Age at Maturity, Fork Length, and Sex Ratio of Upper Willamette River Hatchery Spring Chinook Salmon

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Version of record first published: 06 Mar 2013.

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Abstract

We used data from 17 brood years of coded-wire-tagged hatchery spring Chinook Salmon *Oncorhynchus tshawytscha* from the upper Willamette River to test for changes in mean age at maturity, fork length, and sex ratio. We found only limited evidence for any trend in age at maturity or sex ratio. However, Chinook Salmon sampled from tangle nets, recreational fisheries, spawning grounds, and hatcheries all presented trends of decline in mean fork length. Rates of change in fork length ranged from 0 to 5 mm per year in most sample collections, though fork length declined more rapidly for samples from tangle nets. We also observed a positive relationship between adult fork lengths and the median monthly Pacific Decadal Oscillation index in the year prior to juvenile liberation (the brood year). We suggest that future research should investigate the potential cause(s) for the decline in size of hatchery spring Chinook Salmon from the upper Willamette River, with attention to harvest, broad-scale environmental conditions, and hatchery spawning and rearing practices.

A variety of factors can affect the productivity of Pacific salmon *Oncorhynchus* spp. populations. Numerous studies have demonstrated relationships between variable ocean conditions, survivorship (Cole 2000; Mueter et al. 2002; Logerwell et al. 2003), and growth (Bigler et al. 1996; Hobday and Boehlert 2001; Wells et al. 2006) of diverse species. Size at maturity, determined by growth rate and age at maturity, can in turn affect the reproductive success of salmon through influence on egg size (Quinn et al. 2004; Beacham 2010), egg deposition (Steen and Quinn 1999), fecundity (Quinn et al. 2011), and competitive advantage for mates and redd sites (Foote 1990; Fleming and Gross 1994; Hendry et al. 2001; Ford 2012). However, reproductive advantages gained by larger size at maturity are sometimes offset by the cost of increased vulnerability to size-selective harvest (Hard et al. 2008; Kendall and Quinn 2009) or natural predation (Quinn et al. 2001).

In addition to individual fitness traits, demographics can influence population productivity. For example, skewed sex ratios within a population can reduce the effective number of breeders (Waples 2002) and impact mate choice processes (Garner et al. 2010). Large population size can intensify intraspecific competition, while the probability of encountering mates decreases in small, structured populations (Frank and Brickman 2000). Information on the stability of phenotypic traits and demographics is therefore highly relevant to managers, who sometimes produce hatchery salmon for both harvest and wild population supplementation purposes.

Upper Willamette River (UWR) spring Chinook Salmon *O. tshawytscha* are listed as threatened under the U.S. Endangered Species Act (NMFS 1999, 2005). Thirteen Willamette Project dams constructed in the upper watershed by the U.S. Army Corps of Engineers between 1941 and 1968 blocked 32% of historic spawning habitat (ODFW 2005), reducing natural production within subbasins by up to 95% (ODFW and NMFS 2010). To mitigate for lost production and fishing opportunities, four state-operated hatcheries (Figure 1) release approximately 5.1 million juvenile Chinook Salmon into the upper Willamette River annually (Johnson and Friesen 2010). Fish produced by these facilities are harvested in recreational, commercial, and tribal fisheries and are used for reintroduction programs

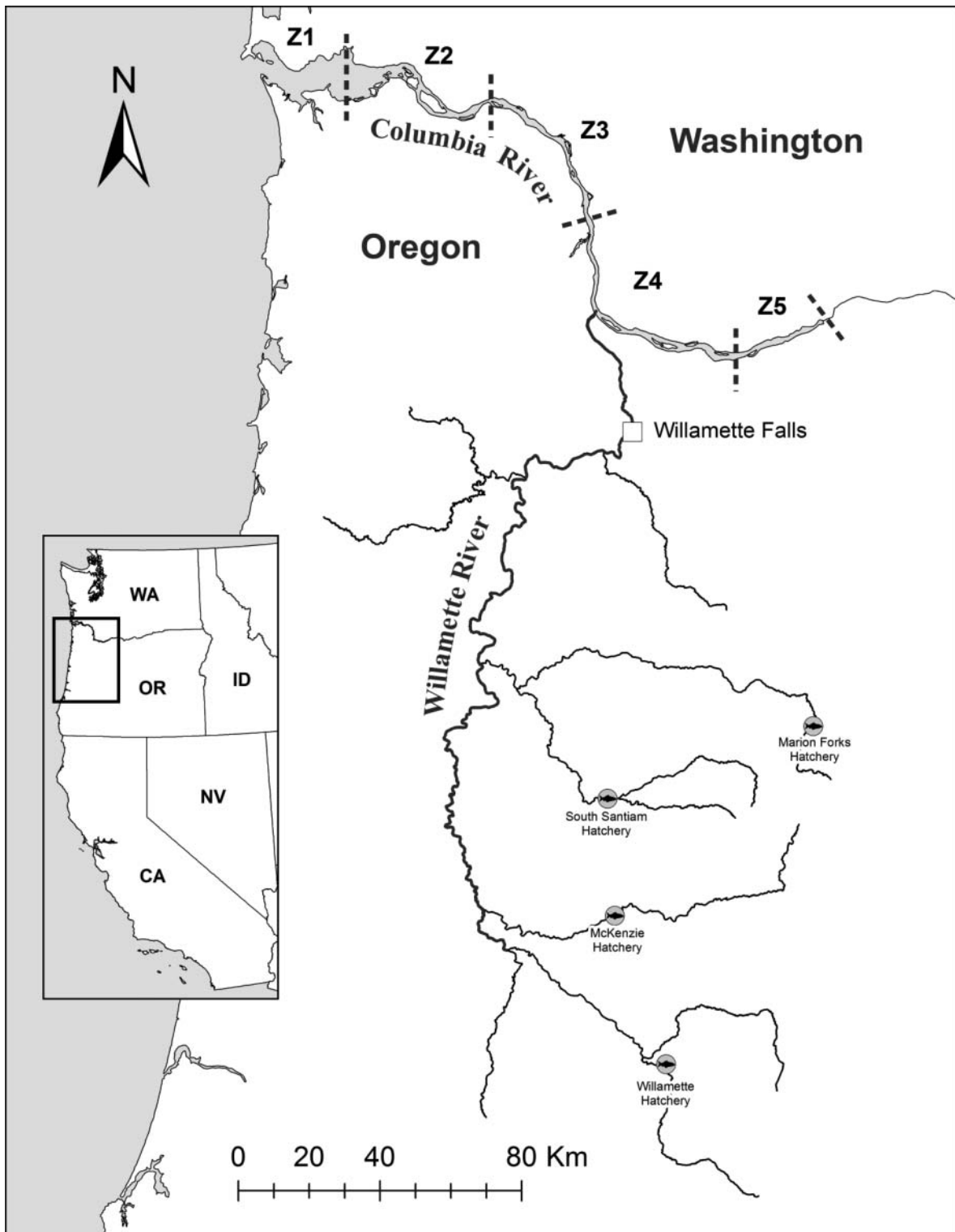*Corresponding author: marc.johnson@oregonstate.edu

FIGURE 1. The lower Columbia and Willamette rivers (major tributaries shown). Fish symbols denote upper Willamette River spring Chinook Salmon hatcheries and Z1–Z5 are lower Columbia River commercial fishery management zones.

intended to establish naturally reproducing populations in vacant or underutilized habitats (NMFS 2008).

Only limited information is currently available for demographic and life history traits of UWR spring Chinook Salmon. Length and sex data are routinely collected from hatcheries and various fisheries but are seldom analyzed across multiple generations. Counts of age-3 jacks and age-2 minijacks (Larsen et al. 2010) are obtained through observations at the Willamette Falls fish passage facility (Figure 1). However, these precocious male phenotypes typically comprise less than 5% of spring Chinook Salmon that return to spawn in the UWR basin (ODFW 2011). Other adult age-classes (ages 4, 5, and 6) cannot be observationally discriminated and are pooled in counts.

For several decades, the Oregon Department of Fish and Wildlife has tagged large numbers of juvenile UWR hatchery spring Chinook Salmon with coded wire tags (CWTs). Tagged Chinook Salmon have been released from all UWR hatcheries in most recent years (Figure 2, top panel), and tag groups have

included both fall and spring juvenile releases (Figure 2, bottom panel). Tags are typically recovered from salmon that return as adults to hatcheries and spawning grounds or are harvested in commercial and recreational fisheries. Coded wire tags provide a source of robust, publically available data (PSMFC 2011) that have been used in other systems to address a wide range of fisheries research and management questions, providing information on marine distributions (Weitkamp and Neely 2002; Weitkamp 2010; Chamberlin et al. 2011), stock structure (Courtney et al. 2000; Tucker et al. 2011), and behavior (Mortensen et al. 2002; Parken et al. 2008).

In this study, we used CWT data from 17 brood years of adult UWR hatchery spring Chinook Salmon sampled from the Willamette and lower Columbia rivers to answer the following questions:

1. Has the mean age at maturity of UWR spring Chinook Salmon changed over time?
2. Has the sex ratio of adult UWR spring Chinook Salmon changed over time?
3. Has the mean fork length of adult UWR spring Chinook Salmon changed over time?

By characterizing the nature or absence of trends for these population traits, we provide managers with basic phenotypic and demographic information, which may help to identify undesirable processes such as unintentional selection.

METHODS

Data collection.—We examined CWT data from hatchery UWR spring Chinook Salmon sampled at (1) UWR hatcheries, (2) UWR spawning grounds, (3) lower Columbia River commercial net fisheries, and (4) combined lower Columbia and Willamette River recreational fisheries. We did not include data from tags collected in ocean fisheries, as our study focused on traits of mature UWR spring Chinook Salmon. From the Regional Mark Information System (RMIS), we downloaded the following data for spring Chinook Salmon produced in brood years 1989–2005 and released as juveniles in the UWR basin: adult run year, fishery and gear used in collection, recovery location, recovery date, sex, fork length, tag code, release location, brood year, and release date. We then calculated the age of each tagged fish at the time of collection (from the brood year and tag collection date).

For CWTs collected in lower Columbia River commercial net fisheries, we analyzed data only for Chinook Salmon released in the upper Willamette River and harvested in Columbia River management zones 1 through 5 (Figure 1). Specifically, we did not analyze data for UWR spring Chinook Salmon released from lower Columbia River net pens (see Claiborne et al. 2011) in any sample collection. These fish are produced by Willamette basin hatcheries and transferred to the lower Columbia River, where they are acclimated in net pens to favor the local return of adult fish to support "select area" commercial fisheries, with
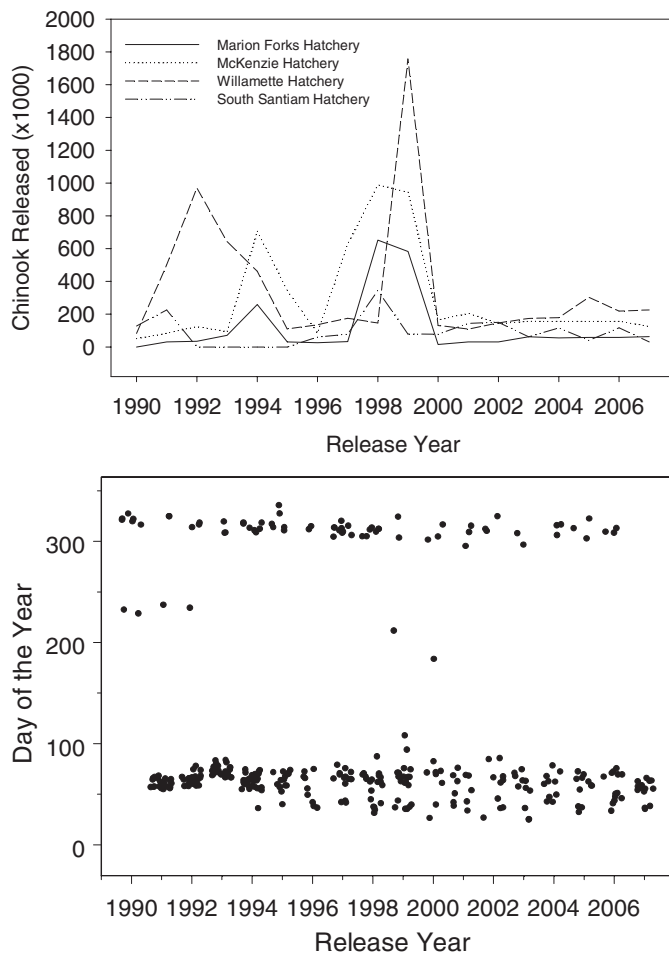

FIGURE 2. Number of tagged juvenile spring Chinook Salmon (top panel) released from upper Willamette River hatcheries into the upper Willamette River, 1990–2007, and day of the year (bottom panel) for release of tagged groups of upper Willamette River spring Chinook Salmon, release years 1990–2007. January 1st is day 1 on the *y*-axis.

a goal of 100% harvest (ODFW and NMFS 2010). Therefore, they are subject to release and harvest practices not common to other UWR hatchery spring Chinook Salmon.

We tested for effects from broad-scale ocean conditions on fork length at maturity. We first obtained monthly data for the Pacific Decadal Oscillation (PDO) index (JISAO 2012) and the Multivariate El Niño–Southern Oscillation index (MEI; NOAA 2012), then tested for a relationship between fork length and the median value for each index during the brood year and the five subsequent years.

Age structure.—As different fish collection methods can produce disparate sampling biases, we first tested for differences in age-class structure between fish harvested in commercial gill nets and tangle nets to determine whether data from these net types should be pooled or treated separately. In the lower Columbia River, gill nets are required to have minimum mesh sizes of between 20.3 and 22.9 cm, whereas tangle nets have maximum mesh sizes of between 10.8 and 14.0 cm (WDFW and ODFW 2011). Gill nets and tangle nets are not used simultaneously in the lower Columbia River, and we used the date of tag collection from these fisheries to determine which net type had been used during harvest. We then used a chi-square test to compare the age structures of fish collected by these two gear types in years that employed both.

Using CWT data from brood years 1989–2004[1], we calculated the mean age of each cohort in each sample collection (hatcheries, spawning grounds, net fisheries, and recreational fisheries). We then used linear regression analyses to test for relationships between brood year and mean age at maturity, weighted by sample size for each brood year. We did not include brood year 2005 for this portion of our study, as data for age-5 adults had not yet been uploaded to RMIS at the time of our analyses.

Sex ratio.—We examined sex ratios for spring Chinook Salmon sampled in Columbia River commercial net fisheries, UWR hatcheries, and UWR spawning grounds. Since these data are typically not recorded for Chinook Salmon taken in Columbia or Willamette River recreational fisheries, we did not analyze sex ratios in this sample collection. As with age structure analyses, we first used a chi-square test to compare the sex ratios of fish harvested by gill nets with those taken by tangle nets.

After plotting the number of females against the number of males recovered from each cohort, we estimated linear regression slopes that characterized the sex ratios in each sample collection, whereby $b = 1$ for 1:1 sex ratio. We calculated the 95% confidence intervals for each slope, then compared the slopes for sex ratios of each sample collection to $b = 1$.

Fork length.—We performed our analyses of mean fork length with data from age-4 and age-5 adults, since small sample sizes of other age-classes precluded formal statistical analyses.

[1]Gill net data were available for brood years 1989–1992 and 1995–2005. Tangle net data were available for brood years 1996–2005.

For each sample collection and the pooled dataset, we tested for relationships between mean fork length and the brood year, age, and sex of spring Chinook Salmon. We also considered all first-order interaction variables. Samples that lacked data for variables included in a given model were omitted from that analysis. We tested for the effects of ocean conditions on size at maturity by evaluating relationships between mean fork length with median monthly PDO and MEI index values for all years from juvenile production until adult collection. For these analyses, we used a mixed linear model approach and treated tag code, grouped by brood years, as a random effects variable. This approach prevented pseudoreplication that would otherwise occur if individual observations (each fish) were treated as samples. We used Akaike's Information Criterion (AIC) to assess model fits and examined residual distributions to verify conformance with linear model assumptions.

RESULTS

We obtained data from RMIS for 34,336 CWTs recovered from UWR spring Chinook Salmon at hatcheries, spawning grounds, and terminal (freshwater) fisheries. Most tags were recovered from adults at UWR hatcheries (75%), followed by Willamette and Columbia River recreational fisheries (12%), Columbia River commercial net fisheries (7%), and UWR spawning grounds (5%).

On average, 74% of CWTs (interannual median and mean) were recovered from fish that had been released as juveniles during February–May. Although we observed no trend in the data for the weight of juvenile fish released in the spring ($t = 0.43$, df = 15, $P = 0.6672$), juvenile Chinook Salmon released in fall months were on average 0.4 g heavier each consecutive brood year ($t = 2.72$, df = 15, $P = 0.0157$, $r^2 = 0.29$).

Age Structure

For all years and sample collections, most tags (52%) were recovered from age-4 adults, followed by age-5 adults (43%) and age-3 jacks (3%). Age-2 minijacks and age-6 adults each comprised only 1% of total tag collections (Table 1).

Despite the overall age structure of the stock, approximately 86% of tagged UWR spring Chinook Salmon harvested in lower Columbia River net fisheries ($n = 2,548$) were from age-5 or age-6 adults (Table 1). In years that both gill nets and tangle nets were used (2002–2009) the age structure of fish taken in gill nets differed significantly from that of tangle nets ($\chi^2 = 31.89$, df = 3, $P < 0.001$), with proportionally more age-4 and age-6 fish harvested with gill nets. The greater proportion of age-4 fish harvested by gill nets, relative to tangle nets, could be explained by May and June catches by gill nets, when 47% of harvested fish were age 4 and tangle nets were not used.

We found no significant relationships between brood year and mean age at maturity for Chinook Salmon sampled from gill nets ($t = -1.18$, df = 12, $P = 0.260$), tangle nets ($t = -2.18$, df = 7, $P = 0.067$), recreational fisheries ($t = -0.92$, df = 14, $P = 0.374$), or hatcheries ($t = -0.68$, df = 14, $P = 0.506$).

TABLE 1. Number of coded wire tags recovered from upper Willamette River hatchery spring Chinook Salmon, ages 2–6, by sample collection type. The percent of each sample collection total represented by various age-classes is in parentheses. Data from brood years 1989–2005.

Sample collection	Age 2	Age 3	Age 4	Age 5	Age 6
Gill nets	0 (0%)	1 (0%)	172 (16%)	905 (83%)	17 (2%)
Tangle nets	0 (0%)	1 (0%)	181 (12%)	1,256 (86%)	15 (1%)
Recreational fisheries	5 (0%)	62 (1%)	2,356 (54%)	1,891 (44%)	32 (1%)
Spawning grounds	1 (0%)	20 (1%)	770 (43%)	996 (55%)	20 (1%)
Hatcheries	353 (1%)	780 (3%)	14,519 (57%)	9,797 (38%)	186 (1%)

However, the mean age of Chinook Salmon sampled on UWR spawning grounds decreased by 4% each year ($t = -2.89$, df = 14, $P = 0.012$) for brood years 1989–2004.

Sex Ratio

We found no significant difference between the sex ratios of fish taken with gill nets and tangle nets ($\chi^2 = 0.80$, df = 1, $P = 0.371$). The number of female Chinook Salmon recovered from a given cohort was highly correlated with the number of males recovered for the same cohort in lower Columbia River net fisheries ($t = 21.23$, df = 12, $P < 0.001$, $r^2 = 0.974$), UWR spawning grounds ($t = 15.27$, df = 14, $P < 0.001$, $r^2 = 0.943$), and UWR hatcheries ($t = 17.40$, df = 14, $P < 0.001$, $r^2 = 0.956$) (Figure 3). Regression slopes (b) for these relationships indicated that the ratio of males to females was not significantly different from 1:1 in lower Columbia River net fisheries ($b = 1.035 \pm 0.087$ for 95% CI) or UWR hatcheries ($b = 1.111 \pm 0.112$ for 95% CI). Yet only half as many tags were recovered from males than females on UWR spawning grounds ($b = 0.450 \pm 0.052$ for 95% CI). The high r^2 values that we observed suggested stable sex ratios in each sample collection among years.

Fork Length

Chinook Salmon taken in gill nets were a mean 27 mm longer than those taken in tangle nets ($t = 3.30$, df = 6, $P = 0.016$), after accounting for differences explained by brood year, sex,

and age. Mean fork lengths of fish taken by gill nets were not, however, different from those of all other sample collections pooled (including tangle nets) after accounting for significant effects from age, sex, PDO, and brood year ($t = 1.37$, df = 12, $P = 0.195$).

Age-5 Chinook Salmon were significantly longer than age-4 fish in all sample collections (Table 2). We also found that sex was associated with size differences for fish in all sample collections except recreational fisheries, where data for sex are typically not recorded (Table 2). In most sample collections, age-4 females were longer than age-4 males. Age-4 males were only longer than age-4 females for samples from spawning grounds. Among age-5 fish, males were longer than females in all sample collections (except where not detectable in recreational fisheries; Table 2).

We found significant evidence for a decline in mean fork length in age-5 Chinook Salmon in all sample collections except gill nets (Table 3). Although we detected no change in fork length among samples collected with gill nets or age-4 females collected at hatcheries, some significant change was detected among samples of both sexes and age-classes in all other collections (Table 3; also see Appendix). Significant first order interaction terms suggested slightly different rates of change in fork length for males, females, and both dominant age-classes sampled at hatcheries (Table 3), whereby fork length of age-5 males declined at the greatest rate (2 mm/year). Patterns observed in the pooled dataset largely reflected those of the hatchery sample collection (Table 3; Figure 4).

TABLE 2. Observed mean fork length (FL) for age-5 male spring Chinook Salmon from various sample collections, and mean relationships with FL for age-5 females, age-5 males, and age-4 females, as estimated from linear mixed models. Estimated mean FL differences for Hatcheries and Pooled represent the range of values for brood years 1989–2005.

			Mean difference in FL from age-5 males		
Sample collection	Observed mean FL for age-5 males[a]		Age-5 females	Age-4 males	Age-4 females
Gill nets	847	($n = 88$)	–4	–125	–108
Tangle nets	814	($n = 110$)	–5	–86	–64
Recreational fisheries	825	($n = 6$)	0	–108	–108
Spawning grounds	865	($n = 39$)	–35	–124	–132
Hatcheries	831	($n = 647$)	–13 to –2	–110 to –96	–106 to –81
Pooled	832	($n = 890$)	–10 to +1	–113 to –96	–106 to –79

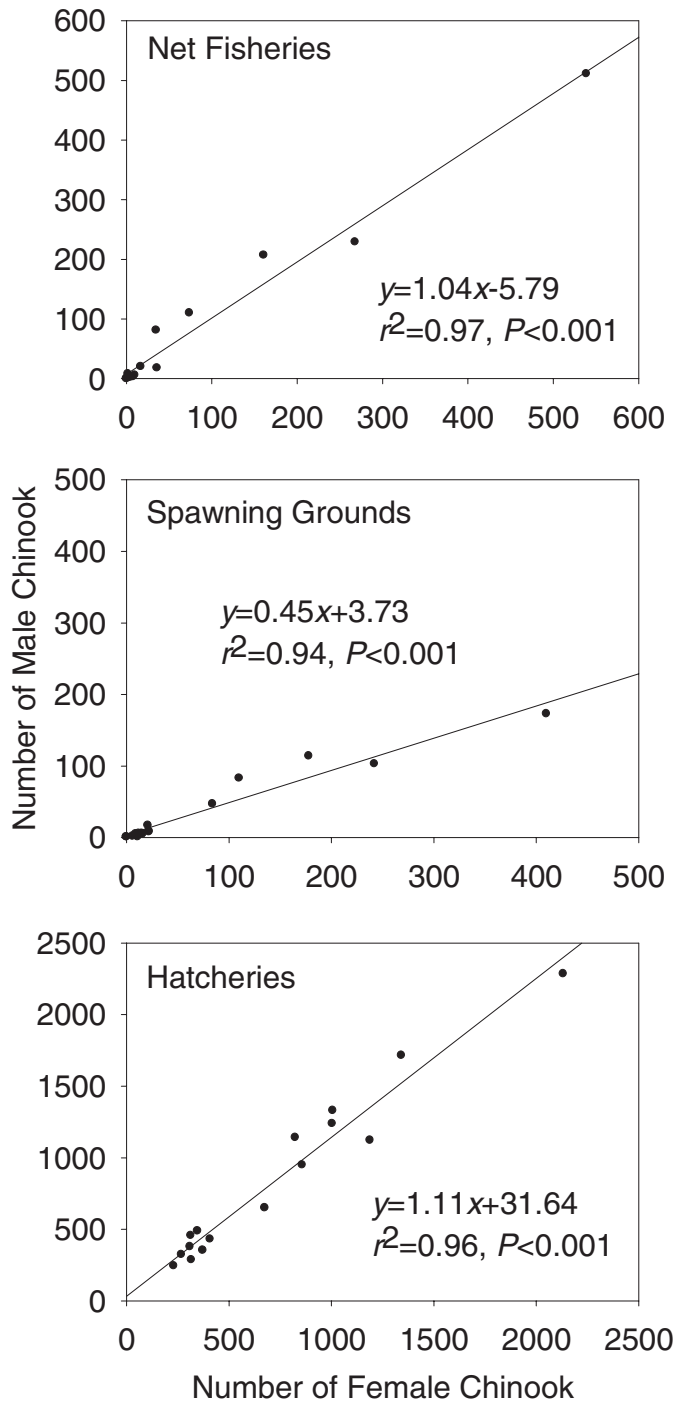[a]For brood year 1999, which presented age and sex data in all collections.

FIGURE 3. Number of tagged female (x-axis) and male (y-axis) upper Willamette River (UWR) spring Chinook Salmon recovered from Columbia River gill net fisheries (top panel), UWR spawning grounds (middle panel), and UWR hatcheries (bottom panel). Data are from age-4 and age-5 adults, brood years 1989–2005. Note scale differences.

In most sample collections, we found that during the year juvenile fish were produced (the brood year), single unit increases in the median monthly PDO index explained a significant increase in adult mean fork length (Table 3; Figure 5). Only samples from tangle nets and spawning grounds showed

TABLE 3. Coefficients and degrees of freedom from linear mixed models for the effects of median monthly PDO and brood year (as b in mm/year) on mean fork length (mm) of Willamette River hatchery spring Chinook Salmon. Data are for brood years 1989–2005, except gill nets (1989–1992 and 1995–2005) and tangle nets (1996–2005). All values are rounded to the nearest whole number and are significantly different from zero ($P < 0.05$), unless indicated as no relationship (NR) or zero. Additional model parameter values are provided in the Appendix.

Sample collection	PDO	Slope (b)				df
		Age-5 males	Age-4 males	Age-5 females	Age-4 females	
Gill nets	8	NR	NR	NR	NR	11
Tangle nets	NR	−18	−18	−18	−18	5
Recreational fisheries	10	−1	−1	−1	−1	14
Recreational fisheries	10	−1	−1	−1	−1	14
Spawning grounds	NR	−5	−5	−5	−5	14
Hatcheries	14	−2	−1	−1	0	14
Pooled	13	−2	−1	−1	0	14

no relationship with the PDO index (Table 3). We found no relationship between fork length and the MEI index (in any year) or the PDO index in years other than the brood year.

DISCUSSION

By examining data from CWTs, we found evidence of modest but statistically significant declines in mean fork length for UWR hatchery spring Chinook Salmon. We also found that while sex ratios and mean ages of UWR hatchery spring Chinook Salmon differed significantly among sample collections, these demographic characteristics generally appeared stable. We believe our study to be the first to examine these important demographic and phenotypic traits across multiple generations of this economically important stock.

Although we did not perform extrapolations from CWT data to formally reconstruct UWR hatchery populations, inferences from our data likely reflect patterns present in the entire hatchery population. According to WDFW and ODFW (2011), an estimated 47% (mean; SE = 0.01) of all adult Willamette River hatchery spring Chinook Salmon that entered the Columbia River from 1995 to 2010 were collected by hatcheries, harvested in Columbia and lower Willamette River recreational fisheries, or in lower Columbia River commercial net fisheries. In most years, the majority of these (collected) fish were recovered by hatcheries (mean ± SE, 61% ± 13%), followed by lower river recreational fisheries (32% ± 12%) and commercial net fisheries (5% ± 4%). Typically, another 5% of the total run was sampled through spawning ground surveys. Therefore, the proportions of CWTs present in each sample collection of our study (75% hatchery, 12% recreational fisheries, 7% commercial net fisheries, and 5% spawning grounds) are similar to
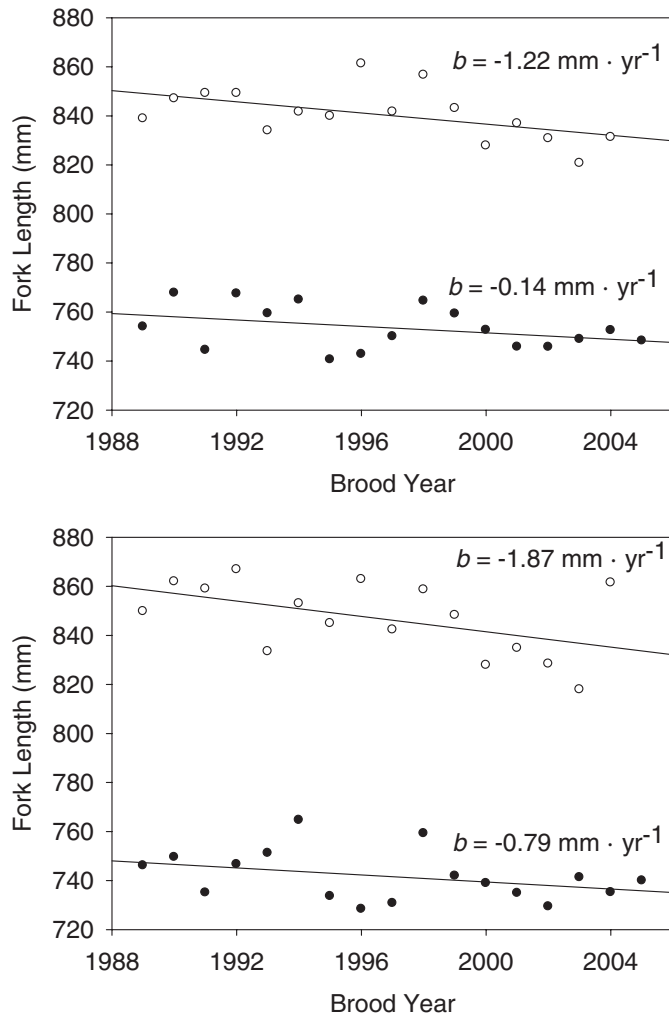
FIGURE 4. Relationships between brood year and mean fork length of mature female (top panel) and male (bottom panel) upper Willamette River spring Chinook Salmon for the dominant year-classes, age 4 (black dots) and age 5 (white dots). Mean fork lengths are for age–sex categories from the pooled dataset, each adjusted for the effect of Pacific Decadal Oscillation in each brood year. Rates of change in fork length (b) are provided for each age–sex class.
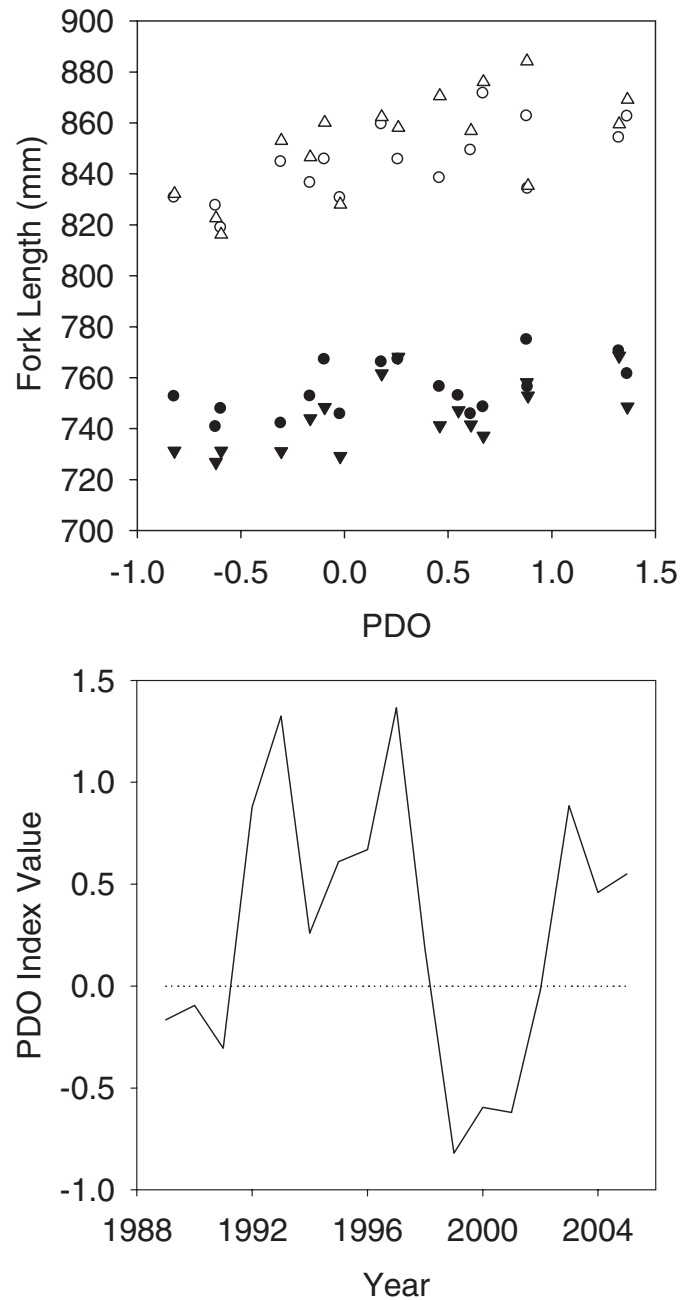

FIGURE 5. Relationship between median monthly Pacific Decadal Oscillation (PDO) index values for years 1989–2005 and the mean fork lengths of UWR hatchery spring Chinook Salmon produced in these brood years (top panel), sampled as age-5 males (white triangles), age-5 females (white dots), age-4 males (black triangles), and age-4 females (black dots). Data are pooled from all sample collections. Median monthly PDO index values (bottom panel) for years 1989–2005. Dashed line is reference for zero PDO anomaly.

average harvest and collection rates, with some underrepresentation of recreational fisheries offset by overrepresentation of hatchery collections.

Our estimates for the rates of decline in mean fork length of UWR spring Chinook Salmon (Table 3) are similar to values reported for other stocks of Pacific salmon. Bigler et al. (1996) found that mean fork lengths of Chinook Salmon from the Yukon and Kenai rivers of Alaska declined by rates that ranged between 1.74 and 6.52 mm per year, depending upon river and age at maturity. Their meta-analysis also revealed that 45 of 47 Pacific salmon populations examined showed some evidence of decreasing body size, which they attributed to broad-scale environmental conditions and density-dependent competition (Bigler et al. 1996). Using 29 years of catch and escapement data, Kendall and Quinn (2011) found that mean fork length of

male Chinook Salmon from Alaska's Nushagak River declined by 2.6 mm per year and females declined by 3.1 mm per year. They concluded that this decline could not be fully explained by the intense fisheries on this river, citing possible effects from

environmental conditions, ocean harvest, and competition with hatchery-reared salmon.

As these studies suggest, apparent trends in the mean size and age of Pacific salmon can be influenced by combinations of environmental factors, selection-driven change, and sampling bias. Ricker (1981) cited eight potential mechanisms that could lead to observed declines in mean age or length of Chinook Salmon. These included (1) increased troll fishing on immature fish that contribute to population estimates, (2) "fishing up" effects that expose late-maturing fish to increased risk of mortality, (3) extirpation of innately larger or late-maturing populations within the composite stock, (4) changes in ocean conditions that affect growth, (5) directional selection by fisheries that predominately harvest older individuals, (6) directional selection by fisheries that predominately harvest larger individuals, (7) changes in regulations governing harvest practices, and (8) some aspect of artificial propagation.

Two of the mechanisms proposed by Ricker (1981) cannot explain the trends in mean fork length that we found in UWR hatchery spring Chinook Salmon. First, because we only used data from fish collected during or after spawning migration, potential biases posed by sampling immature fish (mechanism 1) were largely avoided. Second, we focused our study on hatchery populations, none of which were extirpated during the period of sample collections (mechanism 3). Having excluded these two mechanisms, all others proposed by Ricker (1981) merit consideration.

In their analysis of size trends, Bigler et al. (1996) cited the importance of competition and broad-scale ocean conditions on growth of Pacific salmon. Though we found a strong positive relationship between mean fork length and PDO in most sample collections, this relationship did not explain the 17-year trend for fork length revealed by our data (Figure 5). Instead, the PDO index explained short-term oscillations in mean fork length. Interestingly, evidence of several recent "regime shifts" (Mantua and Hare 2002) were present in the PDO index data during the period of our study. Such regime shifts are typically recorded every 20–30 years (Mantua and Hare 2002). The positive relationship between PDO in the year prior to juvenile release and fork length of mature adults is consistent with the positive PDO–ocean productivity relationship widely recognized to occur in southeast Alaskan waters (Hare et al. 1999). In each year immediately following positive PDO anomaly years, UWR spring Chinook Salmon, which are thought to spend marine residence in southeast Alaskan waters (Weitkamp 2010), likely benefit from abundant forage fish and invertebrate prey species supported by high primary productivity of the previous year. We suspect that this pattern was not detectable for fish from tangle nets and spawning grounds because of the smaller sample sizes in these collections.

Although commercial net fisheries appear to be highly selective for age-5 Chinook Salmon, the declines we observed in mean fork length cannot simply be explained by harvest of these older fish, since size trends for both age-4 and age-5 fish were present, and evidence of a trend in age at maturity was absent for samples from hatcheries and recreational fisheries. Similarly, "fishing up effects" cannot explain the trend for declining size within age-classes. However, because data from spawning grounds suggested a precipitous decline in mean age at maturity and negative t-values were present in all other collections (though not statistically significant), continued monitoring of age at maturity seems warranted for Willamette spring Chinook Salmon populations.

A more direct mechanism than age selectivity might explain the trend in length of UWR hatchery spring Chinook Salmon. It has long been recognized that size-selective fisheries can exert strong evolutionary pressures on salmon populations, generating detectable changes in size within ten or fewer generations (reviewed by Hard et al. 2008). However, our data do not suggest that Chinook Salmon harvested in gill nets are significantly larger than found in other sample collections. Moreover, selection imposed by gill nets is limited by short seasons and strictly enforced quotas. Commercial net harvests of UWR spring Chinook Salmon have been estimated at 0.1–7.4% (median 1.2%) of the total run between 1995 and 2010 (WDFW and ODFW 2011).

Both Ricker (1981) and, more recently, Hankin et al. (2009) proposed that hatchery practices could lead to declines in mean size at maturity for Pacific salmon. Hankin et al. (2009) suggested that random matings at hatcheries could unnaturally boost the fitness of younger, smaller individuals that would otherwise be outcompeted on spawning grounds by older, larger salmon. As age at maturity appears to be a heritable trait in Chinook Salmon (Hankin et al. 1993; Kinnison et al. 2011), random matings could then increase the proportion of early maturing individuals in each generation. Yet jacks are relatively rare in UWR Chinook Salmon populations, and we have shown that there is little evidence for a trend toward earlier age at maturity in this stock. Nevertheless, random matings performed at hatcheries could still increase the fitness of smaller individuals within year-classes, inadvertently relaxing natural selection on heritable size at age. Additional research is still needed to establish how hatchery practices may influence life history and phenotypic traits of salmon. Given the trend toward smaller hatchery fish suggested by our data, we recommend that hatchery managers consider alternative spawning practices that favor the reproductive success of larger, perhaps older, individuals. Such practices may serve to compensate for selection against larger fish (regardless of the mechanism) and more closely mimic mate selection processes that occur in nature (Hankin et al. 2009).

Although we found sex ratios to differ among sample collections, the high r^2 values we obtained from our analyses (Figure 3) suggest that sex ratios within collections are stable among years. The skewed sex ratios that we observed on spawning grounds were likely the consequence of male–female differences in behavior. Female salmon expend considerable energy searching for suitable habitats to establish redd sites. After spawning, females then safeguard their reproductive investment through

active parental care, remaining on redds to tend and fan eggs. In contrast, male salmon increase their fitness by successfully locating additional mates as they become receptive (Esteve 2005; Quinn 2005; Anderson and Quinn 2007). These alternate behaviors place males at a higher risk to enter hatcheries and fish traps, often without the possibility to return to spawning grounds. In agreement with this hypothesis, we found that sex ratios in the large hatchery sample collections were slightly skewed in favor of males, though not significantly different from 1:1. In practice, the skewed sex ratios of hatchery fish on spawning grounds suggests that, in the Willamette River, females may contribute more to the proportion of hatchery spawners on natural spawning grounds than males. A significant reduction in the proportion of hatchery spawners on natural spawning grounds might therefore be achieved by excluding females from programs that return hatchery fish to the river, as females may be less likely than males to enter fish traps a second time.

In conclusion, we found that while sex ratios and age at maturity of UWR hatchery spring Chinook Salmon appeared to be stable, this stock experienced a slow but significant decline in mean fork length between brood years 1989 and 2005, with males experiencing an approximate 2–3% decrease in mean body length over four generations. Positive relationships between body size with fitness traits and reproductive success have been well documented in Pacific salmon (Fleming and Gross 1994; Dickerson et al. 2002; Knudsen et al. 2008; Williamson et al. 2010; but see Dickerson et al. 2005). Thus, even slow declines in fork length, as we have described for UWR spring Chinook Salmon, could have serious individual fitness and population productivity consequences if allowed to continue. Although we have not identified the mechanism(s) responsible for the observed trend in fork length, we recommend that hatchery spawning practices be considered as a possible contributing factor. Other candidate factors, such as climatic variables not considered in this study, should also receive due consideration. Furthermore, we recommend that future research investigate the stability of fork length and other potentially important phenotypic traits in threatened wild UWR spring Chinook Salmon.

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APPENDIX: DETAILED DATA

TABLE A.1.   Linear mixed model variable coefficients, standard errors (SE), degrees of freedom (df), *t*-values, and *P*-values. Variables are significant predictors of mean fork length for upper Willamette River hatchery spring Chinook Salmon derived from samples collected by various methods (see text), brood years 1989–2005. Age5 and Female are indicator variables (value = 0, 1); PDO and BroodYear are continuous. Coefficient units are in millimeters. For example, the mean fork length (FL) of an age-5 male collected from spawning grounds in 2002 is estimated as follows:

$$FL = 11436.46 + (2002 \cdot -5.34) + (1 \cdot 123.80) + (0 \cdot -8.13) + (0 \cdot -26.86) = 871 \text{ (mm)}.$$

Sample collection	Variables	Value	SE	df	*t*-value	*P*-value
Gill nets	Intercept	731.67	5.95	928	122.90	<0.01
	PDO	8.45	2.70	11	3.13	0.01
	Age5	124.92	6.34	928	19.70	<0.01
	Female	16.45	8.45	928	1.95	0.05
	Female:Age5	−20.02	8.98	928	−2.23	0.03
Tangle nets	Intercept	37,431.33	2,695.73	1,371	13.89	<0.01
	BroodYear	−18.36	1.35	5	−13.62	<0.01
	Age5	86.17	5.66	1,371	15.22	<0.01
	Female	22.25	7.43	1,371	3.00	<0.01
	Female:Age5	−26.82	7.95	1,371	−3.37	<0.01
Recreational fisheries	Intercept	2,495.87	822.91	4,120	3.03	0.00
	PDO	10.05	3.33	14	3.02	0.01
	BroodYear	−0.88	0.41	14	−2.13	0.05
	Age5	108.33	2.16	4,120	50.23	<0.01
Spawning grounds	Intercept	11,436.46	2,711.25	1,637	4.22	<0.01
	BroodYear	−5.34	1.36	14	−3.93	<0.01
	Age5	123.80	6.06	1,637	20.43	<0.01
	Female	−8.13	5.35	1,637	−1.52	0.13
	Female:Age5	−26.86	7.39	1,637	−3.63	<0.01
Hatcheries	Intercept	2,590.32	685.66	24,245	3.78	<0.01
	PDO	13.50	2.50	14	5.40	<0.01
	BroodYear	−0.93	0.34	14	−2.70	0.02
	Age5	1,900.50	408.12	24,245	4.66	<0.01
	Female	−1,388.26	373.92	24,245	−3.71	<0.01
	Female:Age5	−17.13	1.50	24,245	−11.44	<0.01
	BroodYear:Female	0.70	0.19	24,245	3.74	<0.01
	BroodYear:Age5	−0.90	0.20	24,245	−4.38	<0.01
Pooled data	Intercept	2,306.70	692.65	28,342	3.33	<0.01
	PDO	13.04	2.53	14	5.16	<0.01
	BroodYear	−0.79	0.35	14	−2.26	0.04
	Age5	2,281.65	401.15	28,342	5.69	<0.01
	Female	−1,285.62	369.79	28,342	−3.48	<0.01
	Female:Age5	−17.03	1.39	28,342	−12.28	<0.01
	BroodYear:Female	0.65	0.19	28,342	3.51	<0.01
	BroodYear:Age5	−1.09	0.20	28,342	−5.41	<0.01