

1 **Temporal variation in intertidal habitat use by nekton at seasonal and diel scales**

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9 **Abstract**

10 Structure provided by temperate seagrasses is expected to reduce encounter rates with predators  
11 and therefore benefit small nekton most in summer, when predation is intense and seagrass  
12 reaches peak biomass, and in the day relative to night, when darkness limits visually-oriented  
13 predators regardless of habitat. Based on seines in eelgrass (*Zostera marina*), unvegetated  
14 habitat, and edges in Willapa Bay, Washington, USA, nekton abundances varied across habitats  
15 and on both diel and seasonal time scales, yet only a few time-by-habitat interactions were  
16 observed, in which habitat distinctions were most pronounced at certain times. One explanation  
17 is that four of the six most abundant species disproportionately occupied unvegetated habitat or  
18 were habitat generalists, but our expectations were based on eelgrass-associated taxa.  
19 Multivariate community structure responded separately to season, habitat, and diel period, in  
20 order of importance. Total abundance showed a significant season-by-habitat interaction. A  
21 summer peak in vegetated habitats was largely driven by shiner perch and sticklebacks, two  
22 eelgrass-associated fishes, while unvegetated habitat showed year-round uniform abundances  
23 due to taxa like English sole and sand shrimp with winter and spring peaks, and no strong habitat

24 associations or association with unvegetated habitat, respectively. In a single diel-by-habitat  
25 interaction, shiner perch were eelgrass-associated during the day but not at night. No evidence  
26 emerged of differences in body size across habitats for any species measured, but many taxa  
27 grew seasonally, likely as cohorts migrating out of the estuary. Seasonality was thus the strongest  
28 signal governing patterns of community structure, abundance, and body size across time and  
29 space, while habitat structure and diel period were less important. Our results are largely  
30 consistent with the other studies showing the primacy of seasonality in structuring estuarine  
31 nekton communities, but also show that this pattern is highly dependent on the seasonal  
32 recruitment patterns and habitat associations of abundant nekton.

### 33 **Keywords**

34 Seagrass, seasonality, diel patterns, nekton, habitat use, nursery habitat

### 35 **1. Introduction**

36 In temperate coastal and estuarine systems, macrophytes such as seagrasses and macroalgae  
37 occur as foundation species that create structurally complex three-dimensional habitat structure,  
38 typically leading to increased species richness and abundances in their associated animal  
39 communities (Jenkins & Wheatley 1998, Hughes et al. 2002, Vega Fernandez et al. 2009, Gross  
40 et al. 2018). These macrophytes often exhibit seasonal variation in biomass, with corresponding  
41 changes in animal abundance and assemblage structure (Heck et al. 1989, Shaffer 2000, Siddon  
42 et al. 2008, Xu et al. 2016). In temperate estuaries around the world, the flexible habitat structure  
43 provided by shallow seagrass beds shows seasonal patterns in growth, density, and canopy height  
44 as a result of variations in light, nutrients, or temperature (Lee et al. 2007, Clausen et al. 2014).  
45 Seagrasses have been well-documented to be associated with greater numbers of fishes and  
46 decapods relative to adjacent unvegetated habitats (Heck et al. 1989, Hughes et al. 2002, Ferraro

47 & Cole 2010, Blandon & Ermgassen 2014, Gross et al. 2017), and while seasonal studies of  
48 seagrass nekton communities exist (Heck et al. 1989, Able et al. 2002, Ribeiro et al. 2012, Xu et  
49 al. 2016), less research has been conducted on how the habitat value of seagrass relative to  
50 unvegetated substrate changes on seasonal scales (but see Able et al. 2002, Ribeiro et al. 2012).  
51 Further, the value of seagrass habitat for a given species may change seasonally not as a function  
52 of the seagrass itself, but due to changes in habitat use across its life history (Hughes et al. 2014,  
53 McDevitt-Irwin et al. 2016). On shorter diel time scales, the habitat value of seagrasses may also  
54 change as nighttime darkness eliminates the need for nekton to use seagrass structure as a screen  
55 from visual predators (Gray & Bell 1986, Horinouchi 2007). The simultaneous changes in age-  
56 specific use of nursery habitats, seagrass structure, and visibility on seasonal and diel timescales  
57 raise the question of whether season, diel period, or habitat type is a primary driver of patterns of  
58 estuarine nekton density and community structure, and if the value of vegetated over unvegetated  
59 habitat changes over time.

60         The structurally-complex environments of seagrass beds provide nekton with seasonally-  
61 variable access to resources like epifauna on seagrass blades (Nakaoka et al. 2001, Parker et al.  
62 2001, Carr et al. 2011), or protection from larger predators by impeding movement or vision  
63 (Irlandi 1994, Horinouchi 2007, Canion & Heck 2009). When biomass and structural complexity  
64 decrease seasonally, the benefit of seagrass as a source of food or protection distinct from  
65 unvegetated areas may also decrease, causing abundances in seagrass habitat to decrease and  
66 leading to muted differences in density between the two habitat types (Able et al. 2002, Xu et al.  
67 2016).

68         The beneficial aspects of seagrass structure may also change on shorter diel time scales.  
69 Nekton may leave dense patches at night due to increased seagrass respiration and resultant

70 hypoxia (Horinouchi 2007), or because they are released from predation pressure by visual  
71 predators (Gray & Bell 1986, Horinouchi 2007). Birds are common piscivores in estuarine  
72 systems, are known to forage mostly during the day due to their reliance on visual prey detection  
73 (Safina & Burger 1985, Terörde 2008, Tweedley et al. 2016), and have been shown to drive  
74 trophic cascades by feeding on fishes in seagrass beds (Huang et al. 2015). Reduced risk of avian  
75 predation has been implicated as a major factor contributing to increased abundance of estuarine  
76 fishes in shallow habitats at night relative to daytime (Yeoh et al. 2017). Diel changes in habitat  
77 value may be species- and habitat-specific. A study in southeastern Australia found that while  
78 total abundance varied only by habitat regardless of diel period, overall community structure  
79 differed between day and night in bare sand, but not seagrass, and that glassfish (*Ambassis*  
80 *jacksoniensis*, a small schooling fish) were more abundant in seagrass than bare sand during the  
81 day, but not at night (Gray et al. 1998).

82         Temperate estuaries often experience substantial seasonal turnover in community  
83 structure (Ribeiro et al. 2012, Xu et al. 2016, Castillo-Rivera et al. 2017). For example, juveniles  
84 of many species use seagrass beds and other estuarine habitats as “nursery habitats”, or juvenile  
85 habitats where productivity (density, survival, growth) and movement to adult habitats are  
86 greater per unit area than other juvenile habitats (Beck et al. 2001, McDevitt-Irwin et al. 2016).  
87 Adults of other species may also enter estuaries at certain times of year to breed (so-called  
88 “semi-anadromous” or “semi-catadromous” species; Elliott et al. 2007, Potter et al. 2015) or feed  
89 (e.g., green sturgeons, *Acipenser medirostris*, Moser & Lindley 2007, Borin et al. 2017). As  
90 cohorts increase in body size, they may show reduced dependence on shallow and/or structured  
91 habitats as shelter from gape-limited piscivorous predators before leaving the estuary entirely.  
92 (Paterson & Whitfield 2000, Munsch et al. 2016). On shorter diel or tidal timescales, different

93 species may move between deep channel habitats and shallow flat habitats to avoid predators or  
94 access prey (Holsman et al. 2006, Castillo-Rivera et al. 2017), contributing to observed diel and  
95 tidal differences in community structure in shallow habitats.

96 Our study presents the results of a natural experiment that used the natural seasonal  
97 variation in seagrass biomass and diel variation in visibility to examine how total nekton  
98 abundance and community structure respond to seagrass habitat structure in a temperate  
99 Northeast Pacific estuary on seasonal and diel temporal scales. In addition to total density, we  
100 also measured the abundances and body sizes of six common species that use estuaries as  
101 nursery habitat and are ecologically and economically important (Hughes et al. 2014). Nekton in  
102 this temperate coastal region have been sampled previously in summer, generally during daylight  
103 hours, and occur at higher densities and form distinct assemblages in seagrass relative to  
104 unvegetated mudflats (Gross et al. 2017, 2018). We expected that nekton densities and  
105 assemblages would show the greatest differences across vegetated and unvegetated habitats (1)  
106 in summer when eelgrass aboveground biomass is greatest relative to other seasons (Ruesink et  
107 al. 2010), and (2) in daytime relative to nighttime as species relying on eelgrass as a protective  
108 screen are more obscured to visually-oriented predators (Irlandi 1994, Horinouchi 2007, Canion  
109 & Heck 2009). We were also interested in whether nekton body sizes would differ across  
110 habitats over time, either because movement is more restricted as shoot density increases, or  
111 because growth to a size refuge reduces the risk of predation and the need for eelgrass as cover.

## 112 **2. Methods**

113 *2.1. Study site and sampling regime.* Willapa Bay (46.52°N, 123.99°W) is a macrotidal  
114 estuary in Washington State, USA, formed from the drowned mouths of several major rivers fed  
115 by winter rains, which drive seasonal salinity patterns in the estuary. About half of the bay area

116 consists of intertidal flats (Hickey and Banas 2003), and approximately 41% of these flats  
117 contain native seagrass habitat (eelgrass, *Zostera marina*) (Dumbauld and McCoy 2015). During  
118 2015-2017, water temperatures were highest in July (20°C) and lowest in December and January  
119 (6°C), while salinity peaked in early fall (30 relative to 17 in winter; supplementary methods,  
120 Table S1). Eelgrass canopy height (shoot length) and density were measured twice in summer  
121 and once in fall during the study period when shoots were fully emersed (supplementary  
122 methods), and these characteristics showed little spatiotemporal variability except that samples  
123 from the edge of eelgrass patches generally had shorter, sparser shoots than inside patches (dots  
124 in Fig. 1A, B; Table S1). However, a general pattern in the central part of Willapa Bay is that  
125 canopy height in summer and fall is 3-4 times that of winter, while densities remain more  
126 consistent seasonally (lines in Fig. 1).

127         We sampled nekton seasonally during daylight low tides for two years, specifically in  
128 July and September 2015, January, April, July, September, and December 2016, and March  
129 2017. Sampling typically occurred at three sites, except one site in September 2015 and January  
130 2016, and four sites in April 2016, all located near the middle of the bay's long (~40 km) north-  
131 south axis, where the mean tidal range is 3.1 m (Folger 1972). In September and July of 2015  
132 and 2016, we also sampled during nighttime low tides to examine diel variation in nekton  
133 communities.

134         Sampling for nekton occurred in three habitat types at each site: unvegetated mudflat, the  
135 vegetated interiors of eelgrass beds, and the edge between these two habitats. Nekton samples  
136 were collected with a custom beach seine (1 m tall, 3 mm mesh) around low tide when the water  
137 above our target habitats was between 0.2 and 0.8 m deep. The seine sampled a circular area of  
138 11 m<sup>2</sup> with wings of 6 m. length, which were then pressed together to chase captured nekton into

139 a cod end. Interior and unvegetated seines were each carried out at least 3 m. from an edge, and  
140 edge seines were conducted to sample half inside and half outside of eelgrass. Animals were  
141 counted, identified to the lowest possible taxonomic level (typically species), and released. Of  
142 these, the first 10 individuals of each species encountered in the seine were measured to the  
143 nearest 0.5 cm (total length for fish and shrimp, carapace width for crabs). Typically, two seines  
144 were carried out in each habitat type per site, for a total of 6 seines per site, but fewer were  
145 carried out in September 2015 (two seines each in unvegetated and interior habitats) and January  
146 2016 (four seines in unvegetated habitat, as eelgrass was inaccessible on this low tide).

147       2.2. *Data analysis.* We divided our nekton samples into two groups to separately evaluate  
148 seasonal and diel effects. One group (seasonal seines) included only daytime seines across the  
149 entire sampling period, with analyses exploring season-by-habitat interactions. The other (diel  
150 seines) included daytime and nighttime seines from July and September, considering season as a  
151 random effect to emphasize diel-by-habitat interactions. To describe and visualize community  
152 variation by habitat and time (seasonal or diel), we generated non-metric multidimensional  
153 scaling (NMDS) plots using Bray-Curtis distances. Densities were  $\log(n+1)$ -transformed to  
154 downweight the most common species and allow rarer species to exert more influence on  
155 distance calculation (Clarke & Warwick 2001). A permutational multivariate ANOVA  
156 (PERMANOVA, maximum permutations = 9,999) was carried out on the sample-by-species  
157 density matrix (each seine as a sample) to determine the significance of habitat and temporal  
158 influences on community structure, and quantify the amount of variation explained by each  
159 factor ( $R^2$ ). For seasonal seines, habitat, season, and their interaction were included as fixed  
160 effects; given two years of data at a consistent set of sites, year and site were considered crossed  
161 random effects. For diel seines, habitat, diel period, and their interactions were included as fixed

162 effects. Site, sampling month (July or September), and year (2015-2016 or 2016-2017) were  
163 treated as crossed random effects to ensure that randomizations occurred only within each site  
164 during a given year and sampling month. For both seasonal and diel seines, statistical  
165 significance of predictor variables required subsequent post-hoc tests to determine which groups  
166 were different. As appropriate, we conducted PERMANOVAs on subsets of the data,  
167 specifically three different habitat combinations (unvegetated-edge, unvegetated-interior, and  
168 edge-interior) and six different pairwise combinations of the four seasons. Bonferroni corrections  
169 were applied to adjust  $\alpha$ -levels in these multiple comparisons.

170         Univariate analyses were applied to total abundance per seine and separately to the six  
171 most abundant species found over the two-year sampling period (Table 1, 2): shiner perch  
172 (*Cymatogaster aggregata* Gibbons), three-spined stickleback (*Gasterosteus aculeatus* L.), sand  
173 shrimp (*Crangon* sp.), English sole (*Parophrys vetulus* Girard), Dungeness crab (*Metacarcinus*  
174 *magister* [Dana]), and staghorn sculpin (*Leptocottus armatus* Girard). These species were  
175 analyzed for patterns in both abundance and body size. As with multivariate analyses, the  
176 complete data set was divided into two parts, one (seasonal) containing only daytime seines to  
177 assess seasonality of habitat associations, and another (diel) containing daytime and nighttime  
178 seines to assess diel patterns in habitat associations. For each response variable (total abundance  
179 and body size, and density of the six focal species), we built linear mixed effects models to  
180 evaluate the significance of habitat, time (season or day/night), and interactions as fixed effects,  
181 and included site, year, and sampling month as random effects where appropriate. Total  
182 abundance was log-transformed to conform to a normal distribution. Species-specific abundance  
183 distributions were heavily right-skewed, and would not conform to normality with standard  
184 transformations. We thus incorporated species-specific abundances into generalized linear mixed



185 effects models with a negative binomial error distribution without transformation. We visually  
186 examined other potential distributions, including lognormal and gamma distributions, but  
187 negative binomial provided the best fit. Body sizes were log-transformed where appropriate to  
188 conform to a normal distribution. In certain seasons, some of the six focal taxa were observed  
189 only once in a particular habitat in both years; these seasons were excluded from body size  
190 analyses for the species in question.

191 The significance of fixed effects in all mixed effects models was determined using  
192 likelihood ratio tests to compare models with and without the fixed effect of interest. For  
193 variables showing significant habitat or seasonal differences, in which there were more than two  
194 levels of a factor, post-hoc tests were carried out comparing each pair of habitats, seasons, or  
195 habitat-by-season groups, using Bonferroni-corrected  $\alpha$ -levels. Analyses were conducted using  
196 the lme4 and vegan packages in R v. 3.4.3 (Bates et al. 2015, Oksanen et al. 2015, R Core Team  
197 2017).

198 *2.3. Data availability.* Data are archived at Gross et al. (2018). Data for: Temporal  
199 variation in intertidal habitat use by nekton at seasonal and diel scales [Data set]. Zenodo.  
200 <http://doi.org/10.5281/zenodo.1434463>.

### 201 **3. Results**

202 *3.1. Community structure.* Differences in community structure across habitats did not  
203 change across seasonal or diel timescales (no interaction). In seasonal seines, multivariate  
204 community structure showed significant habitat and seasonal effects (habitat pseudo- $F_{2, 116} = 2.9$ ,  
205  $p = 0.0060$ ; season pseudo- $F_{3, 116} = 37.4$ ,  $p < 0.001$ ; interaction pseudo- $F_{6, 116} = 0.55$ ,  $p = 0.93$ ;  
206 Fig. 2A, B). Season accounted for most of the explained variation in community structure ( $R^2 =$   
207  $0.473$ ) while habitat had an  $R^2$  of  $0.024$ . Nekton differences across habitats were not reduced in

208 any season (no significant season-by-habitat interaction). Based on post-hoc comparisons,  
209 summer was significantly different from fall, winter, and spring; fall and winter assemblages  
210 were significantly different; and spring assemblages were not significantly different from fall and  
211 winter (Table S2). However, given the relatively low  $R^2$  values assigned to season in these post-  
212 hoc comparisons and the relatively high 2D stress value of the NMDS ordination (0.137), distinct  
213 assemblages were often difficult to visualize (Fig. 2A, B). Unvegetated and interior assemblages  
214 were distinct from each other, but edge assemblages were intermediate (Table S2, Fig. S1). In  
215 diel seines, habitat and diel period significantly influenced community structure (habitat pseudo-  
216  $F_{2, 110} = 4.5$ ,  $p < 0.001$ ,  $R^2 = 0.072$ ; diel pseudo- $F_{1, 110} = 5.3$ ,  $p < 0.001$ ,  $R^2 = 0.043$ ; Fig. 2C, D),  
217 but there was no significant interaction between diel period and habitat (pseudo-  $F_{2, 110} = 0.30$ ,  $p$   
218  $= 0.92$ ). Again, because habitat and diel period only explained 7.2% and 4.3% of the variation in  
219 assemblage structure respectively, and because 2D NMDS stress was so high (0.161) distinct  
220 assemblages were difficult to visualize (Fig. 2C, D). Post-hoc tests revealed that assemblages in  
221 unvegetated habitat were significantly different from those on edges and interior eelgrass, but  
222 edge and interior assemblages were not significantly different (Table S3, Fig. S2). 34 total  
223 species were observed across seasonal and diel seines in all habitats over the two-year study  
224 period, totaling 14,932 individuals, of which 79.8% were fishes, 14.2% were shrimps, and 6%  
225 were crabs (Table 1, Table 2).

226 *3.2. Temporal and habitat effects on total nekton abundance.* Abundance did not differ  
227 between day and night in diel seines, but did between habitats ( $\chi^2_2 = 29.4$ ,  $p < 0.001$ ), increasing  
228 from unvegetated into interior habitat. Seasonal abundances showed a significant season-by-  
229 habitat interaction effect ( $\chi^2_6 = 13.0$ ,  $p = 0.043$ , Fig. 3). In spring, fall, and winter, abundance did  
230 not differ among habitats while in summer, assemblages in unvegetated habitats had significantly

231 fewer individuals per seine than edge and interior, which were not significantly different from  
232 each other. Unvegetated habitat showed no change across seasons in nekton abundance, while  
233 abundance in edge and interior habitat was greatest on average in summer, lowest in winter and  
234 spring, and intermediate in fall.

235         3.3. *Species-specific responses to temporal and habitat variation.* The top six most  
236 abundant species were shiner perch (*Cymatogaster aggregata*; 5,337 individuals observed over  
237 the two-year period), three-spined stickleback (*Gasterosteus aculeatus*; 3,858), sand shrimp  
238 (*Crangon* sp.; 1,953), English sole (*Parophrys vetulus*; 1,394), Dungeness crab (*Metacarcinus*  
239 *magister*; 894), and Pacific staghorn sculpin (*Leptocottus armatus*; 672). Together, these six  
240 species made up 94.5% of the total individuals observed over the entire study period (Table 1, 2).

241         Of the six focal species, only two were strongly associated with eelgrass-vegetated  
242 habitats, while others had no strong habitat associations or were associated with unvegetated  
243 habitat. In the seasonal seines, shiner perch and sticklebacks were more abundant in eelgrass than  
244 unvegetated habitat and seasonally most abundant in summer (shiner perch, Fig. 4A) or summer  
245 and fall (sticklebacks, Fig. 4B). Sand shrimp were the only taxon to show a significant season-  
246 by-habitat interaction effect ( $\chi^2_6 = 14.9$ ,  $p = 0.022$ ; Table S5), due to reduced densities in  
247 eelgrass in summer (opposite to our original hypothesis; Fig. 4C). The other three taxa varied in  
248 abundance seasonally but not by habitat, with English sole peaking earlier (spring) than  
249 Dungeness crabs and sculpins (summer and fall). No evidence emerged of differences in body  
250 size across habitats for any of the six major taxa (Fig. S3), but many taxa appeared as cohorts  
251 that grew seasonally, including 180.9% growth in English sole and 83.7% growth in staghorn  
252 sculpins from spring to fall, and 148.1% growth in shiner perch from summer to spring (Fig. 5).

253 Most focal taxa responded only to diel period when daytime and nighttime abundances  
254 were compared across habitats, but the two eelgrass-associated species showed a significant  
255 habitat effect. Edge and interior habitat had significantly more shiner perches than unvegetated  
256 during the day, but at night all habitats were the same (Fig. 6A, Table S6). No other taxon  
257 showed this predicted diel-by-habitat interaction. Sticklebacks responded both to habitat (more in  
258 eelgrass) and diel period (more during the day; Fig. 6B, Table S6), with no significant interaction  
259 effect. The other four taxa only differed by diel period, with Dungeness crab and staghorn  
260 sculpins more abundant during the day (Fig. 6 E, F) and sand shrimp and English sole at night  
261 (Fig. 6C, D).

262 More detailed descriptions of species-specific responses to season, habitat, and diel  
263 period can be found in the supplemental material.

#### 264 **4. Discussion**

265 In our study of how the habitat value of eelgrass relative to unvegetated substrate changes  
266 across seasonal and diel timescales, we found that seasonality was the most important factor  
267 driving patterns of nekton community structure and abundance (Fig. 2-4), with limited evidence  
268 for time-by-habitat interactions. Further, we observed seasonal changes in the body size of six  
269 abundant taxa, but not differences in body size across habitats (Fig. 5, S1). Temporal variation in  
270 nekton using shallow-water environments of estuaries is widely reported on both diel (Gray et al.  
271 1998, Yeoh et al. 2017) and seasonal scales (Able et al. 2002, Ribeiro et al. 2012, Xu et al.  
272 2016), but it is less common to simultaneously evaluate these two temporal scales and whether  
273 temporal variability in nekton is habitat-specific.

274 We found a significant interaction between season and habitat for total nekton  
275 abundance, with interior eelgrass habitat showing the greatest seasonal variation while seasonal

276 patterns in edge and unvegetated habitats were weaker or absent altogether. In contrast, Ribeiro  
277 et al. (2012) found an inverted habitat pattern in a Portuguese lagoon, where abundances peaked  
278 in unvegetated habitat in summer, driven by two common species, but remained uniformly low  
279 throughout the year in seagrass habitat. On a shorter timescale, we observed no diel effect on  
280 abundance across habitats. While we had expected that nighttime darkness and winter seagrass  
281 senescence would lead to muted habitat distinctions among nekton assemblages, we observed no  
282 significant time-by-habitat interaction effects for multivariate community structure on diel or  
283 seasonal scales.

284         When nekton in multiple habitat types have been studied seasonally, a common result is  
285 for seasonality to result in more variation than habitat-specificity (Cote et al. 2013, Able et al.  
286 2002). Sometimes, however, nekton respond to season-by-habitat effects. In some of these cases,  
287 bare habitats show more seasonality in nekton community structure than do structured habitats  
288 (Ribeiro et al. 2012), while in other cases nekton are more seasonally variable in seagrass than  
289 bare (Cote et al. 2013). Season-by-habitat interactions were present in only a few of our response  
290 variables, yet generally in a manner consistent with summer peaks in shoot density and canopy  
291 height of eelgrass (Fig. 1, Ruesink et al. 2010). In summer we observed significantly greater total  
292 nekton abundance in vegetated habitats (edge and interior) than in unvegetated; other seasons  
293 showed statistically more even numbers across habitats, indicating distinct and favorable  
294 conditions for some nekton in vegetated (edge and interior) habitats during the summer. For  
295 instance, the summer peak in vegetated habitats was consistent with shiner perch and stickleback  
296 densities, two pelagic schooling fishes that are known to be strongly eelgrass-associated (Gross  
297 et al. 2017, 2018). In contrast, the year-round uniform abundances in unvegetated habitat were  
298 due to benthic, sand-colored taxa like English sole and sand shrimp, which showed weaker peaks

299 in winter and spring and had no strong habitat associations or were associated with unvegetated  
300 habitat, respectively. Differences in the direction and magnitude of season-by-habitat interactions  
301 may thus reflect the life histories and functional types of taxa using each habitat.

302         Multivariate community structure showed separate, non-interacting effects of season and  
303 habitat in the daytime; instead of communities in different habitats converging in winter and  
304 diverging in summer with changes in habitat structure, habitats had unique communities  
305 associated with each season (Fig. 2A, B). Four of the most abundant taxa (shiner perch,  
306 sticklebacks, Dungeness crabs, and staghorn sculpins) achieved their greatest densities in  
307 summer and fall, creating the summer peak in total abundance. English sole recruited into  
308 shallow habitats earlier than the other highly seasonal taxa, appearing at their highest densities in  
309 spring at small body sizes. Other less-abundant taxa also showed strong seasonal patterns.  
310 Comparatively large numbers of chum salmon smolt (*Oncorhynchus keta* [Walbaum]) were  
311 observed in spring along with juvenile lingcod (*Ophiodon elongatus* Girard) in unvegetated and  
312 interior habitats, respectively, while bay pipefish (*Syngnathus leptorhynchus* Girard) and Pacific  
313 herring (*Clupea pallasii* Valenciennes) were most common in the fall (Table 1). Ribeiro et al.  
314 (2012) found that pipefish were most abundant in seagrass in fall and winter, while small wrasses  
315 were abundant in the same habitat in summer and fall; unvegetated habitat was dominated by  
316 sand smelt (*Atherina presbyter*) in fall, but gobies (*Pomatoschistus microps*) in summer, leading  
317 to separate effects of habitat and season on multivariate community structure. Our results for  
318 community structure and species-specific abundances both suggest that rather than seasonal  
319 variation in structural complexity altering the distribution of a relatively stable pool of species,  
320 seasons are associated with their own unique complement of species in each habitat which may  
321 be migrating between habitats or to and from the bay throughout the year.

322 Estuarine environmental conditions can fluctuate dramatically between diel periods  
323 (Tyler et al. 2009, Morse et al. 2014), which can thereby influence fish distribution and behavior  
324 (Neilson and Perry 1990, Henderson and Fabrizio 2014). Most studies worldwide show greater  
325 abundance (and diversity and richness) at night than during the day in the shallows (Garcia Raso  
326 et al. 2006, Yeoh et al. 2017). Additionally, during the day, species may burrow or shelter in  
327 physical structures (Gray and Bell 1986). In one study examining diel patterns of habitat use,  
328 distinct daytime and nighttime assemblages occurred only in unstructured habitat (Gray et al.  
329 1998). Because we did not detect diel-by-habitat interactions for total nekton abundance or for  
330 multivariate community structure, and total abundance also did not differ overall from day to  
331 night, the mosaic of small (ca. 100 m) patches of interspersed bare and vegetated habitat in the  
332 present study may play a special role in enabling nekton to use shallow water even in daylight.  
333 Nevertheless, from our species-specific tests, we documented several species that respond in  
334 different ways to diel changes. Sand shrimp and English sole were caught at higher densities at  
335 night, but Dungeness crab, sticklebacks, and staghorn sculpins during the day. Thus, diel shifts in  
336 which taxa were present apparently evened out total abundance, while shifting community  
337 composition from day to night. Two of the taxa (Dungeness crab, staghorn sculpin) detected at  
338 higher numbers during the day than night also have diets most likely to include other nekton  
339 (Hughes et al. 2014), which may be consistent with their using visual cues to forage in shallow  
340 water. Our results for diel patterns of intertidal use by Dungeness crabs run counter to those  
341 documented by video techniques and radio-tagging, which showed that crabs move out of  
342 channels onto extensive unvegetated tideflats to forage at night (Holsman et al. 2006). Possibly  
343 this difference is due to the relatively steep bathymetry where fringing eelgrass occurred in our  
344 study, such that these low intertidal habitats were accessible without long-distance movement

345 from channels. Shiner perch were the only taxon to demonstrate a habitat-by-diel interaction,  
346 matching our initial predictions: their distribution was even across habitats at night, when hiding  
347 in eelgrass might provide little value as protection from predation, but they were strongly  
348 eelgrass-associated during the day.

349         Although the spatiotemporal patterns of abundance supported habitat-by-time interactions  
350 for two of our focal taxa (shiner perch and sand shrimp), we found no significant patterns in  
351 nekton body size across habitats (Fig. S3). The most abundant species observed over our two-  
352 year study period, shiner perch, reached peak abundance in summer (Fig. 4A), corresponding to  
353 the peak in seagrass aboveground biomass and their lowest average body size (Fig. 5A). These  
354 fish live in the water column above the sediment among seagrass leaves, relying on their habitat  
355 to conceal themselves from visual predators such as birds and fishes, and we had hypothesized  
356 this type of habitat may be particularly valuable for smaller individuals that are vulnerable to  
357 gape-limited visual predators. In late spring and early summer, shiner perch move into shallow  
358 estuarine waters to give birth to live young, which can then use structurally complex shallow  
359 habitats like eelgrass beds for shelter from predators while adults retreat to deeper channels  
360 (Hughes et al. 2014). However, for shiner perch (and for all other taxa), their habitat association  
361 with eelgrass was not enhanced at the season of their smallest body size, and body size did not  
362 differ significantly by habitat in any season. It thus appears that while certain species may be  
363 associated with particular habitats, these habitat associations are consistent throughout their  
364 period of residency in Willapa Bay, regardless of body size or season. This suggests that body  
365 size may not affect habitat accessibility as strongly as we previously thought for the relatively  
366 small fishes captured in our seines, or that other dimensions (e.g., body width) may be more  
367 important than total length in dictating the accessibility of structurally complex habitats.



368           Habitat association with eelgrass was a trait of just two of six major taxa in this study  
369 (shiner perch and sticklebacks). The predominance of nekton that do not react to structural  
370 complexity in Willapa Bay may help explain why two prior studies found similar nekton  
371 assemblages and densities across low-intertidal habitats in this bay (Hosack et al. 2006,  
372 Dumbauld et al. 2015). Additionally, these prior studies used methods (fyke nets, tows) covering  
373 a much greater spatial area than the custom beach seine in our study. However, our study  
374 coincides with these prior cases in showing a dominant signal of seasonal changes in the  
375 numbers and types of fish and decapods using the estuary (Hosack et al. 2006, Dumbauld et al.  
376 2015).

377           *4.1. Conclusion.* As has been previously identified, temporal variation in nekton using  
378 shallow-water estuarine habitats makes conclusions about habitat value sensitive to when the  
379 sampling takes place, on both seasonal and diel timescales. Because scientists often sample  
380 during the day in summer field seasons, it is worth asking how conclusions about estuarine  
381 habitat use by nekton might shift with evidence from other seasons or at night. Seasonal seines in  
382 summer identified the greatest habitat differences in abundance, i.e. because total abundance  
383 peaked in eelgrass in summer, and for shiner perch, in eelgrass during the day. Our sampling also  
384 identified that some bare-associated taxa (i.e. sand shrimp) were less abundant among the peak  
385 structural complexity observed in summer seagrass, which was not documented in other seasons.  
386 Seasonal sampling was critical to identifying the spatiotemporal axis of greatest variation in  
387 nekton, as well as in capturing ontogenetic shifts in body size for many taxa that reflect seasonal  
388 recruitment and migration events in the estuary and may determine their trophic roles in shallow  
389 water.

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570 **Figures and Tables**571 **Table 1.** Species observed in seasonal seines (daytime seines across seasons and habitats).

572 Values represent total numbers for each species, summed across years, sites, and seine replicates.

Species	Spring	Summer	Fall	Winter	Unvegetated	Edge	Interior	Total
Shiner perch ( <i>Cymatogaster aggregata</i> )	3	4130	73	0	72	1834	2300	4206
Three-spined stickleback ( <i>Gasterosteus aculeatus</i> )	52	1697	855	13	438	876	1303	2617
Sand shrimp ( <i>Crangon</i> sp.)	691	114	179	468	504	356	592	1452
English sole ( <i>Parophrys vetulus</i> )	500	191	127	9	332	199	296	827
Dungeness crab ( <i>Metacarcinus magister</i> )	5	348	217	0	163	238	169	570
Staghorn sculpin ( <i>Leptocottus armatus</i> )	31	212	205	4	139	176	137	452
Grass shrimp (Hippolytidae)	138	5	4	7	53	44	57	154
Arrow goby ( <i>Clevelandia ios</i> )	102	1	20	3	90	14	22	126
Chum salmon ( <i>Oncorhynchus keta</i> )	137	0	0	0	115	4	18	137
Bay pipefish ( <i>Syngnathus leptorhynchus</i> )	19	19	56	1	11	19	65	95
Saddleback gunnel ( <i>Pholis ornata</i> )	6	36	9	1	7	23	22	52
Bay goby ( <i>Lepidogobius lepidus</i> )	0	3	0	0	1	1	1	3
Redtail surfperch ( <i>Amphistichus rhodoterus</i> )	0	8	0	0	0	5	3	8
Starry flounder ( <i>Platichthys stellatus</i> )	4	0	5	0	3	3	3	9
Unidentified flatfish	4	3	0	2	3	3	3	9
Snake prickleback ( <i>Lumpenus sagitta</i> )	5	0	2	0	0	3	4	7
Tubesnout ( <i>Aulorhynchus flavidus</i> )	3	1	0	1	1	3	1	5
Surf smelt ( <i>Hypomesus pretiosus</i> )	1	0	0	3	2	1	1	4
Coho salmon ( <i>Oncorhynchus kisutch</i> )	2	0	1	0	1	0	2	3
Pacific herring ( <i>Clupea pallasii</i> )	0	0	0	6	3	0	3	6
Lingcod ( <i>Ophiodon elongatus</i> )	5	0	0	0	1	1	3	5
Chinook salmon ( <i>Oncorhynchus tshawytscha</i> )	0	3	0	0	0	3	0	3
Arrow Flounder ( <i>Atheresthes stomas</i> )	0	2	0	0	2	0	0	2
Sand sole ( <i>Psettichthys melanostictus</i> )	0	0	3	0	0	0	3	3

Red rock crab ( <i>Cancer productus</i> )	1	0	0	0	0	0	1	1
Buffalo sculpin ( <i>Enophrys bison</i> )	2	0	0	0	0	1	1	2
Plainfin midshipman ( <i>Porichthys notatus</i> )	0	0	1	0	1	0	0	1
Pandalid shrimp (Pandalidae)	1	0	0	0	0	0	1	1
Snailfish (Liparidae)	1	0	0	0	1	0	0	1
Great sculpin ( <i>Myoxocephalus polyacanthocephalus</i> )	0	1	0	0	1	0	0	1
Total	1713	6774	1757	518	1944	3807	5011	10762

573

574 **Table 2.** Species observed in diel seines (summer and fall seines in daytime and nighttime),

575 Values represent total numbers for each species, summed across years, sites, seasons (summer

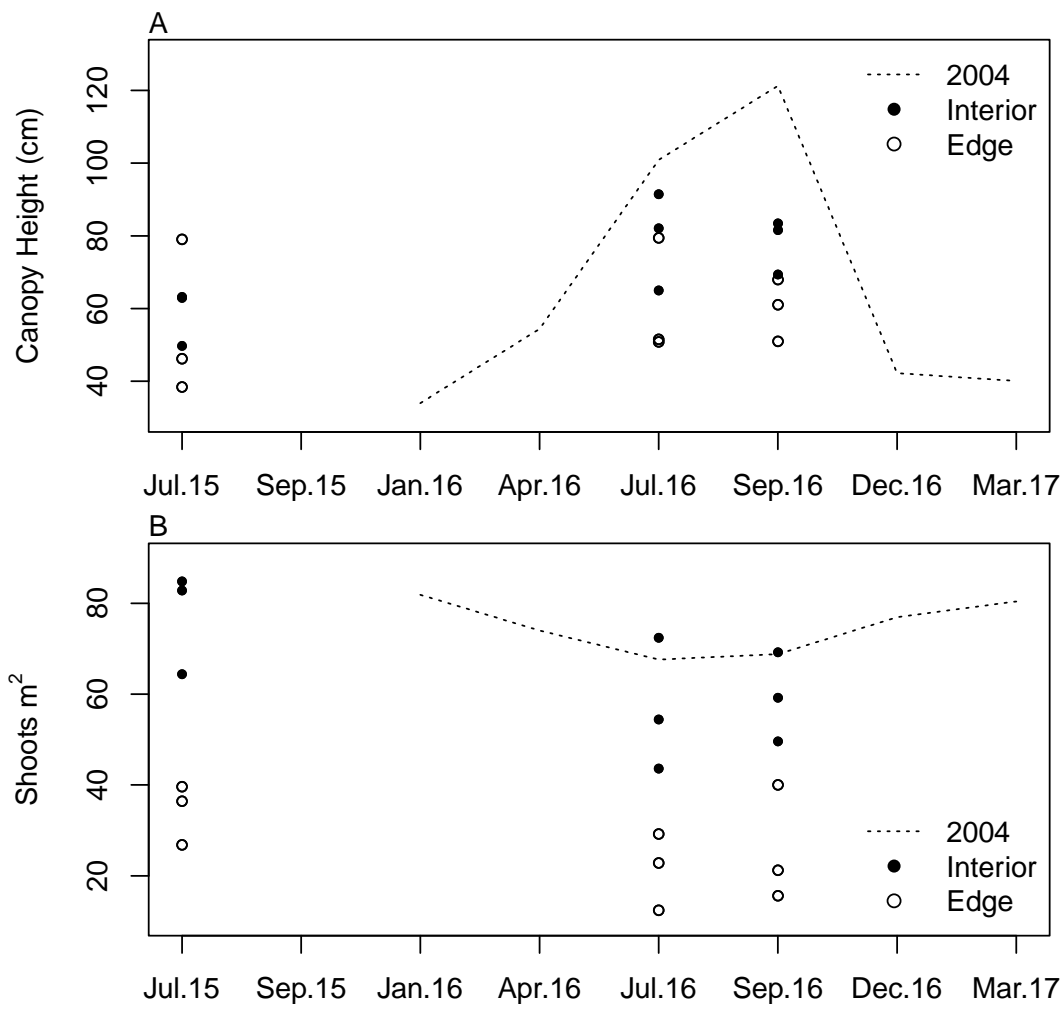
576 and fall only) and seine replicates.

Species	Day	Night	Unvegetated	Edge	Interior	Total
Shiner perch ( <i>Cymatogaster aggregata</i> )	4203	1130	226	2326	2781	5333
Three-spined stickleback ( <i>Gasterosteus aculeatus</i> )	2552	1242	605	1323	1866	3794
Sand shrimp ( <i>Crangon</i> sp.)	293	501	394	156	244	794
English sole ( <i>Parophrys vetulus</i> )	318	567	272	269	344	885
Dungeness crab ( <i>Metacarcinus magister</i> )	565	324	232	357	300	889
Staghorn sculpin ( <i>Leptocottus armatus</i> )	417	220	190	249	198	637
Grass shrimp (Hippolytidae)	9	6	2	6	7	15
Arrow goby ( <i>Clevelandia ios</i> )	21	29	27	9	14	50
Bay pipefish ( <i>Syngnathus leptorhynchus</i> )	75	38	10	22	81	113
Saddleback gunnel ( <i>Pholis ornata</i> )	45	23	12	32	24	68
Bay goby ( <i>Lepidogobius lepidus</i> )	3	60	30	24	9	63
Redtail surfperch ( <i>Amphistichus rhodoterus</i> )	8	6	0	6	8	14
Starry flounder ( <i>Platichthys stellatus</i> )	5	3	1	4	3	8
Unidentified flatfish	3	0	0	0	3	3
Snake prickleback ( <i>Lumpenus sagitta</i> )	2	2	0	3	1	4
Tubesnout	1	3	1	0	3	4

<i>(Aulorhynchus flavidus)</i>						
Surf smelt <i>(Hypomesus pretiosus)</i>	0	4	0	0	4	4
Coho salmon <i>(Oncorhynchus kisutch)</i>	1	4	3	1	1	5
Chinook salmon <i>(Oncorhynchus tshawytscha)</i>	3	0	0	3	0	3
Arrow Flounder <i>(Atheresthes stomas)</i>	2	1	2	1	0	3
Sand sole <i>(Psettichthys melanostictus)</i>	3	0	0	0	3	3
Red rock crab <i>(Cancer productus)</i>	0	1	0	1	0	1
Unidentified sculpin	0	2	1	0	1	2
Plainfin midshipman <i>(Porichthys notatus)</i>	1	1	2	0	0	2
Great sculpin <i>(Myoxocephalus polyacanthocephalus)</i>	1	0	1	0	0	1
Walleye surfperch <i>(Hyperprosopon argenteum)</i>	0	1	0	1	0	1
Asian shrimp <i>(Palaemon macrodactylus)</i>	0	1	0	1	0	1
Kelp crab <i>(Pugettia producta)</i>	0	1	0	1	0	1
Total	8531	4170	2011	4795	5895	12701

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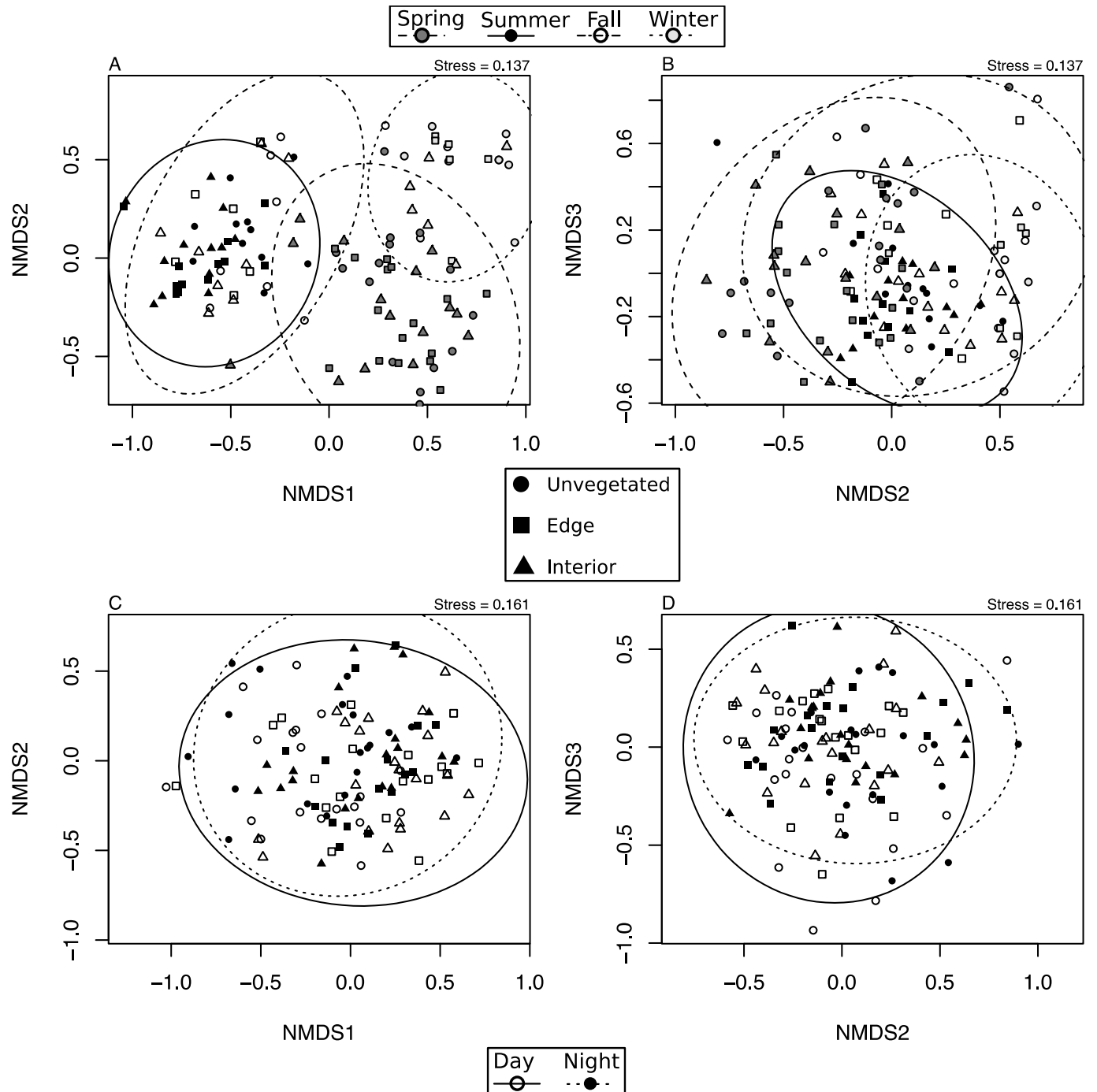
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580 **Figure 1.** Eelgrass (*Zostera marina*) morphometric variables measured concurrently with nekton  
581 sampling, including canopy height (A), and shoot density (B). Points represent eelgrass  
582 morphometric values measured in July 2015 and July and September 2016, while the dotted line  
583 shows values recorded in 2004 (Ruesink et al. 2010).

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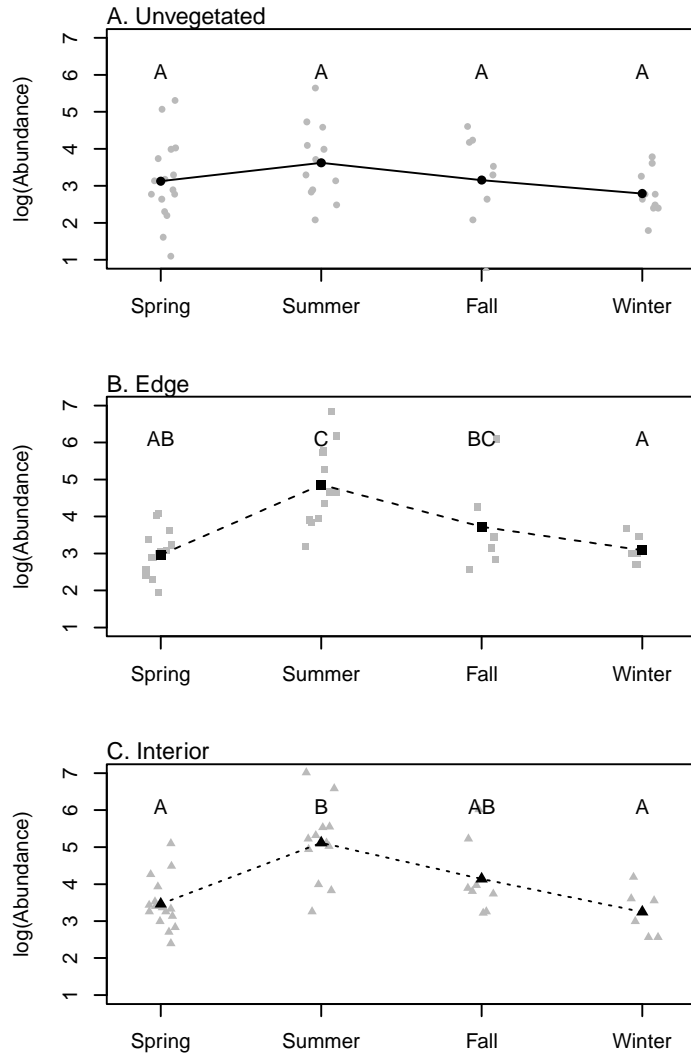


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586 **Figure 2.** Non-metric multidimensional scaling (NMDS) plots of community structure in  
 587 seasonal seines by season and habitat (A, B), and diel seines by diel period and habitat.

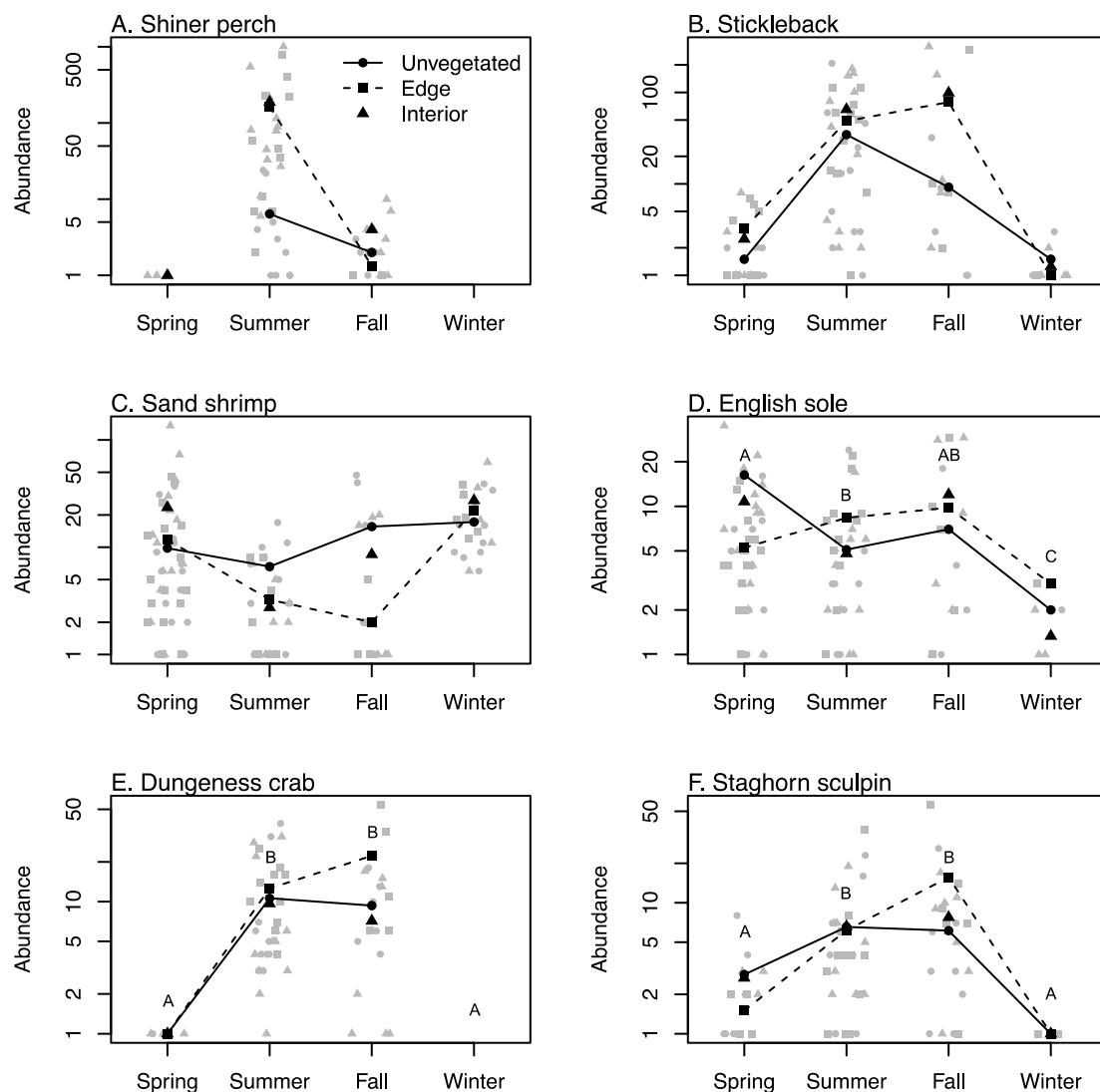
588 Ellipses represent 95% confidence limits around seasons (A, B) and diel period (C, D); A and C

589 show NMDS axes 1 and 2, while B and D show NMDS axes 2 and 3.



590

591 **Figure 3.** Total nekton abundance measured across habitats and seasons. Light-colored points  
 592 represent raw values measured for each sample; dark-colored points and lines represent habitat  
 593 averages. Letters above average points represent results of post-hoc tests. For abundances, post-  
 594 hoc comparisons occurred between seasons within each habitat (significant habitat-by-season  
 595 interaction).



596

597 **Figure 4.** Abundances of the six most abundant nekton species across seasons and habitats.

598 Light-colored points represent raw values of abundance measured for each sample; dark-colored

599 points and lines represent seasonal averages. All abundances are plotted on a log-scaled y-axis;

600 plots shown here include only individuals when present, but analyses included counts of 0

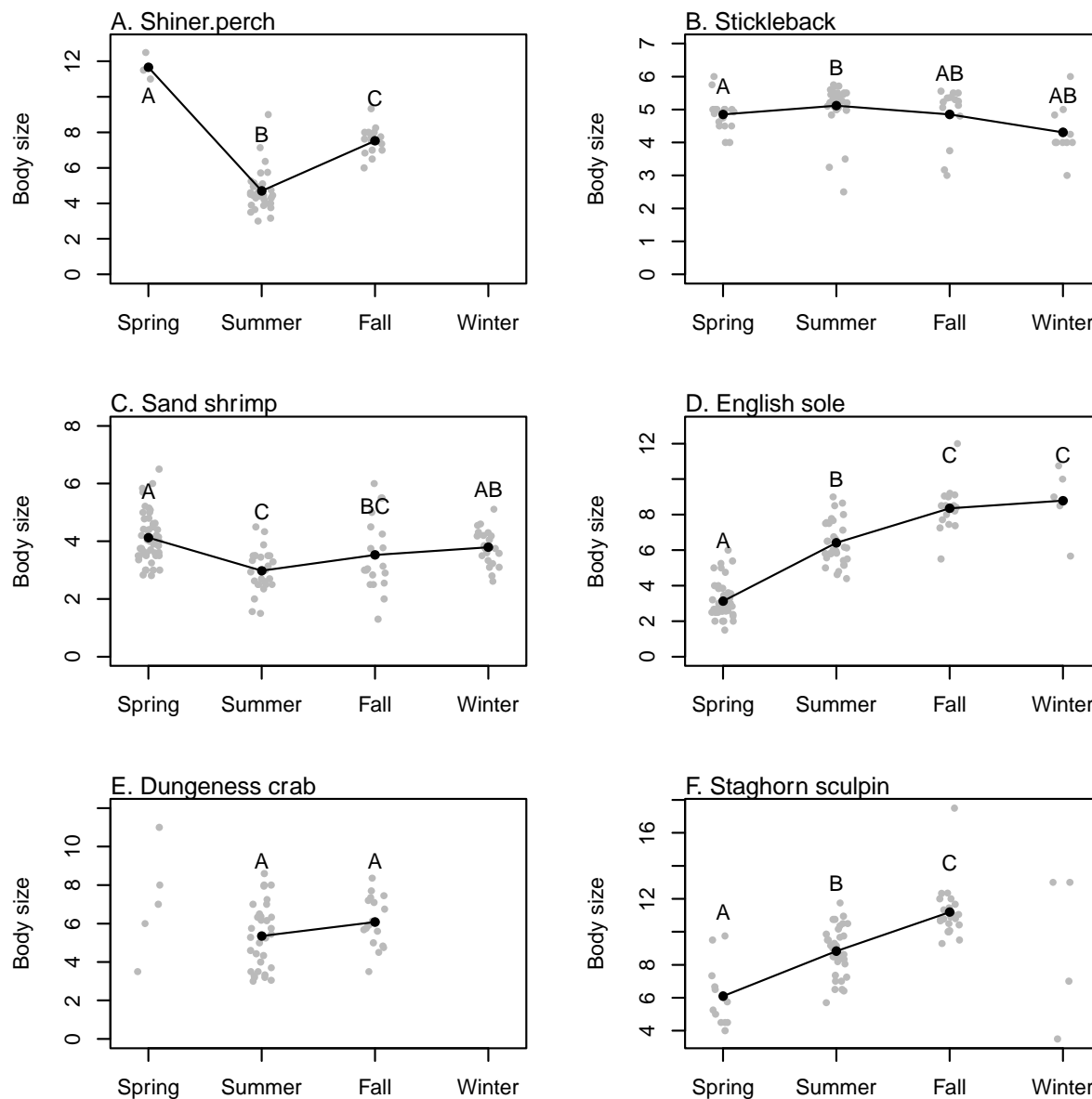
601 individuals for all species. English sole, Dungeness crabs, and staghorn sculpins showed a

602 significant abundance response to season; letters in D-F represent results of post-hoc tests for

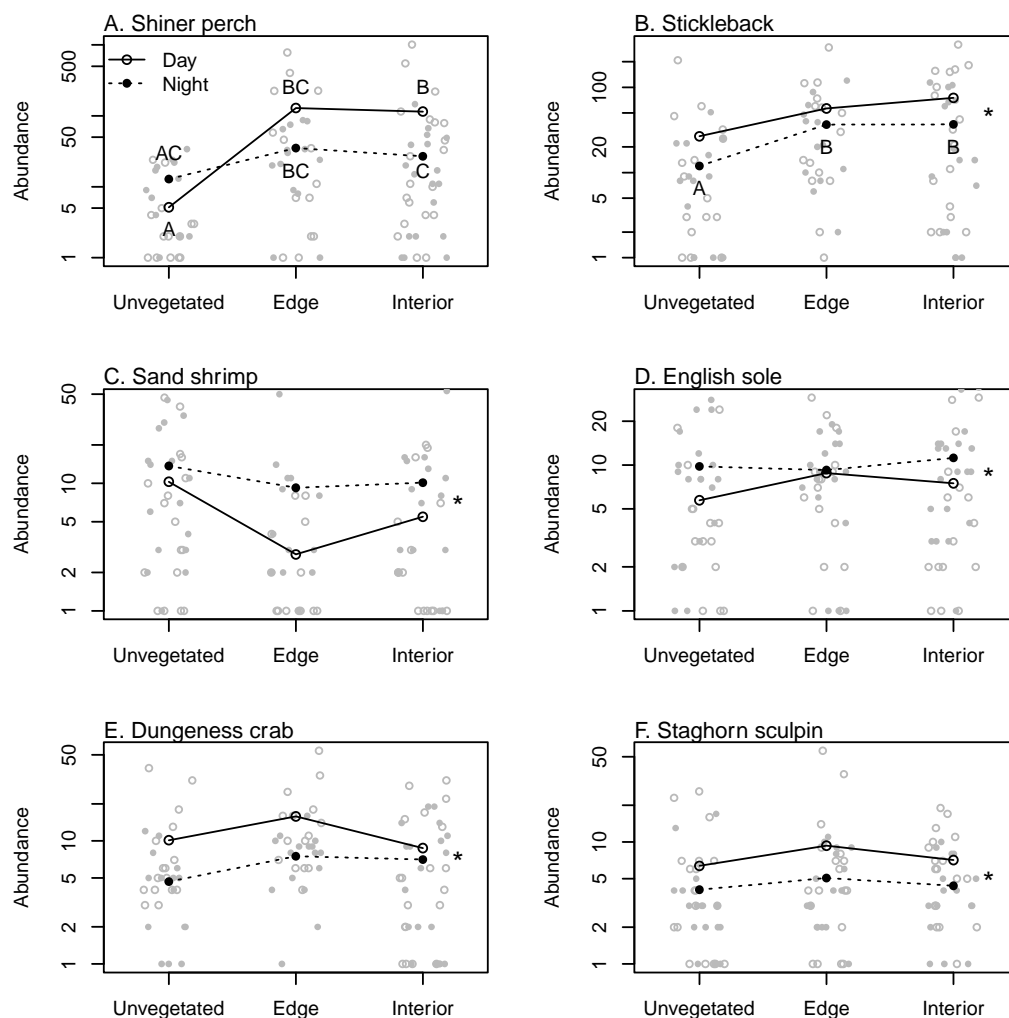
603 these species. Results of post-hoc tests for shiner perch, sticklebacks, and sand shrimp are shown

604 in table S2 and S3.





605  
 606 **Figure 5.** Body sizes of the six most abundant taxa, by season. Light-colored points represent  
 607 raw values of average body size measured in each sample; dark-colored points and lines  
 608 represent seasonal averages, pooled across all habitats. In spring, only five Dungeness crabs were  
 609 found altogether, and in winter, no Dungeness crabs, shiner perch, and only four staghorn  
 610 sculpins were found in total. These seasons were excluded from analysis for those species.  
 611 Letters above points represent results of post-hoc tests.



612  
 613 **Figure 6.** Abundances of the six most abundant nekton species in diel seines across habitats.  
 614 Light-colored points represent raw values of abundance measured for each sample; dark-colored  
 615 points and lines represent averages across habitats. All abundances are plotted on a log-scaled y-  
 616 axis; plots shown here include only individuals when present, but analyses included counts of 0  
 617 individuals for all species. Letters in A and B represent results of post-hoc tests. For shiner  
 618 perch, there was a significant habitat-by-diel interaction; comparisons occurred between all  
 619 habitat-by-diel pairs (Table S4). For sticklebacks, habitat and diel effects were separate;  
 620 comparisons occurred only between habitats. In B-F, stars on the right-hand side of plots  
 621 represent significant differences between nighttime and daytime abundances.

## 622 **Supplemental materials**

### 623 **Methods: environmental variables**

624 At each site in July 2015, July 2016, and September 2016, we sampled eelgrass in 10  
625 0.25 m<sup>2</sup> quadrats along a 50 m transect in edge and interior habitats. We measured shoot density  
626 per quadrat and canopy height by measuring the longest leaf length of five (2015) or 3 (2016)  
627 randomly selected shoots per quadrat. Values were averaged across quadrats to obtain a value  
628 per habitat per site. For sampling periods when we did not measure shoot density and canopy  
629 height, we used values measured in 2004 at one of our study sites (Nahcotta; Ruesink et al.  
630 2010). Water temperature and salinity were recorded hourly by a mooring within 0.5 km of our  
631 sites ([http://nvs.nanoos.org/ShellfishGrowers?action=oiw:fixed\\_platform:PSI\\_Nahcotta:details](http://nvs.nanoos.org/ShellfishGrowers?action=oiw:fixed_platform:PSI_Nahcotta:details)),  
632 and average values during the days of nekton sampling were calculated.

### 633 **Results: Species-specific responses to season, habitat, and diel period.**

634 Sand shrimp daytime abundance varied significantly with a season-by-habitat interaction  
635 effect ( $\chi^2_6 = 14.9$ ,  $p = 0.022$ ; Table S5); in unvegetated habitat, abundance was the same across  
636 all seasons, while in edge and interior habitat, abundances were highest in winter and spring and  
637 lowest in summer and fall (main text Fig. 4C). Average body size changed significantly with  
638 season ( $\chi^2_3 = 27.0$ ,  $p < 0.001$ ), and was greatest in winter and spring and lowest in summer and  
639 fall (main text Fig. 5C), with a 38.6% reduction between spring and summer. In summer and fall  
640 seines, sand shrimp were significantly more abundant at night than during the day ( $\chi^2_1 = 8.0$ ,  $p =$   
641 0.0047; main text Fig. 6C).

642 Shiner perch abundance responded significantly to habitat and season during the day  
643 (habitat  $\chi^2_2 = 19.1$ ,  $p < 0.001$ ; season  $\chi^2_3 = 125.3$ ,  $p < 0.001$ ). Abundance was lowest in  
644 unvegetated and highest in edge and interior habitat, and peaked in summer (main text Fig. 4A);

645 they were absent in winter. Average shiner perch body size changed significantly with the  
646 seasons ( $\chi^2_2 = 64.5$ ,  $p < 0.001$ , main text Fig. 5A), and was greatest in spring and lowest in  
647 summer, changing by 148.1% between these two seasons. Shiner perch abundance also showed a  
648 significant diel-by-habitat interaction in summer and fall ( $\chi^2_2 = 8.5$ ,  $p = 0.014$ ); in daytime  
649 seines, edge and interior habitat had significantly more shiner perches than unvegetated, but at  
650 night all habitats were the same (main text Fig. 6A, Table S6).

651 Stickleback abundance responded significantly to habitat and season during the day  
652 (habitat  $\chi^2_2 = 8.1$ ,  $p = 0.017$ ; season  $\chi^2_3 = 76.2$ ,  $p < 0.001$ ). Abundance was lowest in  
653 unvegetated and highest in eelgrass interiors, and highest in summer and fall and lowest in winter  
654 and spring (main text Fig. 4B). Stickleback average body size changed significantly with the  
655 seasons ( $\chi^2_3 = 12.7$ ,  $p = 0.0055$ ), and was greatest in summer (main text Fig. 5B); average body  
656 size changed by 18.8% between summer and winter. In diel seines, sticklebacks responded to  
657 habitat and diel effects separately (habitat  $\chi^2_2 = 7.9$ ,  $p = 0.019$ ; diel  $\chi^2_1 = 13.2$ ,  $p < 0.001$ ;  
658 interaction  $\chi^2_2 = 0.0013$ ,  $p = 0.99$ ); abundance was lowest in unvegetated and greatest in edge  
659 and interiors, and abundance was higher during the day than at night (main text Fig. 6B, Table  
660 S6).

661 English sole daytime abundance varied significantly by season ( $\chi^2_3 = 46.9$ ,  $p < 0.001$ ),  
662 and was greatest in spring and fall and lowest in winter (main text Fig. 4D). Average body size  
663 varied significantly by season ( $\chi^2_3 = 150.9$ ,  $p < 0.001$ ), and was lowest in spring and greatest in  
664 fall and winter (main text Fig. 5D), with a 180.9% change between spring and winter average  
665 sizes. During summer and fall, English sole were significantly more abundant at night than  
666 during the day ( $\chi^2_1 = 8.6$ ,  $p = 0.0033$ ; main text Fig. 6D).

667 In daytime seines, Dungeness crab abundance varied significantly by season ( $\chi^2_3 = 125.0$ ,  
668  $p < 0.001$ ), with greatest abundances in summer and fall and lowest abundances in spring (main  
669 text Fig. 4E). Dungeness crabs were absent in winter, and in spring only 3 were observed in  
670 interior eelgrass, one on edges, and one in unvegetated habitat over the entire study period; these  
671 seasons were thus excluded from body size analyses, and average body size was not found to  
672 vary between summer and fall. Dungeness crabs were significantly more abundant in daytime  
673 seines than nighttime seines in summer and fall ( $\chi^2_1 = 5.9$ ,  $p = 0.016$ ; main text Fig. 6E).

674 Daytime abundances of staghorn sculpins varied significantly by season ( $\chi^2_3 = 96.2$ ,  $p <$   
675  $0.001$ ), and were greatest in summer and fall and lowest in winter and spring (main text Fig. 4F).  
676 In winter, only one sculpin was observed in interior habitat, two on edges, and one in  
677 unvegetated; winter was thus excluded from body size analyses. Average body size changed  
678 significantly with season ( $\chi^2_2 = 50.6$ ,  $p < 0.001$ ), and was greatest in fall and lowest in spring  
679 (main text Fig. 5F), with an 83.7% change between these seasons. In summer and fall, staghorn  
680 sculpins were significantly more abundant during the day than at night ( $\chi^2_1 = 11.1$ ,  $p < 0.001$ ;  
681 main text Fig. 6F).

682 No species showed significant differences in body size across habitats (Fig. S3).

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690 **Supplemental tables**

691 **Table S1.** Environmental variables across seasons, including temperature and salinity (average  
 692 hourly values one week prior to seining date and standard errors across 24 hours) and canopy  
 693 height and shoot densities along edges and in eelgrass bed interiors.

Season	First Seine Date	Temperature (°C)	Salinity (psu)	Interior canopy height	Edge canopy height	Interior shoot density	Edge shoot density
Summer	3 Jul 2015	19.31 ± 0.062	29.26 ± 0.021	58.59 ± 4.46	54.51 ± 12.46	77.33 ± 6.49	34.27 ± 3.85
Fall	29 Sep 2015	17.37 ± 0.090*	28.00 ± 0.016		85.86 <sup>†</sup>		68.8 <sup>†</sup>
Winter	16 Jan 2016	5.95 ± 0.053	19.60 ± 0.098		33.96 <sup>†</sup>		NA <sup>‡</sup>
Spring	12 Apr 2016	15.16 ± 0.063	21.98 ± 0.016		54.38 <sup>†</sup>		74 <sup>†</sup>
Summer	2 Jul 2016	18.17 ± 0.12	26.50 ± 0.027	79.49 ± 7.75	60.56 ± 9.43	56.8 ± 8.4	21.47 ± 4.90
Fall	31 Aug 2016	18.66 ± 0.61	30.61 ± 0.090	78.13 ± 4.41	59.98 ± 4.93	59.33 ± 5.66	25.6 ± 7.38
Winter	9 Dec 2016	9.66 ± 0.067	18.74 ± 0.32		42.21 <sup>†</sup>		76.9326 <sup>†</sup>
Spring	10 Mar 2017	7.09 ± 0.029	18.34 ± 0.083		40.04 <sup>†</sup>		80.4 <sup>†</sup>

694 \*Temperature data was not available from 9 October to 16 August 2015; we used the average  
 695 temperature from one week prior to 29 September 2016 instead.

696 <sup>†</sup>Eelgrass shoot morphometrics were not measured for these dates; values are taken from Ruesink  
 697 et al. (2010).

698 <sup>‡</sup>Shoot density from Ruesink et al. (2010) was unavailable for this date.

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707 **Table S2.** Results of post-hoc comparisons of multivariate community structure across seasons  
 708 and habitats. Comparisons were made only within the set of three habitats or four seasons,  
 709 because no significant habitat-by-season interaction was observed. Bolded p-values represent  
 710 those significant at the specified Bonferroni-corrected  $\alpha$ -levels, for three habitat comparisons  
 711 and six season comparisons.

Comparison		Pseudo-F	Degrees of freedom	R <sup>2</sup>	Bonferroni $\alpha$	p-value
Habitat					0.01666667	
Unvegetated	Edge	1.3465	1, 84	0.01578		0.2192
Unvegetated	Interior	3.4718	1, 86	0.0388		<b>0.0071</b>
Edge	Interior	0.93386	1, 80	0.01154		0.3614
Season					0.00833333	
Spring	Summer	3.6754	1, 82	0.0429		<b>0.0002</b>
Spring	Fall	3.0243	1, 68	0.04258		0.0719
Spring	Winter	1.6031	1, 68	0.02303		0.435
Summer	Fall	4.7385	1, 56	0.07802		<b>0.0026</b>
Summer	Winter	25.269	1, 56	0.31093		<b>0.0001</b>
Fall	Winter	9.0628	1, 43	0.17748		<b>0.0001</b>

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713 **Table S3.** Results of post-hoc comparisons of multivariate community structure across habitats  
 714 for diel seines. Comparisons were made only within the set of three habitats because no  
 715 significant habitat-by-season interaction was observed. Bolded p-values represent those  
 716 significant at a Bonferroni-corrected  $\alpha$ -level of 0.0167 for three comparisons.

Comparison		Pseudo-F	Degrees of freedom	R <sup>2</sup>	observed p
Unvegetated	Edge	5.1599	1, 74	0.06518	<b>0.0001</b>
Unvegetated	Interior	6.347	1, 78	0.07525	<b>0.0001</b>
Edge	Interior	1.0453	1, 74	0.01393	0.2542

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720 **Table S4.** Results of post-hoc comparisons of shiner perch and stickleback abundances in  
 721 seasonal seines. Abundances of these species responded separately to habitat and season, so post-  
 722 hoc comparisons were made only within the set of three habitats or four seasons (no interaction).  
 723 Bolded p-values represent those significant at the specified Bonferroni-corrected  $\alpha$ -levels, for  
 724 three habitat comparisons and six season comparisons.

Species	Comparison		$\chi^2_1$	Bonferroni $\alpha$	p-value
Shiner perch				0.016666667	
	Unvegetated	Edge	13.53		<b>0.0002348</b>
	Unvegetated	Interior	20.909		<b>4.82E-06</b>
	Edge	Interior	0.0703		0.7909
				0.008333333	
	Spring	Summer	81.618		<b>&lt; 2.2E-16</b>
	Spring	Fall	34.878		<b>3.51E-09</b>
	Spring	Winter	2.4271		0.1193
	Summer	Fall	31.817		<b>1.69E-08</b>
	Summer	Winter	54.004		<b>2.00E-13</b>
	Fall	Winter	29.229		<b>6.43E-08</b>
	Stickleback				0.016666667
Unvegetated		Edge	3.6324		0.05667
Unvegetated		Interior	5.754		<b>0.01645</b>
Edge		Interior	0.4332		0.5104
			0.008333333		
Spring		Summer	76.281		<b>&lt; 2.2E-16</b>
Spring		Fall	249.01		<b>&lt; 2.2E-16</b>
Spring		Winter	3.5233		0.06051
Summer		Fall	3.8806		0.04885
Summer		Winter	57.277		<b>3.79E-14</b>
Fall		Winter	27.517		<b>1.56E-07</b>

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729 **Table S5.** Results of post-hoc comparisons of sand shrimp abundance across season-by-habitat  
 730 pairs, following the result of a significant season-by-habitat interaction effect on sand shrimp  
 731 abundance. Bolded p-values represent those significant at a Bonferroni-corrected  $\alpha$ -level of  
 732 0.00076 for 66 total comparisons.

Comparison		$\chi^2_1$	p-value
Spring, Unvegetated	Spring, Edge	0.3459	0.5564
Spring, Unvegetated	Spring, Interior	3.6447	0.05625
Spring, Unvegetated	Summer, Unvegetated	3.1829	0.07441
Spring, Unvegetated	Summer, Edge	9.3789	0.002195
Spring, Unvegetated	Summer, Interior	12.158	<b>0.0004887</b>
Spring, Unvegetated	Fall, Unvegetated	0.091	0.7629
Spring, Unvegetated	Fall, Edge	8.0863	0.00446
Spring, Unvegetated	Fall, Interior	0.2878	0.5916
Spring, Unvegetated	Winter, Unvegetated	2.8134	0.09348
Spring, Unvegetated	Winter, Edge	5.0671	0.02438
Spring, Unvegetated	Winter, Interior	8.1301	0.004354
Spring, Edge	Spring, Interior	2.357	0.1247
Spring, Edge	Summer, Unvegetated	4.6423	0.03119
Spring, Edge	Summer, Edge	13.418	<b>0.0002493</b>
Spring, Edge	Summer, Interior	14.095	<b>0.0001738</b>
Spring, Edge	Fall, Unvegetated	0.1985	0.656
Spring, Edge	Fall, Edge	9.2403	0.002367
Spring, Edge	Fall, Interior	2.0149	0.1558
Spring, Edge	Winter, Unvegetated	1.09	0.2965
Spring, Edge	Winter, Edge	2.2855	0.1306
Spring, Edge	Winter, Interior	3.3688	0.06644
Spring, Interior	Summer, Unvegetated	10.267	0.001354
Spring, Interior	Summer, Edge	19.319	<b>1.11E-05</b>
Spring, Interior	Summer, Interior	18.682	<b>1.54E-05</b>
Spring, Interior	Fall, Unvegetated	4.3197	0.03767
Spring, Interior	Fall, Edge	11.766	<b>0.0006033</b>
Spring, Interior	Fall, Interior	6.8172	0.009028
Spring, Interior	Winter, Unvegetated	0.8631	0.3529
Spring, Interior	Winter, Edge	0.008	0.9286
Spring, Interior	Winter, Interior	0.041	0.8395
Summer, Unvegetated	Summer, Edge	4.7188	0.02983
Summer, Unvegetated	Summer, Interior	6.3104	0.012

733 Table S5, cont.

Comparison		$\chi^2_1$	p-value
Summer, Unvegetated	Fall, Unvegetated	0.4981	0.4804
Summer, Unvegetated	Fall, Edge	5.0602	0.02448
Summer, Unvegetated	Fall, Interior	0.0691	0.7926
Summer, Unvegetated	Winter, Unvegetated	8.6667	0.003241
Summer, Unvegetated	Winter, Edge	10.401	0.001259
Summer, Unvegetated	Winter, Interior	15.481	<b>8.33E-05</b>
Summer, Edge	Summer, Interior	0.0488	0.8252
Summer, Edge	Fall, Unvegetated	4.4592	0.03471
Summer, Edge	Fall, Edge	0.0113	0.9155
Summer, Edge	Fall, Interior	4.1499	0.04164
Summer, Edge	Winter, Unvegetated	17.623	<b>2.69E-05</b>
Summer, Edge	Winter, Edge	16.881	<b>3.98E-05</b>
Summer, Edge	Winter, Interior	18.763	<b>1.48E-05</b>
Summer, Interior	Fall, Unvegetated	5.6487	0.01747
Summer, Interior	Fall, Edge	0.0668	0.796
Summer, Interior	Fall, Interior	4.2505	0.03924
Summer, Interior	Winter, Unvegetated	21.958	<b>2.79E-06</b>
Summer, Interior	Winter, Edge	21.283	<b>3.96E-06</b>
Summer, Interior	Winter, Interior	20.69	<b>5.40E-06</b>
Fall, Unvegetated	Fall, Edge	1.8075	0.1788
Fall, Unvegetated	Fall, Interior	0.4023	0.5259
Fall, Unvegetated	Winter, Unvegetated	0.3567	0.5503
Fall, Unvegetated	Winter, Edge	1.8698	0.1715
Fall, Unvegetated	Winter, Interior	2.3587	0.1246
Fall, Edge	Fall, Interior	2.0688	0.1503
Fall, Edge	Winter, Unvegetated	18.203	<b>1.99E-05</b>
Fall, Edge	Winter, Edge	20.328	<b>6.52E-06</b>
Fall, Edge	Winter, Interior	19.568	<b>9.71E-06</b>
Fall, Interior	Winter, Unvegetated	3.0466	0.08091
Fall, Interior	Winter, Edge	5.2364	0.02212
Fall, Interior	Winter, Interior	7.189	0.007335
Winter, Unvegetated	Winter, Edge	0.7922	0.3734
Winter, Unvegetated	Winter, Interior	1.9055	0.1675
Winter, Edge	Winter, Interior	0.1872	0.6653

735 **Table S6.** Results of post-hoc comparisons of shiner perch and stickleback abundances in diel  
 736 seines. Shiner perch showed a significant diel-by-habitat interaction, so post-hoc tests compared  
 737 diel-by-habitat paired subsets of the data. Stickleback abundance responded separately to habitat  
 738 and diel period, so post-hoc comparisons were made only within the set of three habitats or day  
 739 vs. night (no interaction); night and day were significantly different ( $\chi^2_1 = 13.2$ ,  $p < 0.001$ ).  
 740 Bolded p-values represent those significant at the specified Bonferroni-corrected  $\alpha$ -levels.

Species	Comparison		$\chi^2_1$	Bonferroni $\alpha$	p-value
Shiner perch				0.003333333	
	Day, Unvegetated	Day, Edge	16.053		<b>6.16e-05</b>
	Day, Unvegetated	Day, Interior	25.768		<b>3.85e-07</b>
	Day, Unvegetated	Night, Unvegetated	3.1506		0.0759
	Day, Unvegetated	Night, Edge	12.209		<b>0.0004755</b>
	Day, Unvegetated	Night, Interior	13.411		<b>0.0002501</b>
	Day, Edge	Day, Interior	0.6851		0.4078
	Day, Edge	Night, Unvegetated	10.456		<b>0.001223</b>
	Day, Edge	Night, Edge	2.3757		0.1232
	Day, Edge	Night, Interior	3.1164		0.07751
	Day, Interior	Night, Unvegetated	16.784		<b>4.19e-05</b>
	Day, Interior	Night, Edge	6.4028		0.01139
	Day, Interior	Night, Interior	8.9236		<b>0.002815</b>
	Night, Unvegetated	Night, Edge	4.7956		0.02853
	Night, Unvegetated	Night, Interior	4.5711		0.03251
	Night, Edge	Night, Interior	0.0621		0.8032
Stickleback				0.016666667	
	Unvegetated	Edge	8.3735		<b>0.003807</b>
	Unvegetated	Interior	7.1705		<b>0.007411</b>
	Edge	Interior	0.1698		0.6803

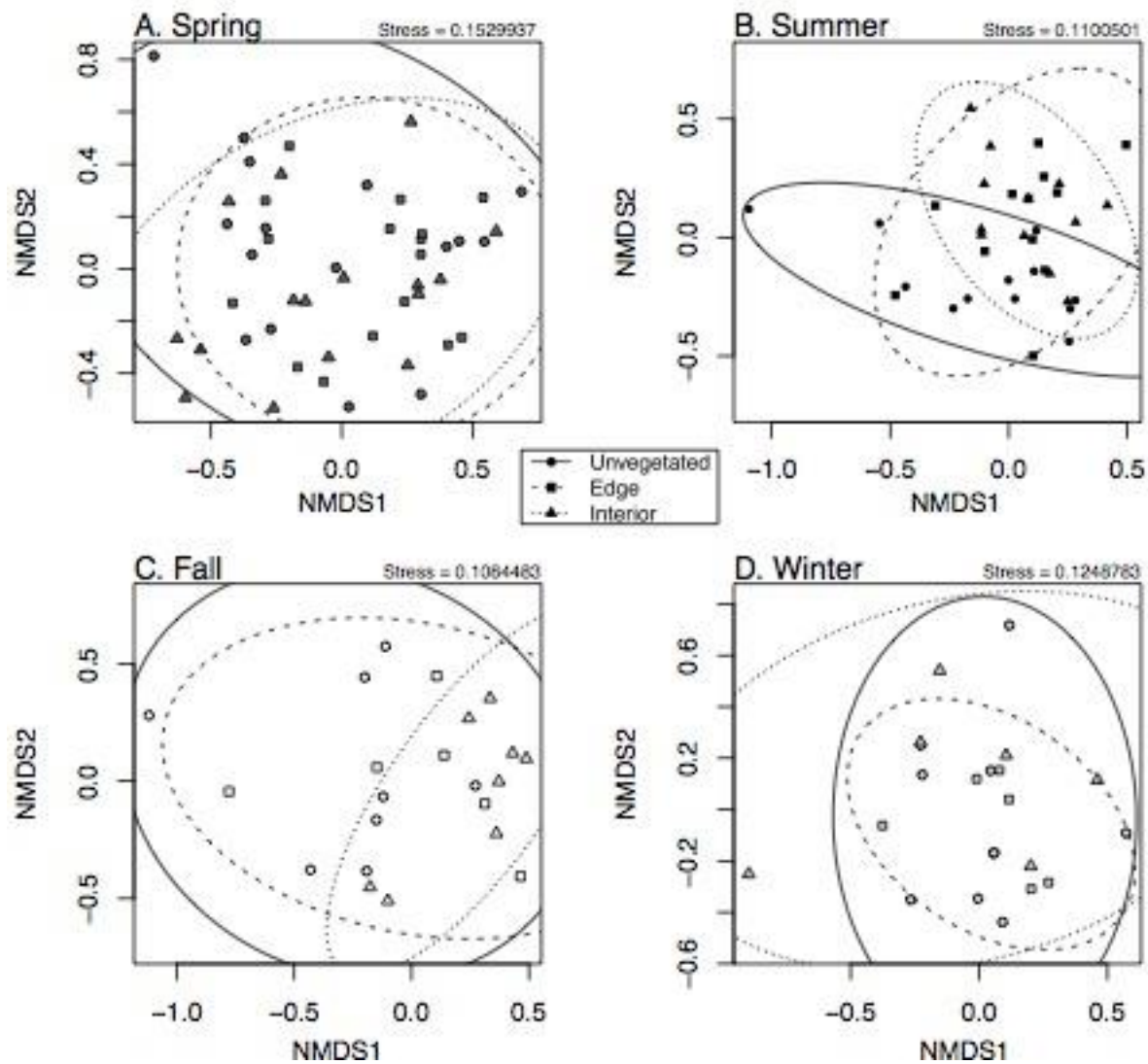
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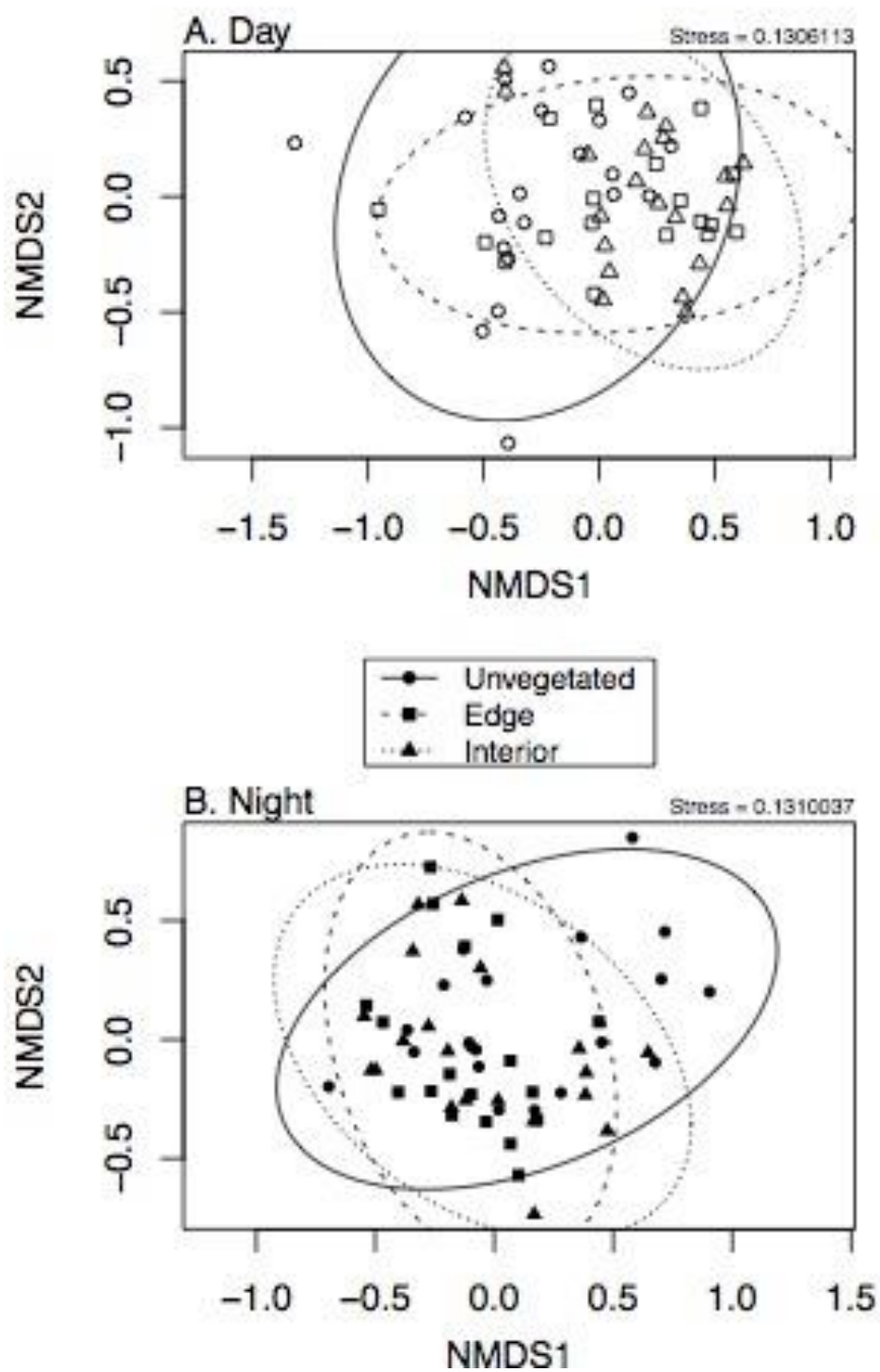
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748 **Figure S1.** Non-metric multidimensional scaling (NMDS) plots of community structure across

749 habitats in seasonal seines. Ellipses represent 95% confidence limits around habitat types.

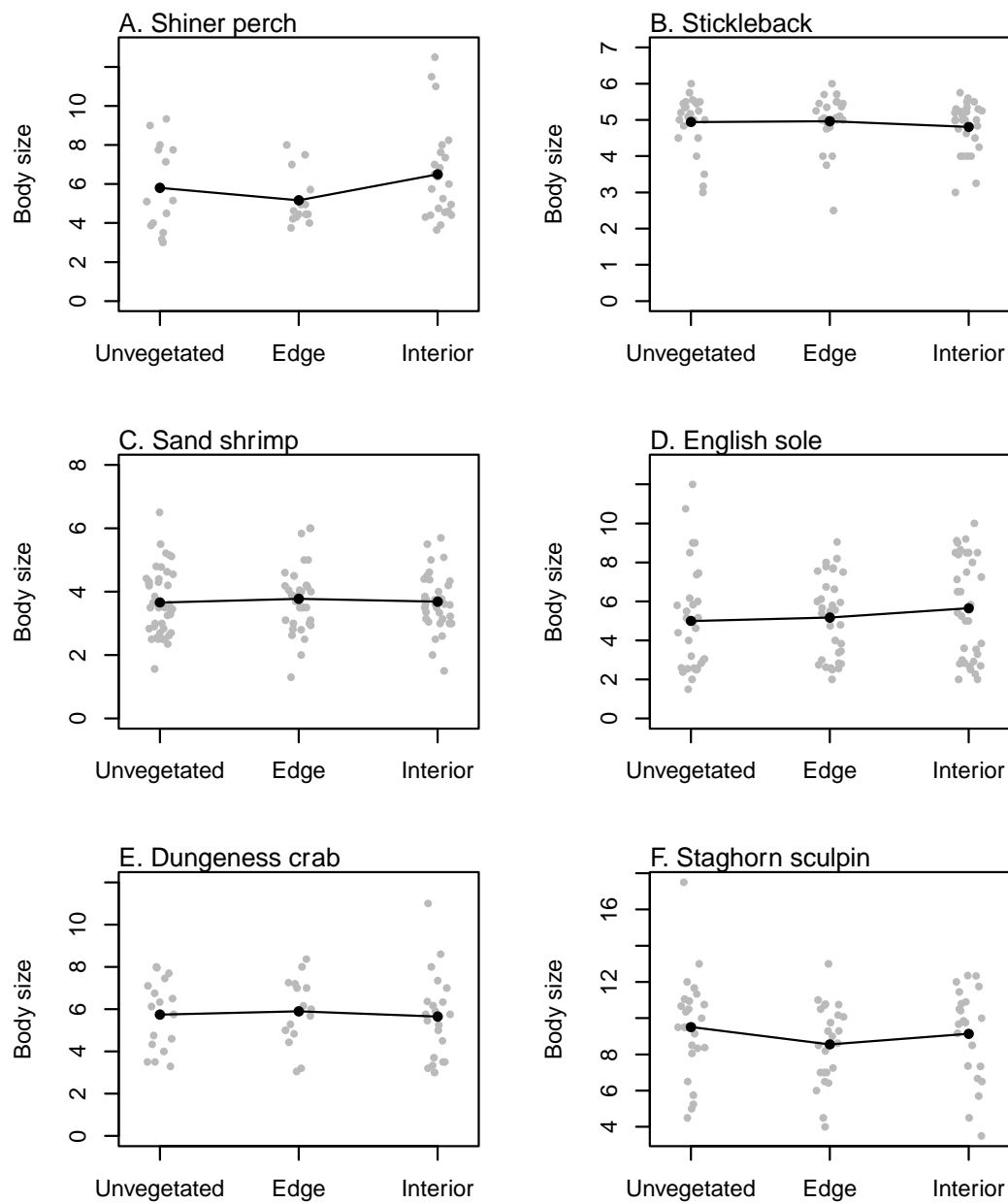


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751 **Figure S2.** Non-metric multidimensional scaling (NMDS) plots of community structure across

752 habitats in diel seines. Ellipses represent 95% confidence limits around habitat types.

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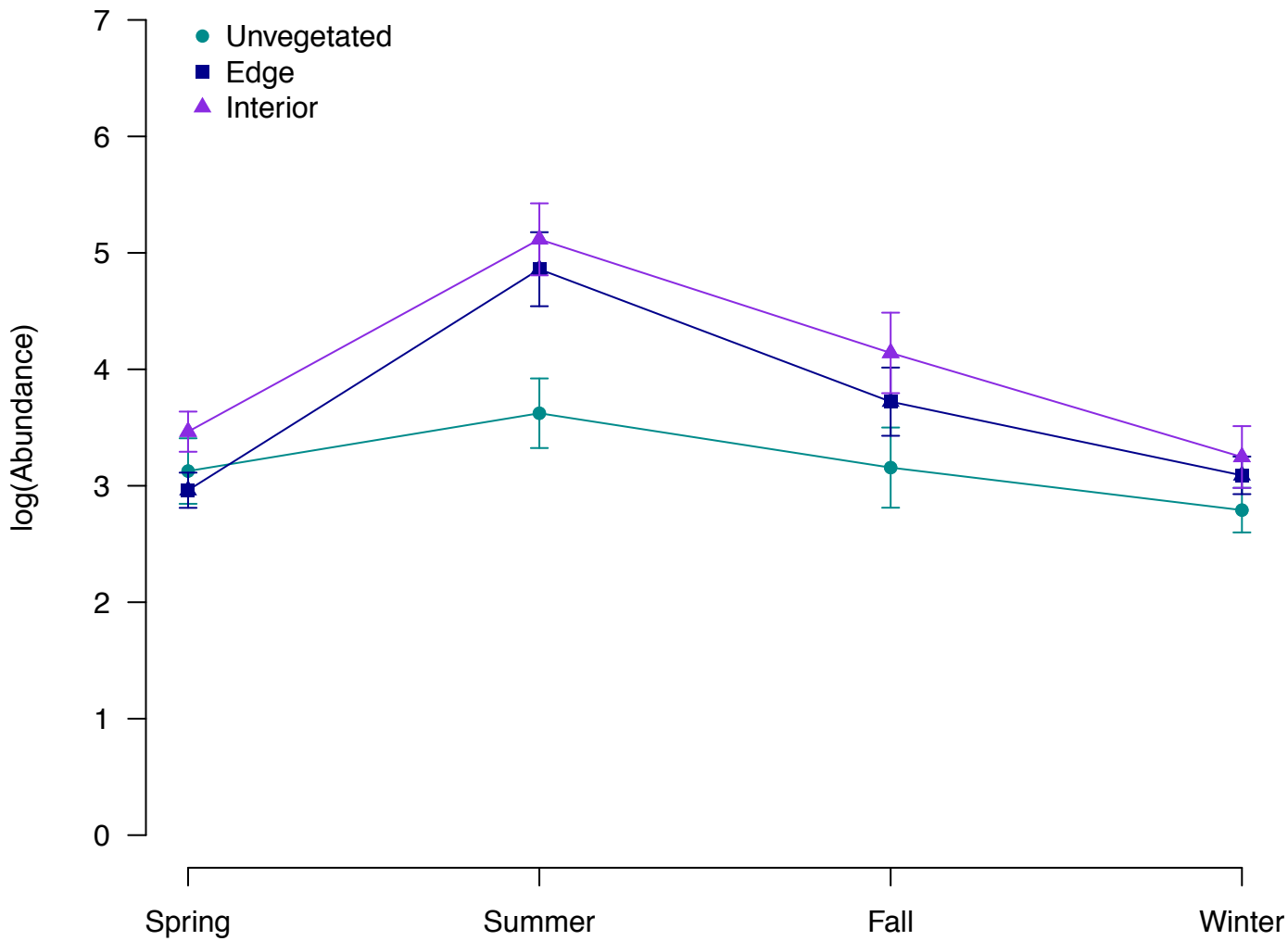


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755 **Figure S3.** Body sizes of the six most abundant taxa across habitats. Light-colored points  
 756 represent raw values of average body size measured in each sample; dark-colored points and  
 757 lines represent habitat averages, pooled across all seasons. No significant effect of habitat on  
 758 body size was observed for any of these species.

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# A. Seasonal Pattern



# B. Diel Pattern

