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Landscape determinants of aquatic estuarine habitat use by juvenile Chinook salmon

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Abstract

Habitat restoration planning and design can be informed by information on spatial patterns in habitat use, which can be obtained from temporally and spatially extensive monitoring efforts. Using records from long-term monitoring in four tidal deltas, we modeled how landscape features (channel types, wetland vegetation types, and a channel network connectivity index) influenced juvenile natural-origin (NOr) and hatchery-origin (HOr) Chinook salmon presence/absence and density when present. Models detected strong effects of landscape characteristics on either presence/absence or density, although the directionality and relative importance of these features differed between NOr and HOr fish. In addition, while interannual differences were stronger for NOr juveniles, the seasonal pattern was much stronger for HOr fish and was in fact the strongest predictor of density. For both types of fish, interactions between landscape features and seasonal pattern existed, indicating that habitat use changed dynamically from the beginning to the end of the rearing period. These findings help provide general principles for prioritizing location and designing habitat restoration projects.

Key words: Chinook salmon, landscape connectivity, estuary wetlands, river deltas

Introduction

Ecologists studying habitat relationships among fish and other aquatic species have long recognized the importance of broad patterns of habitat-forming processes in creating suitable habitat at smaller spatial extents. Stream-living fish respond to channel structure, connectivity, and geomorphology at riverscape extents (Angermeier and Winston 1999; Fausch et al. 2002; Harvey and Railsback 2009; Torgerson et al. 2022). Likewise, fish distribution and abundance in marine waters are influenced by seascape features (Pittman 2018), such as upwelling (Bakun 1996), gyres (Dickey-Collas et al. 1997), fronts (Lough and Manning 2001), and temperature patterns (Shroeder et al. 2022).

Both riverscape and seascape concepts have resonated well in the study of anadromous species like Pacific salmon (e.g., Whited et al. 2012; Bi et al. 2008; Sabal et al. 2020; Torgerson et al. 2022). However, fewer studies have documented how landscape factors influence the distribution and abundance of these fishes during estuarine life stages, which can be ecologically significant (Moore et al. 2016; Chalifour et al. 2021). This is despite evidence that distributions of juvenile salmonids in estuaries are influenced by riverscape processes such as fluvial dynamics (Bottom et al. 2005; Morrice et al. 2020), seascape processes such as currents (Hayes et al. 2011) and tidal hydraulics (Hering et al. 2010), and structural habitat features such as wetland vegetation (Ewing 1986; Sharpe et al. 2019) and channel morphology (Ellings et al. 2016; Munsch et al. 2020).

The lack of a general understanding of how landscape processes and structure influence the distribution and abundance of estuarine life stages of salmon is unfortunate given the large scope of habitat loss and fragmentation in estuaries (Brophy et al. 2019). Estuarine river deltas are the geomorphological outcome of riverine distributary channel networks entering the ocean (Coleman 1988; Syvitski et al. 2005), and these networks mediate hydrological, geological, and ecological processes across deltas. Many river deltas have suffered from the conversion of estuarine wetlands to agriculture, urbanization on the landward side, and dredging on the seaward side. A primary cause of fragmentation is blocking off historical distributaries, which simplifies the channel planform of deltas (Bortelson et al. 1980; Collins et al. 2003). These impacts are exacerbated by climate change impacts on riverine flow regimes and sea level rise (Hood et al. 2016). Wetland habitat restoration for sensitive or declining estuarine species would benefit from a sound understanding of how landscape elements influence fish distributions; this would allow better prioritization of land acquisitions and improved restoration design (Simenstad et al. 2002).

We examined landscape patterns of habitat use in juvenile Chinook salmon, whose threatened and endangered status on the Pacific Coast has advanced estuarine wetland restoration. These anadromous fish are well known for estuarine rearing life histories during outmigration (Reimers 1973*a*, 1973*b*; Healey 1982; Ellings et al. 2016; Levings 2016), particularly in populations where subyearling migrants dominate. Several studies have linked population responses to the availability of estuarine habitats (Levings et al. 1989; Magnusson and Hilborn 2003; Flitcroft et al. 2016), which support the hypothesis that estuarine habitats are vital rearing areas for juvenile Chinook salmon. Studies have also related environmental factors to the estuarine presence or abundance of salmonids (see Levings 2016 for review), but few studies have developed a landscape context describing broad patterns of habitat use and residence. The lack of a landscape perspective may inhibit our ability to re-establish estuarine support functions for salmon populations (Simenstad et al. 2002).

We studied estuarine landscape features associated with habitat use by natural-origin (NOr) and hatchery-origin (HOr) juvenile Chinook salmon in four Puget Sound river deltas. The four systems included in our analysis provide a broad range of habitat variation and contrasting stock status and population size. Populations from all four watersheds are listed as threatened, though some have larger NOr outmigrations than others. The watersheds also vary in their reliance on hatcheries to supplement NOr populations. Hatchery-reared fish are bred to migrate downstream with later timing and at larger sizes than NOr fish, and so they might be expected to use estuarine habitats differently as they move through river deltas (Levings et al. 1986). We focus on several landscape attributes subject to natural variation, anthropogenic stressors, and improvements through restoration. These include different river deltas (systems), wetland vegetation types, channel types, and landscape connectivity.

Specifically, we examined several hypotheses related to landscape configuration, which we expected to be associated with juvenile life history variation as characterized by migrant fry early in the year and larger parr later in the spring (Zimmerman et al. 2015; Apgar et al. 2020).

1) Juvenile NOr Chinook salmon density and occurrence should be higher at sites within the delta with greater spatial connectivity (Fullerton et al. 2010; Flitcroft et al. 2019) relative to the mainstem source of outmigrants.
2) NOr density and occurrence should be higher in blind channels (compared to distributary channels). As hydrodynamics (McNatt et al. 2016) and predation risk (Murphy et al. 2021) disproportionately affect smaller individuals, the timing of use should coincide with outmigrations of fry.
3) NOr density and occurrence should differ among wetland types. These patterns could arise due to variations in insect prey (higher energetic quality, Davis et al. 2019) and effects on water temperature.
4) Some of these patterns should be reversed for HOr fish, which migrate later in the season at larger sizes and would therefore be expected to exhibit reduced habitat use in tidal deltas. Specifically, we predicted shorter cohort residency periods, and higher HOr density and occurrence associated with distributaries and estuary emergent marsh, consistent with rapid outmigration (Moore et al. 2016).

Methods

We took advantage of sampling in four Puget Sound river deltas—the Nooksack, Skagit, Snohomish, and Nisqually—to evaluate how various landscape attributes influence delta rearing by juvenile Chinook salmon. Specifically, we used data collected from 55 sampling sites within the four systems that were repeatedly sampled during later winter though mid-summer for juvenile Chinook salmon by beach seines and fyke traps for up to 20 years, depending on the system. We associated each site with landscape characteristics, including delta system, wetland vegetation type, and channel types.

Our overall analysis approach was a cross-system comparison, which is valuable because variation in biotic and abiotic attributes can have limited range within one system (Boddy et al. 2019). For our purpose, a comparison across systems provided broader distributions of the attributes that may affect juvenile Chinook salmon rearing conditions in deltas. Additionally, anthropogenic activities can differ across systems, so cross-system comparisons can offer insight into potential management effects on juvenile Chinook salmon rearing habitat. Thus, cross-system comparisons provide improved opportunity to generalize juvenile Chinook salmon population responses to estuarine habitat variation.

Four river delta systems

The Nooksack, Skagit, and Nisqually watersheds have prograding tidal deltas, while the Snohomish is a drowned river valley. All of these deltas are estuaries within the Salish Sea, itself a larger estuary system. All have undergone extensive wetland habitat loss, primarily from diking and draining for agriculture, and extant channel area varies fivefold across systems (Table 1). Despite habitat loss and current land use, the Nooksack and Skagit have classic prograding delta fans, while the Nisqually is intermediate between the Nooksack/Skagit and Snohomish. However, the progradation rate in the Skagit delta has been slowing for decades and has recently become negative in some parts of the delta. Anthropogenic changes to sediment routing shelter areas from sediment supply but not from sea level rise or wave attack, thereby facilitating marsh erosion (Hood et al. 2016).

These four systems allow comparisons based on variation in habitat extent, NOr fish population sizes, and hatchery practices, which seasonally increase local densities of fish migrating through the river deltas (Table 1). These factors could be expected to influence the relative importance of estuarine habitats for threatened populations of Chinook salmon in Puget Sound. For example, all four systems have naturally spawning Chinook salmon populations, though the juvenile outmigrant population sizes vary from thousands in the Nooksack to millions in the Skagit. Chinook salmon in much of their range have several juvenile life history types, including yearlings and subyearling parr migrants, with extended rearing in freshwater but not in estuaries. Migrant fry, the smallest migrants with the earliest migration timing, are the principal life history type rearing in estuaries (Healey 1991; Zimmerman et al. 2015; Apgar et al. 2020), and they exhibit more variation across systems than total outmigrants

Table 1. Characteristics of the four estuarine river delta systems examined in this report.

	Nooksack	Skagit	Snohomish	Nisqually
Juvenile Chinook populations				
Years analyzed	2005–2015	1995–2015	2002–2015	2010–2015
Total outmigrants (1000 s)	25.5–669.8	1000.2–7712.3	190.6–1024.3	34.7–245.7
Fry outmigrants (1000 s)	0.2–111.1	444.4–6553.0	119.2–432.9	3.5–93.8
Parr outmigrants (1000 s)	25.3–571.4	116.6–2188.0	28.6–651.2	31.2–151.8
Hatchery releases (M)	0.61–1.94	0.15–0.89	1.82–4.30	3.35–4.26
Landscape characteristics				
Habitat loss (%)[2]	71.2	74.1	89.3	76.6
Estuarine channel area (ha)	43.95[1]	293.96	136.60	248.82[3]
Tidal range (m)	2.59	3.37	3.38	4.12
River discharge				
Mean annual discharge (cfs)	3200	18 000	10 000	2100
Standardized by channel area (cfs ha^{-1})	73	61	73	8
Sediment load				
Annual sediment load (tons year^{-1})	1 400 000	2 800 000	490 000	120 000
Standardized by discharge (tons/year/cfs)	437.5	155.6	49	57.1
Standardized by channel area (tons/year/ha)	31 854	9525	3587	482

Note: Wetland habitat loss data are from Simenstad et al. (2011) summarized for vegetated areas. Wetland channel area is based on GIS analysis completed for this report (see Supplemental text). Total NOr subyearling, fry, and parr outmigrant abundances are from Hall et al. (2018). Hatchery releases (millions) are based on Regional Mark Information System (RMIS) reports (www.rmpc.org). Tidal ranges are from Mofjeld et al. (2002). River discharge and sediment loads from Czuba et al. (2011).

[1] Does not include Lummi River/Red River channels, which are intermittent.

[2] Based on Simenstad et al. (2011), which did not include several large restoration projects in each delta. The largest of these is the Nisqually delta, which underwent a 364 ha increase in tidal footprint (David et al. 2014).

[3] Value includes channel habitat created by restoration of 364 ha tidal footprint in the Nisqually delta.

(Table 1). In addition to NOr outmigrants, all systems have hatchery programs that release thousands to millions of subyearling outmigrants each year within their natal river; these fish also briefly inhabit estuarine habitat after release.

Wetland types

The vegetated tidal delta is exposed to tidal and riverine processes and dominated by three tidal wetland types or zones: forested riverine tidal (FRT), estuarine forest transition (EFT), and estuarine emergent marsh (EEM) (after Cowardin et al. 1979). Because these wetland types are determined by their location relative to fluvial and tidal inundation, they have different abiotic and biotic characteristics. FRT areas are tidal freshwater habitats; EEM areas have greater tidal inundation and highly variable salinity, while EFT areas are intermediate between the two. Wetland types may also vary in temperature due in part to differential shading by vegetation differences (e.g., shrubs and trees vs. sedges and cattails). These varying conditions likely affect invertebrate communities and growth opportunities for fish in these zones (Davis et al. 2019).

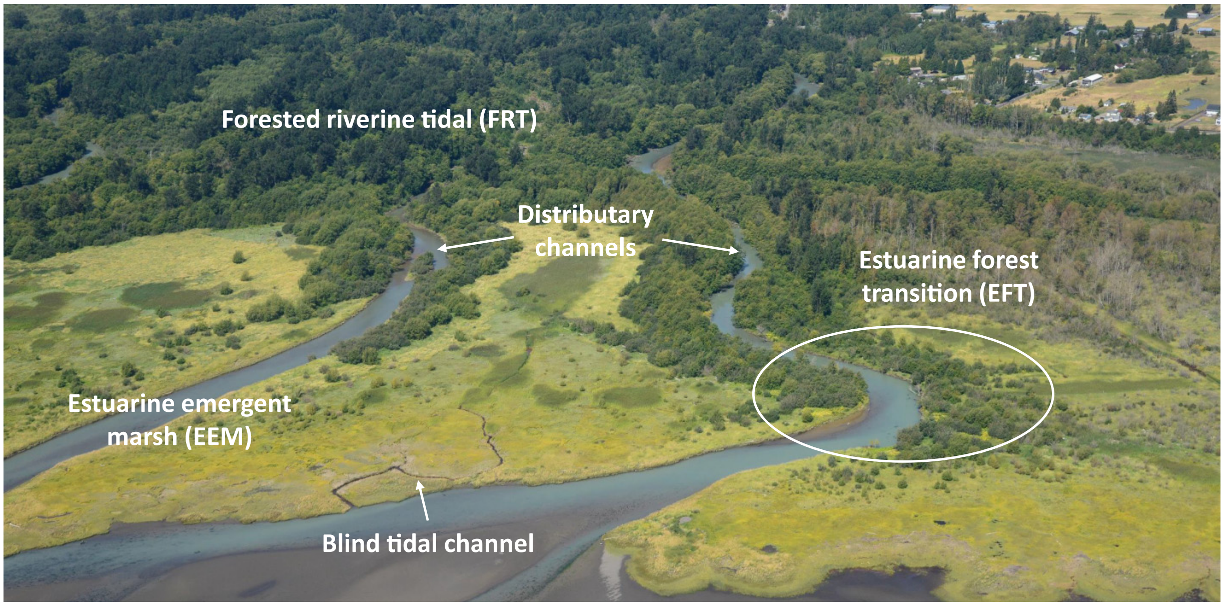
We investigated tidal wetland type effects because (1) juvenile Chinook salmon estuarine rearing success may vary due to abiotic (salinity, temperature) and biotic (prey availability and energy content of food) differences among tidal wetland types; (2) not all tidal wetland types respond similarly to stresses, such as predicted sea level rise or nutrient pollution; and (3) some Puget Sound salmon recovery plans have goals related to specific tidal wetland vegetation types within their river deltas, so comparative analyses could inform management.

We characterized the tidal wetland type of each site, based on indicator habitat types (Fig. 1, Supplemental text and Table S1). We used aerial photographs to determine the dominant vegetation type, following the classifications of Cowardin et al. (1979). Sites were also evaluated in the field to verify aerial photograph interpretations, and the presence/absence of indicator vegetation provided a qualitative evaluation of photogrammetric classification. Note that we evaluated the current tidal wetland type, which could be different from the historical tidal wetland type due to subsidence, vegetation removal, or other processes.

Channel types

We examined two general classes of channels in estuarine deltas. Distributaries connect rivers to marine waters (Fig. 1). While tidally influenced, they are maintained primarily by the constant flow of river water. Blind tidal channels have only one connection to another water body (a distributary or marine embayment) and are flushed only by tidal exchange (Ashley and Zeff 1988; Hood 2006). Both channel types are likely important to juvenile salmon for different reasons. Distributaries are almost always wetted (although the depth can change depending upon tide and river flow), while blind channel sites may significantly dewater or become disconnected during low tides. Distributaries serve as the main pathways by which juvenile salmon move from river to sea, while blind channels are relatively shallow, low energy environments that provide rearing opportunities with high ratios of channel edge to marsh (Simenstad et al. 2002) and a predator refuge function for juvenile salmon (Thorpe 1994). Each

Fig. 1. Aerial photo of the lower Nooksack tidal delta illustrating distinctions among tidal wetland and channel types (Source: Washington Shoreline Photo Viewer, https://apps.ecology.wa.gov/shorephotoviewer/).



site in the four delta systems was attributed to a blind or distributary channel.

Landscape connectivity

The concept of connectivity has been central to explaining habitat use by anadromous fish (Fausch et al. 2002). In estuarine systems, however, connectivity is complicated by opposing river and tidal flows, and channel networks become correspondingly complex (Davis et al. 2012). Therefore, we developed a new metric focused on potential pathways juvenile salmon might encounter while migrating from the river to each sampled site in a bifurcating tidal delta network. Landscape connectivity was defined as a function of both the length, width, and complexity of the pathway that outmigrating juvenile Chinook salmon must follow to access particular estuarine locations. Higher values of landscape connectivity have a shorter and/or less complex pathway to the river mainstem, the source of juvenile Chinook salmon. We created GIS layers of point data representing all sites used in this study. For each point, we calculated a landscape connectivity value by utilizing a fish pathway arc layer. The GIS arc layer uses width measurements of distributary channels to calculate landscape connectivity for each site in this study. It reflects the pathways by which juvenile Chinook salmon are expected to move through the delta channel network and to find and colonize habitat represented by the fish sampling sites. Channel width was measured at each bifurcating channel and used to determine channel order values (see additional methods in the Supplemental text).

Landscape connectivity (LC) for each site was calculated as

$$(1)\qquad \mathrm{LC} = \frac{1}{1 + \sum_{i=1}^{i_{\text{end}}} (B_i * D_i)}$$

where B_i = bifurcation order for distributary channel or nearshore segment i, D_i = distance along segment i of order B_i, i = count $(1 \ldots i_{\text{end}})$ of distributary channel or nearshore segments, and i_{end} = total number of distributary channel or nearshore segments at destination or sample point. See Supplemental text for rules for determining bifurcation order and subsequent channel-specific values of $B_i * D_i$.

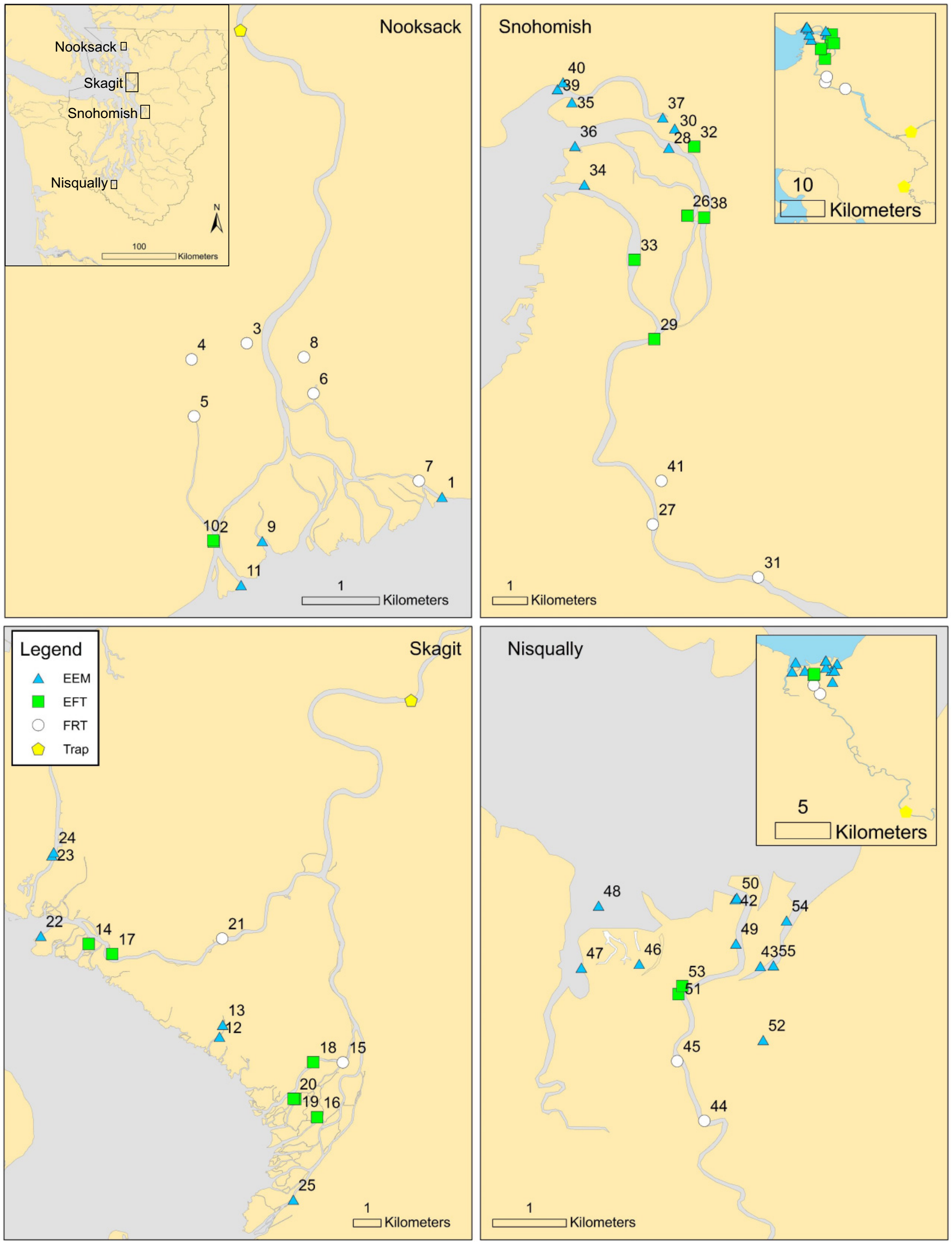
In a bifurcating tidal distributary network, multiple possible pathways exist to reach the same location. We focused on the maximum connectivity value of a site to the freshwater mainstem. Possible landscape connectivity values range from 0 (completely isolated) to 1 (mainstem upstream of all tidal distributary bifurcations).

However, the four delta systems vary in size and distributary channel complexity, so the calculated landscape connectivity values across delta systems are not uniform (Nooksack site landscape connectivity values range from 0.042 to 0.084; Skagit from 0.015 to 0.081; Snohomish from 0.012 to 0.351; and Nisqually from 0.059 to 0.290). To compare landscape connectivity across the four delta systems uniformly, we scaled connectivity values to the highest landscape connectivity value within each delta, thus forcing each system to fit more uniformly with each other. We called the standardized version of landscape connectivity “Maximum Standardized Landscape Connectivity” (Max.Std.Conn., Table S2).

Fish sampling

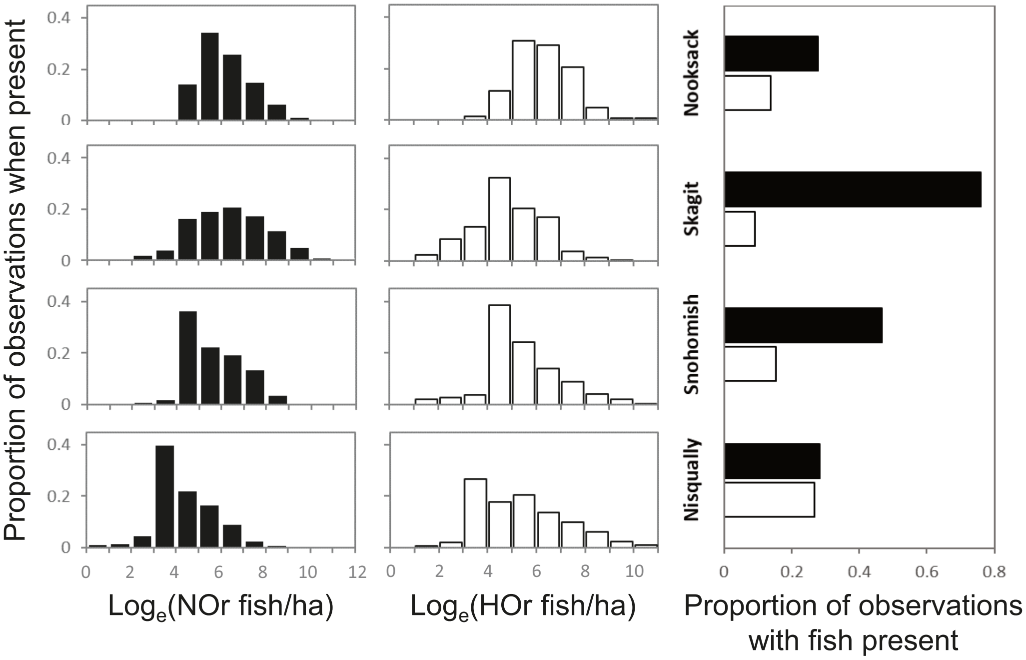
We compiled records of juvenile Chinook salmon abundance from beach seine and fyke trapping sites in all four river deltas (Fig. 2, Table S2) from 1995 to 2015 (Table 1). The two sampling techniques have their individual sampling biases related to gear-specific efficiency and area sampled (see Supplemental methods and Table S3). We converted counts to local density (fish ha^{-1}) by estimating set or channel area and capture efficiency (proportion captured

Fig. 2. Four Puget Sound river delta systems examined in this report. Symbols represent smolt traps (yellow pentagons) and delta sampling sites, with numbers corresponding to the site list in Table S2. White circles, green squares, and blue triangles indicate forest-riverine tidal (FRT), estuarine-forest transition (EFT), and estuarine-emergent marsh (EEM) sites, respectively. Sites not bordering main distributaries are in blind tidal channels or small (unmapped) distributaries. For more information describing sites, see Table S2. Map Projection: NAD 1983 State Plane Washington North (ft). Coordinate System: WGS 1984.



when present, estimated using mark–recapture tests across the season). Hence, density = count/recovery efficiency/area. Density data were log-transformed to correct for geometric variation. This procedure was done separately for NOr and HOr catches, resulting in separate density estimates for NOr and HOr Chinook. All fish captured during the studies were carefully handled, consistent with applicable state and federal laws for ESA-listed species. While recent monitoring across all systems is biweekly or monthly from February to August, earlier years (particularly in the Nooksack and Snohomish systems) sometimes included fewer seasonal observations.

Fig. 3. Proportion of all observations of juvenile Chinook density in Nooksack, Skagit, Snohomish, and Nisqually delta systems (top to bottom) of natural-origin (NOr) (black bars) and hatchery-origin (HOr) (open bars) when juvenile Chinook salmon were present, and proportion of observations of fish presence (right column).



Statistical analysis

Fish abundance (i.e., count data) can be difficult to evaluate because the patchiness (schooling) of fish produces a high number of zeros in the data. Thus, we used a two-stage model, a common tool for handling zero-inflated data (Barry and Welsh 2002), to evaluate how landscape characteristics influenced juvenile Chinook salmon densities in the four deltas. The first stage used logistic regression to estimate the probability of a nonzero response, i.e., presence during a sampling event. The second stage used only positive (i.e., fish present) density values to evaluate magnitude changes in biweekly local density among and within each delta. Because two-stage models include two fits to the data, final model predictions are the product of both the probability (i.e., first stage) and the estimated magnitude as a function of the selected covariates (second stage). Large system differences exist within our dataset for overall juvenile Chinook salmon presence, but there is good system overlap in the frequency of density levels for both NOr and HOr juvenile Chinook salmon when present (Fig. 3).

Juvenile NOr Chinook salmon could display nuanced seasonal patterns reflecting complex life history variation within the species. Given the nonlinear nature of these complex seasonal patterns, we used generalized additive models (GAMs; Hastie and Tibshirani 1990) to fit the presence/absence and the positive density data. GAMs are analogous to generalized linear models, with the added flexibility of model covariates using a set of "smoothing functions" to capture the nonlinear trends. Smoothing functions, although free to take any form, are penalized for excessive overfitting to maximize the trade-off between fit and the degree of smoothness for each predictor (Wood 2017). Thus, GAMs provide a robust tool to evaluate changes in density while accounting for complex nonlinear trends. Two-stage models were fit separately for NOr and HOr juvenile groups.

Covariates included in each stage of analysis were selected to best represent the natural system based on expert knowledge. Our objective was to evaluate how juvenile Chinook salmon presence and density varied as a function of landscape attributes—specifically wetland vegetation type, channel type, and Max.Std.Conn.—within and among the four deltas. To better isolate landscape effects from temporal variation and watershed-specific spatial differences, candidate models (i.e., for both presence/absence and density models) included a week term to account for known seasonal patterns of outmigrating juvenile salmon and a system term to account for known system-level differences (Table 1). The model with the lowest AIC score was selected as the best fit model (Akaike 1973). Models with delta AIC < 2 were considered to have similar support, so we used model weights to evaluate their probability as the correct model based on likelihood estimates.

First-stage GAM models evaluated the presence/absence of Chinook salmon based on the set of covariates described above. Each model included week and system and then successively included single parametric terms for the remaining covariates and their first-order interactions with system. These models took the form:

$$\text{Logit}\,(p) = f_1\,(\text{Week}) + \text{System} + \text{X}\theta \tag{2}$$

Table 2. Model selection table for NOr presence/absence in all systems.

Model	Week	System	Year	Max.Std. Conn	Channel type	Wetland type	Max.Std.Conn × system	Channel type × system	Wetland type × system	df	ΔAICc	Weight
1	X	X	X							14	89.25	0
2	X	X								13	102.86	0
3	X	X		X						14	88.46	0
4	X	X			X					14	104.25	0
5	X	X				X				15	105.1	0
6	X	X		X			X			17	74.95	0
7	*X*	*X*			*X*			*X*		*17*	*0*	*1*
8	X	X				X			X	21	56.46	0

Note: Model covariates include week, system, year, channel type (chan.type; blind vs. distributary), wetland type (wet.type; EEM, EFT, and FRT), and maximum standardized connectivity (max.std.conn; landscape connectivity scores standardized to maximum score within each system). Best-fit model (7) is indicated in italic.

where p = the probability of presence or Pr(density $>$ 0), f_1(Week) represents the smooth function of week, System represents the individual deltas, and **X** is the row of the model matrix for the parametric landscape attributes with their corresponding parameter vector, θ. Model fit, or predictive capability, was evaluated based on the proportion of deviance explained by the best-fit model.

Initial analysis of the positive density data suggested a more complex structure for fitting juvenile Chinook salmon density among the four deltas in our second stage model. We used a hierarchical GAM to explore how the nonlinear components differed within the levels, or groups, of our selected landscape attributes (Pedersen et al. 2018). Specifically, we evaluated how Chinook salmon density varied seasonally (i.e., Week) within each channel type and wetland type. In addition, we asked how Chinook salmon density varied as a function of landscape connectivity within each system. Such terms were fit using sum-to-zero constraints that fit a smooth for the term (week or maximum standardized connectivity) for each level of the factor of interest (channel type, wetland type, or system) which are presented as deviations from the smooth for the main effect term (week or maximum standardized connectivity). Within this structure, we could estimate a global fit for each of our parameters of interest as well as estimate a fit for each level or group as it varied from the global relationship. Due to the complexity of the models and the number of potential terms, we chose to use a double penalty selection procedure (Marra and Wood 2011) on the full model, including all terms and first-order interactions. The double penalty selection procedure imposes an extra penalty on smooth terms, such that those smooth components tending toward zero and thus a straight line (reflected in effective degrees of freedom (EDF)) do not contribute toward model fit. In contrast, terms with positive EDF values and p values less than 0.05 contribute significantly toward model fit. The magnitude of the EDF values indicates the complexity of the smooth function used for model fit.

Our second-stage model took the form:

$$(3) \qquad \ln(\mu_i) = f_1(x_1) + \cdots + f_j(x_i) + f_{1,i}(x_i, x_{i+1}) + X\theta + \epsilon$$

where μ_i = density when present, $f_{1\ldots j}$ represent the smooth functions for single terms and interactions, **X** is the row of the model matrix for the parametric landscape attributes with their corresponding parameter vector, θ, and ϵ is an autocorrelated error term (see below). To evaluate the importance of each individual term in our models, we used a deviance decomposition, or partitioning, method similar to Reum et al. (2011). The portion of the deviance attributable to each single term, including their interactions, was the deviance of the model with all terms that included the one of interest minus the deviance of the model with all the terms of interest removed.

During model fit, we also needed to account for the autocorrelation in biweekly observations of juvenile Chinook salmon density. Prior to analysis, we evaluated autocorrelation plots, determined a lag-1 autoregressive error structure, and estimated that rho = 0.445 fit the data sufficiently. All models were fit with this error structure, and standard diagnostic procedures were used to assess fit and residual structure. All analyses were executed using R statistical software (R Core Team 2019) and specifically the mgcv package (Wood 2011). All plots were produced using the ggplot2 package for R (Wickham 2016).

Results

We found slightly different results when examining presence/absence and density when present. Below, we highlight the model selection results, examining the potential influences of landscape variables on both components. Model comparisons (Tables 2 and 3) provide insight into which variables best explain presence/absence, and summary tables of GAM parameters reveal which variables are important for explaining variation in density when present (Tables 4 and 5). Model predictions with confidence intervals illustrated in figures provide interpretation about variables or variable ranges where landscape predictors are important.

NOr presence/absence

The statistical model that best explained NOr presence/absence included the variables: system, week, channel type, and the interaction between channel type and system (Table 2). Both system and week explained the majority of the variability in the presence/absence of NOr Chinook salmon (Fig. 4, upper left panel). There was a strong seasonal effect

Table 3. Model selection table for HOr presence/absence in all systems.

Model	Week	System	Year	Max.Std.Conn	Channel type	Wetland type	Max.Std. Conn × system	Channel type × system	Wetland type × system	df	ΔAICc	Weight
1	X	X	X							15	95.84	0
2	X	X								14	94.1	0
3	X	X		X						15	95.08	0
4	X	X			X					15	55.92	0
5	X	X				X				16	62.13	0
6	X	X		X			X			18	97.06	0
7	*X*	*X*			*X*			*X*		*18*	*0*	*1*
8	X	X				X			X	22	23.86	0

Note: Model covariates include week, system, year, channel type (chan.type; blind vs. distributary), wetland type (wet.type; EEM, EFT, and FRT), and maximum standardized connectivity (max.std.conn; landscape connectivity scores standardized to maximum score within each system). Best-fit model (7) is indicated in italic.

Table 4. Smoothed term (s) parameters from global model fit to positive NOr densities in all systems.

Model Terms	edf	Ref. df	*p*-Value
s(week)	6.243	24	<0.001
s(year)	20.110	24	<0.001
s(max.std.conn)	0.691	9	0.0483
s(max.std.conn, system)	13.217	30	<0.001
s(week, wet.type)	4.980	20	<0.001
s(week, chan.type)	6.581	10	<0.001

Note: Model covariates include week, system, year, channel type (chan.type; blind vs. distributary), wetland type (wet.type; EEM, EFT, and FRT), and maximum standardized connectivity (max.std.conn; landscape connectivity scores standardized to maximum score within each system). All terms contributed significantly to fit and define the best model.

Table 5. Smooth term parameters from global model fit to positive HOr densities in all systems.

Model terms	edf	Ref. df	*p*-Value
s(week)	6.115	9	<0.001
s(year)	6.478	24	0.015
s(max.std.conn)	2.068	9	<0.001
s(max.std.conn,system)	3.128	28	<0.001
s(week,wet.type)	6.414	20	<0.001
s(week,chan.type)	2.880	10	0.003

Note: Model covariates include week, system, year, channel type (chan.type; blind vs. distributary), wetland type (wet.type; EEM, EFT, and FRT), and maximum standardized connectivity (max.std.conn; landscape connectivity scores standardized to maximum score within each system). All terms contributed significantly to fit and define the best model.

on the probability of NOr presence in all delta systems (Fig. 5A). The Skagit delta had the highest probability of NOr presence, and this high probability was more broadly sustained over time than in the other deltas, spanning from week 8 through week 27 (mid-February to July). All four delta systems had peak probabilities of presence around week 22 (end of May), after which there were steep declines. The Skagit delta showed a higher probability of NOr presence in blind channel habitat than in distributary channels; the reverse was true for the Nooksack. The probability of presence was similar between channel types in the Nisqually and Snohomish deltas.

HOr presence/absence

The statistical model that best explained HOr presence/absence was the same as for NOr, which included the variables: delta system, week, channel type, and the interaction between channel type and delta system (Table 3). Similar to NOr presence/absence, system and especially week explained the majority of the variability in HOr presence (Fig. 4, upper right panel).

There was a strong seasonal effect on the probability of HOr presence in all delta systems. The probability of presence for HOr fish was estimated at zero until roughly week 16 in all systems, after which it increased to a peak around week 25 (mid-June), three weeks later in the year than did the NOr peak. Thereafter, HOr probability of presence sharply decreased, resulting in a more compressed seasonal curve compared to NOr outmigrants (Fig. 5B). These differences reflect a later and more rapid release of hatchery Chinook salmon and shorter cohort residence time in the delta compared to the broader and earlier outmigration timing of NOr migration, especially the fry life history (Zimmerman et al. 2015), from natal streams to the river delta. (Fig. 5A).

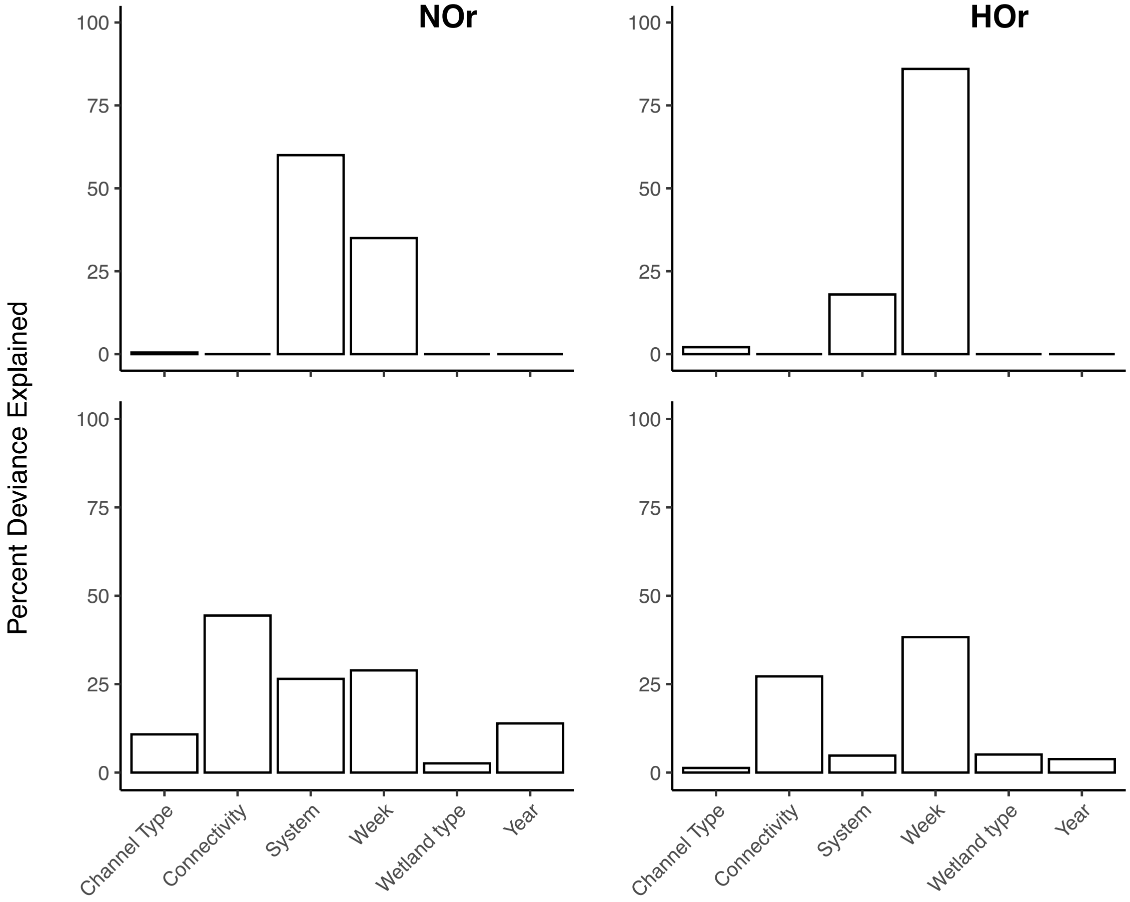
The Skagit Delta had the lowest peak probability of HOr presence, and the Nisqually Delta had the highest, which likely reflects differences in hatchery releases and areal extent of estuarine habitat (Table 1). The Skagit and Nooksack deltas had a higher probability of HOr presence in distributary habitat compared to blind channel habitat. There were no differences in HOr presence between channel types in the Nisqually and Snohomish deltas. However, despite these patterns, NOr and HOr exhibited strong co-occurrences during time periods after HOr releases.

NOr density when present

NOr density (when present) was primarily a function of landscape connectivity and seasonal patterns between channel types and among wetland types. In addition, there was a significant effect of year, likely accounting for interannual and system-level differences in outmigration abundance (Table 4). Week, system, and connectivity explained the majority of variability in NOr density when present (Fig. 4, lower left panel).

Overall, NOr density was significantly greater in blind tidal channels earlier in the season but higher in distributary

Fig. 4. Percent deviation explained by factors for the best-fit model for NOr (left column) and HOr (right column) presence/absence models (top row) and Chinook density when present models (bottom row). The total deviance explained by each factor includes the proportion attributable to each single factor and all interactions for which that particular factor is included.



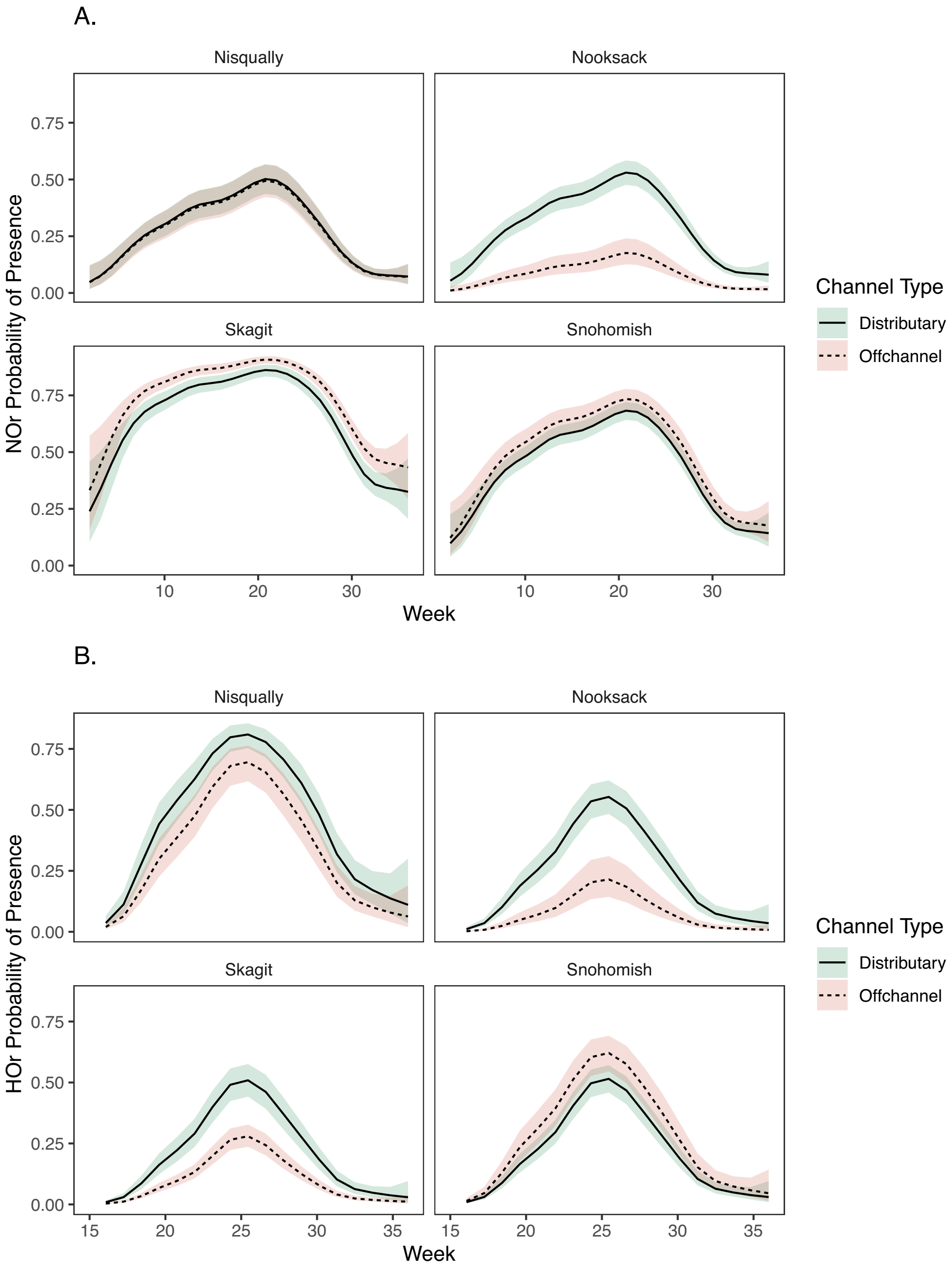
channels late in the season (Fig. 6A). NOr density peaked around weeks 15 and 24 for blind and distributary channels, respectively. Seasonal differences among wetland types were less discernible and were generally similar after week 15 (Fig. 7A). However, the rank order of predicted NOr density among wetland types prior to week 15 indicated a potential switch from FRT to EFT habitats around week 12. While the shapes of the seasonal relationships for channel and wetland types were similar, the overall magnitude of predicted NOr density varied among systems. NOr Chinook salmon densities were highest in the Skagit Delta and lowest in the Nisqually Delta (Figs. 6A and 7A, insets), likely as a function of total outmigrant population size and available channel habitat area (cf. Table 1).

We found a strong global effect (i.e., across all systems) of Max.Std.Conn on NOr density when present, although the effect was modest compared to other variables (Table 4). The global effect of landscape connectivity indicated that NOr density increased positively with standardized connectivity (Fig. 8A and Table 4). Nevertheless, one of the strongest effects on NOr density was the interaction between the system and Max.Std.Conn, which was generally positive but varied by system (Table 4). This interaction, which can be represented by deviation from the global pattern, generally ranged between 0 and 2 for all systems, with the exception of the Nooksack. However, observations were not uniform or complete across the range of connectivity values within any of our systems (Fig. 8B). In particular, the Snohomish and Nooksack had highly skewed observations, generally representing the low and high end of the range, respectively. The largest deviations from the global pattern occurred where observations were not available within a particular system (Fig. 8C).

HOr density when present

HOr density when present was driven by a strong seasonal effect and a similar positive effect of landscape connectivity (Table 5 and Fig. 4, lower right panel). HOr density increased rapidly from week 16 to a peak in week 26 and a subsequent decline through the end of the season. The seasonal effect on HOr density when present was embedded within patterns for both channel and wetland types (Figs. 6B and 7B). HOr density was not significantly different between blind and distributary channels across the season, although the predicted densities in distributary channels encompassed a higher range compared to blind channels after week 21. HOr density was

Fig. 5. Best model predictions for the probability of the presence of NOr (A) and HOr (B) juvenile Chinook by system, week, and channel type. Shaded regions reflect 95% confidence intervals.



significantly higher in EEM habitats compared to EFT and FRT habitats prior to week 24. After the period of peak HOr density, there was no apparent difference in observed differences among the wetland types, and densities consistently decreased throughout the remainder of the rearing period. Similar to NOr densities, the global patterns in HOr density as a function of channel and wetland types differed only by the magnitude of the predicted density (see Figs. 6 and 7 insets).

Landscape connectivity had a similar positive effect on HOr density as observed for NOr density (Fig. 9A). The global effect of standardized connectivity indicated that HOr density increased with an increase in connectivity. Deviations between the global pattern and system-level patterns in connectivity were evident when predicting HOr density but were less discernible than observed for NOr density. System-specific deviations were less consistent and appeared highest in the Skagit and Nisqually compared to the Snohomish and Nooksack (Fig. 9C). Both uneven sampling across the range of connectivity values and the relatively high variation in HOr densities among systems contribute to the observed patterns in deviations.

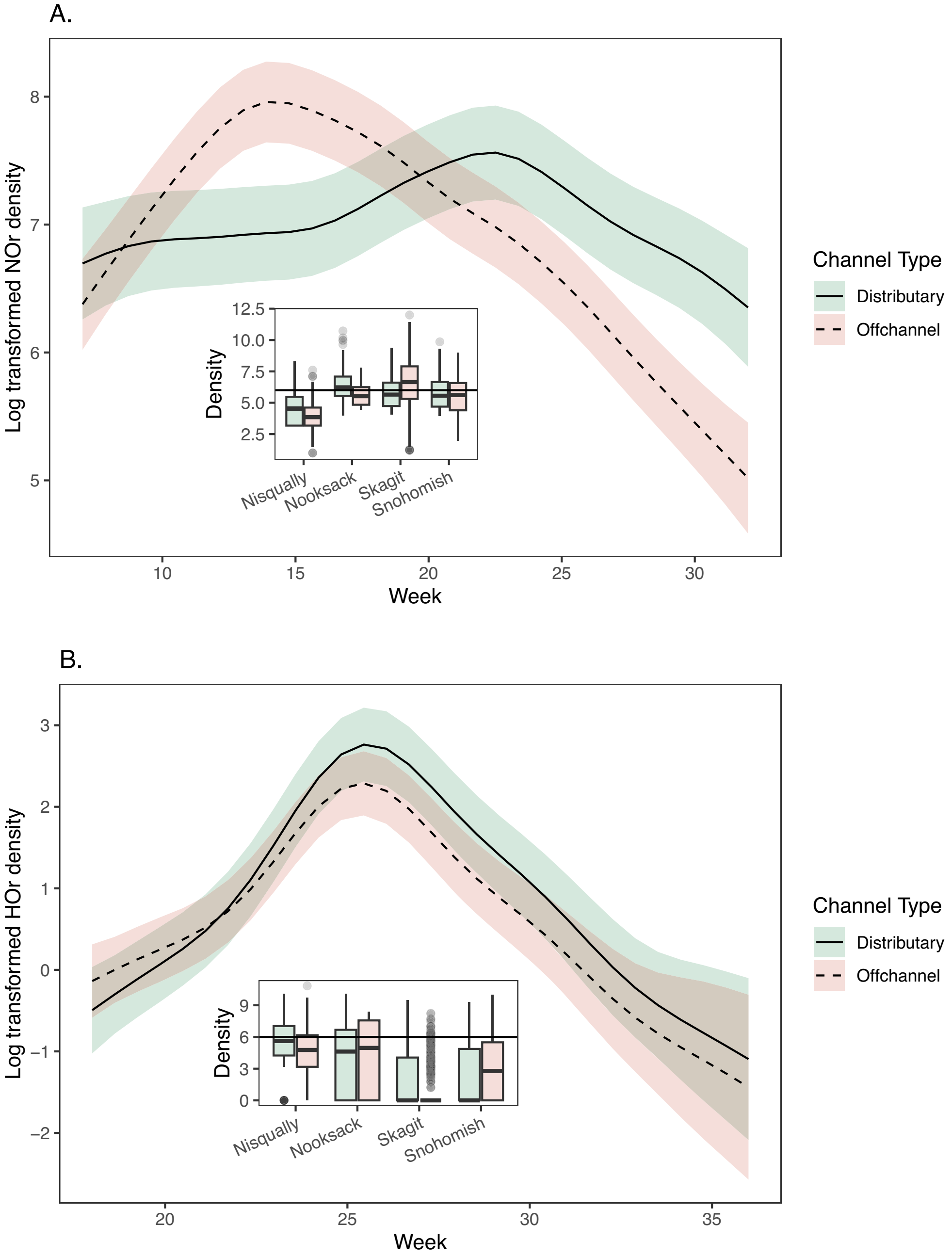
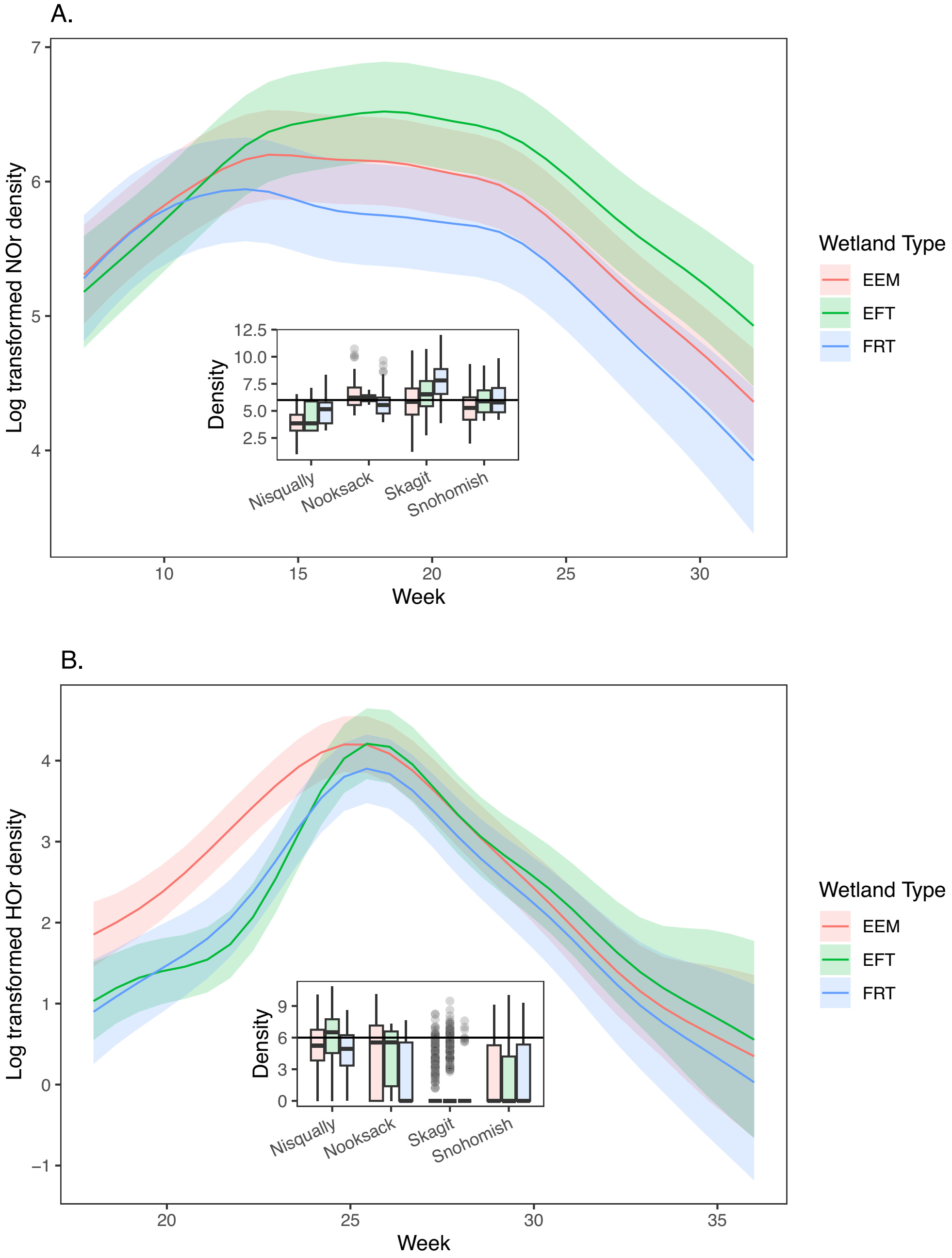


Fig. 6. Model fitted estimates of NOr (A) and HOr (B) juvenile Chinook density when present by week and channel type. Fish density is $\log_e$ transformed number of fish/hectare. The shaded area reflects the 95% confidence interval of the model prediction. Inset boxplots are observed density by channel types within each system. Note the difference in the *x*-axis reflecting the seasonal distribution of NOr and HOr.

Discussion

Our analysis of unmarked, natural-origin, and marked, hatchery-origin juvenile Chinook salmon revealed strong landscape-based patterns, as well as strong intra- and inter-annual effects. Landscape effects included delta system, channel type, landscape connectivity, and their interactions. Seasonal effects were expected from the well-known natural history of juvenile salmon seaward migration timing through river deltas (Healey 1982). Intra-annual density can also vary greatly (Ellings et al. 2016) depending on seasonal variation in local habitat characteristics such as depth (Bottom et al. 2005), temperature (Neilson et al. 1985), and salinity (Levings 2016). These characteristics likely produce variation around the central tendencies generated by landscape features (e.g., channel type and tidal wetland type; Figs. 6 and 7). Inter-annual variation can be caused by variation in outmigration population size (Hall et al. 2018) and by inter-annual climate variation impacting habitat quality, e.g., through variation in river discharge, water temperature, and salinity (Greene et al. 2005).

Fig. 7. Model-fitted estimates of NOr (A) and HOr (B) juvenile Chinook density when present by week and wetland type. Fish density is $\log_e$ transformed number of fish/hectare. The shaded area reflects the 95% confidence interval of the model prediction. Inset boxplots are observed density by wetland types within each system. Note the difference in the *x*-axis reflecting the seasonal distribution of NOr and HOr.



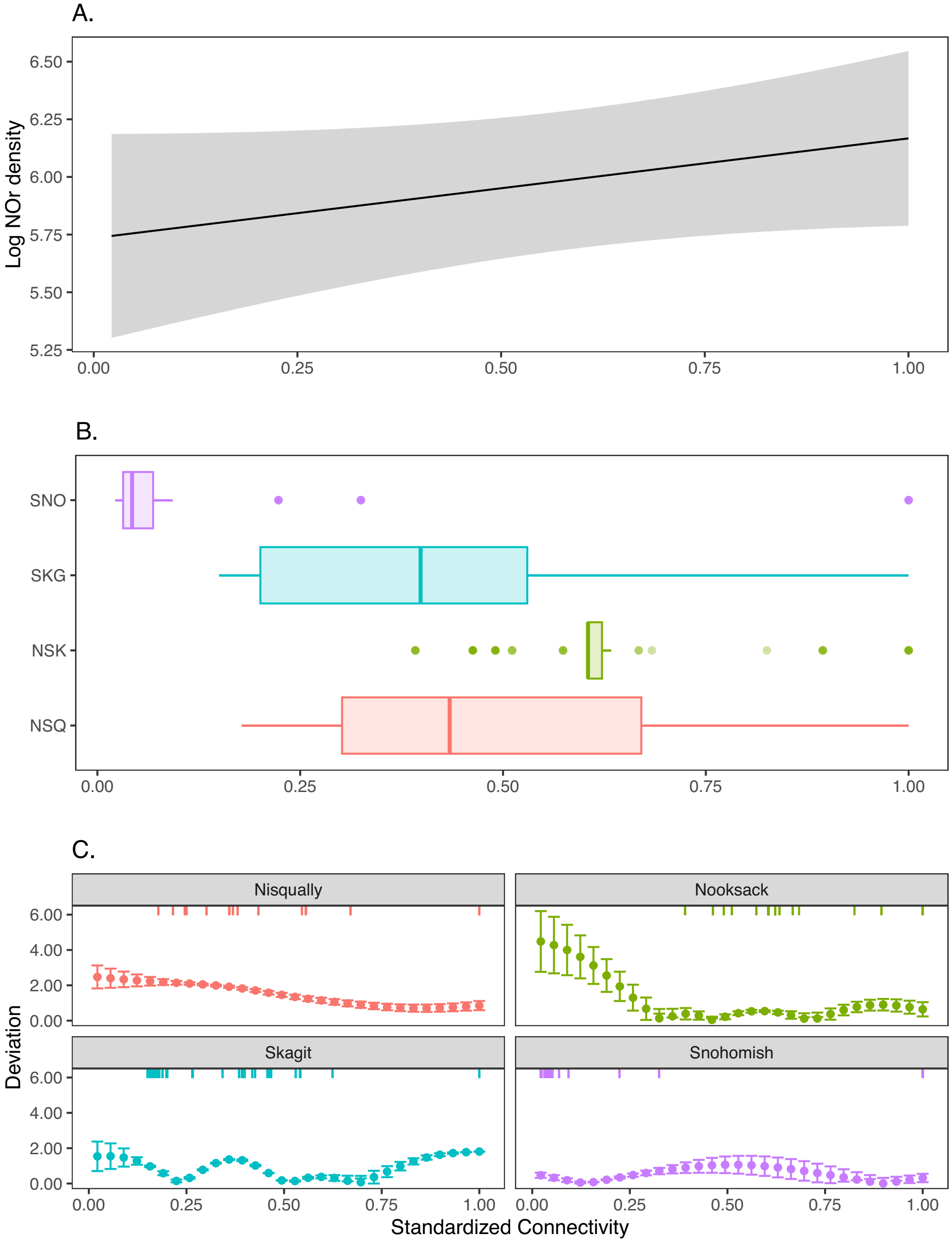
Landscape effects

We focus on why landscape features might directly influence juvenile Chinook salmon rearing patterns. We recognize the potential to overestimate the strength of correlations in analyses of fish abundance, and therefore discuss our interpretations considering the strength of the correlation, its consistency across multiple populations or units of observation (i.e., systems), plausible mechanistic explanations, and alternative or competing explanations (Hilborn 2016).

System

We found support for shared seasonal and landscape patterns of Chinook salmon within the four deltas but also acknowledged nuanced differences among systems that warrant discussion. System differences were primarily attributable to shifts in density across the season within channel and wetland types but also influenced patterns of presence/absence for NOr fish. Two types of system differences may help explain these results: idiosyncratic differences

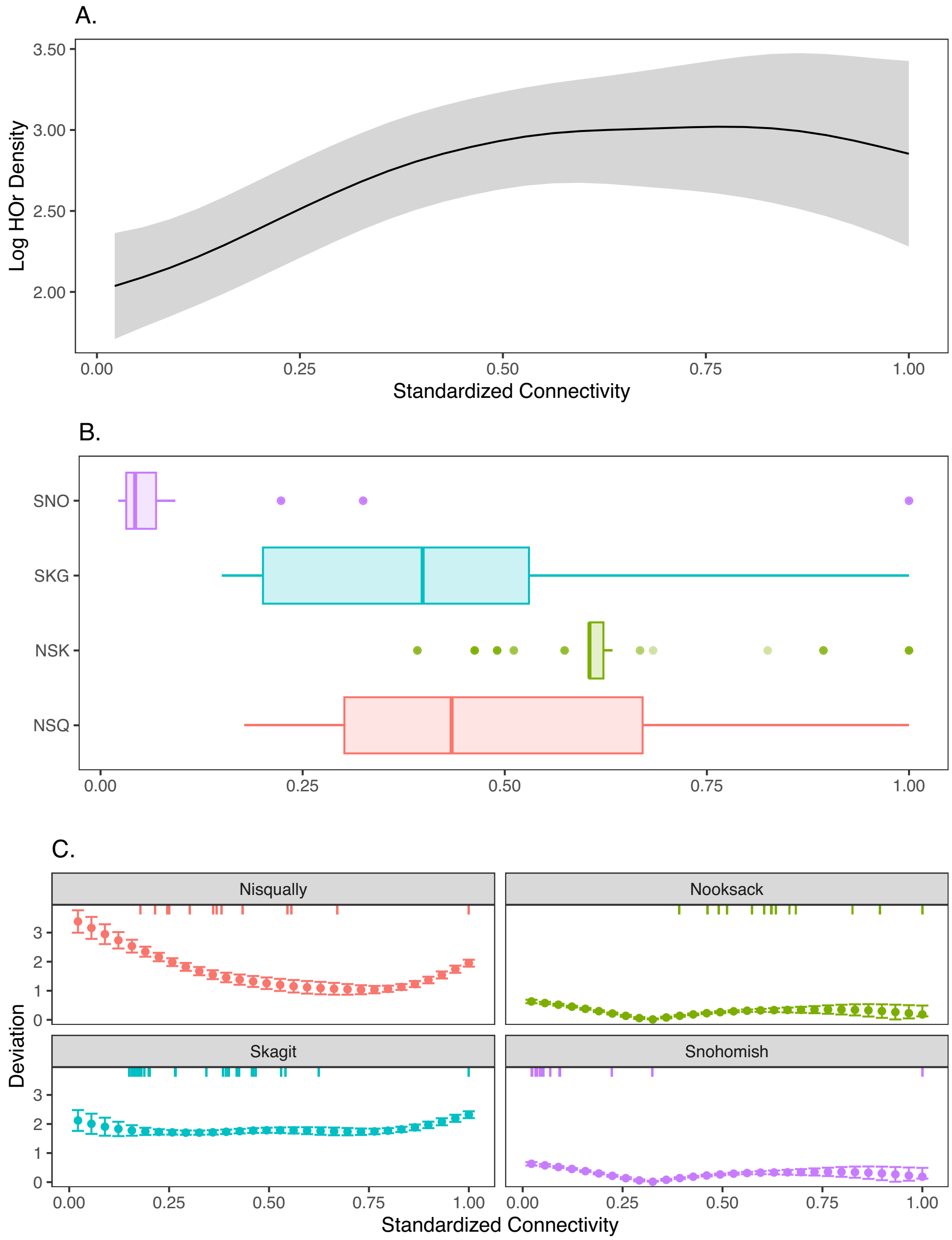
Fig. 8. Estimated effect of landscape connectivity (standardized by maximum value within each system) on NOr juvenile Chinook density when present. (A) Global effect of landscape connectivity across all systems. (B) The distribution of sampling sites within each delta across the range of standardized maximum connectivity values. (C) System-level deviations in predicted density from global fit across the range of standardized connectivity.



between river delta systems and systemic differences related to river basin size.

Idiosyncratic differences include differences in river hydrology and tidal range. Most of the Skagit basin is snow-dominated and has a flow regime that shows a late spring/early summer peak; most of the Snohomish and Nisqually basins are rainfall-dominated with winter peak flows; and most of the Nooksack is transitional between rainfall- and snow-dominated. These hydrographic differences affect Chinook salmon life history traits, such as spawn timing, age at spawning, age at outmigration, and body size (Beechie et al. 2006). The tidal range also varies among the deltas, with a mean range of 2.6 m for the mouth of the Nooksack, 3.4 m for the Skagit and the Snohomish, and 4.1 m for the Nisqually. This tidal variation affects tidal channel geomorphology, such that blind tidal channels are few and small in the Nooksack, large and abundant in the Nisqually, and intermediate in the Skagit and Snohomish, after accounting for

Fig. 9. Estimated effect of landscape connectivity (standardized by maximum value within each system) on HOr juvenile Chinook density when present. (A) Global effect of landscape connectivity across all systems. (B) The distribution of sampling sites within each delta across the range of standardized maximum connectivity values. (C) System-level deviations in predicted density from global fit across the range of standardized connectivity.

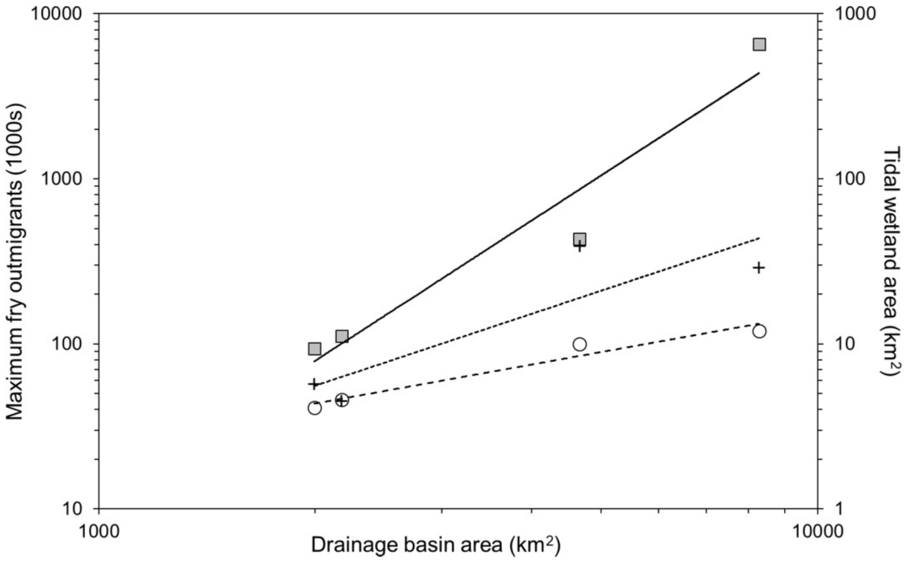


the effects of delta surface area (Hood 2015). Thus, differences in tidal range between systems affect delta rearing habitat availability for juvenile Chinook salmon and, by extension, fish densities differently in each system.

Additionally, variables related to dynamic environmental features such as water temperature, dissolved oxygen, and turbidity vary between systems. For example, systems with large mudflats (e.g., Skagit Bay and large restored areas in the Nisqually delta) might be expected to warm faster than systems with greater vegetation coverage, and estuaries in watersheds that drain abundant, large glaciers (e.g., Skagit) would be expected to have protracted freshwater inundation during the latter portion of the rearing season. Finally, hatchery practices likely vary idiosyncratically among river systems, especially with respect to the number of fish released.

Systemic effects of basin size may be a significant unaccounted factor, with multiple pathways for influencing fish densities and rearing habitat (Hood 2007). When the maximum observed fry migrant population size from Table 1 is plotted against river drainage basin area (from Czuba et al. 2011), a power function describes the positive correlation, with $R^2 = 0.94$ and a scaling exponent of 2.8, which

Fig. 10. Scaling of maximum observed fry outmigrant population size (solid gray squares and left axis, $y = 4{*}10^{-8}x^{2.8}$, $R^2 = 0.94$) with river drainage basin area. Scaling of the late 19th-century tidal wetland area (crosses, $y = 0.00009\ x^{1.4}$, $R^2 = 0.78$) and the 1980 tidal wetland area (white circles, $y = 0.01\ x^{0.8}$, $R^2 = 0.95$) with river drainage basin area is shown for comparison on the right axis.



indicates a strongly nonlinear (allometric) increase in outmigrant population size with increasing basin size (Fig. 10). The scaling exponent of 2.8 indicates that migrant fry population size increases three times faster than basin size. This is likely the result of other nonlinear consequences of basin size on spawning and rearing habitat abundance in the basin. In tropical systems, for example, large rivers have been shown to have disproportionately larger floodplains than do smaller rivers, and this has been related to the scaling of fisheries catches with river size (Perez Filho and Christofoletti 1977; Welcomme 1979; Liermann et al. 2010). In Puget Sound rivers, the lengths of braided and side channel habitats in river floodplains scale with mainstem river length (Hall et al. 2018), with braided channel length and side channel length increasing 50% and 30% faster than mainstem length, respectively.

Basin size and its cascading effects on habitat abundance and diversity, as well as on salmon productivity and life history diversity, likely partially explain the system effects in our analysis. When we compare the scaling of fry migrant population size with river size to the scaling of river delta tidal wetland area with river size (data from Simenstad et al. 1982), it is apparent that modern tidal wetland rearing habitat area does not scale as steeply as does maximum migrant fry population size, although the difference with historical tidal wetland area is much less (Fig. 10). Consequently, juvenile Chinook salmon density effects might be stronger in larger deltas because they produce disproportionately more fish and because, at least in the case of the four river deltas that we examined, larger deltas have had disproportionately greater tidal marsh habitat loss.

Differences in salmon ecology among watersheds have often been seen as idiosyncratic. Every watershed is in some sense unique, and such individual differences have often been emphasized in independent analyses of salmon populations (e.g., Zimmerman et al. 2015; Ellings et al. 2016; Beechie et al. 2021). Conversely, an allometric approach on watershed size and its consequences for habitat, salmon production, and natural history (e.g., Hood 2007; Hall et al. 2018) could allow partitioning of delta system differences in salmon ecology into predictable watershed size effects and idiosyncratic variation. A systematic allometric approach depends on a larger sample size of systems than we could accomplish in this study, but recent studies of systems across the Pacific Northwest (e.g., Apgar et al. 2020) indicate the potential for additional research addressing this question.

Landscape connectivity

This study provides a novel method for calculating landscape connectivity for anadromous fishes and reveals that landscape connectivity is an important predictor of NOr and HOr juvenile Chinook salmon density but not presence in all four river deltas, a finding replicated in other studies (Ellings et al. 2016) and regions (Munsch et al. 2020) using different metrics for landscape connectivity. Overall, the landscape connectivity effect on HOr and NOr density is positive and consistent among deltas for HOr groups but varied slightly among deltas for NOr outmigrants. System-specific deviation from the overall pattern may reflect biological hotspots (or depressions) within each delta system, such as system differences in habitat opportunity across deltas longitudinally (upstream to downstream) or differences in nonlinear branching patterns of distributary channels across deltas, which affect juvenile salmon migration pathways. Alternately, these differences may reflect sampling site bias across the landscape connectivity gradient, an issue that occurred in at least two of the four sampling designs (Fig. 8B).

Connectivity can describe both the direct effects of channel morphology on the physical dispersal of seaward-migrating salmon, as well as spatial gradients in biotic and physical habitat attributes. We observed effects of landscape connectivity in all systems for NOr juveniles, as well as a strong system-connectivity interaction that reflects some nonlinear aspects of connectivity for some deltas. Tidal wetland types (as characterized by dominant vegetation types) also track connectivity gradients because FRT sites are closer to the freshwater mainstem, while EEM sites are farther away and generally dispersed over a greater area of the delta along a network of serial distributary bifurcations. Additionally, because landscape connectivity describes the gradient from river to sea, it is a good predictor of physical habitat attributes such as temperature and salinity, which interact with vegetation as well as the fish community. Any variation in Chinooksalmon densities explained by characteristic vegetation communities and physical habitat attributes can also be explained by landscape connectivity. This autocorrelation likely reduced our ability to detect significant tidal wetland effects, independent of connectivity effects.

Analyses of connectivity in this study assumed that connectivity was related to migration access purely based on distance and bifurcation, essentially using a structural interpretation of connectivity. However, other studies have pointed to additional factors related to connectivity (Fullerton et al. 2010) worth applying in estuarine contexts. For example, studies of freshwater spawning support the idea of incorporating aspects of habitat quality to better predict the occurrence and abundance of spawning salmon (Isaak et al. 2007; Rodeles et al. 2019). Similar approaches may apply in estuarine environments, and habitat quality features related to growth and survival (e.g., temperature regime, food availability, cover from predators) may point to why large differences in occurrence and density existed over time between blind and distributary channels in this study. Other conceptualizations of landscape connectivity integrate individual movement rules based on concepts of landscape resistance and conductance to movement (McRae et al. 2008; Zeller et al. 2012; Morin et al. 2017). Further work on the landscape connectivity of fish in estuarine environments should consider not only distance and structural complexity as highlighted in this study but also physical constraints that increase resistance to movements such as velocity (Hering et al. 2010), high temperatures (Marschall et al. 2011), and other water quality parameters (Tetard et al. 2016). Conversely, tidal inundation of low-elevation wetlands may be one example of conductance, enabling juveniles to by-pass channel structures by cross-wetland movements at higher tides.

Effects of channel type

Juvenile natural origin Chinook salmon clearly exhibit higher densities in blind channel areas early in the season, consistent with extensive observations of the utilization of these areas for rearing (David et al. 2014). This result likely reflects their value as refuge from fish predators and as areas of low velocities that reduce bioenergetic costs for migrating fry (Sommer et al. 2005; Safran et al. 2016). Later in the migration season, NOr Chinook salmon use distributaries more than blind channels as they transition at larger sizes out of rearing habitats and into migratory pathways prior to moving to marine waters. HOr juveniles, which are released later in the year than the early part of the NOr outmigration curve and at a larger and physiologically more mature size, generally spend little time in blind channel rearing habitat, instead quickly migrating through distributaries to marine nearshore and offshore habitats.

We also found strong system-by-channel-type interactions for both presence/absence and density. These results may be explained by systemic differences in outmigrant abundance and life history types. Migrant fry comprise a large proportion of Skagit and Snohomish outmigrations (Table 1) that reside for weeks to months in the deltas (Simenstad et al. 1982); fry residents typically rear in blind tidal channels. However, the Nooksack is dominated by parr that migrate quickly through the delta (Beamer et al. 2016). The Nooksack Delta pattern was distinct in having little difference in NOr density between blind and distributary channels during midseason. Two reasons may account for this: first, the Nooksack is dominated by relatively large and physiologically mature parr outmigrants rather than relatively small and immature fry migrants, and parr spend relatively little time rearing in tidal marshes; and second, the Nooksack Delta has relatively little blind channel habitat available for rearing (Hood 2015), requiring more rearing in distributaries.

Uncertainties

Like many efforts to document landscape effects on populations, our approach relies on determining correlative associations between fish and their habitat. Other types of studies could improve the causal inference of these patterns. For example, two natural experiments add to our confidence in direct landscape connectivity effects on salmon distribution and abundance. In the Skagit delta, a channel avulsion on the north fork distributary increased landscape connectivity to some delta and adjacent nearshore locations, which thereafter increased Chinook salmon densities (Beamer and Wolf 2016). Conversely, a large log jam in the Nooksack delta disconnected sites along a distributary; afterward, the sites had lower Chinooksalmon densities (Beamer et al. 2016).

To better confirm the causal nature of our findings, we recommend a comprehensive analysis of effectiveness monitoring across multiple projects (Flitcroft et al. 2016). Performing experiments to demonstrate cause-and-effect can be difficult at large spatial extents, but it is possible in association with habitat restoration projects, as long as comprehensive effectiveness monitoring is used to document results. For example, our results predict that increasing habitat complexity along distributaries would have smaller effects than enlarging blind channel networks for NOr migrants, especially the early component, which is comprised of fry. Likewise, multiple effectiveness monitoring studies could be used to evaluate whether reconnection of estuarine emergent marsh results in lower rearing densities than reconnection of forested riverine tidal areas. Similar compilations of effectiveness monitoring have enabled comparisons of the efficacy of various tidal reconnection techniques (Greene et al. 2015), although they can be difficult to arrange because they are outcomes of multiple restoration efforts.

An alternative to empirical evaluation of restoration experiments is modeling the movements of fish in estuary systems to determine whether landscape effects are emergent properties of individual behavior. While these models are much better established for riverine species and life stages (Harvey and Railback 2009; Hawkins et al. 2020; Seaborn et al. 2023), several examples have focused on estuarine nursery species. For example, Haas et al. (2004) used an individual-based model to infer habitat characteristics that increased estuary rearing by brown shrimp, and Sridaran et al. (2023) used a particle tracking model to examine the fates of juvenile Chinook salmon migrating through the Sacramento delta. While these models can further corroborate empirical patterns, the assumptions concerning individual behavior and how habitat variation affects behavior are often complex. Nevertheless, movement models afford a means to systematically test how various "rules" of fish movement and residence, based in part on landscape features, can produce systematic patterns in rearing density and other population attributes. As knowledge of fish behavioral dynamics improves (e.g., Hering et al. 2010; McNatt et al. 2016), more accurate rules will emerge to verify these assumptions.

This study relies on two generally accepted methods for sampling fish in tidal deltas (beach seines and fyke traps), and each of these differs in gear selectivity, which in turn can depend on estuarine habitat attributes. We attempted to correct for these differences by integrating area sampled and capture efficiency estimates into density estimates (see fish sampling methods in Supplemental text), but recognize that our results nevertheless depend to some extent on the ability of these methods to effectively sample different life histories or size classes of juvenile Chinook salmon in different portions of the delta and at different times during the season. As juvenile salmon grow, they are less dependent on shallow water and more mobile, making estimates of the occurrence and density of larger size classes more uncertain. Size-dependent biases tend to be most important at the later portions of the season and may help to explain some of the broader confidence intervals illustrated in later weeks (e.g., Figs. 5 and 6B). However, capture efficiency trials were made throughout the season, so we suspect these biases were small.

Finally, our analysis assumed unmarked Chinook salmon represented natural-origin migrants. For much of the rearing season, this assumption is valid, as migrant fry immigration into deltas generally precedes hatchery releases by one to three months. However, later in the season, unmarked fish may be NOr migrant fry that have reared extensively in the delta and grown to parr size, NOr parr migrants swimming to the sea from the river, or unmarked hatchery releases. Marking effort varies across hatchery programs; larger hatchery releases will have more accidentally unmarked fish simply because the small percentage of lost tags or missed marks result in a higher abundance than in smaller hatchery releases. To avoid errors in assigning NOr Chinook salmon that are really unmarked HOr fish, we included data only for years with near-complete marking of hatchery releases. For example, from 2006 to 2015, unmarked hatchery releases of Chinook salmon in the Nooksack River averaged <6000 fish year^{-1} (Beamer et al. 2016). For hatchery Chinook salmon originating from the Skagit, 99.9% of the 764 570 fish released in 2002 (yearlings and subyearlings combined) could be identified as hatchery fish based on the presence of an adipose fin clip or electronic wanding for the presence of a coded-wire tag (Zimmerman et al. 2015). Marking practices in the Skagit have been similar to 2002, starting in 1995 to present. Even with the near-complete marking of HOr migrants, NOr parr migrants can be expected in catches later in the season, particularly if sampling occurs in distributaries conveying NOr parr migrants to the sea. Despite this biological "noise" in our analysis, we believe the observed patterns are robust, as we obtained similar model results when using total Chinook salmon density (marked and unmarked combined). Further efforts to refine analyses could focus on earlier sampling and body size cut-offs for fry observations.

Implications for restoration

Many estuaries are fragmented due to losses of historical distributaries (Bortleson et al. 1980; Collins et al. 2003) and are a fraction of their historical area due to the conversion of tidal wetlands to human land uses (Brophy et al. 2019). In response, many practitioners have completed estuary restoration projects, which are often expensive due to their size as well as societal requirements for drainage and flood control. Such socioeconomic constraints highlight the need for increasing the functional "bang for the buck" of these projects. Our results suggest three general restoration design principles arising from landscape patterns of tidal wetland habitat use by Chinook salmon: (1) include landscape connectivity in restoration planning, (2) reconnect blind channel habitats, and (3) restore the diversity of estuarine wetland types. The positive effect of landscape connectivity on juvenile Chinook density suggests that reconnection of the distributary channel network can improve rearing opportunities by reducing system fragmentation. Likewise, for estuaries with reduced habitat area, restoration at sites with higher landscape connectivity will provide habitat to more juveniles. In addition, for estuaries with reduced habitat area and high proportions of their NOr outmigrants expressing the fry life history, restoration planning could prioritize restoring blind channel rearing areas over restoration that simply "softens" existing channel margins. Because blind channel geomorphology follows allometric norms (e.g., Hood 2007, 2015), establishing the number and density of these channels is directly estimable from project footprints and elevation. Finally, our finding of a seasonal pattern of use by juvenile Chinook in all wetland types suggests that maintaining and restoring estuarine wetland diversity of systems should be a focus. The importance of habitat diversity for population productivity is well documented (Schindler et al. 2010; Brennan et al. 2019). Diverse habitat portfolios likely support increased life history diversity (Campbell et al. 2017), which in turn supports population resilience (Greene et al. 2010).

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This report is dedicated to Casimir Rice and Karen Wolf, who both passed away before they saw the fruits of their labor on this study. Casimir Rice helped frame the initial study and lead sampling in the Snohomish delta. Karen Wolf's efforts were central to the calculation of the landscape connectivity index, and she had her hands in many parts of this project. Numerous people assisted with fish data collection in all four delta systems. The study was greatly improved via extensive reviews overseen by T. Conway-Cranos (ESRP, Washington Department of Fish and Wildlife) and R. Conrad (Northwest Indian Fisheries Commission), as well as two anonymous reviewers. EB, CMG, GH, and JC were involved in study conceptualization, writing, and editing. EB, CMG, and JC were additionally involved in data curation, formal analysis, and project administration. EB, JC, CE, SH, and TZ were involved in methodology, collection, and curation of data from individual tidal deltas.

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Copyright

Data availability

The data used in this study were shared by tribes, and they exercise sovereign authority over it. Requests for data not supplied in tables, figures, or supplemental text may be made by formal request to coauthors.

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Competing interests

The authors have no competing interests in this study.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2023-0249.

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