



Assessing the Relative Importance of Estuarine Nursery Habitats—a Dungeness Crab (*Cancer magister*) Case Study

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Abstract

Estuaries serve as important nurseries for many recreationally and commercially harvested fisheries species. Recent conceptual approaches (i.e., seascape) for assessing the value of estuaries to fisheries have advocated for complex habitat-scale assessments that integrate multiple life-history responses (e.g., abundance, growth, reproduction) and ecological processes across heterogeneous landscapes. Although ecologically compelling, implementing seascape approaches may not be feasible for resource-limited management agencies. In such cases, we propose that resource managers can enhance the identification of fishery important estuarine habitats by integrating attainable aspects of the seascape approach into a more traditional single-response (e.g., abundance) model. Using Dungeness crab (*Cancer magister*) as a case study, we applied a spatially explicit hybrid approach to assess the relative contribution of different estuarine habitats to that important fishery species within three Oregon estuaries (Tillamook, Yaquina, and Alsea bays). We measured the abundance of juvenile *C. magister* from low-tide trawls in estuarine channels and the mosaic of habitat characteristics within defined home range distances for the crabs. After identifying and reducing strong intercorrelations among habitat variable data, we developed a best-fit model that associated crab abundance with the most influential habitat variables. We found that lower estuary side channels supported the highest abundance of juvenile crabs; furthermore, crab abundance was positively associated with high salinity and burrowing shrimp (*Upogebia pugettensis*) density on adjacent unvegetated tidal flats. This hybrid method produced a habitat-specific model that better predicted juvenile *C. magister* abundance than did a model based on generalized habitat categories.

Keywords Estuaries · Nursery · Habitat mosaic · Fisheries · Dungeness crab

Introduction

Fisheries production is an important ecosystem service of estuaries throughout the world (Houde and Rutherford 1993;

Barbier et al. 2011; Jordan and Peterson 2012), largely due to the important nursery function that estuaries provide for many organisms (Houde and Rutherford 1993; Beck et al. 2001; Nagelkerken et al. 2015). Commercial and recreational fisheries in the United States are dominated by species that depend on estuaries at some point in their life cycle (Houde and Rutherford 1993; EPA 2004; Lellis-Dibble et al. 2008). Although the general value of estuaries to marine fisheries has long been recognized at the estuary scale, recent studies have shifted focus toward assessing the nursery importance of estuarine sub-habitats (Beck et al. 2001; Nagelkerken et al. 2015; Litvin et al. 2018). The heterogeneity of estuarine habitat dictates variation in the nursery value of those habitats (Heck et al. 1995; Beck et al. 2001), so habitat-scale assessments are necessary to better inform the restoration, conservation, or enhancement of specific habitats for estuarine-dependent fisheries species.

Early habitat-scale nursery studies compared the production of fish and invertebrate populations among broad and homogenous habitat types, such as vegetated (e.g., seagrass,

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marsh) vs. unvegetated (e.g., sand flat, mudflat) habitats (Heck et al. 1995), or advocated for such an approach (Beck et al. 2001). These straightforward approaches assessed the contributions of categorical habitat types and were attainable for resource managers. However, estuaries are recognized as complex habitat mosaics that include physical, biotic, and chemical components interacting at multiple scales (Eggleston et al. 1999; Jordan and Peterson 2012), and thus assessments of habitat utilization and fisheries production should go beyond comparisons between generalized habitat categories (Nagelkerken et al. 2015; Sheaves et al. 2015; Litvin et al. 2018). Recent literature has suggested further refinement of these assessments with holistic conceptualizations of “nursery seascapes” to identify and manage critical estuarine habitats for important fisheries species—refinements that integrate environmental drivers, ontogeny, migration, and connectivity among a mosaic of habitats at multiple spatial and temporal scales (Nagelkerken et al. 2015; Sheaves et al. 2015; Litvin et al. 2018). The seascape concept presents an ecologically compelling view of the integrated value of estuarine habitats for important fisheries, but its practical implementation can be a substantial limitation for resource managers (Lefcheck et al. 2019).

We posit that resource managers can enhance their understanding of estuarine habitat production for major fisheries species beyond that of generalized habitat types, without developing an elaborate, complex seascape framework. Here, we present a spatially explicit, hybrid approach in which attainable seascape concepts (e.g., heterogeneity, connectivity, migration) were integrated with a traditional single-response (i.e., production of juveniles) approach to identify and assess the relative value of estuarine habitats to an important fishery species, using Dungeness crab (*Cancer magister*; alternatively recognized as *Metacarcinus magister*) as a case study.

C. magister is a highly valued fishery species that supports important recreational and commercial fisheries from southern California to southwestern Alaska (Rasmuson 2013). Crabs are found in NE Pacific estuaries and the adjacent continental shelf, but the contributions of estuarine habitats to their production have not been well characterized. Crab larvae settle and grow in estuaries as well as on the continental shelf (Orcutt 1978; Wainwright et al. 1992), but those that rear in estuaries grow faster (Gutermuth and Armstrong 1989; Gunderson et al. 1990; Wainwright and Armstrong 1993). Estuaries offer favorable growing conditions for juvenile crabs, including warmer water temperatures and more foraging opportunities (Stevens and Armstrong 1984; Gunderson et al. 1990; Wainwright and Armstrong 1993). Armstrong et al. (2003) estimated the contribution of estuaries to the commercial *C. magister* fishery along the US Pacific Northwest (PNW) coast by extrapolating densities of juvenile crabs sampled in three qualitatively defined channel strata to whole-estuary abundances of juvenile *C. magister*. They found that lower side channels, adjacent to

intertidal flats, contained the highest densities of juveniles and thus the greatest average contribution to *C. magister* fishery production among channel strata; those results were primarily attributed to the proximity of extensive intertidal habitats, which are essential foraging grounds for the large populations of *C. magister* in estuaries (Holsman et al. 2003). Armstrong et al. (2003) provided a method to estimate the contribution of estuarine sub-regions to the commercial fishery, but it did not yield direct information on specific habitat variables that drove differences in juvenile *C. magister* densities within the estuaries. Those data are critically needed to manage estuarine lands for the benefit of estuary-supported fisheries and other ecosystem services.

Here, we examine the correspondence between estuarine habitat mosaics and the abundance of juvenile *C. magister* within Oregon estuaries. Quantifying habitat within crab home ranges allows the movement of crabs among interconnected, heterogeneous habitats to be considered. We compare the resulting crab-habitat relationships to those from Armstrong et al. (2003) and discuss the merits of a habitat mosaic approach to estimating the estuarine contribution to adult *C. magister* fisheries. We also use these data to test the hypothesis that a habitat mosaic model, more representative of the ecosystem, would better predict juvenile *C. magister* abundance than would a model based solely on channel strata.

Methods

Estuaries in Oregon are numerous (15) and characterized as small, drowned river basin systems with large intertidal flats (Cortright et al. 1987; Emmett et al. 2000; Hickey and Banas 2003). Diverse faunal communities that inhabit these tidal areas (Ferraro and Cole 2010, 2012) support fisheries harvest of valued infaunal invertebrates (Lewis et al. 2019) and provide an important juvenile foraging source for estuarine-dependent species highly valued by recreational and commercial fisheries (e.g., *Cancer magister* and Pacific salmon) (Holsman et al. 2003; David et al. 2016). This case study focused on three Oregon estuaries with a history of supporting recreational and commercial *C. magister* fisheries (Ainsworth et al. 2012; ODFW 2019): Tillamook Bay (34 km²), Yaquina Bay (15.8 km²), and Alsea Bay (8.7 km²).

Extensive summertime surveys of juvenile *C. magister* abundance were conducted over 2 years (2010–2011) at ~20 replicate sites within each estuary (Fig. 1). Intertidal habitats adjacent to each trawl transect were surveyed after trawling was completed. Yaquina and Alsea bays were trawled in 2010, while Tillamook Bay was trawled in 2011; although this sampling design limited direct comparisons between estuaries or years, the comprehensive dataset provided juvenile *C. magister* data representative of small Oregon estuaries collectively. Throughout the remainder of this

manuscript, we refer to these three “estuary × year” surveys as “sampling events.”

Trawling to measure *C. magister* abundance was conducted during June–August using the same methods as Armstrong et al. (2003). Sampling sites within an estuary were randomly distributed within tidal channels (> 5-m wide and > 1.5-m deep at low tide) that were stratified into lower estuary main channel (LMC), lower estuary side channel (LSC), and upper estuary (UP), as defined in Armstrong et al. (2003). Accordingly, each stratum was defined by a set of environmental characteristics that vary with distance from the estuary mouth. Strata in the marine-dominated portion of the estuary (LMC and LSC) were located proximal to the estuary mouth where salinities were high and summer water temperatures low; however, the LSC stratum was constrained to shallow side channels adjacent to extensive intertidal flats, unlike the deeper channels of the LMC stratum (Armstrong et al. 2003). The UP stratum was located farthest up-estuary and subjected

to more riverine water conditions (i.e., warmer summer temperatures and lower salinities) (Armstrong et al. 2003). Trawls were conducted during daytime low tides—when crabs were concentrated in subtidal channels (Holsman et al. 2003)—using a plumb-staff beam trawl to sample benthic crustaceans, which included a tickler chain to displace buried individuals and a 4-mm mesh liner in the cod-end to capture early-stage juvenile crabs. Trawl gear (effective fishing area of 2.3×0.6 m) was towed from a small boat heading into the prevailing tidal current. The average towing distance was 118 ± 33 m, with the starting position and direction determined a priori, at a speed of 0.5 to 1.0 m s⁻¹ and with the distance trawled and ending position estimated with a differential global positioning system (GPS) on the boat. The captured *C. magister* were counted, measured to the nearest 1 mm (carapace width), and returned to the estuary alive. Salinity at each trawl transect was measured once at 0.5 m below the water surface using a YSI 30 Salinity, Conductivity, and

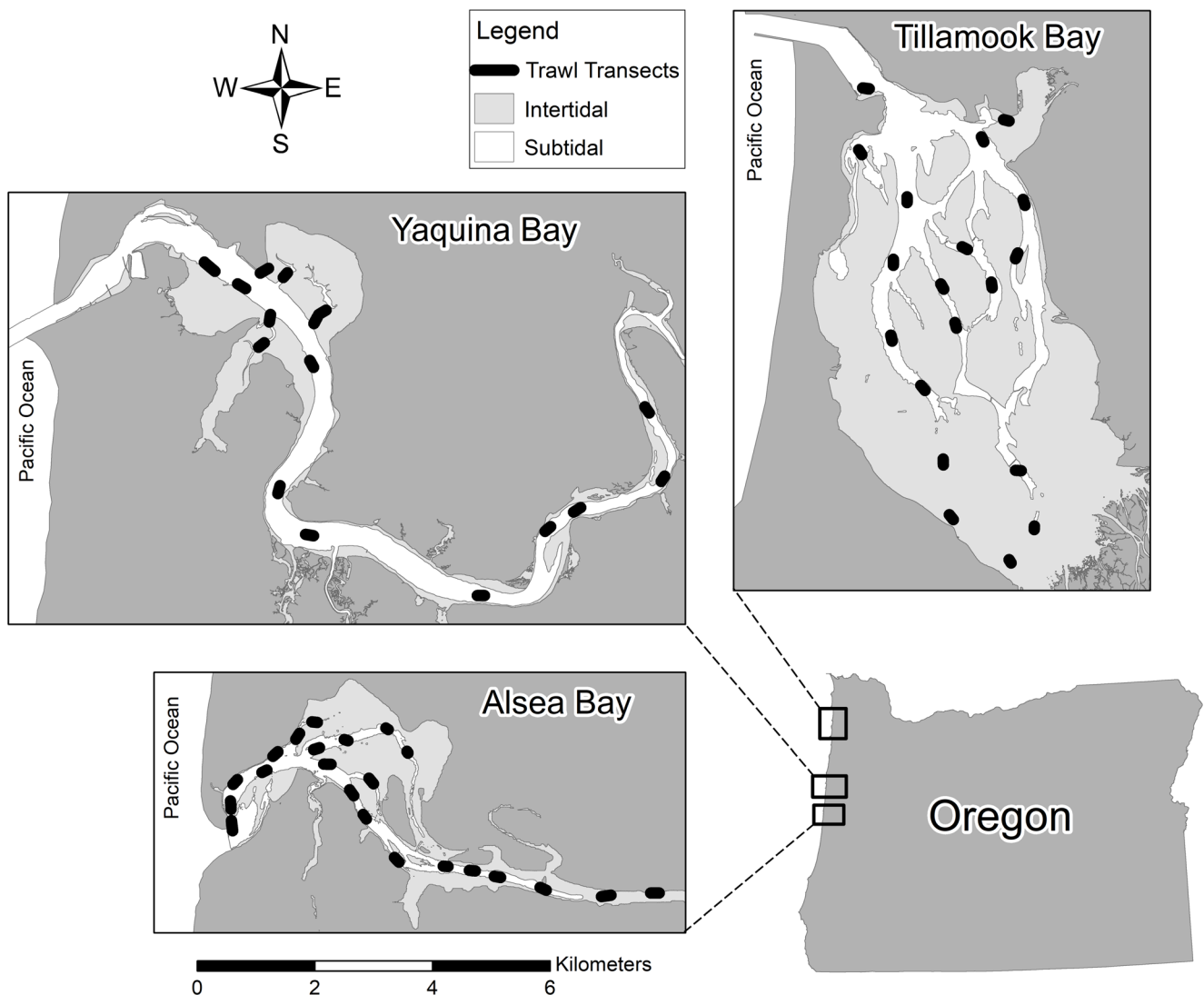


Fig. 1 Study area maps of Tillamook, Yaquina, and Alsea bays, OR

Temperature Meter prior to trawling. Estuarine salinity is highly dynamic, so the point measurement for a given trawl was not representative of the salinity range or average for that transect; however, we find this estimate to be appropriate as a potential predictor for highly mobile *C. magister* captured at that specific point in time.

Intertidal habitat sampling was conducted from September to June after trawling was completed to avoid months of peak green macroalgal abundance which could obscure shrimp burrows. Intertidal habitat (i.e., above – 2-m Mean Lower Low Water [MLLW]) was characterized within 250 m of each trawl transect to assess potential effects of adjacent intertidal habitat on juvenile *C. magister* abundance. We determined this radius to be a suitable “home range” distance as Holsman et al. (2006) found that subadult *C. magister* traveled an average of 225 m from channels during nighttime high tides, when their migration was most pronounced. Three to twenty-nine intertidal habitat stations (arrayed on a 100-m grid) were sampled per trawling site, depending on the area of intertidal habitat within the 250-m radius of the trawl transect and the proximity of adjacent trawl sites. The distribution of trawl transects throughout these diverse estuaries resulted in the differences in adjacent intertidal area, which was largely responsible for the range of intertidal habitat stations sampled at each trawling site (i.e., quantity of intertidal habitat stations was positively correlated with intertidal area). At each habitat station, a 2.25-m² quadrat was used to visually estimate percent cover of *Zostera marina*, *Z. japonica*, *Ulva* spp., and total unvegetated (bare) area. Burrowing shrimp burrows were identified to species (i.e., *Upogebia pugettensis* or *Neotrypaea californiensis*) and counted. Each habitat variable was measured and recorded independently by two trained staff, and the mean of their observations at a station was used to represent the final value for each variable in subsequent analyses.

As another means of habitat characterization at a larger scale, we used a geographic information system (GIS) to calculate the geospatial coverage of National Wetlands Inventory (NWI; <https://www.fws.gov/wetlands/>) habitat classes within 250 m of each trawl transect. These classes included the total intertidal area, total subtidal area, intertidal unconsolidated shore (e.g., sand or mud) area, and intertidal marsh area—the latter two classes also had subclasses for regularly and irregularly flooded areas. NWI habitat classes were included with intertidal habitat survey variables and trawl-sampled salinity as potential predictor variables for the abundance of juvenile *C. magister*.

The 1 + age class of juvenile *C. magister* was used for all analyses in this study, following the methods of Armstrong et al. (2003). This age class was most appropriate because these juveniles inhabited the estuary for more than a year, and thus provided a stable response variable for examining the relative production of juvenile *C. magister* from estuarine

habitats. We determined the age 1 + size class of trawl-sampled juveniles by using size-frequency charts to visually identify thresholds between classes (similar to Wainwright et al. 1992). The size of age 1 + juveniles ranged from approximately 40 to 115 mm in carapace width, depending on the month, year, and estuary in which trawls were conducted; this was similar to the range observed by Armstrong et al. (2003). Juvenile count data were fit to a negative binomial distribution, representative of our dataset. All analyses were conducted using the statistical software R (V 3.6.3; R Development Core Team 2020). We used a generalized linear model (GLM) with a log area offset (to control for trawl area differences) using the “stats” (R Development Core Team 2020) and “MASS” (Ripley et al. 2020) packages to examine the effect of channel strata on juvenile *C. magister* abundance within and across all estuaries. An analysis of deviance via a chi-squared test was then used to determine differences among channel strata and between sampling events.

Multivariate analyses (conducted with “stats” and “vegan” (Oksanen et al. 2019) packages—visualized with “ggfortify” (Horikoshi et al. 2020) and “ggplot2” (Wickham et al. 2020) packages) were used to examine associations among the 14 potentially correlated variables in the full dataset (see Fig. 2) with respect to channel strata and to identify habitat variables to remove from the predictor variable pool for juvenile *C. magister* abundance. Non-metric multidimensional scaling (NMDS) plots were used to identify habitat relationships between samples in multidimensional space using a distance matrix created with the Bray-Curtis dissimilarity index. Permutational multivariate analyses of variance (PERMANOVAs) were then used to determine whether variation in the habitat dataset (via the distance matrix) could be explained by channel strata or sampling event.

A principal component analysis (PCA) was conducted to assess relationships between habitat variables and to examine the contribution of each variable to variance in the habitat dataset. PCA transforms data from a set of potentially correlated variables into uncorrelated principal components (PCs; ranked by degree of explained variance) in order to summarize dataset variance with fewer axes (PCs) in multidimensional space yet retain patterns within the data (Bulger et al. 1993; Johnson and Wichern 2002; Tabachnick et al. 2007; Lever et al. 2017). Correlation coefficients between original variables and PCs are displayed as variable loadings, which provide a means to assess which habitat variables are most influential on the structure of the ecological community. Channel strata could not be included as a non-numeric variable in the PCA but were used to classify trawl samples so the resulting clusters could be assessed against habitat variables. Habitat variables that did not contribute substantially (loading magnitudes < 0.3 absolute value; Tabachnick et al. 2007) to any of the top three PCs (which collectively explained the majority of dataset variance) were removed from the habitat

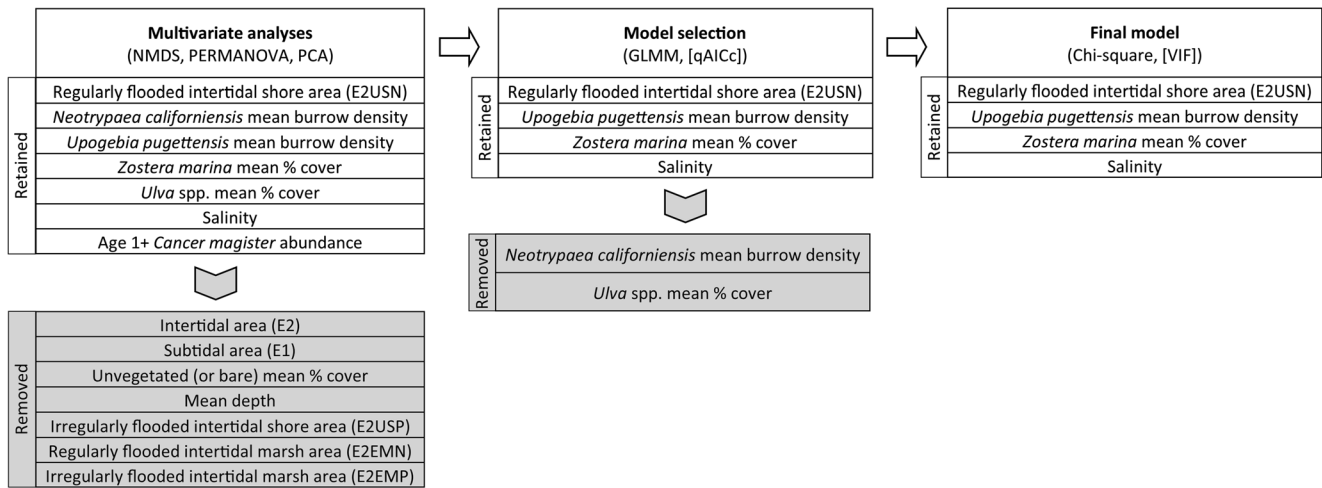


Fig. 2 Diagram showing the variables used within each stage of analysis. The first row in each column shows the general analysis stage, specific analyses used (in parentheses), and calculated metrics [in brackets]. Variables in shaded cells were removed from the variable pool at that

analysis stage; variables in non-shaded cells were passed onto the subsequent analysis stage. Age 1+ *Cancer magister* abundance was used as the response variable for the final two stages of analysis

predictor pool. All remaining potential habitat predictor variables were plotted against one another in a scatterplot matrix to assess relationships between predictors that could lead to problematic multicollinearity (e.g., % *Zostera marina* cover vs. % unvegetated area). Linear regressions were used to determine which of the related habitat variables to remove from the predictor pool based on the strength of their associations with juvenile *C. magister* abundance.

Using the narrowed variable pool of potential predictors, we developed several generalized linear mixed models (GLMMs) for juvenile *C. magister* abundance (using the “lme4” package; Bates et al. 2020). We selected the fixed-effect terms in these models by examining the PCA plot, comparing habitat predictor loadings to the juvenile *C. magister* loading, and developing several candidates from the narrowed variable pool. Estuary and channel strata (nested within estuary) were specified as random effects in all candidate models in order to account for potential group-level variation. The habitat mosaic model that best explained the variance in juvenile *C. magister* abundance was identified using the qAICc metric—a version of Akaike’s Information Criterion that is corrected for small sample size and accounts for overdispersion (calculated with the “bbmle”

package; Bolker 2020). The final model identified (with the lowest qAICc value) was the best-fit for estimating the magnitude and significance of the predictor habitat variables on *C. magister* abundance. To check the final model for multicollinearity, we used the variance inflation factor (VIF) to assess the magnitude of multicollinearity between predictor variables based on conditional associations (calculated with the “performance” package; Lüdecke et al. 2020). We then calculated an asymptotic chi-square statistic based on the deviance (using the “stats” package), as an estimated goodness-of-fit measure for the final habitat mosaic model. Finally, to determine whether the habitat mosaic model was a better predictor of juvenile *C. magister* abundance than a model containing only channel strata (i.e., per Armstrong et al. 2003), we compared the deviance (via a chi-square statistic) between the models.

Results

Consistent with the findings of Armstrong et al. (2003), our data revealed the importance of lower side channels to

Table 1 Mean (\pm SE) age 1+ *Cancer magister* captured per trawl within each channel stratum (lower main channel [LMC], lower side channel [LSC], and upper estuary [UP]) across all bays sampled

	Tillamook	Yaquina	Alesea	All estuaries
LMC	2.83 \pm 1.17	56.6 \pm 19.30	11.25 \pm 3.95	20.53 \pm 7.14
LSC	11.50 \pm 5.74	79.33 \pm 29.38	45.00 \pm 16.19	45.26 \pm 12.29
UP	6.55 \pm 1.42	11.33 \pm 4.56	0.71 \pm 0.29	6.63 \pm 1.76
All strata	6.87 \pm 1.71	43.05 \pm 11.78	18.64 \pm 6.49	

Presented values are not corrected for transect length differences; however, a log area offset was implemented during significance testing (analysis of deviance via a chi-squared test) to account for these differences in transect length

juvenile *Cancer magister* populations within estuaries. The effect of channel strata on juvenile crab abundance differed among estuaries ($p < 0.001$), but the LSC stratum contained the greatest mean abundance in all estuaries (Table 1). Confirming that the relationship between juvenile *C. magister* abundance and channel strata in our dataset (see Online Supplement 1 for entire dataset) was similar to that of Armstrong et al. (2003) allowed us to compare our habitat mosaic model and their channel strata model by attributing differences to predictor variables rather than differences in juvenile crab data.

An NMDS plot showed grouping patterns in the habitat dataset related to channel strata, which provided visual support for our hypothesis that intertidal habitat variables were ultimately driving the differences in juvenile crab abundance among channel strata (Fig. 3). Coupled PERMANOVAs provided strong evidence that channel strata explained a proportion of overall habitat variation ($R^2 = 0.29$, $p = 0.001$), whereas no difference in habitat composition was detected among sampling events.

PCA analysis revealed that the first three principal components explained ~59% of the variation in the complete dataset, as well as how each habitat variable contributed to each principal component (Table 2). In a plot of the first two principal components (Fig. 4), the directions of loading vectors corresponded with channel strata groupings; for example, vegetation types were directed toward the channel stratum in which they typically occur (e.g., *Zostera marina* toward the LSC grouping and irregularly flooded intertidal marsh toward the UP grouping). This too was consistent with the hypothesis that habitat variables drove the differences in crab abundance among channel strata. Multivariate results led to the removal

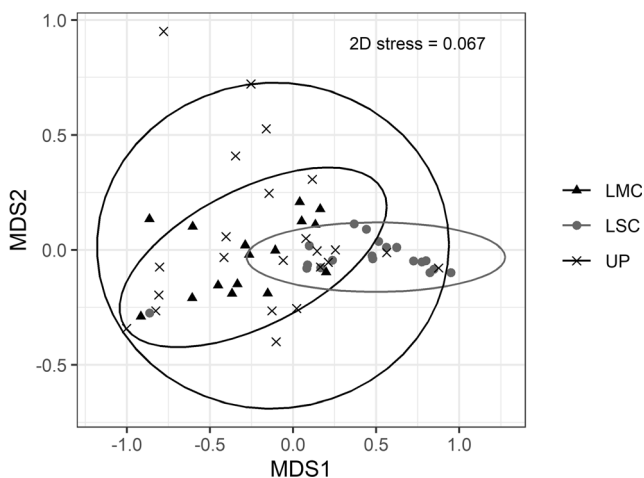


Fig. 3 Non-metric multidimensional scaling (NMDS) plot showing the ordination of trawl transects (points) in two-dimensional space. Transects are represented by the channel stratum in which they were collected (i.e., lower main channel [LMC], lower side channel [LSC], and upper estuary [UP]) and their distribution in the plot is based on habitat composition. Ellipses represent a 95% confidence interval around the centroid of each stratum's point distribution

of several habitat variables from the predictor variable pool in subsequent analyses (Fig. 2). Regularly and irregularly flooded intertidal marsh areas were removed because neither substantially contributed to the top three principal components. Subtidal area, intertidal area, irregularly exposed intertidal shore area, average trawl depth, and percent of unvegetated (or bare) area were removed because of strong correlations with other habitat variables.

The best-fit GLMM for juvenile *C. magister* abundance among the six candidate models (Model 1, Table 3) contained the following predictor variables: regularly flooded intertidal shore area, *Upogebia pugettensis* mean burrow density, *Z. marina* mean % cover, and salinity. Although the top three candidate models produced similar qAICc values ($< 2.0 \Delta qAICc$), Model 1 was selected over the other two models for several reasons. First, the additional predictor variable in Model 3 (*Neotrypaea californiensis* mean burrow density) neither contributed additional explanatory power to the model (i.e., improve the qAICc value) nor provided substantial evidence of an influence on crab abundance in the model output ($p = 0.256$), so Model 3 should not be considered competitive with the simpler models (see Arnold 2010). Secondly, in Model 2, *N. californiensis* mean burrow density replaced regularly flooded intertidal shore area, where it was also uninformative ($p = 0.274$); conversely, output from Model 3 showed that regularly flooded intertidal shore area at least produced very minor evidence of an influence on crab abundance ($p = 0.106$).

A negative binomial regression of the best-fit model revealed that *U. pugettensis* mean burrow density ($p = 0.004$) and salinity ($p = 0.005$) positively affected abundance of juvenile *C. magister*, whereas evidence weakly suggested that *Z. marina* negatively affected juvenile *C. magister* abundance ($p = 0.094$). Variable coefficients (β) from GLMM output (i.e., expected log counts) are not easily interpretable on their own but can be converted to percent change (% change = $100 \times [\exp(\beta) - 1]$; Beaujean and Grant 2016) in juvenile *C. magister* abundance per unit increase in a predictor variable. For example, a 1% increase in mean *U. pugettensis* burrow density resulted in a ~1.6% increase in mean juvenile *C. magister* abundance (Table 4). Variance inflation factors for the included predictor variables ranged from 1.13 to 1.60, indicating low correlation among model terms. Finally, results from the analysis of deviance showed that the negative binomial GLMM with habitat-specific variables was a better predictor of juvenile *C. magister* abundance than the model based solely on channel strata ($p = 0.001$).

Discussion

A key underlying assumption of this study is that juvenile *Cancer magister* favor certain estuarine habitats more than

Table 2 Loading values for ecosystem variables considered in the principal component analysis

	PC1	PC2	PC3
Intertidal area (E2)	-0.42	-0.30	0.06
Subtidal area (E1)	0.30	0.39	-0.18
Regularly flooded intertidal shore area (E2USN)	-0.44	-0.23	0.04
Irregularly flooded intertidal shore area (E2USP)	0.04	0.19	0.40
Regularly flooded intertidal marsh area (E2EMN)	0.11	-0.18	0.04
Irregularly flooded intertidal marsh area (E2EMP)	0.15	-0.15	-0.04
Age 1+ <i>Cancer magister</i> abundance	-0.28	0.08	-0.36
<i>Neotrypaea californiensis</i> mean burrow density	-0.22	0.09	0.44
<i>Upogebia pugettensis</i> mean burrow density	-0.25	0.13	-0.48
<i>Zostera marina</i> mean % cover	-0.34	0.28	-0.01
<i>Ulva</i> spp. mean % cover	-0.03	0.29	0.45
Unvegetated (or bare) mean % cover	0.32	-0.38	-0.11
Salinity	-0.24	0.38	-0.14
Mean depth	0.22	0.37	-0.13
Percent of total variation (100%) explained	27.6%	18.0%	12.9%

National Wetland Inventory (NWI) habitat classes include class codes in parentheses. Values are shown for the top three principal components (PC1, PC2, PC3), which explain the majority (58.8%) of variance in the dataset (shown in bold in the last row). Shaded cells highlight the primary variables contributing to each principal component (i.e., loading magnitudes ≥ 0.3 in absolute value)

others, which can be derived from congregation patterns. That is, juvenile *C. magister* movement allows the highly mobile crabs to congregate in and near preferred habitats. Although juvenile *C. magister* were most abundant in lower side channels, our analysis suggests that variation in crab abundance

was actually driven by higher salinity in the lower estuary and the density of *Upogebia pugettensis* on unvegetated tidal flats adjacent to lower side channels. Lower side channels, in the more saline areas of estuaries, provide refuge for juvenile crabs at low tide, but alone may not support sufficient prey biomass for high densities of juvenile *C. magister* (Holsman et al. 2003). It is likely that age 1 + juvenile crabs foraged on the high densities and diversity of infaunal and epifaunal prey within *U. pugettensis* beds (see Ferraro and Cole 2010, 2012) on intertidal flats, where they fulfill most of their energetic requirements (Holsman et al. 2003). Laboratory studies show that *C. magister* movement provides a mechanism to balance avoidance of unfavorable conditions (e.g., hypoxia and low salinity) with foraging efficiency among different habitats (Fernandez 1999; Bernatis et al. 2007; Curtis and McGaw 2012). Inclusion of the specific habitat variables in our habitat mosaic model better explained variation in age 1 + *C. magister* abundances within Oregon estuaries than did the categorical channel strata model of Armstrong et al. (2003); thus, our results provide a mechanistically supported yet practical approach to managing estuarine areas for the production of juvenile *C. magister*.

Salinity gradients often contribute to the explanation of differences in size and abundance of *C. magister* across estuarine habitats, with larger crabs predominantly inhabiting lower, more saline reaches of NE Pacific estuaries (Stevens and Armstrong 1984; Dunn and Young 2013); so, the positive effect of salinity on the abundance of juvenile *C. magister* in

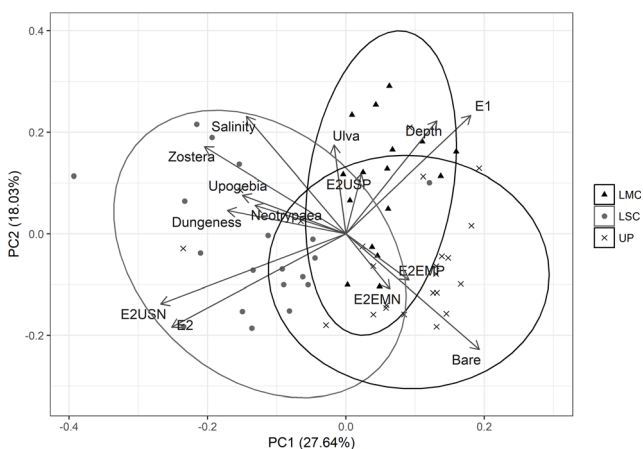


Fig. 4 Results from a principal component analysis (PCA) showing the distribution of trawl transects (points) in relation to the two principal components that explain the highest percentage of variation in the dataset (total dataset variation sums to 100%). Transects are represented by the channel stratum in which they were collected; each stratum also includes a 95% confidence ellipse around transects sampled in that stratum. Magnitude and direction of individual variable loadings (labeled arrows; refer to Table 2 for codes of National Wetlands Inventory habitat classes) indicate the degree to which they contribute to the explanation of each principal component

Table 3 Candidate models assessed with the qAICc metric to identify which model best explained the variance in juvenile (age 1 +) *Cancer magister* abundance

Candidate model	Fixed-effect predictor variables	qAICc
1	Regularly flooded intertidal shore area + <i>U. pugettensis</i> mean burrow density + <i>Z. marina</i> mean % cover + salinity	428.3
2	<i>N. californiensis</i> mean burrow density + <i>U. pugettensis</i> mean burrow density + <i>Z. marina</i> mean % cover + salinity	429.5
3	Regularly flooded intertidal shore area + <i>N. californiensis</i> mean burrow density + <i>U. pugettensis</i> mean burrow density + <i>Z. marina</i> mean % cover + salinity	429.9
4	Regularly flooded intertidal shore area + <i>N. californiensis</i> mean burrow density + <i>U. pugettensis</i> mean burrow density + <i>Z. marina</i> mean % cover + <i>Ulva</i> spp. mean % cover + salinity	432.7
5	Regularly flooded intertidal shore area + <i>N. californiensis</i> mean burrow density + <i>Z. marina</i> mean % cover + salinity	436.9
6	Regularly flooded intertidal shore area + <i>N. californiensis</i> mean burrow density + <i>Z. marina</i> mean % cover + <i>Ulva</i> spp. mean % cover + salinity	439.2

Candidate models were developed from the narrowed pool of potential predictors (Fig. 2) using the PCA plot (Fig. 4) to compare habitat predictor loadings to the *C. magister* loading. All candidate models included random effects of estuary and strata (nested within estuary)

the model we present was expected. Salinity is also an influential factor that affects the distribution of most estuarine organisms, including the ecosystem-engineering species included as predictors in this modeling effort (Dumbauld and Wyllie-Echeverria 2003; Dumbauld and McCoy 2015). The influence of salinity on these sedentary organisms (i.e., burrowing shrimp and *Zostera marina*) would likely be best captured with the long-term salinity average or range for a given area, rather than the point estimate included as a predictor in the juvenile *C. magister* model. Although a general ecological association exists between these variables, our analysis showed that their inclusion as predictors did not lead to problematic multicollinearity in the final model.

Younger (age 0 +) *C. magister* are known to utilize *Z. marina* beds for foraging and protection from predators, including larger conspecifics (Stevens and Armstrong 1984; Fernandez et al. 1993); in contrast, our results potentially show a decrease in abundance of age 1 + *C. magister* with increased coverage of *Z. marina*. This difference may have been due to an ontogenetic shift in habitat for juveniles between the ages of 0 + and 1 +, as previously suggested in categorical habitat comparisons by Stevens and Armstrong (1984) and Holsman et al. (2006). Although *Z. marina* beds harbor a high biomass and diversity of potential prey species

(Hosack et al. 2006; Ferraro and Cole 2010, 2012), larger (age 1 +) juvenile crabs may decrease their utilization of *Z. marina* beds because the high structural complexity likely inhibits their mobility which can decrease foraging efficiency and increase the risk of stranding at low tide (Holsman et al. 2006). Our results also showed that the burrow density of *U. pugettensis*, a dominant inhabitant of unstructured low intertidal mudflats, was a significantly positive predictor for juvenile *C. magister* abundance—a novel finding that advocates for the inclusion of *U. pugettensis* beds in discussions of critical estuarine habitat for juvenile *C. magister*.

Distribution of *U. pugettensis* was historically controlled in PNW estuaries by the oyster aquaculture industry with the pesticide carbaryl (Feldman et al. 2000), but population declines throughout the PNW over the last two decades have been attributed to a parasitic isopod, *Orthione griffenis* (Dumbauld et al. 2011; Chapman et al. 2012). These events may have indirectly affected *C. magister* fisheries by reducing estuarine foraging opportunities for juvenile crabs. The diet of *C. magister* has been documented to shift toward shrimp and fish at age 1 + (Jensen and Asplen 1998; Stevens et al. 1982), so it is possible that age 1 + *C. magister* forage upon *U. pugettensis*, but the more likely explanation is that these crabs are foraging upon prey that occupy the *U. pugettensis*

Table 4 Negative binomial regression results from the habitat mosaic model (via GLMM)

	Estimate (β)	SE	Exp. estimate	% change	z-value	p value
(Intercept)	-5.448	0.669	0.004	-99.570	-8.146	<0.001
Regularly flooded intertidal shore area (ha)	0.060	0.037	1.062	6.184	1.617	0.106
<i>Upogebia pugettensis</i> mean burrow density	0.016	0.006	1.016	1.613	2.851	0.004
<i>Zostera marina</i> mean % cover	-0.018	0.011	0.982	-1.784	-1.674	0.094
Salinity	0.077	0.027	1.080	8.004	2.844	0.005
Null deviance: 899.16 on 57 degrees of freedom						
Residual deviance: 406.5 on 50 degrees of freedom						

Coefficient estimates for each variable are expected log counts, which are not easily interpretable, so also provided are the exponentiated estimates (showing the multiplicative effects) and percent change for a one-unit increase in the corresponding habitat variable

beds. Our findings indicate that the burrowing shrimp *Neotrypaea californiensis* did not have the same influence on crab abundance as did *U. pugettensis*. This is consistent with previous research that demonstrated *N. californiensis* beds contained lower densities and biomass of benthic invertebrates (e.g., fewer potential prey) (Ferraro and Cole 2010, 2012); these beds are also located in the mid to upper intertidal zone (DeWitt et al. 2004), farther from subtidal channels than *U. pugettensis* beds. Stevens et al. (1982) found that intertidal predation of *Crangon* spp., an important prey item for age 1 + juvenile *C. magister*, increased at night when these shrimps were most abundant, which supports the findings of Holsman et al. (2006) that subadults migrate onto unvegetated intertidal flats to forage during nighttime high tides. Our regression analysis is consistent with the findings of Holsman et al. (2003, 2006), which may support the occurrence of a coupled ontogenetic shift in habitat and diet for juvenile *C. magister*. Juvenile crabs may have transitioned from foraging upon small bivalves and diatoms in habitats with epibenthic cover (Fernandez et al. 1993; Jensen and Asplen 1998) to foraging upon shrimp on intertidal sand and mudflats (Stevens et al. 1982; Holsman et al. 2006).

The estuarine-scale importance of these habitat mosaics to *C. magister* fisheries cannot be understated. In addition to the direct contribution that estuaries provide to commercial *C. magister* harvest (see Online Supplement 2), these nurseries provide an important buffer of recruits to the population, particularly when unfavorable oceanic conditions may adversely impact juveniles in the coastal nearshore. Minor fluctuations in nearshore oceanic conditions can lead to substantial fluctuations in crab abundance (Higgins et al. 1997). Seasonal development of hypoxia and anoxia (dissolved oxygen concentrations ≤ 2 mg Γ^{-1} ; Brown and Power 2011; Sutherland and O'Neill 2016) in nearshore coastal waters can impact the behavior, physiology, and survival of invertebrate communities on the continental shelf (Diaz and Rosenberg 1995; Grantham et al. 2004; Bernatis et al. 2007; Chan et al. 2008). Although these oxygen-poor waters are advected into PNW estuaries, physical and biological processes can moderate dissolved oxygen within PNW estuaries such that levels are higher than those experienced in the benthic zone of the continental shelf (Brown and Power 2011; Sutherland and O'Neill 2016). Thus, estuaries may serve as a refuge from prolonged or severe hypoxic and anoxic events for juvenile *C. magister* that settle there or migrate from elsewhere.

Estuarine nurseries provide more value per unit area to the development of recruits to *C. magister* fisheries than the adjacent continental shelf. Higher densities of juvenile *C. magister* are facilitated by higher benthic prey densities and biomass on intertidal flats of NE Pacific estuaries (compared with continental shelf sediments), as indicated by the findings of Gunderson et al. (1990). Coupled with warmer

water temperatures (i.e., relative to the continental shelf) that promote faster growth rates in these crabs (Gutermuth and Armstrong 1989; Gunderson et al. 1990; Wainwright and Armstrong 1993), food-rich estuaries presumably export recruits to the continental shelf that are larger than their shelf cohorts. Faster growth could translate into earlier maturity and recruitment into the fishery for these individuals (Wainwright and Armstrong 1993). If estuarine-reared *C. magister* females are larger at reproductive maturity, they likely have greater reproductive success (Hines 1991; Dunn and Shanks 2012) than those reared in nearshore coastal areas, which would increase the relative contribution of estuarine-reared individuals.

Estuarine habitats were classically considered nurseries if their production was greater than that of alternative settlement or rearing areas based on higher densities, increased growth, or greater survival of organisms per unit area (Heck et al. 1995; Beck et al. 2001). We estimated that small Oregon estuaries contributed an average of ~ 22 adult male crab ha^{-1} to commercial harvest in 2012–2014 as compared with ~ 7.6 adult male crab ha^{-1} from the nearshore settlement area (see Online Supplement 2) within 15 km of the coastline (McConnaughey et al. 1992). The utility of the nursery designation by Beck et al. (2001) is still valuable for major fisheries species when enhancements are made to consider estuarine habitat as a mosaic rather than static units. Lefcheck et al. (2019) recommended that a renewed emphasis in simplicity be considered in the evaluation of estuarine nurseries, particularly where resources or existing information are lacking. Assessments directed at quantifying the overall nursery value of estuaries would benefit greatly from a comprehensive seascape framework; however, the approach we present provides an attainable alternative for resource-limited management agencies looking to improve upon categorical habitat assessments and identify the relative nursery value for economically important species.

Results from this study provide resource managers with valuable information for prioritization of estuarine habitats for restoration, conservation, or enhancement for the purpose of sustaining or increasing the abundance of *C. magister* populations valued by local fisheries. Similar to Armstrong et al. (2003), we examined a single-response variable (abundance) for a single species (*C. magister*); however, we considered estuarine habitats as heterogeneous interconnected mosaics within spatially explicit crab home ranges. We utilized existing research to determine the average range that juvenile *C. magister* would migrate at diel and tidal cycles and to control for ontogenetic shifts by isolating our observations to a single year class (age 1 +). Our small-scale sampling of intertidal habitats and application of large-scale NWI habitat classes allowed us to examine the diverse habitat compositions within observed home ranges and quantitatively assess the potential effect on juvenile *C. magister*

abundance. The hybrid approach we utilized to estimate the relative value of estuarine habitats for juvenile *C. magister* demonstrated that we can improve our understanding of nursery habitat associations for an important fisheries species by integrating several attainable concepts from the seascape approach with existing estuarine production methodologies.

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