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Nekton use of co-occurring aquaculture and seagrass structure on tidal flats

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ABSTRACT: On the extensive tidal flats of Willapa Bay (Pacific coast, USA), oyster culture, seagrass, and mudflats create a mosaic of intertidal habitats. Structured habitats are generally considered to increase abundance and diversity of associated species, but less attention has been paid to roles of different kinds of structure (seagrass meadows, reefs, farm infrastructure) or co-occurring structure in shaping nekton assemblage structure. Here, we investigated the effects of different oyster culture methods (suspended culture and bottom culture) on nekton communities and abundance across a gradient of seagrass habitats, during multiple seasons, and using both seine and video sampling methods. Of 23 major estuarine taxa, 2 were generally associated with vertical structure (eelgrass or suspended culture), 3 were seagrass specialists, and 3 primarily used habitats lacking vertical structure (mudflats and bottom culture). Where oyster culture was present, 5 taxa associated with on-bottom and 2 taxa associated with suspended culture. Assemblage structure responded to co-occurring structure as expected from responses to each structure type independently (i.e. additive effects of seagrass and oyster culture). In contrast to much empirical evidence in structured habitats, seagrass density was a poor predictor of overall fish abundance. These findings together suggest that maintaining a mosaic of available habitats is favorable for promoting diversity in Willapa Bay.

KEY WORDS: Seagrass · Oysters · Aquaculture · Nekton · Fish · Community

1. INTRODUCTION

Structured habitats profoundly change the ecological characteristics of nearshore and estuarine systems. Foundation species provide biogenic structure, increase biodiversity and productivity relative to unstructured habitats, and modify abiotic conditions such as water chemistry, flow, and sediment properties (Dayton 1972, Ellison 2019). Independently, mangrove forests, coral reefs, shellfish reefs, and seagrass beds generate ecological conditions and support ecological communities that depart from what would be present without them (Beck et al. 2003, Kovalenko et al. 2012, Whitfield 2017). However, few studies have evaluated the ecological effects of co-occurring foundation species (Angelini et al. 2011), and the extent to which these structured habitats may be functionally redundant or act non-additively on assemblage structure. Such studies require a study design in which different foundation species co-occur across a range of relative densities.

Historically, seagrass (eelgrass *Zostera marina*) and the Olympia oyster *Ostrea lurida* were the primary foundation species in estuaries along the northeastern Pacific Ocean, providing structurally complex habitats to estuarine mudflats. Today, southwest Washington state (USA) is a globally important producer of the introduced Pacific oyster *Magallana gigas*, and commercial oyster aquaculture makes up about 17% of the total intertidal area (3876 of 22 699 ha) in Willapa Bay (Feldman et al. 2000). Introduced oysters provide biotic structure when

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planted directly on-bottom, while other methods involve stakes, lines, and bags extending up to 1 m above the sediment surface. Oyster aquaculture is able to provide many of the same ecosystem services as natural oyster ecosystems (Alleway et al. 2019), and in some cases enhanced services (i.e. additional dimension of habitat provisioning in suspended culture methods) (Dealteris et al. 2004), such that oysters in culture have the potential to act as a foundation species. While bottom culture is the traditional method of oyster culture in Washington state, there has been a gradual shift towards suspended culture methods, such as longlines and flipbags, to meet market demands and aquaculture regulations. The resulting seascape is a mosaic of (1) oyster culture (bottom culture or suspended culture), (2) eelgrass, (3) mixed eelgrass and oyster culture, and (4) bare mudflat. These habitats vary by type and complexity of structure, including multiple overlapping structure types, and could host distinct communities.

Globally, shellfish aquaculture (particularly suspended mussel and oyster culture) is recognized to increase macrofaunal abundance and species richness by providing habitat and/or food resources (Dealteris et al. 2004, Pinnix et al. 2005, Dumbauld et al. 2009, Gentry et al. 2020, Shinn et al. 2021, Theuerkauf et al. 2022). This has also been seen in fin-fish aquaculture, where a greater abundance of fish was found in the sandy habitats below sea-cages than in nearby submerged aquatic vegetation and sand, with a similar species richness to that found in the vegetated habitats (higher than in bare sand) (Tuya et al. 2005). However, questions remain about how habitat use in shellfish aquaculture compares to seagrass and mixed seagrass–culture habitats, as well as how different methods of oyster aquaculture compare as habitat. In Humboldt Bay, CA, and Rhode Island, shellfish aquaculture gear hosts an even greater overall abundance of nekton than eelgrass (Dealteris et al. 2004, Pinnix et al. 2005). In Willapa Bay, a consistent set of seagrass specialists (bay pipefish *Syngnathus leptorhynchus*, three-spine stickleback *Gasterosteus aculeatus*, shiner perch *Cymatogaster aggregata*, hippolytid or 'grass' shrimp, Hippolytidae spp.) emerges when comparing seagrass and surrounding unstructured habitats (Hosack et al. 2006, Gross et al. 2018, Ruesink et al. 2019), but there is little evidence of whether these taxa would use other vertical structure or mixed seagrass–culture habitats similarly to seagrass. For taxa primarily using structure for refuge, different foundation species may provide functionally redundant habitat. For example, in the Northeast Pacific, suspended aquaculture had similar use to eelgrass habitats by perch species (Muething et al. 2020, Ferriss et al. 2021), a group often associated with seagrass. Alternatively, if taxa are foraging in structure and seeking particular prey, then the resources available could differ between oysters and seagrass as foundation species. While habitat generalists could use any vertically structured habitat, the existence of seagrass (or other aquatic vegetation) and shellfish-culture specialists would result in differences in assemblage structure among habitat types, as found in other past studies in the Northwest Atlantic and the Northeast Pacific (Ferriss et al. 2021, Shinn et al. 2021). There is a notable collection of studies comparing habitat use in seagrass to surrounding areas, some including aquaculture (listed above); however, no past studies have examined the effects of shellfish aquaculture co-occurring in seagrass habitats, which we accomplish here.

Management decision-making around aquaculture is currently limited because past comparisons of habitat value have addressed eelgrass and oyster culture habitats separately (e.g. Hosack et al. 2006) or have focused on eelgrass as habitat without addressing whether aquaculture within eelgrass changes the associated communities. Many regions have regulations in place that prevent shellfish culture from occurring in seagrass beds. However, in Willapa Bay, oyster culture has overlapped with eelgrass for over a century (Dumbauld & McCoy 2015). While eelgrass densities are typically reduced on oyster beds, certain management strategies of oyster culture can result in the co-occurrence of these 2 foundation species (Tallis et al. 2009, Dumbauld & McCoy 2015). The unusual and historical practice of culturing oysters with co-occurring seagrass in Willapa Bay provides an opportunity to study the additivity, or lack thereof, of oyster culture and seagrass habitats with regards to macrofaunal assemblage structure.

In this study, we carefully designed a field sampling method to further our understanding of the effect of oyster culture on nekton communities within and outside of seagrass habitats. First, we employed a crossed design that allows for examination of nekton use of mixed seagrass–aquaculture habitats, which is of significant management interest. Second, we sampled in spring and summer to account for seasonal variation in both seagrass and the structure that it provides, and nekton taxa and life history stages present, which may use habitats differently. Third, we employed 2 methods of sampling, seining and video, in order to account for potential biases that come with different sampling methods (i.e. performance in different structure types, visibility, disturbance, etc.) (Bosch et al. 2017). We asked the following questions:

(1) Do eelgrass and oyster culture, either on-bottom or suspended, support distinct suites of associated taxa during spring and summer, and do these associations differ when the habitat types co-occur (i.e. are mixed seagrass and culture habitats non-additive)?

(2) How do 2 commonly used sampling methods, seining and video, compare in their ability to capture habitat use by nekton?

(3) Does overall fish abundance increase as a function of eelgrass density, within and outside of oyster culture?

2. MATERIALS AND METHODS

2.1. Study sites

Willapa Bay, Washington, USA, is one of the larger estuaries along the Northeast Pacific coast (240 km^2 at mean sea level, Hickey & Banas 2003) and consists of shallow and extensive mudflats with a mosaic of eelgrass, oyster culture, and mixed eelgrass and culture habitats. In order to determine how oyster aquaculture method and amount of eelgrass affect nekton assemblage structure, we sampled using a crossed design of the 3 culture methods (no culture, bottom culture, suspended culture) and 3 eelgrass levels (no eelgrass, sparse eelgrass, dense eelgrass), resulting in 9 distinct habitat types that included the full range of eelgrass densities available (Fig. 1). We sampled 6 regions (Fig. 2) and used a block design in which all habitat types were represented in each of the regions. Three regions had longlines, and 3 regions had flipbags. The 2 suspended culture methods were grouped together for the purpose of this analysis, although it is important to note that longlines consist of clusters of oysters strung on lines, while flipbags are mesh bags suspended from one end, with a buoy on the other, designed to 'flip' with the tide. We included one additional site of 'no eelgrass, no culture' and 'dense eelgrass, no culture' in each region, resulting in 11 sites per region, and a total of 66 sites. In 2020, we sampled 3 southern Willapa Bay regions in May and again in August. In 2021, we sampled 3 regions in the northern part of the Bay, during April and July (Fig. 2). Winter sampling was not feasible due to necessary tides occurring overnight as well as poor field and video conditions. Sites within a region were no more than 1 km apart and were often neighboring habitat patches (sampling at least 50 m apart). Average eelgrass density (shoots per 0.25 m^2) for each site was determined in each season by running a 100 m transect (or 2 parallel 50 m transects) where we counted shoots in 0.25 m^2 quadrats (n = 20), spaced 5 m apart (Fig. 1).

2.2. Seining methods

We used circular beach seines that were customized with a rubber 25 cm lining along the bottom to operate over sharp oyster shells (6 m radius) (Research Nets), and fished in 0.3–0.7 m deep water, as close to slack tide as possible. Nets were set to cover an area of 11 m^2 and then collapsed to collect the organisms present in that area. In each spring and summer, we set 3 consecutive seines at each of the 66 sites. In suspended culture, the seine was set from the end of a line by extending the wings into the

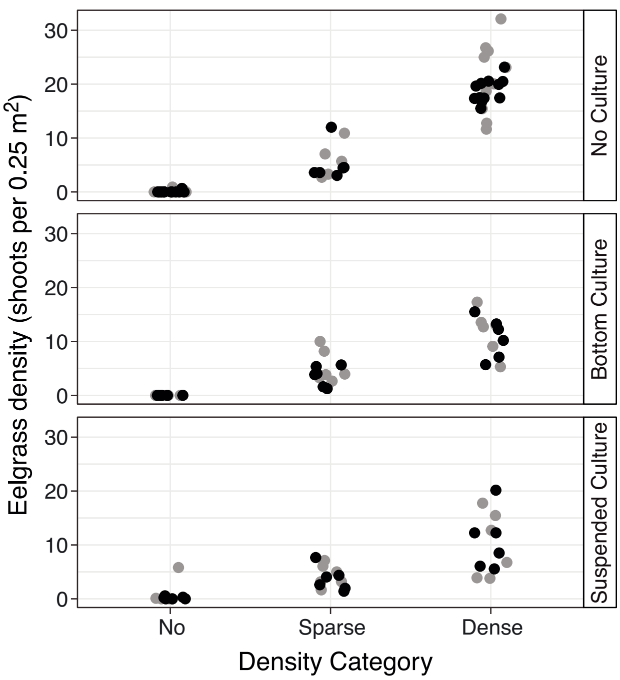

Fig. 1. Eelgrass density of each density category at all sampling sites, by culture type and season (grey = spring, black = summer). Densities varied across regions and oyster culture methods, so categorizations are relative to within region and culture method (e.g. 'Site1 – no culture – sparse eelgrass' might be similar eelgrass density to 'Site1 – bottom culture – dense eelgrass') resulting in some overlap of categories when viewed across all regions and culture types. Eelgrass density was used as a continuous or binary predictor in all analyses (besides methods in Text S1), but the sampling method ensured we sampled the full spectrum of available densities

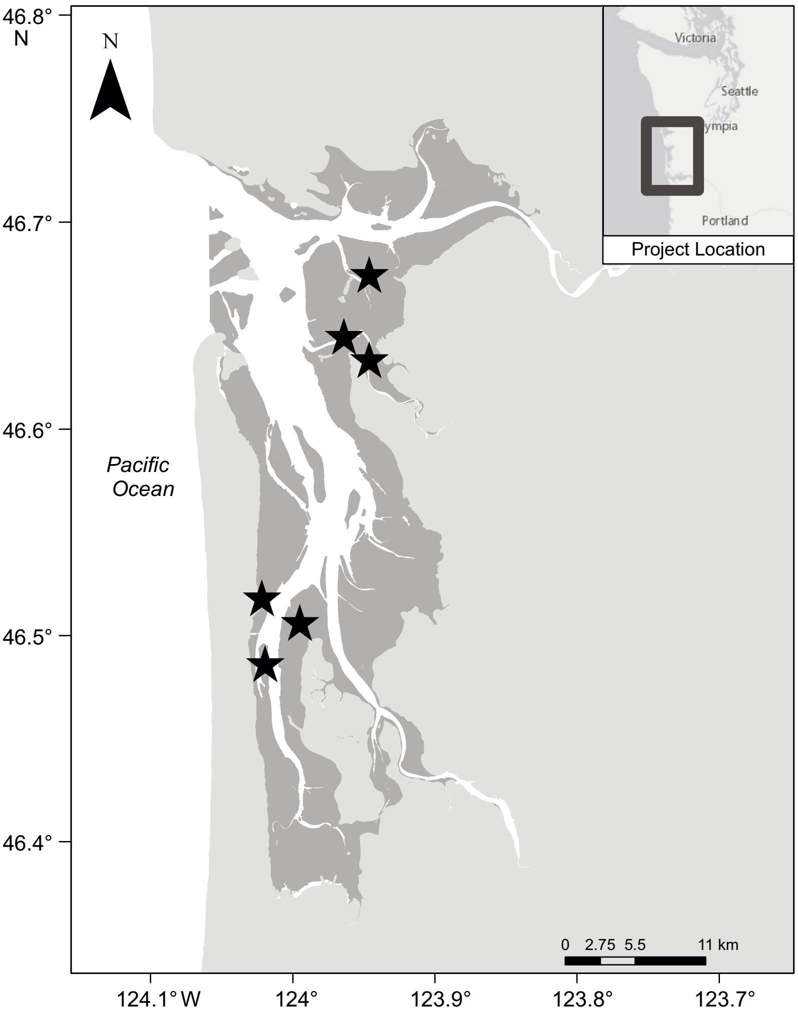

Fig. 2. Willapa Bay, Washington, USA, indicating the 6 sampling regions (stars). The darker grey indicates the intertidal zone. Map modified from Muething et al. (2020) with permission

surrounding rows and carefully collapsing around the central line. All fish, crabs, and shrimp were identified to species (or, in some cases, to family), counted, and released in the field. The first 10 of each taxon caught per seine were measured in centimeters for total length (fish, shrimp) or carapace width (crabs only). Counts and lengths from the 3 seines were pooled within each site and treated as a single sample.

2.3. Video methods

At 54 sites (covering the 9 distinct habitat types in each region), we deployed GoPro Cameras (Hero 3+) to capture 2 min videos every 10 min. Cameras were installed 0.75 m above the sediment at a downward angle, with a marker placed 1 m away to mark the field of view (Fig. 3). Camera video settings were set to be consistent across cameras (1080 p) to give approximately equal field of view areas. Cameras were deployed during the low tide and recorded images during flood tide. Cameras were collected at low tide on the following day. Many sites had 2 camera deployments within each season, while others only had one due to technical difficulties (i.e. camera failures) or unfavorable weather. Videos were then downloaded and systematically reviewed for mobile organisms in the field of view by 2 individuals (reproducibility was confirmed during training and spot checks performed). Nekton identification and visitations were extracted from the videos using the MaxCount method (Ferriss et al. 2021), with the modification that individuals that exited the frame and returned within 5 s were only counted once to avoid excessive repeated counts. We selected the first 22 videos (2 min each) after submersion from each camera, excluding videos with complete camera obstruction (i.e. from algae) or extremely poor visibility due to turbidity (could not ID taxa within 1 m). Sites with fewer than 22 videos were excluded for that season, which led to removal of 5 samples during spring, and 3 samples during summer. Nekton counts were summed across videos from each camera, and sites with duplicate camera deployments had counts averaged and rounded to the next integer. Rare taxa (occurred in only a single sample) were removed, which resulted in removal of 15 species in the spring, and 9 in the summer.

2.4. Analytical methods

2.4.1. Taxa–habitat associations

First, an initial analysis was performed using the 'mvabund' package (Wang et al. 2012) in R (v4.1.3; R Core Team 2022) to determine overall community response to the amount of eelgrass (none, sparse, dense) and type of oyster culture (none, bottom culture, suspended culture), as well as testing for an

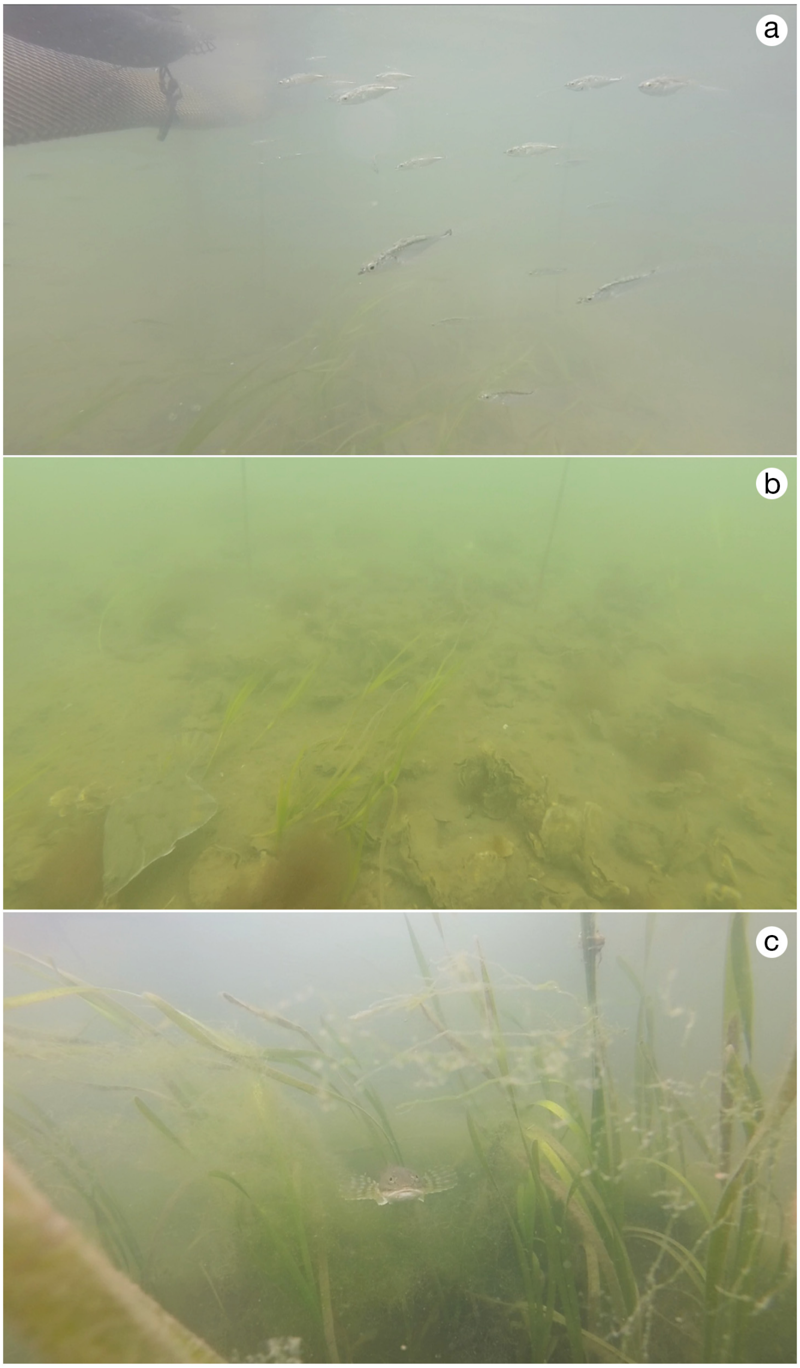

Fig. 3. (a) Three-spine stickleback in flip-bags (suspended culture) and sparse eelgrass, (b) starry flounder in bottom culture with sparse eelgrass, and (c) staghorn sculpin in dense eelgrass with no culture

interaction effect of eelgrass × oyster culture to address a potential non-additive effect of the 2 habitats (refer to Text S1 and Table S1 in the Supplement at www.int-res.com/articles/suppl/q015p307_supp.pdf). Upon finding no evidence of an eelgrass × oyster interaction effect on nekton community composition, we proceeded with a Bayesian analysis of taxa–habitat associations. A Bayesian approach was suitable due to the hierarchical nature of our data, unaccounted variability (typical for this type of ecological field study), and the ability to provide taxon-specific responses while accounting for the entire community.

Based on datasets with columns for each nekton taxon, the 'Bayesian Ordination and Regression AnaLysis (BORAL)' package (Hui 2016) in R was used to fit correlated column generalized linear mixed models (GLMMs) with latent variables (introduces unmeasured predictors to each sample and accounts for correlations among taxa columns in the response matrix) via Markov chain Monte Carlo (MCMC) estimation (Warton et al. 2015: see their Box 1 and Fig. 1 for more on latent variable model structure; Hui 2016). The response matrix included nekton taxon counts for each site (54 sites for videos, 66 for seines), with a separate matrix for each season. Separate analyses were carried out on spring and summer data, due to expected seasonal differences in assemblages, and on seines and videos. For each dataset, we fit 2 models addressing distinct questions. In the first model, oyster culture (presence/absence) and eelgrass (presence/absence) were included as environmental variables, with region included as a random effect. The second model only included summer data from sites where oyster culture was present, with oyster culture method (bottom culture/suspended culture) and eelgrass (presence/absence) included as environmental variables, and region as a random effect. Eelgrass presence/absence was chosen (instead of 'none', 'sparse', 'dense' categories), because categories were relative to each site and did not represent consistent densities, but did ensure that a range of densities were sampled (Fig. 1). All models included 2 latent variables to account for potential correlation among taxa, and default priors ('prior.control') were used. The models were fit using the negative binomial distribution (with log link) and checked with residual analysis. Coefficients and highest posterior density (HPD) intervals were obtained and used to create caterpillar plots of taxon-specific responses. Our results were also compared to those in existing literature by performing a literature search of publications that included taxa identified here and at least 2 of our studied habitat types (*Zostera marina*, mudflat, oyster shell/culture).

2.4.2. Fish abundance across eelgrass densities and culture types

A GLMM with negative binomial errors (link = 'log') was fit using Stan and the 'rstanarm' package for Bayesian estimation (Goodrich et al. 2023) in R. The response variable was total fish counts (invertebrates removed) from the seining data. Predictor variables included average eelgrass shoot density (shoots per 0.25 m^2), season (spring or summer), and oyster culture method (none, bottom culture, or suspended culture) as fixed effects and region as a random effect. Quantitative shoot density was used instead of density categories, as categories were relative to each site, as described in Section 2.4.1. The model fit and MCMC convergence were checked using posterior predictive check and $\hat{r}$ values, respectively (Table 1; Fig. S1), which were acquired using ShinyStan. The posterior predictive check ('ppcheck' in ShinyStan) compares the model prediction (y^{rep}) to the observed data (y), and indicates model adequacy (Fig. S1). $\hat{r}$ values < 1.05 indicated no issues of MCMC convergence. Data were also visualized with scatter plots to illustrate distribution.

3. RESULTS

3.1. Total catch and method comparison

Overall, seining captured a much greater abundance of nekton, as well as greater species richness, relative to videos (see summary of total nekton sampled in spring and summer in Table 2). We sampled 30 taxa in the seines, whereas 17 taxa were identified via video. Furthermore, small and/or cryptic taxa that were abundant in the seines (i.e. gobies, juvenile sole, and small [<3 cm] shrimp species) were not captured in videos. The taxa most sampled by videos were shiner perch and Dungeness crab *Metacarcinus magister*, while the taxa most sampled by seine were English sole *Parophrys vetulus*, shiner perch, and shrimp of the families Hippolytidae (hippolytid shrimp) and Crangonidae (crangonid shrimp) (Table 2). Seasonal variation in abundances and lengths indicate patterns of nekton migration and reproduction. In particular, English sole and Pacific staghorn sculpin *Leptocottus armatus* showed seasonal growth, and shiner perch migrated into intertidal habitats in summer.

3.2. Taxon–habitat associations

3.2.1. Eelgrass and oyster culture

Oyster culture (none, bottom, suspended) and eelgrass density (none, sparse, dense) were statistically significant predictors of nekton community composition (Text S1, Table S1). There was no evidence of an oyster culture × eelgrass interaction effect on nekton

Table 1. Summary parameter statistics for model of fish count. n_eff: effective sample size; $\hat{R}$: convergence diagnostic; MCSE: Monte Carlo standard error; PPD: posterior predictive distribution

	n_eff	$\hat{R}$	Mean	MCSE	SD	2.50%	25%	50%	75%	97.50%
(Intercept)	1733	1	4.4	0	0.2	3.9	4.2	4.4	4.5	4.8
Shoot density	4089	1	0	0	0	0	0	0	0	0
Season – Summer	4741	1	−0.2	0	0.2	−0.5	−0.3	−0.2	−0.1	0.2
Oysters – Bottom	3816	1	−0.2	0	0.2	−0.5	−0.3	−0.2	0	0.2
Oysters – Suspended	3900	1	−1.1	0	0.2	−1.4	−1.2	−1.1	−1	−0.7
[(Intercept) Region:Bay_Center]	1599	1	0.5	0	0.3	0.1	0.3	0.5	0.7	1.1
[(Intercept) Region:Cutoff]	1956	1	−0.2	0	0.2	−0.7	−0.4	−0.2	−0.1	0.3
[(Intercept) Region:Long_Island]	1690	1	0	0	0.2	−0.4	−0.1	0	0.1	0.5
[(Intercept) Region:Middle_Sands]	1896	1	0.1	0	0.2	−0.4	−0.1	0	0.2	0.5
[(Intercept) Region:Port]	1790	1	−0.2	0	0.2	−0.7	−0.4	−0.2	−0.1	0.2
[(Intercept) Region:West_Channel]	2214	1	0	0	0.2	−0.5	−0.2	0	0.1	0.4
reciprocal_dispersion	4443	1	1.5	0	0.2	1.2	1.4	1.5	1.6	1.9
Sigma[Region:(Intercept),(Intercept)]	1646	1	0.2	0	0.2	0	0.1	0.1	0.2	0.8
mean_PPD	4043	1	68.7	0.1	8.1	54.2	63.1	68.2	73.6	86.2

Table 2. Nekton counts used in analysis. Seine counts are summed catches from all 66 sites. Video counts are summed from the first 22 videos (2 min each) at each site. Sites with multiple cameras had counts averaged, resulting in a single set of counts for each site per season. unID: unidentified

Taxon	Common name	Spring			Summer		
		Videos	Seine	Size (cm) ± SE	Videos	Seine	Size (cm) ± SE
Clevelandia ios	Arrow goby	0	154	4.58 ± 0.29	3	57	3.66 ± 0.13
Lepidogobius lepidus	Bay goby	0	7	5.00 ± 0.72	1	2	8.00 ± 1.00
Syngnathus leptorhynchus	Bay pipefish	1	66	16.50 ± 0.44	13	141	13.51 ± 0.52
Scorpaenichthys marmoratus	Cabezon	0	4	3.13 ± 0.59	0	0	
Oncorhynchus keta	Chum salmon	0	95	5.70 ± 0.18	0	0	
Oncorhynchus tshawytscha	Chinook salmon	0	0		30	16	8.07 ± 0.30
Crangonidae spp.	Crangon shrimp	0	770	3.56 ± 0.07	0	610	2.40 ± 0.05
Metacarcinus magister	Dungeness crab	57	56	7.75 ± 0.55	106	253	6.92 ± 0.24
Parophrys vetulus	English sole	5	2715	3.55 ± 0.06	25	383	7.54 ±0.13
Carcinus maenas	European green crab	3	1	5.50	0	10	4.94 ± 0.66
Hemigrapsus spp.	Shore crab	5	42	1.01 ± 0.09	2	21	1.27 ± 0.16
Hippolytidae spp.	Grass shrimp	0	1321	1.92 ± 0.04	0	68	1.83 ± 0.11
Pugettia producta	Kelp crab	0	0			2	4.00 ± 0.0
Hexagrammos decagrammus	Kelp greenling	0	6	5.25 ± 0.21	0	27	7.98 ± 0.21
Cottidae sp.	unID juvenile sculpin	0	31	2.13	0	0	
Ophiodon elongatus	Lingcod	0	3	10.17 ± 0.17	0	0	
Pandalidae sp.	*Pandalus* shrimp	0	1	5.00	0	0	
Porichthys notatus	Plainfin midshipman	0	0		0	1	12.00
Cancer productus	Red rock crab	0	5	10.50 ± 0.32	1	3	8.33 ± 1.20
Pholis ornata	Saddleback gunnel	4	180	6.47 ± 0.18	6	809	7.19 ± 0.13
Cymatogaster aggregata	Shiner perch	76	75	7.29 ± 0.97	468	2317	5.89 ± 0.10
Hyperprosopon ellipticum	Silver surfperch	0	0		0	2	7.50 ± 0.50
Hypomesus pretiosus	Surf smelt	1	306	5.79 ± 0.20	14	0	
Citharichthys stigmaeus	Speckled sanddab	0	1	3.00	0	12	6.25 ± 0.29
Leptocottus armatus	Pacific staghorn sculpin	7	361	5.55 ± 0.15	57	352	10.80 ± 0.16
Platichthys stellatus	Starry flounder	0	11	13.73 ± 0.89	0	32	13.12 ± 0.65
Gasterosteus aculeatus	Three-spine stickleback	1	282	4.72 ± 0.14	26	214	3.18 ± 0.16
Aulorhynchus flavidus	Tubesnout	0	2	13.25 ± 0.25	0	0	
Hyperprosopon argenteum	Walleye surfperch	0	6	7.60 ± 0.19	10	0	
Phanerodon furcatus	White surfperch	0	2	8.50 ± 0.5	7	0	

community composition, so we proceeded with a more in-depth analysis of taxon-specific habitat responses.

Habitat associations are shown for each taxon as estimated coefficients and posterior densities (Figs. 4 & 5, Table 3; extended model output is reported in Tables S2 & S3). In seines in spring, positive associations with eelgrass occurred for crangonid shrimp, hippolytid shrimp, bay pipefish, saddleback gunnel *Pholis ornata*, and three-spine stickleback. Four of these associations persisted in summer (hippolytid shrimp, bay pipefish, saddleback gunnel, three-spine stickleback), and additionally, shiner perch were positively associated with eelgrass. Also in seines in spring, positive associations with oyster culture occurred for arrow goby *Clevelandia ios*, *Hemigrapsus* spp., and hippolytid shrimp. For hippolytid shrimp and *Hemigrapsus* spp., this positive association persisted into summer. Seining data also indicated negative associations of arrow gobies with eelgrass and negative associations of three-spine stickleback and English sole with oyster culture in the spring. In the summer, there were negative associations of English sole with eelgrass, and shiner perch and three-spine stickleback with oyster culture.

In contrast to seines in which several taxa showed positive associations with eelgrass in both seasons, video data resulted in no positive associations with eelgrass. Video results indicated a negative association of *Hemigrapsus* spp. with eelgrass during the spring, and a negative association of Dungeness crab with eelgrass during the summer, whereas seine results indicated no strong association (negative or positive) with eelgrass for both of these taxa. The video results also found shiner perch and staghorn sculpin to be positively associated with oyster culture during the summer, while seine data showed staghorn sculpin to be neutral and shiner perch to be negatively associated with oyster culture during summer (see Section 4.1). Taxa that were not listed as

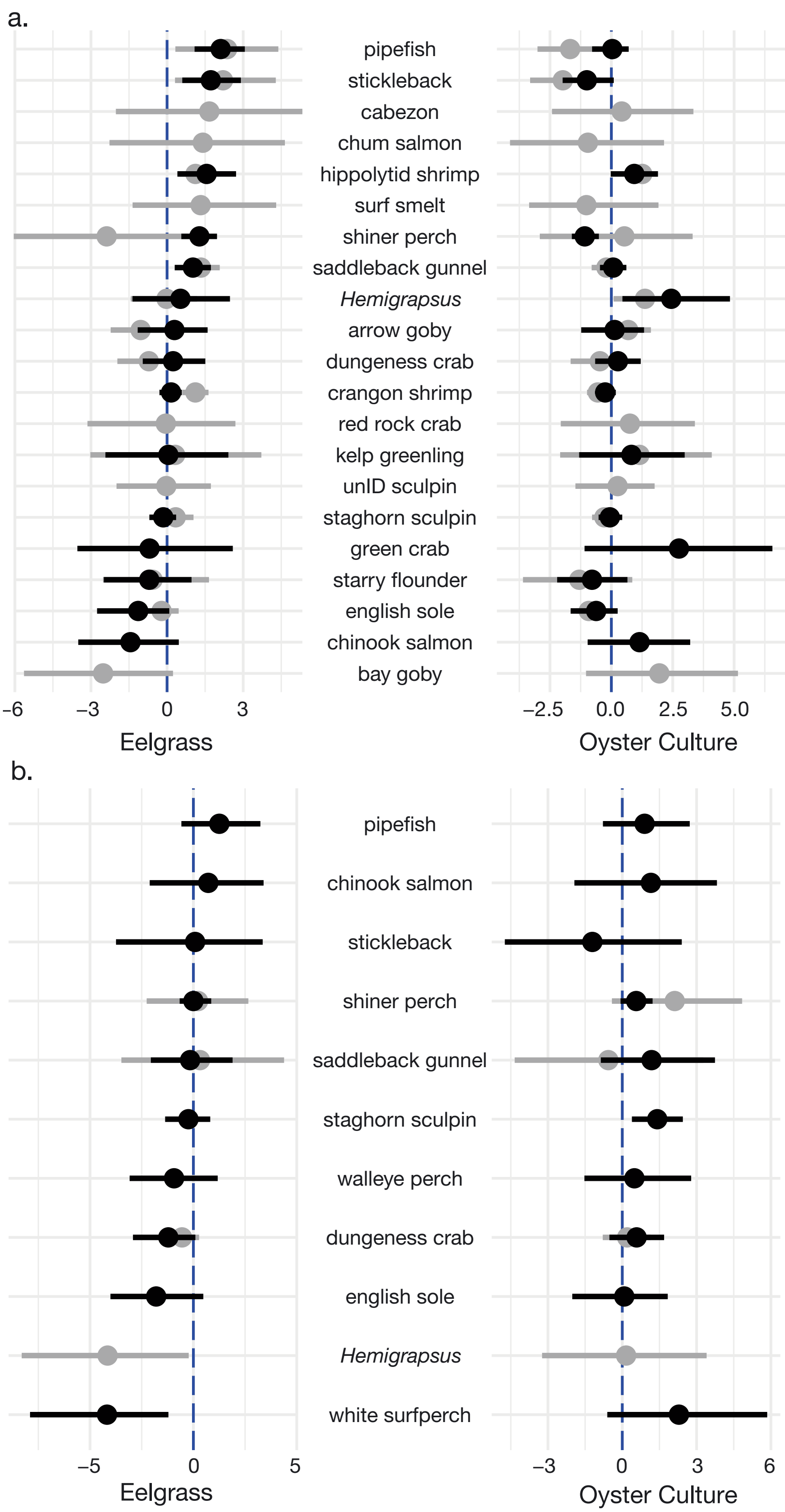

Fig. 4. Coefficients with highest posterior density (HPD) interval from (a) seine and (b) video analysis including all sites (grey = spring, black = summer). Values greater than zero indicate a positive association with eelgrass (left panels) or oyster culture (right panels). Values below zero indicate negative association with respective habitat structure. unID: unidentified

being associated with habitat had HPD intervals that included 0. Some of these HPD intervals were quite narrow, indicating no habitat association with eelgrass or oyster culture, while wider HPD intervals indicate greater uncertainty of the habitat association estimation.

3.2.2. Bottom vs. suspended culture associations

The second model fit for video and seining data examined summer sites where culture was present, in order to compare associations with bottom culture versus suspended culture. Considering only where culture was present, seining results indicate associations of arrow gobies with suspended culture, and associations of Chinook salmon *Oncorhynchus tshawytscha* (hatchery released, indicated by clipped adipose fin), Dungeness crab, English sole, saddleback gunnel, shiner perch and staghorn sculpin with bottom culture (Fig. 5, Table 3). Videos indicate a similar result for Dungeness crab (associated with bottom culture), but an opposite result for shiner perch (associated with suspended culture).

3.3. Fish abundance across eelgrass densities and culture types

Total fish in seines ranged from 0 to 598 across samples but was poorly predicted by habitat or season as shown by mean estimates and confidence intervals close to and overlapping zero (Table 1), and an undistinguishable data pattern (both with exception to suspended culture) (Fig. 6). Fewer fish were caught in seines in suspended culture relative to other habitats (Fig. 6, Table 1); however, this is likely an inaccurate reflection of fish density due to challenges of seining around rigid structures (see Section 4.1).

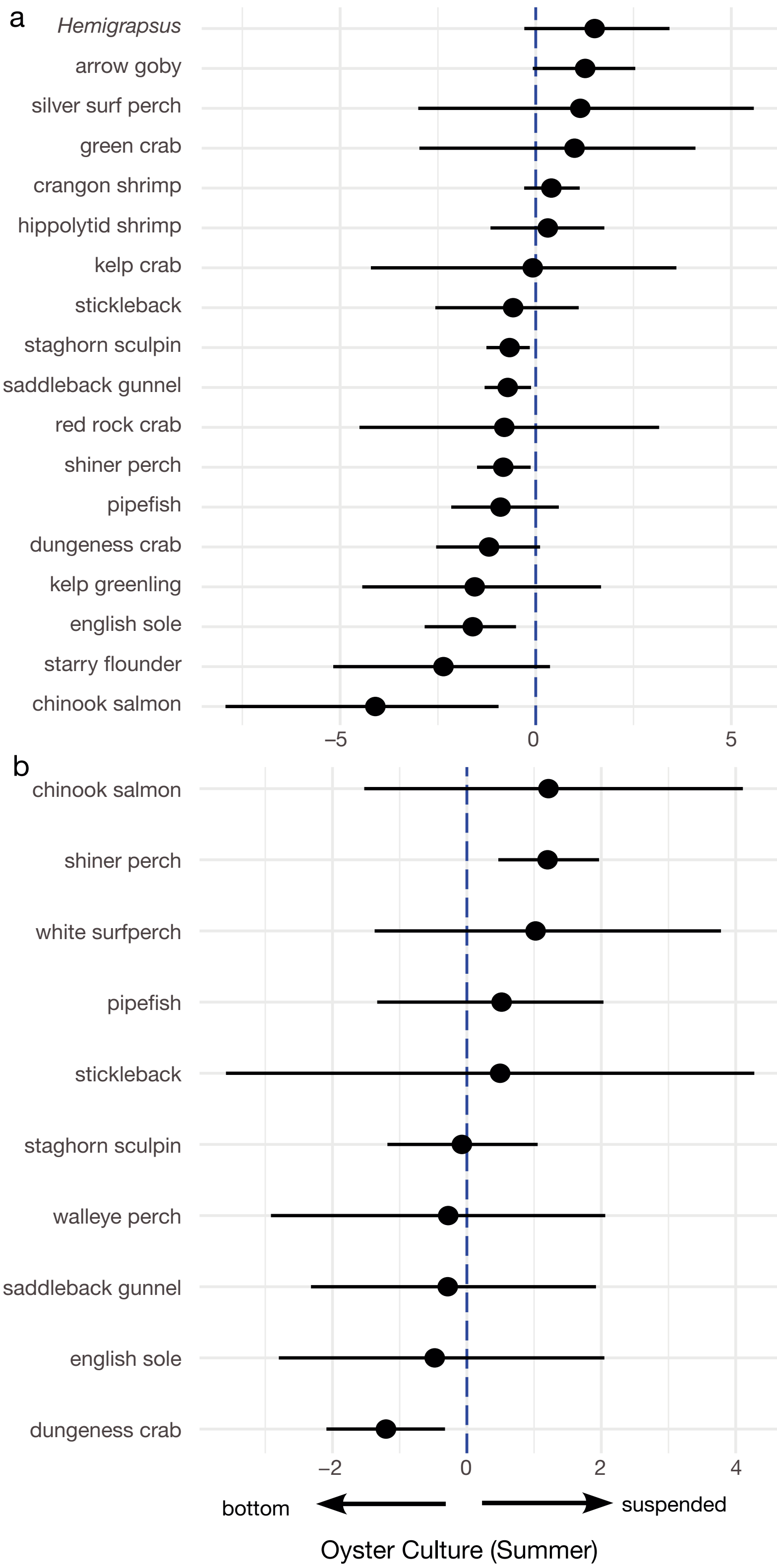

Fig. 5. Coefficients and highest posterior density (HPD) intervals from (a) seine and (b) video analysis, including only sites that have oyster culture. Summer data only. Values below zero (left) indicate association with bottom culture, while values above zero (right) indicate association with suspended culture

4. DISCUSSION

Seagrass and oyster aquaculture both provide habitat to a variety of fish and invertebrate nekton. While certain taxa associate with eelgrass, others associate with oyster culture (one or both methods). Some taxa generally associate with increased vertical habitat structure, in which case the structured habitats (seagrass and suspended culture) may be functionally redundant. Additionally, some taxa associate with habitats lacking vertical structure and were found primarily in unstructured mudflat (negatively associated with eelgrass/culture) or bottom culture habitats. Nekton respond to co-occurring seagrass and oyster culture habitats as they would when occurring separately (Table S1). These different habitat types support distinct nekton assemblage structures and suggest that a mosaic of habitat types can increase overall diversity and support multi-trophic connectivity. Using multiple sampling methods, in this case seining and video footage, is helpful to understand sampling biases, and can reveal strengths and weaknesses of methods in different sampling contexts. Finally, eelgrass density is not a reliable indicator of total fish abundance in Willapa Bay, due to the use of unstructured habitats by highly abundant taxa.

4.1. Method comparison

Comparison of our results sampling the same sites with both seines and videos reveals important sampling biases, as well as strengths and weaknesses of each method. Seining caught more species of nekton and is not affected by visibility. However, in order to fish multiple sites per day, both ebb and flood were used, which could introduce unaccounted variability. Additionally, while our modified seines operated well in eel-

Table 3. Summary table of taxon–habitat associations compared with findings from existing literature. + indicates positive association and – indicates negative associate. Blank cells indicate no strong relationship, while NA indicates the taxon was not captured in the indicated season and/or method

Taxon	This study (seining / videos): Spring Eelgrass	Spring Oyster	Summer Eelgrass	Summer Oyster	Culture preference	Reviewed literature: Eelgrass	Oyster	Culture preference
Arrow goby	–/NA	+/NA			Suspended/			
Chinook salmon (hatchery)	NA	NA			Bottom/	+ Semmens (2008)		
Crangonid shrimp	+/NA	–/NA	/NA	/NA				
Dungeness crab			/–		Bottom/ Bottom		+ Dumbauld et al. (2009) + Fernandez et al. (1993)	Bottom (Dumbauld et al. 2009)
English sole	NA	–/NA	–/		Bottom/	– Ruesink et al. (2019)		
Hemigrapsus spp.	/–	+/	/NA	+/NA				
Hippolytid shrimp	+/NA	+/NA	+/NA	+/NA		+ Ruesink et al. (2019)		
Bay pipefish	+/NA	–/NA	+/			+ Ruesink et al. (2019)		
Saddleback gunnel	+/		+/		Bottom/	+ Ruesink et al. (2019)		
Shiner perch			+/	–/+	Bottom/ Suspended	+ Dumbauld et al. (2015) + Hosack et al. (2006) + Ruesink et al. (2019) + Ferriss et al. (2021) + Gross et al. (2018) + Gross et al. (2017)	+ Ferriss et al. (2021) + Muething et al. (2020)	Suspended (Muething et al. 2020, Ferriss et al. 2021)
Pacific staghorn sculpin	NA	NA		/+	Bottom/		+ Muething et al. (2020) + Ferriss et al. (2021) (regional variation)	Suspended (Muething et al. 2020)
Three-spined stickleback	+/NA	–/NA	+/	–/		+ Ruesink et al. (2019) + Gross et al. (2018) + Gross et al. (2017)		

grass and over oyster bottom culture, maneuvering the seine through and around suspended culture provided a challenge that likely reduced our catch (Fig. 6), thus resulting in a negative sampling bias that must be strongly considered when interpreting the results concerning suspended culture. Escapement of small taxa into rigid bottom culture habitats may also be a source of sampling bias with seines. In contrast, videos provided more controlled sampling in terms of using footage from one period of the tide, although they were severely affected by visibility in the form of (1) turbidity and (2) view interference via macrophytes. This resulted in likely under-sampling of nekton in highly macrophytic (including eelgrass) or turbid videos, as well as under-sampling of more cryptic taxa, such as juvenile English sole. We found that sampling on clear days with little wind provided the best video quality. Overall, the video method sampled fewer taxa and numbers of nekton than seining (although this is also dependent on sampling effort), but provided a useful tool for capturing habitat use, particularly by pelagic fish, in suspended culture. While seining required a much greater field effort (10–15 min per seine pull and 3 pulls per site), the processing effort required for video analysis is much greater than seining (approximately 45–60 min per site), making the 2 methods of similar magnitude in terms of overall effort. However, many more cameras would have to be deployed to reach a similar number of 'captures' as the seining. When selecting methods, we suggest considering factors including habitat structure, turbidity, and cryptic nature of taxa. Careful consideration of potential method biases, project goals, and the strengths and weaknesses of different sampling methods is critical when designing a study, which is clearly demonstrated here.

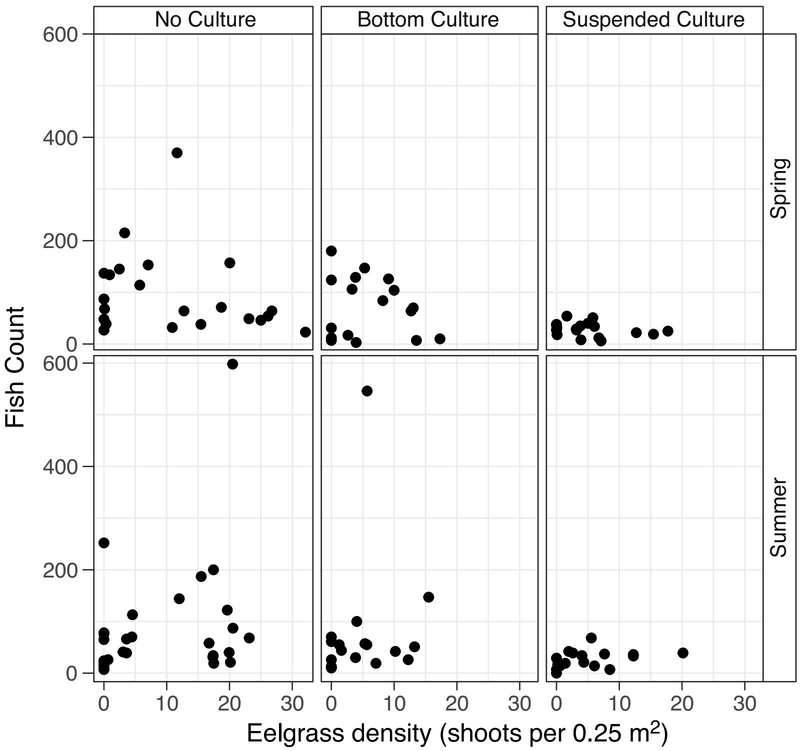

Fig. 6. Fish count from seines as a function of eelgrass shoot density in different culture habitats (no culture, bottom culture, suspended culture), and during spring and summer. Note that fish count in suspended culture was likely affected by negative sampling bias (see Section 4.3)

4.2. Taxon–habitat associations

Our results illustrate that many nekton species utilize multiple estuarine habitat types, and that both the amount of eelgrass and presence/type of oyster culture drive nekton assemblage structure. Where preferences are exhibited, some taxa associate with eelgrass or one method of oyster culture, whereas others respond to degree of structure (i.e. structured vs. unstructured) rather than structure type. Additionally, nekton communities within habitats vary based on season, as organisms migrate and reproduce, thus altering the role of these habitats seasonally. We found no significant statistical interaction of nekton communities in response to eelgrass and oyster culture (Table S1), suggesting that co-occurrence of the 2 habitats does not affect how taxa respond to the habitats relative to when they are independent; in other words, there is no evidence of a non-additive effect of co-occurring seagrass and oyster culture. Eelgrass-associated species (associated in spring and/or summer) include bay pipefish, three-spine stickleback, saddleback gunnel, and crangonid shrimp (Fig. 5, Table 3). Three-spine stickleback were the only taxon in the study that were consistently (both seasons, both methods) negatively associated with oyster culture. Positive oyster culture-associated taxa include shore crabs (*Hemigrapsus* spp.), staghorn sculpin, arrow goby, and shiner perch (videos only) (Fig. 5, Table 3); arrow gobies and shiner perch were associated with suspended culture, while the other taxa were associated with bottom culture (Fig. 5, Table 3). However, observations suggest that gobies reside in holes that occur in the soft sediment under suspended culture, rather than use the culture directly. Another set of taxa showed no overall association with oyster culture presence or absence (i.e. did not prefer or avoid), but were associated with one type of culture when captured within oyster culture habitats. Members of this group are juvenile chinook salmon (hatchery-reared), Dungeness crab, and English sole, which were all found more in bottom culture than suspended culture habitats. Possibly, opposing associations of taxa with different culture types (i.e. positively associated with bottom culture, negatively associated with suspended culture) could mask an overall association with oyster culture. For example, chinook salmon were associated with bottom culture relative to suspended culture, and while there was an overall positive association with oyster culture, a large HPD and low number of individuals result in uncertainty around this conclusion. Hippolytid shrimp and shiner perch showed positive associations with both eelgrass and oyster culture presence (shiner perch in videos only), suggesting that these taxa may respond generally to increased vertical structure for foraging and refuge (Fig. 4, Table 3). Lastly, English sole, Dungeness crab, and *Hemigrapsus* spp. showed tendencies towards habitats without vertical structure (bare or bottom culture), and showed negative correlations with eelgrass in at least one season (Fig. 4, Table 3). English sole also demonstrated seasonal variation in use of oyster culture (negative association in spring), reflecting how different life stages may interact with the habitat mosaic. For example, ~2 cm, translucent sole may primarily use bare habitats for camouflage in the spring, while slightly older and larger summertime sole may utilize bottom culture habitats for foraging.

When comparing our findings to past studies and evaluating habitat function, it is important to consider sampling methods used. Several recent studies corroborate that videos are an effective method of sampling pelagic nekton such as perch species (Gross et al. 2018), including in suspended culture (Muething et al. 2020, Ferriss et al. 2021). However, these studies using video also sampled relatively low numbers of more cryptic taxa, particularly flatfish such as English sole. We see this discrepancy when comparing our own sampling methods, where seines revealed much higher numbers of cryptic taxa than would have been concluded from using exclusively video methods.

Our results also demonstrate that sampling across multiple seasons is a critical component when evaluating habitat value. Eelgrass- and structure-associated organisms tended to be in greater abundance during the summer, when eelgrass itself reaches high biomass (see also Ruesink et al. 2019). In the spring, however, a greater proportion of the community is composed of taxa that prefer unstructured habitats or are habitat generalists, therefore increasing the value of less structured habitats. Seasonal studies of nekton indicate that spring vs. summer encompasses the greatest shift in community composition (Gross et al. 2019b), but many past studies have been restricted to summer sampling. While our findings certainly corroborate that eelgrass and structured habitats (e.g. suspended culture) are of high value to many organisms, using multiple methods of sampling and sampling across seasons allowed us to identify the notable use of unstructured mudflat and bottom culture habitats.

Overall, our results confirm findings from previous work and provide new evidence of habitat associations that expand on past studies. Consistent with past estuarine work (Gross et al. 2018, Ruesink et al. 2019), there is a suite of eelgrass specialist taxa — bay pipefish, three-spine stickleback, saddleback gunnel, and crangonid shrimp — which continuously use eelgrass habitats. Bay pipefish and crangonid shrimp appeared to use eelgrass regardless of the presence of oyster culture, while three-spine sticklebacks avoided culture. Our findings confirm that shiner perch utilize the vertical structure provided by both eelgrass and suspended aquaculture habitats, as previously recorded (Dumbauld et al. 2009, Muething et al. 2020, Ferriss et al. 2021). For taxa found in both eelgrass and suspended culture, such as shiner perch, the vertical structures could provide redundancy in habitat. It is apparent from videos that shiner perch may forage among macroalgae attached to longlines or flipbags. Epifaunal abundance is often increased in oyster aquaculture relative to bare areas (Hosack et al. 2006). In keeping with this trophic explanation, grass shrimp (Hippolytidae) were generally structure-associated in our study and could also serve as a food resource for the larger-bodied nekton we captured.

Two species of management importance cannot be considered to use eelgrass as estuarine nursery habitat, because of lack of positive association or statistical negative association. Our findings from both fishing and videos confirm that juvenile Dungeness crabs prefer habitat lacking vertical structure, but utilize bottom culture habitats, which is consistent with past work (Eggleston & Armstrong 1995, Dumbauld et al. 2000, 2009, their Section 5.3), and suggests that bottom culture is valuable nursery habitat for Dungeness crab. English sole were also found to avoid vertical structure and to use bottom culture habitats during the summer, consistent with past work (Laffargue et al. 2006, Ferriss et al. 2021). The importance of habitats lacking vertical structure, or which have low vertical relief (such as bottom culture) was conspicuous in our study due to the sheer number of juvenile English sole in seines. English sole were our most sampled taxon (followed by shiner perch), with 2715 individuals captured via seines during the spring. The lengths of English sole increased between spring and summer (Table 2), suggesting that there is a cohort of newborn English sole in the spring, a fraction of which survive to be larger juveniles by summer. Like Dungeness crab, English sole are commercially important species that use the mudflat and bottom culture habitats as juveniles. Additionally, abundant young flatfish likely provide trophic resources for resident and migratory mesopredators, many of which would be preparing to reproduce. We highlight the importance of unstructured habitat, not to undermine the value of structured habitats, but to bring attention to an often overlooked feature of estuaries, and to suggest that a mosaic of habitat types supports overall productivity in Willapa Bay.

4.3. Fish abundance across eelgrass densities and culture types

Past studies suggest that overall nekton abundance is higher in structured habitats such as seagrass, oyster culture or reef, and salt marsh habitats (Dumbauld et al. 2009, França et al. 2009, Gross et al. 2019a, Muething et al. 2020, Grabowski et al. 2022). Between structured habitats, nekton abundance has also been documented to be higher in oyster culture habitats than seagrass (Dealteris et al. 2004, Pinnix et al. 2005), or similar between those habitat types (Hosack et al. 2006: slightly more in seagrass than oyster culture on average; Muething et al. 2020: more in suspended culture and eelgrass habitats than bottom culture). However, use of structured habitats is also reliant on the surrounding landscape (Grabowski et al. 2022). For example, elevated nekton abundance in seagrass may be more pronounced when fringing along channels than on wide tidal flats where most oyster culture occurs (Gross et al. 2019a), or some demersal fish may be more likely to use structured habitat with adjacent mudflat (Grabowski et al. 2022). Here, we found that eelgrass and oyster culture presence or absence affects nekton assemblage structure, but that eelgrass shoot density (i.e. degree of habitat structure) does not have a strong effect on overall fish abundance. Culture type (no culture, bottom culture, suspended culture) was shown to have a weak effect on fish abundance (Table 1), but was mostly influenced by low fish counts in suspended culture, which were likely affected by negative sampling bias (see above discussion and Fig. 6). These results continue to highlight the importance of less structured habitats for taxa that are often under-represented in studies due to their cryptic nature and common sampling methods. The presence of habitat generalists and those associated with unstructured habitats are likely driving this lack of association between eelgrass density and overall nekton abundance, and it is expected that a similar analysis just including eelgrass-associated species would show a correlation between eelgrass density and abundance, as seen in Belgrad et al. (2021).

4.4. Concluding remarks about habitat values and management applications

Our findings suggest that the presence of oyster culture in eelgrass habitats is not generally detrimental to the habitat value of eelgrass for nekton. Eelgrass specialists continued to use eelgrass habitat when oyster culture was present (with the exception of three-spine stickleback), structure-associated taxa used oyster culture with or without the presence of eelgrass, and some taxa that were negatively associated with vertical structure (suspended culture and eelgrass) were found to use oyster bottom culture habitats in addition to bare mudflat. However, in order for eelgrass to co-occur with oyster culture, oyster culture must be managed along 2 axes: density of oysters (for instance by low stocking densities or gaps in longlines) (Dumbauld et al. 2009, Tallis et al. 2009, Wagner et al. 2012), and intensity and frequency of disturbance. Processes such as dredging and trampling can occur in ways that limit negative impacts on eelgrass, for instance by small reductions in density or capacity for resilience (branching, seedling success) (Cabaço & Santos 2012, Dumbauld & McCoy 2015, Ferriss et al. 2019, Fales et al. 2020, F. C. Boardman unpubl. data). Existing management of shellfish aquaculture in Willapa Bay has generated a habitat mosaic on which we capitalized for the treatments in this study. Because of the variety of habitat associations among estuarine nekton, overall composition depends on including patches of bare unstructured mudflat, patches of eelgrass, patches of mixed eelgrass/oyster, and patches of oyster culture of different methods. This farmed seascape contains elements of the original habitat mosaic in this region and supports a diverse group of nekton across multiple life history stages.

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