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ARTICLE

Comparative Use of Shallow and Deepwater Habitats by Juvenile Pacific Salmon in the Columbia River Estuary Prior to Ocean Entry

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Abstract

The degree to which fine-scale habitat use by salmonid species and stocks varies within habitat types such as estuaries is not fully resolved. We sampled shallow shoreline and deeper main-stem channel habitats in the Columbia River estuary over 3 years to compare salmon species composition, migration timing, density, size, and production type (hatchery or natural). Results indicated a high degree of spatial heterogeneity in habitat occupancy by the five salmonid species that are native to the basin. Salmonid communities at two channel habitat sites were much more similar to each other than to the community at a shoreline site. Salmonids sampled at the shoreline site were primarily subyearling Chinook Salmon *Oncorhynchus tshawytscha* and Chum Salmon *O. keta* and yearling Coho Salmon *O. kisutch*, with few other salmonids present. In contrast, channel habitat contained a higher diversity of salmon species, with samples representing all species of anadromous salmonids, including Sockeye Salmon *O. nerka* and steelhead *O. mykiss*. Salmonids in deeper channel habitat were generally larger than salmonids found along the shore, and the proportion of hatchery-origin salmon was also higher in deep channel habitats. On a per-area basis, we also found much higher densities of salmon along the shoreline than in channel habitats. For Chinook Salmon, habitat use also differed by genetic stock of origin: upper-river stocks primarily used deeper channels, while lower-river populations used both channel and shoreline areas. We concluded that sampling at both habitat types is required to fully encompass the migration patterns of all salmon evolutionarily significant units in the Columbia River basin. These spatial and temporal variations in salmon timing and density have ramifications for feeding, growth, and competitive interactions. This study provides information that is relevant for conservation efforts targeting specific fish populations and efforts to evaluate the potential impacts of in-water activities in the Columbia River estuary.

A common challenge for species conservation is understanding the spatial and temporal variation in habitat utilization, as this is necessary to target appropriate actions toward restoration of specific habitats. This challenge is especially difficult with regard to anadromous salmonids because of their use of freshwater, estuarine, and marine habitats, with

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fine-scale use varying by species and among genetically distinct stocks within habitat types. Estuarine environments are critical habitats for juvenile salmon yet also are among the most degraded by human activity and are particularly susceptible to future alteration through climate change (Scavia et al. 2002). In the present study, we address the issue of differential habitat use by comparing metrics of salmonids sampled in shallow nearshore and deeper channel environments within the Columbia River estuary.

Five Pacific salmonid species (Chinook Salmon *Oncorhynchus tshawytscha*, Coho Salmon *O. kisutch*, Chum Salmon *O. keta*, Sockeye Salmon *O. nerka*, and steelhead *O. mykiss*; hereafter collectively referred to as "salmon") are extant in the Columbia River basin. Due to concerns about the long-term viability of wild populations, several evolutionarily significant units (ESUs) or distinct population segments (DPSs) are listed and receive protection under the U.S. Endangered Species Act (ESA). Listed stocks include all five steelhead DPSs, five Chinook Salmon ESUs, one Sockeye Salmon ESU, one Coho Salmon ESU, and one Chum Salmon ESU (Ford 2011). Hatchery production is extensive throughout the basin, with combined annual releases averaging 140 million juvenile Chinook Salmon, Coho Salmon, and steelhead during 2007–2010, while substantially lower numbers of Sockeye Salmon and Chum Salmon are released annually (<0.5 million; PSMFC 2014; Weitkamp et al. 2014). The Columbia River estuary serves as a critical migration and rearing environment for all of these anadromous salmonid species regardless of origin or listing status.

Columbia River salmonids display a diversity of juvenile life history patterns. Chinook Salmon stocks include both subyearling and yearling life history types. Subyearlings (age 0) typically migrate to sea during the year of hatch, while yearlings (age 1) spend at least 1 year in freshwater reaches before migrating to sea in the next spring. Columbia River Chum Salmon are subyearling migrants, whereas Coho Salmon and Sockeye Salmon migrate primarily as yearlings (Fresh et al. 2005; Myers et al. 2006). Life histories of steelhead are also complex, with seaward migration occurring after 1–5 years of freshwater rearing (Busby et al. 1996).

The spatial and temporal distribution of salmon within estuarine habitats varies by species and life history stage (Bottom et al. 2005). General patterns are thought to include the use of open-water migratory channels by active migrants, with shallow-water, shoreline, and wetland habitats being preferred by more estuarine-dependent fish (Dawley et al. 1986; Bottom et al. 2005). These distributions may reflect distinct life history characteristics based on genetic lineage, or they may represent the remnants of a wider continuum of evolutionary migration strategies that are now limited by hatchery practices and habitat alterations. The temporal distribution of juvenile salmon in the estuary is influenced by a combination of hatchery release practices and the migration timing of naturally produced individuals. Wild and hatchery-reared yearling Chinook Salmon and Coho Salmon, subyearling Chum Salmon, and steelhead all appear to have a relatively narrow migration period during spring (Dawley et al. 1986; Weitkamp et al. 2012, 2015). In contrast, subyearling Chinook Salmon arrive in the estuary over protracted migration periods depending on the stock of origin (Dawley et al. 1986; Bottom et al. 2005; Roegner et al. 2012; Teel et al. 2014; Weitkamp et al. 2015). Additionally, hatcheries generally produce fish that are larger than naturally reared individuals and that are often smolted (Naish et al. 2008; Tatara and Berejikian 2012).

Habitat segregation by species, abundance (density), size, or life history stage has important implications for interspecific and intraspecific predation and competition and for the influence of these factors on subsequent patterns of mortality. Larger hatchery fish may outcompete smaller wild fish but conversely can be disproportionally selected for by predators (Ryan et al. 2003; Clements et al. 2012). Predation on juvenile salmon in particular may represent a considerable portion of the mortality experienced by a given cohort throughout its life cycle (Bradford 1995); in the Columbia River estuary, avian predation accounts for the mortality of millions of juvenile salmon per year (Ryan et al. 2003; Sebring et al. 2013). Additionally, during the first few months of ocean residency, salmon populations may experience size-selective mortality that is driven by food limitation due to competition or variation in prey abundance (Cross et al. 2008). Therefore, conditions that impact fitness and growth in the estuary may influence subsequent marine survival. However, species- and stock-specific locations of enhanced predation (and, conversely, refuge zones) in the estuary have not been determined, and competitive interactions are also difficult to measure directly.

In the Columbia River estuary, details of salmonid predation and competition are poorly understood (Thom et al. 2013). Therefore, a critical step in elucidating patterns of mortality and competition is to determine the distribution of salmon in estuaries or the pathways they use to transit estuaries, including whether there are species- or population-specific levels of variation. Understanding differential habitat utilization aids the development of effective management strategies to maximize benefits and minimize disturbances for specific species of concern (Hansen et al. 2012). Despite the important influence of species–habitat interactions on salmonid growth and survival in the Columbia River estuary, few studies have concurrently investigated salmon habitat metrics from the range of salmonid species or stocks since the seminal works of Dawley et al. (1986) and Bottom and Jones (1990). We explored the general hypothesis that attributes of salmonid populations do not differ between shoreline and channel habitats in the Columbia River. These attributes include salmonid species, migration timing, density, size, life history stage, and production type (hatchery or natural). For Chinook Salmon, we additionally compared genetic stock of origin between sites. Our results indicate that channel and shoreline habitats have very different juvenile salmon communities, which has implications for salmonid biology and management.

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METHODS

Study region.—The tidal freshwater Columbia River broadens and shoals at the head of Cathlamet Bay (river kilometer [rkm] 80), well upstream from the upper extent of saline intrusion at rkm 40. Here, the main-stem river is flanked by two peripheral bays (Baker and Youngs bays) and divides into two channels that are 10–15 m in depth. These channels are north and south of a large intertidal sandflat (Desdemona Sands) and merge near the estuary mouth (Figure 1). We refer to these deeper, open-water environments as "channel habitats." The banks of the main-stem portion of the estuary (except the peripheral bays) are extensively modified by shoreline armoring and surface deposition of dredged material. Shallow intertidal areas along the shore are generally composed of coarse- to medium-grained sand; we refer to these shallow intertidal areas as "shoreline habitat." The tidal amplitude in the estuary ranges from 1.0 to 3.5 m.

Fish sampling.—Time series of beach seine and purse seine samples were made to compare fish communities between shallow shoreline and deepwater channel habitats (Figure 1). Sampling protocols for shoreline sites were detailed by Roegner et al. (2012), and those for channel sites were described by Weitkamp et al. (2012). In brief, at the shoreline site (0–6-m depth), we used a beach seine with a tapered, 3- × 50-m variable-mesh net and a 1.0-cm knotless-mesh bunt to sample an enclosed area of approximately 400 m^2. Shoreline sampling was conducted at Point Adams Beach (rkm 19.8; Figure 1), a long-term monitoring station that was representative of mesohaline estuarine habitat. Previous studies have indicated that habitat utilization by the fish community at Point Adams Beach was similar to habitat utilization at a paired station on the Washington side (Bottom et al. 2011; Roegner et al. 2012), but sampling logistics and permitting issues with ESA-listed stocks restricted the sampling sites that could be used in this study.

At deepwater channel sites, fish were sampled with a 10.6- × 155-m, fine-mesh purse seine with a 1.7-cm stretched-mesh opening and a 1.5-cm knotless-mesh bunt. Sampling was conducted at depths of 8–10 m and spanned the entire water column. The net was set in one of two configurations, which were termed "round hauls" or "towed hauls." Round hauls were used to acquire quantitative fish density measurements, while towed hauls were used to maximize catch. Each round haul enclosed an area of about 1,913 m^2, and results from those hauls were used in fish density calculations. Data from towed hauls were employed to supplement round-haul data when juvenile salmon densities were below 2 individuals (ind)/1,000 m^2. Juvenile salmon collected from towed hauls were used to estimate the genetic stock of origin, size, and length–weight relationships but not densities. For towed hauls, the net was drawn for 5–10 min while proceeding upstream before closing and pursing. Two deepwater stations were sampled: North Channel (rkm 17) and Trestle Bay (rkm 13; Figure 1). These stations sampled both of the deep channels that bisect the respective north and south portions of the estuary.

In 2010–2012, shoreline beach seine samples were collected biweekly during February–July and monthly thereafter through the remainder of each year. Channel purse seine samples were collected biweekly from mid-April to late June

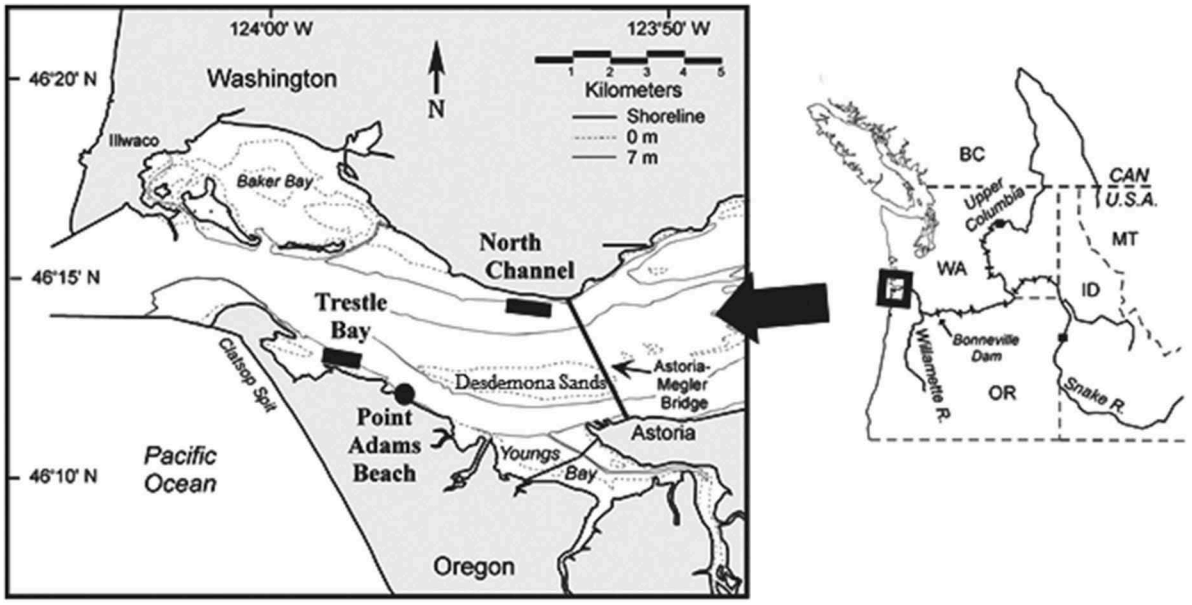


FIGURE 1. Map of the Columbia River study area in Washington and Oregon. Point Adams Beach was the shoreline habitat station (river kilometer [rkm] 19.8; 46.202°N, 123.946°W). Deepwater channel habitat stations were located at North Channel (rkm 17; 46.237°N, 123.903°W) and Trestle Bay (rkm 13; 46.215°N, 123.962°W). Solid and dashed lines indicate the 7-m and 0-m depth contours, respectively.

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or early July and at monthly intervals through October of each year. During the period when sample schedules overlapped, sampling of the two habitats generally took place within 3 d, although adverse weather sometimes lengthened this period for up to 5 d. All purse seining was initiated on morning low tides and continued with the flooding tide (Weitkamp et al. 2012); therefore, for comparative analysis, we used samples that were collected at each habitat type during morning low-tide periods and within a few days of each other. These consecutive samples taken during the overlap period were used for "paired-sample" analyses. This sampling effort represented a compromise between the frequency of sampling events and restrictions on the take of ESA-listed salmon and steelhead.

Catches were processed according to standard protocols (Roegner et al. 2012; Weitkamp et al. 2012). Juvenile salmon were anesthetized (tricaine methanesulfonate), identified to species, and measured to the nearest millimeter FL. Weights (nearest 0.1 g) were measured in the field for beach seine samples; weights of lethally sampled salmon from the purse seine catch were measured in the laboratory. For salmon caught in beach seine hauls (which sometimes numbered in the hundreds), we measured FLs and weighed up to 30 ind/species, measured up to 70 of the remaining salmon, and counted and released the remainder. Salmon that were not needed for laboratory analyses were released after recovery from anesthesia. The nonsalmonid catch was also enumerated, and a subsample was measured (data are available from the authors upon request).

All measured salmon were examined for adipose fin clips or tags (PIT tag, visible implant elastomer, or coded-wire tag) that were indicative of hatchery origin. However, not all hatchery fish are marked, and marking rates differ among species and among hatcheries. Therefore, to estimate the percentages of hatchery salmon and steelhead in the catch, we divided the percentages of marked fish by the average hatchery marking rate for each species, as determined by the Regional Mark Processing Center (PSMFC 2014).

Fish catches were standardized to density for analysis (ind/1,000 m^2 of surface area). This necessitated increases in beach seine densities by a factor of 2.50 and decreases in purse seine densities by a factor of 0.53. Note that these density calculations used a standard factor based on ideal conditions; the actual areas sampled were not routinely determined, and they varied somewhat with hydrological conditions. In addition, these comparisons assumed equal efficiency between nets to catch fish of the target species (i.e., catchability = 1.0). Although we did not test for a possible catch bias between gear types, both nets were effective at retaining fish larger than 40 mm FL, with the exception of some elongate species (primarily Surf Smelt *Hypomesus pretiosus*).

Biomass data were calculated from measured lengths by using species-specific regression equations derived from measured length–weight relationships. For each salmon species and stock, the regression relation was based on several-hundred representative samples collected over a period of years (our unpublished data). Species-specific biomass for each sampling date and habitat type was estimated as the mean weight of a given species multiplied by the abundance of that species.

Numeric and biomass data used for analysis were estimated as the means of two to three replicate daily hauls. For channel habitat, samples were further summarized as the average of means from both of the channel sites (Trestle Bay and North Channel) to ensure equal weighting. Adverse weather prevented sampling at one of the two channel stations on four occasions; therefore, in those cases, data from a single station were used.

Chinook Salmon life history designation.—For our analysis, subyearling and yearling life history designations for Chinook Salmon were determined by length and capture day (day of year) as modified from Dawley et al. (1986). Maximum FL of subyearlings was 115 mm in April and 140 mm in July (Weitkamp et al. 2012). These thresholds effectively captured the break in size distribution between subyearlings and yearlings of most stocks (Weitkamp et al. 2015). We further categorized the subyearlings as fry (≤60 mm FL) or fingerlings (>60 mm FL). Although life history designations based on size are somewhat artificial, we were particularly interested in fry because they represented primarily wild stocks from sources below Bonneville Dam (Roegner et al. 2012).

Genetic stock identification.—Details of our Chinook Salmon genetic methods and analysis were previously described by Roegner et al. (2012), Teel et al. (2014), and Weitkamp et al. (2015). Briefly, tissue storage and data collection followed the protocols of Teel et al. (2009). Regional genetic stock groups were based on the standardized database of microsatellite DNA loci described by Seeb et al. (2007) and on previous genetic studies of Chinook Salmon in the Columbia River basin (Waples et al. 2004; Myers et al. 2006). Baseline genetic data and stock groups were described in detail by Teel et al. (2009, 2014), Roegner et al. (2010), and Johnson et al. (2013). Proportional stock composition was estimated by using the likelihood model of Rannala and Mountain (1997) as implemented by the genetic stock identification program ONCOR (Kalinowski et al. 2007). Precision of the stock composition results was estimated by bootstrapping the baseline and mixture data 100 times (Kalinowski et al. 2007).

Stock composition was estimated for samples that were grouped by habitat and season (spring and summer–autumn). In accordance with the method of Teel et al. (2014), we used estimates of proportional composition to compute standard indices of community diversity for each habitat by using the number of genetic stocks (S_G) and the Shannon–Wiener diversity index (H'_G),

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$$H'_G = -\sum_{i=1}^{R}[p_i \cdot \log_e(p_i)],$$

where p_i is the proportional composition of stocks in the sample. Likewise, we evaluated stock composition with Pielou's evenness index ($J_G{}'$),

$$J_G{}' = \frac{H'}{H_{maxG}},$$

where $H_{maxG} = \log_e(S_G)$.

Statistical analysis.—We employed multivariate techniques based on pairwise Bray–Curtis similarity coefficients to test the general hypothesis that salmon numeric and biomass metrics were similar between shoreline and channel environments. The Bray–Curtis index produces a value between 0 and 1, where 0 indicates that there are no species in common among sites and 1 indicates that species composition is identical among sites (Clarke 1993; Legendre and Legendre 1998). These similarity coefficients are widely used in ecological studies because they are unaffected by changes in scale (e.g., the use of percentages or proportions) or the number of variables (i.e., species or hauls).

Bray–Curtis similarity matrices were calculated between salmon abundance estimates from the two habitat types (shoreline versus channel) or three study sites (shoreline site: Point Adams Beach; channel sites: Trestle Bay and North Channel). One matrix was constructed by using numeric data, and another was obtained by using biomass data. The data set included the five species of juvenile salmon found in the estuary: Chinook Salmon, Chum Salmon, Coho Salmon, Sockeye Salmon, and steelhead. Chinook Salmon subyearlings and yearlings were analyzed separately. In all analyses, numeric or biomass abundances for each species or age-class were first standardized by total abundance or biomass for each date, location, and/or station (sum of abundance or biomass = 1.0) and were then fourth-root transformed. Note that other analytical techniques, such as the use of data sets that contained all recorded species, the use of nonstandardized abundance or biomass data, or the use of different transformations (e.g., square root and log[x + 1]) produced patterns and results that were very similar to those described here.

The multivariate analyses employed included (1) nonmetric multidimensional scaling (NMDS) to examine salmon species composition and biomass based upon habitat type and date; (2) analysis of similarity (ANOSIM; a multivariate analog to ANOVA) to test for the influence of spatial (habitat and sampling station) and temporal variation; and (3) direct comparisons of Bray–Curtis similarity among subsets of pairs to examine fine-scale spatial influences while controlling for date. These comparisons were restricted to paired samples that were made during time periods of overlap between beach seine and purse seine hauls (i.e., as described above), and each comparison employed both standardized numeric data (counts) and biomass data.

We used NMDS plots to graphically explore variation in juvenile salmon community structure between habitat types. The NMDS ordination technique places all points in multidimensional space in relation to their similarity (i.e., points that are further apart in space are less similar than those that are closer together). In all NMDS analyses, random starting locations were used for each of 25 iterations to find the best solution. Minimum stress (a measure of the consistency between the similarity matrix and plotted points) was attained in multiple iterations, suggesting a true minimum solution (Clarke 1993).

We used ANOSIM to quantitatively evaluate variation that was attributable to time (month or year), habitat type (shoreline versus channel), and station (Point Adams Beach, Trestle Bay, or North Channel) using each factor individually or in pairs. This analysis produces global R-values that indicate the degree of separation among groups generated by a particular factor (or pair of factors). The global R-value ranges from 0 (no separation) to 1 (complete separation). The analysis also computes pairwise R-values for the different levels of each factor. Statistical probabilities of both global and pairwise R-values were generated by permutation (Clarke and Gorley 2006).

Both NMDS and ANOSIM employed the entire matrix of pairwise similarities, which included many values based on different sampling dates. To focus on differences between habitat types or sites that were sampled on the same date, we used a subset of pairwise Bray–Curtis similarities that were restricted by sampling event. Specifically, we compared pairwise similarities based on abundance between the two habitat types (the shoreline site versus either of the channel sites) and between the two channel sites (Trestle Bay versus North Channel) during each sampling event. These differences were evaluated by using a Mann–Whitney test for differences in medians. All multivariate analyses were run with PRIMER-E software (Clarke and Gorley 2006).

RESULTS

We collected 29 paired purse seine and beach seine samples between April and October in 2010–2012. The 29 samples contained over 87,000 individuals from 18 fish species within eight families: six salmonid species, three pleuronectid species, three clupeid species, and two osmerid species. Subyearling Chinook Salmon were the only salmonid component of the fish community that were present over the entire sample period; other salmonids made up less than 1.0% of the total catch (Table 1). However, all salmonids except subyearling Chinook Salmon exhibited pronounced seasonality, with high abundances during peak migration periods (described below). The overall frequency of occurrence (FO) was higher along the shoreline than in the channel habitats for subyearling

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TABLE 1. Salmon community structure at shoreline and channel habitats sampled in the Columbia River estuary, calculated from common sampling dates in 2010–2012 (N = number of fish sampled; % = percentage of total catch; FO = frequency of occurrence, %; density = mean density [individuals/10^3 m^2]; SD = standard deviation of mean density).

	Shoreline					Channel				
Species	*N*	%	FO	Density	SD	*N*	%	FO	Density	SD
Chum Salmon	177	0.6	30.0	11.06	33.4	47	0.1	14.9	0.02	0.0
Coho Salmon	107	0.3	22.5	6.69	18.3	267	0.5	32.5	0.09	0.2
Steelhead	0	0.0	0.0	<0.01	0.0	205	0.4	33.1	0.07	0.2
Sockeye Salmon	0	0.0	0.0	<0.01	0.0	38	0.1	9.7	0.01	0.1
Subyearling Chinook Salmon	3,696	11.7	92.5	231.00	354.0	953	1.7	74.0	0.33	0.5
Yearling Chinook Salmon	19	0.1	12.5	1.19	4.0	298	0.5	35.7	0.10	0.3

Chinook Salmon (92.5% versus 74.0%) and Chum Salmon (30.0% versus 14.9%). In contrast, the FO was lower along the shoreline habitat than in channel habitats for yearling Chinook Salmon (12.5% versus 35.7%) and Coho Salmon (22.5% versus 32.5%). For steelhead and Sockeye Salmon, which were captured only in channel habitats, the FO was 33.1% and 9.7%, respectively.

Salmonid Species Composition

Across all years, the proportions of salmonid species varied between shoreline and channel environments (Figure 2). During spring (April–June), the shoreline samples primarily consisted of Chinook Salmon, Chum Salmon, and Coho Salmon, whereas the channel samples contained all five salmonids that are known to spawn in the Columbia River system, as well as incidental numbers of Cutthroat Trout *O. clarkii*. In both habitat types during summer (July–October), all juvenile salmonids in the samples were subyearling Chinook Salmon.

Over the entire sampling period, Chinook Salmon dominated the salmonid abundance in both shoreline (87.4%) and channel (71.5%) environments. Chum Salmon were the second most abundant salmonid along the shoreline (7.4%) but were relatively rare in the channel habitats (1.9%). Coho Salmon, in contrast, made up 14.4% of

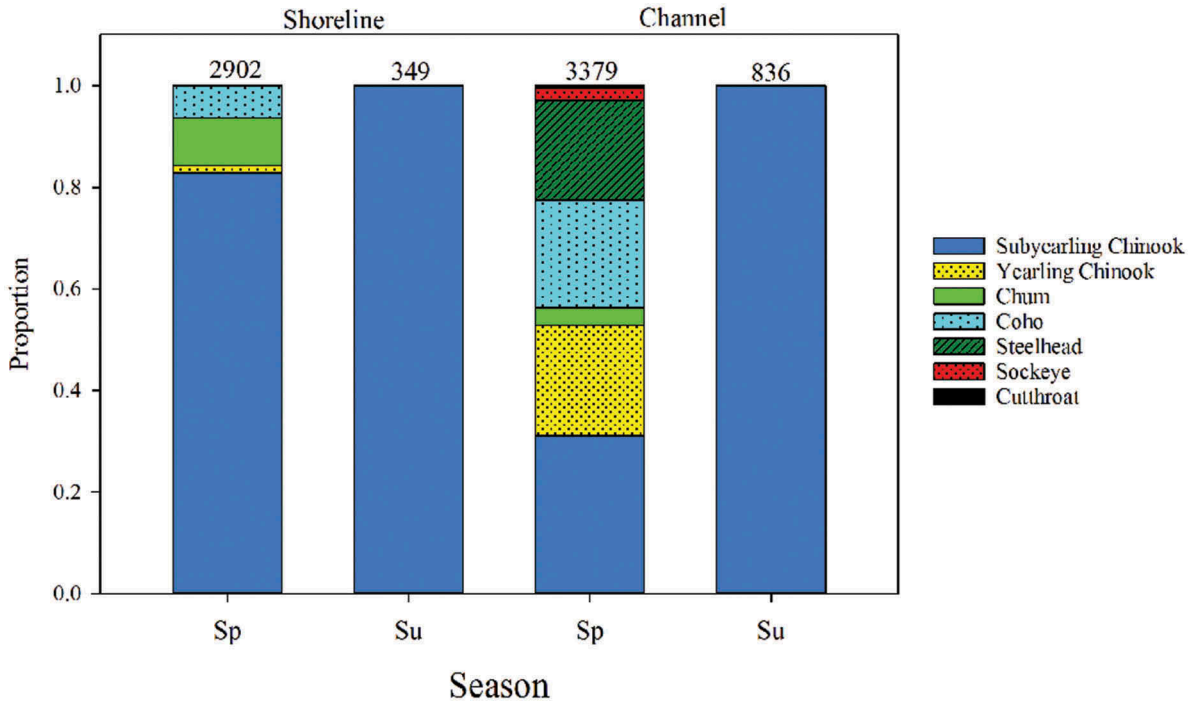


FIGURE 2. Proportional abundances of salmonids within shoreline and channel habitats of the Columbia River estuary during spring (Sp; April–June) and summer (Su; July–October) of 2010–2012. Stippling indicates the yearling life history type; solid fill represents subyearlings. The number at the top of each bar refers to the sample size.

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salmonid abundance in the channel samples but only 5.2% of the salmonids in the shoreline samples. Steelhead and Sockeye Salmon constituted 10.1% and 2%, respectively, of the salmon that were found in channels, and neither of these species was found along the shoreline.

The percentages of salmon at different life history stages also varied by habitat type. For Chinook Salmon, shoreline samples were composed mainly of subyearlings (98.8% of the total), whereas channel samples encompassed a mixture of subyearlings (72.0%) and yearlings (28.0%; Figure 3; Table 2). Size frequency histograms further indicated that fry-sized individuals (≤60 mm FL) contributed 21.1% of the subyearling Chinook Salmon found in shoreline habitat versus only 0.5% of the subyearlings that were found in the channel environment. In contrast, yearlings made up 28.0% of Chinook Salmon in channel habitats versus only 1.2% at the shoreline site. Chum Salmon subyearlings were 99.5% fry along the shore but 49.6% fingerling-sized fish in the channel. In both habitat types, all Coho Salmon (except one individual), steelhead, and Sockeye Salmon were yearlings or older.

Density

Comparison of salmonid density (ind/10^3 m^2) between shoreline and channel habitats also indicated substantial differences (Figure 4a). Standardized densities of Chinook Salmon, Chum Salmon, and Coho Salmon along the shoreline were one to three orders of magnitude higher than the densities observed in paired purse seine samples. The exception was the summer density of subyearling Chinook Salmon, which was of similar magnitude between habitats.

Size

Mean sizes of salmon that occurred in both habitat types were generally larger in the channel than along the shoreline (Figure 4b), with subyearling Chinook Salmon being approximately 15 mm larger at channel stations than at the shoreline station on a given date. Subyearling Chinook Salmon and Chum Salmon mean size increased approximately linearly over the seasonal time scale. In contrast, within the channel, yearling Chinook Salmon and steelhead evinced little size variation over time, whereas the mean sizes of Coho Salmon and Sockeye Salmon tended to decrease with time. For yearling Chinook Salmon and Coho Salmon that were sampled along the shoreline, patterns of mean size in relation to time were also indistinct. Note that subyearling Chinook Salmon captured during late autumn were about as large as the yearling Chinook Salmon that were exiting during the spring.

Migration Timing

Considering all years together, salmon migration timing was generally similar between shoreline and channel habitats, but the peak migration and the duration of migration differed somewhat among species (Figure 4a). Migration periods were well defined for salmon, with the exception of Chinook Salmon subyearlings, which were present throughout the sampling period and were broadly concentrated from March to July. Yearling Chinook Salmon were present along the shoreline as early as February, with peaks observed during March–April; in the channel habitats, migration generally peaked during May. Chum Salmon migration began in March and concluded by June, demonstrating a peak along the shoreline in March or April. Migration of yearling Coho Salmon was confined to a few weeks in May and was consistent between habitats. In the channel habitats, steelhead

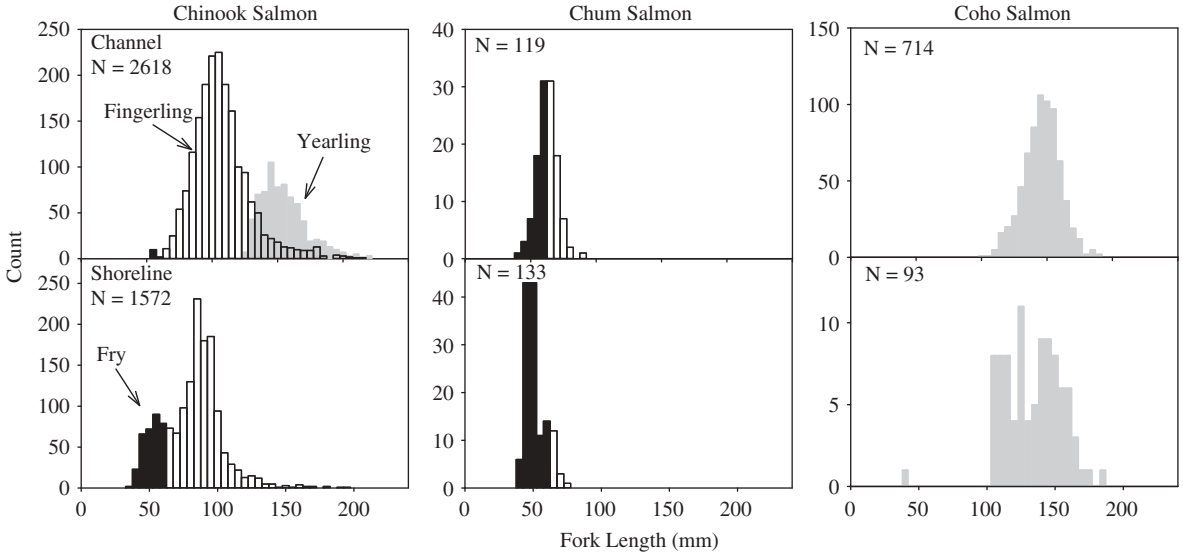


FIGURE 3. Length frequency (FL, mm) plots for Chinook Salmon, Chum Salmon, and Coho Salmon sampled from channel (top row) and shoreline (bottom row) habitats of the Columbia River estuary during April–October of 2010–2012. Shading designates the life history stage based on size at age (black bars = fry [<60 mm]; open bars = fingerling-sized subyearlings; gray bars = yearlings). Note the variation in *y*-axis scale.

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TABLE 2. Salmon life history stages calculated from absolute numbers of measured salmon in paired shoreline and channel samples from the Columbia River estuary (N = number measured; % = percentage of total).

	Shoreline		Channel	
Life history stage	N	%	N	%
Chinook Salmon				
Fry	332	21.1	12	0.5
Fingerling	1,221	77.7	1,873	71.5
Yearling	19	1.2	733	28.0
Total	1,572		2,618	
Chum Salmon				
Fry	117	88.0	60	50.4
Fingerling	16	12.0	59	49.6
Yearling	0	0	0	0
Total	133		119	
Coho Salmon				
Fry	1	1.1	0	0
Fingerling	0	0	0	0
Yearling	92	98.9	714	100
Total	93		714	

were present throughout May, and Sockeye Salmon were present from late May to early June.

Statistical Analysis of Abundance and Biomass

The patterns of variation described above were confirmed in the multivariate analyses of juvenile salmon assemblage data based on numeric and biomass metrics (Figure 5). There was complete separation between habitat types in NMDS space during April–June but complete overlap during August–October, when only subyearling Chinook Salmon were caught at both habitat types. The single factor that produced the best-defined groups in the ANOSIM was month for both numeric and biomass data (global R = 0.24 and 0.23, respectively; both $P < 0.01$) rather than habitat type (global R = 0.18 and 0.19, respectively; $P < 0.02$). However, when used together, month and habitat type produced the highest global R-values for the numeric and biomass data sets: 0.68 and 0.72, respectively, for habitat type; and 0.46 and 0.45, respectively, for month (all $P < 0.01$).

When channel abundance data were segregated by station, the global R-value for month (0.27, $P < 0.01$) was higher than that for either habitat type (global $R = 0.03$, $P > 0.10$) or station (global $R = 0.11$, $P < 0.01$). When two factors were used concurrently, the respective global R-values for habitat type and month (global R = 0.46 and 0.44; all $P < 0.01$) were similar to those for station and month (global R = 0.45 and 0.44; all $P < 0.01$). However, the difference between the shoreline station and the channel stations ($R > 0.49$, $P < 0.01$) was considerably greater than the difference between the two channel stations ($R = 0.14$, $P < 0.05$). These results indicate that there are strong seasonal changes in the juvenile salmon assemblages at all sites, but juvenile salmon communities at the two channel sites were more similar to each other than to the community at the shallow station, especially when seasonal variation was taken into consideration.

We compared the juvenile salmon assemblage between stations that were restricted to the same date (paired samples). Results showed that overall, pairwise similarities between the shoreline habitat and the channel habitats (mean = 72.1, n = 53) were significantly lower than similarities between the two channel stations (mean = 84.4, n = 25; $Z = 2.1$, $P < 0.05$). However, after June 30, pairwise similarities were equal (similarity = 1.0) between habitat types and between the two channel stations because only subyearling Chinook Salmon were caught. Consequently, although overall juvenile salmon communities remained distinct between the two habitat types throughout the season, by mid-summer they had merged into a single community. During summer, the predominance of subyearling Chinook Salmon in both habitats resulted in much lower species and life history diversity compared to spring.

Production Type

The contribution and size frequency of hatchery- and naturally produced salmon also differed among species and between environments (Figure 6; Table 3). In the channel habitats, marked and unmarked subyearling Chinook Salmon occurred at approximately equal frequencies, but unmarked salmon had a slightly higher size mode than marked fish. In contrast, along the shoreline, most of the subyearling Chinook Salmon smaller than 70 mm FL were unmarked, and the majority of these were fry of presumed natural origin. Size modes of marked subyearling Chinook Salmon were similar between shoreline and channel habitats, but the size range was narrower for subyearlings that were captured along the shore.

Chinook Salmon yearlings sampled at both shoreline (90.5%) and channel (83.5%) environments were predominately marked, although they were found at a much lower frequency along the shore. In both habitats, Coho Salmon were also predominately marked (68% in the shoreline habitat; 71.5% in the channel habitats), and marked fish had higher size modes than their unmarked conspecifics. Only 2 of 232 Chum Salmon had been fin clipped. Neither steelhead nor Sockeye Salmon were found along the shoreline, but among individuals that were sampled from channel habitats, the steelhead were predominately marked (89.8%), whereas the Sockeye Salmon were all unmarked. Seasonally, proportions of unmarked subyearling Chinook Salmon increased from spring to autumn in both habitats. This was likely due in part to a decreased prevalence later in the year of fall-run fish (i.e., fall = the season of adult return to freshwater) released from Spring Creek National Fish Hatchery and other hatcheries in the Columbia River basin (Teel et al. 2014; Weitkamp et al. 2015).

Chinook Salmon Genetics

Proportional stock composition of Chinook Salmon varied between habitat types and seasons (Figure 7; Table 4.)

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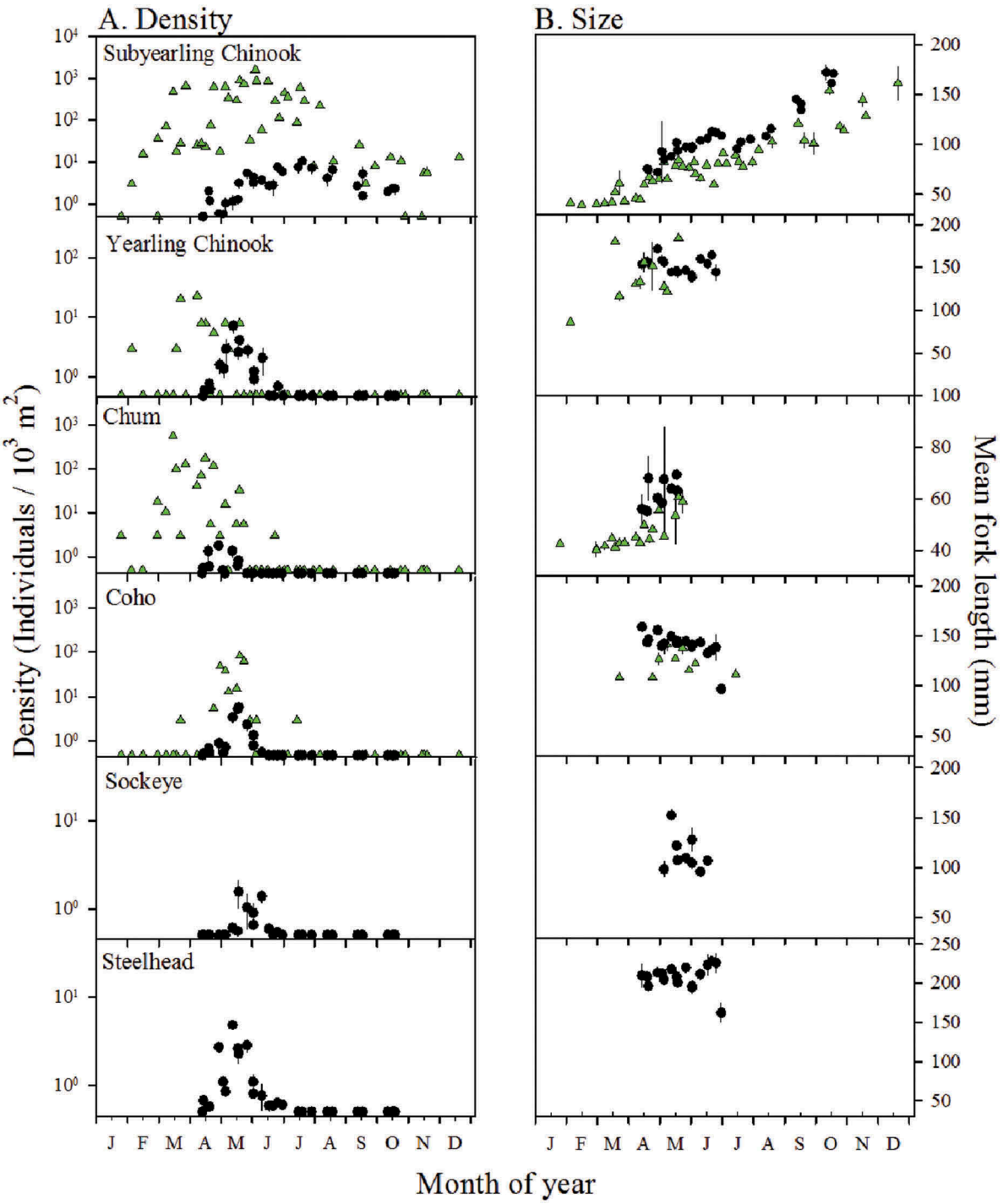


FIGURE 4. Time series comparing the density (left column) and mean FL (right column) of salmonids sampled at channel (circles; ±SE) and shoreline (triangles) habitats of the Columbia River estuary. Note the differences in *y*-axis scale between plots. No Sockeye Salmon or steelhead were sampled at the shoreline.

Shoreline samples were dominated by lower Columbia River fall-run fish, with West Cascade tributary fall-run and Spring Creek group tule fall-run fish contributing an estimated 85% of the total stock composition. The third-largest component of shoreline juveniles was the upper Columbia River summer–fall stock (7%). These same three stocks were also the largest

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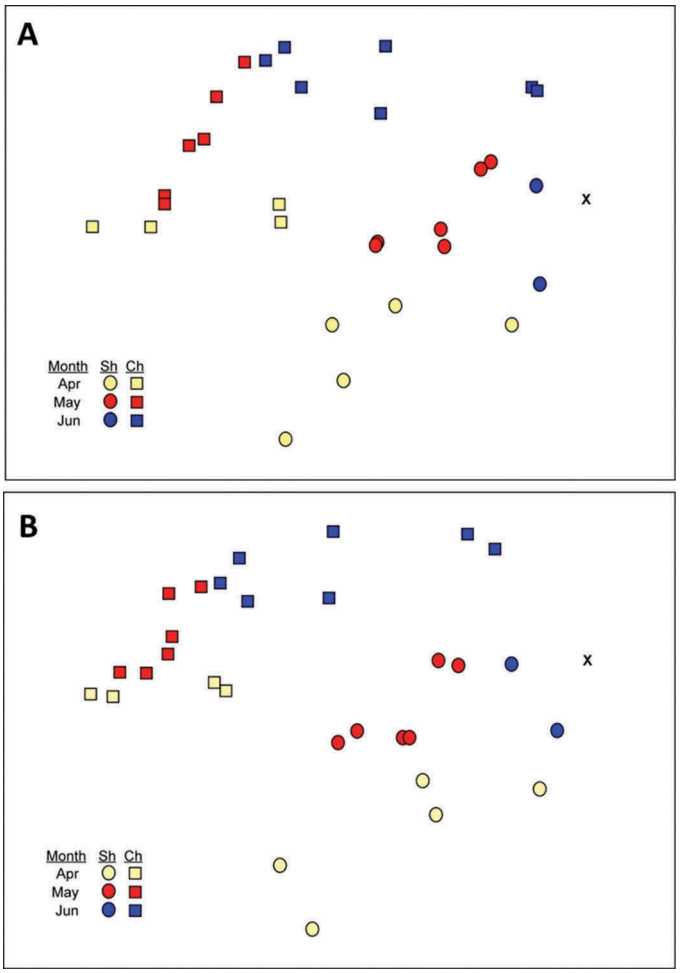


FIGURE 5. Nonmetric multidimensional scaling (NMDS) plots based on **(A)** numeric data or **(B)** biomass data describing the juvenile salmon community sampled from shoreline (Sh) or channel (Ch) habitats of the Columbia River estuary. Colors indicate the month of each sampling event. The "X" indicates shoreline and channel sampling dates (July–October) occupying the same position on both plots.

contributors to channel samples but in very different proportions than at the shoreline site. The largest stock proportion in the channel habitats consisted of upper Columbia River summer–fall fish (31%) followed by the Spring Creek group (23%) and West Cascade fall-run (14%) stocks.

Interior basin spring-run Chinook Salmon were present in channel samples, including yearling fish from the middle and upper Columbia River spring-run (9%) and Snake River spring-run (7%) stocks. These two interior spring stocks were apparently absent from our shoreline samples: proportional estimates were near zero, and no individuals were assigned to these stock groups with a probability above 0.90. However, several other genetic stocks comprised small (1–5%) proportions of both shoreline and channel samples, including the Willamette River and West Cascade tributary spring-run stocks, the Rogue River stock, and the coastal stock.

Measures of genetic stock diversity were higher for channel samples than for shoreline samples. We found more genetic stocks (S_G = 11 versus 10), higher genetic diversity (H'_G = 1.91 versus 1.20), and greater genetic evenness (J_G' = 0.80 versus 0.52) in channel samples than in shoreline samples. Seasonal changes were observed in both habitats—especially in spring, with higher proportions of the Spring Creek group stock, and in summer, with increased proportions of West Cascade fall-run and upper Columbia River summer–fall stocks. In channel habitats, genetic stock diversity metrics decreased from spring to summer, reflecting a near-total absence of spring-run fish later in the season.

DISCUSSION

We compared a series of metrics contrasting attributes of juvenile salmon communities sampled at channel and shoreline habitats in the Columbia River estuary. With the exception of salmon migration timing, nearly all of the evaluated metrics differed between the two habitat types, even though one channel site and the beach seine site were a short distance apart on the same side of the river. Along the shoreline, salmon densities were higher but mean sizes were lower, whereas in the channel habitat, there was a higher diversity of salmonid species and Chinook Salmon genetic stocks. Channel environments supported all salmon species and all genetic stocks of Chinook Salmon present in the Columbia River basin, although Chinook Salmon, Coho Salmon, and steelhead samples were composed primarily of large, hatchery-reared individuals. Shoreline samples contained higher proportions of smaller, presumably wild Chinook Salmon and Chum Salmon as well as lower occurrences of hatchery-reared yearling Coho Salmon and Chinook Salmon. The shoreline was particularly well populated by Chinook Salmon and Chum Salmon fry, which were rare in the channels. Yearling Chinook Salmon, yearling Coho Salmon, and larger subyearling Chinook Salmon each exhibited a more continuous distribution that spanned the habitat types. These results reinforce the concept that shallow estuarine environments function as nursery or refuge habitats for small, fry-sized salmonids, whereas channels are migratory corridors that are occupied by fast-moving stocks of larger body size. These large differences in the salmon community indicate that both habitat types must be sampled so as to obtain a comprehensive understanding of salmon migration patterns and habitat use.

The goal of this study was to examine the general similarity of salmon metrics between shallow and deepwater habitats. Because these habitats were physically dissimilar, we were obligated to sample them with different gear types. There are well-known issues related to comparing fish catches based on different gear types (Steele et al. 2006; Hayes et al. 2013). In the literature, capture efficiencies based on mark–recaptures for both beach seines and purse seines range widely (typically 30–80%; e.g., Charles-Dominique 1989; Bayley and Herendeen 2000). However, beach seines and purse seines are effective methods for

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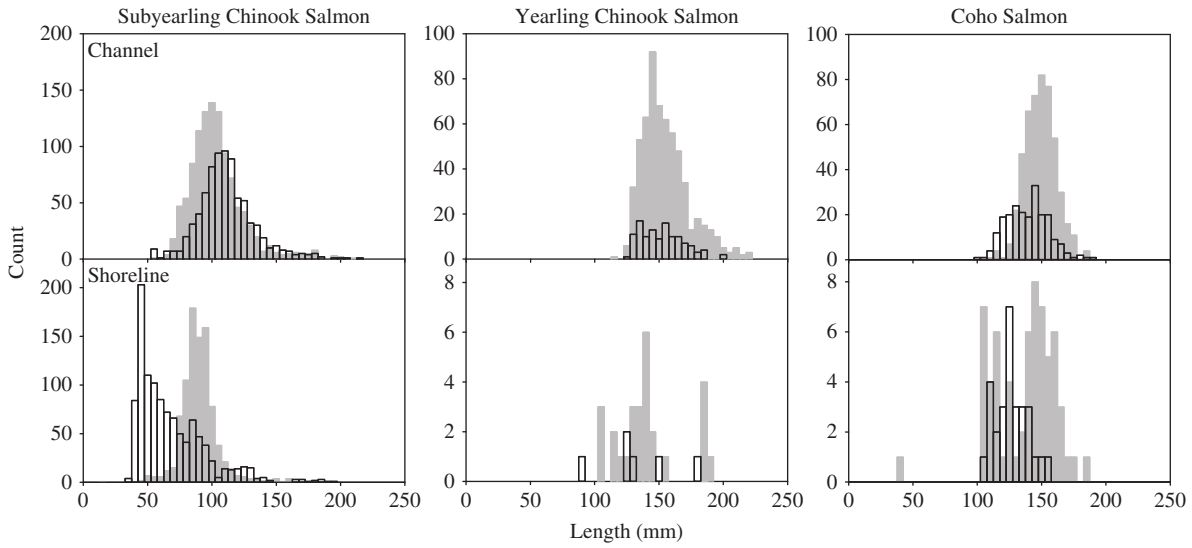


FIGURE 6. Length frequency (FL, mm) plots for marked (hatchery-cultured; gray bars) and unmarked (open bars) Chinook Salmon and Coho Salmon that were sampled from channel and shoreline habitats of the Columbia River estuary during April–October of 2010–2012. Note the variation in the *y*-axis scale.

capturing juvenile salmon, and gears with similar mesh sizes have been extensively utilized in the lower Columbia River and estuary over the last 40 years (Dawley et al. 1986; Bottom and Jones 1990; McCabe et al. 1993; Roegner et al. 2012; Weitkamp et al. 2012, 2015; Sather et al. 2016). Given that both types of gear are able to catch a wide size range of fish (from 25-mm fry to adult salmon), gear effects are unlikely to have produced the observed patterns in relative abundance, stock composition, migration timing, or relative size. Thus, we consider the differences in metrics to accurately reflect the differences in habitat utilization by salmon species and stocks. However, as with any comparative gear study, one must accept certain assumptions and caveats when interpreting the data. In our case, each gear type has its own unknown selectivity and efficiency based on fish species, size, and behavior; local physical conditions; and characteristics of the target area sampled. Selectivity was not measured in our study, and we assumed that both gear types undersampled the true populations. Nevertheless, we are confident that the general findings will prove robust given (1) the use of standard techniques for both gear types, (2) the similar mesh sizes of the nets, and (3) past research that has obtained similar results when employing similar gear types (Dawley et al. 1986; Bottom and Jones 1990).

Salmon Migration Timing

Salmon migration timing was the one metric that was generally comparable between habitats, although densities

TABLE 3. Hatchery marking rates for Pacific salmon (averaged across all facilities in the Columbia River basin) captured at shoreline and channel sampling locations in the Columbia River estuary and for the combined field data (age 0 = subyearling; age 1 = yearling; total = number of salmon sampled; hatchery % = estimated hatchery contribution). Hatchery data are from the Regional Mark Processing Center (PSMFC 2014).

	Hatchery		Shoreline			Channel			Combined	
Species	Mark (%)	*N* released ($\times 10^6$)	Total	Mark (%)	Hatchery (%)	Total	Mark (%)	Hatchery (%)	Mark (%)	Hatchery (%)
Chinook Salmon, age 0	82.6	66.7	1,551	46.8	56.7	1,884	60.2	72.9	54.1	65.6
Chinook Salmon, age 1	88.3	35.3	21	90.5	100[a]	726	83.8	94.9	84.0	95.1
Chum Salmon	10.8	0.3	133	0	0	119	1.7	15.7	0.8	7.4
Coho Salmon	78.9	18.5	93	68.8	87.2	715	72.2	91.5	71.8	91.0
Steelhead	83.0	14.6	0		0	665	76.3	91.9	76.3	91.9
Sockeye Salmon	68.2	0.4	0		0	84	0	0	0	0

[a]Capped at 100% because mark rates observed in the estuary exceeded mark rates reported for hatcheries.

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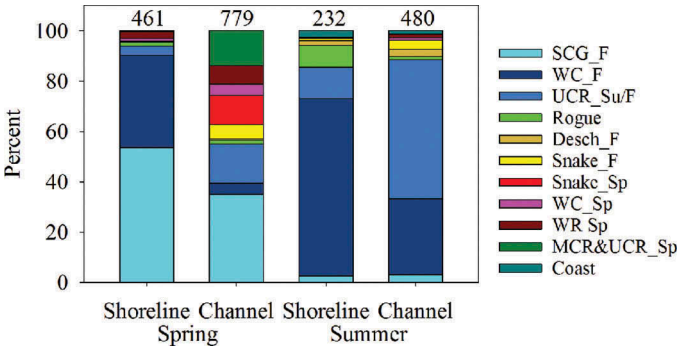


FIGURE 7. Genetic stock composition of Chinook Salmon that were sampled from channel and shoreline habitats of the Columbia River estuary during spring (April–June) and summer (July–October) of 2010–2012. The number of fish that were used to estimate stock proportions is shown above each bar. Codes for the genetic groups are defined in Table 4..

appeared to increase slightly earlier along the shoreline. This increase was obscured in part because the channel time series did not sample the earliest migrating Chinook Salmon or Chum Salmon (Weitkamp et al. 2015). Notable were the narrow migration windows of all groups except subyearling Chinook Salmon, which occupy estuarine habitats year-round (Dawley et al. 1986; Roegner et al. 2012). Chum Salmon, Coho Salmon, Sockeye Salmon, and steelhead were abundant only for about 1 month in the spring. For Sockeye Salmon, migration timing was several weeks later than the timing observed for the other species.

Migration timing of smaller, more vulnerable juvenile Chum Salmon preceded that of Coho Salmon and steelhead, overlapping only at the end of the Chum Salmon out-migration. In contrast, Chinook Salmon fry were present through July, and their migration timing overlapped extensively with those of larger, piscivorous salmon. Although fry predation by yearling salmon has been observed in wetlands (Roegner et al. 2010), it has not appeared prevalent in the estuary (Weitkamp et al. 2012; L. Weitkamp, unpublished data) or nearshore ocean (Daly et al. 2014). These migration timing differences were confirmed by results from the seasonal variable in multivariate tests, which indicated separate habitats during the spring migrations of yearling Chinook Salmon, Chum Salmon, Coho Salmon, Sockeye Salmon, and steelhead, with increased similarity during the summer and autumn migration of subyearling Chinook Salmon.

Whether our habitat-specific species and size results are comparable to patterns observed for juvenile salmon in other West Coast estuaries is difficult to determine, as similar studies with concurrent sampling of parallel habitat types are lacking. The migration timing patterns we observed in shoreline and channel habitats are generally similar to those reported for other large estuaries within the region (Quinn 2005; Weitkamp et al. 2014). This similarity suggests that habitat-specific differences observed in the Columbia River likely apply to other large estuaries, but directed research exploring this assumption is clearly warranted.

Genetic Composition of Chinook Salmon

The shoreline and channel habitats we studied are both used by Chinook Salmon from throughout the basin. Nevertheless, genetic stock diversity was greater in the channel habitats than along the shoreline. The greater diversity in the channel was largely due to the presence of upriver Chinook Salmon stocks, which were relatively rare in shoreline samples—a pattern that is consistent with previous research (Dawley et al. 1986; Teel et al. 2014). In channel habitats, the upriver stock component displayed a strong seasonal shift: a change in composition during April–June due to the migration of yearlings from interior basin spring-run populations was followed by a change in July–October during the migration of a large proportion (55%) of upper Columbia River summer–fall subyearlings.

Despite these striking differences in upriver stock composition, fall-run Chinook Salmon subyearlings from the Spring Creek group stock were predominant during April–June in both shoreline (54%) and channel (35%) habitats. After June, these subyearlings left the estuary relatively rapidly and constituted very minor proportions (3%) of the Chinook Salmon in both habitat types. The Spring Creek group stock primarily comprises large subyearlings that are released from a number of hatcheries each spring. After release, this stock is pervasive throughout the estuary, including in tidal freshwater habitats upriver (Roegner et al. 2012; Teel et al. 2014). It is noteworthy that our April–July sampling encompassed the peak migration period for juvenile spring-run yearling Chinook Salmon in the basin, yet during this period, fall-run Chinook Salmon representing the Spring Creek group were nearly as abundant in the channel as all of the spring-run stocks from throughout the basin.

One caveat to this discussion is that our data collected at Point Adams Beach represented the stock composition at the shoreline prior to ocean entry but does not represent the stock composition for the entire lower river. A downstream–upstream spatial structure of estuarine stocks has been reported previously (Roegner et al. 2012; Teel et al. 2014). For example, Teel et al. (2014) reported that the upper Columbia River summer–fall stock was the most common Chinook Salmon stock at shallow, tidal freshwater habitats of the lower Columbia River. This stock presumably changes its habitat distribution during the migration downstream. An increased sampling frequency during the main migration periods for yearling Chinook Salmon, Coho Salmon, Sockeye Salmon, and steelhead would likely confirm the presence of some stocks that were rare or absent in our shoreline collections, especially those with relatively low population abundances (e.g., Snake River fall-run subyearlings) or those with migration timing of short duration. Targeted sampling would

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TABLE 4. Genetic stock composition (percentages; with 95% confidence intervals in parentheses) and genetic stock diversity for Chinook Salmon that were sampled by shoreline beach seines and channel purse seines in the Columbia River estuary during the spring and summer of 2010–2012. Codes next to stock names (in parentheses) correspond to the genetic groups depicted in Figure 7.

	Apr–Jun (%)		Jul–Oct (%)		All samples (%)	
Genetic stock	Shoreline	Channel	Shoreline	Channel	Shoreline	Channel
N	461	779	232	480	693	1,259
West Cascade fall (WC_F)	36.6 (30.3–41.8)	4.3 (3.0–8.1)	70.4 (58.4–72.4)	30.3 (23.7–32.2)	47.3 (39.6–51.5)	14.0 (11.4–16.3)
West Cascade spring (WC_Sp)	1.1 (1.6–6.1)	4.4 (3.6–6.8)	0 (0.0–5.1)	1.0 (0.8–5.3)	0.6 (1.0–4.6)	3.4 (3.2–5.8)
Willamette River spring (WR_Sp)	2.7 (0.9–4.1)	7.3 (4.8–8.7)	0.4 (0.0–1.2)	1.4 (0.4–2.3)	1.9 (0.4–2.7)	4.9 (3.3–5.8)
Spring Creek group fall (SCG_F)	53.6 (45.2–56.3)	35.1 (29.3–37.3)	2.6 (0.5–9.2)	3.0 (1.4–5.2)	37.2 (30.8–40.2)	23.0 (18.9–24.0)
Deschutes River fall (Desch_F)	0.3 (0.0–1.3)	0.7 (0.0–2.3)	1.9 (0.0–5.6)	3.0 (1.7–6.7)	0.8 (0.0–1.7)	1.5 (1.1–3.7)
Upper Columbia River summer–fall (UCR_Su/F)	3.7 (2.0–6.4)	15.7 (13.5–19.1)	12.5 (8.3–19.6)	55.2 (46.9–57.0)	6.8 (5.0–9.4)	30.6 (26.2–33.9)
Mid- and upper Columbia River spring (MCR&UCR)	0 (0.0–0.4)	13.9 (10.3–15.5)	0 (0.0–0.0)	0 (0.0–0.0)	0 (0.0–0.3)	8.5 (6.4–9.8)
Snake River fall (Snake_F)	0 (0.0–0.5)	5.5 (3.4–7.5)	0.9 (0.0–4.2)	3.5 (2.0–8.9)	0.3 (0.0–1.5)	4.8 (3.6–7.5)
Snake River spring–summer (Snake_Sp)	0.2 (0.0–0.7)	11.8 (10.0–15.2)	0 (0.0–0.2)	0 (0.0–0.2)	0.1 (0.0–0.5)	7.3 (5.3–9.3)
Rogue River (Rogue)	1.6 (0.7–2.6)	1.3 (0.4–2.1)	8.7 (4.1–11.6)	1.2 (0.1–2.8)	4.0 (2.4–5.2)	1.4 (0.7–1.9)
Coastal (Coast)	0.2 (0.0–1.0)	0 (0.0–0.5)	2.6 (0.7–5.5)	1.4 (0.6–3.3)	1.0 (0.4–2.3)	0.6 (0.2–1.2)
Shannon–Weiner diversity index (H'_G)	1.07	1.90	0.95	1.18	1.20	1.91
Number of genetic stocks (S_G)	9	10	8	9	10	11
Pielou's evenness index (J_G')	0.49	0.82	0.46	0.54	0.52	0.80

also likely reveal higher genetic diversity of Chinook Salmon. For example, Teel et al. (2014) sampled monthly at Point Adams Beach and detected seven genetic stocks of Chinook Salmon, whereas we sampled the site biweekly and detected 10 genetic stocks. Our sampling schedule allowed for the discernment of periods of habitat use by salmon species and stocks before ocean entry.

Density Variation by Habitat Type

A striking finding from the present study was that maximum salmon densities were considerably higher at the shoreline habitat than at channel habitats. Relative to other sites within the Columbia River estuary (Thom et al. 2013), salmon densities at our shoreline site would likely be classified as "medium-high" (>10^1 to 10^2 ind/10^3 m^2). In contrast, salmon densities at our channel sites would be considered "low" (<10^1 ind/10^3 m^2). This was also the case for most of the nonsalmonid densities; the only species for which channel densities rivaled shoreline densities were the Northern Anchovy *Engraulis mordax* and Threespine Stickleback *Gasterosteus aculeatus* (data not shown). The large difference in salmon density (up to two orders of magnitude per paired sample) was not accounted for by differences in catchability alone, and similar variability in fish densities between habitats was found by Dawley et al. (1986) and Bottom and Jones (1990). We conclude that on a per-area basis, Chinook Salmon, Chum Salmon, and Coho Salmon exhibit periods of intensive occupation of shoreline habitat.

Simple scaling calculations illustrate how these variations in salmon density relate to comparative habitat use. As an example,

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TABLE 5. Density, percentage of total, and estimated number of Pacific salmon in shoreline and channel habitats of the Columbia River estuary as determined from average salmon densities (age 0 = subyearling; age 1 = yearling). Percentage of total is the percent of shoreline values relative to the entire reach area modeled (105 m^2 of shoreline plus 5 × 106 m^2 of channel).

Species	Habitat	Density (individuals/10^3 m^2)	Percentage of total	Estimated number of fish in reach (*n*)
Chinook Salmon, age 0	Shoreline	321.7	67.1	32,168.9
	Channel	3.2	32.9	15,786.2
Chinook Salmon, age 1	Shoreline	3.5	18.4	350.0
	Channel	0.3	81.6	1,550.0
Chum Salmon	Shoreline	39.9	66.8	3,987.5
	Channel	0.4	33.2	1,982.6
Coho Salmon	Shoreline	11.9	14.5	1,188.9
	Channel	1.4	85.5	6,995.3
Steelhead	Shoreline	0.0	0.0	0.0
	Channel	0.92	100.0	4,611.9
Sockeye Salmon	Shoreline	0.0	0.0	0.0
	Channel	0.37	100.0	1,844.3

we compare total salmon abundance at shoreline and channel environments by integrating salmon density by the area of the two habitats. Consider the estuarine channel environment encompassed by a 1-km reach of river that is 5 km wide (5×10^6 m^2) and the estuarine shoreline environment as a strip that is 1 km long × 50 m wide (with two shorelines, the area equals $2 \times 5 \times 10^4 = 10^5$ m^2). Extracting mean densities from our surveys, assuming a constant density across the respective habitats, and integrating by area yield the total number of salmonids in each habitat (Table 5.). Given these conditions, subyearling Chinook Salmon and Chum Salmon along the shoreline both constituted, on average, about 67% of the fish within the total 5.1-km^2 area, whereas yearling Chinook Salmon and Coho Salmon along the shoreline comprised only 18% and 14%, respectively. In contrast, 100% of the steelhead and Sockeye Salmon were occupying the channels.

Thus, despite representing only one-fiftieth of the total area, the shoreline habitat was significantly enriched in Chinook Salmon and Chum Salmon relative to the channel environment. There was also a significant seasonal effect on subyearling Chinook Salmon abundance: during spring, 78% of the total number of subyearlings were found along the shoreline, but this proportion dropped to 35% during summer. Note that the use of a volumetric standardization (e.g., fish/m^3) would magnify these habitat differences by an order of magnitude. Additionally, if we had used a narrower section of river reach (typical of upriver tidal freshwater zones), with all other variables remaining unchanged, the proportions of shoreline use would have been even higher (due to a reduction of channel habitat area). Our data and this scaling exercise emphasize the enrichment of smaller salmon along the shore. The data also support the concept that a sizeable minority of yearling Chinook Salmon and Coho Salmon do not simply migrate through the estuary in channel habitats but in fact utilize shallow-water areas. In contrast, steelhead and Sockeye Salmon are confined to the channel environment.

Natural versus Hatchery Production

In our study, evidence of naturally produced fish was most apparent for small subyearling Chinook Salmon and Chum Salmon that occupied shoreline habitats. These species exhibit life history strategies that include ocean migrations by fry and small fingerlings (Bottom et al. 2005). For example, nearly all Chum Salmon and about 13% of the subyearling Chinook Salmon sampled from shoreline sites in the lower estuary regularly enter the ocean at sizes smaller than 60 mm FL (Roegner et al. 2012). Chum Salmon reportedly once had annual adult returns exceeding 1 million (Good et al. 2005), and Chinook Salmon that migrate to the ocean as fry still contribute significantly to adult returns (Miller et al. 2010, 2011). Small, naturally produced juvenile subyearling Chinook Salmon that occupy shoreline habitats are primarily fall-run fish originating from lower-river sources (Table 4; Roegner et al. 2012; Teel et al. 2014; Sather et al. 2016). Although less is known about the sources of Chum Salmon in our samples, this species also spawns primarily in lower-river tributaries (Good et al. 2005; Small et al. 2011). Shallow-water habitat conservation and restoration are particularly important for this life history type.

In contrast to subyearling Chinook Salmon and Chum Salmon, we estimated that more than 90% of steelhead, Coho Salmon, and yearling Chinook Salmon in our study were hatchery produced. The size distributions of these larger migrants also reflected hatchery practices that concentrate salmon into a narrower range of larger size-classes relative to naturally spawned fish (Bottom et al. 2005). As a result, the observed narrow size composition and migration

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timing of these stocks at ocean entry were largely a function of hatchery rearing and release procedures (Weitkamp et al. 2015). Notably, the proportions of wild fish were similar to those previously observed in adjacent marine habitats for juveniles of the same species (Teel et al. 2003; Van Doornik et al. 2007; Daly et al. 2012, 2014). This is consistent with the premise that conditions and management practices with impacts on juvenile salmon during their out-migration in riverine and estuarine habitats have consequences for subsequent marine distribution and survival.

Conclusions

Pacific salmon in the Columbia River basin evolved in a system that was vastly different from the conditions that are present today. The river has been diked and channelized, peak flows have been reduced, the timing of peak flows has been altered, and spawning and rearing areas have been degraded or destroyed (Williams 2006). Much of the historic diversity of salmon in the Columbia River has been lost (Gustafson et al. 2007). Climate change will likely apply additional stressors to salmon and to estuarine environments (Scavia et al. 2002; Isaak et al. 2012). Our data have clarified contemporary juvenile salmon migration timing and habitat use in the lower Columbia River estuary prior to ocean entry. Sampling at both habitat types is required to fully encompass the migration patterns of all salmon ESUs.

Our analysis of juvenile salmon in the estuary also suggests that for many salmon stocks and species, migration timing continues to largely reflect hatchery management practices. Most of the hatchery fish are larger and fall within a narrower size range than their natural counterparts, reflecting a decrease in life history diversity that may reduce resilience to environmental variation. In light of these differences, future research efforts investigating the effects of hatchery programs on rebuilding threatened Columbia River salmon populations (e.g., Paquet et al. 2011) should evaluate ecological interactions between hatchery- and naturally produced fish in estuarine and nearshore ocean habitats (Fresh 1997; Rand et al. 2012). Furthermore, the extent to which fine-scale habitat use patterns observed in this part of the estuary apply to reaches further upstream is unclear (Roegner et al. 2012; Teel et al. 2014; Sather et al. 2016); additional research is needed to elucidate patterns of habitat use elsewhere in the system.

Finally, our data can also guide the design of restoration actions for multiple salmon stocks and runs in the Columbia River estuary and can inform the potential benefits of such efforts. The contemporary juvenile migration timing we have described clearly demonstrates that benefits to the highest diversity of salmonid species and stocks will occur during the critical migration window in the spring. Mitigation programs, such as the restoration of shallow wetlands and shorelines as sources of insect prey, will directly benefit the smaller salmon that inhabit these wetlands throughout the year as well as the larger fish occupying channel habitats via indirect food web connectivity during spring.

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