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ARTICLE

Stock Differences in Growth, Smolting, and Early Male Maturation in Hatchery Spring Chinook Salmon: a Common-Garden Experiment

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Abstract

Hatchery spring Chinook Salmon *Oncorhynchus tshawytscha* from Parkdale Hatchery on the Hood River, Oregon, and Carson National Fish Hatchery (CNFH) on the Wind River, Washington, were reared under a common-garden experimental regime at CNFH over three consecutive brood years (2008–2010) to assess the effects of stock on smoltification and early male maturation. Rearing groups were monitored for size, percent solid (a surrogate for whole-body lipid), gill Na^+, K^+ -ATPase activity, and rate of precocious maturation in males (i.e., age-2 minijack rate). Despite rearing of the stocks under identical conditions, the out-of-basin Hood River stock was significantly smaller throughout the study and at release as smolts, had lower whole-body lipid at release, and had lower gill Na^+, K^+ -ATPase activity at release than the Carson stock; furthermore, the Hood River stock exhibited much higher mean minijack rates than the Carson stock (45% versus 23% of males). Using logistic regression, we demonstrated that the threshold size for initiation of early male maturation was significantly lower for the Hood River stock than for the Carson stock, suggesting a genetic basis for this life history difference. The present study highlights the importance of understanding how specific genotypes may respond differently to the unique environmental conditions in a given hatchery environment. These differences may in turn influence physiological and life history pathways that affect smolt-to-adult return rates and the demography of returning adults.

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In salmonids, male age at maturation is phenotypically plastic and is influenced by environmental (Shearer and Swanson 2000; Campbell et al. 2003; Larsen et al. 2013) and genetic (Hard et al. 1985; Hankin et al. 1993; Heath et al. 1994, 2002) factors. Several recent studies of Chinook Salmon *Oncorhynchus tshawytscha* have described the occurrence, prevalence, and distribution of early maturing males (commonly referred to as “minijacks”) in Columbia River basin hatchery programs (Beckman and Larsen 2005; Harstad et al. 2014; Spangenberg et al. 2014). These studies have documented that hatchery rearing conditions can promote early male maturation through physiological and endocrine processes related to high growth rates or fat levels during seasonally sensitive windows (Silverstein et al. 1998; Shearer and Swanson 2000; Larsen et al. 2006; Shearer et al. 2006). Moreover, male maturation as minijacks has been reported to occur at rates as high as 71.4% in some hatchery programs, and an average minijack rate of 31% was calculated for male Chinook Salmon in 14 Columbia River hatchery programs (Harstad et al. 2014).

High rates of early male maturation may have implications for the long-term genetic integrity of natural and hatchery populations, and there may be ecological consequences associated with releasing significant numbers of precociously mature fish into streams and rivers. A complete evaluation of such consequences has not been conducted, but clearly if a semelparous Chinook Salmon matures as an age-2 minijack (and subsequently dies), that same fish cannot return as a full-sized age-4 or age-5 adult for harvest or broodstock. Early male maturation represents an important component of a diverse life history portfolio in naturally rearing salmonids by serving as a potential conduit for gene flow across cohorts and by increasing the effective population size (Myers et al. 1986; Jones and Hutchings 2001; Johnstone et al. 2013). However, recent evidence suggests that the relative reproductive success of hatchery minijacks spawning in the wild is low (Ford et al. 2012). The phenomenon of early maturation is therefore worthy of further study within the context of optimizing salmon hatchery operations and for understanding and evaluating the effectiveness of hatchery programs for potential supplementation of Endangered Species Act-listed and unlisted salmon populations.

The primary purpose of salmon hatchery programs in the Columbia River basin is to produce juvenile salmon that will smolt, migrate to the sea, rear for one or more years, initiate maturation, and then return to freshwater and (1) contribute to harvest opportunities or (2) successfully spawn either in hatcheries or naturally in rivers. Smoltification is a developmental process that initiates the physiological and behavioral cascade associated with migration to the ocean. The physiological changes associated with smolting have been positively correlated with the spring growth rate and the adult return rate (Beckman et al. 1999). The survival rate (or smolt-to-adult return rate [SAR]) is one of the key metrics of hatchery performance, assessing the proportion of released smolts that eventually return as adults. One factor that is believed to contribute to

high SARs is simply the size of individual fish. Previous studies have found that among hatchery fish (Martin and Wertheimer 1989) and wild fish (Zabel and Achord 2004), larger smolts have higher rates of survival than smaller smolts. However, elevated summer and autumn growth rates, which are used to generate larger hatchery smolts, also stimulate early maturation in males. Hatchery managers must therefore balance the benefits of higher growth and increased smolt size against the costs associated with elevated rates of early male maturation (Larsen et al. 2013; Spangenberg et al. 2014).

Optimization of salmon hatchery programs might best be accomplished through experimental testing, monitoring, and evaluation. However, hatchery-scale experiments are relatively rare; they are both expensive and time consuming, as obtaining adult return data for Chinook Salmon can take up to 4 years after the smolts are released. In the present paper and in our companion paper (Spangenberg et al. 2014), we describe a multiple-year study examining smolt development and early male maturation in spring Chinook Salmon from different stocks—some reared in common and others reared separately—at middle Columbia River basin hatcheries. Previously, we (Spangenberg et al. 2014) detailed the results of rearing spring Chinook Salmon of the Hood River, Oregon, stock at three different hatcheries, and we found that minijack rates significantly differed among the hatcheries. In the current investigation, we take the reciprocal approach and use a common-garden experimental construct to test the null hypothesis that spring Chinook Salmon of the Carson stock (Carson National Fish Hatchery [CNFH], Carson, Washington) and the Hood River stock would be phenotypically indistinguishable with regard to growth, energetics, smoltification, and early male maturation when reared under identical conditions at CNFH.

At the local scale, the motivation for this experiment was the limited rearing capacity at Parkdale Hatchery on the Hood River; the facility’s lack of capacity prevented it from meeting spring Chinook Salmon production needs in the Hood River basin. Thus, we investigated the efficacy of rearing Hood River-stock fish at CNFH, which lies in close geographic proximity to the Hood River (~80-km driving distance) and has excess rearing capacity. On a broader scale, similar scenarios are relatively common in Pacific Northwest salmon hatcheries that conduct broodstock transfers among facilities—most notably, when the number of returning adults in one basin is inadequate to meet production goals during a given year. In those cases, managers obtain excess broodstock from other facilities with adequate adult returns, and the progeny from the out-of-basin broodstock are reared at the hatchery facility that is lacking adult returns. Thus, results from this investigation may have broader implications for hatchery management practices throughout the Pacific Northwest.

METHODS

Chinook Salmon stocks.—Spring Chinook Salmon of the Carson and Hood River stocks were reared at CNFH, which is

located at river kilometer (rkm) 29 (rkm 0 = confluence with the Columbia River) on the Wind River in Washington (45°50'28.9386"N, 121°56'43.6668"W). The Carson stock is typically reared for production at CNFH. Historically, spring Chinook Salmon were not native to the Wind River. Initial broodstock for CNFH were collected from the adult fish ladder at Bonneville Dam (Columbia River) in 1958–1959 and included a mixture of spring Chinook Salmon that were returning to the Snake River and the middle and upper Columbia River (Howell et al. 1984). The spring Chinook Salmon program at CNFH is a segregated hatchery program. By definition, segregated hatchery programs generally use only hatchery-origin returning adults (marked with adipose fin clips, coded wire tags, PIT tags, etc.). Thus, in theory, the hatchery population is genetically isolated from naturally rearing populations (HSRG 2009).

Hood River-stock spring Chinook Salmon were from Parkdale Hatchery, which is located at rkm 30.2 (rkm 0 = confluence with the Columbia River) on the West Fork Hood River, Oregon (45°31'25.0608"N, 121°37'18.0408"W). Spring Chinook Salmon were extirpated from the Hood River basin in the late 1960s to early 1970s as a result of both natural and anthropogenic factors (HDR FishPro 2008). The Oregon Department of Fish and Wildlife (ODFW) conducted direct releases of Carson-stock smolts in the West Fork Hood River from 1986 to 1991 to provide a sport fishery. Beginning in 1993, the Confederated Tribes of Warm Springs and the ODFW began a deliberate effort to re-establish a naturally reproducing population of spring Chinook Salmon in the Hood River basin by using acclimated releases of Deschutes River (Oregon)-stock smolts originating from Round Butte Hatchery (44°36'20.5776"N, 121°16'37.9056"W; HDR FishPro 2008). In more recent years, hatchery-origin adults that return to the Hood River are used for broodstock each year in an attempt to "localize" the population, but during years when adult returns do not meet broodstock needs at Parkdale Hatchery, they are supplemented with Chinook Salmon eggs from Round Butte Hatchery. The ultimate objective for this program was to develop an integrated, localized brood source utilizing only natural-origin returning adults (HSRG 2009). In conclusion, although the two stocks used in our study shared some Carson-stock lineage in the late 1980s to early 1990s, they have essentially been genetically isolated from one another since that time. To date, comprehensive testing to establish specific genetic differences between the Hood River stock and either the Carson stock or the Deschutes River stock has not been undertaken.

During 2008–2010, Hood River broodstock adults were collected at an adult trap (rkm 7.2) during their return migration in the Hood River, were held in adult ponds at Parkdale Hatchery for 3–4 months until fully mature, and then were artificially spawned over a 3-week period (August 4–20). Eggs at the eyed stage of development ($n = 50,000$ – $65,000$ depending on the brood year [BY]) were subsequently transferred to

CNFH for final incubation. Likewise, during 2008–2010, Carson broodstock adults were collected at CNFH and were held in adult ponds for 3–4 months prior to artificial spawning, which took place over 3 weeks (August 11–27). Water at CNFH is sourced from Tye Springs, and water temperature ranges from a low of 5–6°C throughout most of the year to a high of 8°C in late summer.

Hatchery rearing.—In accordance with standard hatchery protocols (Stickney 1991), eggs from each stock were reared to the swim-up stage in indoor egg incubation trays. Fry were then transferred to outdoor raceways and were reared to the smolt stage. Ponding dates in 2008–2010 ranged from January 27 to February 20 for both stocks but varied by only 1 or 2 d between stocks within years. Throughout rearing, the fish were fed Bio-Diet Starter and then Bio-Diet Grower (Bio-Oregon, Longview, Washington) according to the standard practices at CNFH. The Hood River stock was reared in a single adjacent raceway under conditions (including density) that were identical to those experienced by the Carson stock.

Carson-stock fish remained at CNFH until their forced release directly into the Wind River during early April of 2010–2012. Fish of the Hood River stock were reared at CNFH until March 24, 2010 (BY 2008); March 23, 2011 (BY 2009); or February 22, 2012 (BY 2010). Hood River-stock fish were then transferred by tanker truck to an acclimation site on the West Fork Hood River, approximately 16 km from Parkdale Hatchery (BY 2008 and BY 2009: Blackberry acclimation site [45°31'16.0824"N, 121°44'37.2192"W], rkm 34.3 from the Columbia River confluence; BY 2010: Moving Falls acclimation site [45°34'22.3566"N, 121°39'25.8372"W], rkm 23.9 from the Columbia River confluence). For all three BYs, the final sampling of the Hood River stock occurred at the acclimation site prior to the fish's forced release, which took place during mid-April.

Sample collection.—For each BY, Hood River-stock and Carson-stock fish were each sampled from a single raceway during October and then monthly (same raceway) from January to their release in April. In October, a nonlethal size-census was conducted by sampling 300 fish/stock. In October, January, February, March, and April, a lethal sample of 25 fish/stock was obtained for use in analysis of physiological variables. Just prior to release, a lethal size-census ($n = 25$ fish) and minijack census ($n = 275$ additional fish) were conducted for each stock. Censuses took place on April 8, 2010 (BY 2008), April 7, 2011 (BY 2009), and April 11, 2012 (BY 2010), for the Carson stock (at CNFH). Censuses occurred on April 20, 2010 (BY 2008), April 19, 2011 (BY 2009), and April 17, 2012 (BY 2010), for the Hood River stock (at the acclimation site).

All fish were randomly collected by dipnetting from the hatchery raceways. For nonlethal sampling, fish were lightly anesthetized in a buffered 0.01% solution of tricaine methane-sulfonate (MS-222; Argent Chemical Laboratories, Redmond, Washington); after measurements were recorded, the fish were allowed to recover in freshwater and were subsequently

returned to the raceway. For lethal sampling, fish were individually euthanized in a 0.05% solution of MS-222.

Each fish was measured for FL (nearest 1.0 mm) and weight (nearest 0.1 g). Phenotypic sex of the fish was determined by visual examination of the gonads. Filaments from the first gill arch on the left side of the fish were placed in a solution of sucrose, EDTA, and imidazole according to the methods described by Zaugg (1982); the gill filament samples were frozen on dry ice for transport and were stored at -80°C prior to being analyzed for gill Na^+ , K^+ -ATPase activity. For collection of whole bodies (BY 2009 and BY 2010 only), the gut contents of each fish were removed from the stomach and intestine to control for variation in the contents of the digestive tract. Carcasses were individually labeled, bagged, and frozen for future measurement of percent solid, which was used as a surrogate for whole-body lipid. During the minijack census in April, fish were euthanized and measured for FL and weight. The caudal peduncle was severed, and blood was collected from the caudal vein by using heparinized Natelson tubes (VWR Scientific, Radnor, Pennsylvania). The blood samples from all males were then centrifuged at $3,000 \times g$ for 5 min; the plasma was transferred to a new tube, frozen and transported on dry ice, and stored frozen at -80°C for future measurement of plasma 11-ketotestosterone (11-KT).

Laboratory analyses.—Shearer (1994) demonstrated that whole-body moisture is inversely related to whole-body lipid in salmonids. Thus, total dry solid provides a relative index of whole-body lipid. To determine percent solid, frozen fish were cut into 0.5-cm^3 pieces, placed on aluminum weighing pans, and dried to a consistent weight in an oven at 40°C (~ 48 h). Wet and dry weights were then used to calculate the percent solid for each fish. Larsen et al. (2010) found that gill Na^+ , K^+ -ATPase activity is suppressed in maturing male spring Chinook Salmon; therefore, we only measured gill Na^+ , K^+ -ATPase activity in females and immature males (i.e., minijacks were excluded) so as to obtain an accurate measure of smolt status that would be independent of the proportion of fish maturing in each stock. Gill Na^+ , K^+ -ATPase activity was measured according to the methods of McCormick (1993); all values are reported in micromoles of inorganic phosphate per milligram of protein per hour ($\mu\text{mol PO}_4\text{-mg prot}^{-1}\text{-h}^{-1}$). Plasma 11-KT levels (ng/mL) were determined by an enzyme-linked immunosorbent assay (ELISA) adapted from the method of Cuisset et al. (1994) using acetylcholinesterase tracer and pre-coated (mouse anti-rabbit immunoglobulin G) 96-well plates (Cayman Chemical, Ann Arbor, Michigan). To control for potential interference from steroid-binding proteins, the plasma was heat extracted and then analyzed according to the method of Schulz et al. (1994). Plasma was diluted 1:3 in sterile water and was placed in a water bath at 80°C for 1 h. Extracts were centrifuged at 13,000 rotations/min ($\sim 18,000 \times g$) for 6 min, and the supernatant was transferred to a new tube prior to ELISA.

Data analyses.—Fork length, percent solid, and gill Na^+ , K^+ -ATPase activity were analyzed by using two-way ANOVA models for stock and BY (main effects) and the stock \times BY interaction. For clearer interpretation of main effects in the two-way ANOVAs, we report results from additive models (those excluding the interaction term). To test for (1) differences between stocks within a BY and (2) differences among BYs within a stock, we conducted one-way ANOVAs with Bonferroni multiple comparison tests to compare FL, percent solid, and gill Na^+ , K^+ -ATPase activity for all stock and BY combinations. The minijack rates were arcsine transformed (Zar 1988) and the mean minijack rate was analyzed for differences between stocks by using an unpaired *t*-test with BYs as replicates. The incidence of minijack maturation is a binary variable, so the relationship between male size at age (FL measured during the minijack census; age = 20 months post-parental spawning [PPS]) and the minijack rate was determined for each stock via logistic regression. Finally, to test for differences between stocks, we calculated estimates of FL at 50% minijack maturation from the individual logistic regression models for each stock and each BY separately and analyzed the estimates by using unpaired *t*-tests with BYs serving as replicates. STATA version 12 (StataCorp LP, College Station, Texas) was used to analyze all data except size at 50% minijack maturation, which was analyzed by using the R package “doBy.” The statistical significance level α was set at 0.05.

RESULTS

Length, Weight, and Percent Solid

In both stocks and for all three BYs of spring Chinook Salmon, the mean FL increased from October through release in April (Figure 1). Overall, Carson-stock fish were less variable in FL across BYs, and they were larger than the Hood River-stock fish both in October (mean difference = 7.3 mm; stock: $F_{1, 1,797} = 780.2$, $P = 0.000$; Figure 2A) and in April (mean difference = 7.6 mm; stock: $F_{1, 146} = 35.35$, $P = 0.000$; Figure 2B). The BY main effect and the stock \times BY interaction effect were also significant for October FL (stock: $F_{2, 1,797} = 90.7$, $P = 0.000$; stock \times BY interaction: $F_{2, 1,795} = 84.2$, $P = 0.000$) and April FL (BY: $F_{2, 146} = 15.67$, $P = 0.000$; stock \times BY interaction: $F_{2, 144} = 4.63$, $P = 0.011$). There were size differences among BYs within each stock (Figure 2A, B). The FL of Hood River fish in October was smaller for BY 2009 than for BY 2008 (mean difference = 8.3 mm; $P = 0.000$) or for BY 2010 (mean difference = 4.5 mm; $P = 0.000$). This trend in size differences among BYs of Hood River fish continued through April (BY 2008 versus BY 2009: mean difference = 12.2 mm, $P = 0.000$; BY 2009 versus BY 2010: mean difference = 9.4 mm; $P = 0.001$). Weight (data not shown due to the high correlation between FL and weight) followed the same trends as FL. The mean (\pm SE) weight of Carson-stock fish at release was 23.9 ± 1.1 g for BY 2008, 22.0 ± 0.8 g for BY 2009, and 23.9 ± 1.2 g for BY 2010. The mean weight of Hood

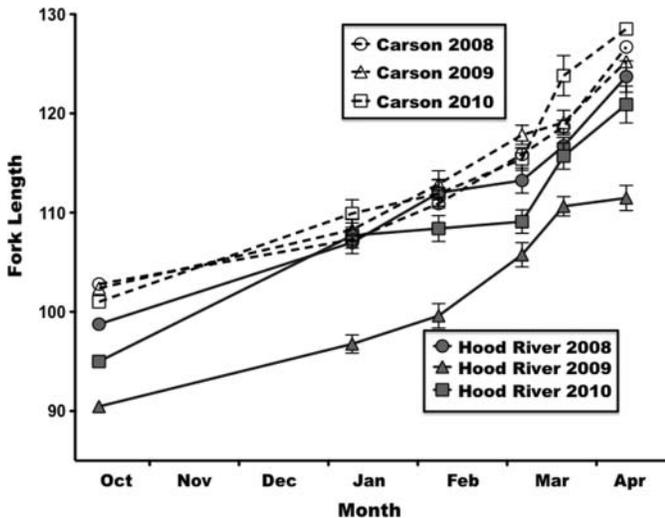


FIGURE 1. Mean FL (mm; \pm SE) from October to April for spring Chinook Salmon (Hood River and Carson stocks; brood years 2008–2010) reared at Carson National Fish Hatchery, Carson, Washington ($n = 25$ fish/sample). Statistical differences between stocks and among brood years were observed at all sampling dates; for visual clarity, data from the first (October) and last (April) sampling dates are presented in Figure 2A and B.

River-stock fish at release was 22.3 ± 1.1 g for BY 2008, 16.4 ± 0.6 g for BY 2009, and 20.3 ± 1.1 g for BY 2010.

Percent solid was determined only for BY 2009 and BY 2010. In October (Figure 2C), the mean percent solid was not significantly different between BYs within stocks (BY: $F_{1, 98} = 0.02$, $P = 0.88$) but was higher in Carson-stock fish than in Hood River-stock fish across BYs (mean difference = 1.3%; stock: $F_{1, 98} = 65.38$, $P = 0.000$). The stock \times BY interaction effect for percent solid in October was significant ($F_{1, 97} = 5.32$, $P = 0.023$), indicating that the degree of difference in percent solid between the two stocks varied between BYs. In April (Figure 2D), the mean percent solid differed between BYs within stocks (stock: $F_{1, 97} = 35.81$, $P = 0.003$) and between stocks within BYs (stock: $F_{1, 97} = 0.000$); percent solid was higher overall in Carson-stock than Hood River-stock fish (mean difference = 1.0%). The stock \times BY interaction effect for percent solid in April was not significant ($F_{1, 96} = 0.01$, $P = 0.938$).

Smolt Development

Gill Na^+ , K^+ -ATPase activity increased between January and April for all three BYs of both stocks, indicating that fish of each stock underwent smoltification (Figure 2E, F). Overall, gill Na^+ , K^+ -ATPase activity was higher in Carson-stock fish than in Hood River-stock fish during both January (mean difference = $0.22 \mu\text{mol PO}_4 \cdot \text{mg prot}^{-1} \cdot \text{h}^{-1}$; stock: $F_{1, 119} = 15.01$, $P = 0.000$; Figure 2E) and April (mean difference = $0.85 \mu\text{mol PO}_4 \cdot \text{mg prot}^{-1} \cdot \text{h}^{-1}$; stock: $F_{1, 113} = 17.56$, $P = 0.000$; Figure 2F). The BY main effect and the stock \times BY

interaction effect were significant for April (BY: $F_{2, 113} = 5.09$, $P = 0.008$; stock \times BY interaction: $F_{2, 111} = 3.3$, $P = 0.04$) but not for January (BY: $F_{2, 119} = 0.68$, $P = 0.509$; stock \times BY interaction: $F_{2, 117} = 1.55$, $P = 0.217$). The significant BY effect and stock \times BY interaction effect in April were driven by Hood River-stock fish from BY 2010, for which Na^+ , K^+ -ATPase levels were significantly lower than those of Carson-stock fish from BY 2010 (mean difference = $1.36 \mu\text{mol PO}_4 \cdot \text{mg prot}^{-1} \cdot \text{h}^{-1}$; $P = 0.002$) and Hood River fish from BY 2009 (mean difference = $1.35 \mu\text{mol PO}_4 \cdot \text{mg prot}^{-1} \cdot \text{h}^{-1}$; $P = 0.003$).

Precocious Maturation in Males

Minijack rates were variable among BYs within stocks and between the two stocks overall. Minijack rates ranged from 35% to 57% of the Hood River-stock males and from 19% to 29% of the Carson-stock males (Figure 3). With BYs serving as replicates, the mean (\pm SE) minijack rate for Hood River-stock males ($45 \pm 6.5\%$) was significantly higher than that of Carson-stock males ($23 \pm 3.4\%$; $t = 3.02$, $df = 4$, $P = 0.039$). Logistic regression of the incidence of minijack maturation against male size at age (i.e., FL at 20 months PPS) suggested that the maturation threshold differed between the Hood River stock and the Carson stock (Figure 4A). The predicted FL (mm) at 50% minijack maturity was higher for Carson-stock fish (mean \pm SE = 136.3 ± 1.8 mm) than for Hood River-stock fish (125.2 ± 0.9 mm; $t = 5.70$, $df = 4$, $P = 0.005$; Figure 4B), representing a 9% increase in threshold maturation size relative to that of the Hood River stock.

DISCUSSION

We used a common-garden experimental design to demonstrate the importance of genetics \times environment interactions for determining differences in smolt development and early male maturation between two spring Chinook Salmon stocks that were reared under identical conditions at the same hatchery. The present results have significant implications for managers who are considering the transfer of salmonid stocks between culture facilities for supplementation purposes. One might anticipate that two stocks of spring Chinook Salmon from mid-Columbia River basin hatchery facilities in close geographic proximity would respond in a relatively similar manner when reared under common-garden conditions. However, the null hypothesis was rejected, as fish of the two stocks differed significantly—sometimes unpredictably so—in a number of characteristics. Hood River-stock fish were smaller than Carson-stock fish throughout the study from the first sampling in October to the time of release in April. Percent solid, serving as an index of whole-body lipid level, was consistently lower in Hood River-stock fish than in Carson-stock fish. Gill Na^+ , K^+ -ATPase activity measured at the time of release in the spring was significantly lower in the Hood River stock

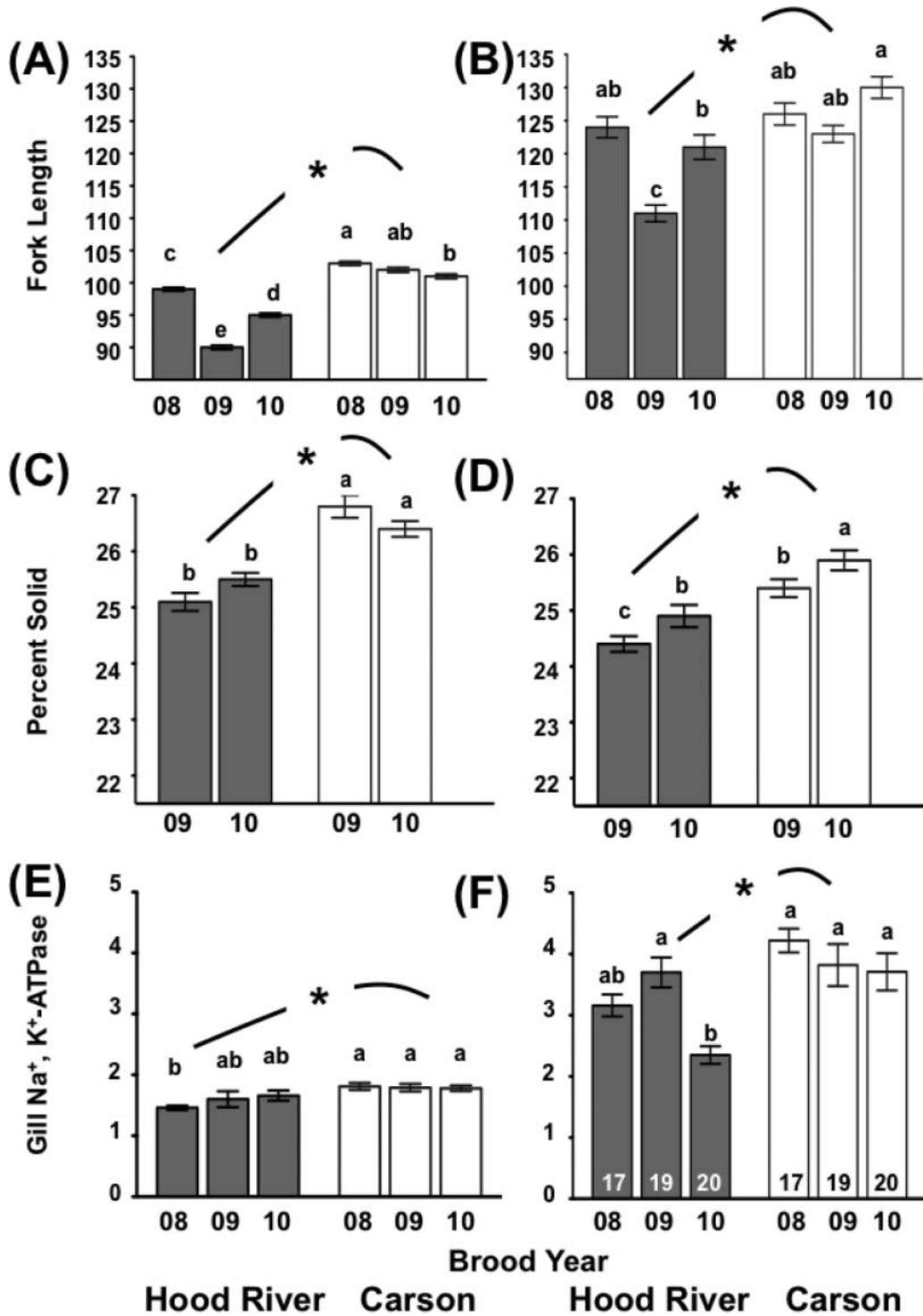


FIGURE 2. Mean (\pm SE) attributes of spring Chinook Salmon (Hood River and Carson stocks; brood years [BY] 2008 [08], 2009 [09], and 2010 [10]) reared at Carson National Fish Hatchery: (A), (B) FL (mm) in October ($n = 300$ fish/stock) and April ($n = 25$ fish/stock); (C), (D) percent solid (for BY 2009 and BY 2010 fish) in October and April ($n = 25$ fish/stock); and (E), (F) gill Na⁺, K⁺-ATPase activity ($\mu\text{mol PO}_4\text{-mg protein}^{-1}\cdot\text{h}^{-1}$) in January ($n = 25$ fish/stock) and April (minijacks were excluded from ATPase analysis; April n [shown on each bar] varied based on the number of minijacks excluded from the sample of 25 fish). On each graph, means without a letter in common are significantly different (Bonferroni multiple comparison test). Asterisks indicate a significant overall effect of stock (two-way ANOVA, $\alpha = 0.05$).

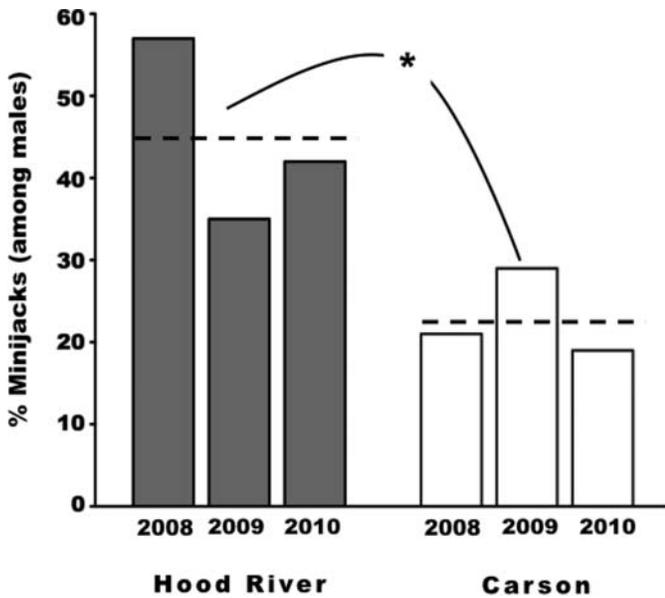


FIGURE 3. Percentage of spring Chinook Salmon males (Hood River and Carson stocks; brood years 2008–2010) that were sampled in the April prior to release and were identified as minijacks. Brood years served as replicates for calculation of the mean minijack rate (dashed line) for each stock. The asterisk indicates a significant difference in arcsine-transformed minijack rates ($\alpha = 0.05$).

than in the Carson stock. We found that minijack rates were significantly higher (approximately twofold) in the Hood River-stock males than in Carson-stock males; the threshold size at age for 50% minijack maturity was significantly lower for the Hood River stock than for the Carson stock.

Despite the fact that spring Chinook Salmon of the Carson and Hood River stocks were ponded within 1–2 d of each other and were reared under similar conditions, the Carson-stock fish were consistently larger and had higher whole-body lipid levels than Hood River-stock fish. The differences in size measured at the first sampling date in October were established during the first year of life and were maintained throughout the remainder of the study. From a genetic perspective, the Hood River stock may not be as well adapted as the Carson stock to the rearing conditions typical of CNFH. Genetic differences in feed intake, growth, and feed utilization have been observed in studies of Atlantic Salmon *Salmo salar* (Thodesen et al. 2001), and such differences may similarly exist between the Hood River and Carson stocks examined here. Ultimately, the between-stock difference in fish size at release is a basic but potentially very important factor, especially considering the positive correlation between smolt size and SARs in salmonids (Martin and Wertheimer 1989; Zabel and Achord 2004). Unfortunately, a simple increase in rations for Hood River-stock fish reared at CNFH may not be a viable strategy for improving their sizes at release or their SARs because (1) Hood River fish were already fed at a maximal rate for the water temperatures at CNFH and (2) larger size

might only serve to further increase the minijack rates in the males.

Increases in growth rate and dietary lipid are associated with increased minijack rates (Silverstein et al. 1998; Shearer and Swanson 2000; Larsen et al. 2006, 2013). Based on the observed differences in growth and lipid levels, one might anticipate that the Carson-stock fish would have higher minijack rates than Hood River-stock fish. However, the opposite relationship was observed: on average, 45% of the Hood River-stock males matured as minijacks, whereas 23% of the Carson-stock males did so. This result suggests that the two stocks vary with regard to their intrinsic growth and energetic threshold for initiating maturation. Thus, the Carson stock might have to grow to a larger body size at release and to achieve higher whole-body lipid levels than the Hood River stock at CNFH before realizing comparable minijack rates; alternatively, Carson-stock fish might never express a similar minijack rate regardless of their size at release. Finally, it should be reiterated that the Hood River-stock fish were sampled 6–12 d (depending on year) later in April than the Carson stock, so the Hood River stock had an opportunity for additional growth prior to final sampling. Therefore, our observations of size-at-age differences for comparisons of 50% minijack maturity were relatively conservative and may in fact underestimate the actual differences between the two stocks.

Studies of Atlantic Salmon have shown that individuals whose size, growth rate, and/or energy stores exceed some genetically determined threshold at a specific age are more likely to initiate the maturation process (Myers and Hutchings 1986; Aubin-Horth and Dodson 2004; Piche et al. 2008). Piche et al. (2008) modeled the threshold graphically as a discontinuous norm of reaction for size at age (7 months old) for different populations of naturally rearing Atlantic Salmon in Nova Scotia, Canada. Using a common-garden experimental design with pure and mixed crosses, Piche et al. (2008) provided evidence of genetic variation in the size threshold for precocious maturation in age-1 parr. To our knowledge, the current investigation is the first to apply this approach to modeling the relationship between size at age (20 months PPS) and the age-2 minijack maturation rate in spring Chinook Salmon (Figure 4). It should be noted that 20 months PPS is approximately 5–7 months after the “physiological decision” to mature as a minijack, and spawning by minijacks occurs at 24 months of age (Campbell et al. 2003). However, the threshold analysis allows for a comparison of sizes among individuals at a point in development when immature and maturing males can be differentiated based on simple visual inspection, the gonadosomatic index, or the plasma 11-KT level (Larsen et al. 2004). Furthermore, in the aforementioned studies of Atlantic Salmon, fish size was determined at 7 months of age—approximately 5 months prior to spawning as 12-month-old precocious parr. The physiological maturation decision in age-1 male Atlantic Salmon (Thorpe et al. 1998) or Chinook

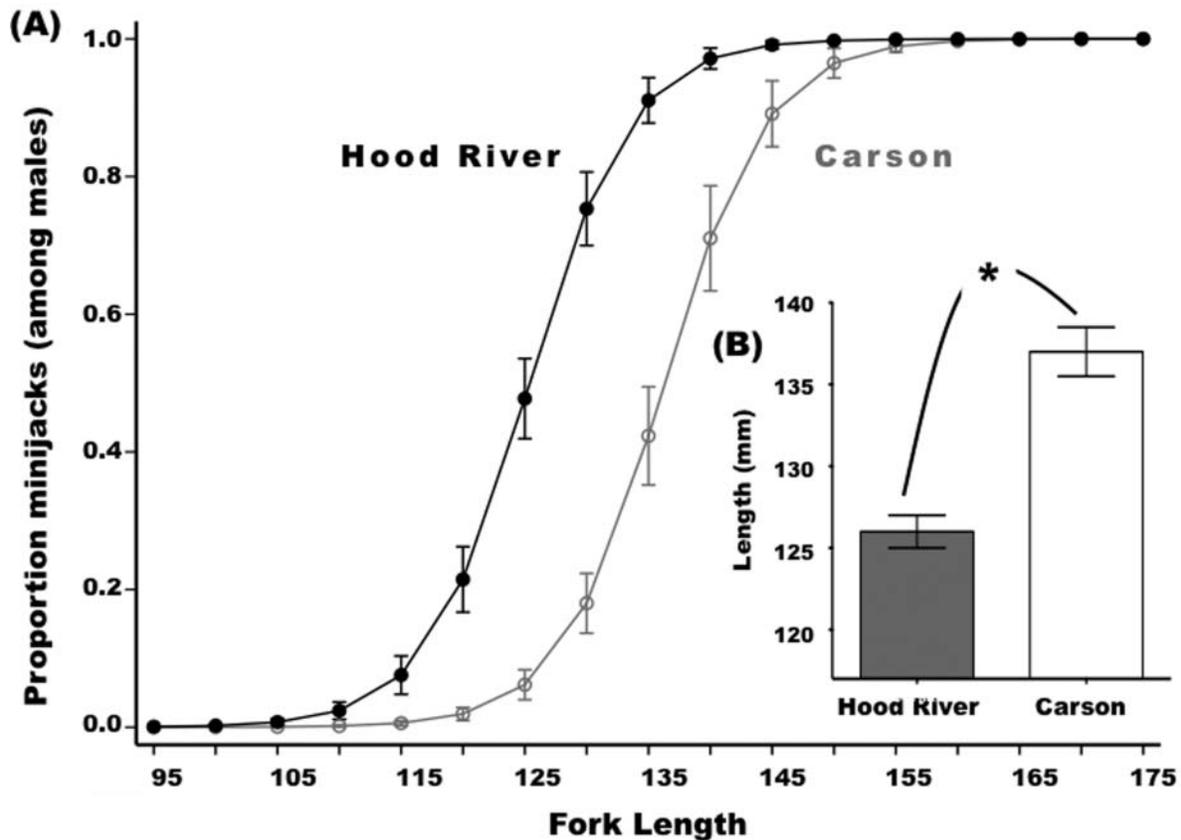


FIGURE 4. (A) Binomial regression of the incidence of minijack maturity against male size at age (FL at 20 months post-parental spawning; values are means $[\pm SE]$ for three brood years [2008–2010]); and (B) FL (mm; $\pm SE$) at 50% minijack maturation for spring Chinook Salmon (Hood River and Carson stocks) reared at Carson National Fish Hatchery. The asterisk indicates a significant difference between stocks ($\alpha = 0.05$).

Salmon (Beckman et al. 2007) is likely made shortly after fry emergence and dictated by the photoperiod at emergence and the very early growth rate.

It is important to understand that fish size at release is not always the best predictor of early maturation rates among males. In our companion study (Spangenberg et al. 2014), the rearing of Hood River-stock spring Chinook Salmon at Round Butte Hatchery's satellite facility (Pelton Ladder [PL]) on the Deschutes River produced fish that were nearly twice the weight (30 g, 140 mm) of the Hood River fish reared at CNFH (18 g, 120 mm; present study), but the minijack rate at the PL facility (14.5%; Spangenberg et al. 2014) was only one-third that observed at CNFH (45%; present study). Variation in results between the present study and our previous study could be due to growth history differences, largely driven by differing seasonal profiles of ambient water temperature at the two hatchery locations. The PL facility typically has a warmer, more variable water temperature than CNFH (Spangenberg et al. 2014). The Hood River-stock fish at the PL facility accumulated much of their body size during their first summer of rearing and then experienced reduced growth and mobilization

of lipid stores during the subsequent autumn and winter, when the physiological decision to mature is typically made (Campbell et al. 2003). The end result of rearing Hood River-stock fish at the PL facility might be described as "the best of all worlds": production of a comparatively large smolt at release while achieving low minijack rates. These results clearly demonstrate the extent to which rearing environment and phenotypic plasticity can affect this important life history pathway.

Further complicating the relationship between hatchery fish size and minijack rate is the potential influence of domestication selection. Recent studies provide empirical evidence that in Atlantic Salmon, domestication leads to a lower probability of precocious maturation among age-1 male parr (Debes and Hutchings 2014). Harstad et al. (2014) quantified minijack rates of Chinook Salmon at both segregated hatchery programs (only hatchery-origin broodstock) and integrated programs (some natural-origin broodstock) throughout the Columbia River basin; minijack rates were found to vary approximately 10-fold across hatchery programs. A highly significant, positive relationship between size at release and the proportion of minijacks released was observed for the integrated hatchery

programs but not for the segregated programs. Furthermore, despite the lower minijack rates in the segregated programs, the average size at release was significantly higher for the segregated programs than for the integrated programs. Minijacks are never used as broodstock in segregated hatchery programs; therefore, these results provide evidence that domestication selection over several generations in culture may also influence the relationship between size and minijack rate. The extent to which domestication selection played a role in the present investigation is unclear, but the lower minijack rates we observed for Carson-stock fish relative to Hood River-stock fish are congruent with the fact that CNFH has been operated as a segregated hatchery program since the early 1960s, whereas the Hood River stock has had a mixed lineage incorporating some level of unmarked wild broodstock throughout the past two decades.

Gill Na^+ , K^+ -ATPase activity is generally considered one of the best physiological indicators of smolt development in salmonids (Hoar 1988). We found that gill Na^+ , K^+ -ATPase activity was higher in Carson-stock fish than in Hood River-stock fish. The gill Na^+ , K^+ -ATPase activity levels were measured only in the nonmaturing male and female smolts. Therefore, the observed differences between stocks were not attributable to the greater proportion of maturing minijacks in the Hood River stock, as minijacks were excluded from the gill Na^+ , K^+ -ATPase analysis (minijacks have a lower gill Na^+ , K^+ -ATPase activity than smolts; Larsen et al. 2010). April sampling of the Carson-stock fish occurred at CNFH, whereas the Hood River-stock fish were sampled at the acclimation sites on the West Fork Hood River. Several weeks had passed since the transfer of Hood River fish (in February or March, depending on BY) from CNFH to the acclimation sites, and water temperatures at CNFH and the acclimation sites were nearly identical ($\sim 5^\circ\text{C}$). Therefore, it is unlikely that either transfer stress or a change in water temperature was responsible for differences in gill Na^+ , K^+ -ATPase activity between the two stocks. Although the differences were relatively modest, gill Na^+ , K^+ -ATPase activity does represent another physiological performance indicator that differs between these two stocks and could influence downstream survival and seawater acclimation (reviewed by Beckman et al. 1999).

Throughout this investigation, there were some significant stock \times BY interaction effects: for FL in October and April, percent solid in October, and gill Na^+ , K^+ -ATPase activity in April. As discussed in our companion paper (Spangenberg et al. 2014), unexplored sources of interannual variation may include genetic characteristics of the adults used as broodstock during a given BY or variation in early incubation temperature or photoperiod. Beckman et al. (2007) demonstrated that variation in photoperiod at the time of emergence significantly altered smolt development and subsequent rates of early male maturation in experimental groups of winter-run Chinook Salmon from the Sacramento River, California. The degree to

which such variation may have had a role in the interactions observed during our present study is unclear.

In conclusion, our results emphasize that specific rearing conditions at a given hatchery facility are not necessarily well suited to every stock. Just as naturally rearing populations are evolutionarily adapted to specific river basins, hatchery populations may become adapted to the environmental conditions at a specific hatchery facility, and this process may occur within a few generations. Rapid evolution in salmonids has been well documented (Hendry et al. 2000; Quinn et al. 2000); thus, it is reasonable to expect that after more than 50 years of segregated culture at CNFH, the Carson stock would be well adapted to the relatively cold, stable water temperatures typical of that facility. Our current results have already been used to support the management decision to discontinue the rearing of Hood River—stock fish at CNFH for the Hood River production program. Complete adult return data from the differentially tagged rearing groups (three BYs) described here and in the Spangenberg et al. (2014) study will be available after the return of age-5 adults from BY 2010 (i.e., autumn 2015). The SARs and demography of these returning adults will be the ultimate measure of whether our pre-release assessment provided accurate predictive power in evaluating the current management strategy for the Hood River production program. Finally, from a broader management perspective, our findings (from this investigation and Spangenberg et al. 2014) emphasize that broodstock transfer among hatchery facilities to fulfill short-term production goals may result in either positive or negative long-term consequences for a hatchery program depending on the specific stock and facility. Care must be taken to avoid such transfers where possible and to carefully monitor and evaluate transfers that are deemed absolutely necessary.

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REFERENCES

- Aubin-Horth, N., and J. J. Dodson. 2004. Influence of individual body size and variable thresholds on the incidence of a sneaker male reproductive tactic in Atlantic Salmon. *Evolution* 58:136–144.
- Beckman, B. R., W. W. Dickhoff, W. S. Zaugg, C. Sharpe, S. Hirtzel, R. Schrock, D. A. Larsen, R. D. Ewing, A. Palmisano, C. B. Schreck, and C. V. W. Mahnken. 1999. Growth, smoltification, and smolt-to-adult return of spring Chinook Salmon from hatcheries on the Deschutes River, Oregon. *Transactions of the American Fisheries Society* 128:1125–1150.
- Beckman, B. R., B. Gadberry, P. Parkins, K. A. Cooper, and K. D. Arkush. 2007. State-dependent life history plasticity in Sacramento River winter-run Chinook Salmon (*Oncorhynchus tshawytscha*): interactions among photoperiod and growth modulate smolting and early male maturation. *Canadian Journal of Fisheries and Aquatic Sciences* 64:256–271.
- Beckman, B. R., and D. A. Larsen. 2005. Upstream migration of minijack (age-2) Chinook Salmon in the Columbia River: behavior, abundance, distribution, and origin. *Transactions of the American Fisheries Society* 134:1520–1541.
- Campbell, B., J. T. Dickey, and P. Swanson. 2003. Endocrine changes during onset of puberty in male spring Chinook Salmon, *Oncorhynchus tshawytscha*. *Biology of Reproduction* 69:2109–2117.
- Cuisset, B., P. Pradelles, D. E. Kime, E. R. Kuhn, P. Babin, S. Davail, and F. Le Menn. 1994. Enzyme immunoassay for 11-ketotestosterone using acetylcholinesterase as label: application to the measurement of 11-ketotestosterone in plasma of Siberian Sturgeon. *Comparative Biochemistry and Physiology Part C* 108:229–241.
- Debes, P. V., and J. A. Hutchings. 2014. Effects of domestication on parr maturity, growth, and vulnerability to predation in Atlantic Salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 71:1371–1384.
- Ford, M., A. Murdoch, and S. Howard. 2012. Early male maturity explains a negative correlation in reproductive success between hatchery-spawned salmon and their naturally spawning progeny. *Conservation Letters* 5:450–458.
- Hankin, D. G., J. W. Nicholas, and T. W. Downey. 1993. Evidence for inheritance of age of maturity in Chinook Salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 50:347–358.
- Hard, J. J., A. C. Wertheimer, W. R. Heard, and R. M. Martin. 1985. Early male maturity in two stocks of Chinook Salmon (*Oncorhynchus tshawytscha*) transplanted to an experimental hatchery in southeastern Alaska. *Aquaculture* 48:351–359.
- Harstad, D. L., D. A. Larsen, and B. R. Beckman. 2014. Variation in minijack rate among Columbia River basin Chinook Salmon hatchery populations. *Transactions of the American Fisheries Society* 143:768–778.
- HDR FishPro. 2008. Revised master plan for the Hood River production program. Technical Report to the Bonneville Power Administration, Project 1988-053-05, Portland, Oregon.
- Heath, D. D., R. H. Devlin, J. W. Heath, and G. K. Iwama. 1994. Genetic, environmental and interaction effects on the incidence of jacking in *Oncorhynchus tshawytscha* (Chinook Salmon). *Heredity* 72:146–154.
- Heath, D. D., L. Rankin, C. A. Bryden, J. W. Heath, and J. M. Shrimpton. 2002. Heritability and Y-chromosome influence in the jack male life history of Chinook Salmon (*Oncorhynchus tshawytscha*). *Heredity* 89:311–317.
- Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290:516–518.
- Hoar, W. S. 1988. The physiology of smolting salmon. Pages 275–344 in W. S. Hoar and D. J. Randall, editors. *Fish physiology*. Academic Press, San Diego, California.
- Howell, P., K. Kones, D. Scarnecchia, L. LaVoy, W. Kendra, D. Ortmann, C. Neff, C. Petrosky, and R. Thurow. 1984. Stock assessment of Columbia River anadromous salmonids I. Chinook, Coho, Chum, and Sockeye salmon stock summaries. Final Report to the Bonneville Power Administration, Contract DE-AI79-84BP12737, Portland, Oregon.
- HSRG (Hatchery Scientific Review Group). 2009. Hood River spring Chinook and related hatchery programs. HSRG. Available: http://www.hatcheryre.com.us/hrp_downloads/reports/columbia_river/system-wide/4_appendix_e_population_reports/gorge-hood_river_spring_chinook_01-31-09.pdf. (October 2015).
- Johnstone, D. L., M. F. O'Connell, F. P. Palstra, and D. E. Ruzzante. 2013. Mature male parr contribution to the effective size of an anadromous Atlantic Salmon (*Salmo salar*) population over 30 years. *Molecular Ecology* 22:2394–2407.
- Jones, M. W., and J. A. Hutchings. 2001. The influence of male parr body size and mate competition on fertilization success and effective population size in Atlantic Salmon. *Heredity* 86:675–684.
- Larsen, D. A., B. R. Beckman, and K. A. Cooper. 2010. Examining the conflict between smolting and precocious male maturation in spring (stream-type) Chinook Salmon. *Transactions of the American Fisheries Society* 139:564–578.
- Larsen, D. A., B. R. Beckman, K. A. Cooper, D. Barrett, M. Johnson, P. Swanson, and W. W. Dickhoff. 2004. Assessment of high rates of precocious male maturation in a spring Chinook Salmon supplementation hatchery program. *Transactions of the American Fisheries Society* 133:98–120.
- Larsen, D. A., B. R. Beckman, C. R. Strom, P. J. Parkins, K. A. Cooper, D. E. Fast, and W. W. Dickhoff. 2006. Growth modulation alters the incidence of early male maturation and physiological development of hatchery-reared spring Chinook Salmon: a comparison to wild fish. *Transactions of the American Fisheries Society* 135:1017–1032.
- Larsen, D. A., D. L. Harstad, C. R. Strom, M. V. Johnston, C. M. Knudsen, D. E. Fast, T. N. Pearsons, and B. R. Beckman. 2013. Early life history variation in hatchery- and natural-origin spring Chinook Salmon in the Yakima River, Washington. *Transactions of the American Fisheries Society* 142:540–555.
- Martin, R. M., and A. Wertheimer. 1989. Adult production of Chinook Salmon reared at different densities and released as two smolt sizes. *Progressive Fish-Culturist* 51:194–200.
- McCormick, S. D. 1993. Methods for nonlethal gill biopsy and measurement of Na⁺, K⁺-ATPase activity. *Canadian Journal of Fisheries and Aquatic Sciences* 50:656–658.
- Myers, R. A., and J. A. Hutchings. 1986. Selection against parr maturation in Atlantic Salmon. *Aquaculture* 53:313–320.
- Piche, J., J. A. Hutchings, and W. Blanchard. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic Salmon, *Salmo salar*. *Proceedings of the Royal Society B* 275:1571–1575.
- Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook Salmon populations. *Evolution* 54:1372–1385.
- Schulz, R. W., L. van der Corput, J. Janssen-Dommerholt, and H. J. Th. Goos. 1994. Sexual steroids during puberty in male African Catfish (*Clarias gariepinus*): serum levels and gonadotropin-stimulated testicular secretion in vitro. *Journal of Comparative Physiology* 164:195–205.
- Shearer, K. D. 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. *Aquaculture* 119:63–88.
- Shearer, K. D., P. Parkins, B. Gadberry, B. R. Beckman, and P. Swanson. 2006. The effects of growth rate/body size and a low lipid diet on the incidence of early sexual maturation in male spring Chinook Salmon (*Oncorhynchus tshawytscha*). *Aquaculture* 252:545–556.
- Shearer, K. D., and P. Swanson. 2000. The effect of whole-body lipid on early sexual maturation of 1+ age male Chinook Salmon (*Oncorhynchus tshawytscha*). *Aquaculture* 190:343–367.
- Silverstein, J. T., K. D. Shearer, W. W. Dickhoff, and E. M. Plisetskaya. 1998. Effects of growth and fatness on sexual development of Chinook Salmon (*Oncorhynchus tshawytscha*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2376–2382.
- Spangenberg, D., D. A. Larsen, R. Gerstenberger, C. Brun, and B. R. Beckman. 2014. The effects of variation in hatchery rearing conditions on growth, smolt quality and minijack rate in spring Chinook Salmon, *Oncorhynchus tshawytscha*: a hatchery scale experiment in the Hood

- River basin, Oregon. Transactions of the American Fisheries Society 143:1220–1230.
- Stickney, R. R., editor. 1991. Culture of salmonid fishes. CRC Press, Boca Raton, Florida.
- Thodesen, J., B. Gjerde, B. Grisdale-Helland, and T. Storebakken. 2001. Genetic variation in feed intake, growth and feed utilization in Atlantic Salmon (*Salmo salar*). Aquaculture 194:273–281.
- Thorpe, J. E., N. B. Mengel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modeling the proximate basis of life history variation, with application to Atlantic Salmon, *Salmo salar* L. Evolutionary Ecology 121:581–600.
- Zabel, R. W., and S. Achord. 2004. Relating size of juveniles to survival within and among populations of Chinook Salmon. Ecology 85:795–806.
- Zar, J. H.. 1988. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey.
- Zaugg, W. S. 1982. A simplified preparation for adenosine triphosphatase determination in gill tissue. Canadian Journal of Fisheries and Aquatic Sciences 39:215–217.