



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

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ABSTRACT

Structure provided by temperate seagrasses is expected to reduce encounter rates with predators and therefore benefit small nekton most in summer, when predation is intense and seagrass reaches peak biomass, and in the day relative to night, when darkness limits visually-oriented predators regardless of habitat. Based on seines in eelgrass (*Zostera marina*), unvegetated habitat, and edges in Willapa Bay, Washington, USA, nekton abundances varied across habitats and on both diel and seasonal time scales, yet only a few time-by-habitat interactions were observed, in which habitat distinctions were most pronounced at certain times. One explanation is that four of the six most abundant species disproportionately occupied unvegetated habitat or were habitat generalists, but our expectations were based on eelgrass-associated taxa. Multivariate community structure responded separately to season, habitat, and diel period, in order of importance. Total abundance showed a significant season-by-habitat interaction. A summer peak in vegetated habitats was largely driven by shiner perch and sticklebacks, two eelgrass-associated fishes, while unvegetated habitat showed year-round uniform abundances due to taxa like English sole and sand shrimp with winter and spring peaks, and no strong habitat associations or association with unvegetated habitat, respectively. In a single diel-by-habitat interaction, shiner perch were eelgrass-associated during the day but not at night. No evidence emerged of differences in body size across habitats for any species measured, but many taxa grew seasonally, likely as cohorts migrating out of the estuary. Seasonality was thus the strongest signal governing patterns of community structure, abundance, and body size across time and space, while habitat structure and diel period were less important. Our results are largely consistent with the other studies showing the primacy of seasonality in structuring estuarine nekton communities, but also show that this pattern is highly dependent on the seasonal recruitment patterns and habitat associations of abundant nekton.

1. Introduction

In temperate coastal and estuarine systems, macrophytes such as seagrasses and macroalgae occur as foundation species that create structurally complex three-dimensional habitat structure, typically leading to increased species richness and abundances in their associated animal communities (Jenkins and Wheatley, 1998; Hughes et al., 2002; Vega Fernandez et al., 2009; Gross et al., 2018). These macrophytes often exhibit seasonal variation in biomass, with corresponding changes in animal abundance and assemblage structure (Heck et al., 1989; Shaffer, 2000; Siddon et al., 2008; Xu et al., 2016). In temperate estuaries around the world, the flexible habitat structure provided by shallow seagrass beds shows seasonal patterns in growth, density, and canopy height as a result of variations in light, nutrients, or temperature

(Lee et al., 2007; Clausen et al., 2014). Seagrasses have been well-documented to be associated with greater numbers of fishes and decapods relative to adjacent unvegetated habitats (Heck et al., 1989; Hughes et al., 2002; Ferraro and Cole, 2010; Blandon and Ergassen, 2014; Gross et al., 2017), and while seasonal studies of seagrass nekton communities exist (Heck et al., 1989; Able et al., 2002; Ribeiro et al., 2012; Xu et al., 2016), less research has been conducted on how the habitat value of seagrass relative to unvegetated substrate changes on seasonal scales (but see Able et al., 2002; Ribeiro et al., 2012). Further, the value of seagrass habitat for a given species may change seasonally not as a function of the seagrass itself, but due to changes in habitat use across its life history (Hughes et al., 2014; McDevitt-Irwin et al., 2016). On shorter diel time scales, the habitat value of seagrasses may also change as nighttime darkness eliminates the need for nekton to use

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seagrass structure as a screen from visual predators (Gray and Bell, 1986; Horinouchi, 2007). The simultaneous changes in age-specific use of nursery habitats, seagrass structure, and visibility on seasonal and diel timescales raise the question of whether season, diel period, or habitat type is a primary driver of patterns of estuarine nekton density and community structure, and if the value of vegetated over unvegetated habitat changes over time.

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

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

Temperate estuaries often experience substantial seasonal turnover in community structure (Ribeiro et al., 2012; Xu et al., 2016; Castillo-Rivera et al., 2017). For example, juveniles of many species use seagrass beds and other estuarine habitats as “nursery habitats”, or juvenile habitats where productivity (density, survival, growth) and movement to adult habitats are greater per unit area than other juvenile habitats (Beck et al., 2001; McDevitt-Irwin et al., 2016). Adults of other species may also enter estuaries at certain times of year to breed (so-called “semi-anadromous” or “semi-catadromous” species; Elliott et al., 2007, Potter et al., 2015) or feed (e.g., green sturgeons, *Acipenser medirostris*, Moser and Lindley, 2007, Borin et al., 2017). As cohorts increase in body size, they may show reduced dependence on shallow and/or structured habitats as shelter from gape-limited piscivorous predators before leaving the estuary entirely. (Paterson and Whitfield, 2000; Munsch et al., 2016). On shorter diel or tidal timescales, different species may move between deep channel habitats and shallow flat habitats to avoid predators or access prey (Holsman et al., 2006; Castillo-Rivera et al., 2017), contributing to observed diel and tidal differences in community structure in shallow habitats.

Our study presents the results of a natural experiment that used the natural seasonal variation in seagrass biomass and diel variation in visibility to examine how total nekton abundance and community structure respond to seagrass habitat structure in a temperate Northeast Pacific estuary on seasonal and diel temporal scales. In addition to total density, we also measured the abundances and body sizes of six common species that use estuaries as nursery habitat and are ecologically and economically important (Hughes et al., 2014). Nekton in this temperate coastal region have been sampled previously in summer, generally during daylight hours, and occur at higher densities and form distinct assemblages in seagrass relative to unvegetated mudflats (Gross

et al., 2017, 2018). We expected that nekton densities and assemblages would show the greatest differences across vegetated and unvegetated habitats (1) in summer when eelgrass aboveground biomass is greatest relative to other seasons (Ruesink et al., 2010), and (2) in daytime relative to nighttime as species relying on eelgrass as a protective screen are more obscured to visually-oriented predators (Irlandi, 1994; Horinouchi, 2007; Canion and Heck, 2009). We were also interested in whether nekton body sizes would differ across habitats over time, either because movement is more restricted as shoot density increases, or because growth to a size refuge reduces the risk of predation and the need for eelgrass as cover.

2. Methods

2.1. Study site and sampling regime

Willapa Bay (46.52°N, 123.99°W) is a macrotidal estuary in Washington State, USA, formed from the drowned mouths of several major rivers fed by winter rains, which drive seasonal salinity patterns in the estuary. About half of the bay area consists of intertidal flats (Hickey and Banas, 2003), and approximately 41% of these flats contain native seagrass habitat (eelgrass, *Zostera marina*) (Dumbauld and McCoy, 2015). During 2015–2017, water temperatures were highest in July (20 °C) and lowest in December and January (6 °C), while salinity peaked in early fall (30 relative to 17 in winter; supplementary methods, Table S1). Eelgrass canopy height (shoot length) and density were measured twice in summer and once in fall during the study period when shoots were fully emerged (supplementary methods), and these characteristics showed little spatiotemporal variability except that samples from the edge of eelgrass patches generally had shorter, sparser shoots than inside patches (dots in Fig. 1A, B; Table S1). However, a general pattern in the central part of Willapa Bay is that canopy height in summer and fall is 3–4 times that of winter, while densities remain more consistent seasonally (lines in Fig. 1).

We sampled nekton seasonally during daylight low tides for two years, specifically in July and September 2015, January, April, July, September, and December 2016, and March 2017. Sampling typically

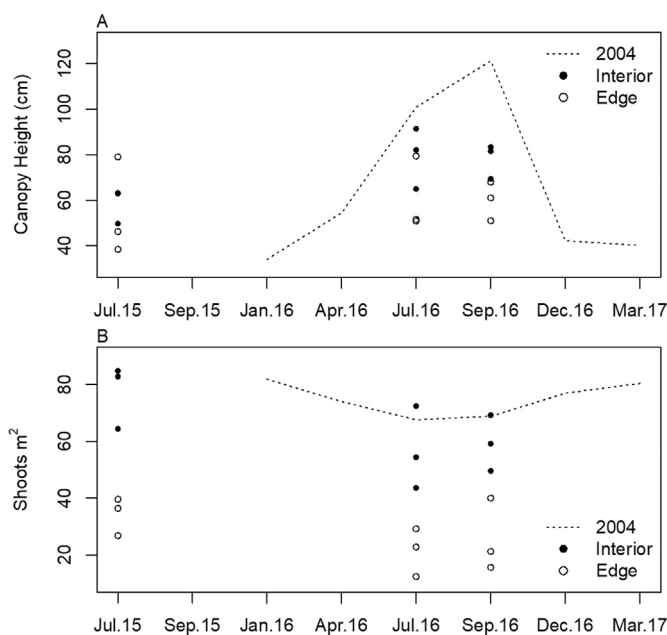


Fig. 1. Eelgrass (*Zostera marina*) morphometric variables measured concurrently with nekton sampling, including canopy height (A), and shoot density (B). Points represent eelgrass morphometric values measured in July 2015 and July and September 2016, while the dotted line shows values recorded in 2004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

occurred at three sites, except one site in September 2015 and January 2016, and four sites in April 2016, all located near the middle of the bay's long (~40 km) north-south axis, where the mean tidal range is 3.1 m (Folger, 1972). In September and July of 2015 and 2016, we also sampled during nighttime low tides to examine diel variation in nekton communities.

Sampling for nekton occurred in three habitat types at each site: unvegetated mudflat, the vegetated interiors of eelgrass beds, and the edge between these two habitats. Nekton samples were collected with a custom beach seine (1 m tall, 3 mm mesh) around low tide when the water above our target habitats was between 0.2 and 0.8 m. deep. The seine sampled a circular area of 11 m² with wings of 6 m. length, which were then pressed together to chase captured nekton into a cod end. Interior and unvegetated seines were each carried out at least 3 m. from an edge, and edge seines were conducted to sample half inside and half outside of eelgrass. Animals were counted, identified to the lowest possible taxonomic level (typically species), and released. Of these, the first 10 individuals of each species encountered in the seine were measured to the nearest 0.5 cm (total length for fish and shrimp, carapace width for crabs). Typically, two seines were carried out in each habitat type per site, for a total of 6 seines per site, but fewer were carried out in September 2015 (two seines each in unvegetated and interior habitats) and January 2016 (four seines in unvegetated habitat, as eelgrass was inaccessible on this low tide).

2.2. Data analysis

We divided our nekton samples into two groups to separately evaluate seasonal and diel effects. One group (seasonal seines) included only daytime seines across the entire sampling period, with analyses exploring season-by-habitat interactions. The other (diel seines) included daytime and nighttime seines from July and September, considering season as a random effect to emphasize diel-by-habitat interactions. To describe and visualize community variation by habitat and time (seasonal or diel), we generated non-metric multidimensional scaling (NMDS) plots using Bray-Curtis distances. Densities were log (n + 1)-transformed to downweight the most common species and allow rarer 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 sample-by-species density matrix (each seine as a sample) to determine the significance of habitat and temporal influences on community structure, and quantify the amount of variation explained by each factor (R²). For seasonal seines, habitat, season, and their interaction were included as fixed effects; given two years of data at a consistent set of sites, year and site were considered crossed random effects. For diel seines, habitat, diel period, and their interactions were included as fixed effects. Site, sampling month (July or September), and year (2015–2016 or 2016–2017) were treated as crossed random effects to ensure that randomizations occurred only within each site during a given year and sampling month. For both seasonal and diel seines, statistical significance of predictor variables required subsequent post-hoc tests to determine which groups were different. As appropriate, we conducted PERMANOVAs on subsets of the data, specifically three different habitat combinations (unvegetated-edge, unvegetated-interior, and edge-interior) and six different pairwise combinations of the four seasons. Bonferroni corrections were applied to adjust α -levels in these multiple comparisons.

Univariate analyses were applied to total abundance per seine and separately to the six most abundant species found over the two-year sampling period (Table 1, Table 2): shiner perch (*Cymatogaster aggregata* Gibbons), three-spined stickleback (*Gasterosteus aculeatus* L.), sand shrimp (*Crangon* sp.), English sole (*Parophrys vetulus* Girard), Dungeness crab (*Metacarcinus magister* [Dana]), and staghorn sculpin (*Leptocottus armatus* Girard). These species were analyzed for patterns in both abundance and body size. As with multivariate analyses, the

complete data set was divided into two parts, one (seasonal) containing only daytime seines to assess seasonality of habitat associations, and another (diel) containing daytime and nighttime seines to assess diel patterns in habitat associations. For each response variable (total abundance and body size, and density of the six focal species), we built linear mixed effects models to evaluate the significance of habitat, time (season or day/night), and interactions as fixed effects, and included site, year, and sampling month as random effects where appropriate. Total abundance was log-transformed to conform to a normal distribution. Species-specific abundance distributions were heavily right-skewed, and would not conform to normality with standard transformations. We thus incorporated species-specific abundances into generalized linear mixed effects models with a negative binomial error distribution without transformation. We visually examined other potential distributions, including lognormal and gamma distributions, but negative binomial provided the best fit. Body sizes were log-transformed where appropriate to conform to a normal distribution. In certain seasons, some of the six focal taxa were observed only once in a particular habitat in both years; these seasons were excluded from body size analyses for the species in question.

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

2.3. Data availability

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

3. Results

3.1. Community structure

Differences in community structure across habitats did not change across seasonal or diel timescales (no interaction). In seasonal seines, multivariate community structure showed significant habitat and seasonal effects (habitat pseudo-F_{2, 116} = 2.9, p = 0.0060; season pseudo-F_{3, 116} = 37.4, p < 0.001; interaction pseudo-F_{6, 116} = 0.55, p = 0.93; Fig. 2A, B). Season accounted for most of the explained variation in community structure (R² = 0.473) while habitat had an R² of 0.024. Nekton differences across habitats were not reduced in any season (no significant season-by-habitat interaction). Based on post-hoc comparisons, summer was significantly different from fall, winter, and spring; fall and winter assemblages were significantly different; and spring assemblages were not significantly different from fall and winter (Table S2). However, given the relatively low R² values assigned to season in these post-hoc comparisons and the relatively high 2D stress value of the NMDS ordination (0.137), distinct assemblages were often difficult to visualize (Fig. 2A, B). Unvegetated and interior assemblages were distinct from each other, but edge assemblages were intermediate (Table S2, Fig. S1). In diel seines, habitat and diel period significantly influenced community structure (habitat pseudo-F_{2, 110} = 4.5, p < 0.001, R² = 0.072; diel pseudo-F_{1, 110} = 5.3, p < 0.001, R² = 0.043; Fig. 2C, D), but there was no significant interaction between diel period and habitat (pseudo-F_{2, 110} = 0.30, p = 0.92). Again, because habitat and diel period only explained 7.2% and 4.3% of the variation in assemblage structure respectively, and because 2D NMDS stress was so high (0.161) distinct assemblages were difficult to visualize (Fig. 2C, D). Post-hoc tests revealed that assemblages in

Table 1

Species observed in seasonal seines (daytime seines across seasons and habitats). 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>Clevalandia 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	10,762

Table 2

Species observed in diel seines (summer and fall seines in daytime and nighttime), Values represent total numbers for each species, summed across years, sites, seasons (summer 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>Clevalandia 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 (<i>Aulorhynchus flavidus</i>)	1	3	1	0	3	4
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	12,701

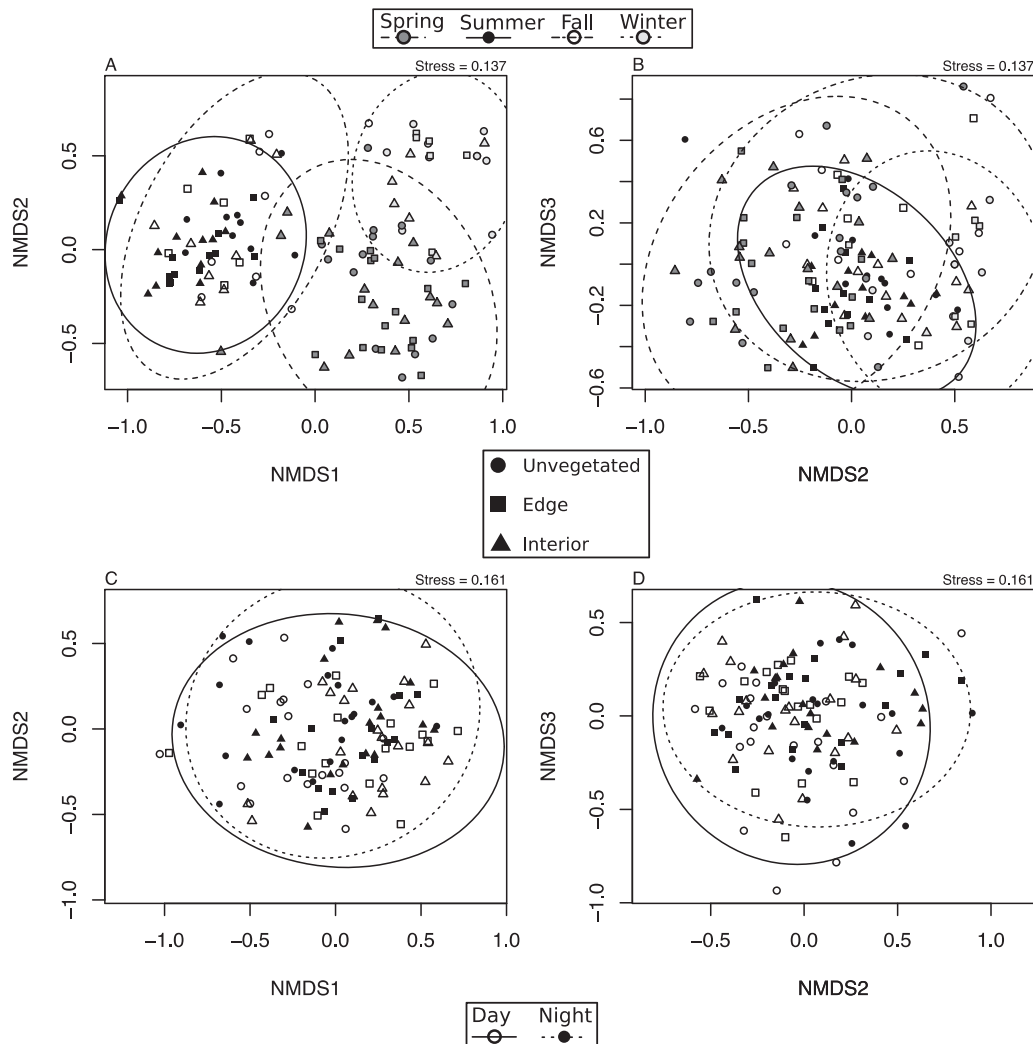


Fig. 2. Non-metric multidimensional scaling (NMDS) plots of community structure in seasonal seines by season and habitat (A, B), and diel seines by diel period and habitat (C, D). Ellipses represent 95% confidence limits around seasons (A, B) and diel period (C, D); A and C show NMDS axes 1 and 2, while B and D show NMDS axes 2 and 3.

unvegetated habitat were significantly different from those on edges and interior eelgrass, but edge and interior assemblages were not significantly different (Table S3, Fig. S2). 34 total species were observed across seasonal and diel seines in all habitats over the two-year study period, totaling 14,932 individuals, of which 79.8% were fishes, 14.2% were shrimps, and 6% were crabs (Table 1, Table 2).

3.2. Temporal and habitat effects on total nekton abundance

Abundance did not differ between day and night in diel seines, but did between habitats ($\chi^2_2 = 29.4$, $p < 0.001$), increasing from unvegetated into interior habitat. Seasonal abundances showed a significant season-by-habitat interaction effect ($\chi^2_6 = 13.0$, $p = 0.043$, Fig. 3). In spring, fall, and winter, abundance did not differ among habitats while in summer, assemblages in unvegetated habitats had significantly fewer individuals per seine than edge and interior, which were not significantly different from each other. Unvegetated habitat showed no change across seasons in nekton abundance, while abundance in edge and interior habitat was greatest on average in summer, lowest in winter and spring, and intermediate in fall.

3.3. Species-specific responses to temporal and habitat variation

The top six most abundant species were shiner perch (*Cymatogaster aggregata*; 5337 individuals observed over the two-year period), three-spined stickleback (*Gasterosteus aculeatus*; 3858), sand shrimp (*Crangon* sp.; 1953), English sole (*Parophrys vetulus*; 1394), Dungeness crab (*Metacarcinus magister*; 894), and Pacific staghorn sculpin (*Leptocottus armatus*; 672). Together, these six species made up 94.5% of the total individuals observed over the entire study period (Table 1, Table 2).

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

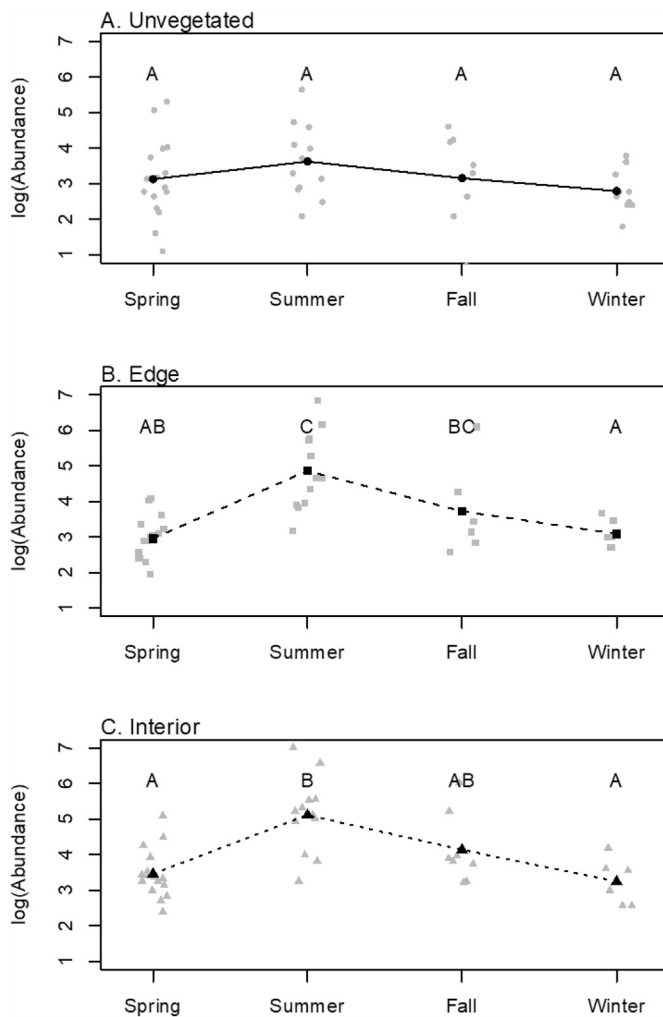


Fig. 3. Total nekton abundance measured across habitats and seasons. Light-colored points represent raw values measured for each sample; dark-colored points and lines represent habitat averages. Letters above average points represent results of post-hoc tests. For abundances, post-hoc comparisons occurred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

growth in English sole and 83.7% growth in staghorn sculpins from spring to fall, and 148.1% growth in shiner perch from summer to spring (Fig. 5).

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

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

4. Discussion

In our study of how the habitat value of eelgrass relative to unvegetated substrate changes across seasonal and diel timescales, we found that seasonality was the most important factor driving patterns of

nekton community structure and abundance (Fig. 2, Fig. 3, Fig. 4), with limited evidence for time-by-habitat interactions. Further, we observed seasonal changes in the body size of six abundant taxa, but not differences in body size across habitats (Fig. 5, S1). Temporal variation in nekton using shallow-water environments of estuaries is widely reported on both diel (Gray et al., 1998; Yeoh et al., 2017) and seasonal scales (Able et al., 2002; Ribeiro et al., 2012; Xu et al., 2016), but it is less common to simultaneously evaluate these two temporal scales and whether temporal variability in nekton is habitat-specific.

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

When nekton in multiple habitat types have been studied seasonally, a common result is for seasonality to result in more variation than habitat-specificity (Able et al., 2002; Cote et al., 2013). Sometimes, however, nekton respond to season-by-habitat effects. In some of these cases, bare habitats show more seasonality in nekton community structure than do structured habitats (Ribeiro et al., 2012), while in other cases nekton are more seasonally variable in seagrass than bare (Cote et al., 2013). Season-by-habitat interactions were present in only a few of our response variables, yet generally in a manner consistent with summer peaks in shoot density and canopy height of eelgrass (Fig. 1, Ruesink et al., 2010). In summer we observed significantly greater total nekton abundance in vegetated habitats (edge and interior) than in unvegetated; other seasons showed statistically more even numbers across habitats, indicating distinct and favorable conditions for some nekton in vegetated (edge and interior) habitats during the summer. For instance, the summer peak in vegetated habitats was consistent with shiner perch and stickleback densities, two pelagic schooling fishes that are known to be strongly eelgrass-associated (Gross et al., 2017, 2018). In contrast, the year-round uniform abundances in unvegetated habitat were due to benthic, sand-colored taxa like English sole and sand shrimp, which showed weaker peaks in winter and spring and had no strong habitat associations or were associated with unvegetated habitat, respectively. Differences in the direction and magnitude of season-by-habitat interactions may thus reflect the life histories and functional types of taxa using each habitat.

Multivariate community structure showed separate, non-interacting effects of season and habitat in the daytime; instead of communities in different habitats converging in winter and diverging in summer with changes in habitat structure, habitats had unique communities associated with each season (Fig. 2A, B). Four of the most abundant taxa (shiner perch, sticklebacks, Dungeness crabs, and staghorn sculpins) achieved their greatest densities in summer and fall, creating the summer peak in total abundance. English sole recruited into shallow habitats earlier than the other highly seasonal taxa, appearing at their highest densities in spring at small body sizes. Other less-abundant taxa also showed strong seasonal patterns. Comparatively large numbers of chum salmon smolt (*Oncorhynchus keta* [Walbaum]) were observed in spring along with juvenile lingcod (*Ophiodon elongatus* Girard) in unvegetated and interior habitats, respectively, while bay pipefish (*Syngnathus leptorhynchus* Girard) and Pacific herring (*Clupea pallasii* Valenciennes) were most common in the fall (Table 1). Ribeiro et al. (2012) found that pipefish were most abundant in seagrass in fall and winter, while small wrasses were abundant in the same habitat in summer and fall; unvegetated habitat was dominated by sand smelt

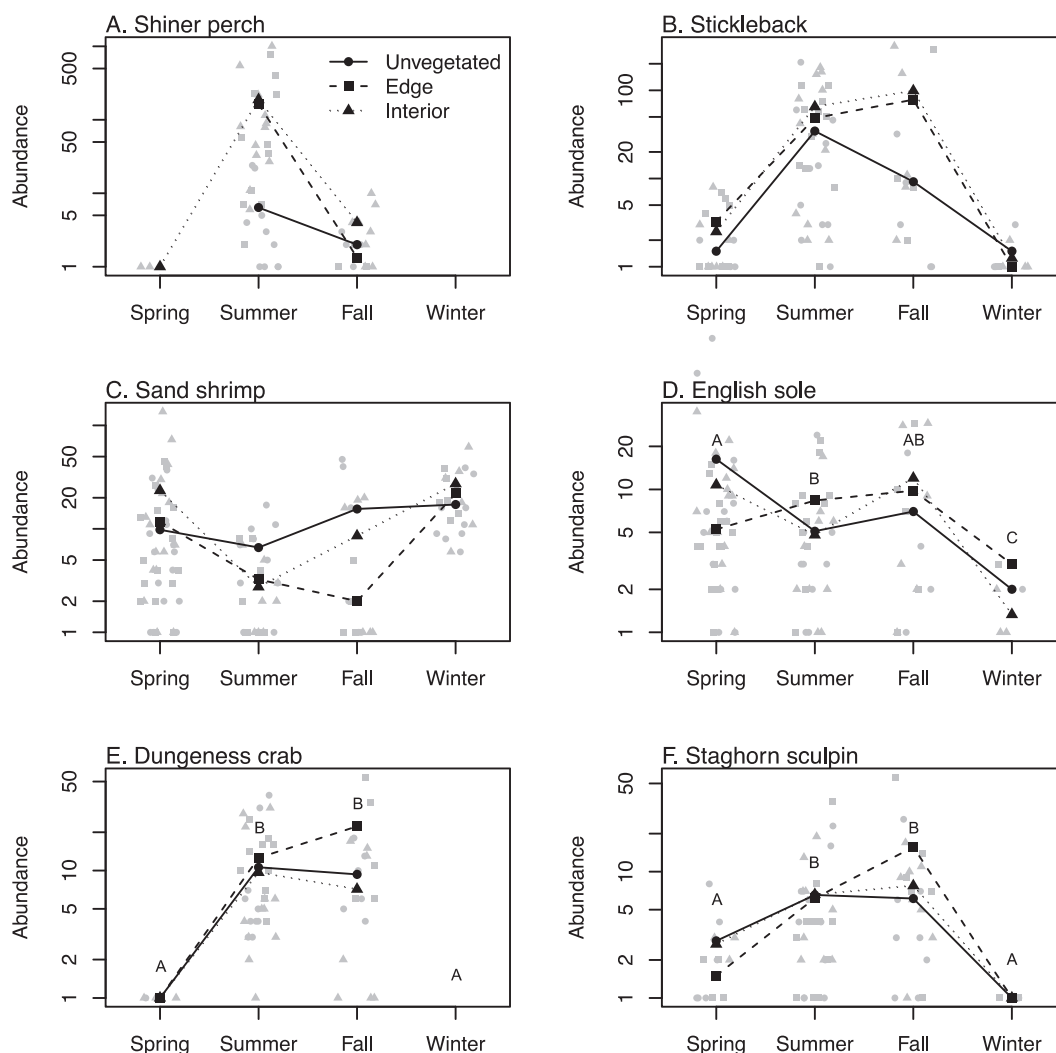


Fig. 4. Abundances of the six most abundant nekton species across seasons and habitats. Light-colored points represent raw values of abundance measured for each sample; dark-colored points and lines represent seasonal averages. All abundances are plotted on a log-scaled y-axis; plots shown here include only individuals when present, but analyses included counts of 0 individuals for all species. English sole, Dungeness crabs, and staghorn sculpins showed a significant abundance response to season; letters in D-F represent results of post-hoc tests for these species. Results of post-hoc tests for shiner perch, sticklebacks, and sand shrimp are shown in Tables S2 and S3.

(*Atherina presbyter*) in fall, but gobies (*Pomatoschistus microps*) in summer, leading to separate effects of habitat and season on multivariate community structure. Our results for community structure and species-specific abundances both suggest that rather than seasonal variation in structural complexity altering the distribution of a relatively stable pool of species, seasons are associated with their own unique complement of species in each habitat which may be migrating between habitats or to and from the bay throughout the year.

Estuarine environmental conditions can fluctuate dramatically between diel periods (Tyler et al., 2009; Morse et al., 2014), which can thereby influence fish distribution and behavior (Neilson and Perry, 1990; Henderson and Fabrizio, 2014). Most studies worldwide show greater abundance (and diversity and richness) at night than during the day in the shallows (Garcia Raso et al., 2006; Yeoh et al., 2017). Additionally, during the day, species may burrow or shelter in physical structures (Gray and Bell, 1986). In one study examining diel patterns of habitat use, distinct daytime and nighttime assemblages occurred only in unstructured habitat (Gray et al., 1998). Because we did not detect diel-by-habitat interactions for total nekton abundance or for multivariate community structure, and total abundance also did not differ overall from day to night, the mosaic of small (ca. 100 m) patches

of interspersed bare and vegetated habitat in the present study may play a special role in enabling nekton to use shallow water even in daylight. Nevertheless, from our species-specific tests, we documented several species that respond in different ways to diel changes. Sand shrimp and English sole were caught at higher densities at night, but Dungeness crab, sticklebacks, and staghorn sculpins during the day. Thus, diel shifts in which taxa were present apparently evened out total abundance, while shifting community composition from day to night. Two of the taxa (Dungeness crab, staghorn sculpin) detected at higher numbers during the day than night also have diets most likely to include other nekton (Hughes et al., 2014), which may be consistent with their using visual cues to forage in shallow water. Our results for diel patterns of intertidal use by Dungeness crabs run counter to those documented by video techniques and radio-tagging, which showed that crabs move out of channels onto extensive unvegetated tideflats to forage at night (Holsman et al., 2006). Possibly this difference is due to the relatively steep bathymetry where fringing eelgrass occurred in our study, such that these low intertidal habitats were accessible without long-distance movement from channels. Shiner perch were the only taxon to demonstrate a habitat-by-diel interaction, matching our initial predictions: their distribution was even across habitats at night, when

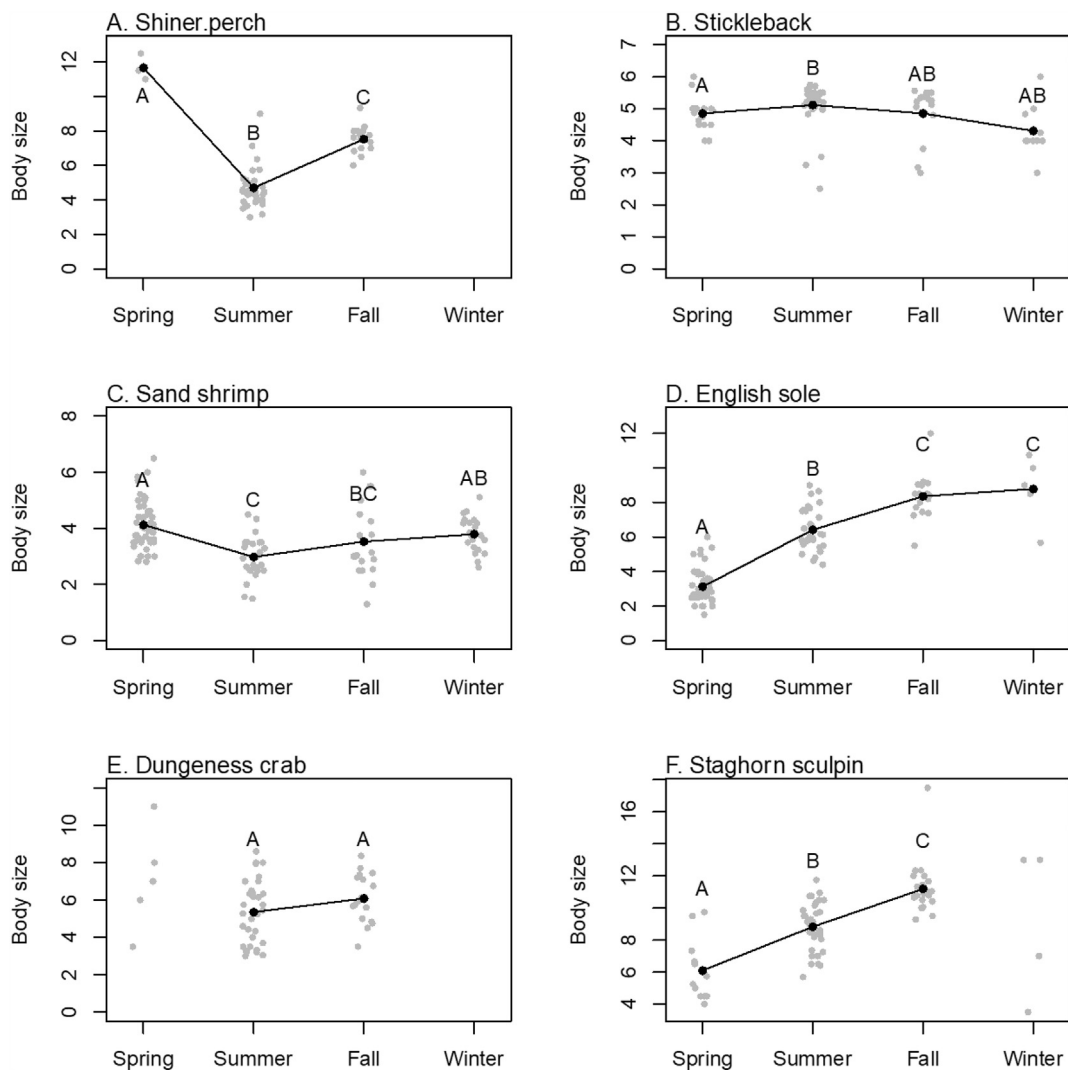


Fig. 5. Body sizes of the six most abundant taxa, by season. Light-colored points represent raw values of average body size measured in each sample; dark-colored points and lines represent seasonal averages, pooled across all habitats. In spring, only five Dungeness crabs were found altogether, and in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

hiding in eelgrass might provide little value as protection from predation, but they were strongly eelgrass-associated during the day.

Although the spatiotemporal patterns of abundance supported habitat-by-time interactions for two of our focal taxa (shiner perch and sand shrimp), we found no significant patterns in nekton body size across habitats (Fig. S3). The most abundant species observed over our two-year study period, shiner perch, reached peak abundance in summer (Fig. 4A), corresponding to the peak in seagrass aboveground biomass and their lowest average body size (Fig. 5A). These fish live in the water column above the sediment among seagrass leaves, relying on their habitat to conceal themselves from visual predators such as birds and fishes, and we had hypothesized this type of habitat may be particularly valuable for smaller individuals that are vulnerable to gape-limited visual predators. In late spring and early summer, shiner perch move into shallow estuarine waters to give birth to live young, which can then use structurally complex shallow habitats like eelgrass beds for shelter from predators while adults retreat to deeper channels (Hughes et al., 2014). However, for shiner perch (and for all other taxa), their habitat association with eelgrass was not enhanced at the season of their smallest body size, and body size did not differ significantly by habitat in any season. It thus appears that while certain species may be associated with particular habitats, these habitat associations are

consistent throughout their period of residency in Willapa Bay, regardless of body size or season. This suggests that body size may not affect habitat accessibility as strongly as we previously thought for the relatively small fishes captured in our seines, or that other dimensions (e.g., body width) may be more important than total length in dictating the accessibility of structurally complex habitats.

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

4.1. Conclusion

As has been previously identified, temporal variation in nekton using shallow-water estuarine habitats makes conclusions about habitat

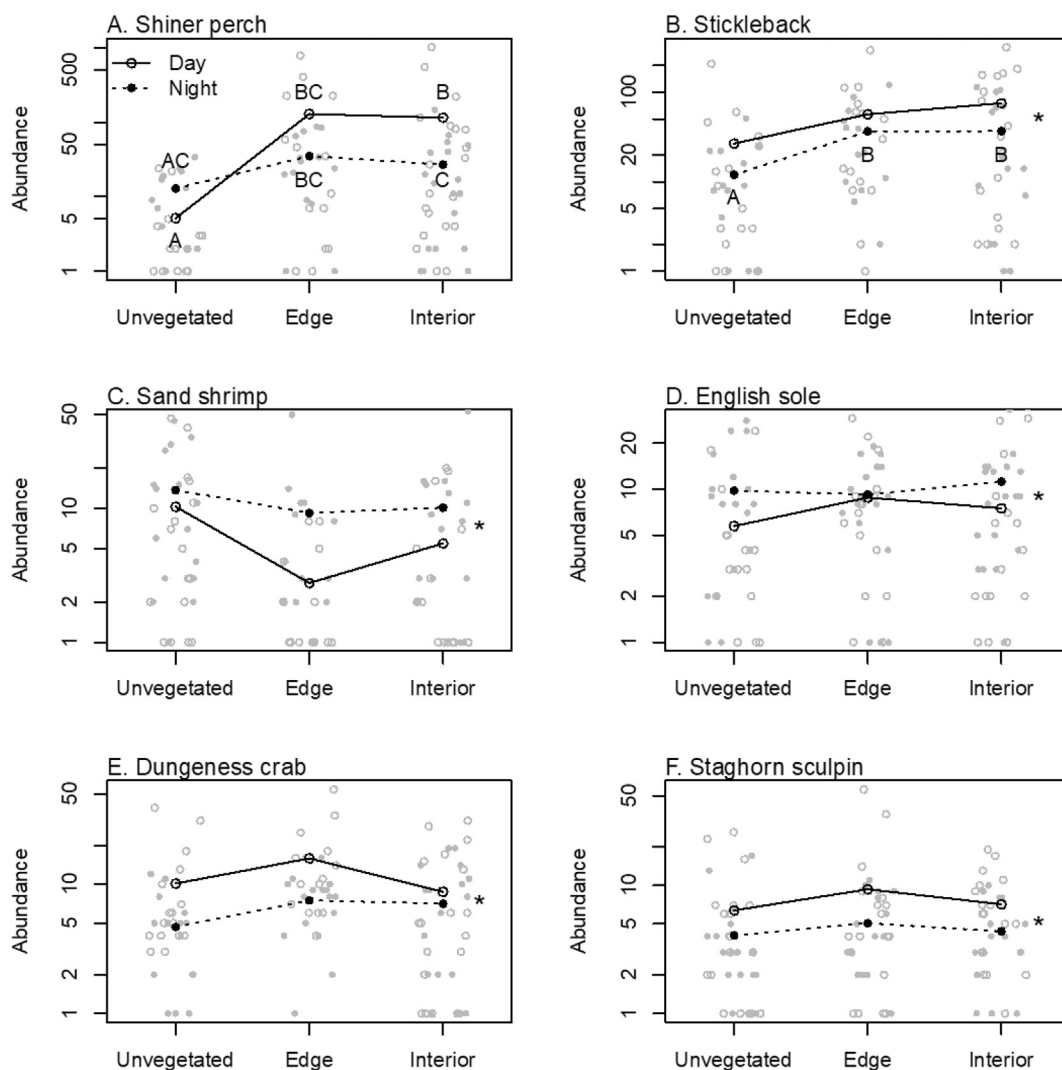


Fig. 6. Abundances of the six most abundant nekton species in diel seines across habitats. Light-colored points represent raw values of abundance measured for each sample; dark-colored points and lines represent averages across habitats. All abundances are plotted on a log-scaled y-axis; plots shown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

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2019.04.009>.

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