



Spatiotemporal Dynamics of Eelgrass (*Zostera marina*), Oyster Aquaculture, and Channel-Fringing Habitat Provided to Managed Nekton Species Throughout Willapa Bay, WA, USA

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Abstract

In estuaries where native eelgrass (*Zostera marina*) and Pacific oyster (*Magallana gigas*) aquaculture co-occur along the US Pacific Coast, contemporary landscape-scale distributions are essential to properly assess the interaction between these habitats and balance priorities of eelgrass conservation and sustainable aquaculture. We classified eelgrass distribution and delineated active oyster aquaculture throughout Willapa Bay, WA, using orthoimagery to examine eelgrass coverage among aquaculture practices and compare current and historical estimates. Eelgrass covered an estimated 5550 ha (or 25.7%) of the intertidal area and had not substantially changed from that of 2009. Active oyster aquaculture encompassed approximately 3096 ha of intertidal area, wherein eelgrass coverage differed among aquaculture management practices ($p < 0.001$), exhibiting the highest proportional coverage (0.60) within off-bottom culture beds. Bottom-culture beds that were harvested mechanically contained lower proportional eelgrass coverage (0.27) than those harvested by hand (0.44, $p < 0.001$). We further demonstrated the utility of these landscape-scale datasets by integrating nekton data to develop novel abundance estimates for two managed nekton species within channel-fringing habitats. Estimated seasonal densities of juvenile Dungeness crab (*Metacarcinus magister*) and English sole (*Parophrys vetulus*) differed among aquaculture methods ($p \leq 0.03$, except for *P. vetulus* in spring ($p = 0.05$)), with bottom culture generally containing the highest densities of both species. Species densities did not differ between areas of eelgrass presence and absence. Collectively, channel-fringing habitat composed 9% of the estuary's expansive lower intertidal area and was estimated to support just 1.3–2.1% of the juvenile *M. magister* but a relatively high 13.6–23.5% of the juvenile *P. vetulus* throughout the same intertidal zone. These landscape-scale methodologies, datasets, and findings provide valuable information on the spatiotemporal dynamics of eelgrass and oyster aquaculture that can support stakeholder efforts to navigate the dual challenges of preserving eelgrass and supporting sustainable aquaculture.

Keywords Seagrass · Bivalve aquaculture · Dungeness crab · Estuarine habitat · Orthoimagery

Introduction

Estuaries of the Northeast (NE) Pacific are composed of a mosaic of habitats that support diverse faunal communities (Boardman et al., 2023; Ferraro & Cole, 2007; Hosack et al., 2006). Native seagrass (eelgrass, *Zostera marina*) is a primary contributor to this mosaic, with other intertidal constituents including burrowing shrimp populations, bare sediments, macroalgal mats, and in some estuaries, Pacific oyster (*Magallana gigas*) aquaculture. In estuaries where eelgrass and oyster aquaculture co-occur, these habitats are inextricably linked as they occupy the same intertidal elevation range (Dumbauld & McCoy, 2015), both provide structured nekton habitat (Boardman et al., 2023), and aquaculture is regulated for the benefit of eelgrass (Boardman et al.,

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2023; NMFS, 2017; NOAA, 2007; NOAA, 2011). Outdated or nonexistent estimates of eelgrass coverage and aquaculture distribution limit the potential to examine relationships between these estuarine habitats at both a habitat-specific level and throughout the mosaic of habitats at a landscape scale.

Eelgrass and Pacific oyster aquaculture have co-existed in estuaries of the US Pacific Coast for more than a century, each serving important ecological roles and offering substantial economic value. Pacific oysters were introduced to US aquaculture in the early twentieth century to replace native oysters (*Ostrea lurida*) populations that were depleted by the industry (reviewed by Dumbauld et al., 2009). Today, Washington state is the largest commercial oyster producer in the USA, generating an estimated \$184 million annually for the state economy (NMFS, 2024; Northern Economics 2013). Willapa Bay is the largest producer in the state, contributing 10–20% of the cultured oysters annually produced in the country (Lowe & Ruesink, 2021; Patten, 2014). Both oysters and eelgrass offer indirect economic value through the provision of essential ecosystem services, including improving water quality and cycling nutrients (Namba et al., 2018; Newell, 2004; Röhr et al., 2018; Sandoval-Gil et al., 2016; Wheat & Ruesink, 2013), stabilizing sediments against erosion (Hansen & Reidenbach, 2012; Meysick et al., 2022; Scyphers et al., 2011; Ysebaert et al. 2019), offering foraging habitat for shorebirds (Boardman & Ruesink, 2023; Connolly & Colwell, 2005; Frazier et al., 2014; Herbert et al., 2018), and providing structured habitat for nekton (Boardman et al., 2023; Muething et al., 2020; Veggerby et al., 2024).

Overlapping oyster aquaculture and eelgrass habitats exhibit mixed interactions that depend on the spatial and temporal scales considered, which present management considerations to balance sustainable industry and eelgrass conservation goals. At the scale of individual aquaculture beds, culture can reduce eelgrass density and biomass due to competition for space with on-bottom oysters (Tallis et al., 2009; Wagner et al., 2012), alter light and sediment dynamics through the placement of anthropogenic gear for off-bottom oysters (Ferriss et al., 2019; Forrest et al., 2009; Howarth et al., 2022), and cause periodic sediment disturbances from maintenance and harvesting activities like harrowing and mechanical harvest (Boardman & Ruesink, 2025; Dumbauld et al., 2009). Eelgrass can be highly resilient to biomass removal, including enhanced reproduction on aquaculture beds and rapid clonal branching at low density (Boardman & Ruesink, 2025; Ferriss et al., 2019; Ruesink, 2018; Wisheart et al., 2007). At larger spatial and temporal scales where areal extent is studied, oyster aquaculture may have little net impact on eelgrass distribution (Martin et al., 2010; Ward et al., 2003). In Willapa Bay,

WA, USA, prior modeling efforts estimated eelgrass distribution across aquaculture beds to be just 1.5% below expected distribution in the absence of aquaculture (Dumbauld & McCoy, 2015). Currently, US federal incentives promote the expansion of domestic aquaculture (Executive Office of the President 2020; NOAA, 2011), while federal regulations protect native eelgrass as essential fish habitat to counter global declines in seagrasses (NOAA, 2007, 2022; Unsworth et al., 2019; Waycott et al., 2009). These regulations restrict certain activities and expansions of aquaculture that overlap with eelgrass, creating complex permitting requirements for shellfish growers (NMFS, 2017). Competing values also present challenges for resource managers, policymakers, and shellfish growers as they seek adaptive solutions for preserving eelgrass while supporting sustainable aquaculture (Green et al., 2023; NMFS, 2017; Ward et al., 2003). Effectively balancing these priorities requires landscape-scale perspectives of eelgrass and aquaculture to assess the contemporary distribution and interaction of these habitats throughout the estuary.

In US Pacific Coast estuaries, economically important species like salmonids, English sole (*Parophrys vetulus*), and Dungeness crab (*Metacarcinus magister*) utilize both eelgrass and oyster culture as important nursery habitats (Boardman et al., 2023; Dumbauld et al., 2015; Holsman et al., 2006; Rooper et al., 2003). Different intertidal aquaculture methods provide distinct structures—bottom culture forms complex structure at or near the sediment surface, whereas off-bottom methods elevate oyster structure above the sediment (Dumbauld et al., 2009). Some nekton species associate with eelgrass and off-bottom aquaculture similarly, whereas other species favor the lower-profile structure provided by bottom culture (Boardman et al., 2023). Another consideration potentially modulating the use of these structured habitats is their occurrence in relation to tidal channels. Channel-fringing habitats, or edge habitats adjacent to estuarine channels, are recognized as unique contributors to the mosaic of estuarine nekton habitats (Bostrom et al. 2011; Gross et al., 2019; Smith et al., 2008; Visintainer et al., 2006), often containing a higher abundance and diversity of nekton taxa. Although the use of estuaries as nursery habitat is well accepted for economically valuable nekton of the US Pacific Coast (Hughes et al., 2014), productivity across these different components of the intertidal habitat mosaic has not been addressed.

Accurate distribution estimates are necessary to appropriately assess the status and relative contributions, both spatially and temporally, of these important habitats throughout the estuary. Landscape-scale estimates provide stakeholders valuable context in discussions, research, regulatory actions, and farming decisions that often take place at a much smaller scale. In Willapa Bay, an initial

habitat characterization of eelgrass and oyster aquaculture from the mid-to-late 2000s (Dumbauld & McCoy, 2015) supported stakeholders and the broader seagrass–aquaculture research field. However, the data and methodologies of that study are more than 15 years old, dynamic intertidal environments are constantly subject to natural and anthropogenic change, and methods for the capture and analysis of remotely sensed data have improved. Here, our objectives are to develop contemporary distribution estimates for both eelgrass and oyster aquaculture at the landscape scale, assess eelgrass distribution across specific culture-harvest practices, and compare current distribution estimates to those from the mid-to-late 2000s. Furthermore, we aim to demonstrate the utility of these landscape-scale habitat datasets to broadly address secondary ecological endpoints—production estimates for economically important fisheries species within channel-fringing habitats—using a proof-of-concept approach to integrate both bathymetric data and disparate nekton data (see Fig. 1 for workflow summary). We hypothesize that eelgrass coverage will differ among aquaculture types and harvest practices, with mechanically harvested aquaculture beds containing less eelgrass than hand-harvested beds. We further hypothesize that channel-fringing habitats will support greater densities of both *P. vetulus* and *M. magister* than adjacent tideflats.

Methods

Study Area

Willapa Bay—located in southwestern Washington State—is one of the largest estuaries on the US Pacific Coast (Hedgepeth & Obrebski, 1981; Hickey & Banas, 2003) and contains approximately 216 km² of intertidal flats (Fig. 2). Shellfish growers employ a variety of techniques to cultivate oysters in Willapa Bay, the most common being bottom culture, where oysters are grown directly on the seafloor (Dumbauld & McCoy, 2015). A more gear-intensive method is off-bottom culture, where oysters are suspended up to 1 m above the seafloor using stakes, longlines, bags, and baskets. In the southern part of the bay, oysters form hummocks—where growers actively place oyster shell on top of shell mounds or existing reefs to encourage natural settlement by larvae. Oysters are harvested either manually or mechanically: bottom-cultured oysters are hand-picked or mechanically “dredged” with metal bags dragged across the seafloor, off-bottom oysters are pulled by hand or with specialized equipment via boat, and hummocks are hand-picked for market-sized oysters, then re-shelled for the next set (Dumbauld et al., 2009; Trimble et al., 2009). The vast majority of oyster aquaculture in Willapa Bay

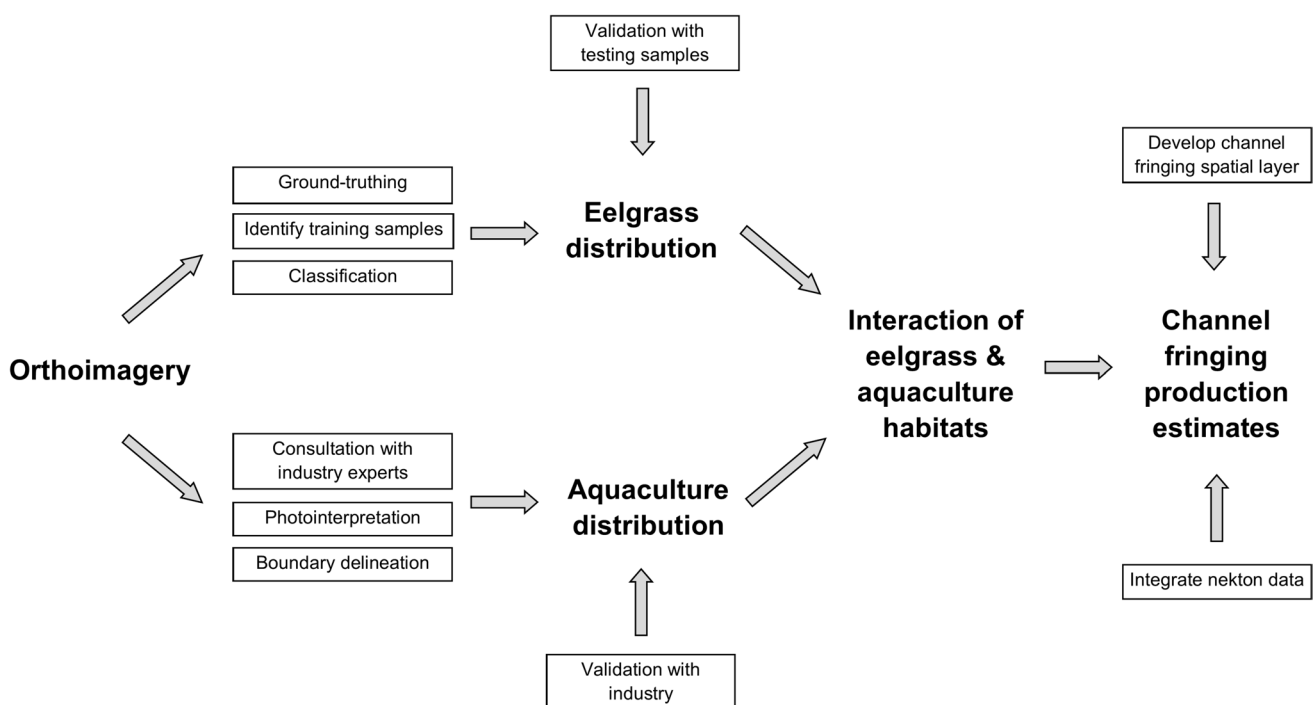


Fig. 1 Generalized workflow that provides a visual summary of the research, including products (in bold) and the methodological steps (in text boxes) required to develop each product

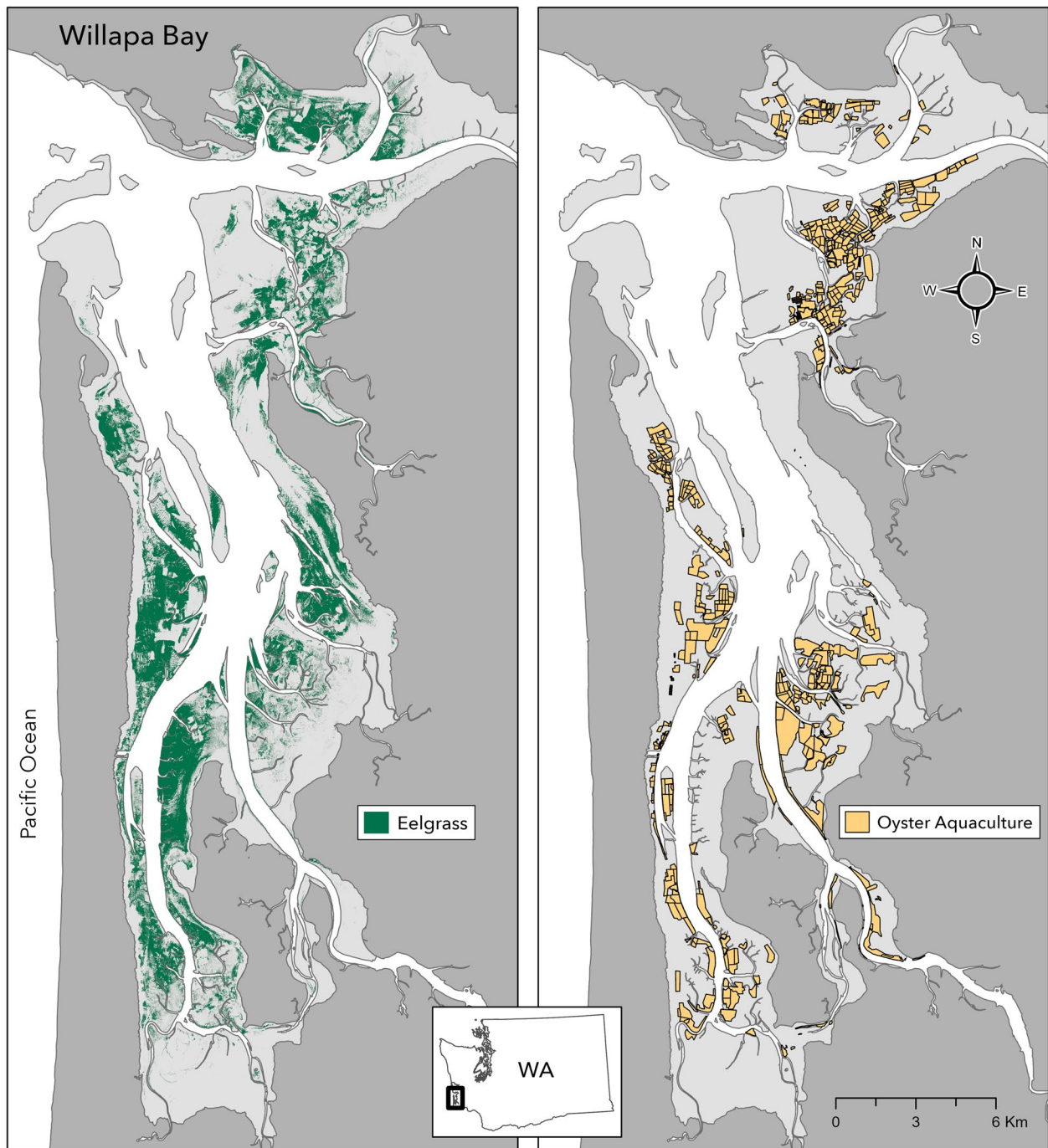


Fig. 2 Estimated distributions of eelgrass (*Zostera marina*; left panel) and active oyster (*Magallana gigas*) aquaculture (right panel) throughout Willapa Bay, WA, in 2020—both distributions were developed from 0.25 m² orthoimagery

occurs below elevations of 1.2 m MLLW (Dumbauld & McCoy, 2015), which is the upper observed threshold of native eelgrass (*Zostera marina*) in the estuary, although meadow formation typically occurs at tidal elevations < 0.6 m MLLW (Ruesink et al., 2010).

Orthoimagery

Contracted capture of orthoimagery was conducted during optimal conditions (low tide: −0.58 m MLLW, cloud cover: 0%, sun angle: 25–40°) on June 22, 2020, from a fixed-wing

aircraft (approximate altitude: 13,600 ft) using a Vexcel UltraCam Falcon P and produced to meet the positional accuracy standards (± 1.22 m @ 95% CI) of the American Society for Photogrammetry and Remote Sensing (ASPRS) for digital geospatial data in a 0.5 m RMSE_x/RMSE_y horizontal accuracy class. Orthorectified images had a pixel resolution of 0.25 m and were captured in 4-band, RGBIR. Images were mosaicked together in a single raster and resampled to 1 m cells to better account for location variability.

Eelgrass Classification

Ground-truthing was conducted in concert with the capture of orthoimagery to create a dataset from which habitat classification of the orthoimagery could be trained and validated. Sampling locations for ground-truthing were randomly established throughout the estuary using ArcGIS Pro 3.0. Distribution of sampling locations was proportionate between habitats with and without eelgrass, and limited to areas within 500 m of channels due to the large size of the estuary. Two teams of two people conducted the ground-truthing from June 22–26, 2020, during the lowest daily tides, which ranged from -0.58 to -0.34 m (MLLW). Samplers navigated to the target sampling locations, collected percent cover estimates of exposed habitat (e.g., *Zostera* spp., sediment) within a 1-m² quadrat, and recorded detailed location coordinates on Trimble handheld GPS units—GeoXT 6000 series (2.5 cm + 1.2 ppm) and Geo 7X (1 cm + 1 ppm). The resulting dataset contained 149 points to be used in the training and testing of the habitat classification.

Preliminary examination of the estuary-wide orthoimagery showed that slight regional differences in spectral characteristics were apparent, so for habitat classification, four regional orthoimagery rasters were extracted to improve classification of characteristics unique to each region. Factors contributing to photometric variation among regions included differences in sun angle at time of capture, leaf angle or density, and sediment with a higher infrared signature due to diatom accumulation or marsh runoff (Clinton et al. 2007; Young et al., 2010). Regional determinations were based on general differences in spectral characteristics by an experienced photointerpreter and delineated along natural breaks in the estuary (e.g., tidal channels). The orthoimagery rasters were constrained to the same *Z. marina* elevation threshold (< 1.2 m MLLW) surveyed by Dumbauld and McCoy (2015) to maintain consistency in the areas being classified.

Habitat classification was developed from a schema with nine classes or subclasses of habitat cover, including: eelgrass (light, vibrant, and dark), green macroalgae, sand (saturated, typical, and dry), mud, and water. Approximately 15% of ground-truthing samples were used to train

the classifier, each training sample contained $\geq 90\%$ cover of the habitat class being trained. Each training sample consisted of a circular area ($r = 5$ m; ~ 78.5 m²) encompassing the raster cells around a selected training point. Supervised, pixel-based classification was then conducted within each regional raster using a support vector machine (SVM) learning model (Mountrakis et al., 2011). Synthetic training samples—samples in which the habitat cover was inferred from the orthoimagery rather than by ground-truthing (Congalton, 1991)—were created to further distinguish habitat classes. No more than 50% of the training samples for any habitat class (except water) consisted of synthetic training samples, allowing $\geq 85\%$ of all ground-truthing samples to be retained for testing the final classification (see Supplementary Material for more details on classification training and development). No synthetic samples were used for testing, to remove undue influence of interpretation and uphold rigor of the validation process. Testing was conducted with a confusion matrix to assess user, producer, and total accuracy of the final classified habitat raster, as well as calculate Cohen's kappa—methods that have become standard for such assessments (Chand & Bollard, 2021; Congalton, 1991; Doukari & Topouzelis, 2022; O'Neill & Costa, 2013).

Aquaculture Delineation

A similar effort was conducted in 2006–2007 via extensive interviews with shellfish growers to determine the location of aquaculture beds and specific culture details, the results of which were synthesized in a GIS layer (Dumbauld & McCoy, 2015) and have remained the most comprehensive and oft-cited aquaculture distribution data for Willapa Bay to date. Evaluation in that effort was limited to “active” oyster aquaculture, which excluded inactive beds and partially active beds (where only a portion of the bed was active or used opportunistically). One aim of the current effort was to create an updated, comprehensive, and more spatially precise layer of active aquaculture by leveraging the estuary-wide orthoimagery captured in 2020. First, an experienced photointerpreter familiar with Willapa Bay analyzed the orthoimagery and digitized boundaries of active aquaculture beds (where oyster culture was present or harvest activity was evident) throughout the estuary. Aquaculture bed delineations were based on visible differences in color, texture, and shape, as well as physical boundary markers (e.g., PVC poles) when visible in the imagery. Human interpretation is advantageous for integrating spatial associations—at multiple scales—between these orthoimage parameters while also considering adjacent objects and information (see Young et al., 2010). Second, each bed was examined to determine culture species (clam or oyster), type (bottom, off-bottom, or hummocks), and harvest method (hand or mechanical); the training for which was largely based on the correspondence

between perceived texture in the imagery and the photointerpreter's ground-based knowledge of the aquaculture beds. During development, collaboration with the Willapa-Grays Harbor Oyster Growers Association (WGHOA) benefited the process by confirming bed categorizations or providing valuable information to help improve the photointerpreter's training process. Third, in areas of uncertainty, available aquaculture data were reviewed from county tax lot information, publicly available permit applications, and consultations with experienced stakeholders. Lastly, the final product was validated through a review by industry stakeholders.

Landscape-Scale Comparisons of Eelgrass and Oyster Aquaculture

Updated distributions of eelgrass and aquaculture throughout the estuary allowed the habitats to be compared spatially, temporally, and within the context of landscape-scale habitat provision. The elevation range of oyster aquaculture in Willapa Bay coincides with that of *Z. marina*; with 98.7% of observed active oyster culture occurring below the upper threshold of *Z. marina* (1.2 m MLLW), we generally limited our analyses to areas below that threshold. Distribution of each habitat was summarized to derive estuary-wide areal estimates (ha) of each habitat, and in the case of aquaculture, subcategorized by culture type and harvest method. Off-bottom aquaculture methods were grouped together due to the comparatively low occurrence of these methods in Willapa Bay. Total eelgrass coverage within the collective acreage of oyster aquaculture was then summarized by culture type and harvest method to observe differences potentially related to aquaculture practices. Similar summaries were produced for data from 2005 to 2009 (Dumbauld & McCoy, 2015), which provided a prior dataset to qualitatively compare against. Eelgrass distribution was also examined at the scale of individual aquaculture beds using a generalized linear model (GLM) ("glmmTMB" package; Brooks et al., 2024) with a beta distribution to analyze eelgrass coverage as a proportion of aquaculture bed area among unique combinations of culture types and harvest methods. We combined these attributes for bed-scale analysis because most culture types were harvested using only one method, thus the statistical comparison would not be fully crossed. To determine whether differences in the proportion of eelgrass coverage within beds existed among specific culture-harvest practices, an analysis of deviance via Wald chi-square test ("car" package; Fox et al., 2024) was first performed on the model output. Specific differences between predictor levels were then assessed with the GLM-produced estimated marginal means (EMMs)—which considered all variables in the model and accounted for sample size differences among predictors—and associated *z*-test significance testing.

Landscape-Scale Production of Managed Nekton Species from Channel-Fringing Habitats

Distribution estimates of eelgrass and oyster culture provided the opportunity to assess landscape-scale habitat provision for managed species of crab and fish when coupled with species-use data from within those habitats (similar to Armstrong et al., 2003; Lewis et al., 2021). To demonstrate this utility, we leveraged nekton data from a habitat-specific seining study in Willapa Bay, WA (Boardman et al., 2023), to estimate the landscape-scale production of juvenile *M. magister* and *P. vetulus* from these habitat types within channel-fringing portions of the estuary. Boardman et al. (2023) used a modified beach seine to capture nekton within multiple eelgrass and aquaculture habitats across six locations throughout the estuary ($n = 374$ seines spanning spring and summer of 2 years); however, the study was not designed to specifically evaluate the use of channel-fringing habitat by juvenile nekton. Such an assessment required that channel-fringing habitats first be identified, so geospatial layers were developed to model physical estuarine attributes that often describe or define these habitats adjacent to channels, including bathymetric elevation, bathymetric slope, distance to channel, and channel order (Dowty et al., 2005; Gross et al., 2019; Visintainer et al., 2006). These physical geospatial data were then examined against the structure of available nekton data to identify confounding issues between potential fringe habitat attributes and nekton sampling locations. Distance to channel was identified as the only suitable identifier of channel-fringing habitat. Existing studies in Washington State broadly interpret fringe habitats to exist within tens of meters of channel edges, reaching up to 100 m in perpendicular distance (Dowty et al., 2005; Gross et al., 2019). We established a distance of 25 m from the channel edge as the threshold between fringe and non-fringe habitats to encompass sufficient nekton sampling sites ($n = 76$), while remaining close enough to channels to minimize inclusion of broad intertidal flat habitat.

Seasonal differences in community composition were noted in Boardman et al. (2023), which we confirmed within the subset of channel-fringing nekton data using NMDS coupled with PERMANOVAs ("vegan" package; Oksanen et al., 2024). Kruskal–Wallis tests ("stats" package; R Development Core Team, 2024) were then applied to *M. magister* and *P. vetulus* counts to determine that seasonal differences also existed among each of these species. Therefore, fringe datasets were further categorized by season (i.e., spring vs. summer) for each species. We assessed each seasonal fringe dataset for interaction effects between eelgrass (presence/absence) and oyster aquaculture method (none, bottom, or off-bottom), however, limited crossed-factor sample sizes led to overparameterization, so we assumed there was no eelgrass $\times$ aquaculture interaction effect, as we found to be

generally true in the larger seasonal datasets for each species (not limited to fringe habitats), and as Boardman et al. (2023) found at the community level. Seasonal count data for each species were modeled with a generalized linear mixed model (GLMM) (“glmmTMB” package; Brooks et al., 2024) within both fringe and non-fringe areas using the categorical habitat variables, eelgrass (present/absent) and oyster aquaculture (none, bottom, or off-bottom), with location as a random variable. An analysis of deviance (via Wald chi-square test) was performed on the output of each seasonal species model to determine whether eelgrass presence or oyster aquaculture type affected abundance. Output coefficients (i.e., EMMs) from both fringe and non-fringe seasonal count models (“emmeans” package; Lenth et al., 2024) were exponentiated to produce expected counts for each specific habitat type, which were then applied to areal estimates of fringe and non-fringe habitats—produced from geospatial distribution layers—to develop expected habitat production estimates for each species at the landscape scale.

Results

Eelgrass Distribution

Validation of the 2020 classified eelgrass raster produced an overall accuracy of 85% and a Cohen’s kappa statistic of 0.70, indicating substantial agreement between the eelgrass classification and the ground-truthed habitat dataset.

The classified eelgrass distribution (Fig. 2) showed that eelgrass covered an estimated 5550 ha of intertidal area at tide heights < 1.2 m MLLW (Table 1), which was 32.8% of the intertidal area below 1.2 m MLLW, or 25.7% of the total intertidal area. Intertidal eelgrass coverage throughout the entire estuary decreased marginally from the most recent estimate in 2009 (27.6%) and from the average coverage between 2005 and 2009 (32.3%), but was still within estimated ranges presented in the literature (Dumbauld & McCoy, 2015; Ruesink et al., 2006). Estimated eelgrass coverage in areas that were both outside of oyster aquaculture and < 1.2 m MLLW in elevation decreased from 38.3 in 2009 to 32.9% in 2020, indicating that interannual decreases also occurred in areas not directly influenced by aquaculture practices.

Aquaculture Distribution

Delineation of 2020 intertidal aquaculture encompassed an estimated area of 3818 ha (Fig. 2) that was actively being used to culture bivalves, the majority of which (3096 ha) was dedicated to Pacific oysters at tide heights < 1.2 m MLLW (Table 1). The total area encompassed by bivalve aquaculture decreased by 1070 ha from the estimate developed in 2006–2007 (Dumbauld & McCoy, 2015), whereas active oyster culture increased by 1332 ha; most of these changes in culture area were likely due to improvements in delineation methodology and accuracy. Active oyster aquaculture comprised 14.4% of the entire intertidal area and 18.3% of the

Table 1 Estimates of the collective area cultured for oysters (*Magallana gigas*) among harvest methods and culture types, as well as the total eelgrass (*Zostera marina*) area contained within respective harvest methods and culture types, for both the 2000s data (via Dum-

bould & McCoy, 2015) and the present (2020) data. Also provided are estimates of the respective percentages comprised by eelgrass in relation to total areas of estuarine eelgrass and culture management practices

	Oyster aquaculture (< 1.2 m MLLW)		Eelgrass (< 1.2 m MLLW)					
	Area (ha)		Area (ha)		% of total eelgrass area		% of total harvest method (or culture type) area	
Oyster harvest method	2006–2007	2020	2009	2020	2009	2020	2009	2020
Mechanical	876.4	1645.8	416.9	453.2	7.0%	8.2%	47.6%	
Hand-picked	554.2	1450.1	224.3	541.3	3.8%	9.8%	40.5%	37.3%
Mixed	328.9		140.2		2.4%		42.6%	
Unknown	4.7		2.5		0.0%		53.2%	
None (outside of aquaculture)	~ 13,450	13,827	5154	4555	86.8%	82.1%	38.3%	32.9%
Total	15,214	16,923	5938	5550				
Oyster culture type								
Bottom culture	1501.6	2259.5	646.7	733.8	10.9%	13.2%	43.1%	32.5%
Hummocks	3.3	580.5	0.8	137.5	0.0%	2.5%	24.2%	23.7%
Off-bottom culture	66.2	193.8	31	102.1	0.5%	1.8%	46.8%	52.7%
Mixed	168.1	62.2	90.4	21.2	1.5%	0.4%	53.8%	34.1%
Unknown	25.1		15		0.3%		59.8%	
Total	1764	3096	784	995				

intertidal area < 1.2 m MLLW, similar to previous estimates by Feldman et al. (2000) and Dumbauld et al. (2009). Bottom culture and hummocks accounted for 73% and 18.8% of active oyster aquaculture, respectively, whereas off-bottom culture collectively comprised 6.3% of observed aquaculture, an increase of 3.8% from the 2009 estimate presented by Dumbauld and McCoy (2015).

Interaction of Eelgrass and Aquaculture at a Landscape Scale

Total intertidal eelgrass coverage across collective oyster aquaculture acreage varied among culture types and harvest methods in 2020. In intertidal areas outside of aquaculture, eelgrass comprised 32.9% of the collective area < 1.2 m MLLW, providing a contextual baseline against which to qualitatively contrast the coverage of eelgrass within different culture types and harvest methods. Similarly, 32.2% of the aggregate area of active oyster aquaculture < 1.2 m MLLW was occupied by eelgrass. The total area with observed off-bottom oyster culture contained the highest percentage of eelgrass among defined culture types, followed by bottom culture and hummocks (Table 1). Collectively, the area of mechanically harvested oyster culture contained 27.5% eelgrass by area, compared to 37.3% for the total area of hand-harvested culture.

Coverage of eelgrass by proportion of aquaculture bed area also differed among specific culture-harvest practices ($p < 0.001$, analysis of deviance). GLM output showed that off-bottom culture (harvested only by hand) was estimated

to contain the highest average proportion of eelgrass (0.60) among culture-harvest practices (all comparisons: $p < 0.001$), followed by hand-harvested bottom culture (0.44), hand-harvested hummocks (0.29), and mechanically harvested bottom culture (0.27). Bottom culture was the only culture type that allowed for a direct comparison between harvest methods, showing that mechanically harvested beds had a significantly lower estimated proportion of eelgrass than those harvested by hand (z -value = 6.05, $p < 0.001$).

Production of Managed Nekton Species from Channel-Fringing Habitats

Composition of eelgrass and aquaculture habitats within channel-fringing areas (< 25 m from channels) was quite similar to that outside of channel-fringing areas, and specific combinations of those habitat types differed only slightly in areal composition between fringe and non-fringe areas (Table 2)—see Fig. 3 for an example of the intersection between channel-fringing areas, eelgrass, and aquaculture. Fringe areas composed 9% (or 1514 ha) of the lower intertidal area (< 1.2 m MLLW) of Willapa Bay, wherein community composition of nekton displayed seasonal differences between spring and summer ($R^2 = 0.159$, $p < 0.001$, PERMANOVA), as did counts of *P. vetulus* ($p < 0.001$, Kruskal–Wallis test) and *M. magister* ($p = 0.05$, Kruskal–Wallis test). To focus on the effects of eelgrass and aquaculture within channel-fringing areas, we minimized variation within the dataset by analyzing the data within seasons via GLMM and including location as a random variable rather than a fixed variable. Seasonal counts

Table 2 Estimated total coverage (ha) of eelgrass (*Zostera marina*) and oyster (*Magallana gigas*) aquaculture habitats within both fringe (< 25 m of channels) and non-fringe (> 25 m of channels) areas of Willapa Bay, WA, as well as the specific habitat combinations used to produce landscape-scale abundance estimates for Dungeness crab (*Metacarcinus magister*) and English sole (*Parophrys vetulus*)

	Fringe habitat totals (< 25 m of channels)		Non-fringe habitat totals (> 25 m of channels)	
	Area (ha)	% of total fringe area	Area (ha)	% of total non-fringe area
Total area	1514	—	15,410	—
Eelgrass (total)	389	25.66	5162	33.50
On-bottom culture (total)	173	11.44	2667	17.31
Off-bottom culture (total)	7	0.47	187	1.21
Eelgrass × on-bottom culture	128	8.45	765	4.97
Eelgrass × off-bottom culture	6	0.42	96	0.62
Eelgrass only	254	16.79	4301	27.91
On-bottom culture only	45	2.99	1,902	12.34
Off-bottom culture only	1	0.05	91	0.59
Bare habitat (no eelgrass or aquaculture)	1080	71.30	8255	53.57

throughout the expansive lower intertidal. Areal estimates were calculated from eelgrass and aquaculture distribution layers using the habitat categories in which Boardman et al. (2023) sampled nekton. Hummocks were grouped with on-bottom culture as the most compatible structural habitat category for this estimation, as no hummock category existed in Boardman et al. (2023)

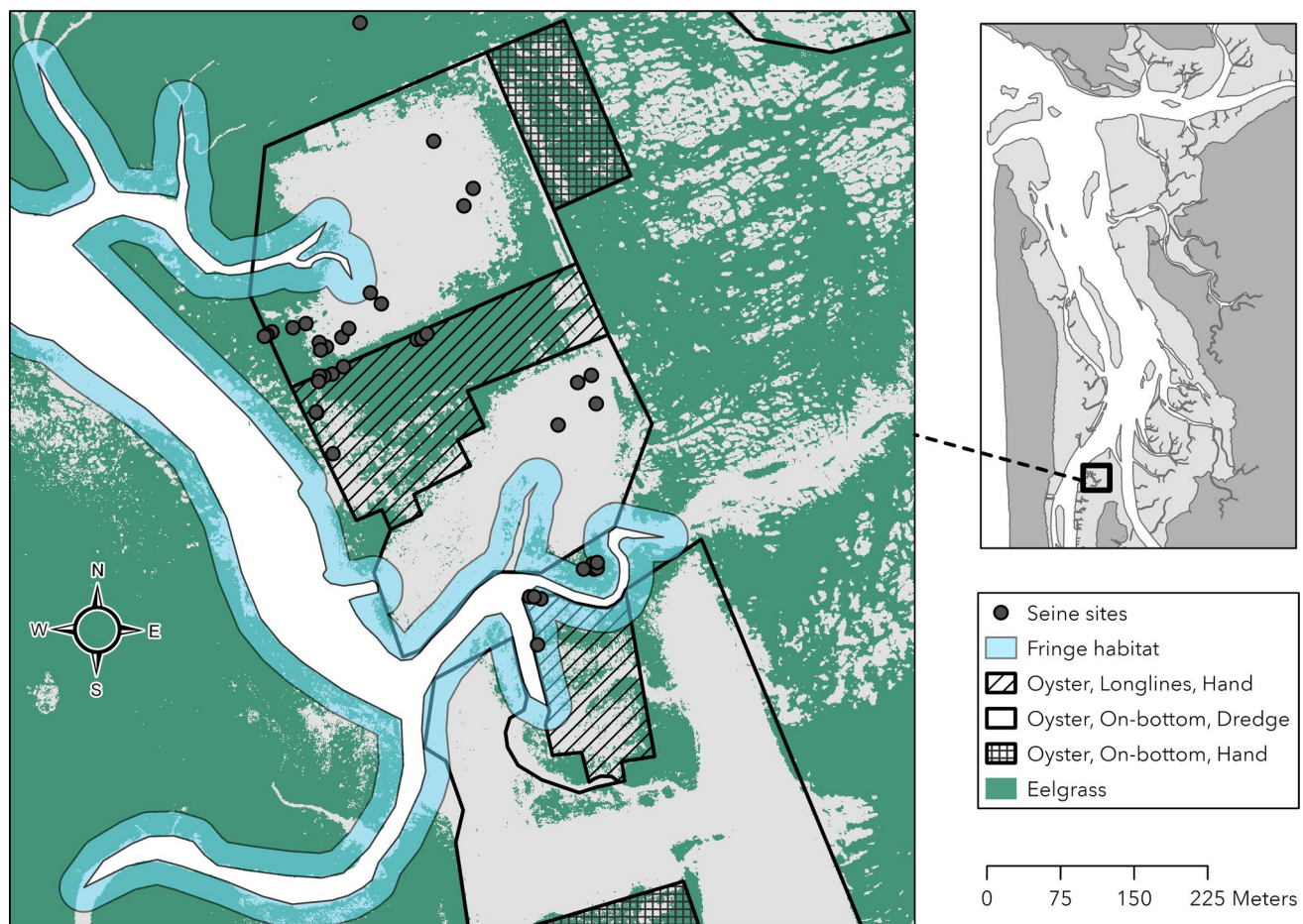


Fig. 3 Subsection of Willapa Bay, WA, that provides a visual example of the intersection of channel-fringing area (<25 m from channels), eelgrass (*Zostera marina*) distribution, and multiple oyster

(*Magallana gigas*) beds of varying culture practices. Also included are the locations of seine sites in this particular location

for both species differed among aquaculture types (analysis of deviance comparisons: $p \leq 0.03$, except for *P. vetulus* in spring; $p = 0.05$). Model output showed evidence of a positive effect of bottom culture on the estimated densities of both species in each season (all comparisons: $p \leq 0.03$), apart from springtime when the estimated bottom culture densities of *M. magister* and *P. vetulus* were not significantly greater than those within off-bottom culture and areas without culture, respectively. Habitats with bottom culture generally contained the highest estimated densities (or expected counts m^{-2} from GLMM output) among habitats within seasons for both species of interest (Table 3). No significant differences in estimated density were observed for either species between areas of eelgrass presence and absence, although *P. vetulus* densities were nearly higher within eelgrass habitats during the summer season ($p = 0.07$, analysis of deviance). Application of habitat-specific expected densities to the corresponding area estimates for specific habitats, both inside and outside of channel-fringing habitats, produced expected abundance estimates for each species at the estuary scale (Tables 3 and 4).

Metacarcinus magister had higher expected densities in fringe habitat types containing aquaculture than in corresponding non-fringe habitat types during the spring, whereas summer expected densities were lower in most fringe habitat types compared to corresponding non-fringe habitats. Conversely, *P. vetulus* had higher expected densities within all fringe habitat types than in corresponding non-fringe habitats during both seasons. Channel-fringing habitats were collectively estimated to support 1.3–2.1% of the juvenile *M. magister* and 13.6–23.5% of the *P. vetulus* throughout the expansive lower intertidal area, depending on season, suggesting that *M. magister* is less reliant upon fringe habitats than *P. vetulus*.

Discussion

Eelgrass and oyster aquaculture co-occur throughout Willapa Bay much as they have for decades; the landscape-scale distributions of these habitats have not substantially changed from those 15–20 years ago. Total estuarine eelgrass area

Table 3 Seasonal count and abundance estimates for Dungeness crab (*Metacarcinus magister*) and English sole (*Parophrys vetulus*) per m² of specific channel-fringing habitat type, total area of fringe habitat type, and collective area of intertidal fringe habitat

	Abundance per habitat type														Collective intertidal estimates	
	Expected count m ⁻²															
	Eelgrass × on-bottom	Eelgrass × off-bottom	Eelgrass × no aqua	Bare × on-bottom	Bare × off-bottom	Bare × no aqua	Eelgrass × on-bottom (128 ha)	Eelgrass × off-bottom (6 ha)	Eelgrass × no aqua (254 ha)	Bare × on-bottom (45 ha)	Bare × off-bottom (1 ha)	Bare × no aqua (1080 ha)	Total fringe abundance	Proportion of total abundance		
<i>M. magister</i> (spring)	0.009	0.047	0.001	0.009	0.047	0.001	12,022	2819	2807	4184	465	11,934	34,231	0.013		
<i>M. magister</i> (summer)	0.134	0.013	0.007	0.087	0.008	0.005	171,867	753	18,954	39,305	81	52,426	283,386	0.021		
<i>P. vetulus</i> (spring)	2.807	0.620	1.669	3.533	0.780	2.121	3,592,918	37,205	4,238,752	1,589,782	7804	22,911,772	32,378,233	0.136		
<i>P. vetulus</i> (summer)	0.189	0.020	0.040	0.871	0.093	0.185	241,464	1205	101,700	392,035	927	1,997,010	2,734,341	0.235		

Expected count m⁻² = exponentiated model results from seasonal GLMMs. Abundance per habitat type = expected count m⁻² × total area of fringe habitat type. Collective intertidal estimates show the summarized fringe habitat abundances and the fringe proportion of estuary-wide abundance throughout the lower intertidal. Aqua, aquaculture

Table 4 Seasonal count and abundance estimates in non-fringe intertidal habitat for Dungeness crab (*Metacarcinus magister*) and English sole (*Parophrys vetulus*) per m² of specific habitat type, total area of habitat type, and collective area of non-fringe habitat

	Expected count m ⁻²		Abundance per habitat type								Collective intertidal estimates			
	Eelgrass × on-bottom	Eelgrass × off-bottom	Eelgrass × no aqua	Bare × on-bottom	Bare × off-bottom	Bare × no aqua	Eelgrass × on-bottom (765 ha)	Eelgrass × off-bottom (96 ha)	Eelgrass × no aqua (4301 ha)	Bare × on-bottom (1902 ha)	Bare × off-bottom (91 ha)	Bare × no aqua (8255 ha)	Total non-fringe abundance	Proportion of total abundance
<i>M. magister</i> (spring)	0.005	0.014	0.021	0.005	0.012	0.018	41,453	13,723	908,044	86,952	10,974	1,485,140	2,546,286	0.987
<i>M. magister</i> (summer)	0.090	0.024	0.063	0.125	0.032	0.087	688,535	22,625	2,727,914	2,381,179	29,534	7,210,288	13,060,075	0.979
<i>P. vetulus</i> (spring)	0.898	0.344	1.394	0.934	0.358	1.451	6,867,570	329,982	59,951,588	17,771,495	325,561	119,762,294	205,008,490	0.864
<i>P. vetulus</i> (summer)	0.041	0.012	0.032	0.086	0.025	0.067	312,488	11,577	1,382,008	1,628,396	23,001	5,559,504	8,916,974	0.765

Expected count m⁻² = exponentiated model results from seasonal GLMMs. Abundance per habitat type = expected count m⁻² × total area of non-fringe habitat type. Collective intertidal estimates show the summarized non-fringe habitat abundances and the non-fringe proportion of the estuary-wide abundance throughout the lower intertidal. Aqua, aquaculture

decreased from 2009 by approximately 2%, which is minimal at a decadal interval, considering the change is substantially less than the interannual decrease of 11.2% estimated from 2005 to 2009 by Dumbauld and McCoy (2015). Total oyster aquaculture area decreased by approximately 10% from 2006–2007 to 2020; however, the 2006–2007 estimate included areas designated as partially active, mixed, or unknown culture/harvest (Dumbauld & McCoy, 2015). The dynamic interaction between eelgrass and oyster aquaculture across beds was, not surprisingly, influenced by specific culture-harvest practices. However, the observed impact that aquaculture had on eelgrass distribution at the landscape scale appeared minor. For instance, consider the difference in eelgrass coverage throughout the estuary if mechanically harvested oyster beds were converted to natural intertidal areas without aquaculture. In the intertidal elevation range that these habitats share, mechanically harvested oyster culture collectively contained 5.4% less eelgrass cover (by percent area) than natural areas outside of oyster aquaculture, which equates to 89 ha of the mechanically harvested area or approximately 1.6% of all eelgrass observed in the estuary. Although oyster aquaculture practices had significant effects on eelgrass coverage at the bed scale, the degree of impact at the landscape scale appears limited by the current extent of aquaculture within the bay and the minor differences in eelgrass coverage between cultured ground and non-cultured ground.

Methodological Improvements and Considerations

The classification of seagrasses from orthoimagery has improved the accuracy of distribution estimates over the last two decades (Doukari & Topouzelis, 2022; Klemas, 2016); but sources of variability and uncertainty still exist that require acknowledgement in any such effort, primarily relating to photometric variation as well as associated training and testing datasets. Appropriate methodologies for image capture, orthorectification, and mosaicking can limit intraphoto and interphoto variation or distortion due to technological or procedural causes; however, variation caused by environmental factors (e.g., sun angle, epiphyte presence, eelgrass blade angle/density, sediment variation, and presence/absence of moisture) is more difficult to explicitly account for (Young et al., 2010). We limited the impact of this variation by classifying habitat regionally within the estuary and creating subclasses to better capture the full range of spectral characteristics for each habitat type and minimize misclassifications. Imperative to minimizing misclassifications is the development of suitable training and testing datasets, which provide the foundation for habitat and spectral reflectance associations as well as the framework for validating the final classified product (Congalton, 1991). These datasets should ideally be developed from

secondary ground-truthing surveys, which can be difficult to comprehensively do with time and effort constraints when conducting an estuary-wide intertidal ground-truthing survey. However, Chand and Bollard (2021) argue that high-resolution data from unmanned aerial systems (UAS) have sufficient detail to visually assess accuracy. Survey limitations required us to restrict the quantity and distribution of ground-truthing locations, which could have impacted classification accuracy, particularly in areas not surveyed—notably, intertidal areas < 1.2 m in elevation that were > 500 m from tidal channels. Although training data were supplemented with a limited quantity of synthetic training points, the testing data were composed only of those ground-truthed data in order to appropriately exclude photointerpretation from that process and maintain independence of the dataset. Inclusion of synthetic testing points (interpreted from the orthoimagery) could potentially influence validation statistics and unduly inflate user confidence in a classified product in two primary ways: 1) the synthetic testing dataset could contain points where habitat types were misinterpreted from the orthoimagery, leading to validation inaccuracy (Congalton, 1991); 2) an excessive quantity of synthetic points included in testing could lead to exaggerated precision and accuracy statistics without definitive field confirmation of habitat types. The empirical validation process—and subsequent results—of the classified eelgrass distribution against the field-verified testing dataset provide end-users assurance in the rigor and accuracy of the final product.

The associated scale and resolution of airplane-captured orthoimagery were best suited for this research effort, as they provided a low tide snapshot in time of the entire estuary at a resolution that we demonstrated to be effective at discerning between habitats of interest. Utilization of aerial orthoimagery in seagrass research has increased substantially in recent years as technological advances have made these tools more accessible and affordable to researchers (Chand & Bollard, 2021). The various platforms (e.g., UAS, aircraft, and satellite) used to capture orthoimagery all provide valuable data, however, the associated cost and time required for capture can dictate the choice of platform for resource-limited organizations (Doukari & Topouzelis, 2022; Nahirnick et al., 2019). When considering the suite of platforms, the most important factors are scale and resolution, ensuring the platform of choice provides sufficient detail and coverage (spatially and temporally) to address the research question of interest, given the available resources (Dahdouh-Guebas, 2002; O'Neill & Costa, 2013; Young et al., 2010). Unmanned aerial systems provide unparalleled detail (cm^2) and accessibility but are limited on a single flight to the small scale (1000s of m^2) of an eelgrass bed or aquaculture lease (Doukari & Topouzelis, 2022). Satellites offer the broadest spatial coverage (1000s of km^2), typically at resolutions of 10–30 m^2 for affordable research uses,

which may obscure habitat details and interactions of interest in small estuaries (Chand & Bollard, 2021). Fixed-wing aircraft occupy a niche at the scale of an estuary (100s of km²), providing resolutions at or near 0.25 m², but often with higher cost and more weather limitations than other platforms. There is no one-size-fits-all approach or platform to capture orthoimagery for the purpose of mapping benthic habitats—that determination should be driven by the goals, timeline, and budget of the effort. However, we emphasize that all classification efforts require accuracy assessment to be considered valid for user interpretation (Congalton, 1991).

Methodological improvements to the delineation of active aquaculture boundaries and determination of culture/harvest details allowed for more representative aquaculture estimates than previous efforts. Dumbauld and McCoy (2015) developed aquaculture estimates throughout Willapa Bay in the mid-to-late 2000s using the best available science and orthoimages at the time, however, they relied on interviews with industry members, and many aquaculture beds were broadly designated as partially active, mixed culture/harvest, or unknown culture/harvest due to this methodology, which required the authors to remove those beds (approximately 49% of mapped oyster aquaculture) from consideration within the active oyster aquaculture estimates and analyses. Utilizing photointerpretation and digitization of contemporary orthoimagery in the present study allowed for the inclusion of more cultured area, as there was sufficient detail to better determine the activity, culture, and harvest within areas of the estuary that were previously underrepresented due to their designation as partially active, mixed, or unknown. Hummocks were particularly underrepresented in the 2006–2007 aquaculture layer because they were often designated as partially active and mixed culture. The area dedicated to off-bottom aquaculture methods increased nearly threefold from the mid-2000s to 2020, an increase that we expect accurately reflects a slight shift in culture practice given the easy identification of those collective culture types from orthoimagery. Estimates produced by the comprehensive aquaculture dataset provide a means to accurately account for benthic oyster structure, quantify the distribution of eelgrass among culture management practices, and compare the provision of nekton habitat among these structured habitat types.

Landscape-Scale Interaction of Eelgrass and Aquaculture—Contemporary vs. Historic

Landscape-scale summary statistics suggest that percent eelgrass coverage within mechanically harvested aquaculture substantially decreased (by approximately 20%) between 2009 and 2020 (Table 1); however, we posit the magnitude of this difference is mostly spurious. Potentially accounting

for an initial portion of the interannual decrease observed in mechanically harvested beds was the slight bay-wide decrease in eelgrass outside of aquaculture. In addition, aquaculture beds designated as active in the mid-2000s by Dumbauld and McCoy (2015) may not have included beds in areas less suitable for eelgrass due to designation as “inactive” or “mixed” (e.g., on-bottom culture mixed with hummocks); thus, average eelgrass cover could have been inflated. Relevant to this argument is that, by 2009 cover estimates, mechanically harvested oyster acreage was estimated to have the highest coverage of eelgrass (by total percent area) among defined harvest methods, including natural areas outside of aquaculture. When 2009 cover data were analyzed among beds with the same methodology as the 2020 data (i.e., GLM followed by analysis of deviance), no significant differences were observed in eelgrass coverage (as a proportion of bed area) among specific culture-harvest practices. On- and off-bottom oyster beds harvested by hand had similarly high proportions of eelgrass, 0.49 and 0.46 respectively, as did mechanically harvested bottom culture beds (0.47). We suspect that higher-than-expected eelgrass coverage within mechanically harvested beds during 2009 was, in part, a product of that classification process. Aquaculture beds were underrepresented in the 2009 eelgrass classification, potentially leading to a higher proportion of misclassified cells within those areas. The ground-truthing dataset used by Dumbauld and McCoy (2015) to develop eelgrass distribution estimates was largely conducted (via hovercraft) outside of active aquaculture beds to avoid interfering with active culture, which resulted in a disproportionately low quantity of training points within aquaculture beds. Ground-truthing for that effort was also conducted throughout the summer months of 2006 and 2007, which could have further increased misclassification of the 2009 orthoimagery (captured in June 2009) due to natural variability of eelgrass in the bay, both seasonally and annually. Orthoimages captured at different time periods generally require unique training and testing datasets due to differences that exist in environmental factors, such as ephemeral blooms of green macroalgae or diatoms.

Although eelgrass distribution differed among culture-harvest practices, the specific impacts of bed management on eelgrass are more difficult to explicitly quantify. Physical removal of eelgrass as a result of mechanical oyster harvest—albeit a minimal quantity at the landscape scale—is a direct and obvious impact at the bed scale; however, cultured bivalves also impact eelgrass by less direct or indirect means, both positively and negatively. Reviews that jointly evaluated hundreds of studies on bivalve-seagrass interactions found that approximately 50% reported positive interactions through various pathways (Fales et al., 2020; Gagnon et al., 2020). For example, bivalves can facilitate seagrasses by attenuating waves to stabilize sediment and enhance seed

retention (Meysick et al., 2019; Smith et al., 2009), filtering water to increase light availability (Newell & Koch, 2004), and cycling nutrients that fertilize sediments (Newell et al., 2002; Peterson & Heck, 2001; Reusch et al., 1994). Areal coverage of eelgrass was greater within manually harvested culture and off-bottom culture acreage compared to other harvest methods and culture types, as well as the collective area outside of oyster aquaculture. However, there are potential factors that might dictate culture management decisions (see Dumbauld et al., 2009) in areas that are naturally more or less beneficial to eelgrass (e.g., along elevation and salinity gradients), which could confound interpretation of these eelgrass-aquaculture interactions.

Eelgrass classification of remotely sensed imagery only captures the above-ground presence of plants; however, the below-ground (non-visible) portion of the plant plays a pivotal role in resilience and resistance of eelgrass to disturbances such as aquaculture (Cabaço & Santos, 2012; Ruesink et al., 2024; Vermaat, 2009). Bottom oyster culture was shown by Ruesink et al. (2024) to decrease the above-ground traits (e.g., size) of the plant while below-ground traits (e.g., biomass) were maintained, indicating that eelgrass retained its capacity for resistance. The authors also noted that bottom culture increased the flowering and rhizome expansion of eelgrass. Similarly, a global meta-analysis conducted by Ferriss et al. (2019) showed that while bottom culture decreased eelgrass density, growth and reproduction metrics increased. Timing and intensity of harvest-related disturbance are important factors that can influence the degree of impact that harvest has on eelgrass resilience (Boardman & Ruesink, 2025). Mechanically harvested bottom culture beds have the potential to act as productive locations for eelgrass seed production and storage post-disturbance (Wisehart et al., 2007), as well as areas of increased seedling growth and survival among aquaculture types, albeit primarily due to removal of competition (Tallis et al., 2009; Wisehart et al., 2007). Alternatively, off-bottom culture relies on placement of structures that can impede eelgrass, primarily via light limitation and sedimentation, and this culture-eelgrass interaction has also been shown to decrease above-ground traits and some below-ground traits in eelgrass (Everett et al., 1995; Ferriss et al., 2019; Ruesink et al., 2024; Wisehart et al., 2007). In the present study, off-bottom aquaculture was estimated to contain the highest eelgrass cover among culture types. In areas where off-bottom culture structures (i.e., stakes, lines, and bags), eelgrass, and macroalgae were co-mingled, classification could have encountered difficulty discerning between these spectral signatures in small areas, potentially decreasing accuracy. However, this contrasting result is more likely due to effect modulation in off-bottom culture at the local or regional scale that was found in previous studies (Ferriss et al., 2019; Ruesink et al., 2024).

Below-ground and reproductive traits of eelgrass within Willapa Bay aquaculture beds may have increased to mitigate disturbance, potentially indicated by the relative temporal stability in eelgrass coverage throughout the entire estuary.

A non-native eelgrass species, *Zostera japonica*, also exists in the upper intertidal areas of many US Pacific Coast estuaries, inhabiting higher elevations than *Z. marina* (Ruesink et al., 2006; Young et al., 2015). Differentiating *Z. marina* from *Z. japonica* via classification of four-band orthoimagery at the landscape scale is extremely difficult due to nearly identical spectral characteristics (Dumbauld & McCoy, 2015; Young et al., 2015). We used the same elevation established by Dumbauld and McCoy (2015) as a maximum threshold for classification to avoid the upper intertidal where the majority of *Z. japonica* beds occur, which allowed us to compare our eelgrass distribution directly with the distribution from that study. This methodology minimized the signature of *Z. japonica* within the classification but did not entirely preclude its inclusion; as the elevation ranges of the congeners have been observed to overlap within the upper elevation range of *Z. marina* (Ruesink et al., 2010), where *Z. marina* exists in depressions and narrow drainage channels (Dumbauld & McCoy, 2015). Thus, the classified *Z. marina* distribution presented here could be slightly inflated at its upper elevation range if the classification included sparse *Z. japonica* below its contiguous distribution. We anticipate any inflation to be minor and also present in the Dumbauld and McCoy (2015) classification against which we compared.

Differences between classification methods could have contributed to differences observed between the interannual (2009 vs. 2020) estimates of eelgrass coverage among aquaculture management practices. The aforementioned differences in ground-truthing datasets (i.e., age relative to orthoimagery and distribution within aquaculture beds) could certainly impact the resulting classification, as could differences in cover estimation methods. Dumbauld and McCoy (2015) estimated eelgrass density categorically at each ground-truthing station (~10 m² area) into one of four bins and used those densities to train the classification process, in which cells were classified as probable eelgrass cover, subsequently taken to be eelgrass area (e.g., 0.5 probable cover × 1 m² cell = 0.5 m² eelgrass area). Classified estimates were then used to statistically model eelgrass distribution from input habitat variables and ultimately contrast differences between the modeled and classified eelgrass estimates within aquaculture beds. Despite the methodological differences between studies, resulting eelgrass distribution estimates at the landscape scale were quite similar, and we suspect that differences due to these methodological aspects were more evident at smaller scales.

Production of Managed Nekton Species from Channel-Fringing Habitats

Channel-fringing eelgrass and aquaculture structures provided unique habitat for two managed nekton species of interest, although the effect appeared to be species-specific. A higher proportion of the estuarine *P. vetulus* population remained closer to tidal channels than did *M. magister*, a species known to forage across tidal flats during the sub-adult stage (Holsman et al., 2003), which was the primary age class (age $\geq 1+$; approximately 40–115 mm) captured in nekton seines by Boardman et al. (2023). Proximity to tidal channels and use of channel-fringing habitat are still critical to the life history of *M. magister*; however, these highly mobile organisms display ontogenetic differences in utilization of these estuarine habitats, with younger 0+ crabs favoring eelgrass (Stevens & Armstrong, 1984) and oyster habitats (Dumbauld et al., 2021), and older 1+ crabs utilizing unstructured tidal flats for foraging (Holsman et al., 2006; Lewis et al., 2021). Subadult crabs retreat with ebbing tides to low intertidal and subtidal habitats (Holsman et al., 2006), passing through or into channel-fringing habitats. We suspect this aspect of utilization was not entirely captured by our study, as seining was conducted at water depths of 0.3–0.7 m, when 1+ crabs were potentially still foraging on tidal flats above the channel-fringing habitat. Bottom culture facilitated generally higher densities of *M. magister* and *P. vetulus* than both off-bottom aquaculture and areas without aquaculture, whereas no density differences were found between habitats with and without eelgrass. Juvenile *P. vetulus* have been shown to exhibit risk-prone behavior in response to predators (Lemke & Ryer, 2006), so use of bottom culture habitat could be related to predator abundance. The nekton data we utilized were not from a study specifically designed to analyze fringe habitats, which should be considered when interpreting the general estuary-wide estimates modeled here. This effort was, in part, a proof-of-concept exercise to integrate small-scale field abundance data and large-scale geospatial habitat data within a defined area of interest to address meaningful habitat use questions from disparate datasets, which produced the first areal estimates of channel-fringing eelgrass and oyster aquaculture throughout the estuary and a unique first-order abundance comparison of important fisheries species among channel-fringing habitats estuary-wide.

Implications and Applications

This landscape-scale habitat mapping effort is intended to support resource managers, shellfish growers, and policymakers navigating the challenges of preserving eelgrass while supporting sustainable shellfish aquaculture.

Contemporary distributions of eelgrass and aquaculture not only provide stakeholders with valuable estuary-wide coverages but also unique estimates of eelgrass coverage among specific culture practices. This broader perspective on eelgrass and aquaculture spatiotemporal dynamics is an important contrast to smaller-scale efforts that are focused at the scale of an eelgrass or aquaculture bed, particularly in supporting decisions occurring at a regional or estuary scale, such as culture management choices or regulation assessments. Adaptation of these landscape-scale distributions to estimate fringe habitat production of juvenile fisheries species further demonstrates the utility of these datasets to develop novel secondary endpoints. In this case, the secondary endpoints can be used to further support stakeholders balancing eelgrass and aquaculture priorities by comparing the provision of habitat for important fisheries species. The detailed methodology presented here also offers a blueprint for efforts in other estuaries where similar priorities exist.

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Author Contribution NL designed the study, developed models, performed data analyses, interpreted results, and drafted the manuscript; BM contributed to field sampling and writing/revising the manuscript; JR and FB provided valuable nekton data and manuscript revisions; BD conceived the research topic and participated in study design, field sampling, results interpretation, and manuscript revision.

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Data Availability The datasets developed for this study are available from the corresponding author on reasonable request, except for those data that contain sensitive or identifiable information on aquaculture farms.

Declarations

Ethics Approval Not applicable.

Consent for Publication Not applicable.

Competing interests The authors declare no competing interests.

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