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ARTICLE

Shallow Tidal Freshwater Habitats of the Columbia River: Spatial and Temporal Variability of Fish Communities and Density, Size, and Genetic Stock Composition of Juvenile Chinook Salmon

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Abstract

We investigated the spatial and temporal variability of the fish community and the density, size, and genetic stock composition of juvenile Chinook Salmon *Oncorhynchus tshawytscha* in shallow tidal freshwater habitats of the Columbia River. We sought to address data gaps related to juvenile Chinook Salmon in this portion of the Columbia River and thereby inform habitat restoration efforts. We examined fish communities, juvenile salmon life history characteristics, and relationships between salmon density and habitat conditions by using beach seine data collected over a 63-month period (2007−2012) from two tidal freshwater areas: the Sandy River delta (river kilometer [rkm] 188–202) and the lower river reach (rkm 110–141). We found few differences in the fish community across the two study areas. Fish community patterns were largely attributable to seasonal changes as opposed to spatial gradients and habitat types. Juvenile Chinook Salmon were the most common salmon species in our catches; this species was the only salmonid encountered during all four seasons. Chinook Salmon density differed among three distinct habitat strata (main channel, off-channel, and wetland channel), but FL and genetic stock

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composition did not. Across all habitat strata, environmental covariates (mean percent tree cover, dissolved oxygen level, and mean percent emergent vegetation) were positively associated with juvenile Chinook Salmon density. Although comparisons of environmental metrics and salmon density helped to establish a quantitative relationship between biotic and abiotic conditions, we found that juvenile salmon occupied a range of habitats. Our findings support a strategy that involves restoring a diversity of shallow tidal freshwater habitats to facilitate the recovery of threatened and endangered salmon populations in the Columbia River basin.

Tidal freshwater habitats support high levels of primary productivity (Baldwin et al. 2009) and diverse biotic communities (Odum et al. 1984). Tidal freshwater segments within an estuarine–riverine ecotone are those that reside in the uppermost portions of tidal influence and are characterized by salinities less than 0.5‰ (Odum et al. 1984; Mitsch and Gosselink 1993; Baldwin et al. 2009). The longitudinal extent of tidal freshwater zones is determined by a combination of factors, such as tidal amplitude and river discharge, both of which operate at varying temporal scales (Odum et al. 1984; Baldwin et al. 2009).

In western North America, tidally influenced habitats in rivers and estuaries support early life phases for anadromous Pacific salmon *Oncorhynchus* spp. (Healey 1982, 1991), but these habitats have suffered substantial losses in size and extent (NRC 1996). The anthropogenic reduction of shallow-water habitats (e.g., dikes and levees) in the lower Columbia River and estuary (LCRE; e.g., Thomas 1983) may be a factor limiting the production and diversity of Columbia River basin salmon (Bottom et al. 2005b; Fresh et al. 2005; Quinn 2005). Currently, 13 populations of Pacific salmon and steelhead *O. mykiss* in the Columbia River basin are listed as threatened or endangered under the Endangered Species Act (Ford 2011). The restoration of these habitats would likely enhance performance (e.g., foraging success and growth) of juvenile salmonids via direct and indirect mechanisms and thus would increase their survival rates during downstream migration and early ocean residence (Diefenderfer et al. 2013). Improved growth and survival in LCRE habitats are hypothesized to lead to increased population size and stability and to aid in the recovery of listed species (Fresh et al. 2005).

The LCRE encompasses the tidal environment from the ocean (river kilometer [rkm] 0) to the head of tide at Bonneville Dam (rkm 234), which includes 176 rkm of tidal freshwater (Figure 1). Research on juvenile salmon in the LCRE (e.g., Dawley et al. 1986; Maier and Simenstad 2009; Spilseth and Simenstad 2011; Roegner et al. 2012) has largely focused on the lowest 75 km of the Columbia River, where tidal forces dominate (Jay et al., in press). In contrast, the migratory characteristics of juvenile salmon and steelhead in shallow tidal freshwater habitats upstream of rkm 75, where riverine forces predominate (Jay et al., in press), are not well understood (ISAB 2000; ISRP 2004; Fresh et al. 2005). However, a recent genetic study by Teel et al. (2014) showed that stock composition of juvenile Chinook Salmon *O. tshawytscha* varied among LCRE tidal freshwater areas. Based on that geographically broad survey, Teel et al. (2014) concluded that strategic estuary restoration would benefit from additional studies to quantify differences in tidal freshwater habitat use at finer spatial scales.

Here, we describe the early life history characteristics of Chinook Salmon sampled from shallow (<3-m depth) tidal freshwater habitats of the Columbia River during 2007–2012. We focused on two study areas (Figure 1): the Sandy River delta (SRD), located at rkm 188–202; and the lower river reach (LRR), located at rkm 110–141. We characterized the fish community and the juvenile Chinook Salmon density, size distribution, and genetic stock composition in each study area. The objectives were to (1) describe seasonal and annual patterns of these characteristics in the SRD; (2) describe seasonal and spatial (habitat type) patterns of these characteristics in the LRR; (3) compare the characteristics between the SRD and LRR study areas; and (4) determine relationships between the density of juvenile Chinook Salmon and environmental covariates in the LRR. This study provides insight into characteristics of juvenile Chinook Salmon and fish community composition in understudied tidal freshwater habitats by offering a comprehensive understanding of seasonal and interannual patterns as well as habitat linkages that support habitat restoration planning in the LCRE.

METHODS

Study areas and sampling design.—We chose the SRD as a study area (Figure 1) because it is within the tidal freshwater portion of the LCRE, is readily accessible by boat, and includes a diversity of shallow tidal freshwater habitats. Sampling sites were selected to represent a diversity of habitat conditions with respect to beach slope, emergent and overhanging vegetation, sediment grain size, and connectivity to the main-stem river. The study design included sites that were adjacent to (1) the main channel, (2) off-channel areas, or (3) wetland channels (Figure 2). At the SRD, a minimum of four sites were sampled monthly from June 2007 through December 2012 (Figure 1), except when very high or very low river discharge prevented data collection, which happened for 11% of the total monthly sampling trips. To describe monthly and seasonal changes in early life history characteristics (e.g., size and stock composition), the predesignated sites at the SRD were systematically sampled each month.

In January 2009, we expanded the geographic extent of the sampling effort in response to a previous recommendation by the Independent Scientific Review Panel (ISRP 2005). We selected

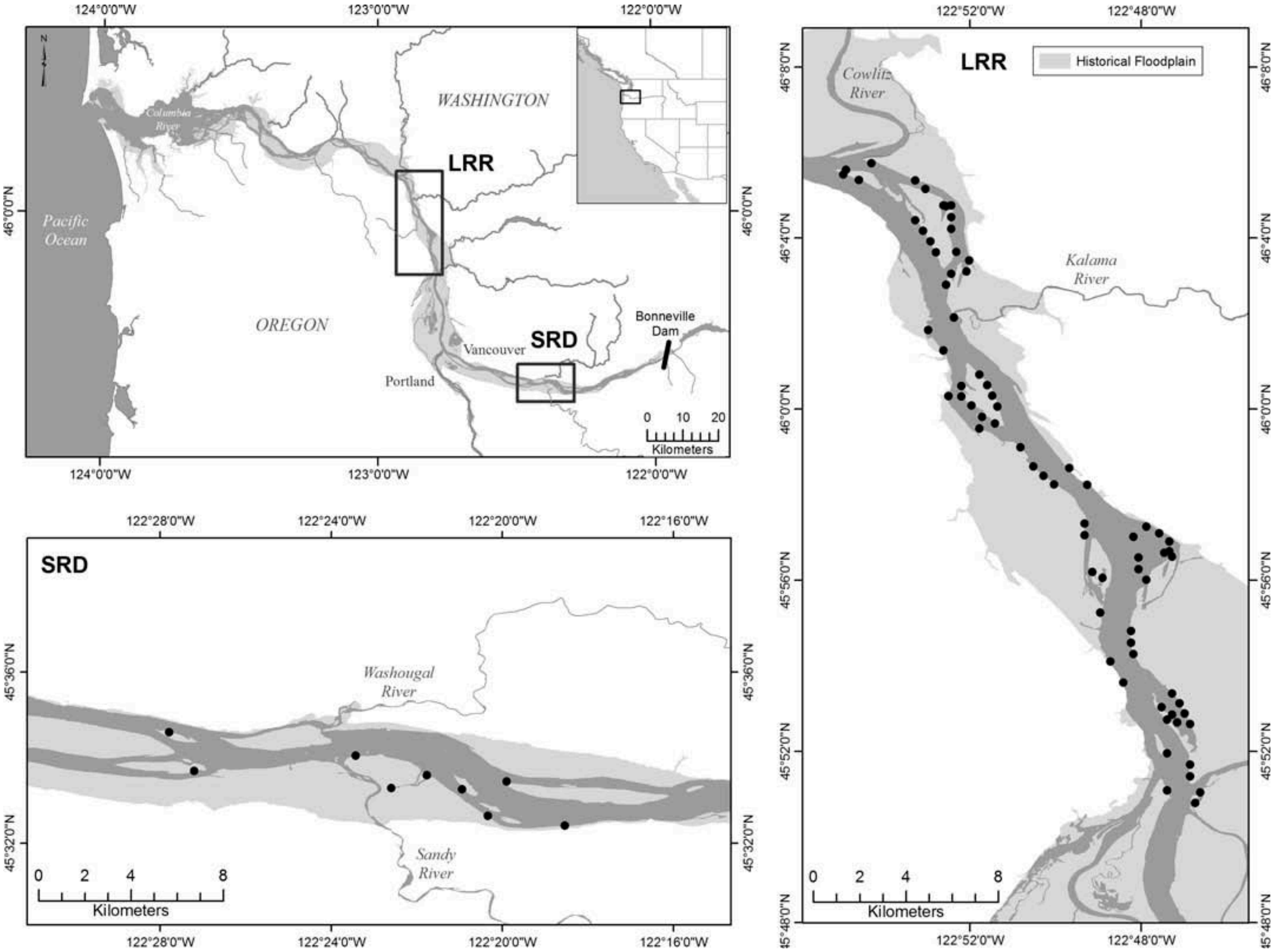

FIGURE 1. Map of the two study areas and the tidal freshwater sampling locations in the lower Columbia River and estuary. Sandy River delta (SRD; river kilometer [rkm] 188–202) fixed sites were sampled monthly during 2007–2012. Lower river reach (LRR; rkm 110–141) sites were randomly sampled seasonally during 2009–2012.

the LRR as an additional study area because of the potential for habitat restoration in this part of the Columbia River (USACE et al. 2007) and because the LRR is downstream of the Willamette River, a major LCRE tributary. We implemented a study design with three strata for sampling: main channel (shorelines along the main river channel), off-channel (shorelines in secondary channels behind islands), and wetland channel (shorelines of wetland areas connected to off-channel areas; Figure 2). Within each stratum, we defined potential sampling sites as 500-m segments along the shoreline. Field reconnaissance supported the 500-m size criterion because most sites yielded little change in habitat features within this distance. Additionally, a 500-m linear segment permitted adequate space for deployment of a beach seine while providing flexibility within a site in the event of unforeseen sampling impediments. Sites were excluded if they were deemed impossible to sample with a beach seine (e.g., sites that exhibited heavy shoreline development, armoring, pile structures, or extremely shallow water). This process yielded a total of 167 potential sampling sites within three habitat strata (Figure 1). We applied a stratified random sampling approach for each seasonal sampling episode. To capture seasonal and spatial patterns at each habitat type in the LRR, sites (depending on availability) were randomly selected from each stratum for seasonal sampling (February, May, July, and November) during 2009–2012. Our LRR sampling protocol targeted five sites within each stratum per event. However, the number of sites sampled varied from the target due to unforeseen environmental factors and habitat conditions (river discharge, tidal elevation, and beach slope). Over the entire study period, we sampled 92 main-channel sites, 73 off-channel sites, and 37 wetland channel sites. The relative number of sites sampled per habitat stratum was similar across seasons.

Habitat conditions.—Water quality measurements were collected in conjunction with fish sampling. Using a YSI 85 or YSI 556 handheld meter (Yellow Springs Instruments,

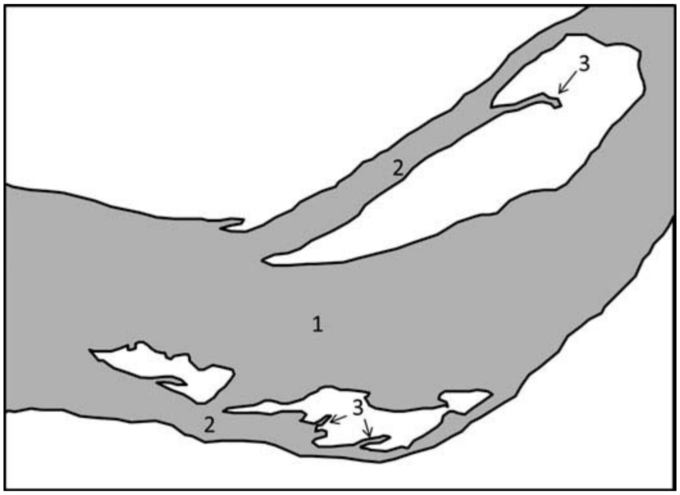

FIGURE 2. Types of tidal freshwater habitats that were sampled in two study areas (Sandy River delta and lower river reach) of the lower Columbia River and estuary. Main-channel habitats (1) are shoreline areas along the main-stem Columbia River. Off-channel areas (2) occur in secondary channels behind islands. Wetland channels (3) are blind channels that are located on islands and hydraulically connected to off-channels.

Yellow Springs, Ohio), we measured temperature (°C), salinity (‰), and dissolved oxygen concentration (mg/L). The YSI probes were suspended approximately 0.3 m below the water's surface, and measurements were taken from a boat or by wading into the water near the locations that corresponded to the beach seine hauls. Using transect-based surveys that extended 50 m perpendicular from the shoreline to the upland, we adapted methods from Borde et al. (2009) to determine mean percent bare ground cover, mean percent emergent vegetation, mean percent shrubs, mean percent tree cover, and substrate type (fines, sand, gravel, and cobble) at the SRD and LRR study areas. In total, three transects were surveyed immediately after fish were captured and processed from each site, and the transects were spaced to encompass the upland shoreline area adjacent to beach seine locations.

Fish sampling.—To capture fish, we deployed a 46-m beach seine (1.5–3.0 m deep; 13-mm knotless-mesh wings; 3-mm knotless-mesh bag; and 15-m haul lines). In some cases, deployment of the 46-m seine was not possible, so a 30.5-m beach seine (3 m deep; 5-mm knotless mesh) was used during approximately 30% of the sampling effort at the SRD. Due to potential biases between the two gear types, data from the small seine were excluded from statistical analyses for the SRD but were used for general characterization of the fish community. All LRR data were collected with the 46-m beach seine. Beach seines were set by boat except when water depths were prohibitively low or when site accessibility was poor; in these instances, the net was deployed on foot. Two nonoverlapping hauls were performed at each site, with a minimum interval of 30 min between sets. The length and width of the sampled area were recorded during each deployment event and were later used to calculate fish density (individuals/m^2). To the extent possible, two seine hauls were performed at each site during each sampling event. The same sampling methods were used at both study areas.

After each haul, all salmon and steelhead were immediately removed from the net and placed in holding buckets filled with oxygenated, ambient-temperature river water. The remaining individuals (i.e., nonsalmonid taxa) were placed in separate holding buckets until processing. Catches were processed by enumerating all taxa and measuring the lengths (nearest mm) of up to 20 individuals within various size-classes for each species. Size-class modes for salmonids were used to distinguish life history characteristics as described by Johnson et al. (2014). Fish were identified to the lowest practical taxonomic level. Occasionally, when catches were large, nonsalmonid fish were subsampled from the seine. Subsampling of the catch was implemented (1) to provide a standardized approach for documenting large numbers of fish over a short time period and (2) ultimately to reduce handling stress and fish mortality. Using a plastic scoop drilled with holes, we counted the fish in a known number of scoops to estimate the number of fish per scoop. We then scooped out the remaining fish from the net, counting the number of scoops as we worked. The total number of scoops was multiplied by the number of fish per scoop to estimate the total catch. In addition to enumeration and length measurements, salmon were checked for marks indicating hatchery origin: adipose fin clips, coded wire tags, and passive integrated transponder tags. Although marks identify hatchery fish, unmarked fish can include both natural- and hatchery-origin individuals. Prior to processing, all salmonids were anesthetized with tricaine methanesulfonate (MS-222; 40 mg/L). Fin clips to be used in genetic stock identification were collected from a subset of Chinook Salmon; if a particular beach seine haul yielded numerous Chinook Salmon, priority was placed on sampling unmarked fish, although some marked fish were also included. Fin clips were stored in nondenatured ethanol. Fish were placed in holding buckets after processing. Aerators maintained dissolved oxygen levels in the buckets as the fish recovered from the anesthesia. Fish that were processed from the first haul were released downstream of the sampling site to minimize the potential for contamination of the second sample; fish from the second haul were released at the site of capture.

Genetic stock identification.—Genetic stock identification of Chinook Salmon samples was conducted in accordance with the methods outlined by Teel et al. (2014). Fin clips were genotyped at 13 microsatellite DNA loci. Proportional stock composition of samples grouped by study area, season, and habitat type was estimated by using a standard mixture modeling approach to genetic stock identification (Manel et al. 2005). A "baseline" of standardized microsatellite DNA data (Seeb et al. 2007) that were collected from spawning populations throughout the Columbia River basin (Teel et al. 2014) was used along with the genetic stock identification program ONCOR (Kalinowski et al. 2007).

To investigate the occurrence of rare stocks in our samples, we also used ONCOR to estimate the most likely stock membership of each individual fish. We included fish whose individual probability of assignment to a genetic stock was greater than or equal to 0.80. Proportional contributions and individual fish assignments were made for 10 Columbia River basin genetic stocks (see Johnson et al. 2013 and Teel et al. 2014 for detailed descriptions). Briefly, the stocks originate both from lower Columbia River sources (e.g., the Willamette River and tributaries draining the western Cascade Mountains) and from the interior basin (the upper Columbia River and Snake River). However, stock transfers in the Columbia River have been extensive; for several stocks, both hatchery production and natural production currently occur downriver of their natal ranges.

Data analysis.—The average density (count per volume sampled) was calculated for each sampling event at each site on a given day. Seasonal and interannual differences in fish community composition at the SRD were evaluated by using ANOVA with the main effects of season and year. All data were used in the analysis of interannual variability by seasons because the autocorrelation for all lag times was less than 40%. A $\log_{10}(x + 1)$ transformation of density was used to reduce within-class heterogeneity. When ANOVA assumptions could not be met, a nonparametric Kruskal–Wallis multiple comparison test with a Bonferroni correction (family error rate $\alpha = 0.05$) was conducted between years for each season. For analysis, months were grouped into the following seasons based on water temperature and river discharge: winter (January–March), spring (April–June), summer (July–September), and fall (October–December). For the LRR, the mean density of unmarked Chinook Salmon was compared using a generalized linear model (GLM) with dissolved oxygen as a covariate: main effects included habitat stratum, season, and year; and interaction effects included stratum × season and stratum × year. The within-season interannual variability in density of unmarked Chinook Salmon was evaluated by using the coefficient of variation (CV; %), calculated as 100 × [(SD of annual means)/(average of annual means)]. Seasonal and interannual differences in dissolved oxygen at the LRR were evaluated by using an ANOVA with the main effects of habitat stratum, season, and year as well as the stratum × season interaction.

To examine for homogeneity of size-class composition (across seasons in the SRD and across habitat strata in the LRR), we used a chi-square test (Snedecor and Cochran 1980) for three size-classes of Chinook Salmon (<61, 61–90, and >90 mm FL; described by Johnson et al. 2014). In addition, to compare size distributions between the study areas, the number of unmarked Chinook Salmon within each of three size-classes was standardized based on sampling effort and was compared between the SRD and LRR by using analysis of similarity (ANOSIM) in PRIMER version 6 (Clarke and Gorley 2006).

Bray–Curtis similarity matrices of genetic stock composition were generated by using data that were standardized across samples (as described by Clarke and Warwick 2001) and were square-root transformed. Using individual stock assignments with probabilities greater than 0.80, the similarity matrices for genetic stocks represented among marked and unmarked Chinook Salmon from the SRD and LRR were visualized with nonmetric multidimensional scaling. Differences between groups were evaluated with the ANOSIM statistic R based on the following criteria: R-values greater than 0.75 indicated distinct groups; mid-range R-values (e.g., 0.50) inferred separation among groups but with some overlap; and R-values less than 0.25 indicated that the groups were indistinguishable (Clarke and Warwick 2001).

To examine relationships between Chinook Salmon density and environmental covariates, we concentrated on the LRR study area during 2009–2012 because concurrent collection of environmental covariate data with the fish density data was more systematic, comprehensive, and extensive than that for SRD. The covariates were Bonneville Dam outflow (m^3/s), depth (m), dissolved oxygen concentration (mg/L), habitat stratum (main channel, off-channel, and wetland channel), mean percent bare ground cover, mean percent emergent vegetation, mean percent shrubs, mean percent tree cover, substrate type (fines, sand, cobble, and gravel), temperature (°C), total native fish (nonsalmon) density, and total nonnative fish density. Only samples with measurements of all variables were included in the fish–habitat analysis. We applied GLMs using a Poisson error, log-link model of fish density. After first adjusting for temporal (season and year) effects, we performed two analyses: single variable and stepwise forward-selection multiple regression. Analysis of deviance was used to test the significance of each individual variable (McCullagh and Nelder 1983).

RESULTS

Environmental Conditions

During 2007−2012, environmental conditions varied seasonally and annually. River discharge at the SRD and LRR study areas (measured as outflow at Bonneville Dam) was generally lowest during fall and increased through winter and spring (Figure 3). Discharge typically peaked during May and June. The highest daily discharge (14 m^3/s) was observed during May 2011, and the lowest (2 m^3/s) occurred during September 2009. Water temperature recorded at the SRD sites displayed an annual cycle with a low of about 5°C in winter to a high of about 20°C in summer. The 7-d daily average maximum exceeded 18°C throughout most of the summer months at each of the SRD sites as well as for some time periods during late spring and early fall. In the LRR, water temperature also differed seasonally and across years for each habitat stratum.

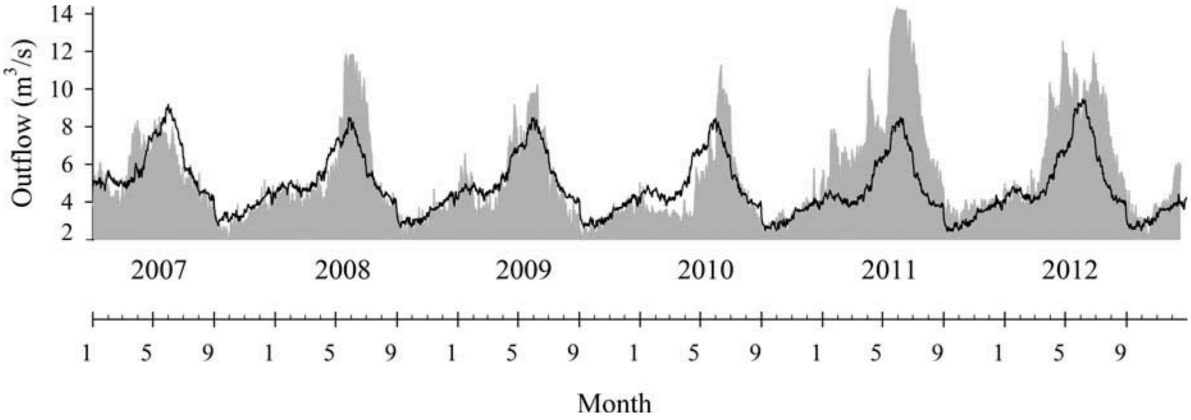

FIGURE 3. Daily average outflow (m^3/s; gray bars) and 10-year average outflow (black line) at Bonneville Dam (river kilometer 234) on the Columbia River (data source: Columbia River Data Access in Real Time, www.cbr.washington.edu/dart/).

Fish Community

During 2007–2012, we conducted 715 individual beach seine hauls at SRD sites, capturing a total of 476,208 fish. Twenty-four of the 47 taxa observed were native fishes. Numerically, native nonsalmon taxa composed 81% of the total catch, and nonnative taxa contributed 17% of the total catch. Juvenile salmon made up 2% of the total catch. The abundance of nonsalmon species was highest during summer and fall and lowest during winter and spring (Table 1). Unmarked Chinook Salmon were the most commonly captured juvenile salmonid in the SRD, accounting for 69% of the total salmon catch, and were captured during all seasons. The remaining salmonid taxa were most abundant during spring and were less prevalent during the other seasons (Table 2).

During 2009–2012, we made 13 seasonal sampling trips to the LRR, where we performed 396 individual beach seine hauls and captured 563,726 fish; 44 taxa, of which 21 taxa were native. Juvenile salmon contributed 2% of the total catch in the LRR. Native nonsalmon taxa accounted for 71% of the total catch, and nonnative taxa composed 27% of the catch. Similar to the results observed for the SRD, the abundance of nonsalmon species was highest during summer and fall and lowest during winter and spring (Table 1). Unmarked Chinook Salmon were present during all seasons and were the most abundant salmonid group captured in the LRR, accounting for 84% of the total salmon catch. With the exception of Chum Salmon *O. keta*, the remaining salmon taxa were most abundant during spring (Table 2).

Chinook Salmon Density

In the SRD, mean density of unmarked Chinook Salmon was generally greatest during spring followed by winter (Figure 4). The highest density was observed in spring 2010 (0.118 individuals/m^2). The density of unmarked Chinook Salmon was lowest (0.004 individuals/m^2) during summer and fall in most years. There was considerable interannual variability in unmarked Chinook Salmon density (CV = 24–38% in fall and winter; CV = 93–108% in spring and summer). Pairwise comparisons of spring density between years were not significant (Kruskal–Wallis multiple comparison test [Bonferroni-corrected $\alpha = 0.005$]: $P > 0.015$); summer, fall, and winter densities also did not differ between years (Kruskal–Wallis multiple comparison test: $P > 0.26$).

In the LRR, the mean density of unmarked Chinook Salmon was greatest during winter (0.048 individuals/m^2) and spring (0.070 individuals/m^2; Figure 4). Mean density was greatest in off-channel habitats (0.043 individuals/m^2), lowest in main-channel habitats (0.021 individuals/m^2), and intermediate in wetland channel habitats (0.037 individuals/m^2). The habitat stratum × season interaction and the habitat stratum × year interaction from the GLM with dissolved oxygen as a covariate were not significant ($F_{6,\ 102} = 1.8$, $P = 0.11$ and 0.31, respectively). The main effects of habitat stratum and year were not significant (stratum: $F_{2,\ 102} = 2.2$, $P = 0.114$; year: $F_{3,\ 102} = 1.2$, $P = 0.302$). The mean density of unmarked Chinook Salmon was significantly different among seasons ($F_{3,\ 102} = 12.2$, $P < 0.001$).

Size Distributions

In the SRD, the smallest unmarked Chinook Salmon were generally encountered during winter and spring (Figures 5, 6). The size of unmarked Chinook Salmon generally increased during the course of a year; larger fish were captured during summer and fall. The proportions contributed by the three size-classes of unmarked individuals were not equal across years during winter ($\chi^2 = 219$, df = 6, $P < 0.001$) or spring ($\chi^2 = 72.4$, df = 6, $P < 0.001$). Winter was dominated by fry (<60 mm FL), yet during 3 of 5 years, there was a bimodal size distribution with noticeable proportions of larger (>90 mm FL) fish in addition to fry-sized fish. Fry were also prevalent during spring, along with moderate-sized (60−90 mm FL) fish, which contributed over 20% of the spring

TABLE 1. Proportional contribution of fish taxa to the total catch (for taxa comprising > 1% of the catch) in the Sandy River delta and lower river reach study areas within the lower Columbia River and estuary.

Taxon	Community status	Total proportion	Winter	Spring	Summer	Fall
Sandy River delta						
Threespine Stickleback *Gasterosteus aculeatus*	Native	0.62	0.03	0.01	0.31	0.65
Banded Killifish *Fundulus diaphanus*	Nonnative	0.13	0.03	0.07	0.06	0.85
Peamouth *Mylocheilus caurinus*	Native	0.10	0.00	0.07	0.86	0.06
Northern Pikeminnow *Ptychocheilus oregonensis*	Native	0.04	0.02	0.13	0.25	0.59
Suckers *Catostomus* spp.	Native	0.03	0.03	0.05	0.74	0.19
Chinook Salmon *Oncorhynchus tshawytscha*	Native	0.01	0.21	0.73	0.03	0.03
Bluegill *Lepomis macrochirus*	Nonnative	0.01	0.28	0.10	0.24	0.38
Sculpins *Cottus* spp.	Native	0.01	0.03	0.05	0.56	0.37
Smallmouth Bass *Micropterus dolomieu*	Nonnative	0.01	0.00	0.01	0.85	0.14
Lower river reach						
Threespine Stickleback	Native	0.67	0.10	0.06	0.43	0.41
Banded Killifish	Nonnative	0.23	0.01	0.02	0.21	0.77
Yellow Perch *Perca flavescens*	Nonnative	0.03	0.00	0.08	0.91	0.01
Chinook Salmon	Native	0.02	0.56	0.29	0.14	0.01
Northern Pikeminnow	Native	0.01	0.02	0.01	0.36	0.62
Peamouth	Native	0.01	0.01	0.06	0.93	0.01

TABLE 2. Proportional contribution of salmonids in the Sandy River delta and lower river reach study areas. Origin is used to distinguish hatchery fish (marked) from these of unknown origin (unmarked).

Taxon	Origin	Total proportion	Winter	Spring	Summer	Fall
		Sandy River delta				
Chinook Salmon *Oncorhynchus tshawytscha*	Unmarked	0.69	0.21	0.73	0.03	0.03
Chum Salmon *O. keta*	Unmarked	0.14	0.31	0.69	0.00	0.00
Coho Salmon *O. kisutch*	Unmarked	0.08	0.28	0.40	0.01	0.31
Chinook Salmon	Marked	0.07	0.05	0.80	0.14	0.01
Coho Salmon	Marked	0.01	0.00	0.91	0.00	0.09
Steelhead *O. mykiss*	Unmarked	0.002	0.00	0.94	0.00	0.06
Steelhead	Marked	0.001	0.33	0.67	0.00	0.00
		Lower river reach				
Chinook Salmon	Unmarked	0.84	0.56	0.29	0.14	0.01
Chinook Salmon	Marked	0.09	0.03	0.56	0.34	0.07
Coho Salmon	Marked	0.03	0.00	1.00	0.00	0.00
Coho Salmon	Unmarked	0.03	0.02	0.42	0.09	0.47
Chum Salmon	Unmarked	0.01	0.92	0.07	0.00	0.01
Steelhead	Marked	0.002	0.06	0.89	0.00	0.06
Steelhead	Unmarked	0.0003	0.00	0.25	0.00	0.75

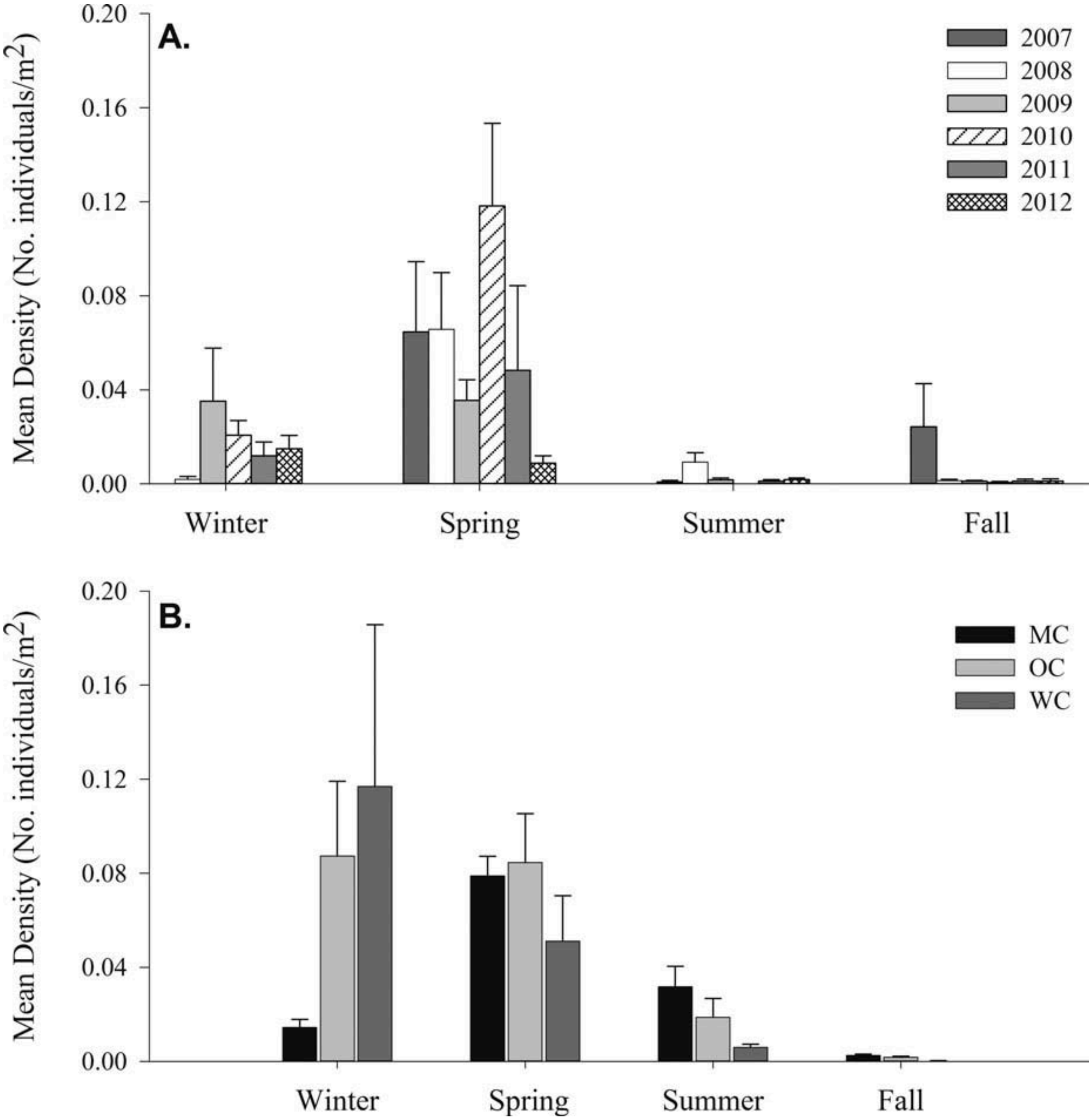

FIGURE 4. Seasonal mean (+SE) density (individuals/m^2) of unmarked Chinook Salmon captured from the **(A)** Sandy River delta during spring 2007 through fall 2012 and **(B)** lower river reach during 2009–2012 (habitat strata: MC = main channel; OC = off-channel; WC = wetland channel).

catch during most years. The sizes of unmarked Chinook Salmon were least variable during summer and fall, and the proportional representation of the three size-classes was not significantly different across years (summer: $\chi^2 = 7.96$, df = 4, $P = 0.093$; fall: $\chi^2 = 1.70$, df = 4, $P = 0.637$). Summer was dominated by moderate-sized fish (60–90 mm), and fish larger than 90 mm were the most predominant group during fall.

In the LRR, the proportions of unmarked Chinook Salmon size-classes (≤60, 61–90, and >90 mm) varied across strata and seasons (Figure 6). Fish sizes increased from winter through fall (Figure 7). For example, during winter, two distinct size-classes of unmarked Chinook Salmon were present in the main-channel and off-channel habitats. This contrasted with the spring, when fewer 61–90-mm fish were observed in the main-channel stratum and many were in the off-channel stratum ($\chi^2 = 17.1$, df = 4, $P = 0.002$). Across the two study areas, the counts by size-classes of unmarked Chinook Salmon showed little spatial distinction (ANOSIM: $R = 0.21$, $P = 0.046$); however, differences in size-classes were distinguishable across seasons (ANOSIM: $R = 0.785$, $P < 0.001$).

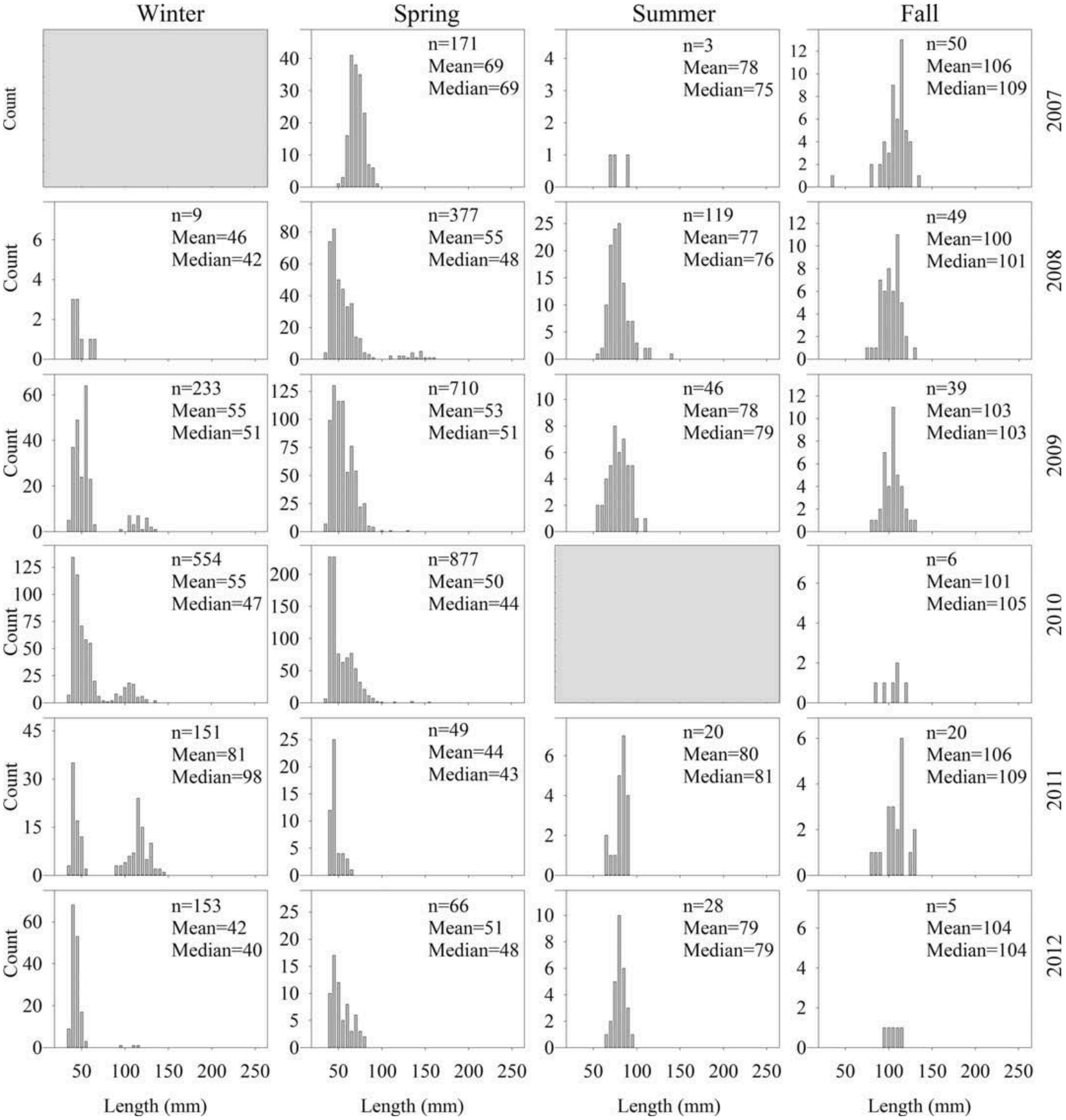

FIGURE 5. Fork lengths (mm) of unmarked Chinook Salmon that were captured at the Sandy River delta during 2007–2012. Shaded panels (winter 2007 and summer 2010) represent time periods when data were not collected.

Genetic Stock Composition

Based on the 1,706 unmarked Chinook Salmon that were genotyped from the 2007–2012 sampling effort at the SRD, proportional stock composition analysis revealed that the major contributors to the catch were the Spring Creek group fall stock (35%) and the upper Columbia River summer/fall stock (34%; Table 3). Intermediate proportions were estimated for the West Cascade fall (13%) and Willamette River spring

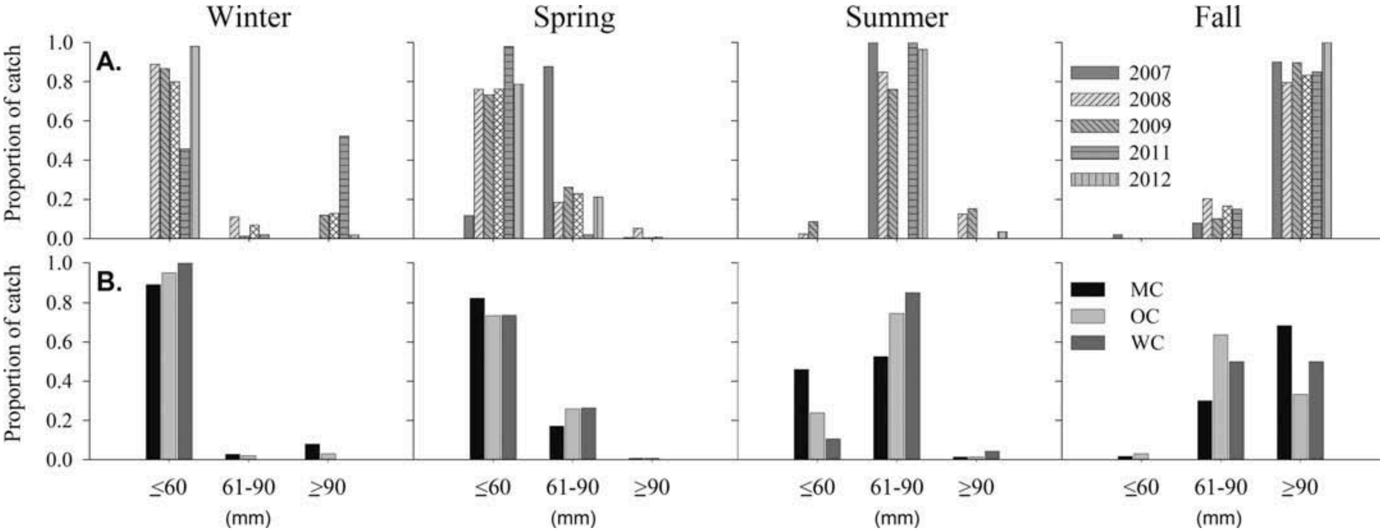

FIGURE 6. Proportion of unmarked Chinook Salmon by size-class (mm) and season of capture from the **(A)** Sandy River delta and **(B)** lower river reach (habitat strata: MC = main channel; OC = off-channel; WC = wetland channel). Proportions are segregated among the three distinct size-classes that were used to differentiate juvenile life history characteristics of Chinook Salmon (see Johnson et al. 2014).

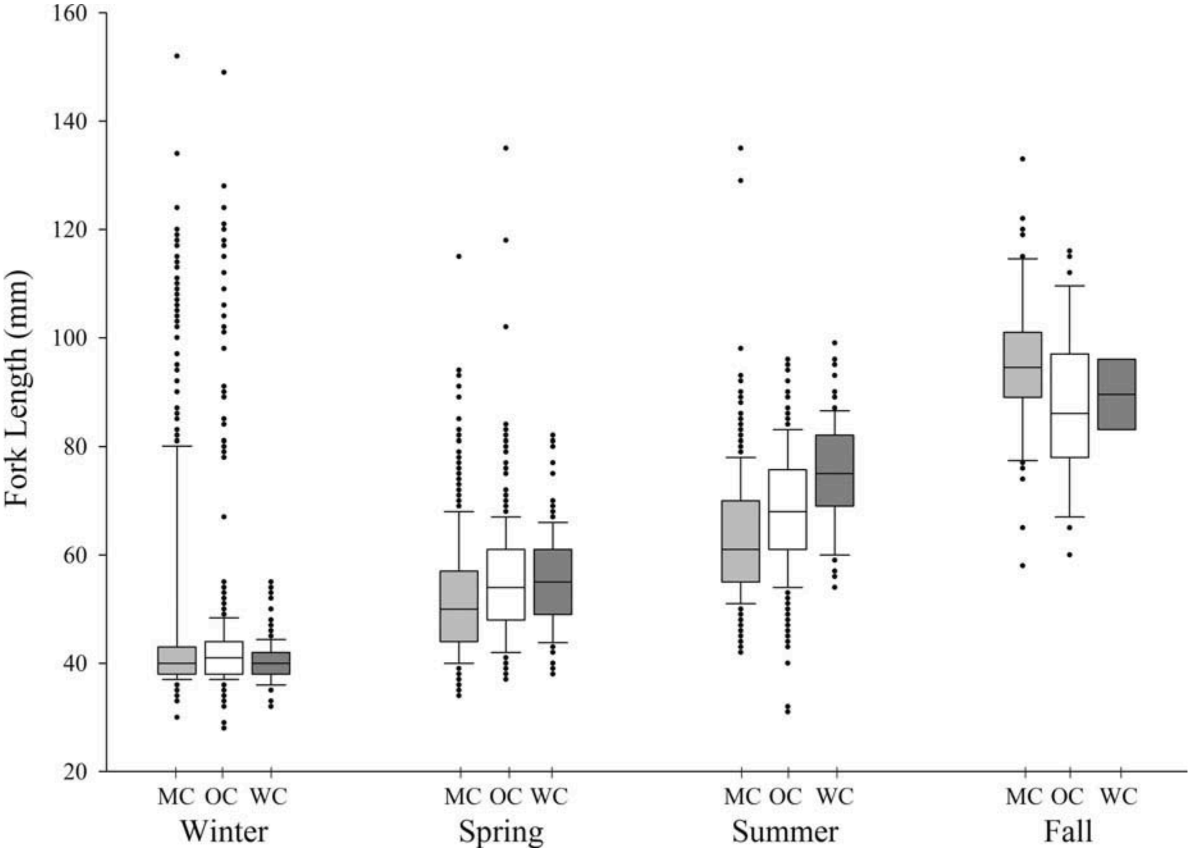

FIGURE 7. Box plots of FLs for unmarked Chinook Salmon captured from main-channel (MC), off-channel (OC), and wetland channel (WC) habitats in the lower river reach during 2009–2012. The upper and lower bounds of each box are equivalent to the 25th and 75th percentiles, respectively. The solid line within the box is the median fork length (mm). Box whiskers are the 10th and 90th percentiles and the black dots are outliers.

TABLE 3. Sample sizes and estimated percent composition of seven genetic stocks of unmarked juvenile Chinook Salmon sampled from Sandy River delta and lower river reach sites in the lower Columbia River and estuary, 2007–2012. All estimates for mid- and upper Columbia River spring, and introduced Rogue River stocks were less than 1% and are not shown.

Season	*N*	West Cascade Fall	West Cascade Spring	Willamette River spring	Spring Creek group fall	Deschutes River fall	Upper Columbia summer/fall	Snake River fall
Sandy River delta								
All	1,706	13	2	9	35	3	34	3
Winter	568	5	4	10	74	1	5	1
Spring	848	18	1	3	20	6	48	4
Summer	199	12	0	11	1	1	68	7
Fall	91	13	14	63	2	1	4	2
Lower river reach								
All	1,193	73	5	2	6	1	11	2
Winter	388	71	8	5	15	0	0	0
Spring	357	68	2	0	6	2	18	5
Summer	360	74	3	1	0	2	19	0
Fall	88	88	4	2	4	0	2	1

(9%) stocks. The Deschutes River fall (3%), Snake River fall (3%), and West Cascade spring (2%) stocks were also present in the samples. Seasonally, winter samples were dominated by the Spring Creek group fall stock (74%); spring and summer samples largely contained upper Columbia River summer/fall stock (48% and 68%); and fall samples were dominated by the Willamette River spring stock (63%). Genetic stock composition of unmarked Chinook Salmon sampled from the SRD did not differ across years (ANOSIM: global R = 0.078, P = 0.052) but was significantly different across seasons (ANOSIM: global R = 0.57, P = 0.001; Figure 8). Genetic stock composition observed during fall was distinct from that observed during winter (R = 0.644, P = 0.001), spring (R = 0.835, P = 0.001), and summer (R = 0.709, P = 0.001). Genetic stock composition in winter also differed from the stock composition observed in spring (R = 0.538, P = 0.001) and summer (R = 0.832, P = 0.001). There was considerable overlap in genetic stock groups that were sampled from the SRD during spring and summer (R = 0.273, P = 0.002).

The genetic stock composition of marked Chinook Salmon sampled from the SRD differed across seasons (one-way ANOSIM: global R = 0.441, P = 0.008; Figure 8). Genetic stock composition of marked Chinook Salmon differed between winter and summer (R = 0.583, P = 0.02) and between spring and summer (R = 0.444, P = 0.048). Genetic stock groups of marked Chinook Salmon overlapped considerably during spring and winter (R = 0.284, P = 0.095). The Spring Creek group fall hatchery stock predominated in winter (87%) and spring (81%), whereas the upper Columbia River summer/fall stock was predominant in summer samples of marked fish (89%).

Of the 1,193 unmarked Chinook Salmon that were genotyped from LRR samples collected during 2009–2012, 73% were identified as belonging to the West Cascade fall stock (Table 3). Smaller proportions were estimated for the upper Columbia River summer/fall (11%), Spring Creek group fall (6%), and West Cascade spring (5%) stocks. Snake River fall (2%), Willamette River spring (2%), and Deschutes River fall (1%) stocks were also present in the LRR samples. Genetic stocks of unmarked Chinook Salmon in the LRR did not differ among habitat strata (ANOSIM: global R = –0.19, P = 0.973). There was considerable overlap in genetic stock groups across seasons (ANOSIM: global R = 0.332, P = 0.004); the largest difference occurred between winter and summer stock groups (R = 0.594, P = 0.001; Figure 8). Genetic stock composition of marked Chinook Salmon sampled in the LRR did not differ among habitat strata (ANOSIM: global R = –0.201, P = 0.864) or among seasons (ANOSIM: global R = 0.02, P = 0.439; Figure 8).

Fish–Habitat Relationships

There were several significant relationships associated with dissolved oxygen (mg/L) in the LRR. Dissolved oxygen levels were significantly different among habitat strata (GLM: F_{109} = 8.5, P < 0.001) and among seasons (ANOVA: F_{109} = 95.6, P < 0.001; Table 4). Based on Tukey's pairwise comparisons with a family error rate α of 0.05, the wetland channel stratum had a significantly lower mean dissolved oxygen concentration, but the difference was probably not biologically meaningful (Table 5). Mean dissolved oxygen levels in the spring and summer were significantly lower than those measured in the fall and winter. Furthermore, dissolved oxygen level had a negative linear relationship with water temperature for each of the three habitat strata. The slopes (ranging from –0.27 to –0.30) for dissolved oxygen level as a function of water temperature for each habitat stratum were not significantly different (F-test comparison of common versus separate slopes: $F_{2,\ 107}$ = 0.37, P = 0.692), and the R^2 values for each stratum were greater than 74%. However, the wetland channel stratum had a significantly lower intercept (F-test comparison of common versus separate intercepts with a common slope: $F_{2,\ 109}$ = 15.4, P < 0.0001) than the main-channel and off-channel strata, reflecting the overall lower dissolved oxygen concentration in wetland channels.

The density of unmarked Chinook Salmon within the LRR study area was significantly related (P < 0.10) to 4 of the 10 explanatory variables we considered (Table 6). From the single-variable analysis, habitat stratum (main channel < wetland channel < off-channel), depth (negative), and mean percent tree cover (positive) were the top-three ranked variables. Total native fish density (excluding salmonids) was significantly correlated with total nonnative fish density but not with the density of unmarked Chinook Salmon. The multiple stepwise regression (Table 7) indicated that seven of the covariates entered the model at P-values less than 0.10: habitat stratum, depth, dissolved oxygen concentration, mean percent tree cover, water temperature, mean percent bare ground cover, and mean percent emergent vegetation. Four interaction terms—most of which included habitat stratum, dissolved oxygen level, or both—were also significant. Seasonal effects explained 48.2% of the variability in the data. The seven covariate main effects explained another 16.5% of the total variance, and the interaction terms explained an additional 9.9%.

DISCUSSION

To address the paucity of data available to guide the ecosystem restoration program in the LCRE, we implemented a 5-year investigation of tidal freshwater habitat use by juvenile salmon with year-round sampling at two study areas (SRD [rkm 188–202] and LRR [rkm 110–141]). Different spatial and temporal sampling regimes were employed in the two areas, allowing us to investigate different aspects of juvenile Chinook Salmon life history. Sampling at the SRD generated information on seasonal and interannual patterns associated with abundance, size, and genetic stock, whereas the spatially extensive sampling effort at LRR provided additional information on early life history characteristics of juvenile salmon and habitat attributes. Together, the two approaches provided a comprehensive means by which to assess juvenile salmon use of the LCRE tidal freshwater zone.

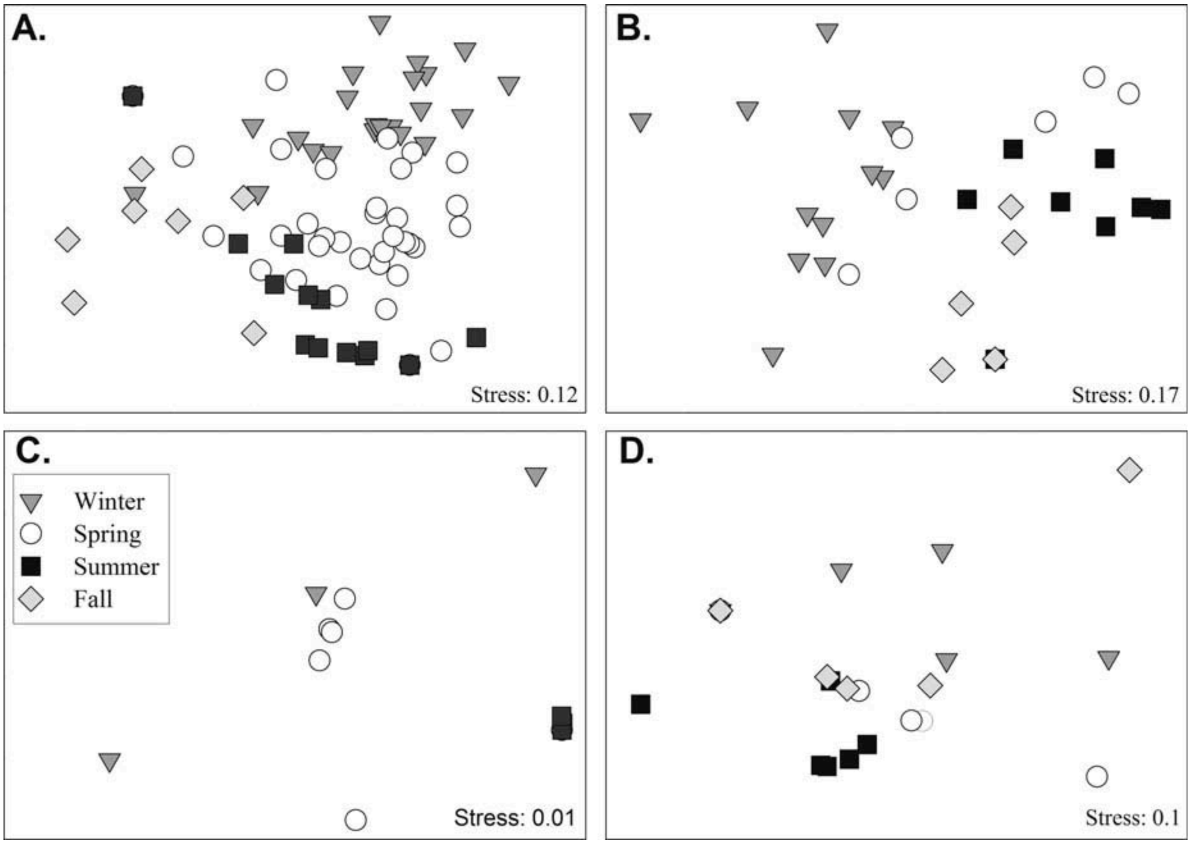

FIGURE 8. Multidimensional scaling plot based on Bray–Curtis similarities calculated for genetic stock groups of unmarked Chinook Salmon that were collected from the **(A)** Sandy River delta (SRD) and **(B)** lower river reach (LRR); and marked Chinook Salmon that were sampled from the **(C)** SRD and **(D)** LRR during 2007–2012.

TABLE 4. Results of ANOVA examining dissolved oxygen concentration (mg/L) in the lower river reach relative to the main effects of habitat stratum (main channel, off-channel, and wetland channel), season, and year and the habitat stratum × season interaction (SS = sum of squares; MS = mean square).

Factor	df	SS	MS	*F*	*P*
Habitat stratum	2	13.5	6.7	8.5	<0.001
Season	3	226.1	75.4	95.6	<0.001
Year	3	4.0	1.3	1.7	0.17
Habitat stratum × season	6	6.1	1.0	1.3	0.26
Error	109	85.9	0.79		

TABLE 5. Mean dissolved oxygen concentration (mg/L; with 95% confidence intervals [CIs]) from Tukey's pairwise comparisons (family error rate α = 0.05) for habitat stratum and season in the lower river reach.

	Habitat stratum			Season			
Statistic	Main channel	Off-channel	Wetland channel	Winter	Spring	Summer	Fall
Mean (mg/L)	11.2	11.2	10.2	13.4	11.1	9.7	9.2
95% CI	10.8–11.5	10.9–11.5	9.8–10.7	13.1–13.8	9.2–10.3	8.8–9.8	10.8–11.4

TABLE 6. Analysis of deviance results for each individual covariate evaluated in relation to the density of unmarked Chinook Salmon (× 10,000) in the lower river reach. The *P*-values are for each term added separately to a model with sampling occasions. Covariates are listed in order of *P*-value reduction. Covariates with multiple levels are ranked from the smallest to largest effect on Chinook Salmon density (i.e., lower versus higher density).

Source	df	Deviance	$P > F$	Sign or rank of regression coefficient
Initial model				
Total	168	86,468.1		
Sampling occasion (year and season)	6	41,712.4	<0.0001	
Additional covariates				
Habitat stratum	2	5,554.2	<0.0001	Main channel < wetland channel < off-channel
Depth (m)	1	3,221.2	0.0005	–
Mean percent tree cover	1	2,709.4	0.0015	+
Dissolved oxygen (mg/L)	1	2,371.3	0.0031	+
Mean percent emergent vegetation	1	650.2	0.1252	+
Temperature (°C)	1	511.0	0.1744	+
Mean percent bare ground cover	1	325.8	0.2786	–
Substrate type	3	288.1	0.3805	Sand < cobble < fine < gravel
Mean percent shrubs	1	8.9	0.8584	–
Bonneville Dam outflow (m^3/s)	1	2.6	0.9226	+
Total nonnative fish density	1	1.2	0.9488	+
Total native (nonsalmon) fish density	1	505.8	0.1766	+

The fish community composition and the densities of salmonids, nonnative fishes, and native nonsalmon fishes were similar across the two tidal freshwater areas. These findings contrast with those noted by Roegner et al. (2008) for the lower segments of the Columbia River estuary (rkm 8–60), where longitudinal differences in fish community composition were attributed to environmental gradients, particularly salinity. Furthermore, the areas sampled by Roegner et al. (2008) were more tidally dominated than our study areas—that is, water elevation in their study reach exhibited greater

TABLE 7. Multiple regression analysis of deviance results for the density of unmarked Chinook Salmon (× 10,000) in the lower river reach. The *P*-values are for each term added sequentially to a model with sampling occasions. There were seven significant two-way interactions. Variable types are aquatic (A), terrestrial (T), and interaction (I).

Source	Variable type	df	Deviance	$P > F$
Initial model				
Total		168	86,468.1	
Sampling occasion (year and season)		6	41,712.4	<0.0001
Additional covariates				
Habitat stratum	A	2	5,554.2	<0.0001
Depth (m)	A	1	2,159.3	0.0027
Dissolved oxygen (mg/L)	A	1	1,101.6	0.0291
Mean percent tree cover	T	1	1,168.0	0.0229
Temperature (°C)	A	1	2,182.9	0.0015
Mean percent bare ground	T	1	1,172.2	0.0173
Mean percent emergent vegetation	A	1	957.3	0.0292
Habitat stratum × temperature	I	2	4,610.9	<0.0001
Mean percent tree cover × mean percent bare ground	I	1	2,196.2	0.0003
Dissolved oxygen × mean percent emergent vegetation	I	1	916.5	0.0150
Habitat stratum × dissolved oxygen	I	2	815.7	0.0149
Error		148	21,877.6	

fluctuations coinciding with semidiurnal tidal cycles. Our two tidally influenced study areas were located upstream of the Roegner et al. (2008) study area and were characterized by a reduced tidal range and greater influence from Columbia River discharge (Jay et al., in press).

The LRR and SRD study areas occurred within a single hydrologic zone and encompassed several wetland vegetative zones (Jay et al., in press). Although the environmental conditions (e.g., vegetation and hydrology) resulted in spatial segregation across the LCRE, we did not observe longitudinal "zonation" in the fish community. Across an approximately 60-km expanse of the LCRE, Roegner et al. (2012) noted that Chinook Salmon from the tidal freshwater zone (near rkm 60) were more abundant and smaller than those sampled downriver at middle- and lower-estuary sites. Similarly, Quinones and Mulligan (2005) reported that juvenile Chinook Salmon densities were greater in the middle and upper reaches (including tidal freshwater) of the Smith River estuary (California) than in the lowest segments. Although our study areas (centered at rkm 125 and 195) were segregated by greater distances than those sampled by Roegner et al. (2012) and Quinones and Mulligan (2005), the two areas did not differ in salmon density or in the proportional representation of size-classes among unmarked Chinook Salmon. Temporal trends in Chinook Salmon size in our study and that of Roegner et al. (2012) were similar; fry were predominant during winter and spring, and fish size generally increased with time. Irrespective of study area, juvenile Chinook Salmon appeared to use a diversity of shallow-water habitats similarly across broad spatial expanses of tidal freshwater habitats in the LCRE.

Variation in fish communities within the SRD and LRR was more closely linked to seasonal conditions than to spatial gradients. Native nonsalmonid fishes and nonnative fishes followed similar seasonal cycles, with abundances peaking during summer and fall and then declining during winter and spring. This pattern was the inverse of that observed for juvenile salmon, which exhibited the greatest densities during spring and winter. Low salmonid densities during summer and fall in the shallow-water habitats could be the result of higher water temperatures and lower water surface elevations in comparison with winter and spring. Peak migrations for juvenile salmon in estuarine environments are common during spring and summer (Healey 1982; Levy and Northcote 1982); however, late-summer and early fall migrations have been reported from coastal rivers, such as the Salmon River, Oregon (Bottom et al. 2005a), and the Sixes River, Oregon (Reimers 1971). The trend of high winter and spring densities for unmarked Chinook Salmon in our study was similar to that documented by Dawley et al. (1986). In contrast, Roegner et al. (2012) found that catches of Chinook Salmon in tidal freshwater at rkm 60 were lower during winter months than during other seasons. Seasonal trends in density can be driven by life history characteristics (Bottom et al. 2005a), and the lower Chinook Salmon density observed during winter by Roegner et al. (2012) may have been driven by differences in spatial patterns of genetic stock groups in the LCRE (Teel et al. 2014).

Habitat requirements of seaward-migrating fish include food, shelter, space, and suitable environmental conditions (Chapman 1966; Bjornn and Reiser 1991). Juvenile salmon must maximize energy intake while minimizing energy expenditure, and gains from feeding in profitable habitats must be balanced against the risk of predation (Fausch 1984; Harvey 1991). Parameters regulating this balance change with body size and, in turn, with energetic demands, the ability to detect and avoid predators, and the nature of suitable environmental conditions. The observed mismatch in seasonal densities between salmonids and other fishes could lead to improved juvenile salmon performance through resource partitioning in space and time. However, the predominance of species such as the Threespine Stickleback and the occurrence of numerous nonnative taxa have given rise to concerns about the consequences of competitive interactions between these taxa and threatened and endangered salmonids (Spilseth and Simenstad 2011; Naiman et al. 2012).

Focusing on the LRR study area, we captured juvenile Chinook Salmon in all three habitat types (strata). During the summer, the greater density of Chinook Salmon encountered in the main channel compared with the other habitats was likely driven by the thermal constraints of the wetland channel and off-channel habitats. Summer temperatures in wetland channels, especially those in the LCRE, typically exceed 19°C—a threshold that is considered stressful for juvenile salmon (Brett 1952; Baker et al. 1995). Within tidal freshwater reaches of the LCRE, Roegner and Teel (2014) found that densities of subyearling Chinook Salmon were lower when water temperatures exceeded 19°C than when temperatures ranged from 10°C to 19°C. After seasonal and interannual effects were removed, our analyses indicated that habitat stratum was an important factor explaining variability in juvenile salmon density (Table 6). Salmon densities were generally higher in off-channel habitats than in wetland channel and main-channel habitats. Off-channel habitats are intermediate to main channel and wetland channel habitats in terms of hydraulic connectivity (Figure 2), which may influence biotic and abiotic elements that are critical to the survival of juvenile salmon. Increased growth of juvenile Chinook Salmon in floodplain and off-channel habitats, as described by Sommer et al. (2001) and Jeffres et al. (2008), was attributed to higher productivity of prey resources and more favorable habitat conditions that supported rearing and growth to a greater extent than did main-channel habitats.

We found significant positive associations between juvenile salmon density and percent tree cover, dissolved oxygen level, and percent emergent vegetation (Tables 6, 7). Trees provide shade to shallow waters, thus reducing water temperature to the benefit of juvenile salmon (e.g., Theuerer et al. 1985). In the Smith River estuary, Quinones and Mulligan (2005) found that overhanging riparian vegetation was positively correlated with salmonid densities across different habitats. Shoreline vegetation supports the production of salmon prey resources through inputs of terrestrial invertebrates as well as through the production of detritus (Bottom et al. 2005b; Maier and Simenstad 2009; Storch and Sather 2011). Dissolved oxygen levels were similar across the three habitat strata, and although not biologically significant, we did observe that dissolved oxygen concentrations were lower in wetland channel sites than in main-channel and off-channel habitats. The negative association of juvenile salmon with mean percent bare ground cover was consistent with the positive association observed for emergent vegetation. The positive relationship between salmon density and water temperature was likely attributable to the higher salmon densities found in warmer off-channel and wetland channel habitats relative to the cooler main-channel habitats.

Although we found that juvenile Chinook Salmon occupied LCRE tidal freshwater habitats throughout the year, the timing of migration and estuarine rearing differs greatly among genetically distinct populations. Consistent with other recent LCRE studies (Roegner et al. 2012; Teel et al. 2014), we found that the genetic stock composition of Chinook Salmon varied depending on the river reach. These life history differences were readily apparent in our genetic analysis of unmarked juveniles, as stock composition shifted significantly across seasons within each of the two study areas. The sequence of genetic stocks occupying SRD habitats was particularly striking; winter samples were primarily composed of Spring Creek group fall stock; spring and summer samples were dominated by upper Columbia River summer/fall fish; and autumn samples mostly contained Willamette River spring stock. Although the majority of juveniles sampled from LRR habitats throughout the year were from a single stock (West Cascade fall), minor contributing stocks (i.e., Spring Creek group fall and upper Columbia River summer/fall) exhibited timing in the LRR that was similar to the timing observed in the SRD. The resulting shifts in seasonal stock composition were reflected similarly in all three of the habitat types in the LRR. In addition, major differences in the stock composition of juveniles sampled at the same time in different estuarine regions illustrated that stock-specific occurrence varies across the longitudinal gradient of the estuary and tidal freshwater segments of the LCRE (Teel et al. 2014). In both the SRD and LRR, all of the sampled habitats were used by juvenile Chinook Salmon from both lower-river and upper-river stocks exhibiting a diversity of life histories.

As expected, most of the Chinook Salmon that occupied habitats in both the SRD and LRR were from populations with fall and summer/fall adult run timing, since those populations make extensive use of shallow estuarine habitats for juvenile rearing (Fresh et al. 2005). However, small proportions of juveniles from spring-run populations were also observed in both the SRD (11%) and the LRR (7%). The greatest percentage of spring Chinook Salmon was detected in the SRD during fall, when 63% of juveniles were estimated to be members of the Willamette River stock. Those naturally produced juveniles likely originated in the nearby Sandy River, where the spring-run fish are genetically similar to Willamette River populations due to a history of hatchery stock transfers (Myers et al. 2006; Teel et al. 2014). A fall/winter-migrant life history has been documented for Willamette River spring-run subyearlings (Mattson 1962; Myers et al. 2006), and our data indicate a similar strategy for Sandy River spring Chinook Salmon. Shallow SRD areas likely provide important rearing habitats for fall subyearling migrants, some of which may overwinter in tidal freshwater (Johnson et al. 2015).

Our findings demonstrate spatial and temporal variation in juvenile salmon density, size, and stock composition across a broad range of habitats. This variability suggests that habitat restoration for juvenile salmon in the LCRE should restore a diverse suite of habitats that in turn support a diversity of life history traits expressed by juvenile salmon during seaward migration. We have established a spatially and temporally extensive baseline pertaining to juvenile salmon characteristics and fish community composition in an understudied region—tidal freshwater—within the LCRE. Our study, along with the Roegner et al. (2012) and Teel et al. (2014) studies, provides a baseline with which to aid the management and evaluation of future restoration actions. The current restoration strategy aimed at reconnecting shallow-water areas to the main-stem river (Johnson et al. 2003; BPA and USACE 2014) is supported by our findings that juvenile salmon of various life stages and genetic stocks occupied a wide range of habitat types. We recommend a restoration approach that (1) focuses on maintaining a diversity of habitats and (2) protects existing tidal freshwater habitats.

It is important to put the results in context given the fish sampling methods we employed. We prioritized beach seine sampling along main-channel and off-channel shallow-water shorelines as well as wetland habitats, thus studying a variety of habitat conditions through time. Despite offering versatility for sampling across different habitat gradients, beach seines are unable to sample shorelines that feature heavy armoring and pilings, high densities of shrubs and trees that extend into the water or occur at the water's edge, or areas with submerged large woody debris. The diversity of habitats and environmental conditions at the SRD necessitated the use of two different sizes of beach seine; this may have introduced sampling bias into our catch data. Statistical analyses of the SRD data excluded sampling events in which the smaller seine was used (30% of the effort), but we used all of the SRD data to provide general insights into the temporal characteristics of fish communities. The infrequent occurrence of large fish in our beach seine catches may reflect the general absence of large fish (>125 mm) in the shallow-water habitats (i.e., size segregation), but it may also be related to the seine's poor capture efficiency for large fish. Furthermore, beach seining could not be conducted at night and was not performed or was ineffective during periods of high river discharge (>8.5 m^3/s) during spring 2011 and 2012. Sampling periodicities (monthly for SRD and quarterly for LRR), although sufficient for general characterization, provided only snapshots of fish characteristics, whereas more frequent sampling would have facilitated analyses with a higher degree of temporal resolution. Notwithstanding these limitations, our results address a critical gap in data describing the characteristics of juvenile salmon in shallow tidal freshwater habitats of the LCRE.

Due to the inherent physical and biological variability in conditions, we caution against a narrow focus on a single habitat type, season, or response metric in future studies of juvenile salmon ecology within tidal freshwater habitat. To obtain comprehensive information about juvenile salmon characteristics, sampling should be conducted year-round in multiple habitat types because the complexity of early life history necessitates a broad spatial and temporal view. Elucidating the connections between juvenile salmon and other ecological elements, such as prey production, bioenergetics, and interspecific competition (e.g., nonnative fishes), within tidal freshwater habitats likely requires spatially and temporally intense sampling regimes. Systematically incorporating higher-order metrics of realized function (Simenstad and Cordell 2000) at appropriate scales will provide a much-needed basis for evaluating the success of restoration.

Our findings provide new data on juvenile Chinook Salmon density, size distribution, genetic stock identities, and fish–habitat relationships in tidal freshwater habitats of the Columbia River. The findings support a strategy for restoring a diversity of shallow tidal freshwater habitats and making them available year-round to support the recovery of endangered salmon populations in the Columbia River basin.

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