel, while flats are shown separately. Numbers correspond to subsites as shown in Fig. 1. **a, b** Fidalgo Bay; **c–e** Skokomish River delta; **f, g** Willapa Bay. **a, c, d, f** fringing eelgrass beds; **b, e, g** eelgrass flats

Nekton samples (fishes and decapods) were collected with a custom beach seine (circular area of 11 m²; 3 mm mesh) in each habitat. Edge seines contained approximately 50% each interior and unvegetated habitat, or about 1.5 m each of vegetated and unvegetated substrate, including the border of the eelgrass patch. Animals were counted, identified to the lowest

possible taxonomic level (typically species), and released. Of these, up to 10 individuals per species were measured to the nearest 0.5 cm (total length for fish and shrimp, carapace width for crabs). The first 10 measured individuals were averaged and used to extrapolate the lengths of unmeasured individuals of the same species per seine. Two seines were

carried out in each habitat type per subsite, for a total of 24 seines per site.

Multivariate Analysis of Nekton Assemblages Non-metric multidimensional scaling (NMDS) analyses were conducted on Bray-Curtis dissimilarities derived from a sample-by-species abundance matrix (each seine as a sample) to describe and visualize community variation. Because samples often exhibited high dominance of one or two species, we $\log(n + 1)$ -transformed the species abundance data per seine to downweight the most abundant species and allow less common species to exert more influence on distance calculation (Clarke and Warwick 2001). A permutational multivariate ANOVA (PERMANOVA, maximum permutations = 9999) was carried out on the abundance matrix to test whether communities differed according to habitat type, shoreline slope, and their interaction. Subsites were treated as strata within sites to ensure that randomizations occurred only among habitat patches within subsites. Post-hoc tests were conducted on subsets of the sample-by-species abundance matrix grouped by three different habitat combinations (unvegetated-edge, unvegetated-interior, and edge-interior) after multivariate analyses showed significant differences in community structure among habitats. When assemblages varied statistically, we applied a similarity percentage (SIMPER) analysis to determine which taxa contributed to this variation. Multivariate analyses were conducted using the vegan package in R (Oksanen et al. 2015; R Core Team 2015).

Univariate Analyses of Eelgrass Biometrics, Nekton Abundance, Diversity, and Size Two-factor linear mixed effects models were applied to the following response variables, with each seine as a sample: total abundance (log-transformed), body size (average across all individuals in a seine), Shannon-Weiner species diversity (H'), species richness, log-transformed shoot density, and canopy height. Habitat type (three levels: unvegetated, edge, and interior) and slope (two levels: fringe and flat) were included as fixed effects in the models, while site and subsite were used as nested random effects. Likelihood ratio tests were used to compare models with and without the fixed effects of interest to test for significance. The error structure in all models except those used for assessing species richness was assumed to be Gaussian-distributed based on residual plots, and models were constructed using the lmer() function in the lme4 package in R (Bates et al. 2015). Error structure in species richness models was assumed to be Poisson-distributed, and we used the function glmer() with a log-link function.

Similar models (differing in error structure and nested random effect) were constructed to examine responses of abundance to habitat and shoreline slope on a taxon-specific basis for nine focal taxa (Table 1). These taxa included species contributing most to habitat and fringe-flat differences

according to SIMPER analyses (seven species). We also included bay pipefish (*Syngnathus leptorhynchus*) based on their known site fidelity within eelgrass habitats (Howe and Simenstad 2015), and English sole (*Parophrys vetulus*) because of their documented use of local estuaries as nursery habitat (Hughes et al. 2014), for a total of nine species. Based on residual plots and overdispersion analyses, the error structure for these models was assumed to conform to a negative binomial distribution (glmer.nb() function). Subsite was excluded as a random effect from these models in order to facilitate model convergence. Significance of slope (flat or fringe) and habitat (unvegetated, edge, or interior) was determined using likelihood ratio tests.

As a post-hoc test for analyses in which we found a significant habitat-by-slope interaction, we grouped samples according to their habitat and shoreline slope (six groups). In a pairwise approach, with 15 total comparisons, each group was compared to every other group by mixed effects models, maintaining site and subsite as random effects. To account for multiple comparisons, we used the Bonferroni correction and considered significant only those comparisons for which $p < 0.0033$.

Finally, a direct evaluation of body size as a function of eelgrass structural complexity was carried out by including the shoot density of each habitat in each subsite as a covariate in the analysis of body size, replacing habitat and slope as fixed effects.

Results

Vegetation Structure Shoot density and canopy height varied significantly across habitats, but not between shoreline slopes. Density and canopy height were greatest in interior eelgrass relative to edges, but these parameters did not depend on whether the eelgrass was growing on a fringe or a flat (Table 2, Fig. 3).

Multivariate Analysis of Nekton Assemblages Based on multivariate analyses, taxonomic composition differed significantly by slope (pseudo- $F_{1,67} = 3.77$, $p < 0.001$) and by habitat (pseudo- $F_{2,67} = 4.84$, $p < 0.001$). No habitat-by-slope interaction was evident (pseudo- $F_{2,67} = 0.93$, $p = 0.16$), which was inconsistent with our expectation that assemblages in fringe habitats would be well-mixed relative to those on flats. Post-hoc tests showed that unvegetated, edge, and interior assemblages differed significantly from each other at the $\alpha = 0.0005$ level, although high NMDS plot stress made these distinctions difficult to visualize (Fig. 4). The taxa with the largest contribution to habitat differences included taxa living above (sticklebacks, shiner perch, grass shrimps) and on the sediment (sand shrimp, Dungeness crab, saddleback gunnels; Table 3); sticklebacks, shiner perch, grass shrimps, as well

Table 1 Abundances of the nine focal taxa across all seines. χ^2 values are the result of likelihood comparison tests between a null model containing only the nested random effects of site and subsite and models containing the fixed effect of interest (slope, habitat, and their

interaction). Abundance values represent the total across 24 seines per habitat level, or 54 seines on fringes and 18 on flats. Significance values are shown as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Taxon	Habitat				Shoreline slope			Interaction $\chi^2(2)$
	$\chi^2(2)$	Unvegetated	Edge	Interior	$\chi^2(1)$	Fringe	Flat	
<i>Gasterosteus aculeatus</i> Stickleback	11.82 **	356	355	2018	9.18 **	2620	109	7.65 *
<i>Crangon</i> sp. Sand shrimp	13.79 **	598	567	216	1.91	967	414	1.02
<i>Cymatogaster aggregata</i> Shiner perch	28.17 ***	78	229	979	0.00080	948	338	3.24
<i>Pholis ornata</i> Saddleback gunnel	7.88 *	73	235	326	9.35 **	622	12	4.33
Hippolytidae Grass shrimps	7.52 *	65	155	315	8.77 **	513	22	0.39
<i>Leptocottus armatus</i> Staghorn sculpin	0.21	97	111	129	3.51	278	59	12.98 **
<i>Metacarcinus magister</i> Dungeness crab	0.42	129	102	98	3.33	284	45	10.60 **
<i>Parophrys vetulus</i> English sole	12.63 **	132	58	16	0.39	114	92	16.49 ***
<i>Syngnathus leptorhynchus</i> Bay pipefish	19.01 ***	19	31	102	3.46	131	21	3.04
Other		154	163	161		447	31	
Total abundance	14.32 ***	1701	2002	4364	3.7428	6924	1143	9.01 *

as sand shrimp and staghorn sculpins contributed to differences between fringes and flats (Table 4).

Nekton Diversity and Abundance Overall, there was a significant habitat-by-slope interaction effect on total abundance, which was greater in interior eelgrass than edges or unvegetated habitat on fringes, but remained uniformly low across habitats on flats (Table S3, Fig. 5). Of the 8067 individuals detected in seines, approximately 71% were fishes, and the remainder were crabs and shrimp. As expected, abundances of pelagic and shoot-associated taxa, including bay pipefish (*Syngnathus leptorhynchus*), grass shrimps (Hippolytidae), shiner perch (*Cymatogaster aggregata*), and three-spined stickleback (*Gasterosteus aculeatus*), were elevated in interior eelgrass (Table 1, Table S4). Bay pipefish and

shiner perch showed a significant response to habitat only (interior > edge > unvegetated for shiner perch, interior > edge = unvegetated for bay pipefish; Table S4), whereas grass shrimps additionally showed a slope effect and were more abundant in fringes than on flats (Table 1). The greatest response of three-spined sticklebacks to eelgrass appeared on fringes—while there were significantly more in flat eelgrass bed interiors than unvegetated habitat, this taxon was relatively low on flats (Fig. 5, Table S4). Saddleback gunnels (*Pholis ornata*) increased in abundance from unvegetated to interior eelgrass habitat, and were an order of magnitude more abundant on fringes than flats (Table 1, Table S4). Some benthic taxa were uniformly distributed across habitat types: staghorn sculpin (*Leptocottus armatus*) regardless of shoreline slope, and English sole (*Parophrys vetulus*) and Dungeness crab

Table 2 Eelgrass (*Zostera marina*) biometrics on edge and interior of fringes and flats. χ^2 and p values are the result of likelihood comparison tests between a null model containing only the nested random effects of site and subsite and models containing the fixed effect of interest (habitat, slope). Significance of the habitat-by-slope interaction was tested by

comparing a full model containing the fixed effects and the interaction with a model containing only the additive fixed effects. Values for metrics are averages \pm standard error across subsites, where data from each subsite ($n = 10$ quadrats) were first averaged. Significance values are shown as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Biometric	Habitat			Shoreline slope			Interaction $\chi^2(1)$
	$\chi^2(1)$	Edge	Interior	$\chi^2(1)$	Fringe	Flat	
Density (shoots m^{-2})	25.26 ***	53.8 \pm 13.9	118.7 \pm 31.4	0.018	88.4 \pm 22.3	79.9 \pm 31.0	0.55
Canopy height (cm)	10.09 **	69.4 \pm 10.1	86.4 \pm 11.7	2.13	74.4 \pm 9.6	88.4 \pm 11.5	0.27

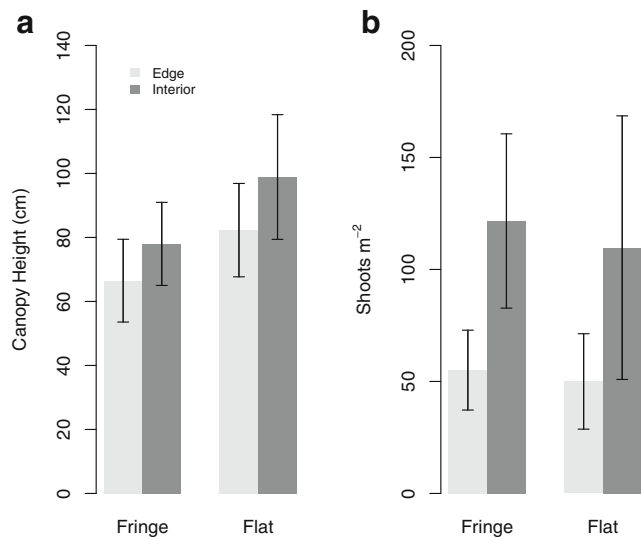
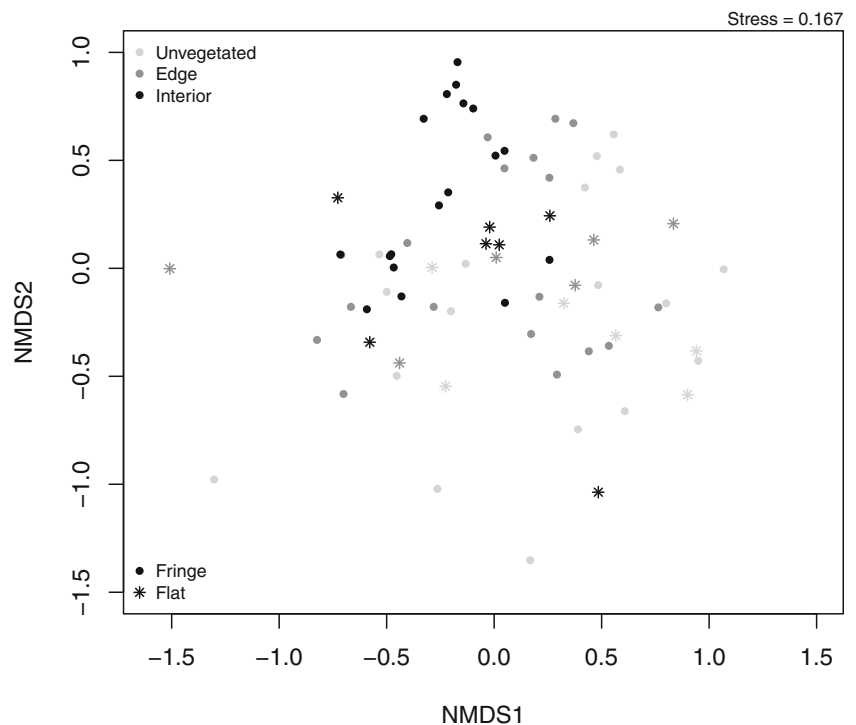


Fig. 3 Vegetation structure measured as canopy height (a) and shoot density (b) for eelgrass (*Zostera marina*) occupying fringes and flats in Washington State (USA). Both metrics responded significantly to habitat only, with greater canopy height and shoot density exhibited in interior eelgrass than edges. Error bars indicate standard error of the mean, based on shoots present in each habitat across nine fringe subsites and three flat subsites (10 quadrats per habitat per subsite)

(*Metacarcinus magister*) on fringes (Table S4). Other benthic taxa decreased in abundance into eelgrass: sand shrimp (*Crangon* sp.) regardless of shoreline slope, and English sole and Dungeness crab on flats. Despite many taxon-specific responses to habitat, species richness and diversity differed only by shoreline slope, not habitat (richness: $\chi^2(2) = 4.66$, $p = 0.097$; diversity: $\chi^2(2) = 1.85$, $p = 0.40$; Fig. 6). Both

Fig. 4 Community structure of fish and decapods across eelgrass, edge, and bare habitats on fringes and flats in Washington State (USA), plotted by non-metric multidimensional scaling. There were significant habitat (pseudo- $F_{2,67} = 4.84$, $p < 0.001$) and slope (pseudo- $F_{1,67} = 3.77$, $p < 0.001$) effects, but no significant interaction effect on community structure. Post-hoc analyses revealed significant differences among interior, edge, and unvegetated assemblages



species richness ($\chi^2(1) = 4.62$, $p = 0.039$) and Shannon-Weiner diversity ($\chi^2(1) = 5.45$, $p = 0.020$) were significantly higher on fringes than on flats.

Body Size The average size of nekton in our samples showed no significant patterns across habitat types ($\chi^2(3) = 1.02$, $p = 0.60$) or slopes ($\chi^2(1) = 0.59$, $p = 0.44$; Fig. 7a). Moreover, body size was not significantly related to local shoot density ($\chi^2(1) = 0.0597$, $p = 0.81$; Fig. 7b).

Discussion

A common pattern in seascapes worldwide is that nekton show increased abundance in vegetated areas relative to adjacent unvegetated areas (Heck et al. 1989; Hughes et al. 2002; Ferraro and Cole 2010; Blandon and Ermgassen 2014), but these habitat benefits often accrue only to specific taxa or functional groups (Hori et al. 2009; Gross et al. 2017). Such was the case in our study, with taxa favored in eelgrass that typically dwell in the water column directly above or among the blades (Fig. 4). Previous research on nekton in seagrass has demonstrated that these assemblages can differ depending on the surrounding seascape, for instance the depth profile (Francour 1997) or other habitat types in the vicinity (De Angelo et al. 2014; Henderson et al. 2017). The spatial arrangement of seagrass and the patchiness of a seascape can also modify local nekton assemblages (Yeager et al. 2016); as in our case, Hensgen et al. (2014) found high animal density in small and reticulated seagrass patches relative to continuous

Table 3 Results of SIMPER analyses, showing percent contribution to pairwise differences in assemblage structure for the six most influential taxa among habitats, and their average per-sample abundance in each habitat. Abundance values represent the average abundance \pm standard

Taxon	Average abundance			Contribution %		
	Unvegetated	Edge	Interior	Unvegetated-edge	Edge-interior	Unvegetated-interior
Sand shrimp	24.92 \pm 5.19	23.63 \pm 6.15	8.64 \pm 3.48	11.72%	10.55%*	10.63%**
Stickleback	14.83 \pm 8.95	14.79 \pm 5.66	80.72 \pm 20.54	10.98% ^a	14.70% ^a	14.97% ^a
Shiner perch	3.25 \pm 1.44	9.54 \pm 3.45	39.16 \pm 7.50	10.13%*	12.62%**	15.93%***
Dungeness crab	5.38 \pm 2.23	4.25 \pm 1.55	3.92 \pm 1.78	8.20% ^a	7.16% ^a	6.73% ^a
Saddleback gunnel	3.04 \pm 1.65	9.79 \pm 4.46	13.04 \pm 5.22	7.87%	8.49%	6.82%*
Grass shrimps	2.71 \pm 1.16	6.46 \pm 2.46	12.6 \pm 4.45	7.56%	8.83%	7.79%*

^a Sticklebacks and Dungeness crabs showed a significant interaction between shoreline slope and habitat

meadows in their summer sampling, but different patch morphologies were not attributed to underlying differences in shoreline slope. We took advantage of the mosaic of differently shaped eelgrass beds and unvegetated habitat along Washington shorelines to evaluate the ways in which factors beyond the simple presence/absence of eelgrass shoots contribute to assemblage structure. In the crossed design of habitat (unvegetated, edge, interior) and slope (flat, fringe), we expected only main effects for total nekton abundance, and an interaction effect for multivariate assemblage structure. Instead, augmented abundance of nekton in interior eelgrass only appeared on fringes, not flats (habitat-by-slope interaction), while multivariate assemblage structure among habitats was equally distinguishable on fringes and on flats (no habitat-by-slope interaction). These results suggest that nekton in this region consists of characteristically habitat-specific taxa, but that some feature of fringing eelgrass makes it particularly favorable.

Table 4 Results of SIMPER analyses, showing percent contribution to pairwise differences in assemblage structure for the five most influential taxa between fringes and flats, and their average abundance per sample in each shoreline slope type. Abundance values represent the average abundance \pm standard error, based on 54 seines on fringes and 18 on flats. Asterisks next to contribution percentages indicate significant differences between fringes and flats. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Taxon	Average abundance		Contribution %
	Fringe	Flat	
Stickleback	48.52 \pm 11.18	5.74 \pm 2.89	13.42% ^a
Shiner perch	17.56 \pm 3.70	17.79 \pm 7.71	12.38%
Sand shrimp	17.91 \pm 3.80	21.79 \pm 4.01	11.61%
Grass shrimps	9.50 \pm 2.38	1.16 \pm 0.43	7.99%**
Staghorn sculpin	5.15 \pm 0.93	3.11 \pm 0.92	7.85% ^a

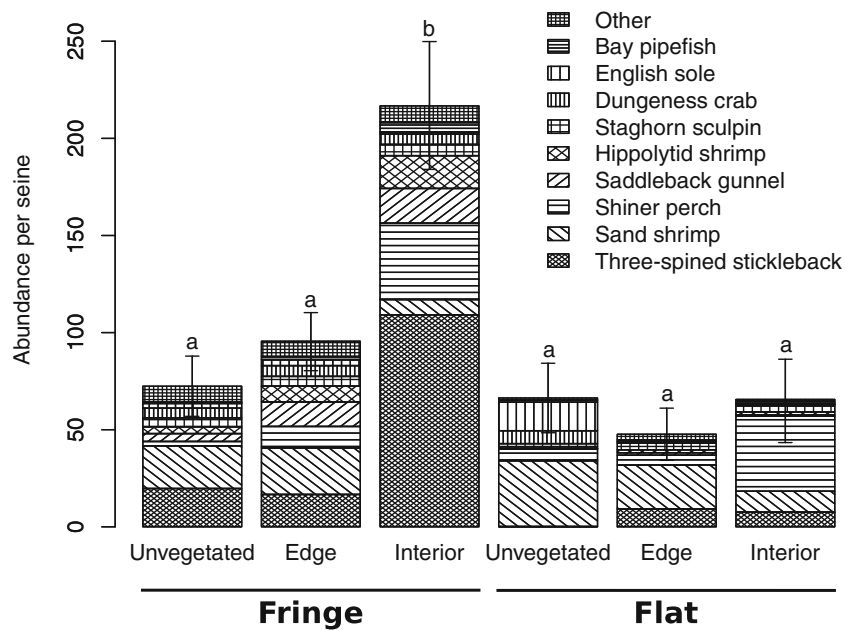
^a Sticklebacks and staghorn sculpins showed a significant interaction between shoreline slope and habitat

error ($n = 24$ for interior, edge, and unvegetated). Asterisks next to contribution percentages indicate significant differences between habitats at a Bonferroni-corrected alpha level of 0.017 for three pairwise habitat comparisons. * $p < 0.017$, ** $p < 0.0017$, *** $p < 0.00017$

Shoreline slope has three mechanisms that could influence the habitat response of nekton, including two at large scales (proximity to channels, eelgrass patch size) and one at a smaller scale (eelgrass density or canopy height). At the scale of individual shoots, eelgrass had similar density and size regardless of whether it grew in fringes or flats (Fig. 3), and therefore could not directly act to increase nekton abundance only in fringing eelgrass (Fig. 4), increase richness and diversity on fringes relative to flats (Fig. 5), or generate distinct assemblages for eelgrass on fringes and flats (Fig. 7). In contrast, on both slope types, shoot density and length decreased from eelgrass interior to edge. Thus, the lack of significant difference in total nekton abundance between fringe edges and adjacent unvegetated habitat may reflect a shoot density threshold required for structural complexity to augment nekton abundance (Horinouchi 2007; Yeager et al. 2016). Intermediate shoot structure may also provide a reason for nekton community structure to differ on edges relative to interior and unvegetated habitats, regardless of slope (Fig. 7). Another possibility is that nekton perceive edges, at the scale at which we sampled, to contain two habitat types, thus resulting in intermediate assemblages.

Our inclusion of edge samples on both fringes and flats allowed us to evaluate if fringing eelgrass had augmented nekton abundance due to the large amount of edge relative to interior habitat. Horinouchi (2007) predicted that small pelagic schooling fishes associated with sparse seagrass or edge habitat would have higher abundance in smaller, fragmented seagrass patches. However, none of our focal taxa showed augmented abundance at edges relative to any other habitat type in our study, suggesting that nekton do not directly benefit from edges as a distinct habitat. Rather than using edges per se, nekton may have better access to interior eelgrass with edges in close proximity, or the greater amount of edge relative to interior habitat in fringing eelgrass beds may be perceived by nekton as less dense

Fig. 5 Total abundances of fish and decapods across habitats (interior, edge, and unvegetated) and slopes (flats and fringes) in Washington State (USA), subdivided into the nine focal taxa and others. Bars represent habitat × slope pairings. There was a significant interaction effect between habitat and slope ($\chi^2(2) = 9.01, p = 0.01$). Error bars represent the standard error of total abundance, based on 18 seines per habitat on fringes and 6 seines per habitat on flats; letters indicate the results of post-hoc pairwise comparisons within a given slope, based on a Bonferroni-corrected alpha level of 0.0033

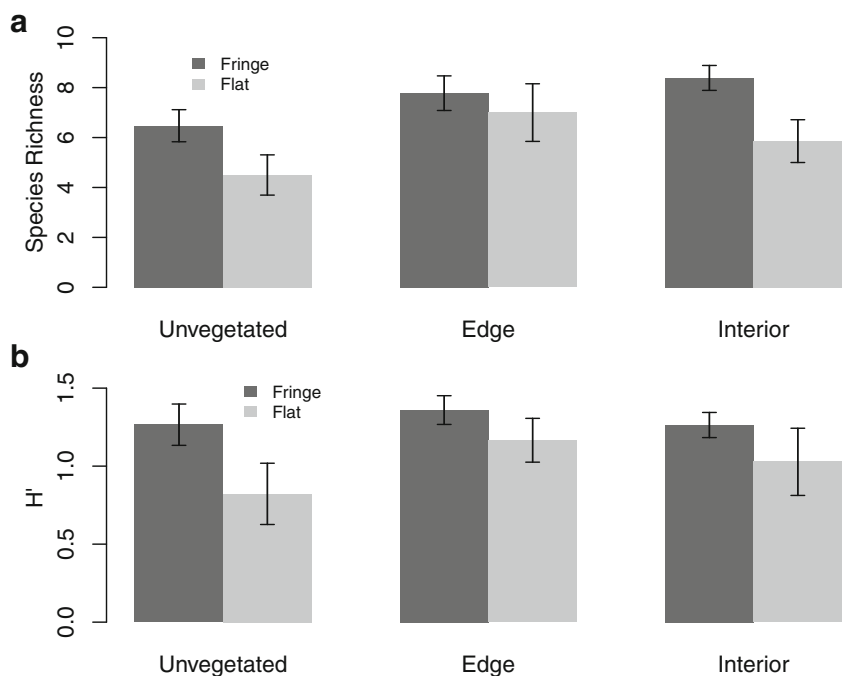


than a continuous flat eelgrass meadow at a coarser scale. Consistent with Horinouchi’s (2007) prediction, three-spined sticklebacks, a pelagic schooling fish and the most abundant species observed in our surveys, showed elevated abundance in fringing eelgrass relative to flats. Other studies have shown no consistent direct effects of fragmentation or patch size on overall nekton abundance (reviewed in Connolly and Hindell 2006; Lefcheck et al. 2016, but see Hensgen et al. 2014). This, however, may be due to highly variable species-specific responses (Horinouchi 2007; Pfeifer et al. 2017; Gross et al. 2018), and driven

by broader-scale patterns in shoreline slope or proximity to other habitats.

Several reasonable connections can be made to link differences between flat and fringe assemblages to the underlying bathymetry of the shoreline, which could result in all three habitats (interior, edge, and unvegetated) on flats having uniformly low abundances (Fig. 4), and diversity and species richness being greater on fringes than flats across all habitats (Fig. 5). These effects may be the result of increased topographic and land-cover habitat heterogeneity (sensu Stein et al. 2014) on fringes relative to flats; the steeper slopes of

Fig. 6 Species richness (a) and Shannon-Weiner diversity (b) of fish and decapods in interior, edge, and unvegetated habitats on fringes and flats in Washington State (USA). Both richness and diversity were higher on fringes than on flats (richness: $\chi^2(1) = 4.62, p = 0.039$; Shannon-Weiner: $\chi^2(1) = 5.45, p = 0.020$). Error bars represent standard error based on 18 seines per habitat on fringes and 6 seines per habitat on flats



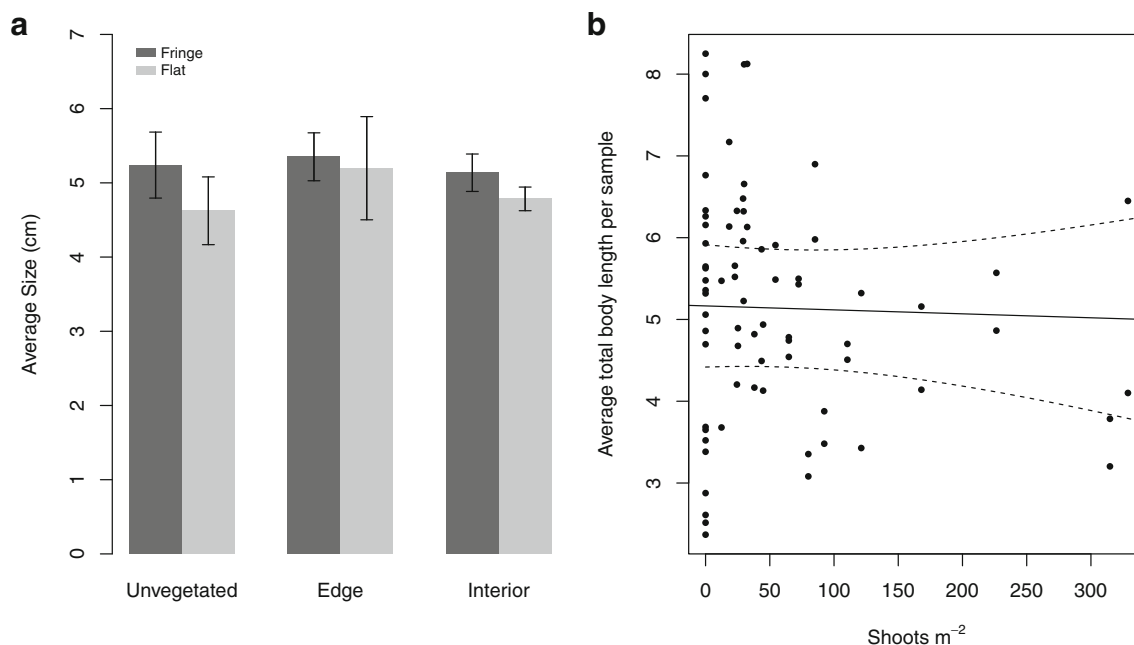


Fig. 7 Average body size of fishes and decapods across interior, edge, and unvegetated habitats on fringes and flats in Washington State (USA). Body size was based on total length for fishes and shrimps and carapace width for crabs. No significant pattern was observed in size distributions across habitats or shoreline slopes (**a**), and body size did not have any significant relationship with local shoot density (**b**). Error bars in **a**

represent the standard error of the mean body size per seine based on measured individuals; dotted lines in **b** represent a 95% confidence interval around the regression line across all subsites. Eighteen seines per habitat were conducted on fringes and six seines per habitat were conducted on flats

fringes may present a steeper gradient in light conditions, food availability, and eelgrass morphology than shallow-sloping flats. Variation in these characteristics in such a small area may have interacted with the presence of eelgrass structure to increase abundance, diversity, and richness on fringing beds by pooling together animals from multiple habitats (Whitfield 2017). Jackson et al. (2006) observed that deep seagrass beds were more species-rich and had more fishes and decapods than shallower seagrass beds, possibly due to decreased predation risk from birds and a refuge from the more extreme physical changes that may occur in shallow seagrass beds over diel and tidal cycles. Species that associate with fringes more than flats may do so because of increased connectivity to nearby subtidal habitats when the tide recedes, sheltering them from desiccation, temperature, and oxygen stress (Holsman et al. 2006; Ferraro and Cole 2010; Good et al. 2010). These habitats are often home to diverse and abundant assemblages of larger adult fishes and invertebrates that may use seagrasses and other shallow estuarine habitats as nursery habitats (Ribeiro et al. 2005; Hughes et al. 2014; Hemery and Henkel 2015), further contributing to assemblage connectivity, a feature often associated with greater numbers and diversity of fish and invertebrate species in structurally complex habitats (Whitfield 2017), and which may override the effects of small-scale structural complexity in increasing diversity and abundance (Olds et al. 2012).

Despite substantial evidence that assemblages differed in taxonomic composition with habitat and shoreline slope, body size did not. We had expected larger individuals to be associated with unvegetated habitat and areas with more sparsely distributed vegetation (MacArthur and Hyndes 2001; Hyndes et al. 2003; Nanjo et al. 2014), but we found no significant patterns in body size across shoot density, habitat, or slope (Fig. 6). This result for body size was unexpected both from first principles, because it seemed likely that dense eelgrass would be less accessible to individuals of larger body size (Hyndes et al. 2003), and also because some taxa that exhibited distinct responses to eelgrass (such as grass shrimps) tended to be much smaller than others (such as staghorn sculpins) that had no response. We are comfortable with our sampling scheme as a sensitive indicator of body size of mesopredators, but also recognize that body size distribution may shift more if a wider variety of functional types were sampled, including epifaunal mesograzers and top predatory fish.

Fringes and flats contained statistically distinct assemblages across all habitats, with sticklebacks, shiner perch, sand shrimp, grass shrimps, and staghorn sculpins contributing the most to differences between the two shoreline slopes. Most of these species and others showed greater abundances on fringes than flats when differences were significant (Table 1). In aggregate, nekton responded most positively to fringing eelgrass, but taxon-specific responses were highly

variable. Overall, the diversity of responses to habitat and shoreline slope may have decoupled community structure from our results for abundance; the habitat-by-slope interaction was evident for total abundance, but multivariate community structure had strictly additive responses to slope and habitat type.

Estuarine nekton communities responded to both the structural complexity provided by eelgrass habitat and variation in patch size and shape due to local bathymetric conditions, but shoreline slope seemed to determine the ultimate effect of eelgrass habitat on nekton abundance and was the only significant driver of richness and diversity. One of the key conclusions of this study is that topographic and seascape heterogeneity as well as habitat connectivity may play key roles in the value of nearshore estuarine habitats for nekton in the Northeast Pacific. The generally positive response of diversity and abundance to naturally patchy seascapes is not necessarily an analog to the consequences of fragmenting seagrass through human activities, but does reinforce the conservation value of fringing eelgrass in Washington State. Of Washington shorelines occupied by eelgrass, a large fraction of linear shoreline consists of fringes (87% in Puget Sound, relative to 13% of flats measured in 2000–2002), but in terms of shallow-water area, eelgrass flats and fringes are more evenly represented (53% fringes and 47% flats), due to the larger width of eelgrass meadows occupying flats (Berry et al. 2003). Future research comparing seagrass use by nekton will benefit from simultaneous consideration of larger-scale factors (amount of edge, connection to adjacent habitats) to determine if and how they interact with smaller-scale structural complexity provided by seagrass shoots. Experiments are ideal for decoupling eelgrass biometrics and fragmentation from underlying bathymetry, as well as other biotic and abiotic factors that may covary with larger spatial scales, to address how and why nekton communities appear to respond to shoreline slope. As seagrass populations are increasingly threatened and fragmented (Short and Wyllie-Echeverria 1996; Orth et al. 2006; Waycott et al. 2009; Short et al. 2011), our understanding of how different levels of habitat complexity impact nekton communities becomes increasingly important.

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References

- Bates D., Maechler M., Bolker B., Walker S. 2015. lme4: linear mixed-effects models using Eigen and S4 (version 1.1–8). *Journal of Statistical Software*.
- Berry, H.D., A.T. Sewell, S. Wyllie-Echeverria, B.R. Reeves, T.F. Mumford Jr., J.R. Skalski, R.C. Zimmerman, and J. Archer. 2003. *Puget Sound Submerged Vegetation Monitoring Project: 2000–2002 monitoring report*. Olympia: Nearshore Habitat Program, Washington State Department of Natural Resources 60pp.
- Blandon, A., and P.S.E.Z. Ermgassen. 2014. Quantitative estimate of commercial fish enhancement by seagrass habitat in southern Australia (vol 141, pg 1, 2014). *Estuarine Coastal and Shelf Science* 151: 370–370. <https://doi.org/10.1016/j.ecss.2014.10.006>.
- Bostrom, C., S.J. Pittman, C. Simenstad, and R.T. Kneib. 2011. Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Marine Ecology Progress Series* 427: 191–217. <https://doi.org/10.3354/meps09051>.
- Canion, C.R., and K.L. Heck. 2009. Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. *Marine Ecology Progress Series* 393: 37–46. <https://doi.org/10.3354/meps08272>.
- Clarke, K.R., and R.M. Warwick. 2001. *Change in marine communities: an approach to statistical analysis and interpretation*. 2nd ed. Plymouth: PRIMER-E 172pp.
- Connolly, R.M., and J.S. Hindell. 2006. Review of nekton patterns and ecological processes in seagrass landscapes. *Estuarine Coastal and Shelf Science* 68 (3-4): 433–444. <https://doi.org/10.1016/j.ecss.2006.01.023>.
- De Angelo, J.A., P.W. Stevens, D.A. Blewett, and T.S. Switzer. 2014. Fish assemblages of shoal- and shoreline-associated seagrass beds in eastern Gulf of Mexico estuaries. *Transactions of the American Fisheries Society* 143 (4): 1037–1048. <https://doi.org/10.1080/00028487.2014.911209>.
- Dowty, P., B. Reeves, H. Berry, S. Wyllie-Echeverria, T. Mumford, A. Sewell, P. Milos, and R. Wright. 2005. *Puget Sound Submerged Vegetation Monitoring Project 2003–2004 Monitoring Report*. Olympia: Washington Department of Natural Resources.
- Ferraro, S.P., and F.A. Cole. 2010. Ecological periodic tables for nekton usage of four US Pacific northwest estuarine habitats. *Canadian Journal of Fisheries and Aquatic Sciences* 67 (12): 1957–1967. <https://doi.org/10.1139/f10-114>.
- Francour, P. 1997. Fish assemblages of *Posidonia oceanica* beds at Port Cros (France, NW Mediterranean): assessment of composition and long-term fluctuations by visual census. *Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I* 18 (2): 157–173. <https://doi.org/10.1111/j.1439-0485.1997.tb00434.x>.
- Good, T.P., J.A. June, M.A. Etnier, and G. Broadhurst. 2010. Derelict fishing nets in Puget Sound and the Northwest Straits: patterns and threats to marine fauna. *Marine Pollution Bulletin* 60 (1): 39–50. <https://doi.org/10.1016/j.marpolbul.2009.09.005>.
- Gorman, A.M., R.S. Gregory, and D.C. Schneider. 2009. Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*). *Journal of Experimental Marine Biology and Ecology* 371 (1): 1–9. <https://doi.org/10.1016/j.jembe.2008.12.008>.
- Gross, C., C. Donoghue, C. Pruitt, A.C. Trimble, and J.L. Ruesink. 2017. Taxonomic and functional assessment of mesopredator diversity across an estuarine habitat mosaic. *Ecosphere* 8 (4): 13. <https://doi.org/10.1002/ecs2.1792>.
- Gross, C., C. Donoghue, C. Pruitt, and J.L. Ruesink. 2018. Habitat use patterns and edge effects across a seagrass-unvegetated ecotone depend on species-specific behaviors and sampling methods. *Marine Ecology Progress Series* 598: 21–33. <https://doi.org/10.3354/meps12609>.

- Heck, K.L., K.W. Able, M.P. Fahay, and C.T. Roman. 1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows—species composition, seasonal abundance patterns and comparison with unvegetated substrates. *Estuaries* 12 (2): 59–65. <https://doi.org/10.2307/1351497>.
- Heithaus, M.R. 2004. Fish communities of subtropical seagrass meadows and associated habitats in Shark Bay, Western Australia. *Bulletin of Marine Science* 75: 79–99.
- Hemery, L.G., and S.K. Henkel. 2015. Patterns of benthic mega-invertebrate habitat associations in the Pacific Northwest continental shelf waters. *Biodiversity and Conservation* 24 (7): 1691–1710. <https://doi.org/10.1007/s10531-015-0887-7>.
- Henderson, C.J., B. Gilby, S.Y. Lee, and T. Stevens. 2017. Contrasting effects of habitat complexity and connectivity on biodiversity in seagrass meadows. *Marine Biology* 164 (5): 9. <https://doi.org/10.1007/s00227-017-3149-2>.
- Hensgen, G.M., G.J. Holt, S.A. Holt, J.A. Williams, and G.W. Stunz. 2014. Landscape pattern influences nekton diversity and abundance in seagrass meadows. *Marine Ecology Progress Series* 507: 139–152. <https://doi.org/10.3354/meps10818>.
- Holmer, M., S. Baden, C. Bostrom, and P.O. Moksnes. 2009. Regional variation in eelgrass (*Zostera marina*) morphology, production and stable sulfur isotopic composition along the Baltic Sea and Skagerrak coasts. *Aquatic Botany* 91 (4): 303–310. <https://doi.org/10.1016/j.aquabot.2009.08.004>.
- Holsman, K.K., P.S. McDonald, and D.A. Armstrong. 2006. Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Marine Ecology Progress Series* 308: 183–195. <https://doi.org/10.3354/meps308183>.
- Hori, M., T. Suzuki, Y. Monthum, T. Srisombat, Y. Tanaka, M. Nakaoka, and H. Mukai. 2009. High seagrass diversity and canopy-height increase associated fish diversity and abundance. *Marine Biology* 156 (7): 1447–1458. <https://doi.org/10.1007/s00227-009-1184-3>.
- Horinouchi, M. 2007. Review of the effects of within-patch scale structural complexity on seagrass fishes. *Journal of Experimental Marine Biology and Ecology* 350 (1-2): 111–129. <https://doi.org/10.1016/j.jembe.2007.06.015>.
- Howe, E.R., and C.A. Simenstad. 2015. Using stable isotopes to discern mechanisms of connectivity in estuarine detritus-based food webs. *Marine Ecology Progress Series* 518: 13–29. <https://doi.org/10.3354/meps11066>.
- Hughes, J.E., L.A. Deegan, J.C. Wyda, M.J. Weaver, and A. Wright. 2002. The effects of eelgrass habitat loss on estuarine fish communities of southern New England. *Estuaries* 25 (2): 235–249. <https://doi.org/10.1007/bf02691311>.
- Hughes, B.B., M.D. Levey, J.A. Brown, M.C. Fountain, A.B. Carlisle, S.Y. Litvin, C.M. Greene, W.N. Heady, and M.G. Gleason. 2014. *Nursery functions of U.S. west coast estuaries: the state of knowledge for juveniles of focal invertebrate and fish species*. Arlington: The Nature Conservancy 168pp.
- Hyndes, G.A., A.J. Kendrick, L.D. MacArthur, and E. Stewart. 2003. Differences in the species- and size-composition of fish assemblages in three distinct seagrass habitats with differing plant and meadow structure. *Marine Biology* 142 (6): 1195–1206. <https://doi.org/10.1007/s00227-003-1010-2>.
- Irlandi, E.A. 1994. Large-scale and small-scale effects of habitat structure on rates of predation—how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98 (2): 176–183. <https://doi.org/10.1007/bf00341470>.
- Jackson, E.L., M.J. Attrill, and M.B. Jones. 2006. Habitat characteristics and spatial arrangement affecting the diversity of fish and decapod assemblages of seagrass (*Zostera marina*) beds around the coast of Jersey (English Channel). *Estuarine Coastal and Shelf Science* 68 (3-4): 421–432. <https://doi.org/10.1016/j.ecss.2006.01.024>.
- Jaxion-Harm, J., and M.R. Speight. 2012. Algal cover in mangroves affects distribution and predation rates by carnivorous fishes. *Journal of Experimental Marine Biology and Ecology* 414: 19–27. <https://doi.org/10.1016/j.jembe.2012.01.007>.
- Keller, M., and S.W. Harris. 1966. Growth of eelgrass in relation to tidal depth. *Journal of Wildlife Management* 30 (2): 280. <https://doi.org/10.2307/3797815>.
- Lefcheck, J.S., S.R. Marion, A.V. Lombana, and R.J. Orth. 2016. Faunal communities are invariant to fragmentation in experimental seagrass landscapes. *PLoS One* 11 (5): 24. <https://doi.org/10.1371/journal.pone.0156550>.
- MacArthur, L.D., and G.A. Hyndes. 2001. Differential use of seagrass assemblages by a suite of odacid species. *Estuarine Coastal and Shelf Science* 52 (1): 79–90. <https://doi.org/10.1006/ecss.2000.0728>.
- MacArthur, R., and J.W. MacArthur. 1961. On bird species-diversity. *Ecology* 42 (3): 594–598. <https://doi.org/10.2307/1932254>.
- Macreadie, Peter I., Hindell, Jeremy S., Keough, Michael J., Jenkins, Gregory P., Connolly, Rod M. 2010. Resource distribution influences positive edge effects in a seagrass fish. *Ecology* 91 (7): 2013–2021.
- Nanjo, K., H. Kohno, Y. Nakamura, M. Horinouchi, and M. Sano. 2014. Effects of mangrove structure on fish distribution patterns and predation risks. *Journal of Experimental Marine Biology and Ecology* 461: 216–225. <https://doi.org/10.1016/j.jembe.2014.08.014>.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R.B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. 2015. *vegan: Community Ecology Package (version 2.2-1)*.
- Olds, A.D., R.M. Connolly, K.A. Pitt, and P.S. Maxwell. 2012. Primacy of seascape connectivity effects in structuring coral reef fish assemblages. *Marine Ecology Progress Series* 462: 191–203. <https://doi.org/10.3354/meps09849>.
- Orth, R.J., T.J.B. Carruthers, W.C. Dennison, C.M. Duarte, J.W. Fourqurean, K.L. Heck Jr., A.R. Hughes, G.A. Kendrick, W.J. Kenworthy, S. Olyarnik, F.T. Short, M. Waycott, and S.L. Williams. 2006. A global crisis for seagrass ecosystems. *Bioscience* 56 (12): 987–996. [https://doi.org/10.1641/0006-3568\(2006\)56\[987:agcfse\]2.0.co;2](https://doi.org/10.1641/0006-3568(2006)56[987:agcfse]2.0.co;2).
- Peterson, C.H. 1991. Intertidal zonation of marine invertebrates in sand and mud. *American Scientist* 79: 236–249.
- Pfeifer, M., V. Lefebvre, C.A. Peres, C. Banks-Leite, O.R. Wearn, C.J. Marsh, S.H.M. Butchart, V. Arroyo-Rodriguez, J. Barlow, A. Cerezo, L. Cisneros, N. D'cruze, D. Faria, A. Hadley, S.M. Harris, B.T. Klingbeil, U. Kormann, L. Lens, G.F. Medina-Rangel, J.C. Morante-Filho, P. Olivier, S.L. Peters, A. Pidgeon, D.B. Ribeiro, C. Scherber, L. Schneider-Maunoury, M. Struebig, N. Urbina-Cardona, J.I. Watling, M.R. Willig, E.M. Wood, and R.M. Ewers. 2017. Creation of forest edges has a global impact on forest vertebrates. *Nature* 551 (7679): 187–191. <https://doi.org/10.1038/nature24457>.
- R Core Team. 2015. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Ribeiro, C., A.J. Almeida, R. Araujo, M. Biscoito, and M. Freitas. 2005. Fish assemblages of Cais do Carvao Bay (Madeira Island) determined by the visual census technique. *Journal of Fish Biology* 67 (6): 1568–1584. <https://doi.org/10.1111/j.1095-8649.2005.00861.x>.
- Short, F.T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23 (01): 17–27.
- Short, F.T., B. Polidoro, S.R. Livingstone, K.E. Carpenter, S. Bandeira, J.S. Bujang, H.P. Calumpang, T.J.B. Carruthers, R.G. Coles, W.C. Dennison, P.L.A. Erfteimeijer, M.D. Fortes, A.S. Freeman, T.G. Jagtap, A.H.M. Kamal, G.A. Kendrick, W.J. Kenworthy, Y.A. La Nafie, I.M. Nasution, R.J. Orth, A. Prathep, J.C. Sanciango, B. Van Tussenbroek, S.G. Vergara, M. Waycott, and J.C. Zieman. 2011. Extinction risk assessment of the world's seagrass species.

- Biological Conservation* 144 (7): 1961–1971. <https://doi.org/10.1016/j.biocon.2011.04.010>.
- Smith, T.M., J.S. Hindell, G.P. Jenkins, and R.M. Connolly. 2008. Edge effects on fish associated with seagrass and sand patches. *Marine Ecology Progress Series* 359: 203–213. <https://doi.org/10.3354/meps07348>.
- Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* 17 (7): 866–880. <https://doi.org/10.1111/ele.12277>.
- Stevens, A.W., and J.R. Lacy. 2012. The influence of wave energy and sediment transport on seagrass distribution. *Estuaries and Coasts* 35 (1): 92–108. <https://doi.org/10.1007/s12237-011-9435-1>.
- Tews, J., U. Brose, V. Grimm, K. Tielborger, M.C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31 (1): 79–92.
- Waycott, M., C.M. Duarte, T.J.B. Carruthers, R.J. Orth, W.C. Dennison, S. Olyarnik, A. Calladine, J.W. Fourqurean, K.L. Heck Jr., A.R. Hughes, G.A. Kendrick, W.J. Kenworthy, F.T. Short, and S.L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 106 (30): 12377–12381. <https://doi.org/10.1073/pnas.0905620106>.
- Whitfield, A.K. 2017. The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Reviews in Fish Biology and Fisheries* 27 (1): 75–110. <https://doi.org/10.1007/s11160-016-9454-x>.
- Yang, S., E.E. Wheat, M.J. Horwith, and J.L. Ruesink. 2013. Relative impacts of natural stressors on life history traits underlying resilience of intertidal eelgrass (*Zostera marina* L.). *Estuaries and Coasts* 36 (5): 1006–1013. <https://doi.org/10.1007/s12237-013-9609-0>.
- Yeager, L.A., D.A. Keller, T.R. Burns, A.S. Pool, and F.J. Fodrie. 2016. Threshold effects of habitat fragmentation on fish diversity at landscape scales. *Ecology* 97 (8): 2157–2166. <https://doi.org/10.1002/ecy.1449>.