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ARTICLE

Distribution, Size, and Origin of Juvenile Chinook Salmon in Shallow-Water Habitats of the Lower Columbia River and Estuary, 2002–2007

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Abstract

We monitored fish assemblages monthly at estuarine and tidal freshwater sites in the lower Columbia River and estuary from January 2002 through September 2007 in order to identify specific salmon stocks and migration stages that may benefit from habitat restoration initiatives. We report landscape-scale and seasonal variation in abundance, size, hatchery production (based on adipose fin clips), and genetic stock of origin of juvenile Chinook salmon *Oncorhynchus tshawytscha*. From fish implanted with coded wire tags (CWTs), we also determined the sites of release and inferred migration patterns. Chinook salmon were found in diverse life history stages and forms, including fry migrants, fingerlings, and (fewer) yearlings. Abundance increased in February and decreased in August, but salmon were present in all months each year. Spatial gradients in abundance and size were strong, with fewer but larger fish in brackish than in tidal freshwater zones. Overall, 30% of the Chinook salmon measured were fry (≤60 mm) that were likely naturally produced fish. These occurred at higher mean monthly proportions in tidal freshwater than in estuarine zones. In contrast, most larger fish were probably raised in hatcheries. Genetic stock assessment revealed that the majority of the Chinook salmon analyzed were from fall-run stock groups originating in the lower Columbia River, with 15% originating from other stock groups. Of these minority contributors, about 6% were identified as upper Columbia River summer–fall-run Chinook salmon while seven other stock groups accounted for the remainder, including 3% from transplants originating in southern Oregon's Rogue River. Recaptures of tagged fish revealed maximum migration times of 143 d for subyearlings and 52 d for yearlings, and both CWT and genetic data indicated that fall Chinook salmon from coastal rivers occasionally entered the estuary. These data demonstrated a widespread temporal and spatial distribution of subyearling Chinook salmon in shallow-water habitats of the lower Columbia River and estuary.

The abundance of salmonid populations in the Columbia River basin has declined through the past 150 years due in part to alterations of salmon habitat (Myers et al. 2006), including the degradation and loss of spawning and rearing areas, alteration of river flows from historical patterns, and impediments to juvenile and adult migrations (Sherwood et al. 1990; Sheer and Steel 2006). The lower Columbia River and estuary (LCRE), which we define here to encompass the continuum of tidal freshwater through nearshore plume environments, has been highly modified. Diking, dredging, and filling have eliminated or reduced access to large areas that historically were biologically productive tidal swamps and marshes (Thomas 1983; Sheer and Steel 2006). Dam and jetty construction have changed the timing and magnitude of river flow, affecting water depth and velocity, sedimentation rates, and the extent of salinity intrusion (Kukulka and Jay 2003). Mitigation practices, including hatchery supplementation and measures to offset the many anthropogenic impacts, were attempted throughout the 20th century but to date

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have been insufficient to maintain fish stocks at high abundance. Restoration of degraded wetlands intended to improve juvenile rearing opportunities is presently being implemented or planned in many regions of the LCRE, yet questions remain concerning the benefits of these actions to specific stocks and life history types of salmon.

Major divisions in salmonid life history types include the subyearling and yearling rearing strategies, which refer to whether juveniles migrate to sea during their first year or reside for one or more years in lotic, riverine, tidal freshwater, or brackish environments (Myers et al. 2006). For subyearling Chinook salmon *Oncorhynchus tshawytscha*, life history stages include fry (defined as fish $\leq$60 mm fork length) that can move rapidly to the ocean or linger and grow and fingerlings that may be present for various periods in a variety of freshwater and brackish habitats (Bottom et al. 2005b). Subyearling life history diversity can be categorized broadly by (1) migration timing and size at ocean entry, (2) residence within the physiochemical gradient of riverine, tidal freshwater, and estuarine regimes, and (3) the use of particular habitats (e.g., channels, tidal sloughs, and tidal freshwater versus brackish wetlands). The ability of many salmon stocks to express diverse life histories during the juvenile phase is thought to be an important adaptive mechanism for mitigating natural environmental variability (Healey 1991; Waples et al. 2009). Extensive use of estuaries by subyearling Chinook salmon has been well documented in other Pacific Northwest rivers (e.g., Reimers 1973; Healey 1980; Myers and Horton 1980; Levy and Northcote 1982; Bottom et al. 2005a), and Healey (1982) suggests that Chinook salmon are the most estuary dependent of salmon species, due in part to this wide variation in their life history patterns.

In the LCRE, historical knowledge of Chinook salmon life history diversity is based on a limited study of fork length, timing, and scale circuli data dating from 1914 to 1916 (Rich 1920). This early investigation indicated that a variety of subyearling migration patterns were present. The years 1934 to 1971 saw dam construction on the Columbia and Snake rivers and on many of their tributaries, which severely eliminated habitat and curtailed salmon migration patterns (Bottom et al. 2005b). Subsequently, Reimers and Loeffel (1967) found differences in emergence rates, growth, and residency between the larger, colder rivers draining Mt. St. Helens and the smaller, warmer rivers draining Coast Range watersheds. From 1966 to 1983, an extensive beach- and purse-seining effort documented the abundance, distribution, migration patterns, and postrelease survival of wild and hatchery-reared salmon and steelhead, including subyearling Chinook salmon (e.g., Durkin 1982; Dawley et al. 1985, 1986). The studies by Dawley et al. (1985, 1986) allow direct comparisons from a period soon after the completion of major dam construction with contemporary salmon abundance and size distributions. The latest assessment of fish assemblages and prey resources in the Columbia River estuary was completed more than 20 years ago (Bottom and Jones 1990). Since that time, 13 Columbia River basin Pacific salmon and steelhead evolutionarily significant units (ESUs) have been listed as threatened or endangered under the U.S. Endangered Species Act (Good et al. (2005), prompting changes to the way the Federal Columbia River Power System (FCRPS) has been operated and managed. For example, modifications to the infrastructure of the FRCPS have been made to improve passage for juvenile salmon. Protected Chinook salmon ESUs in the basin are Snake River spring–summer, Snake River fall, upper Columbia River spring, lower Columbia River, and upper Willamette River spring stocks.

Estuary restoration activities have expanded rapidly in recent years in an effort to help recover at-risk populations (LCREP 2011). However, it is not clear which specific stocks of concern will benefit from these restoration efforts. Most recent studies have concentrated on the migration and mortality patterns of larger salmon fingerlings and especially smolts that can be fitted with passive integrated transponder (PIT), acoustic, or radio tags (e.g., Collis et al. 2001; Ledgerwood et al. 2005; Clemens et al. 2009) in order to track the downstream movements or estimate the survival of various groups of marked hatchery fish. These later studies provide no information on the spatial–temporal distribution and genetic stock of origin of the smaller subyearling fish known to be estuarine dependent in other systems (Healey 1982).

In this paper, we summarize the results of a 6-year monitoring program to determine the distribution patterns of Chinook salmon in shallow, tidal fresh and brackish habitats of the lower Columbia River and estuary. The monthly sampling periodicity was designed to resolve broad patterns of salmon abundance and size at the landscape and seasonal scales. Our objectives were to (1) establish salmonid species presence and determine life history characteristics based on size and capture date and (2) identify stock-specific patterns of shallow-water habitat use and migration.

METHODS

Landscape-scale beach seine sites.—Fish communities were sampled by beach seine at six primary sites, ranging from tidal freshwater to marine-dominated estuarine habitats (Figure 1). Sites were paired between Washington and Oregon sides of the Columbia River and grouped into three spatial zones based on salinity characteristics. The tidal freshwater zone was characterized by two sites located above the uppermost extent of salinity intrusion at the head of Cathlamet Bay: lower Elochoman Slough at river kilometer (rkm) 79.2 and upper Clifton Channel (rkm 83.6). A third site, East Tenasillahe Island (rkm 81.4) was sampled from 2002 to 2005, and only data from CWT recoveries are reported here. The estuarine mixing or middle estuary zone included two sites located near the seasonally fluctuating boundary of the salt–freshwater interface: Pt. Ellice (rkm 22.0) and Pt. Adams Beach (rkm 19.8). The marine or lower estuary zone was comprised of two sites near the mouth of the river: Clatsop Spit (rkm 7.7) and West Sand Island (rkm 9.9). Note

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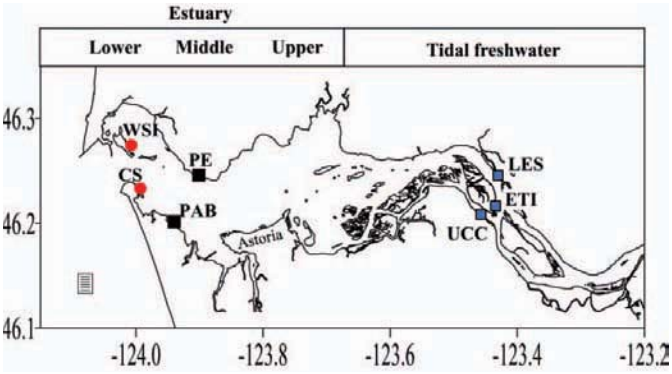


FIGURE 1. Map of the lower Columbia River and estuary showing beach seine sites. Abbreviations are as follows: UCC = upper Clifton Channel, LES = lower Elochoman Slough, PAB = Pt. Adams Beach, PE = Pt. Ellice, CS = Clatsop Spit, and WSI = West Sand Island.

that tidal, wind, and river flow generate widely varying salinities and temperatures in the estuary (Jay and Smith 1990; Roegner et al. 2011). All sampling sites were sandy beaches subjected to tidal fluctuations, but they varied in slope, submerged vegetation cover, and wave exposure (caused by wind waves, swell, and ship traffic). No attempt was made to quantify these site characteristics.

Sites were sampled monthly from January 2002 through September 2007, although adverse weather prevented sampling on 25 of 460 (5.4%) sample dates, usually in November through February. During 2008 we continued sampling for fish with fin clips or tags at Pt. Adams Beach and upper Clifton Channel from March through September, and these data were used to document the results of changes in adipose fin clip procedures for hatchery salmon.

Fish sampling.—Fish species composition was sampled with a tapered 3-m × 50-m, variable-mesh (19.0, 12.7, and 9.5 mm) beach seine with knotless webbing in the bunt to reduce descaling injuries to fish. Beach seine samples were generally acquired within 2 h of low tide. During deployment, one end of the seine was anchored on the beach while the other was towed by a skiff to enclose a semicircular surface area of ~400 m^2. For each sample, we randomly selected and measured (fork length to the nearest 1.0 mm) and weighed (to the nearest 0.1 g) up to 70 salmonids of each species, and fin tissue samples were collected from a maximum of 30 Chinook salmon for genetic analysis. All measured salmonids were examined for fin clips and tags, which are generally indicative of a hatchery origin. However, because Columbia River hatcheries also released juvenile Chinook salmon without such identifying marks during our study period, our samples of unmarked fish likely included both natural and hatchery-origin fish. The remaining salmon were counted and released. For nonsalmonids, we measured and released a representative sample of up to 30 individuals of each species, and the remaining nonsalmonids were counted and released (summary in Roegner et al. 2008).

Genetic stock of origin.—We used microsatellite DNA loci that have been standardized among several West Coast genetics laboratories (Seeb et al. 2007) to estimate the stock origins of Chinook salmon collected in the LCRE from 2002 to 2006. Tissue storage and data collection methods followed the protocols of Teel et al. (2009). The proportional stock compositions of LCRE samples were estimated using a "baseline" of genotypic data from potential source populations (Milner et al. 1985) and the likelihood model of Rannala and Mountain (1997), as implemented by the genetic stock identification computer program ONCOR (Kalinowski et al. 2007).

Population baseline data were compiled from a multilaboratory standardized Chinook salmon genetic database (Seeb et al. 2007). Baseline data for populations in rivers both north and south of the Columbia River were included to estimate the proportions of juveniles migrating into our study area from coastal sources and to identify individuals descended from past transfer of coastal hatchery stocks into the Columbia River basin. Information and data sources for the 45 Columbia River basin and coastal populations in our baseline are given in Table A.1 in the appendix. Allocations to individual baseline populations were summed to estimate the respective proportions contributed by each of the 11 regional stock groups (Table A.1). Regional genetic stock groupings were based on the stock identification analysis described by Seeb et al. (2007) and on previous genetic studies of Chinook salmon in the Columbia River basin (e.g., Waples et al. 2004; Myers et al. 2006; Roegner et al. 2010).

In the interior Columbia River, regional genetic groups identified using the microsatellite baseline included populations from the Snake River spring–summer and Snake River fall ESUs. A single genetic stock group was comprised of populations from the middle and upper Columbia River spring-run ESUs populations (Seeb et al. 2007). Also in the interior Columbia River genetic stock groups were fish from the Deschutes River summer–fall ESU and the upper Columbia River summer–fall ESU. The Columbia River summer–fall stock group included summer-run Chinook salmon populations in the upper Columbia River and "upriver bright" fall populations, including those in the Hanford Reach area. The Hanford Reach fall stock was used to develop the run at Priest Rapids Hatchery and is used at several other hatcheries that release fish in upper Columbia River locations as well as locations lower in the river, such as Bonneville Hatchery (Regional Mark Processing Center; www.rmpc.org).

The lower Columbia River was represented by three genetic stock groups, including the Spring Creek group, which is a "tule" fall stock originating in the Columbia River Gorge area that has been widely propagated for over a century throughout the lower Columbia River (Myers et al. 2006). Also in the lower Columbia River ESU are the West Cascade tributaries spring and fall stock groups, which comprise fish originating in several tributaries and hatcheries (Myers et al. 2006). Populations from the upper Willamette River spring-run ESU form a

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single genetic stock group in our analysis. Chinook salmon in the lower Columbia River also include both hatchery and naturally produced individuals from the Rogue River fall stock, which was introduced from southern Oregon into the Columbia River beginning in the 1980s (North et al. 2006; Roegner et al. 2010). We therefore used genetic data from the southern Oregon and California coastal ESU to estimate the proportions of Rogue River stock in our samples. Another nonnatal stock group in the genetic analysis is fall Chinook salmon from the Oregon and Washington coast ESUs.

The precision of the stock composition results was estimated by bootstrapping baseline and mixture data (100 times) as implemented by ONCOR (Kalinowski et al. 2007). We also used ONCOR to estimate the most likely stock group of origin for individual fish in order to plot stock-specific size-frequency distributions grouped spatially and seasonally. Data for the plots were restricted to assignments made with at least a probability of 0.90 relative to other groups. Power analyses conducted on the baseline data indicated that excluding individuals with lower probability assignments (approximately 25% of our samples) improves overall assignment accuracy and results in only small changes in the stock composition estimates. However, the Deschutes River summer–fall and middle and upper Columbia River spring runs are not represented in the individual fish genetics plots because no fish from those two stocks met the 0.90 probability threshold.

Analysis and data presentation.—Yearling and subyearling life history types were determined by size-at-capture and size-frequency distributions (adjusted from Dawley et al. 1985). Subyearling life history stages were further categorized into fry ($\leq$60 mm) and fingerling size-classes (Bottom et al. 2005b). We assume from hatchery release procedures, which discourage the "dumping" of slower-growing animals, that the majority of fry-sized animals were naturally spawned (although data from 2007 indicate that some larger fry are occasionally released from hatcheries). Therefore, the distribution patterns of fry were analyzed separately from those of fingerlings.

To investigate possible differential habitat use across the longitudinal gradients of the estuary, we grouped salmon abundance (measured as CPUE) and size by region of capture (lower estuary, middle estuary, and tidal freshwater zones). To examine seasonal patterns of abundance and size, we grouped salmon into one of three seasonal periods: winter (November–February), spring (March–June), and summer–fall (July–October). These temporal divisions reflect seasonal variability in water temperature, river flow, and expected salmon abundance patterns (Simenstad et al. 1990); patterns of interannual variation are summarized in Bottom et al. 2008 and Roegner et al. 2008. A two-way analysis of variance (ANOVA) with Tukey's honestly significantly different test was employed to test for differences in mean CPUE and size by spatial zone and season (StatSoft 2010). These data were $\log_{10}$ transformed to reduce heteroscedasticity. To increase temporal resolution, we also computed the mean CPUE and mean proportion of fry-sized animals by month and zone. Finally, we used linear regression of mean size by time to compare salmon sizes among the three zones.

Individual genetic stock assignments were combined with length-frequency histograms to gain a broad sense of stock-specific estuary use across spatial and temporal continua. To further examine use of the estuary by specific life history stages and types, we partitioned the data by fry and fingerling life history stage and by subyearling and yearling type and used stock composition analysis to produce proportional abundances.

We were able to assess the release location and date, genetic stock of origin, and life history type on an individual basis for a subset of individual fish that had been coded-wire tagged. Tag data were used to calculate time since release and migration rate (travel distance divided by travel time; e.g. Fisher and Percy 1995; MacFarlane and Norton 2002; Morris et al. 2007). Migration rate encompasses a variety of behaviors between release and recapture events, including extended rearing periods, and is not intended to be a measure of swimming velocity. In cases where fish were released over a range of dates, we report the average days postrelease and migration rate.

RESULTS

Salmon in Shallow-Water Habitat

From 2002 to 2007, we caught 11,988 Chinook salmon, 2,970 chum salmon *O. keta*, 202 coho salmon *O. kisutch*, 23 steelhead *O. mykiss*, 23 cutthroat trout *O. clarkii*, and 2 sockeye salmon *O. nerka*. Chinook and chum salmon were a relatively high proportion (4.5 and 1.1%, respectively) of the total fish assemblage (salmonids and nonsalmonids). We encountered fewer coho salmon or steelhead, as these species are dominated by yearling life history types that tend to migrate swiftly through the lower river system in main-channel environments (Dawley et al. 1986). Threespine stickleback *Gasterosteus aculeatus* was the dominant species at all sites and times, and surf smelt *Hypomesus pretiosus* and shiner perch *Cymatogaster aggregata* were seasonally abundant in the lower and middle estuary. See Roegner et al. (2008) for a summary of the fish assemblage sampled from 2002 to 2004.

In all years, we found Chinook salmon during every month, although at low abundance during October–January (Figures 2, 3). Shallow-water habitat use varied by life history type among Chinook salmon. Of the 6,195 fish that were measured, 97.4% were subyearlings and only 156 were yearlings (Figure 2; Table 1). Yearling abundance was concentrated in March and early April in the tidal freshwater zone, where they composed 2.9% of the measured population. In the middle estuary, yearling abundance (2.5% of the salmonid population) was concentrated in late March to early May. The fewest number and smallest proportion of yearlings were found in the lower estuary zone (1.4%), where abundance peaked during April and May. However,

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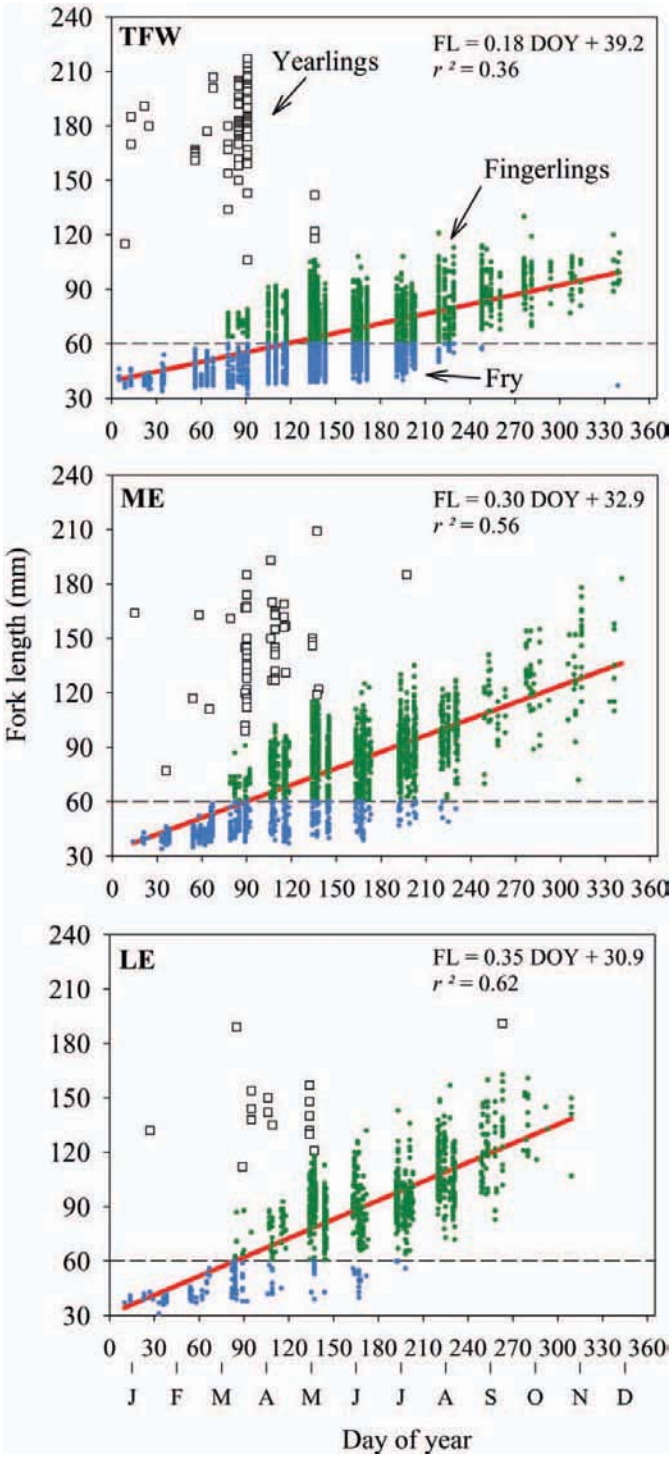


FIGURE 2. Chinook salmon fork length by day of year for each habitat zone (tidal freshwater [TFW], middle estuary [ME], or lower estuary [LE]) and life history stage, 2002–2007. The regression lines and statistics pertain only to subyearlings (fry and fingerlings). The dashed lines indicate the 60-mm threshold dividing fry from fingerlings.

individual yearling fish were captured at all landscape zones outside this window (Figure 2).

Subyearling Variation in Abundance and Size

Spatial gradients in subyearling Chinook salmon abundance were evident, with fewer fish at lower and middle estuary than at tidal freshwater sites. The highest mean monthly catches of subyearlings occurred in the tidal freshwater zone, with a broad peak from April to June (Figure 3). In the middle estuary zone, abundance followed a bimodal distribution, with peaks occurring in May and July and maximum abundance levels about half of those seen in the tidal freshwater zone. The lowest abundances were found in the lower estuary zone, where abundance peaked in July. At all sites, high variance was evident in the monthly averages.

Tests for differences in CPUE and for size grouped by zone and season indicated significant main effects and interaction terms (ANOVA; both $P < 0.001$). We therefore performed separate one-way ANOVA tests by zone, season, site within season, and season within zone. Overall, mean ± SE catches trended from 46.3 ± 7.3 in the tidal freshwater zone to 10.8 ± 2.6 in the lower estuary zone, with significantly lower catches near the mouth of the estuary (Figure 4A).

There were significant differences among catches across seasons (Figure 4B), with catches being highest during spring (50.7 ± 6.9), intermediate in summer–fall (21.4 ± 3.6), and lowest during winter (5.9 ± 1.5). Catches by zone varied within seasons (Figure 4C). During winter, abundance was significantly lower in the lower estuary than in the middle estuary or tidal freshwater zones. In spring, catches increased in all zones, but there was a significant gradient of decreasing catch with downstream location. During summer–fall, catches were moderate throughout the tidal gradient but significantly higher in the tidal freshwater zone. Comparing seasons within zones also revealed significant differences (Figure 4D). In the lower estuary, catches were significantly lower in winter than in other seasons, while in the middle estuary, spring catches were significantly larger than those in other seasons. In the tidal freshwater zone, all seasons differed, with spring having the highest and winter the lowest catches.

We found the opposite trend in the mean fork length of subyearling Chinook salmon along the salinity gradient (Figure 5A). Mean ± SE fork length was significantly greater in the lower (85.2 ± 4.2 mm) and middle estuary zones (84.1 ± 3.8 mm) than in the tidal freshwater zone (68.7 ± 2.4 mm). Seasonally (Figure 5B), length was greater in summer–fall (99.5 ± 2.5 mm) than in spring (69.0 ± 1.7 mm) or winter (62.9 ± 5.4 mm). No size differences were found among the three zones in winter, mainly due to high variance (Figure 5C). In spring and summer–fall, salmon at the lower and middle estuary sites were significantly larger than those in the tidal freshwater zone. Significant differences also were found in mean salmon size between seasons within each zone (Figure 5D). In the lower estuary, mean size increased from winter

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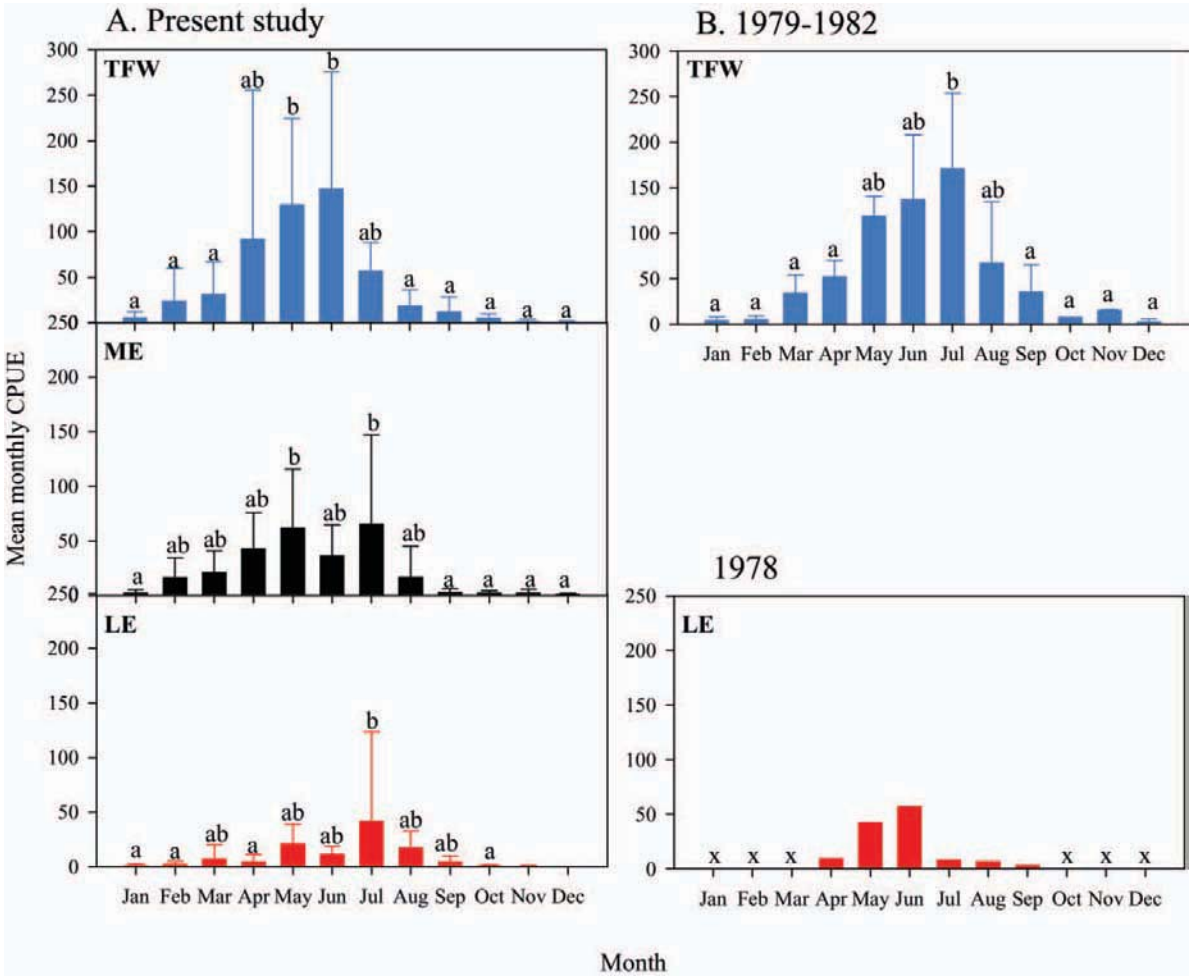


FIGURE 3. Mean monthly CPUE and ANOVA results for subyearling Chinook salmon at tidal freshwater, middle estuary, and lower estuary beach seine sites from **(A)** the present study and **(B)** Dawley et al. (1985) for the years 1979–1982. Within sites, common letters denote groups that are not significantly different. In (B), the lower estuary data were collected for 6 months during 1978. Error bars are SDs.

to summer–fall, while in the other zones fish were significantly larger in summer–fall than in other seasons. The mean size of salmon in the tidal freshwater zone remained near the fry size threshold (60 mm) in both winter and spring.

In all years and zones, subyearling Chinook salmon mean size increased with time (Figure 6). However, the slopes of the regression lines were substantially greater for lower and middle estuary zones than for the tidal freshwater zone. As a result, by the summer–fall season, salmon in tidal freshwater habitats were 20–50 mm smaller than those caught further downstream during the same time period. For example, by November mean fork lengths in the tidal freshwater zone remained <100 mm while

TABLE 1. Numbers (*n*) and proportions of Chinook salmon at different life history stages sampled by beach seine at estuarine and tidal freshwater habitat zones, 2002–2007.

	Tidal freshwater		Middle estuary		Lower estuary		Total	
Life history	*n*	%	*n*	%	*n*	%	*n*	%
Yearling	84	2.9	56	2.5	16	1.4	156	2.5
Fingerling	1,601	55.6	1,640	74.3	939	84.8	4,180	67.5
Fry	1,196	41.5	511	23.2	152	13.7	1,859	30.0
Total	2,881		2,207		1,107		6,195	

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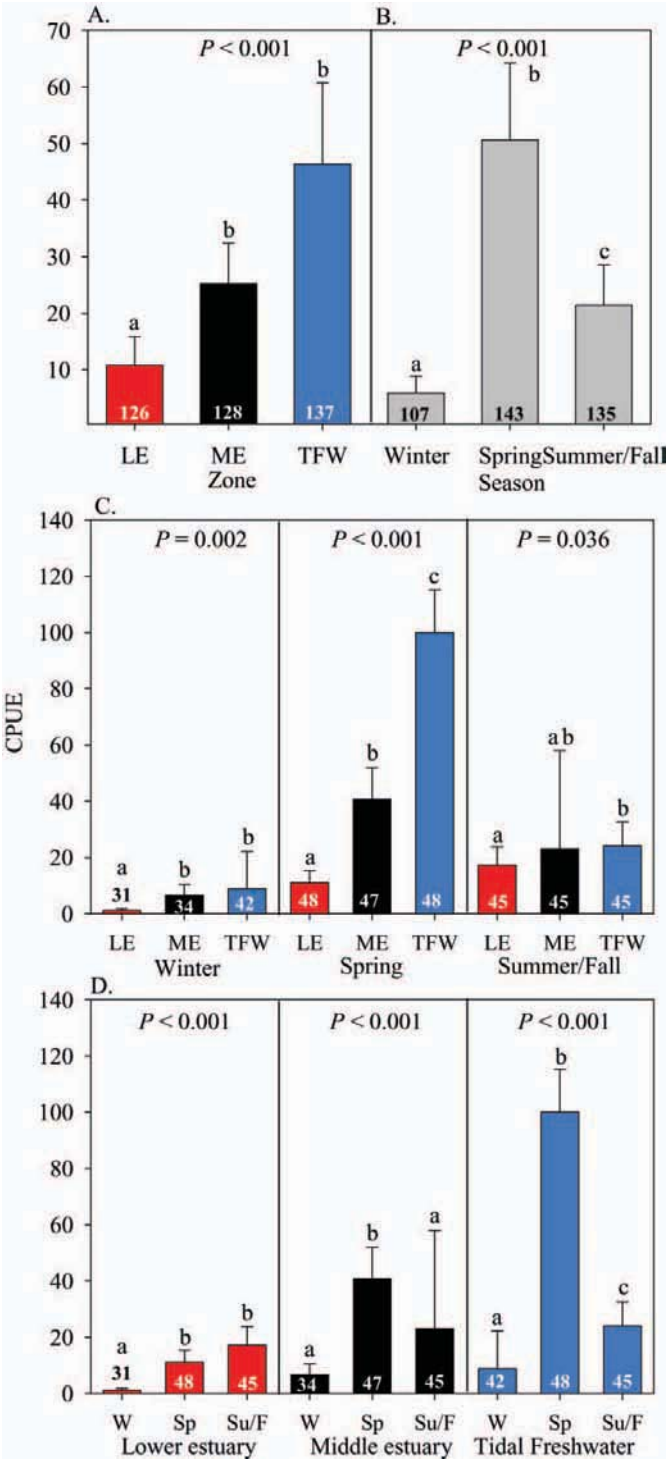


FIGURE 4. Mean CPUE and ANOVA results for subyearling Chinook salmon by **(A)** zone, **(B)** season (winter [W], spring [Sp], or summer–fall [Su/F]), **(C)** zone within season, and **(D)** season within zone. The error bars represent the upper portions of the 95% confidence intervals; within comparisons, common letters denote groups that are not significantly different. The number at the bottom of each bar is the sample size (number of seine hauls).

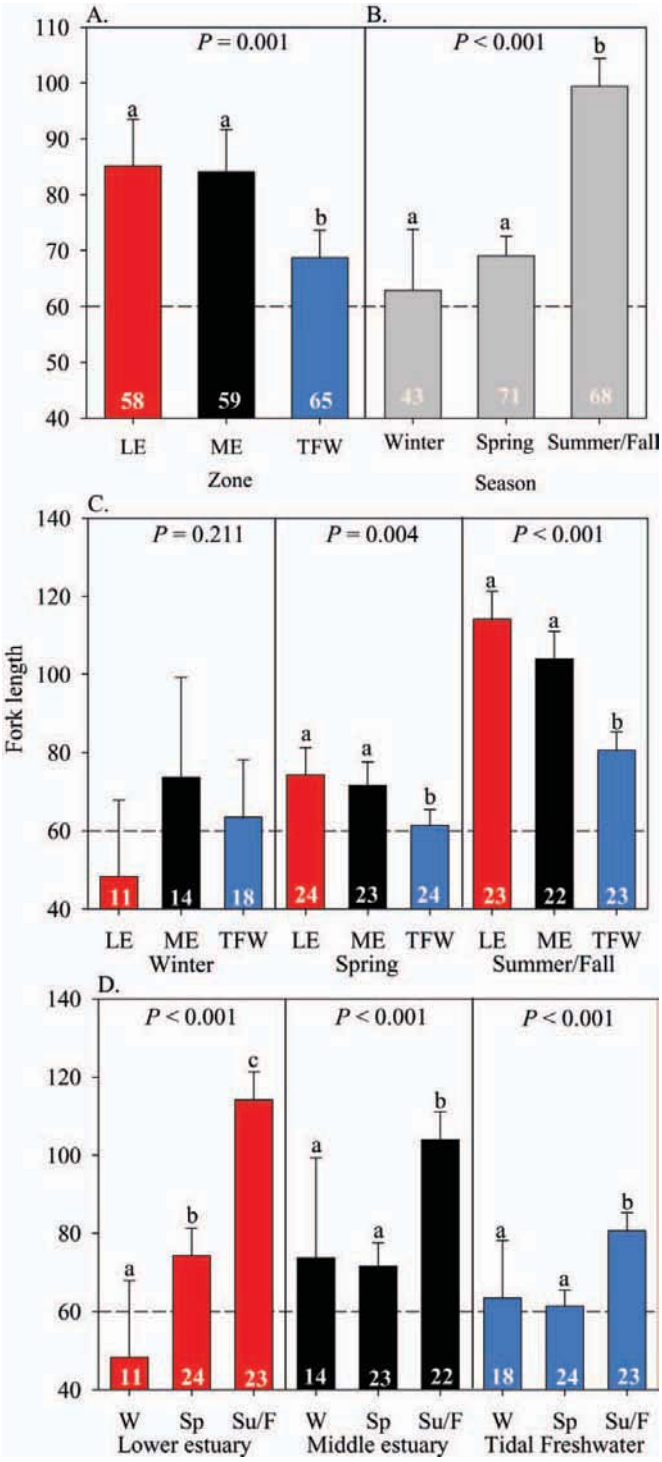


FIGURE 5. Mean fork length and ANOVA results for subyearling Chinook salmon by **(A)** zone, **(B)** season, **(C)** zone within season, and **(D)** season within zone. The dashed lines indicate the 60-mm threshold dividing fry from fingerlings; see Figure 4 for additional information.

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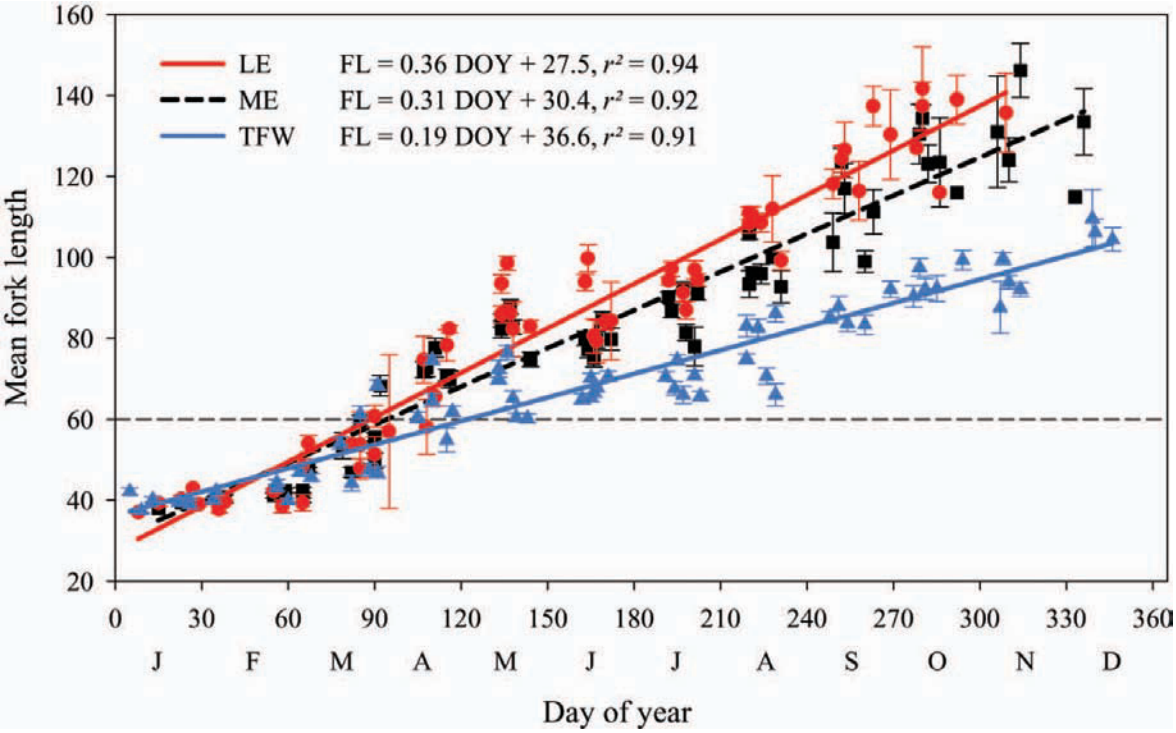


FIGURE 6. Regressions of mean fork length of subyearling Chinook salmon on day of year (DOY) for each zone. The dashed horizontal lines indicate the 60-mm threshold dividing fry from fingerlings. Error bars are SEs.

fish at the lower and middle estuary stations averaged between 120 and 150 mm. Additionally, mean sizes at all sites tended to increase sharply during April through June each year, which may reflect hatchery releases of larger fish (>80 mm fork length).

Distribution of Fry

Thirty percent of all Chinook salmon measured were fry (≤60 mm; Table 1; Figure 2). Fry were present at all sites, and recently emerged individuals (31–45 mm) appeared simultaneously throughout the LCRE in early spring. Fry comprised a relatively high percentage (>25%) of the salmon catch from January through April. The highest overall percentage of fry occurred in the tidal freshwater zone (41.5%), followed by the middle (23.2%) and lower estuary (13.7%) zones (Figure 7).

Based on regression statistics for size at capture (Figure 6), salmon reached the fry-to-fingerling size threshold much earlier at middle and lower estuary sites (31 March and 5 April) than in tidal freshwater areas (3 May). At the tidal freshwater sites, fry in the size range of 40–60 mm were abundant from March to July and were present as late as September. Upper Clifton Channel had the highest overall percent fry abundance (42.2%) and exhibited high mean monthly percentages from January through July, which identified this site as a rearing zone for small fish.

Fewer fry were captured in the middle estuary zone, where they were most abundant from March through June but were present as late as August. The lowest numbers of fry were found in the lower estuary zone, where they were most abundant in March but were largely absent after June. However, the presence of fry at Clatsop Spit at the river mouth indicates the potential for Chinook salmon to enter the ocean with minimal rearing, either in natal streams or the estuary.

Genetic Stock of Origin

Genetic data from 2,174 yearling, fingerling, and fry Chinook salmon collected from 2002 to 2006 were used to estimate genetic stock composition (Table A.2). Of the 11 genetic stock groups identified, eight contributed at least 1% to the samples (Figure 8). However, just two stock groups, the West Cascade tributary fall (51%) and Spring Creek group tule fall (34%), accounted for the majority of the samples. Smaller stock proportions included the upper Columbia River summer–fall (6%), West Cascade tributary spring (3%), Rogue River fall (3%), and Willamette River spring (1%) stocks (Table A.2). Approximately 1% of the juveniles analyzed were from the coastal fall–spring stock group and originated outside the Columbia River basin.

Relatively few yearling Chinook salmon were sampled in our study, and the genetic stock composition estimate was derived from 36 individuals (Figure 8). Of these, 87% were spring-run stocks, with 46% from West Cascade tributaries, 37% from the Willamette River, 3% from the Snake River, and 1% from the mid-Columbia River. Several fall-run stocks also contributed to yearling life-histories; these included the upper Columbia River

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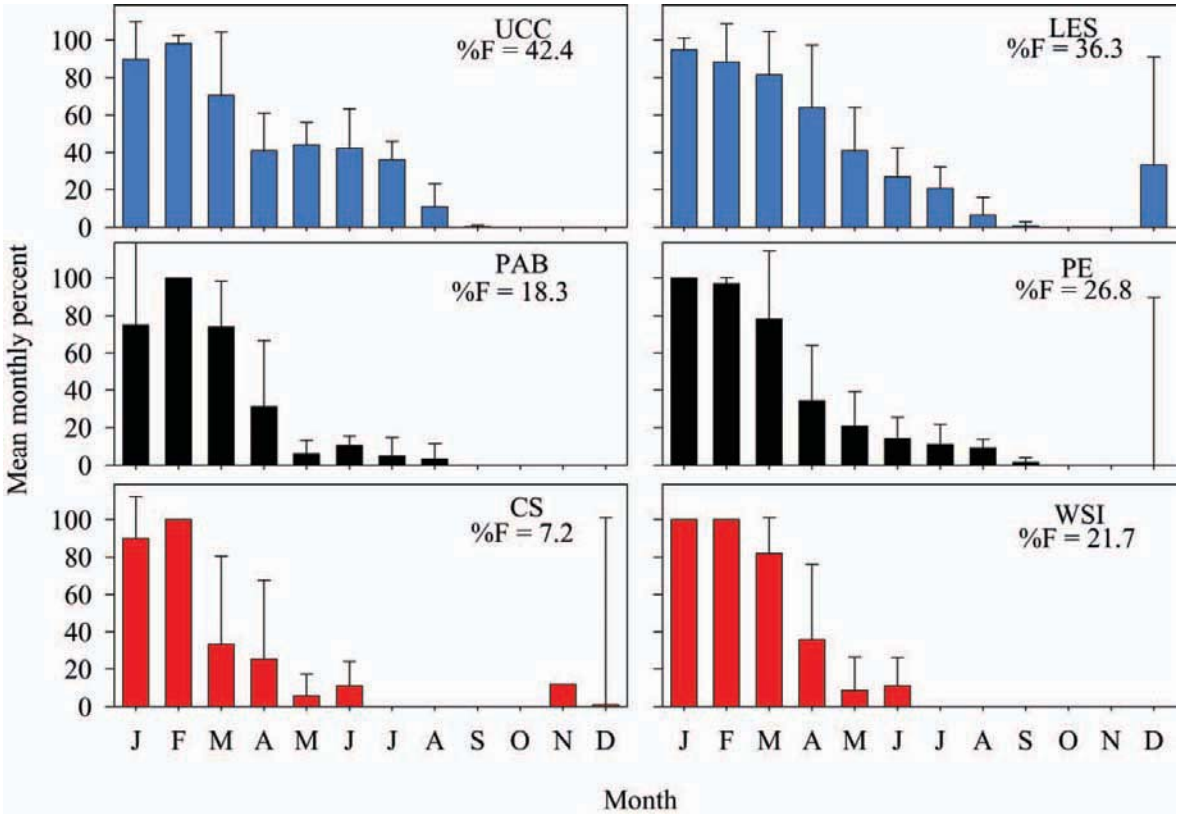


FIGURE 7. Mean monthly percentages (%F) of fry-sized Chinook salmon at tidal freshwater (UCC and LES [see Figure 1]), middle estuary (PAB and PE), and lower estuary beach seine sites (CS and WSI) sites. Error bars are SDs.

summer–fall (6%), Spring Creek group (3%), and West Cascade tributary fall (3%).

We examined the data for patterns of habitat use by life history type and stage, stock, and season by merging size-frequency and genetic data into seasonal categories (Figures 9–11). Even at this broad scale, stock-specific migration windows were observed. Fingerlings were not present during winter. During spring, the Spring Creek group fall stock was predominant among fingerlings, with proportional abundances of 51% in the tidal freshwater, 70% in the middle estuary, and 86% in the lower estuary zones (Figures 9–11). West Cascade Tributary fall fingerlings were the second most abundant stock, with the highest proportion occurring in the tidal freshwater (45%) and the lowest proportion in the lower estuary zone (5%). However, during summer–fall (July–October), the proportion of Spring Creek group fingerlings declined to less than 10% in all regions and West Cascade tributary fall stocks dominated with respective proportional abundances of 83, 62, and 52% in the tidal freshwater, middle estuary, and lower estuary zones.

There were also seasonal differences in the proportional abundance of fingerlings of less dominant stocks. Upper Columbia River summer–fall fingerlings made up a larger proportion in summer–fall than in spring, most notably in the lower estuary zone, where the stock contributed 1% in spring and 20% in summer–fall. Increased contributions of Rogue River fall (11% at middle and 8% at lower estuary sites) and Coastal fall (6% at middle and 4% at lower estuary sites) fingerlings also occurred from the spring to summer–fall periods.

The seasonal stock composition of fry varied somewhat relative to the pattern of fingerlings in the tidal freshwater and middle estuary zones, the only two habitat types for which sufficient samples were collected for analysis (Figures 9–11). Again, the West Cascade tributary fall and Spring Creek group fall were the two dominant stock groups of Chinook salmon fry. However, the Spring Creek group stock played a lesser role in the proportional abundances of fry than of fingerlings, a pattern that was consistent across years (D. Teel, unpublished). At tidal freshwater sites in spring, the Spring Creek group stock accounted for 16% of the catch for fry but 51% for fingerlings, as noted above. Similarly, at middle estuary sites, the Spring Creek group fish contributed 34% to the fry population, but more than double that amount (70%) to fingerling life histories. During summer–fall, the West Cascade tributary fall stock comprised 97% of the fry population at tidal freshwater sites, the only zone where enough samples for analysis were found. The Spring Creek group fall stock contributed the greatest proportion of fry during winter, comprising 40% in the tidal freshwater zone and 75% in the middle estuary zone. These are likely naturally spawned salmon. We also observed small proportions of spring-run stock contributing to fry life history stages (Figures 9–11). The West Cascade tributary spring stock and, to a lesser extent, the Willamette River spring stock fry were present in both winter and spring. The West

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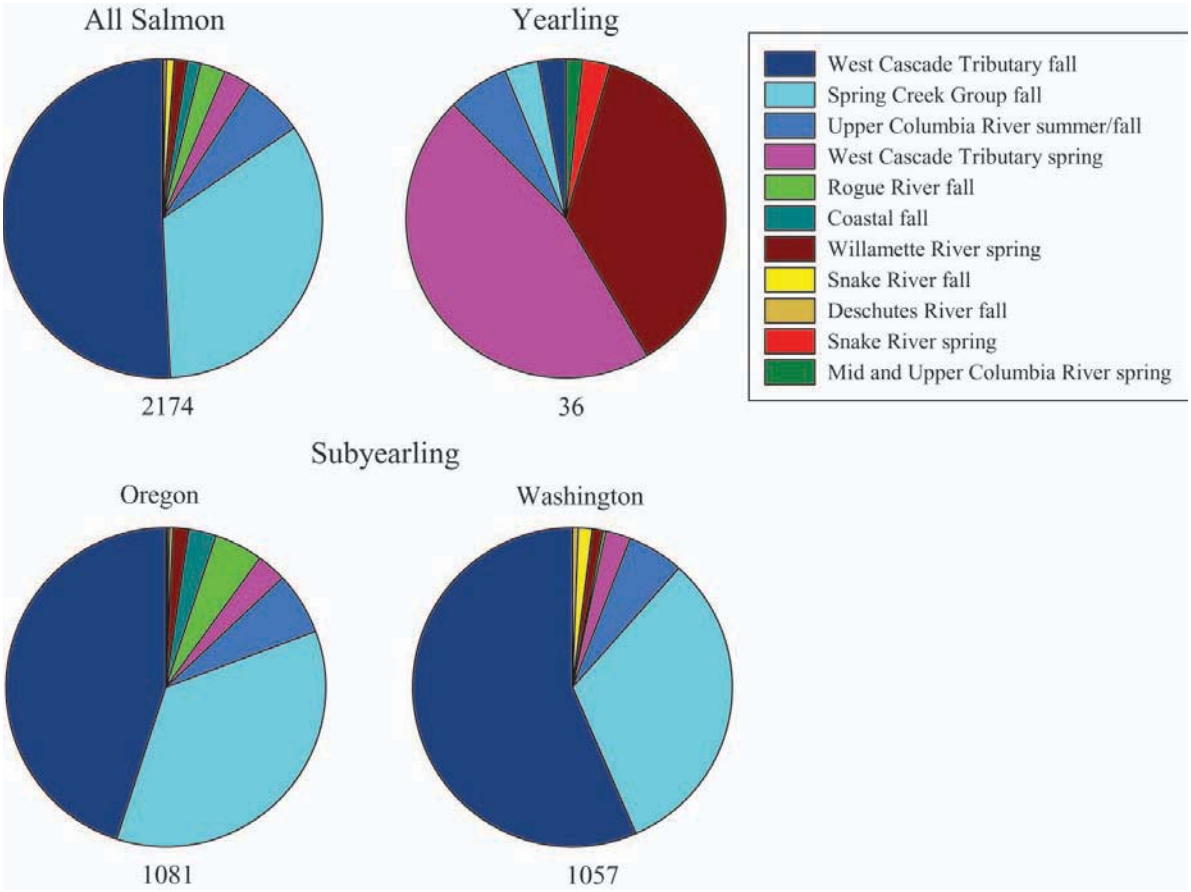


FIGURE 8. Proportional distributions of all Chinook salmon, yearlings, subyearlings from Oregon sites, and subyearlings from Washington sites, by genetic stock of origin.

Cascade tributary spring stock had the greatest contribution (12%) in winter at tidal freshwater sites.

Marks and Tags

Overall, from 2002 to 2007, 16.1% of the Chinook salmon we examined were marked or tagged to indicate a probable hatchery origin. Most marks were adipose fin clips. From 2002 to 2006, 8.0 ± 2.0% of subyearling Chinook salmon were adipose fin clipped (Table 2), but during 2007–2008 this rate increased to 53.2 ± 13.7% (range, 30.1–65.9%). No corresponding difference was observed in the percent of yearling fish that were adipose fin clipped (70.8 ± 7.8 versus 73.7 ± 15.7). We captured only three PIT-tagged fish; two were from lower river tributaries, and the other was a subyearling migrant released from the Snake River 10 km above the confluence with the Clearwater River.

Migration Behavior Inferred from CWTs

From 2002 to 2007, we recaptured 204 Chinook salmon that had been tagged with CWTs. Of these, 143 had retrievable data from which we determined release location and time and calculated migration duration and rate (Figure 12). The release information from the tag codes reflected stock compositions similar to those obtained through genetic analysis. Although our sample size was small, 26 of 30 genetic stock estimates with assignment probabilities of 0.90 or greater agreed with the origins determined using CWTs (Table 3). All coded-wire-tagged fish were hatchery raised except two naturally produced individuals from the Lewis River.

The majority of tagged subyearling Chinook salmon had been released from hatcheries below Bonneville Dam (likely composed predominately of West Cascade tributary fall stock) or from the Spring Creek Hatchery (Spring Creek group fall stock). These catch data again reflected the findings from the genetic analysis. Most tagged yearling Chinook salmon originated in the Kalama and Lewis rivers (West Cascade tributary spring stock) or in the Willamette River (Willamette River spring stock).

The recoveries of tagged fish also reflected some minor stock contributors. For example, three fish originated from hatcheries outside the Columbia River basin: two were from the Nemah River in Willapa Bay, Washington, and one was from the Quinault River on the Washington coast. These catches again agreed with the genetic data and demonstrated that juveniles from coastal fall stocks can migrate into the Columbia River. The

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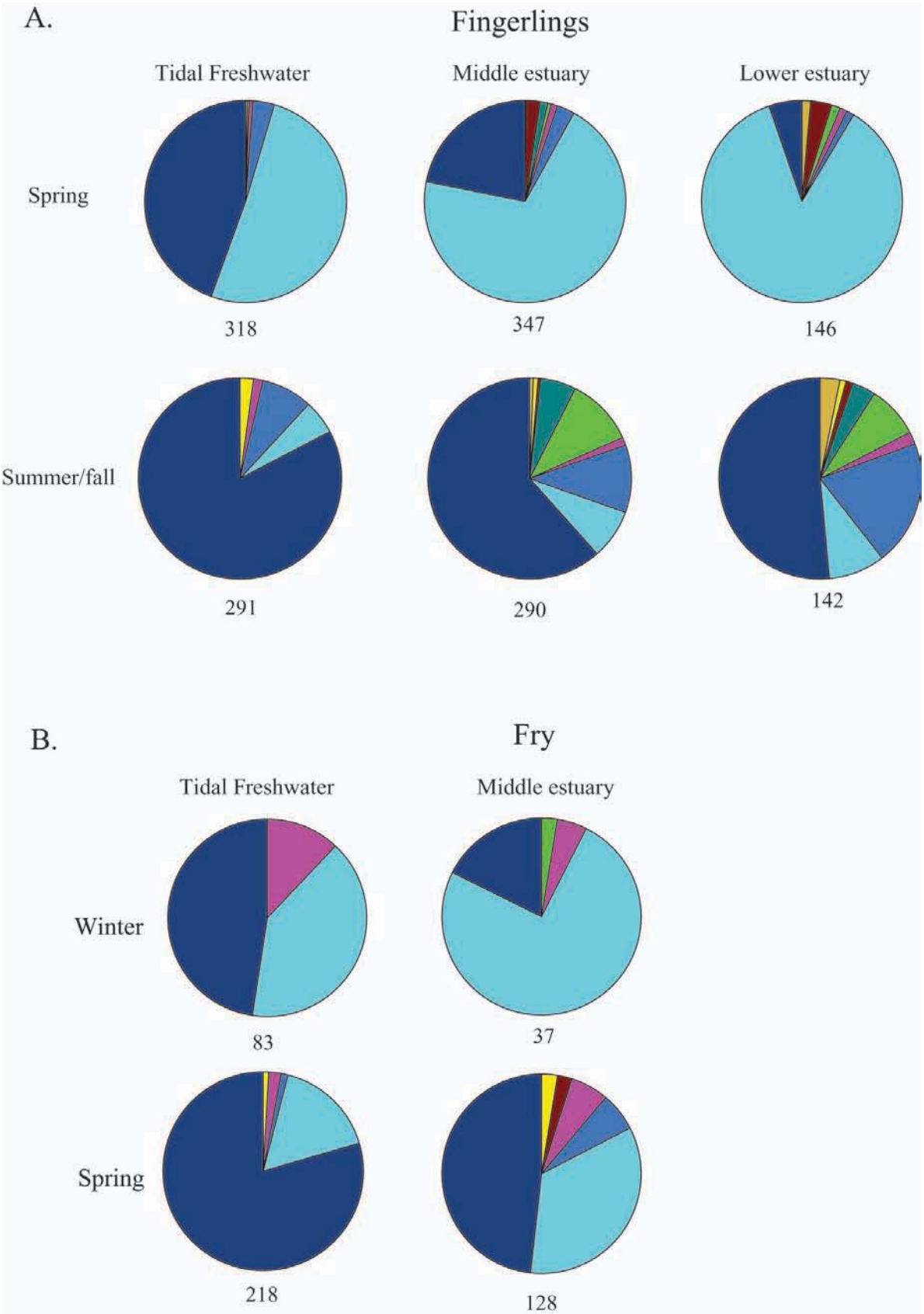


FIGURE 9. Spatiotemporal distributions of **(A)** Chinook salmon fingerlings and **(B)** fry. Too few fry were found in the lower estuary for analysis.

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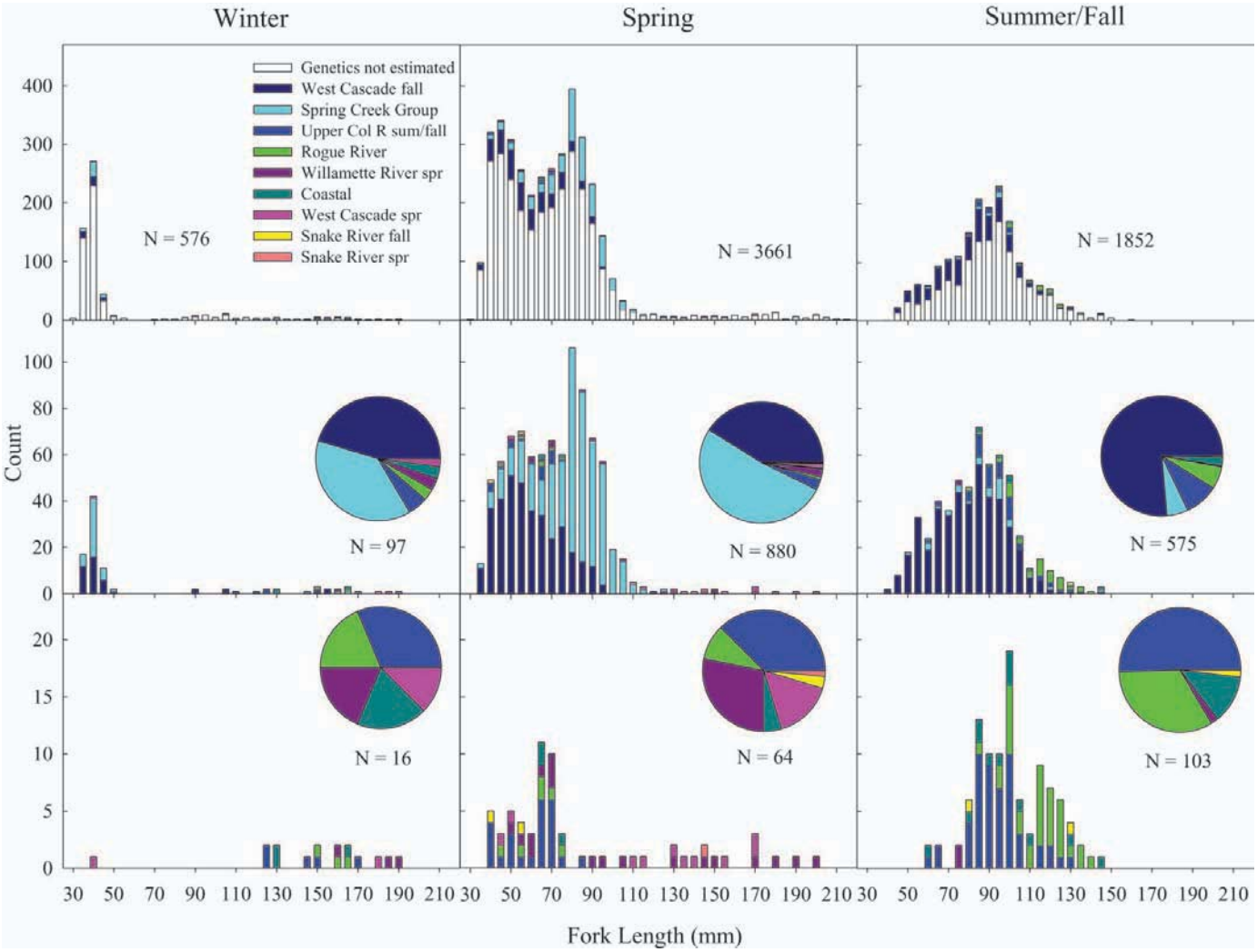


FIGURE 10. Size frequency distributions (bar graphs) and proportional distributions (pie charts) of Chinook salmon sampled from beach seine sites during the winter, spring, and summer–fall seasons, by genetic stock of origin. The upper row shows the distributions of genetically analyzed fish in relation to all measured fish, the middle row the distributions of majority genetic stock contributors, and the bottom row the distributions of minority genetic stock contributors; N = the number of fish evaluated. The data for the plots were restricted to individual fish stock assignments made with at least 0.90 probability.

furthest migrant was a yearling Chinook salmon that had originated in the Tucannon River, Washington (rkm 680), and represented the Snake River spring stock.

Information from the CWTs revealed diverse timing and duration of migration for both the subyearling and yearling life history types (Figure 12; Tables 4, 5). Subyearling recoveries were dominated by releases from the Spring Creek, Big Creek, and Elochoman River hatcheries. Tagged fish were recovered from March through October and were migrating from 1 to 143 d at rates between 0.25 and 42 km/d. Thirteen percent of subyearlings migrated at rates >20 km/d, 28% at rates between 10 and 20 km/d, and 58% at rates <10 km/d. Sixty-eight percent of subyearlings had been migrating for <30 d, 21% between 30 and 60 d, and 11% for >60 d. Fish released from Spring Creek Hatchery exhibited the highest migration rate as well as some of the lowest migration rates, along with fish released from the Kalama and Cowlitz hatcheries. Size at capture was positively related to capture date (Figure 12; linear regression $P < 0.001$; $r^2 = 0.56$). This slope was similar to that derived for fish captured at lower and middle estuary sites (Figure 2). Yearling Chinook salmon with CWTs were present from March through May (Figure 12). Days postrelease ranged from 4 to 52, and migration rates ranged from 2 to 26 km/d; however, most tagged yearling Chinook migrated at rates less than 10 km/d. There was no relation between migration rate and either size at capture or release location (Figure 12).

DISCUSSION

This study identified contemporary spatiotemporal patterns in salmonid species and stock composition, life history type,

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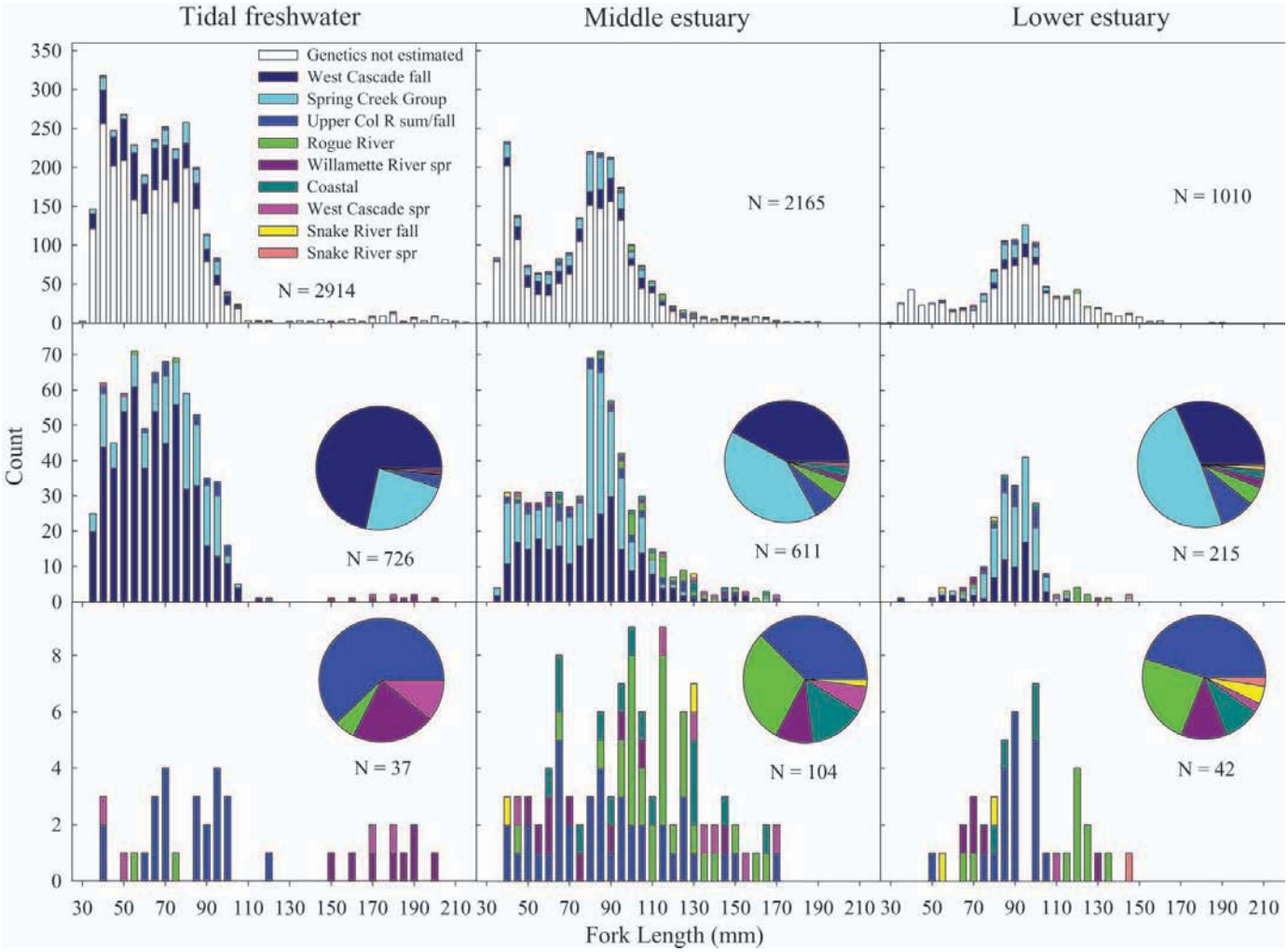


FIGURE 11. Size frequency distributions (bar graphs) and proportional distributions (pie charts) of Chinook salmon, by genetic stock of origin and zone (tidal freshwater, middle estuary, and lower estuary). See Figure 10 for additional information.

and migration behavior at shallow tidal freshwater and estuarine sites in the lower Columbia River and estuary. The predominant species and life history types utilizing the monitored sites were subyearling Chinook and chum salmon. The chum population was composed almost entirely of fry-sized animals and was most prevalent in estuarine sites over a contracted migration period during March–May (Roegner et al. 2008). Few yearling Chinook or other salmon species were present.

Based on size at capture and adipose fin clips, 30% of the Chinook salmon were fry and likely of natural origin, while the remaining 70% were fingerlings and yearlings and probably predominantly of hatchery origin. There were strong spatiotemporal patterns to Chinook salmon life history stages, with smaller fish (and especially fry) being concentrated in the tidal freshwater zone and contemporaneously larger fish at brackish-water sites. Yearling fish were generally present during March–May, while subyearlings were present year-round.

The genetic composition of juvenile salmon in shallow-water habitats of the Columbia River estuary was dominated by fish from the lower Columbia River ESU. Approximately 85% of all fish analyzed were from the West Cascade tributary and Spring Creek group fall Chinook salmon stocks (Figure 8). However, all of the other genetic stock groups in our analysis also contributed 1% or more to our samples grouped by life history type, season, and zone (Table A.2) Coded wire tag information supported the findings from the genetic stock analysis and proved that there is wide variation in migration timing, rate, and duration within and among hatchery releases. This contemporary assessment of juvenile salmon spatiotemporal distribution can help managers to identify which stocks can be expected to benefit from habitat restoration activities in the region.

Spatiotemporal Distribution of Yearling Chinook Salmon

In contrast to studies of deep, midchannel habitats in the Columbia River estuary, which found high proportions of

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TABLE 2. Comparison of adipose-fin-clipped (hatchery) Chinook salmon among sites, measurement periods, and life history types. A much larger marking effort was employed for subyearling fish after 2006.

		2002–2006			2007–2008		
Zone	Site	Total	*n*	(%)	Total	*n*	(%)
				Subyearlings			
Tidal freshwater	Lower Elochoman Slough	1,436	115	8.0	189	99	52.4
	Upper Clifton Channel	1,664	86	5.2	657	198	30.1
Middle estuary	Pt. Adams Beach	1,307	133	10.2	520	320	61.5
	Pt. Ellice	1,043	85	8.2	131	84	64.1
Lower estuary	Clatsop Spit	647	65	10.1	55	25	45.5
	West Sand Island	433	28	6.6	85	56	65.9
Total/mean		6,530	512	8.0 ± 2.0	1637	782	53.2 ± 13.7
				Yearlings			
Tidal freshwater	Lower Elochoman Slough	21	16	76.2	1	1	100.0
	Upper Clifton Channel	60	39	65.0	10	6	60.0
Middle estuary	Pt. Adams Beach	31	21	67.7	0		
	Pt. Ellice	25	19	76.0	8	6	75.0
Lower estuary	Clatsop Spit	10	6	60.0	3	2	66.7
	West Sand Island	5	4	80.0	3	2	66.7
Total/mean		152	105	70.8 ± 7.8	25	17	73.7 ± 15.7

yearling Chinook salmon (Dawley et al. 1986; L. Weitkamp, unpublished), yearlings comprised only 2.5% of the shallow-water population in our study (Figures 2, 9). Yearling abundance was concentrated during March and April, although individual yearling fish were captured at all landscape zones outside these main migration periods. In samples taken during 1977–1983, Dawley et al. (1986) found that yearling migration in the tidal freshwater reach at Jones Beach, Oregon (rkm 75), occurred from February through June, with a consistent peak during May, while the mean size of yearlings decreased with time. Judging by the high proportion of adipose-fin-clipped fish found in our study (Table 2), most yearling fish originated in hatcheries, and the observed abundance patterns were likely due to hatchery releases and smolt transportation practices (Ledgerwood et al. 2005).

Genetic analysis of 36 yearling fish revealed that 83% were spring Chinook salmon from West Cascade tributaries and the Willamette River (Figure 8). Similarly, CWT recoveries from yearling fish indicated that most came from hatcheries between rkm 100 and 200, primarily the Lewis and Kalama Rivers, or else from the Willamette River (Table 5). From CWT data, we found no relation between the number of days postrelease or migration rate and size at capture (Figure 12), although Dawley et al. (1986) found that larger fish tended to migrate faster than smaller fish.

Beeman and Maule (2006) and Tiffan et al. (2009) documented that radio-tagged yearlings moved more quickly in unimpounded sections of the Snake River (63–107 km/d) than in reservoirs (37–39 km/d). Ledgerwood et al. (2005) determined that the migration rate of PIT-tagged yearling Chinook salmon from Bonneville Dam to Jones Beach was related to river flow and averaged around 90 km/d with a travel time of 1.7–2.3 d. These data indicate that yearling fish are capable of rapidly transiting from Bonneville Dam to the ocean. In our study, CWT-derived migration rates ranged from 2.4 to 25.8 km/d, with postrelease periods up to 52 d (Figure 12). Thus, we concluded that while the majority of yearling Chinook salmon move quickly through deep areas of the river inaccessible to beach seines, a proportion of yearlings have a more protracted migration accessing shallow, nearshore habitats and do not travel immediately to the sea.

Subyearlings

Chinook salmon subyearlings were found year-round but were broadly distributed in time from February through August. Mean monthly catches differed between zones (Figure 3), and CPUE was significantly higher in the tidal freshwater zone in all seasons except winter, when catches were low and variable in all zones (Figure 4C). McCabe et al. (1986) found that subyearling Chinook salmon abundance peaked from May to June in estuarine and tidal freshwater sites sampled during 1980 and 1981. From samples collected from 1966 through 1983, Dawley et al. (1986) documented a trend of increasingly later fall Chinook salmon abundance over the years sampled. For a comparison with our data, we calculated monthly mean abundances from weekly catches made by Dawley et al. (1985) at tidal freshwater and lower estuary sites during 1979–1983. This comparison

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TABLE 3. Comparison of genetic stock estimates and origins determined from coded wire tags for 30 hatchery Chinook salmon sampled at estuarine and tidal freshwater habitat zones, 2002–2007. Genetic stock assignments with relative probabilities >0.90 are shown.

	Genetic stock assignments		
Stock determined from tags	Agree (*n*)	Disagree (*n*)	Genetic estimate
Snake River spring–summer	1	0	
Spring Creek group tule fall	14	2	West Cascade tributary fall
Willamette River spring	1	0	
West Cascade tributary spring	3	0	
West Cascade tributary fall	3	2	Spring Creek group tule fall
Rogue River	4	0	
Total	26	4	

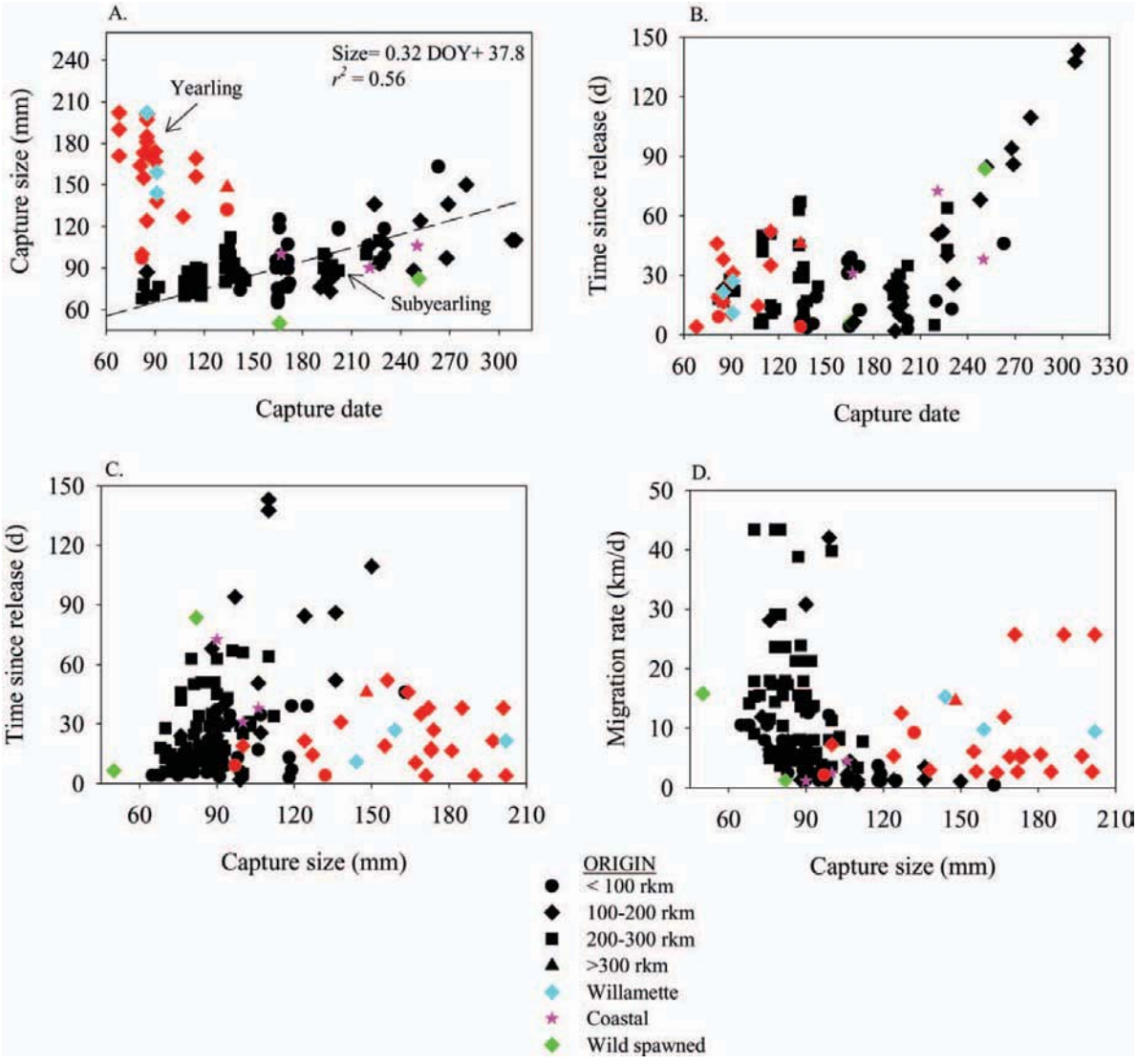


FIGURE 12. Metrics derived from Chinook salmon implanted with coded wire tags, 2002–2008: **(A)** capture size by recovery date (the regression is for subyearling fish), **(B)** days postrelease by capture date, **(C)** days postrelease by capture size, and **(D)** migration rate by capture size. The different symbols denote different release locations. Red symbols pertain to yearlings, black symbols to subyearlings; other colors denote fish of notable origin.

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TABLE 4. Recoveries of coded-wire-tagged subyearling Chinook salmon comparing recapture data from fish in common release groups. Abbreviations are as follows: PAB = Pt. Adams Beach, CS = Clatsop Spit, LES = lower Elochoman Slough, WSI = West Sand Island, PE = Pt. Ellice, ETI = East Tenasillahe Island, UCC = upper Clifton Channel, OR = Oregon, and WA = Washington.

Release location	Release state	Release group	Release date	Capture location	Capture state	Time (d)	Migration (km/d)
Klaskanine River	OR	1	8 May 2005	PAB	OR	13	0.85
				CS	OR	46	0.30
Big Creek	OR	1	2 May 2006	CS	OR	39	1.21
				CS	OR	39	1.21
		2	1 May 2007	PAB	OR	15	2.93
				PAB	OR	15	2.93
		3	7 May 2007	PAB	OR	9	4.89
				PAB	OR	9	4.89
				PAB	OR	9	4.89
				CS	OR	37	1.27
Elochoman River	WA	1	7 Jun 2007	LES	WA	4	10.50
				LES	WA	4	10.50
				LES	WA	4	10.50
				LES	WA	4	10.50
Kalama River	WA	1	18 Jun 2002	ETI	OR	137	0.61
				CS	OR	50	2.26
				WSI	WA	109	1.06
Fallert Creek	WA	1	29 Jun 2006	UCC	OR	68	1.35
				UCC	OR	14	6.57
		2	2 Jul 2007	PAB	OR	15	7.93
				CS	OR	86	1.42
Little White Salmon	OR	1	28 Jun 2007	PAB	OR	19	13.37
				CS	OR	19	13.53
Spring Creek	OR	1	11 Mar 2002	LES	WA	63	3.71
				PE	WA	22	11.59
		2	29 Mar 2002	ETI	OR	63	3.70
				UCC	OR	45	5.18
		3	8 Mar 2003	UCC	OR	66	3.53
				PAB	OR	67	3.88
		4	14 Apr 2003	UCC	OR	29	8.03
				WSI	WA	31	8.55
		5	15 Mar 2005	UCC	OR	13	17.92
				LES	WA	13	18.00
				PAB	OR	11	23.64
				PAB	OR	11	23.64
				UCC	OR	13	17.92
				LES	WA	13	18.00
				PAB	OR	11	23.64
				ETI	OR	13	17.92
				CS	OR	11	23.91
		6	17 Apr 2006	LES	WA	29	8.07
				LES	WA	29	8.07
				LES	WA	29	8.07
		7	5 May 2006	LES	WA	11	21.27
				LES	WA	11	21.27
				LES	WA	11	21.27
				LES	WA	11	21.27

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TABLE 4. Continued.

Release location	Release state	Release group	Release date	Capture location	Capture state	Time (d)	Migration (km/d)
		8	5 Mar 2007	UCC	OR	46	5.07
				PE	WA	18	14.17
		9	9 Mar 2007	UCC	OR	42	5.55
				PAB	OR	17	15.29
		10	12 Apr 2007	PAB	OR	34	7.65
				UCC	OR	8	29.13
				UCC	OR	8	29.13
				WSI	WA	34	7.79
		11	1 May 2007	UCC	OR	17	13.71
				LES	WA	17	13.76

indicated that contemporary abundance patterns appear to have shifted to an earlier peak migration in the tidal freshwater zone, while there is a suggestion of a later migration peak in the lower estuary zone at present (Figure 3). It is uncertain whether these results depict real differences in migration timing (perhaps due to hatchery practices or temperature increases in river water) or simply a higher temporal resolution in the samples of Dawley et al. (1985).

Mean salmon fork length differed significantly among zones, with the smallest mean size being found at tidal freshwater sites and the largest at lower estuary sites (Figure 5). Mean size also increased significantly over time. Regression coefficients implied that size at capture in tidal freshwater regions was half that in the lower estuary zone (Figure 6) and differed as much as 40 mm by late summer. Dawley et al. (1985) and McCabe et al. (1986) also found general increases in mean size over time in subyearling Chinook salmon; however, they found that later-migrating yearling Chinook, coho salmon, and steelhead were generally smaller than earlier migrants. Multiple causes could explain the differences in subyearling size among sites: (1) growth during migration (Healey 1980), (2) higher migration rates of larger subyearlings (Dawley et al. 1986), (3) increased mortality of smaller subyearlings during migration to the estuary (Bottom et al. 2005a), and/or (4) continued input of small subyearlings from different tributary sources (Reimers and Loeffel 1967; Healey 1980). Although the causes of this spatial variation in size cannot be definitively determined with our data, the high percentage and persistence of fry found in the tidal freshwater zone indicates that small fish were intensively utilizing these areas.

From the genetic composition of fingerlings (>60 mm), we observed distinct spatial and seasonal shifts in stock groups that

TABLE 5. Recoveries of coded-wire-tagged yearling Chinook salmon comparing recapture data from fish in common release groups. See Table 4 for additional information.

Release location	Release state	Release group	Release date	Capture location	Capture state	Time (d)	Migration km/d
Fallert Creek	WA	1	3 Mar 2004	UCC	OR	16.5	5.58
				UCC	OR	16.5	5.58
Gobar Creek, Kalama River	WA	1	1 Mar 2004	ETI	OR	21.5	5.40
				ETI	OR	21.5	5.40
		2	1 Mar 2005	PAB	OR	52	2.75
				PAB	OR	27	5.30
		3	1 Mar 2007	PE	WA	19	7.26
				UCC	OR	46	2.52
Lewis River	WA	1	2 Feb 2004	LES	WA	38	2.74
				ETI	OR	38	2.71
				ETI	OR	38	2.71
		2	1 Mar 2005	ETI	OR	4	25.75
				ETI	OR	4	25.75
				ETI	OR	4	25.75

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illustrate varied migration timing and habitat use (Figures 9–11). The Spring Creek group fall fish migrated through the system early in the year, and by summer and fall few of this stock were present at our shallow-water sampling sites. Summer and fall samples were dominated by the West Cascade tributary fall stock group and included increasing proportions of Upper Columbia summer–fall juveniles, particularly in the lower estuary (20% of fingerlings). Similar seasonal shifts in stock composition were observed by Sather et al. (2009), who sampled juvenile Chinook salmon in tidal freshwater habitats near the confluence of the Sandy River (upstream from our study sites) and found that the proportion of fish from upper Columbia and Snake River genetic stock groups increased throughout the migration period and that these groups were predominant in summer and fall. However, more than half of the unmarked juveniles observed by Sather et al. (2009) were stocks from the interior Columbia River basin, a much greater proportion than we observed at our shallow-water sites.

During summer and fall months, fingerlings from several stocks not native to the Columbia River basin were collected in the estuary (Figures 9, 10). The presence of stocks from the Rogue River in southern Oregon is explained by a fishery enhancement program that released these fish into the lower Columbia River (North et al. 2006). Rogue River fish are known to have become naturalized in the Grays River, a tributary that enters along the Washington shore of the upper estuary (Roegner et al. 2010) and have perhaps naturalized elsewhere in the Columbia River basin. While most Rogue River fish were sampled in summer and at sites along the Oregon shoreline and many were marked (indicating that they originated in the enhancement program), others captured in spring prior to the summer releases suggest some contribution from natural production sources. Somewhat surprisingly, we also identified the presence of south Washington–north Oregon coastal fall Chinook salmon juveniles in the estuary during summer and fall (Figures 9, 10). Both CWT recoveries and stock group assignments for fish captured on the Oregon shoreline confirmed that some juvenile Chinook salmon from coastal rivers move from the ocean into the Columbia River estuary.

Coded wire tags confirmed genetic source data, which showed that the fingerlings found in shallow-water habitat were primarily from a variety of lower-river hatchery stocks (Table 3; Figure 12). Analysis of release groups provided evidence of both schooling and wide spatial dispersion, along with variations in migration rate within and between groups (Table 4). Migration rates ranged from <1 to 29 km/d, and many fish from below Bonneville Dam resided for an extended period in the lower river and/or brackish estuary. Thirty-two percent of migrants were captured more than 1 month after release. In comparison, Dawley et al. (1986) found that for marked hatchery fish, migration rates from Jones Beach to the lower estuary ranged from 2 to 59 km/d, and that most marked fall Chinook salmon resided in the estuary for less than 6 d.

Fry

The presence of fish in the 30–40-mm range was generally synchronous across all sample sites in January–March (Figures 2, 7), indicating a rapid dispersion of newly emerged fish from their natal streams, as has been observed elsewhere (e.g., Healey 1980; Bottom et al. 2005a). Fry comprised a high percentage of the catch at most sites from January through April; the proportion of fry diminished at lower and middle estuary sites after April, while remaining relatively high in the tidal freshwater zone until August (Figure 7). Dawley et al. (1985) found the mean size of Chinook subyearling salmon exceeded 60 mm by March of most years in the tidal freshwater zone, whereas regression statistics indicate the contemporary fry threshold in the tidal freshwater zone occurs in late April (Figure 6). This may be a consequence of the higher fry densities found at the semiprotected site at upper Clifton Channel than at the more open area at Jones Beach sampled by Dawley et al. (1985). Volk et al. (2010) found a wide dispersal of fry into estuarine marshes of the Salmon River in spring, and many fish resided in saline waters for weeks or months. In the Columbia system, fry predominate salmon catches in Cathlamet Bay tidal wetlands (Bottom et al. 2008) as well as in newly restored wetlands in the Grays River (Roegner et al. 2010). However, many such estuarine and tidal freshwater marsh habitats presently have limited connectivity to the main-stem Columbia River and without restoration action can no longer serve as nursery areas for small salmon.

Most Chinook salmon fry used in the genetic analysis were sampled from tidal freshwater sites and were identified as belonging to the West Cascade tributary fall stock group in both the spring (78%) and summer–fall (97%) sampling periods (Figures 9, 10). For the latter period, the sources of these fish included cold rivers such as those draining Mt. St. Helens in Washington, where salmon would have later hatch times and reduced growth rates (Reimers and Loeffel 1967; Brannon et al. 2004), and this could explain their small size late in the season. The other tule fall-run stock in our analysis, the Spring Creek group, was also present in spring samples but was largely absent during summer–fall. These seasonal shifts in the proportions of West Cascade tributary fall and Spring Creek group fry were similar to those observed for fingerlings, suggesting that the pattern is not simply a result of hatchery operations but rather reflects natural differences between the stocks in migration and habitat use.

Fry from several other genetic groups also used the shallow estuary beach habitats, including small proportions of Upper Columbia summer–fall and Snake fall stocks during spring. It is especially noteworthy that spring Chinook salmon fry from the West Cascade tributary and Willamette River spring-run stocks were identified in the samples (Figures 9–11). While few in number, these data are consistent with recent evidence of subyearling spring Chinook salmon juveniles rearing in lower Willamette River wetlands during winter and spring (Teel et al. 2009). The new data therefore support earlier observations that

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the life histories of spring Chinook salmon stocks include not only yearlings but fry and fingerling migrants that rear in shallow habitats and enter the ocean as subyearlings (Craig and Townsend 1946; Hymer et al. 1992).

Together, abundance, size, and stock data support the premise that many small juvenile Chinook salmon reside and accumulate in shallow, tidal freshwater sites, with larger fish moving down into the estuary. We note however, that 13.7% of the Chinook salmon measured in the lower estuary zone were fry-sized animals in close proximity to the ocean (Table 1). While the ultimate contribution of fry migrants to adult returns in the Columbia River basin is unknown, Miller et al. (2010) found that 20% of the adult Chinook salmon originating from streams in the Central Valley of California had migrated to saline waters as juveniles at less than 55 mm. Chinook salmon are known to migrate as fry from the Salmon (Bottom et al. 2005a), Sixes (Reimers 1973), and Rogue Rivers (Schluchter and Lichatowich 1977). For comparison, chum salmon are predominantly fry migrants and historically comprised a large biomass of adults returning to the lower Columbia River basin (Johnson et al. 1997). Based on the above examples, one might expect that a fry migrant life history type continues to contribute to Chinook salmon spawner success in the Columbia River basin, especially to the lower-river populations.

Consequences for Restoration

The lower Columbia River and estuary serve as both a migration corridor to the ocean and, for particular stocks, an important habitat for juvenile rearing. In many estuaries, salmon migrating along main-stem sections enter and utilize nonnatal, off-channel, and low-velocity sloughs and wetlands (Murray and Rosenau 1989; Scrivener et al. 1994; Bradford et al. 2001; Baker 2008; Teel et al. 2009; Roegner et al. 2010). The salmon using these habitats are generally, but not exclusively, fry- and fingerling-sized fish. In the CRE, mass hatchery production of large Chinook and coho salmon and steelhead smolts, particularly upper-river spring–summer yearlings, accentuates the contribution of freshwater-rearing phenotypes, which tend to enter the estuary at large sizes and move rapidly to the ocean. The focus of recent hatchery management practices thus belies both historical and recent evidence of protracted use of shallow-water habitats by a variety of salmon species, stocks, and life history stages (Reimers 1973; Healey 1980, 1982; Levy and Northcote 1982; Levings et al. 1986, 1991; Levings 1994; Magnusson and Hilborn 2003; Bottom et al. 2005a; Hering et al. 2010; Roegner et al. 2010).

Restoration projects designed to reestablish habitat opportunity through dike breaches and tide-gate replacements are increasing in the region (LCREP 2011) and have been shown to be used by migrating salmon (Baker 2008; Teel et al. 2009; Roegner et al. 2010). Our study confirmed that subyearling Chinook salmon were prevalent in shallow-water habitats of the LCRE and identified the life history types and genetic stocks expected to be among the primary beneficiaries of restoration activities along the lower-river migration route. Sites further upriver are likely to have a different stock component utilizing shallow-water habitat in those areas (Sather et al. 2009; Teel et al. 2009). Based on size at capture, genetics, marks, and coded wire tags, the majority of these fish were hatchery reared, subyearling, fall-run salmon derived from lower-river sources. However, 11 of the 13 Columbia River stock groups were also represented among the samples collected; moreover, CWT data indicate relatively long migration times for both subyearling and yearling fish and show a protracted residency for a portion of the salmon population. Perhaps most significantly, up to 30% of the Chinook salmon measured in these shallow areas were fry, which we presume were mostly of natural origin and which have an affinity for shallow, low-velocity environments (Healey 1980, 1991).

By combining our spatiotemporal and stock-specific distribution data, managers can predict the windows of opportunity available to salmon migrants at extant and potential rearing habitats. For example, habitat restoration projects to benefit Spring Creek group fry should enhance rearing conditions during spring, when those fry are most abundant. Recovery of Columbia River salmon stocks requires supporting the diversity of life history patterns that historically mitigated for environmental variability (Bottom et al. 2005b; Waples et al. 2009); thus, restoring and preserving habitat formerly available to these various life history types and stages is critical to recovery efforts. Habitat restoration in the lower river and estuary will likely benefit all stocks with populations whose life history patterns utilize shallow-water environments, including those which are at present severely depressed.

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APPENDIX: BASELINE DATA FOR AND RESULTS FROM GENETIC STOCK IDENTIFICATION

TABLE A.1. Chinook salmon populations used as baseline data for genetic stock identification analysis in this study. Genetic stock group, evolutionarily significant unit (ESU), source, run time (Sp = spring, Su = summer, F = fall), and sample size are given. The ESUs (Good et al. 2005) are as follows: 1 = Snake River spring–summer, 2 = Snake River fall, 3 = Middle Columbia River spring, 4 = upper Columbia River spring, 5 = upper Columbia River summer–fall, 6 = Deschutes River, 7 = lower Columbia River, 8 = upper Willamette River, 9 = southern Oregon and northern California coastal, 10 = Washington coast, and 11 = Oregon coast. Populations with asterisks are outside the geographic boundary of the given ESU but are included in the stock group based on genetic similarity. Genetic data are from Seeb et al. (2007) except where noted.

Genetic stock group (ESU)	Source population(s)	Run time	Sample size
Snake River spring–summer (1)	Imnaha River	Summer	144
	Minam River	Spring	144
	Rapid River Hatchery	Spring	144
	Secesh River	Summer	144
	Tucannon River[a]	Spring	136
	Tucannon Hatchery	Spring	42
	Newsome Creek[b]	Spring	95
	West Fork Yankee Creek[b]	Spring	60
Snake River fall (2)	Lyons Ferry Hatchery	Fall	186
Mid and upper Columbia River spring (3, 4)	Carson Hatchery*	Spring	144
	John Day River	Spring	143
	Upper Yakima River	Spring	199
	Warm Springs Hatchery	Spring	143
	Wenatchee River	Spring	62
	Wenatchee Hatchery[a]	Spring	49
Upper Columbia River summer–fall (5)	Hanford Reach	Fall	284
	Methow River	Summer	143
	Wells Hatchery	Summer	144
	Wenatchee River[a]	Summer	135
Deschutes River fall (6)	Lower Deschutes River	Fall	144
	Upper Deschutes River[c]	Fall	144
Spring Creek group tule fall (7)	Spring Creek Hatchery	Fall	144
	Big Creek Hatchery[d]	Fall	99
	Elochoman River[d]	Fall	95
	Willamette River*[d]	Fall	46
Willamette River spring (8)	North Fork Clackamas River*[d]	Spring	80
	North Santiam Hatchery	Spring	143
	North Santiam River[d]	Spring	96
	Mckenzie Hatchery	Spring	142
	Mckenzie River[d]	Spring	98
West Cascade tributary spring (7)	Cowlitz Hatchery	Spring	140
	Kalama Hatchery	Spring	144
	Lewis Hatchery	Spring	144
West Cascade tributary fall (7)	Cowlitz Hatchery	Fall	140
	Lewis River	Fall	93
	Sandy River	Fall	124
Rogue River (9)	Cole Rivers Hatchery	Spring	142
	Applegate River	Fall	143

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TABLE A.1. Continued.

Genetic stock group (ESU)	Source population(s)	Run time	Sample size
Washington and Oregon coastal (10, 11)	Forks Creek Hatchery[a]	Fall	142
	Humptulips Hatchery[a]	Fall	83
	Necanicum River[e]	Fall	77
	Nehalem River[e]	Fall	151
	Kilchis River[e]	Fall	58
	Wilson River[e]	Fall	139
	Trask River[e]	Fall	162

[a]S. Blankenship, Washington Department of Fish and Wildlife, unpublished data.
[b]Narum et al. (2007).
[c]Narum et al. (2010).
[d]D. Teel, Northwest Fisheries Science Center, unpublished data.
[e]R. Bellinger, Oregon State University, unpublished data.

TABLE A.2. Sample sizes and estimated proportional composition of the 11 genetic stock groups observed in samples of yearling, fingerling, and fry-sized Chinook salmon in the Columbia River estuary, 2002–2006. The range below each estimate is the 95% confidence interval derived from 100 bootstrap resamplings of the baseline and mixed-stock genotypes. Abbreviations are as follows: TFW = tidal freshwater, ME = middle estuary, and LE = lower estuary.

		Proportional stock composition (%)										
Estuary sample zone	*N*	West Cascade tributary		Willamette River spring	Spring Creek group fall	Deschutes River fall	Mid- and upper Columbia River spring	Upper Columbia summer–fall	Snake River		Rogue River fall	Coast fall–spring
		Fall	Spring						Fall	Spring		
All samples, all seasons												
All zones	2,138	0.508	0.028	0.013	0.338	0.003	0.000	0.062	0.008	0.001	0.025	0.014
		0.468–0.551	0.028–0.066	0.008–0.019	0.259–0.333	0.000–0.011	0.000–0.002	0.051–0.081	0.002–0.022	0.000–0.003	0.017–0.032	0.009–0.021
All yearlings, all seasons												
All zones	36	0.028	0.462	0.371	0.034	0.000	0.017	0.062	0.000	0.028	0.000	0.000
		0.000–0.186	0.188–0.593	0.231–0.496	0.000–0.109	0.000–0.061	0.000–0.083	0.000–0.157	0.000–0.028	0.000–0.111	0.000–0.000	0.000–0.000
Fingerlings, spring												
TFW	318	0.445	0.006	0.000	0.509	0.003	0.000	0.034	0.000	0.000	0.003	0.000
		0.361–0.497	0.003–0.086	0.000–0.009	0.398–0.531	0.000–0.017	0.000–0.004	0.018–0.071	0.000–0.018	0.000–0.000	0.000–0.011	0.000–0.009
ME	347	0.217	0.010	0.022	0.697	0.002	0.000	0.028	0.000	0.005	0.006	0.012
		0.178–0.302	0.000–0.060	0.009–0.041	0.598–0.711	0.000–0.013	0.000–0.011	0.012–0.046	0.000–0.009	0.000–0.011	0.000–0.019	0.001–0.029
LE	146	0.053	0.012	0.034	0.862	0.014	0.000	0.012	0.000	0.000	0.014	0.000
		0.034–0.166	0.000–0.035	0.007–0.055	0.729–0.882	0.000–0.034	0.000–0.007	0.000–0.044	0.000–0.021	0.000–0.007	0.000–0.028	0.000–0.000
Fingerlings, summer–fall												
TFW	291	0.827	0.015	0.000	0.055	0.000	0.000	0.082	0.022	0.000	0.000	0.000
		0.733–0.844	0.010–0.074	0.000–0.002	0.022–0.093	0.000–0.023	0.000–0.007	0.054–0.124	0.000–0.051	0.000–0.000	0.000–0.009	0.000–0.013
LE	290	0.616	0.013	0.004	0.080	0.006	0.000	0.107	0.008	0.000	0.109	0.057
		0.497–0.657	0.008–0.073	0.000–0.012	0.021–0.101	0.000–0.034	0.000–0.003	0.063–0.145	0.000–0.043	0.000–0.010	0.071–0.146	0.033–0.094
ME	142	0.516	0.020	0.011	0.091	0.032	0.000	0.200	0.010	0.000	0.084	0.038
		0.404–0.592	0.000–0.074	0.000–0.038	0.022–0.134	0.000–0.079	0.000–0.010	0.118–0.267	0.000–0.048	0.000–0.000	0.033–0.113	0.014–0.101
Fry, spring												
TFW	218	0.787	0.020	0.000	0.163	0.000	0.000	0.011	0.009	0.000	0.004	0.005
		0.698–0.850	0.008–0.082	0.000–0.009	0.070–0.201	0.000–0.018	0.000–0.000	0.004–0.070	0.000–0.025	0.000–0.007	0.000–0.015	0.000–0.022
ME	128	0.479	0.062	0.023	0.341	0.000	0.000	0.062	0.026	0.000	0.008	0.000
		0.343–0.597	0.026–0.144	0.006–0.047	0.199–0.378	0.000–0.033	0.000–0.000	0.011–0.129	0.000–0.067	0.000–0.000	0.000–0.023	0.000–0.022
Fry, summer–fall												
TFW	57	0.971	0.000	0.000	0.027	0.000	0.000	0.000	0.000	0.000	0.001	0.000
		0.815–0.988	0.000–0.097	0.000–0.000	0.000–0.084	0.000–0.018	0.000–0.000	0.000–0.017	0.000–0.043	0.000–0.000	0.000–0.068	0.000–0.000
Fry, winter												
TFW	83	0.472	0.120	0.008	0.400	0.000	0.000	0.000	0.000	0.000	0.000	0.000
		0.340–0.688	0.048–0.278	0.000–0.055	0.175–0.491	0.000–0.000	0.000–0.000	0.000–0.022	0.000–0.019	0.000–0.000	0.000–0.015	0.000–0.024
ME	37	0.177	0.049	0.000	0.748	0.000	0.000	0.000	0.000	0.000	0.026	0.000
		0.101–0.546	0.000–0.196	0.000–0.018	0.364–0.771	0.000–0.000	0.000–0.000	0.000–0.086	0.000–0.000	0.000–0.000	0.000–0.054	0.000–0.000

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