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## ARTICLE

# Stock-Specific Size and Timing at Ocean Entry of Columbia River Juvenile Chinook Salmon and Steelhead: Implications for Early Ocean Growth

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## Abstract

**Juvenile salmon transitioning from freshwater to marine environments experience high variation in growth and survival, yet the specific causes of this variation are poorly understood. Size at and timing of ocean entry may contribute to this variation because they influence both the availability of prey and vulnerability to predators. To**

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explore this issue, we used stock assignments based on genetic stock identification and internal tags to document the stock-specific size and timing of juvenile hatchery and presumed wild Columbia River Chinook Salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* at ocean entry during 2007–2011. We found that juvenile salmon and steelhead had consistent stock-specific capture dates, with lower-river stocks typically having earlier timing than those originating farther upstream. Mean size also varied among stocks and was related to hatchery practices. Hatchery yearling Chinook Salmon and steelhead were consistently larger than wild fish from the same stocks, although timing in the estuary was similar. In contrast, hatchery subyearling Chinook Salmon were of similar size to wild fish but entered the ocean up to a month earlier. We evaluated the potential importance of these traits on early marine growth by estimating stock-specific growth rates for Chinook Salmon caught in estuarine and ocean habitats. Growth rates were related to relative ocean entry timing, with lower growth rates for stocks that had only recently arrived in marine waters. Our results demonstrate that stocks within a single basin can differ in their size and timing of ocean entry, life history traits that contribute to early marine growth and potentially to the survival of juvenile salmon. Our results also highlight the necessity of considering stock-specific variation in life history traits to understand salmon ecology and survival across the entire life cycle.

The movement of juvenile salmon from freshwater to marine habitats is a poorly understood but critical transition (Pearcy 1992; Percy and McKinnell 2007). During this transition, fish must not only physiologically adapt to salt water, but also contend with entirely new prey, predators, and habitats (Spence and Hall 2010). The size at and timing of ocean entry have been identified as important factors during this period. Minor variation in timing can have major consequences for survival (Holtby et al. 1990; Scheuerell et al. 2009; Chittenden et al. 2010; Beamish et al. 2013), while size affects growth and survival via vulnerability to predators and the availability of appropriately sized prey (Ivlev 1961; Mittelbach and Persson 1998). Several recent studies of Pacific salmon *Oncorhynchus* spp. have shown that individuals that survive to adulthood were often larger than average as juveniles (Beamish et al. 2004; Zabel and Achord 2004; Moss et al. 2005; Claiborne et al. 2011; Thompson and Beauchamp 2014), and growth rates during initial marine residence are often correlated with survival in both Atlantic Salmon *Salmo salar* and Pacific salmon (Holtby et al. 1990; Jonsson et al. 2003; Miller et al. 2014) and marine fish in general (Sogard 1997). However, while variation in timing and size at ocean entry is well documented between species or populations occupying independent river basins (e.g., Groot and Margolis 1991; Quinn 2005; Spence and Hall 2010), far less is known about the variation among populations within basins that enter the ocean at a common location (Beamish et al. 2013).

A first step to understanding the influence of size and timing of ocean entry is to document whether these traits vary between stocks, species, or production types (hatchery versus wild) occupying common environments. The Columbia River basin is ideal for this because its ecologically diverse subbasins support numerous populations of Chinook Salmon *O. tshawytscha* and steelhead *O. mykiss* (hereafter referred to collectively as “salmon”) that are genetically and phenotypically distinct yet that all enter the ocean at a common location (Rich 1920; Busby et al. 1996; Waples et al. 2004). Although a variety of factors likely influence migration timing (Whalen et al. 1999; Beckman et al. 2000; Achord et al. 2007; Sykes et al.

2009), our fundamental hypothesis was that ocean entry timing would largely be a function of distance to the ocean, i.e., that stocks lower in the basin (closer to the ocean) would enter the ocean earlier than those farther upstream.

The Columbia River also provides an opportunity to document differences between hatchery and wild salmon because of its extensive hatchery production and—in sharp contrast—numerous wild populations that receive protection under the U.S. Endangered Species Act (ESA). Approximately 140 million hatchery salmon are released into the basin each year (Fish Passage Center Web site [www.fpc.org]), while five evolutionarily significant units (ESUs) of Chinook Salmon and five distinct population segments (DPSs) of steelhead are listed under the ESA (Table 1), in large part because of severely depressed population sizes (Ford 2011). We expected that juvenile hatchery salmon would be larger than wild fish, as has been shown in many studies (Quinn 2005; Tatara and Berejikian 2012). However, very little is known about differences in ocean timing between hatchery and wild stocks. We also expected that wild fish would have more variable timing than hatchery fish (Teel et al. 2014) because wild fish respond to environmental cues to initiate migration (Beckman et al. 2000) whereas the downstream movements of hatchery fish are restricted by hatchery release dates. However, it is uncertain whether hatchery fish would tend to have earlier or later timing than wild fish.

While documenting stock-specific variation in the size and timing of hatchery and wild salmon at ocean entry is important to understand the estuarine and marine ecology of salmon, it also provides insight into other processes that may affect depressed wild populations. In particular, there are concerns about potential behavioral interactions between hatchery and wild fish in estuarine or marine habitats where populations that are segregated in freshwater may co-occur (Naish et al. 2008; Rand et al. 2012). The extent of such spatial and temporal overlap and potential size differences between hatchery and wild fish has not been well documented in the Columbia River estuary. In addition, far more is known about hatchery than wild salmon in the Columbia River because of their

TABLE 1. Columbia River evolutionarily significant units (ESUs) for Chinook Salmon and distinct population segments (DPSs) for steelhead as well as genetic stocks and typical hatchery smolt ages (years) for the juvenile salmon used in the analysis. In the first column, the stock's status under the federal Endangered Species Act is indicated by the following abbreviations: N = not warranted, T = threatened, and E = endangered.

ESU/DPS (status)	Genetic stock	Smolt age (years)
<b>Chinook Salmon</b>		
Lower Columbia River (T)	West Cascade, fall	0
	West Cascade, spring	1
	Spring Creek Group, fall	0
Mid Columbia River, spring (N)	Mid Columbia River, spring	1
Upper Columbia River, spring (E)	Upper Columbia River, spring	1
Upper Columbia River, summer/fall (N)	Upper Columbia River, summer	0, 1
	Upper Columbia River, fall	0
Snake River, fall (T)	Snake River, fall	0, 1
Snake River, spring/summer (T)	Snake River, summer	1
	Snake River, spring	1
Upper Willamette River (T)	Willamette River, spring	1
<b>Steelhead</b>		
Lower Columbia River (T)	Lower Columbia River, summer–winter	1–3
Mid Columbia River (T)	Mid Columbia River, summer–winter	1–3
Upper Columbia River (T)	Upper Columbia River, summer	1–3
Snake River (T)	Snake River, summer	1–3
Upper Willamette River (T)	Upper Willamette River, winter	1–3

numerical dominance as both out-migrating juveniles (e.g., Roegner et al. 2012; Weitkamp et al. 2012) and returning adults (NRC 1996; Fish Passage Center Web site). Consequently, it is unclear whether the life history traits documented for hatchery fish can serve as valid proxies for those of relatively scarce wild fish.

In this article we document stock-specific variation in size and timing of ocean entry for juvenile hatchery and presumed wild Chinook Salmon and steelhead in the Columbia River estuary, one of the first studies of its kind in a large river basin. We also use data from sampling these same stocks in marine waters to examine the influence of timing on ocean growth. Despite numerous anthropogenic alterations to both salmon and salmon habitats throughout the Columbia River basin (NRC 1996; Williams 2006), our results show that there is variation between stocks and production types that is associated with growth opportunities in marine waters.

## METHODS

Our primary objective was to determine whether there were differences in the size and date of capture of different groups of juvenile salmon caught in the Columbia River estuary immediately before ocean entry. These groups included both different stocks (defined by geographic origin, genetic distinctiveness, and life history type) and production types (known hatchery versus presumed wild). A secondary objective was to estimate early ocean growth rates for the Chinook Salmon stocks based on differences in size and timing among the

individuals collected in the estuary and those collected during our ocean surveys.

## Collection of Fish

The juvenile salmon used in this analysis came from two studies conducted by NOAA Fisheries' Northwest Fisheries Science Center and Oregon State University during 2007–2011. The objective of both studies was to sample juvenile Columbia River salmon, either in the open waters of the lower Columbia River estuary or in marine waters off the Washington and Oregon coasts. We considered the fish collected by the estuary study to represent fish at ocean entry because the study area is close to the mouth of the Columbia River (a passive particle released at the site would exit the estuary within 3 h during a typical ebb tide). Our methodologies are described in detail in Weitkamp et al. (2012) for the estuary study and Teel et al. (2015) for the ocean study and summarized here.

In the Columbia River estuary, juvenile salmon were sampled during daylight hours at two stations, North Channel (46°14.2'N, 123°54.2'W) and Trestle Bay (46°12.9'N, 123°57.7'W) (Figure 1). These stations are located in the lower estuary 17 and 13 km, respectively, from the river's entrance (rkm 0 is the seaward end of the jetties) and adjacent to the deep north and south channels of the lower estuary. Sampling was conducted every 2 weeks from mid-April until late June or early July during 2007–2011. In 2007 and 2008 we also made a single sampling trip in September, while in

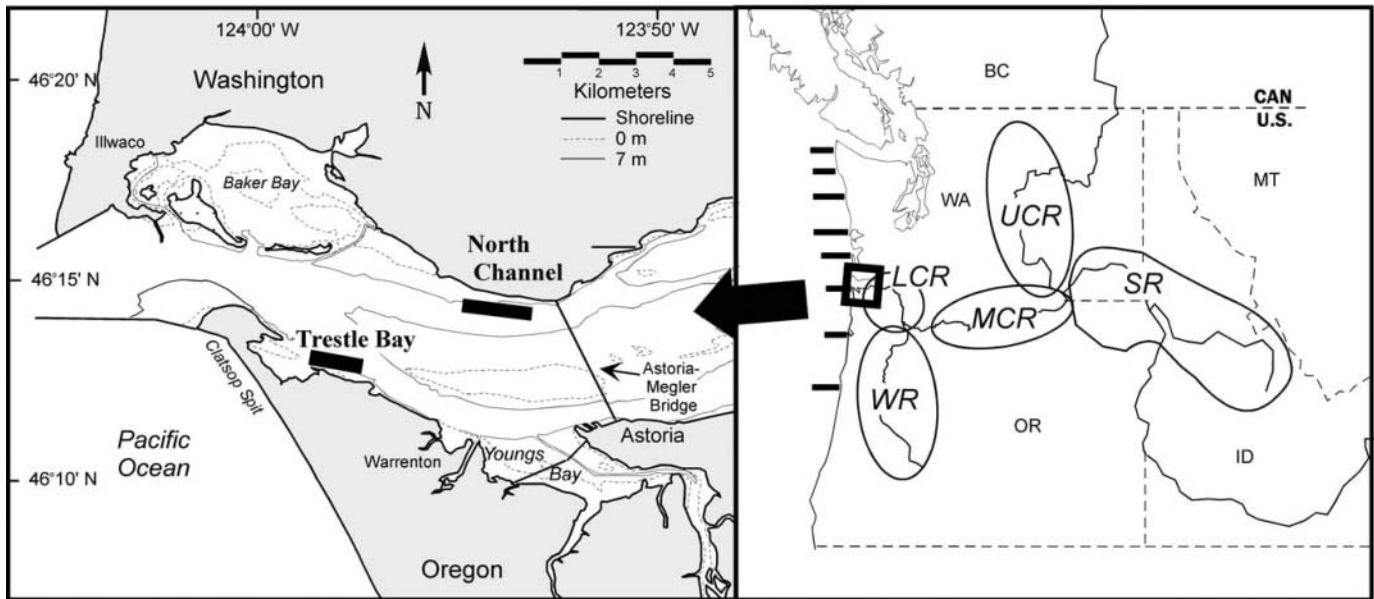


FIGURE 1. Maps showing the locations of the two sampling stations (North Channel and Trestle Bay) in the lower Columbia River estuary (left panel) and the ocean sampling transects (black horizontal lines) and freshwater regions (circles or polygons) within the Columbia River basin (right panel). Region abbreviations are as follows: LCR = Lower Columbia River, WR = Willamette River, MCR = Mid Columbia River, UCR = Upper Columbia River, and SR = Snake River.

2009–2011 we sampled at roughly monthly intervals during July–October.

Estuarine sampling used a fine-mesh purse seine (10.6 m deep  $\times$  155 m long; stretched mesh opening, 1.7 cm; knotless bunt mesh, 1.5 cm) set in water 8–10 m deep. All of the juvenile salmon captured were kept in running water until processed, then anesthetized with MS-222, identified to species, and measured (FL [mm]). The fish were checked for the presence of internal tags (passive integrated transponder [PIT] tags and coded wire tags [CWTs]) and fin clips, which are indicative of hatchery origin (see below). We randomly collected (i.e., lethally sampled) 50 individuals each of juvenile steelhead and yearling (age-1) and subyearling (age-0) Chinook Salmon on each cruise. These fish were given a lethal dose of MS-222, processed as above, individually labeled and bagged, and then frozen. Juvenile salmon that were not needed for laboratory analyses were allowed to fully recover and then released. In some cases (e.g., steelhead caught in 2007 and 2008), fin clips were collected from fish prior to release for genetic analysis; these tissues were immediately placed in labeled containers filled with 95% ethanol.

In marine waters, juvenile salmon were caught with a pelagic rope trawl along a series of seven or eight east-west-oriented transects from 48°14'N (Cape Flattery, Washington) to 44°40'N (Newport, Oregon; Figure 1) in late May, late June, and late September. Each transect had 6–7 stations where fishing was conducted with a Nordic 264 rope trawl (mouth opening, 30 m wide  $\times$  20 m high). The trawl was towed at the surface at 6 km/h for 30 min at each station, sampling approximately 3 km or 90,000 m<sup>2</sup> of water. The ship-board processing of the juvenile salmon collected in marine

waters was similar to that of fish collected in the estuary: all salmon were identified to species, measured (FL [mm]), checked for fin clips, individually labeled and bagged, and immediately frozen.

In the laboratory, we reconfirmed the species of the fish from both studies, remeasured them (FL and total wet weight [g]), and rechecked them for tags and clipped fins. Fin tissue was collected for genetic stock identification (GSI) analysis and placed in 95% ethanol. Snouts were removed from fish with CWTs (see below), and PIT tags were read electronically.

### Stock Assignments

Our analysis was restricted to juvenile salmon for which we were able to identify the stock. Stock information came from GSI analysis and PIT or CWT tags. The genetic stocks for both Chinook Salmon and steelhead correspond to ESUs and DPSs, respectively (Busby et al. 1996; Myers et al. 1998; Table 1); by definition, each represents an important component of the evolutionary legacy of the species (Waples 1991). We also caught large numbers Coho Salmon *O. kisutch*, but their limited genetic population structure in the Columbia River does not allow for the genetic differentiation of stocks (Van Doornik et al. 2007) and too few tagged fish were available for analysis.

Our GSI analysis used microsatellite DNA loci and standard DNA preparation techniques (e.g., Teel et al. 2014). We used 13 loci described by Seeb et al. (2007) for Chinook Salmon and the 13 described by Blankenship et al. (2011) for steelhead. Individual fish were assigned to regional genetic stocks using the likelihood model of Rannala and Mountain

(1997) as implemented in the GSI computer program ONCOR (Kalinowski et al. 2007). The origins of the Chinook Salmon sampled in the estuary were estimated using genetic stocks described by Teel et al. (2014), while the genetic baseline for the ocean-caught Chinook Salmon included the same baseline supplemented with populations ranging from California to southern British Columbia (Teel et al. 2015). Genetic stock assignment of the steelhead sampled in the estuary was made using baseline population data reported by Stephenson et al. (2009) and Blankenship et al. (2011). Steelhead caught in marine waters were not genetically analyzed because regional standardized DNA baselines do not exist at present (D. M. Van Doornik, unpublished data).

For both the Chinook Salmon and steelhead, we used probabilities of 0.8 or greater to assign individual fish to a genetic stock. Comparisons of our genetic estimates with the known origins (from internal tags) of 536 Chinook Salmon and 62 steelhead indicated that this restriction resulted in correct assignments for 85.3% of the Chinook Salmon and 97.8% of the steelhead (the tags were assumed to be correct; L. Weitkamp, unpublished data).

We also used information available for fish tagged with CWTs or PIT tags to determine stock, production type (hatchery or wild; see the next section), and Chinook Salmon age. For these fish, the tags were extracted, the codes were read, and release information was downloaded from the appropriate online database: the Regional Mark Information System for CWTs (Pacific States Marine Fisheries Commission [www.rmpc.org]) or the PIT Tag Information System for PIT tags (Pacific States Marine Fisheries Commission [www.ptagis.org]). Release information included the hatchery, stock, release location, run timing, production type, release size, and release date. This information was used to assign tagged fish to a genetic stock using the criteria provided by Fisher et al. (2014).

### Size-Based Age Designations

Juvenile Chinook Salmon enter marine waters as either sub-yearling (age-0) or yearling (age-1) smolts. These two age-classes are associated with specific life history types (Healey 1983, 1991). In the Columbia River basin, spring runs of Chinook Salmon typically have yearling smolts, fall runs have subyearling smolts, and summer runs can have subyearling or yearling smolts (Waples et al. 2004; the terms “spring,” “summer,” and “fall” refer to the season in which adults return to freshwater). However, hatchery practices have allowed the production of smolts outside the typical smolt age (e.g., fall Chinook Salmon released as yearlings).

Juvenile Chinook Salmon were assigned to age categories based on their length. In the estuary the cutoff length ranged from 115 mm in April to 140 mm on July 1, while the cutoff used in ocean collections ranged from 120 mm in May to 250 mm in September. These cutoffs were derived from (1) seasonally adjusted length frequency histograms, (2) known

ages based on scale analysis, and (3) known ages determined from PIT tags or CWTs (Percy and Fisher 1990; Fisher and Percy 1995; Weitkamp, unpublished data; J. Fisher, Oregon State University, unpublished data).

The validity of this age assignment was confirmed by stock-specific plots of fish size versus capture date, which typically indicated a clear separation between yearling and subyearling individuals in both estuarine and marine environments. However, several small unclipped (presumed wild) mid and upper Columbia River and Snake River spring Chinook Salmon caught in the estuary were reassigned as yearlings due to a continuous size distribution (i.e., no obvious size break between small and large individuals) and timing identical to that for larger individuals (i.e., much earlier than that of individuals identified as subyearlings from these stocks). In contrast, several yearling-sized hatchery Spring Creek Group fall Chinook Salmon were known to be subyearlings (from CWTs) and formed a continuous size distribution within this stock. Accordingly, all Spring Creek Group fish caught in the estuary were assigned as subyearlings, as were those less than 300 mm caught in marine waters. These changes involved age reassignments of only small numbers of Chinook Salmon (<3%).

It should be noted that Columbia River steelhead also exhibit variation in smolt age, with hatchery fish typically being released as yearlings (Fish Passage Center Web site) and wild steelhead smolting after 1–3 years in freshwater (Busby et al. 1996). Unlike with Chinook Salmon, however, this age difference is not associated with other life history traits (Busby et al. 1996), so the steelhead in our study were not segregated by age.

### Production Types

We determined production type—hatchery or presumed wild—based on both external marks and information from internal tags. Mass-marking programs in the Columbia River externally mark most (>75%) hatchery fish by clipping their adipose fins (Regional Mark Processing Center; Table A.1.1 in the appendix to this article). However, because large numbers of unmarked hatchery fish are released each year, fish with unclipped adipose fins may be either unmarked hatchery fish or wild fish. We were able to determine production type (largely hatchery) for unclipped fish with internal tags (PIT or CWT) from release information, although most unclipped juvenile salmon were not tagged. Consequently, our analysis relies on comparisons between two production types of fish: known hatchery and a combination of wild and unclipped hatchery fish (hereafter referred to as “unclipped” fish).

### Data Analysis

*Size and capture date in the Columbia River estuary.*—For our primary analysis, we compared the size (length and weight) and date at capture in the estuary for yearling and

subyearling Chinook Salmon and steelhead by stock, production type, and year. Comparisons of body shape (condition factor) between stocks and production types did not show consistent differences and are not provided here (Weitkamp, unpublished data). Due to changes in sampling effort during the summer months, comparisons of subyearling Chinook Salmon size and timing were restricted to the years 2009–2011.

We modeled differences in length and weight by year, stock, and production type using Bayesian multilevel models (Gelman and Hill 2006). This provides ANOVA-like results while allowing for nonconstant variance and random effects. When modeled as a random effect, a category's batch of parameters (e.g., means for each stock) are allowed to have different values but are assumed to come from a common normal distribution (with estimated mean and standard deviation). This tends to shrink the individual estimates toward the overall mean, with more shrinkage being applied to individual estimates further from the overall mean and/or with higher uncertainty. This is referred to as partial pooling and provides a compromise between complete pooling across a category (e.g., assuming that groups are equal and combining all stocks into a single group) and making independent estimates for each group.

The models for each species and age-class included all main effects (year, stock, and production type) and all two- and three-way interactions. Within-group variance was assumed to be equal across groups except for subyearling Chinook Salmon length and weight, where the variance varied visibly by stock and was therefore allowed to vary by stock. The group means for production type were modeled independently (i.e., no partial pooling) since there were only two categories (hatchery and unclipped).

The fish sampled in this study do not represent random samples from the populations of interest due to the constraints of this type of sampling. However, the regular timing of the sampling events likely produced samples that were approximately representative of the larger population. For the lengths and weights, the variability within sampling events was large relative to the differences between adjacent sampling events. Therefore, ignoring the discrete-sampling-event structure (a violation of the assumption of independence) is unlikely to have had a large effect on the results.

However, in the timing data all of the arrival times are exactly the same within each event. This introduces a strong violation of the assumption of independence. In addition, any changes in the spacing of the sampling events (as occurred later in the season) or truncation of the season (e.g., for yearling Chinook Salmon) could introduce substantial bias. Migration timing for groups of fish was therefore modeled by summing the total number of fish within the group for the individual biweekly sampling events and modeling these counts using a smooth function that increased and then decreased as a function of the day of the year. Specifically, we used the normal density function in which the date of predicted highest

abundance (the mean) was modeled like length, with all main effects and two- and three-way interactions being included. The standard deviation (which controls the width of the normal density function) was modeled in the same way as the mean.

Individual models for length, weight, and timing were fit to each species and age-class (yearling and subyearling Chinook Salmon and steelhead). As an overall model summary, we plotted the variance components associated with the different main effects and interactions. This is comparable to conducting a classic analysis of variance (ANOVA) while taking advantage of partial pooling (Gelman 2005; Gelman and Hill 2006). We also plotted the main effects along with their 95% credible intervals (similar to confidence intervals; Gelman et al. 2013). The group-specific 95% credible intervals are also superimposed on plots of the data. We focus on the overall and relative magnitudes of the differences and their biological relevance as opposed to significance tests, as it is unlikely that any two groups would be exactly equal. For specific comparisons we report the mean difference and the 95% credible interval. For other comparisons, nonoverlapping credible intervals serve as an approximate (conservative) test of the difference between two groups.

A complete description of the models, the method of fitting them, and the approaches used to assess model fit are described in Appendix A.2.

*Ocean growth rates.*—We estimated growth rates during the first weeks or months in marine waters by comparing the mean size and timing of fish from each stock caught in the estuary with those caught in marine waters during our ocean surveys. This analysis was restricted to hatchery fish due to the small numbers of unclipped fish caught in both environments. Ocean growth rates were estimated both across all years (to provide robust sample sizes) and by year for years in which at least five fish from a stock were caught in both estuarine and marine waters. As the two growth rates were highly correlated (Spearman correlation:  $r > 0.9$ ,  $P < 0.05$ ), annual growth rates averaged across years are provided (the standard deviations reflect the interannual variation). Too few steelhead of known origin (from tags) were caught in marine waters to estimate growth rates.

Early ocean growth rates estimated from changes in length ( $G_L$  [mm/d]) were calculated as

$$G_L = (L_o - L_e)/(t_o - t_e),$$

where  $L_o$  is the mean fork length in the ocean at mean recovery time  $t_o$  and  $L_e$  is the mean length in the estuary at recovery time  $t_e$ . Because changes in weight typically assume an exponential rather than a linear form (Ricker 1975), instantaneous changes in weight ( $G_W$  [ $g \cdot g^{-1} \cdot d^{-1}$ ]) were calculated as

$$G_W = [\ln(W_o) - \ln(W_e)]/(t_o - t_e),$$

where  $W_o$  is the mean weight in the ocean at mean recovery time  $t_o$  and  $W_e$  is the mean weight in the estuary at recovery time  $t_e$ . We expressed  $G_w$  as percent body weight per day (% BW/d) by taking the antilog and multiplying it by 100.

Many juvenile salmon were still being caught in the estuary during the ocean surveys. To minimize the influence of possible size differences between early- and late-migrating fish within a stock, we restricted estimates of  $L_e$  and  $W_e$  to fish caught in the estuary before the 20th of each month in the estuary surveys because the mean start dates for the ocean surveys were May 22 (range, May 19–24), June 21 (range, June 20–23), and September 22 (range, September 20–23), respectively.

## RESULTS

### Available Data

We had information on the time and length at capture for 724 yearling and 1,289 subyearling Chinook Salmon and 641 steelhead of known origin that were collected in the lower Columbia River estuary during 2007–2011. These fish belonged to 5 different stocks of steelhead and 11 stocks of Chinook Salmon (Table 1). The totals represent stock information provided by 604 CWTs and 58 PIT tags. Chinook Salmon stocks that were abundant in the estuary were then compared with the same groups collected in marine waters, specifically 1,668 yearling and 664 subyearling Chinook Salmon.

### Stock-Specific Size and Timing in the Estuary

We observed considerable variation in the size and timing of juvenile salmon in the Columbia River estuary. These differences were generally largest among stocks, with occasional large differences between production types and in almost all cases much smaller differences among years (Figure 2). The variances associated with the length and weight residuals were higher than those of any factor, indicating high within-stock variation (Figure 2). Yearling Chinook Salmon and steelhead originating from lower-river locations generally had earlier timing than those from upper-river locations. In contrast, the timing of subyearling Chinook Salmon was related to hatchery release timing and was more variable between hatchery and unclipped fish (Figures 3–5). The length and weight data showed comparable patterns (see Appendix A.2 for the weight data).

**Steelhead.**—The estimated peak arrival date of juvenile steelhead in the estuary varied primarily by stock, with the two stocks originating closest to the river's mouth (the lower Columbia and Willamette River stocks) arriving several days earlier than other stocks (Figure 3). There was some evidence of slightly earlier arrival times for hatchery fish, but this varied by stock and year. Length varied primarily by stock and origin (Figure 2), with the lower Columbia River steelhead being

more than 10 mm shorter than the other stocks (Figure 3) and hatchery fish an estimated 25 mm longer (95% CI = 18–31 mm) than unclipped fish.

**Yearling Chinook Salmon.**—The timing of yearling Chinook Salmon varied primarily by stock and to a lesser degree by year (Figure 2), with the estimated peak arrival date for the Willamette River spring stock being 30 d earlier (95% CI = 19–41 d) than that for the upper Columbia River summer–fall stock (Figure 4). Length varied most by stock and production type, with the Snake River spring and mid and upper Columbia River spring stocks being 10–20 mm shorter than the other stocks. The estimated average length of hatchery fish was 11 mm longer (95% CI = 5–16 mm) than that of unclipped fish. However, this result was driven primarily by the mid and upper Columbia River spring stock, since the other stocks had very few unclipped fish (Figure 4).

**Subyearling Chinook Salmon.**—The timing of subyearling Chinook Salmon varied by stock and to a lesser extent by production type (Figure 2). The estimated peak arrival date for the earliest-arriving stock (the Spring Creek Group fall stock) was 89 d earlier (95% CI = 64–126 d) than that for the latest stock (the west Cascade fall stock; Figure 5). The estimated peak arrival date for hatchery fish was on average 22 d earlier than that for wild fish (95% CI = 8–37 d). Length varied by stock, following the same pattern as peak arrival date (i.e., stocks with smaller fish arrived earlier). The Spring Creek Group fall stock was estimated to be 30 mm shorter (95% CI = 22–38 mm) than the west Cascade fall stock (Figure 5).

### Early Ocean Growth Rates

Juvenile salmon from stocks that had been in the ocean more than a few weeks had higher growth rates than those that had just arrived in marine waters. This pattern was consistent across the yearling and subyearling Chinook Salmon age-classes.

**Yearling Chinook Salmon.**—Willamette River and west Cascade spring Chinook Salmon had the earliest capture dates in the estuary (Figure 4) and the highest estimated growth rates ( $\geq 1.6$  mm/d,  $> 3.6\%$  BW/d) when captured in the ocean in late May, 3–4 weeks after ocean entry (Figure 6). In contrast, the growth rates estimated for later-migrating stocks were much lower ( $\leq 1.1$  mm/d,  $\leq 2.9\%$  BW/d) by the May ocean surveys, consistent with their recent arrival ( $\sim 2.5$  weeks) in marine waters. By the June surveys, however, the growth rates of both early- and late-migrating stocks were similar (Figure 6), reflecting an extended residence ( $\geq 4$  weeks) in marine waters for all stocks.

**Subyearling Chinook Salmon.**—The relationship between time of ocean entry and growth rate for subyearling Chinook Salmon followed the same pattern as for yearling Chinook Salmon (i.e., at the time of ocean sampling, earlier migrants had grown more than later migrants). The early-migrating Spring Creek Group fall and Snake River fall Chinook Salmon stocks were the only subyearling stocks caught in sufficient



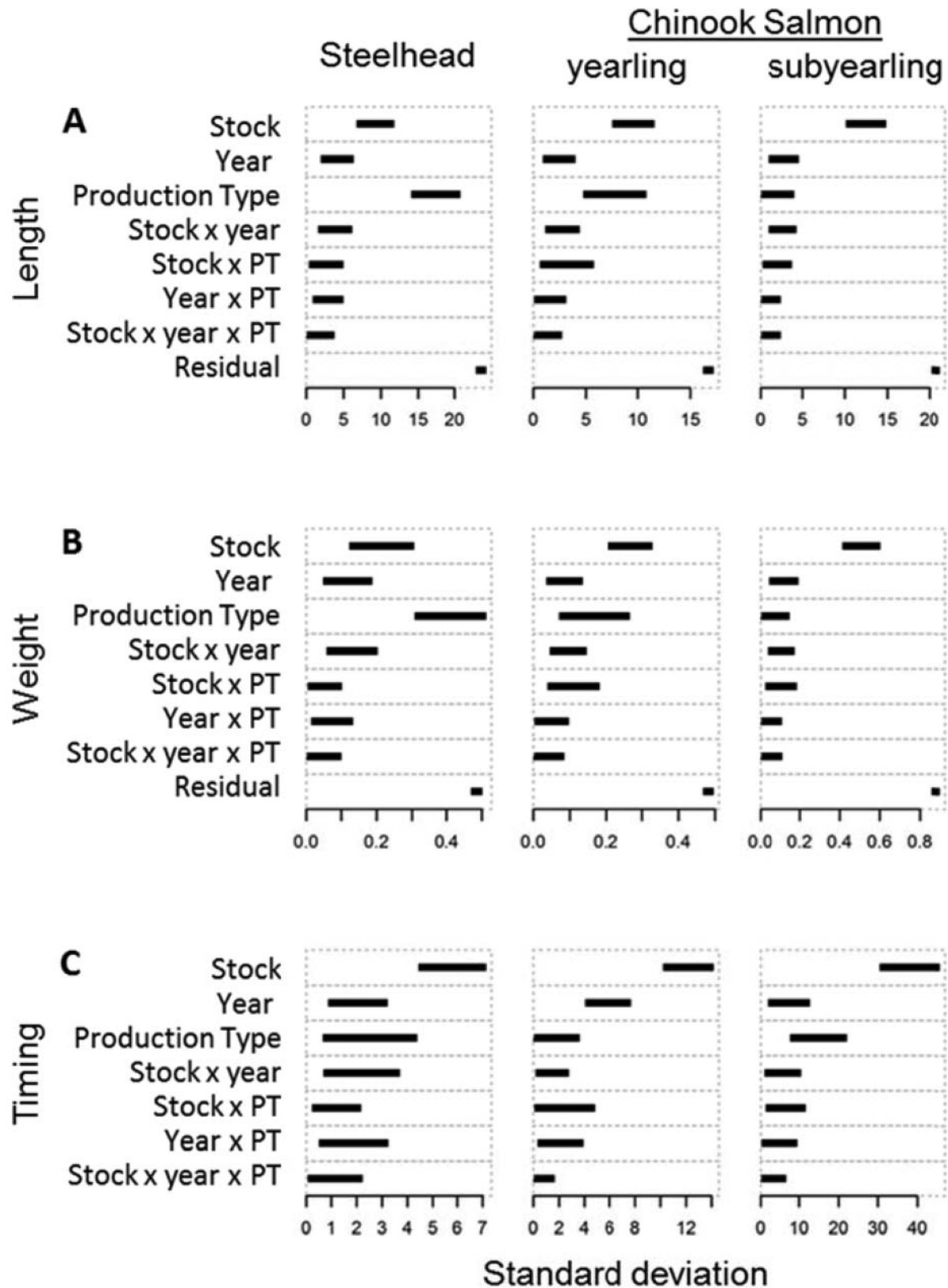


FIGURE 2. Summary of the variance components for each model (rows) for the three species and/or age groups of juvenile salmonids (columns) from analyses of (A) length, (B) weight, and (C) timing of ocean entry using Bayesian multilevel models. The bars represent 80% credible intervals for the estimated standard deviations between groups for the main effects (stock, year, and production type [PT, i.e., hatchery or unclipped {presumed wild} fish]) and their interactions. Due to the highly unbalanced data, this variation does not indicate the degree of variability explained.

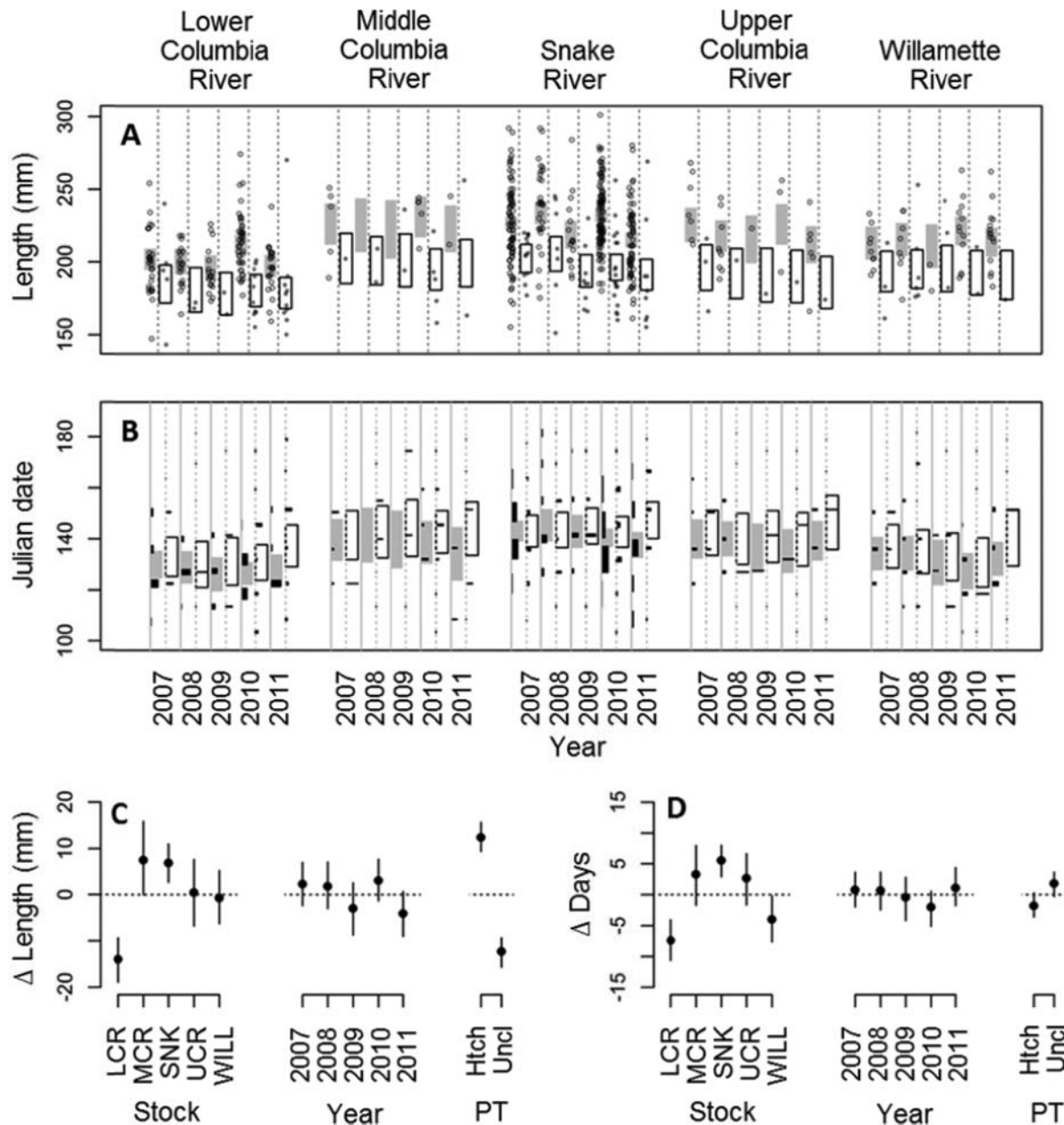


FIGURE 3. Comparisons of mean length and date at capture in the estuary for juvenile steelhead by stock, production type, and year. Panels (A) and (B) show plots of mean length and peak migration date, with model-based 95% credible intervals. The dots indicate individual fish. Gray bars and gray dots represent hatchery fish, open bars and black dots represent uncollected fish. Panels (C) and (D) pertain to the main effects for length and timing. The points are the estimated deviations from the mean for each level of the main effect, and the vertical lines are the corresponding 95% credible intervals. The stock abbreviations are as follows: LCR = lower Columbia River, MCR = mid Columbia River, SNK = Snake River, UCR = upper Columbia River, and WILL = Willamette River. The production type (PT) abbreviations are as follows: Htch = hatchery and Uncl = uncollected.

numbers during the June ocean survey to estimate growth, at which time Spring Creek Group fish had higher growth rates (1.0 mm/d, 2.6% BW/d) than Snake River fall Chinook Salmon (0.1 mm/d, 0.3% BW/d; Figure 7), consistent with the former's approximately 2-week-earlier timing (Figure 5). By the September ocean surveys, however, juveniles from all sub-yearling stocks had been in marine waters for at least 1 month; at that time the estimated growth rates were fairly similar (0.8–

1.1 mm/d, 2.1–2.6% BW/d) among stocks (Figure 7) despite the fact that the average dates of ocean entry varied by nearly 90 d (Figure 5).

## DISCUSSION

We have demonstrated that there are stock-specific differences in the size at and timing of ocean entry for juvenile

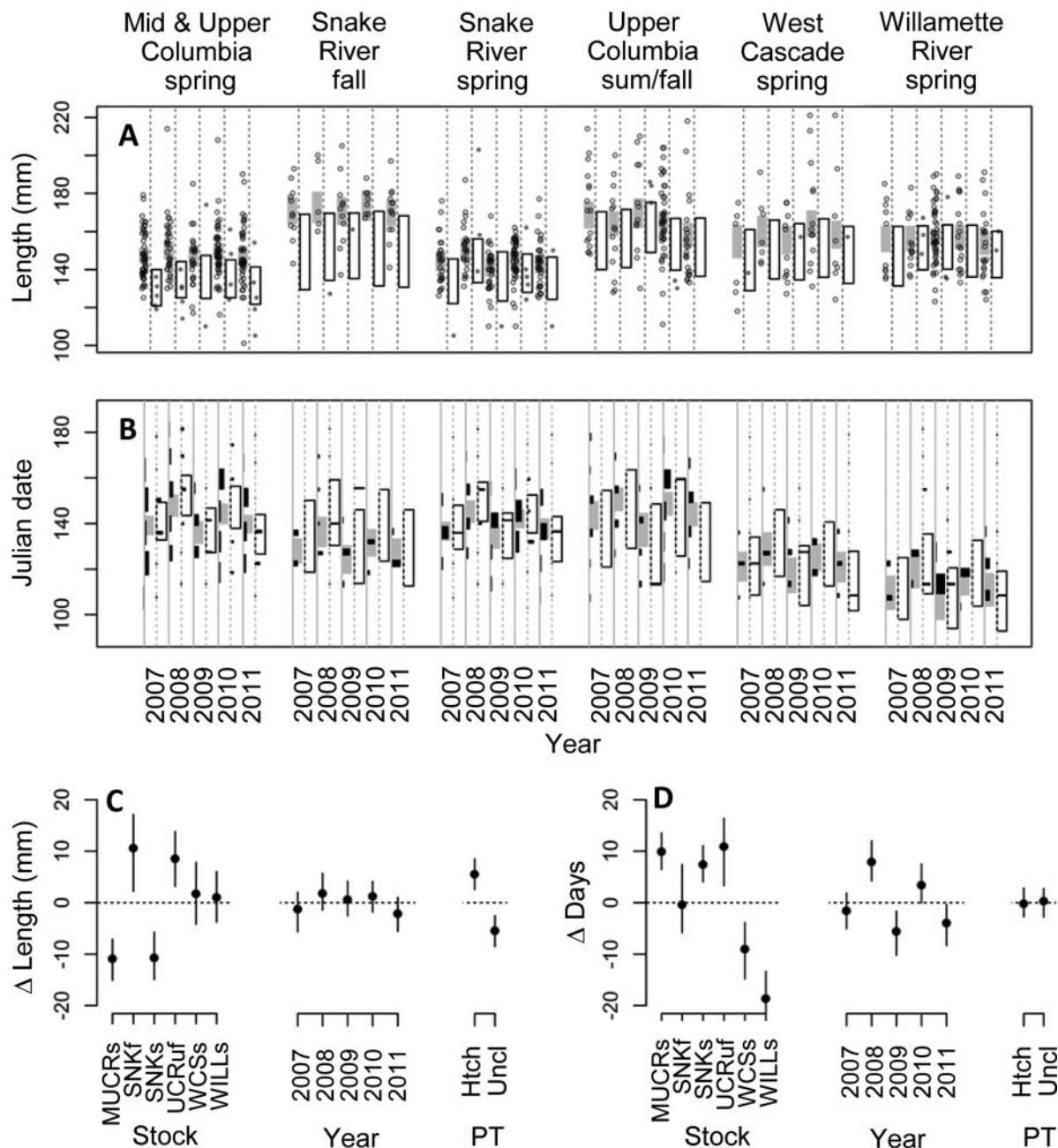


FIGURE 4. Comparisons of mean date and length at capture in the estuary for yearling Chinook Salmon by stock, production type, and year. The stock abbreviations are as follows: MUCRS = mid and upper Columbia River, spring; SNKf = Snake River, fall; SNKS = Snake River, spring; UCRuf = upper Columbia River, summer–fall; WCSS = west Cascade, spring; and WILLS = Willamette River, spring. See Figure 3 for additional details.

Columbia River Chinook Salmon and steelhead that correspond to differences in initial growth opportunities in marine waters. These size and timing differences likely interact with a suite of other factors, including prey availability and predator abundances, to influence survival in estuarine and marine waters. For example, stock-specific variation in the consumption of juvenile salmon by avian predators in the Columbia River estuary has been attributed to stock differences in size,

timing, and behavior (Collis et al. 2001; Ryan et al. 2003; Sebring et al. 2013). While there may be conditions under which early timing results in beneficial growth opportunities or survival (Scheuerell et al. 2009; Satterthwaite et al. 2014), other conditions may select against early timing, leading to survival advantages for later timing (Ryan et al. 2003; Beamish et al. 2013). Similar advantages and disadvantages also likely occur for variation in fish size (e.g., Willette et al.

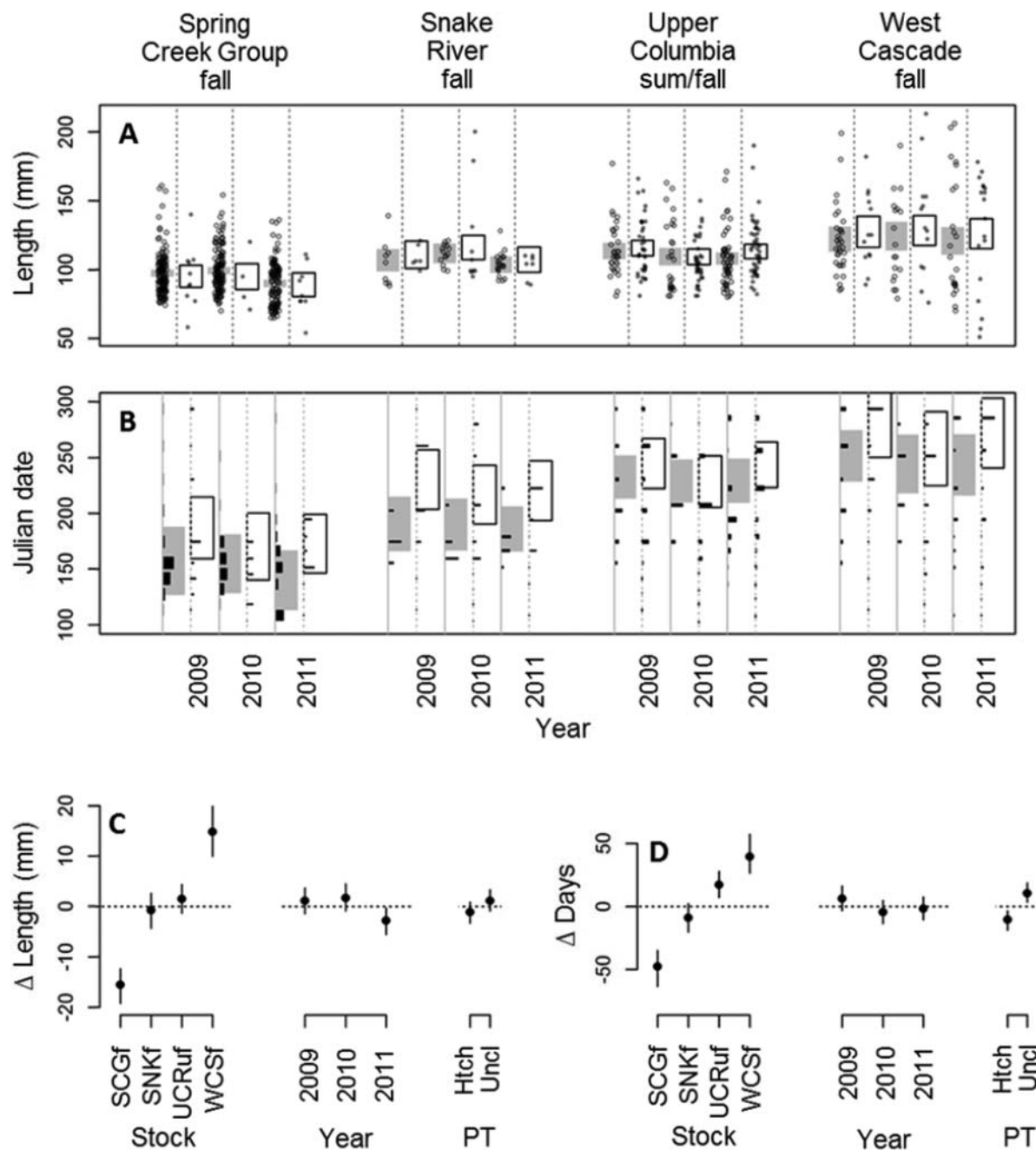


FIGURE 5. Comparisons of mean date and length at capture in the estuary for subyearling Chinook Salmon by stock, production type, and year. The stock abbreviations are as follows: SCGf = Spring Creek Group, fall; SNKf = Snake River, fall; UCRuf = upper Columbia River, summer-fall; and WCSf = west Cascade, fall. See Figure 3 for additional details.

2001). This idea is supported by studies which demonstrate that early timing or large size has survival advantages in some years but not others (Fisher and Percy 1988; Tomaro et al. 2012; Miller et al. 2014).

Although we observed stock-specific differences in timing, high within-stock variability resulted in many stocks being present in the estuary for a month or more. Consequently, multiple stocks of salmon from throughout the Columbia River

basin were present in the estuary at the same time, including hatchery and uncaptured individuals (Figures 3–5). This high temporal and spatial overlap, which has also been observed in shallow habitats in the Columbia River estuary (Teel et al. 2014), suggests high potential for competitive interactions between hatchery and presumed wild fish if resources are limited. The larger size of hatchery individuals may also give them a competitive advantage over small wild fish if larger

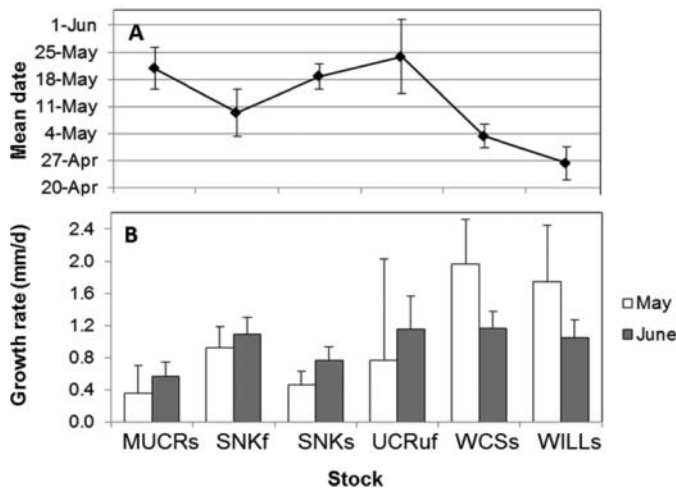


FIGURE 6. (A) Mean dates found in the Columbia River estuary and (B) growth rates as estimated by changes in length for yearling Chinook Salmon, by stock. The stock abbreviations are as follows: MUCRs = mid and upper Columbia River, spring; SNKf = Snake River, fall; SNKs = Snake River, spring; UCRuf = upper Columbia River, summer-fall; WCSs = west Cascade, spring; and WILLs = Willamette River, spring. The error bars represent standard deviations (estimated between years).

size is beneficial in such interactions (Tatara and Berejikian 2012).

High temporal overlap among stocks in the estuary may force wild fish to interact with abundant hatchery fish from other basins, even if hatchery production in their “home” basin is deliberately limited to minimize ecological or behavioral

interactions (Paquet et al. 2011). Whether wild fish are negatively affected by interactions with hatchery fish in the estuary has not been evaluated, but our findings, paired with those of Teel et al. (2014) for shallow habitats, indicate that the opportunity for such interactions clearly exists in the Columbia River estuary.

Comparisons of size and timing between hatchery and presumed wild salmon in the estuary also indicate the extent to which the patterns documented for abundant hatchery fish may serve as proxies for those for scarce wild fish. The timing of hatchery yearling Chinook Salmon and steelhead stocks was generally similar to that of wild stocks, suggesting that the timing of hatchery fish can be used to represent that of wild fish in the absence of data on the latter. By contrast, the size of yearling Chinook Salmon and steelhead and the size and timing of subyearling Chinook Salmon differed markedly between hatchery and wild fish. For these groups, using data from hatchery fish for wild fish would clearly misrepresent the timing and/or size of wild fish. While there may be situations in which the complete absence of data for wild populations requires the use of hatchery-based data, our results provide insight into when it might (and might not) be appropriate.

Our results also emphasize the direct connection between freshwater and marine habitats for juvenile salmon, because freshwater conditions that affect ocean entry timing also influence initial marine growth opportunities. For example, the large size difference between Willamette River (202 mm, 100 g) and Snake River (149 mm, 35 g) spring Chinook Salmon caught in marine waters in May might be explained by differential use of marine habitats of differing quality (e.g., Tucker et al. 2009). However, when one considers that Willamette River spring Chinook Salmon have occupied marine waters for a month longer than Snake River spring Chinook Salmon (Figure 4), it is apparent that the size difference largely reflects time spent in productive marine waters rather than location (and therefore habitat quality) within those waters. A similar conclusion was reached by a recent study of juvenile Sockeye Salmon *O. nerka* in marine waters, which found that stock-specific size at recovery was related to smolt size and ocean entry timing in addition to marine growth rates (Beacham et al. 2014). Furthermore, if the ocean entry timing of hatchery fish largely reflects hatchery practices (see the next section), hatchery practices can directly influence initial marine growth opportunities.

### Influence of Hatchery Practices on Observed Patterns

Our results indicate that the size at and timing of the ocean entry of hatchery fish largely results from hatchery practices, including release timing, distance to the river’s mouth, and size at release. Our prediction that stocks with early migration timing would originate closer to the Columbia River mouth than those with later timing was strongly supported by our results for yearling Chinook Salmon and steelhead (Figures 3, 4).

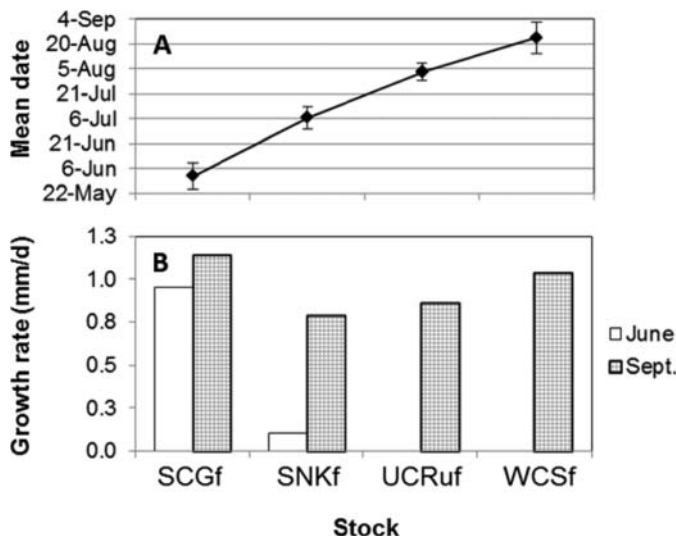


FIGURE 7. (A) Mean dates found in the Columbia River estuary and (B) growth rates as estimated by changes in length for subyearling Chinook Salmon, by stock. The stock abbreviations are as follows: SCGf = Spring Creek Group, fall; SNKf = Snake River, fall; UCRuf = upper Columbia River, summer-fall; WCSf = west Cascade, fall. The error bars represent standard deviation (estimated between years).

Data from tagged individuals also indicate that this earlier timing is influenced by migration distance rather than migration speed because lower-river stocks migrated at slower rates than those farther upriver (Table A.1.2), a phenomenon also observed by Dawley et al. (1986). However, ocean entry timing is also affected by hatchery release timing, as illustrated by the late release date and late timing of west Cascade fall subyearling Chinook Salmon despite their location near the river's mouth (Table A.1.1; Figure 5). The extremely early timing of Willamette and west Cascade spring Chinook Salmon likely results from their location low in the basin and their early hatchery release times (Table A.1.1).

The size of yearling hatchery Chinook Salmon and steelhead in the estuary can be explained by hatchery release size. The unusually large size of Snake River steelhead in the estuary (Figure 3) is consistent with their large size at release (97 g) relative to other stocks (<90 g; Table A.1.1). Yearling Chinook Salmon stocks that were exceptionally large (Snake River, spring) or small (mid and upper Columbia River, spring) when captured in the estuary (Figure 3) were also large (63 g) or small (28 g) at their release from hatcheries. Overall, the size at recovery in the estuary of individuals tagged with CWTs was positively related to the size at hatchery release for both yearling Chinook Salmon and steelhead (linear regression:  $r^2 \geq 0.23$ ,  $P < 0.01$ ;  $n = 322$  yearling Chinook Salmon, 57 steelhead).

In contrast, the relationship between the size of hatchery subyearling Chinook Salmon in the estuary and their size at release was much weaker (linear regression:  $r^2 = 0.04$ ,  $P < 0.01$ ;  $n = 197$ ). This is likely because some subyearling Chinook Salmon stocks have extended residency in the estuary before entering marine waters (Reimers and Loeffel 1967; Sebring et al. 2013) and continue to grow throughout the summer (Campbell 2010). This is particularly true for west Cascade fall Chinook Salmon, which are released at approximately the same size (8.5–8.8 g) as other subyearling stocks (Table A.1.1) but which are recovered at the mouth much later and at larger sizes than other stocks (Figure 5).

### Differences between Hatchery and Wild Fish

We predicted that hatchery fish would be consistently larger than unclipped fish, and our expectations were confirmed for yearling Chinook Salmon and steelhead. This size difference was most pronounced for upper Columbia River steelhead, with hatchery fish being up to 15% longer and weighing 42% more than unclipped fish from the same stock, even though hatchery fish were 1–2 years younger than wild fish (Busby et al. 1996). In contrast, hatchery subyearling Chinook Salmon were not larger than wild fish from the same stocks, but their timing was up to a month earlier. The size of subyearling Chinook Salmon increases throughout the summer (Roegner et al. 2012; Weitkamp, unpublished data), so that if the timing of hatchery and wild subyearling Chinook Salmon from the same

stock were identical hatchery fish would be larger than wild fish, as we predicted.

We did not expect that the timing of hatchery and presumed wild yearling Chinook Salmon and steelhead would be as similar as they were (Figures 3, 4), given that the release timing of hatchery fish is artificially controlled. This suggests that once fish leave a hatchery they initiate active migration by responding to the same environmental cues that wild fish use (e.g., temperature, flow, and photoperiod; Whalen et al. 1999; Beckman et al. 2000; Achord et al. 2007; Sykes et al. 2009). Evidence that fish released from hatcheries do not begin migrating immediately comes from comparisons of the migration rates to the river's mouth estimated for juvenile salmon tagged with CWTs and released from hatcheries with the "active" migration rates for salmon tagged with PIT tags and detected at intermediate dams (Table A.1.2). The active migration rates that we estimated (61–79 km/d) and that others have reported (>50 km/d; Welch et al. 2008; Harnish et al. 2012) were much higher than the CWT-based migration rates that we estimated (3–35 km/d; Table A.1.2) or those reported by Dawley et al. (1986) (3–36 km/d), suggesting that fish do not immediately initiate downstream migration when released from hatcheries.

Subyearling Chinook Salmon were unique because the timing of hatchery fish caught in the estuary was up to a month earlier than that of unclipped fish from the same stock (Figure 5). This large difference may be explained by differential habitat use by hatchery and wild fish. Wild subyearling Chinook Salmon in the Columbia River estuary make greater use of shallow-water habitats and have broader temporal distributions than subyearling hatchery fish, which are abundant in deep-channel habitats (Dawley et al. 1986; Roegner et al. 2012; Weitkamp et al. 2012; Teel et al. 2014). Consequently, the environmental conditions experienced by wild fish are likely different from those experienced by hatchery fish, which results in differences in timing cues and migration timing. Although the range of ocean entry size and timing that we observed for subyearling Chinook Salmon may be less than that reported historically (Rich 1920; Burke 2004), our findings suggest that substantial diversity still exists in the use of estuarine habitats by both hatchery and wild subyearling Chinook Salmon, resulting in ocean entry times spanning the period from May through October (Figure 5).

### Validity of Ocean Growth Assumptions

We estimated initial marine growth rates by sampling the same stocks of salmon in estuarine and marine environments. This analysis was based on the assumption that the fish caught in the estuary and ocean were representative of their respective stocks and that the changes in size were due to growth rather than to other factors, such as emigration/immigration in either habitat, interannual variation in size or timing among stocks, and size-selective mortality. Several lines of evidence indicate

that this assumption is reasonable, as is our primary finding: stocks that have only recently arrived in marine waters have lower growth rates than those that have spent more than a few weeks in productive marine habitats.

An important feature of our analysis of growth rates is that our sampling was conducted in the primary freshwater emigration and early-ocean rearing habitats for the stocks we examined. Research over the last four decades has consistently demonstrated that yearling and subyearling Chinook Salmon are abundant in the deep waters of the Columbia River estuary (Dawley et al. 1986; Bottom and Jones 1990; Harnish et al. 2012; Weitkamp et al. 2012) and that the adjacent marine region offers major rearing and migration habitats for these same stocks (Fisher and Pearcy 1995; Fisher et al. 2014; Teel et al. 2015). We also captured over 1,000 Chinook Salmon from 197 CWT release groups (i.e., individuals within a group have the same tag code) in both estuarine and marine habitats. These recoveries confirm that we sampled the same groups of fish in the two habitats, and the growth rates estimated from this subset of fish showed the same pattern of slow growth for stocks that had just arrived in marine waters (Weitkamp, unpublished data).

Although annual variability is an important consideration in evaluating growth, we estimated growth rates across years to maximize our sample sizes for comparisons among stocks. Our analysis likely benefited from consistent hatchery releases (in terms of size, timing, and abundance), river flow, and ocean conditions during our study years (Fish Passage Center Web site; Peterson et al. 2014), factors which could alter stock-specific growth patterns.

Whether our reported growth rates are influenced by size-specific mortality is more difficult to determine—and a source of potential bias for all of the studies that use this method (e.g., Fisher and Pearcy 1988; Beamish et al. 2008; MacFarlane 2010). We recalculated the May growth rates for the two stocks with the earliest ocean entry timing (Willamette and west Cascade spring Chinook Salmon) using ocean recovery sizes that were 10% smaller than those we observed (to mimic size-selective predation), and the resulting growth rates (0.9 mm/d, 2.2% BW/d) were still generally higher than our estimated growth rates for stocks with later timing (Figure 6). Numerous predators are known to prey on juvenile salmon in estuarine and marine habitats (Emmett 1997; Collis et al. 2001; Emmett et al. 2006; Zamon et al. 2013), although the extent to which this predation is size selective is not known. However, it is difficult to imagine a predation scenario that would result in the patterns that we observed in marine waters in May and June: high predation (to produce high growth rates) on some stocks but not on others within the same general area.

Studies designed to evaluate size-selective mortality have either failed to find evidence of it or have found mixed results (occurring in some but not all years) for Chinook Salmon, including studies focused on Columbia River salmon

(Claiborne et al. 2011, 2014; Tomaro et al. 2012; Miller et al. 2013, 2014). Early ocean growth rates estimated from otoliths for three of the stocks included here (and some of the same individuals) were very close to our estimated growth rates (Tomaro et al. 2012; Claiborne et al. 2014; Miller et al. 2014), suggesting that our results are reasonably representative of the true growth rates.

We may have overestimated growth rates in two cases: those of Willamette River spring and west Cascade spring Chinook Salmon caught in marine waters in late May, for which our rates are extremely high ( $\geq 1.75$  mm/d,  $> 3.7\%$  BW/d; Figure 6). We suspect that these high rates are due, in part, to poor estimates of ocean entry timing. The abundance of the Willamette River spring stock in the estuary was highest when sampling commenced in mid-April, while that of the west Cascade spring stock peaked approximately 1 week later (Figure 4), so that our sampling schedule might miss early-migrating individuals. Juvenile Willamette River spring Chinook Salmon are caught off the west coast of Vancouver Island (300–550 km from the mouth of the Columbia River) in April, and both Willamette River and west Cascade spring Chinook Salmon are caught in Southeast Alaska (over 1,300 km from the river) in June (Tucker et al. 2011; Fisher et al. 2014), which is consistent with extremely early ocean entry. Consequently, the high growth rates that we report for these two stocks may exceed the actual growth rates if we missed early migrants in the estuary and therefore estimated a later date of ocean entry than actually occurred. For example, the growth rates for Willamette River and west Cascade spring Chinook Salmon calculated using ocean entry dates 3 weeks earlier (April 4 and 11, respectively; 0.9 mm/d, 2% BW/d) are similar to those of yearling stocks with later ocean entry timing that were caught in June. Our estimates of ocean entry time for other stocks are consistent with back-calculated ocean entry dates determined by otolith chemical and structural analyses (Tomaro et al. 2012; Claiborne et al. 2014; Miller et al. 2014).

### Variation in Life History Traits

It has long been recognized that different stocks of salmon—including those originating from the same river—often differ in life history traits that are easily measured while the fish are in freshwater (e.g., Rich 1920; Groot and Margolis 1991; Quinn 2005). Our study adds to an increasing body of literature demonstrating that stock-specific variation in marine life history traits rivals that of freshwater traits. This variation begins with stock-specific size and timing at ocean entry (Roegner et al. 2012; our study), continues as stock-specific migration rates, routes, and behaviors during the first summer or two of ocean residence (e.g., Trudel et al. 2009; Tucker et al. 2011; Burke et al. 2013; Fisher et al. 2014; Teel et al. 2015), includes a poorly-understood winter period when salmon may occupy mid-ocean habitats and are logistically difficult to sample

(Groot and Margolis 1991; Myers et al. 1996; Larson et al. 2013), and concludes with stock-specific differences in marine distributions as adult salmon return to their natal streams (Milne 1957; Wright 1968; Weitkamp 2010; Sharma and Quinn 2012)—differences which have long been exploited by managers to structure fisheries (e.g., Killick 1955).

While our ability to detect such differences in marine life history has only recently been made possible by advances in genetic technology and extensive tagging programs, we should not be surprised that they exist given the life history variation that salmon exhibit in freshwater. Furthermore, this stock-specific variation likely contributes to the overall resilience of salmon populations, allowing species to persist despite unpredictable environmental variation that may favor some strategies over others in given time periods (e.g., Thorpe 1999; Schindler et al. 2010; Bottom et al. 2011). Clearly, stock-specific traits are critical to successfully transitioning from one life stage to another, yet they are often overlooked when different stocks originate from a common river basin.

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**Appendix A.1: Additional Data**TABLE A.1.1. Mean size at and time of release of juvenile salmon from Columbia River hatcheries, 2007–2011, by stock. Data are from the Regional Mark Processing Center ([www.rmhc.org](http://www.rmhc.org)) and Fish Passage Center ([www.fpc.org](http://www.fpc.org)) databases.

Stock	Number released (millions)	% Fin clipped	Release date	Release weight (g)
<b>Steelhead</b>				
Lower Columbia River	3.0	86.5	Apr 19	75.1
Mid Columbia River	1.2	54.3	Apr 22	88.6
Snake River	8.3	86.8	Apr 14	97.3
Upper Columbia River	1.1	71.1	Apr 26	70.5
Willamette River	1.0	99.6	Apr 15	89.8
All steelhead	14.6	83.7		
<b>Yearling Chinook Salmon</b>				
Mid Columbia River, spring	6.3	87.0	Apr 12	27.9
Snake River, fall	0.9	56.9	Apr 9	47.4
Snake River, spring	9.8	92.3	Apr 20	62.7
Snake River, summer	2.3	93.9	Apr 9	23.0
Upper Columbia River, spring	3.1	67.6	Apr 24	28.7
Willamette River, spring	4.8	97.2	Mar 11	42.1
Upper Columbia River, summer	2.3	98.8	Apr 21	42.0
Upper Columbia River, fall	0.4	37.7	Mar 22	39.8
West Cascade, spring	3.8	92.7	Mar 11	46.2
All yearling Chinook Salmon	33.7	88.7		
<b>Subyearling Chinook Salmon</b>				
Spring Creek Group, fall	18.8	96.3	Apr 23	5.0
Upper Columbia River, fall	19.9	52.7	May 15	8.8
West Cascade, fall	23.8	88.0	Jun 17	8.7
Snake River, fall	4.4	42.6	May 27	8.5
Upper Columbia River, summer	1.4	65.3	May 27	15.1
All subyearling Chinook Salmon	72.6	75.7		

TABLE A.1.2. Downstream migration rates for juvenile salmon tagged with coded wire tags (CWTs) or passive integrated transponder (PIT) tags and collected in the Columbia River estuary. Only groups for which at least five coded-wire-tagged or three PIT-tagged individuals were recovered are included.

Stock	CWT fish <sup>a</sup>				PIT fish <sup>b</sup>	
	<i>n</i>	Days at large	Distance (km)	Rate (km/d)	<i>n</i>	Rate (km/d)
<b>Steelhead</b>						
Snake River	61	37.7	1,033	27.4	14	79.5
Upper Columbia River	12	33.3	841	25.2		
<b>Yearling Chinook Salmon</b>						
Mid Columbia River, spring	53	44.1	386	11.2		
Snake River, fall	52	30.2	697	24.6	3	61.4
Snake River, spring	58	51.1	853	18.1	11	67.1
Snake River, summer	10	63.3	1,100	19.0		
Upper Columbia River, fall	10	24.1	588	31.3		
Upper Columbia River, spring	65	42.1	830	21.6		
Upper Columbia River, summer	80	37.6	790	24.1		
Willamette River, spring	18	49.1	326	10.9		
Lower Columbia River, spring	14	56.0	143	2.6		
<b>Subyearling Chinook Salmon</b>						
Spring Creek, fall	77	37.8	180	7.9		
Snake River, fall	54	27.2	814	35.2	7	64.8
Upper Columbia River, fall	55	30.0	369	17.2		
Upper Columbia River, summer	6	35.5	813	24.1		
West Cascade, fall	24	44.7	181	5.1		

<sup>a</sup>Estimated from release at the hatchery to recovery in the estuary. Release locations and dates were determined from the Regional Mark Processing Center database (www.rmpc.org).

<sup>b</sup>Estimated from detection at an intermediate dam to recovery in the estuary. Dates and intermediate detection locations were determined from the PTAGIS database (www.ptagis.org).

## Appendix A.2: Model Details

### Models

**Length and weight models.**—The application of traditional ANOVA models to the length and weight data was not possible due to the extreme lack of balance and differences in variance between groups. Thus we used a Bayesian multilevel model in which group means within a category (i.e., different stocks) were assumed to come from a normal distribution for which the mean and standard deviation were estimated. This is comparable to a random effect in a mixed-effects model. We used the same models for length and weight. Here we present the model in terms of length.

Length was assumed to have a normal distribution,

$$L_i \sim N(\text{mean}_i, s_{\text{resid}}),$$

with the mean

$$\alpha + \beta_{\text{year}} + \gamma_{\text{stock}} + \delta_{\text{year, stock}} + \eta_{\text{hat}} + \theta_{\text{year, hat}} + \zeta_{\text{stock, hat}} + \iota_{\text{year, stock, hat}},$$

where “hat” indicates the ratio of hatchery-origin fish to wild ones and the other subscripts are self-explanatory. The year,

stock, and interaction specific constants have normal distributions:

$$\begin{aligned}\beta_{\text{year}} &\sim N(0, s_{\text{year}}) \\ \gamma_{\text{stock}} &\sim N(0, s_{\text{stock}}) \\ \delta_{\text{year, stock}} &\sim N(0, s_{\text{year, stock}}) \\ \theta_{\text{year, hat}} &\sim N(0, s_{\text{year, hat}}) \\ \zeta_{\text{stock, hat}} &\sim N(0, s_{\text{stock, hat}}) \\ \iota_{\text{year, stock, hat}} &\sim N(0, s_{\text{year, stock, hat}})\end{aligned}$$

The constant term  $\alpha$  (the intercept) and groups in categories with less than three groups (i.e., hat) were assigned diffuse normal priors, namely,  $N(0, 1,000)$ . The residual standard deviation ( $s_{\text{resid}}$ ) was assumed to follow an inverse gamma distribution  $\text{InvGamma}(0.01, 0.01)$  unless there were obvious differences in the variance between groups within a category (e.g., stocks). In that case the group residual standard deviations were assumed to follow a normal distribution in the same way as the main effects and interactions above. The standard deviation parameters describing between-group variability (e.g., variability between years,  $s_{\text{year}}$ ) were assumed to follow a uniform distribution,  $\text{uniform}(0, 100)$ , (e.g., Gelman 2006).

**Migration timing model.**—The number of fish observed during a particular sampling event is assumed to follow the negative binomial distribution,

$$\text{count}_i \sim \text{negative binomial}(\text{mean}_i, \text{dispersion}_i),$$

where the mean is a function of time (a normal density function) that first increases and then decreases over the period of migration as function of the day of the year (Figure A.2.1):

$$\text{mean}_i = \text{scale}_i \times N(\text{day of the year}_i, \text{center}_i, \text{spread}_i).$$

The center parameter represents the date with highest expected count and is modeled in the same way as length above, namely,

$$\begin{aligned} \text{center}_i = & \alpha + \beta_{\text{year}} + \gamma_{\text{stock}} + \delta_{\text{year, stock}} + \eta_{\text{hat}} \\ & + \theta_{\text{year, hat}} + \zeta_{\text{stock, hat}} + \iota_{\text{year, stock, hat}}. \end{aligned}$$

The spread parameter is the standard deviation of the normal density function, which describes how the counts are spread across time. It is modeled in the same way as center. The scale parameter accounts for the total number of fish counted over the migration period (by adjusting the height of the normal density curve) and is allowed to vary by group:

$$\text{scale}_i = \exp(\nu + \mu_{\text{year, stock, hat}}).$$

In this equation the constant  $\nu$  (the intercept) is assumed to follow a diffuse normal distribution, i.e.,  $N(0, 1,000)$ .

The dispersion parameter for the negative binomial distribution describes the relationship between the mean and the variance, where decreasing values equate to a larger variance for a given mean and the distribution collapses to a Poisson distribution as the dispersion gets very large. We assigned a

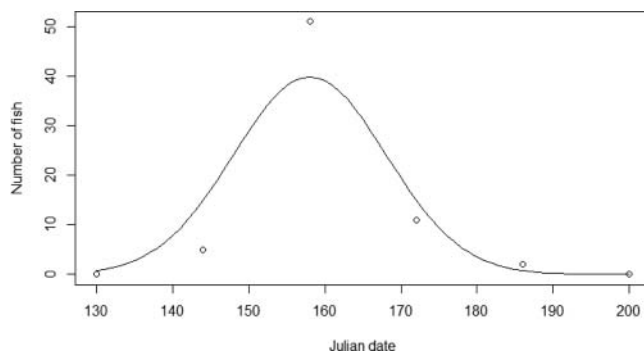


FIGURE A.2.1. Example data and the normal density function used to describe the temporal pattern. The values on the y-axis are the number of fish from a particular group caught during a given sampling event. The points are the counts, and the curve represents the normal density function fit to the data (i.e., the model of migration timing for the group).

diffuse normal distribution to the log of the dispersion parameter.

For all size and timing models, we transformed the main effects and interactions to satisfy the constraint that they sum to zero. That is, all of the main effects sum to zero and the margins of the interactions are zero. For example,

$$\sum_{\text{stock}} \sum_{\text{year}} (\mu_{\text{year, stock, hat}}) = \begin{bmatrix} 0 \\ 0 \end{bmatrix}.$$

This is equivalent to treating the categories as fixed effects or the groups as a finite population (Gelman 2006), where one is interested in making comparisons between specific levels (e.g., between the lower and upper Columbia River stocks). This is independent of whether or not there is partial pooling for the category.

### Assessing Model Fit

We assessed the fit of the model to the data by means of plots. The plots of the data for length and weight (length: Figures 2–5 in the main text; weight: Figures A.2.2–A.2.4)<sup>1</sup> include 95% credible intervals for the group-specific means. This allowed us to look for poor fits for the individual groups, unequal variances across groups, and severe violations of the normal-distribution assumption. Because the group means were assumed to come from a common distribution across the category (e.g., stock-specific means), they will be shrunk slightly toward the grand mean for that category. Therefore, groups with few observations may have 95% credible regions that are not precisely centered over the data. In addition, it is possible to estimate the group mean for groups without data. The observed residuals from the length and weight models were compared with the posterior predictive distributions using quantiles.

For the timing model we again used the plots of the data, along with estimates of peak arrival time, to look for any obvious lack of fit. To assess the fit of the normal-distribution curve to the timing distributions, we examined the data along with several fitted curves from the posterior distribution for each group. We examined the fit of the negative binomial distribution by comparing the observed and expected quantiles.

### Markov Chain–Monte Carlo Convergence Diagnostics

We assessed the convergence of the Markov chain–Monte Carlo algorithm by means of trace plots of individual chains and the difference between the estimates and

<sup>1</sup>Because the length and weight data were very similar and there were more missing weight data, we only presented the length data in the main text. Here we provide comparable plots for the weights of the steelhead, yearling Chinook Salmon, and subyearling Chinook Salmon in our samples.

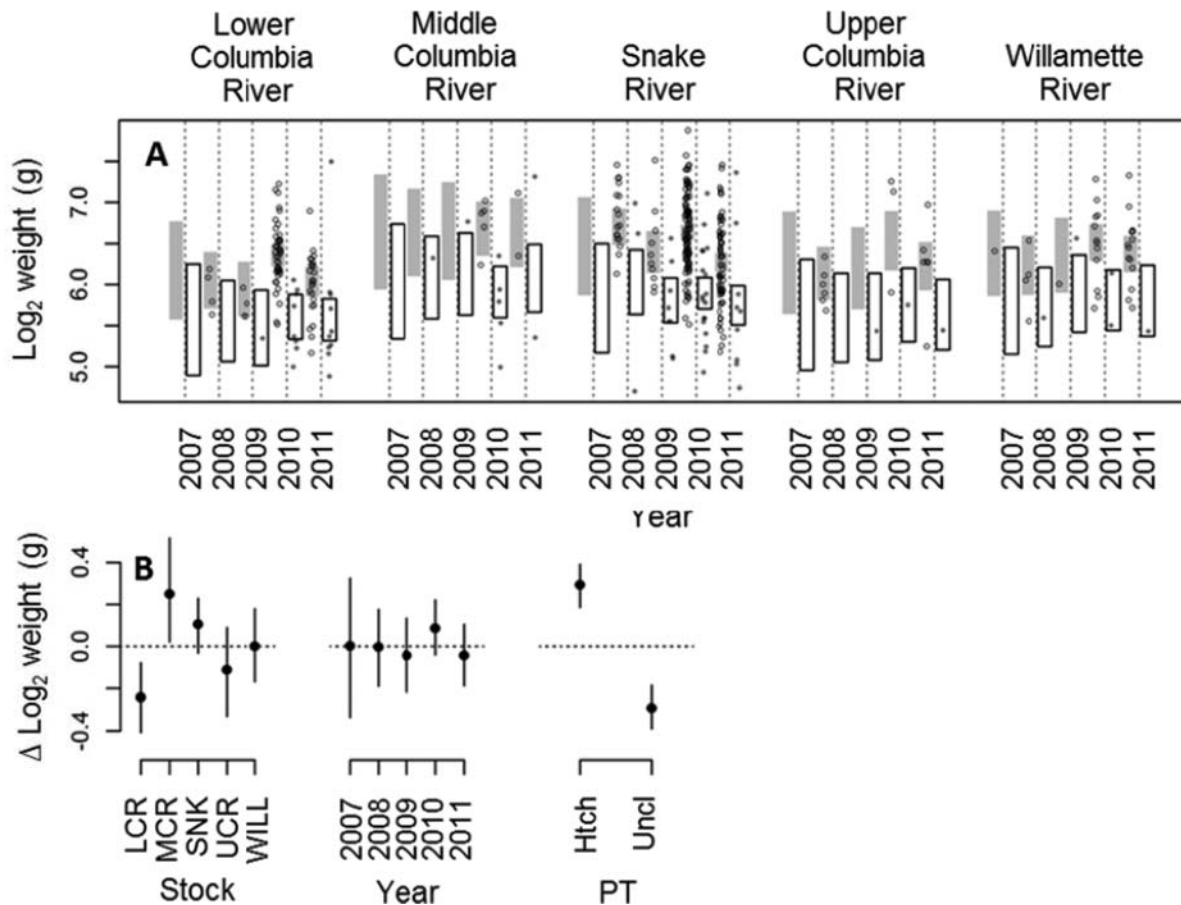


FIGURE A.2.2. Comparisons of log<sub>2</sub> transformed mean weight at capture in the estuary for juvenile steelhead by stock, production type, and year. Panel (A) shows plots of weight, with model-based 95% credible intervals. The dots indicate individual fish. Gray bars and gray dots represent hatchery fish, open bars and black dots represent unclipped fish. Panel (B) pertains to the main effects in the weight model. The points are the estimated deviations from the mean for each level of the main effect, and the vertical lines are the corresponding 95% credible intervals. The stock abbreviations are as follows: LCR = lower Columbia River, MCR = mid Columbia River, SNK = Snake River, UCR = upper Columbia River, and WILL = Willamette River. The production type (PT) abbreviations are as follows: Htch = hatchery and Uncl = unclipped.

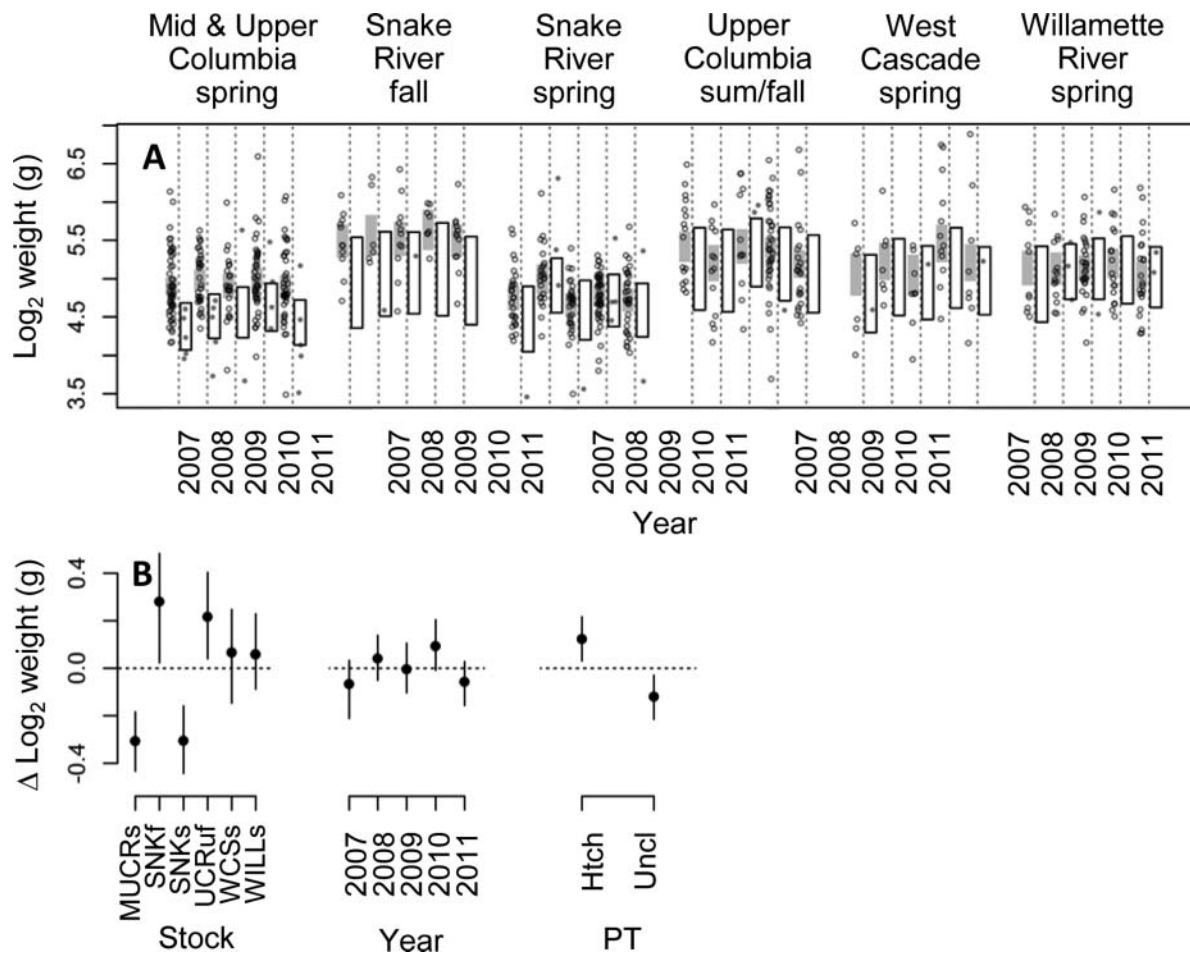


FIGURE A.2.3. Comparisons of  $\log_2$  transformed mean weight at capture in the estuary for yearling Chinook Salmon by stock, production type, and year. The stock abbreviations are as follows: MUCRs = mid and upper Columbia River, spring; SNKf = Snake River, fall; SNKs = Snake River, spring; UCRuf = upper Columbia River, summer–fall; WCSSs = west Cascade, spring; and WILLs = Willamette River, spring. See Figure A.2.2 for additional details.

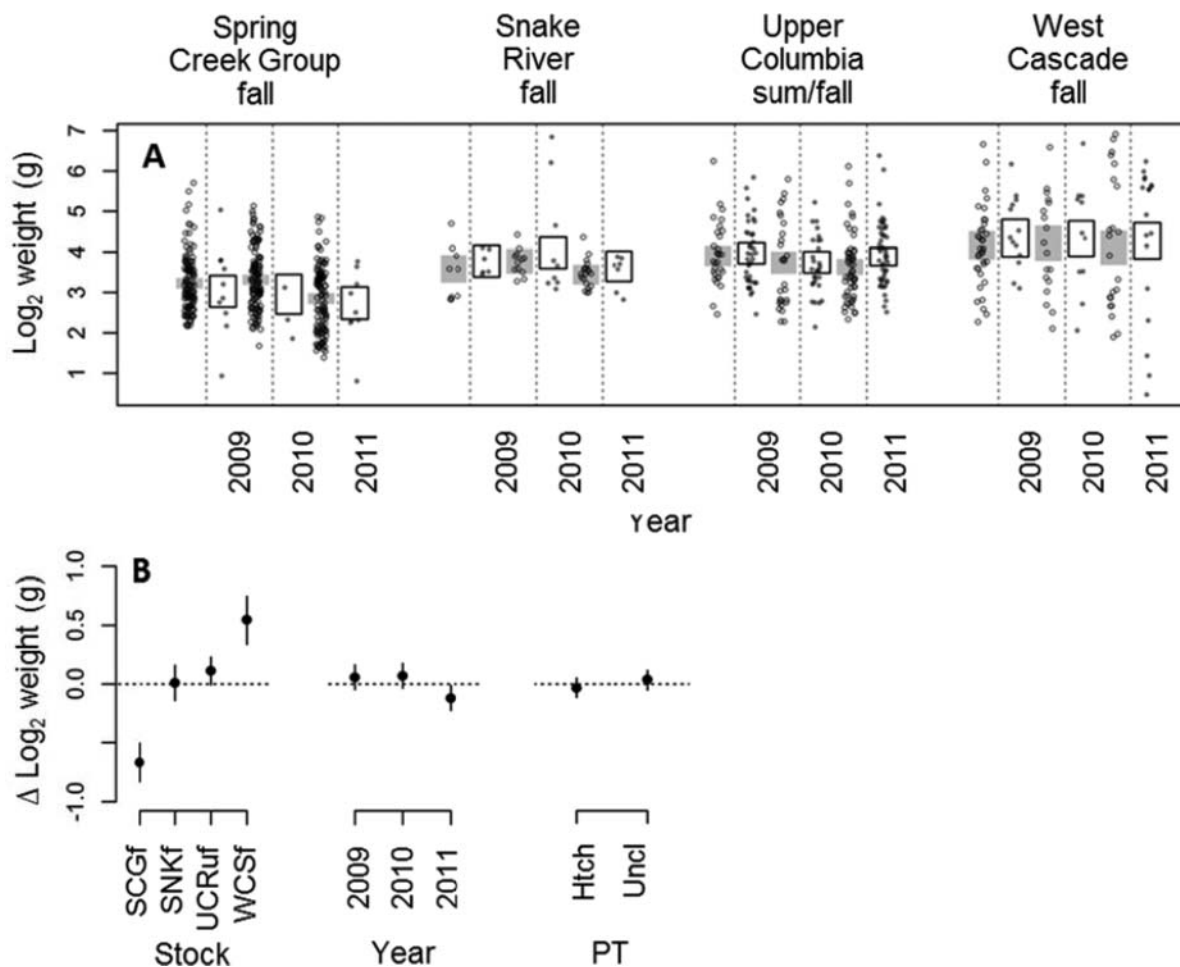


FIGURE A.2.4. Comparisons of  $\log_2$  transformed mean weight at capture in the estuary for subyearling Chinook Salmon by stock, production type, and year. The stock abbreviations are as follows: SCGf = Spring Creek Group, fall; SNKf = Snake River, fall; UCRuf = upper Columbia River, summer–fall; and WCSf = west Cascade, fall. See Figure A.2.2 for additional details.

the credible intervals resulting from multiple chains. Chains were run until the thinned trace plots indicated good mixing and the estimates and credible intervals from separate chains converged.

### Software

The models were fit using Markov chain–Monte Carlo sampling as implemented in JAGS software (Plummer 2003). The R language (R Core Team 2014) was used for data manipulation and plotting.

### APPENDIX REFERENCES

- Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Analysis* 1:515–534.
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- R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.