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Winter-rearing temperature affects growth profiles, age of maturation, and smolt-to-adult returns for yearling summer Chinook Salmon in the upper Columbia River basin

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Abstract

In this investigation, we assessed the effects of rearing conditions on survival and demographics for four yearling summer Chinook Salmon *Oncorhynchus tshawytscha* hatchery programs from the upper Columbia River basin over four release years. Juveniles from each hatchery program were initially reared at Eastbank Hatchery near Wenatchee, Washington (which uses groundwater for fish rearing), and experienced similar rearing temperatures until their first autumn in culture. Fish from two of the programs were subsequently transferred to surface water acclimation sites, where they were reared until release the following spring (surface water winter rearing). Fish from the other two programs were overwintered at the Eastbank Hatchery and then transferred to their acclimation and release sites one to two months prior to spring release (groundwater winter rearing). These two rearing strategies resulted in contrasting temperature profiles experienced by the fish, which in turn affected winter growth, age at maturation, and smolt-to-adult survival (SAS). Overall, the two release groups that were overwintered on colder surface water experienced reduced winter growth, reduced minijack rate, and smaller size at release, but achieved a two- to threefold higher SAS compared to the two release groups overwintered on warmer groundwater at Eastbank Hatchery. In addition, based on migration data compiled from fish tagged with passive integrated transponder tags, smaller juveniles tended to mature at older age-classes than larger smolts. We conclude that rearing of yearling hatchery summer Chinook Salmon under more natural thermal regimes (surface water) may result in the return of larger, older adults that have a higher survival rate compared with fish

reared under constant or less natural thermal regimes (ground water). These results highlight the importance of the hatchery-rearing environment in shaping the survival and life history of summer Chinook Salmon juveniles released into the Columbia River basin.

INTRODUCTION

Chinook Salmon *Oncorhynchus tshawytscha* are an ecologically, culturally, and economically valuable species of the Columbia River basin. Their distribution has been reduced to approximately 40% of their historic range in the contiguous USA (Gustafson et al. 2007). In the upper Columbia River basin, habitats available to Chinook Salmon terminate at Chief Joseph Dam, located at river kilometer (RKM) 877, which limits access to more than 500 km of historic spawning habitat (Fulton 1968). Downstream, the Columbia River contains nine major hydropower dams that allow salmon passage but also create a loss of spawning habitat due to inundation of the river. Tributaries often include dams or other anthropogenic structures that limit access for returning adult salmon or have changed available historic habitats. The combined effect of these alterations is a truncation of Chinook Salmon habitats and reduced survival due to mortality associated with dam passage (Haesaker et al. 2012). To mitigate for habitat loss, hatchery programs have been implemented throughout the Columbia River basin to augment wild populations and increase opportunities for tribal, recreational, and commercial fisheries (Lichatowich 1999). Major challenges associated with hatchery culture include designing rearing strategies to optimize survival to adulthood, reducing negative ecological interactions between hatchery and wild fish and developing methods to assess the success or failure of a given strategy.

Chinook Salmon life history includes variation in duration of freshwater residency as juveniles and age of maturation. Smolts are generally categorized as either “ocean-type” (subyearling smolts), with short freshwater residencies, or “stream-type” (yearling smolts), which spend a winter in freshwater prior to outmigration. Historically, the upper Columbia River summer- and fall-run Chinook Salmon adults produced primarily subyearling smolts (Myers et al.1998; Waples et al. 2004; Miller et al. 2011). However, some hatchery programs release smolts as yearlings. Age of maturation ranges from 1 to 6 years after parental spawning (Myers et al. 1998) for upper Columbia River summer- and fall-run Chinook Salmon. Males can mature precociously at age 1 (microjacks), or 2 (minijacks), sometimes forgoing migration to the ocean, or as anadromous adults at age 3 (jacks) - 6 years (Larsen et al. 2013). Overall, females tend to predominate the higher age-classes compared to males, particularly in stream-type Chinook

Salmon populations (Healey 1991). The physiological “decision” to mature at a given age is affected by genotype (Hard et al. 1985), environmental conditions that impact growth, and energy stores (Clarke and Blackburn 1994; Shearer and Swanson 2000; Larsen et al. 2006; Shearer et al. 2006), and their interaction (Spangenberg et al. 2014, 2015).

In the upper Columbia River basin, summer Chinook Salmon hatchery programs employ a variety of rearing and release strategies including: (a) use of groundwater vs. surface water for rearing, (b) a subyearling vs. yearling smolt release strategy, (c) in-basin vs. out-of-basin rearing relative to release location, and (d) seasonal timing of transfer to off-site acclimation and release facilities. This variety of management approaches has been driven by a combination of water quality and availability, availability of land and facilities, funding, and co-managerial jurisdiction. While these approaches may be challenging to reconcile from a management perspective, they can have profound impacts on the rearing conditions experienced by each population and, in turn, potentially affect the demography and survival to adulthood of respective populations.

In this study, we examined how variation in winter-rearing conditions (groundwater vs. surface water) can affect growth, age at maturation, and survival to adulthood of yearling summer Chinook Salmon in the upper Columbia River basin. Fish from all of the hatchery programs examined in this study are part of the same evolutionary significant unit (upper Columbia River summer- and fall-run Chinook Salmon) and limited genetic diversity exists between broodstock for each program (Kassler et al. 2011). In addition, spawning of broodstock, egg incubation and early rearing for each hatchery program is conducted at a single central hatchery facility. The common early rearing across programs within brood year (BY) allowed us to directly compare the effects of variation in timing of transfer to acclimation sites associated with the different release groups (hatchery program by BY combinations). This study combines data on precocious male maturation (previously published in Harstad et al. 2014), hatchery growth data, and publicly accessible coded wire tag (CWT) and passive integrated transponder (PIT) tag data to compare age at return and survival to adulthood for each program across four release years. These collective data provided a unique opportunity to explore how phenotypic plasticity affects fish attributes under different winter rearing regimes. Specifically, these data allowed us to test (1) the effect of winter-rearing environment on fish size and growth rates, (2) the effect of size and winter growth rate on incidence of age 2 male maturation, and (3) the effect of winter-rearing environment on survival to adulthood and age structure at adult return.

<A>METHODS

<B>Hatchery Rearing

This investigation monitored four yearling summer Chinook Salmon hatchery programs from the upper Columbia River basin (Figure 1, Table 1) over four consecutive BYs. For simplicity, we will refer to these hatchery programs by the names of the final acclimation sites: Dryden, Carlton, Similkameen, and Chelan Falls. Each program uses broodstock from a specific population and rears, acclimates and releases fish from distinct locations. A release group consists of fish from a specific program originating from a specific brood year. Broodstock is sourced from three different stocks: Methow-Okanogan (Similkameen and Carlton Programs; broodstock collected at Wells Dam [RKM = 830]), Wells (Chelan Falls Program; broodstock collected at Wells Hatchery [adjacent to Wells Dam]), and Wenatchee (Dryden Program; broodstock collected at Dryden [RKM = 754.028] and Tumwater [RKM = 754.044] diversion dams on the Wenatchee River). Fish from all release groups of each program began rearing, either at the eyed-egg stage (after transport from other facilities) or their parents were spawned, at Eastbank Hatchery adjacent to Rocky Reach Dam (RKM = 763) on the Columbia River in Washington. All groups were reared in traditional raceways after fry emergence. Also, each release group had the same smolt size target at release of 10 fish/lb (45.4 g/fish). But fish from each program experienced differences in the date of transfer to their respective acclimation sites and subsequently, differences in their seasonal water temperature profiles (Figure 2).

Fish from the Chelan Falls and Similkameen hatchery programs (surface water winter rearing) were transported to their acclimation sites in the fall, a year post-fertilization, and overwintered in river water prior to release from these sites. Fish from the Dryden and Carlton hatchery programs continued to rear at Eastbank Hatchery for an additional three to four months (groundwater winter rearing) prior to transfer to their corresponding acclimation sites in late winter to early spring. In contrast to the acclimation sites, Eastbank Hatchery uses groundwater that ranges in temperature from 8°C in May to above 14.5°C in November, providing higher winter growth potential compared to fish reared at the ambient surface water temperatures (Similkameen and Chelan Falls). Water temperature data were provided by Chelan County Public Utility District for Eastbank Hatchery, Similkameen, Dryden and Carlton acclimation sites. Water temperature data for Chelan Falls were obtained from Lake Chelan Annual Flow Reports available online (clio.chelanpud.org/lc-Resource-Documents-WaterQuality.cfm).

<B>Data Collection

We are reporting on three different types of data in this investigation: (1) Program level winter growth rates were determined using monthly batch weights conducted at the rearing facilities in combination with size at release data collected during minijack assessments (see below) for each release group. (2) All release groups were monitored for prevalence of age-2 maturation among males (minijack rates) prior to their release from the acclimation sites as yearling smolts. (3) Survival to adulthood and age of return were estimated from CWT recoveries and PIT tag returns for each release group.

<C>*Monthly size evaluation.*—Monthly batch weights were collected at Eastbank Hatchery for most release groups by netting approximately 100 fish in each of three grabs and averaging across grabs to calculate fish per pound estimates. Similar size data was also collected at the Chelan Falls acclimation site. These data, in combination with the size data collected during minijack assessment, were used to create growth profiles and to estimate winter-specific growth rates (SGR). Winter SGR (% weight gain/day) was calculated as

$$\text{Winter SGR} = [(\ln W_2 - \ln W_1) / (t_2 - t_1)] \times 100$$

where W_1 and W_2 are mean fish weight at time t_1 (October) and t_2 (April), respectively. Monthly size data were not available for the Similkameen fish after they were moved to their acclimation site at the end of October. Therefore, winter growth rates had to be estimated over the broad span of October to April. Growth rate typically increases in the spring as surface water temperatures begin to warm, therefore our wider winter growth window most likely overestimates the true winter growth rate (October - February) of fish from programs on surface water during overwinter rearing, particularly for fish from the Similkameen program which has water temperatures near freezing during this period (Figure 2).

<C>*Minijack rates.*—For each minijack assessment, we lethally sampled approximately 300 fish from each release group just prior to release from their acclimation sites (dates ranged from 4/6 to 4/29, Table 2). Fish were anaesthetized using a buffered solution of MS-222 (tricaine methanesulfonate: Argent Chemical Laboratories, Redmond, Washington). We measured fork length (FL) to the nearest mm and weight to the nearest 0.1 g; condition factor was calculated from these measures as $K = \text{weight}/\text{length}^3 \times 10^5$. The sex of each fish was determined by

visually inspecting gonads. To determine the maturation status of males, blood plasma was collected to measure 11-ketotestosterone (11-KT) levels using an enzyme-linked immunosorbent assay adapted from the method of Cuisset et al. (1994). Whole blood was collected by severing the caudal vein and placed into heparinized Natelson tubes (VWR International, Radnor, Pennsylvania). The blood was then centrifuged for 5 min at 3,000 x *g* to separate plasma from the whole blood and the plasma was stored at -80°C. The resulting plasma 11-KT data were $\log_{10}$ transformed to detect bimodality in the 11-KT levels according to the method of Larsen et al. (2004). Due to variation in date of sampling and inter-assay variability, the threshold 11-KT value that discriminated maturing males from immature males was evaluated individually for each release group. The mean 11-KT threshold across years and groups was 1.3 ng/mL (range = 0.5-2.3 ng/mL).

<C>*Survival and age at return estimates.*—Survival to adulthood for fish from each release group was assessed by both CWT and PIT tags. CWTs contain a group code (release group) and PIT tags include an individual code. All fish within each release group were marked with CWTs during hatchery rearing; release numbers across release groups ranged from 53K to 931K (Table 3). The CWTs were used to estimate smolt-to-adult survival (SAS), which is the percent of estimated CWTs recovered out of the total number of CWTs released for each release group. To derive SAS, we queried the Regional Mark Information System (RMIS) database (available at www.rmpc.org) maintained by Pacific States Marine Fisheries Commission for survival and harvest contribution estimates on 17 May 2016. SAS estimates from RMIS include contribution to fisheries in addition to adult escapement (hatchery return or recovery on spawning grounds). The few age-2 CWT recovery estimates in the RMIS database were excluded from SAS estimation. Seven of the 14 release groups also included PIT-tagged fish. The number of PIT-tagged fish released by the hatcheries for each release group was obtained from the PIT Tag Information System database (available at www.ptagis.org); PIT-tagging rates ranged from 1 to 18% of total fish released and PIT-tagging dates ranged from July to March, just a month prior to smolt release (Table 3). Returning PIT-tagged adults were detected as they ascended adult fish ladders at Bonneville Dam (RKM = 234) on the Columbia River. Bonneville Dam was chosen as return site because the adult fish ladder has high detection rates for PIT-tagged adult Chinook Salmon (Burke et al. 2006) and is downstream from all spawning reaches for these hatchery programs. These detections were accessed using the Columbia River Data

Access in Real Time website (www.cbr.washington.edu/dart). Smolt-to-adult return (SAR) rates were based on these detections and calculated as the percent of PIT-tagged fish that were detected out of the total number of PIT-tagged fish in each release group. Age-2 PIT tag return detections were excluded from "adult" SAR estimates but specific age-2 "minijack" returns were calculated.

Age at adult return was also assessed by both CWT and PIT tags. Summary reports of CWT recoveries from the RMIS database include estimated recoveries by age and estimated minimum survival rate for each release group. Age at return for PIT-tagged fish detected at Bonneville Dam was calculated by comparing the return year of the fish to the release year (i.e. age 2 minijacks returned the same year they were released). The PIT tag data is unique compared to CWT data because it allows you to track the fate of individual fish. Individual lengths of fish were recorded at the time of PIT tagging, allowing us to assess relationships between individual size of juvenile fish and age at adult return using the PIT tag return data.

Both CWT and PIT tags are known to have different biases that can affect estimates of survival to adulthood and estimates of age at return. Our major goal was to compare characteristics between programs and not to produce precise estimates of survival for any one program. Instead, we endeavored to use all the data available to us (both tag types) to generate as complete a comparison as possible. Since all the fish we considered were from the same evolutionary significant unit and were released at similar times and in similar places, the biases related to each tag type would have affected our assessments similarly; therefore, our comparisons should be valid. However, we clearly delineate here some of the biases inherent to each tag type. Estimates of survival based on CWT recoveries reported to the RMIS database can underestimate survival to adulthood due to inconsistencies of reporting by commercial and recreational fisheries (Hankin et al. 2005) and underestimation of freshwater escapement on spawning grounds (Zhou 2002, Murdoch et al. 2010). Although CWT recoveries derived from the RMIS database may underestimate survival, Hall and Cooper (2013) found that locally derived survival estimates (that included known freshwater harvests that are underreported or not reported to the RMIS database) are still highly correlated with the RMIS estimates. The CWT recovery rates are also skewed toward upper age-classes (age 4+) of Chinook Salmon as these larger fish are targeted in commercial and recreational fisheries and are also more likely to be recovered on spawning ground surveys (Zhou 2002, Murdoch et al. 2010). Estimates of survival based on detections of PIT-tagged fish at Bonneville do not include any commercial or recreational harvest of PIT-tagged fish in the ocean or in the Columbia River downstream of Bonneville Dam. PIT tag model, swimming behaviors and fish size can also affect probability of detection of PIT-tagged fish (Burke et al. 2006). For this study, we used data from both tag types as the results they generate are complementary and provided us the best opportunity to compare characteristics of fish released from these hatchery programs.

<B>Data Analysis

Statistical analyses were conducted using STATA v.12 (StataCorp LP, College Station, TX) or Prism v.6 (GraphPad software, Inc., La Jolla, CA) software. Statistical significance was set at $\alpha = 0.05$. Program, BY, and winter water source were treated as categorical variables in all regression analyses. All other variables (minijack rate, SAS, length, weight, winter SGR) were treated as continuous variables. BY 2007 Dryden fish were infected with high levels of *Renibacterium salmoninarum,* the causative agent of bacterial kidney disease, (D. McCarver, Washington Department of Fish and Wildlife, personal communication). The added stress of this infection may have reduced the potential for initiation of minijack maturation as the peak mortality occurred during January (fish were treated with medicated feed after this outbreak). In previous surveys, we have found evidence of reduced minijack rates in populations infected with bacterial kidney disease (D. A. Larsen, unpublished data). Thus, the minijack rate from this release group was excluded from any regression analyses. These fish were included in the survival to adulthood analyses as we don’t have any reason to think that the fish that survived to smolt release were potentially subject to reduced survival (this release group had fewer mortalities during acclimation at Dryden Pond [less than 1%] than the other BYs in this study [1.8-10%]).

<C>*Size, winter growth and minijack rate analyses.*—Fish size (g), in October and April, and winter SGR comparisons between hatchery programs were compared using one-way ANOVAs with Tukey’s multiple comparisons test with BYs as replicates. The effect of the categorical predictor variable, hatchery program, on the probability of age-2 male maturation was analyzed using logistic regression, excluding females. Post-test comparisons were done using the linear combination “lincom” command in STATA to compare the different minijack levels of different hatchery programs. Simple linear regression was used to examine the

relationship between minijack rate and the predictor variables October size, size at release, and winter SGR across release groups.

<C>*Survival analyses.*—SAS was used for analyses of survival over SAR because we were able to generate this estimate for all release groups. Nine linear regression models were compared in their ability to predict SAS (Table 4) using Akaike's Information Criterion (AIC) to find the most parsimonious model. Brood year was included as a predictor variable of SAS as year-to-year variation occurs in both freshwater and ocean conditions, such as spill at hydropower dams (Haeseker et al. 2012) or ocean temperatures indexed by the Pacific Decadal Oscillation (Mantua et al. 1997), which may be related to Chinook Salmon survival. Five simple linear regression models (models 1, 2, 4, 6 and 8 in Table 4) were run using the following predictor variables: BY, program, water source (ground vs. surface), minijack rate, and weight at release. Four multiple regression models (models 3, 5, 7 and 9 in Table 4) were run using BY in combination with the other predictor variables from the simple linear regression models to account for BY effect on SAS. Interactions with BY were tested using the "mfpigen" command in STATA, which models interactions between pairs of covariates. The significance of the predictor variables within multiple regression models was determined by Wald tests. These regression models were used to generate linear prediction of SAS estimates for BY, hatchery program, water source, minijack rate, and size at release. Post-test comparisons to compare levels within categorical variables were done using the "lincom" command in STATA.

<C>*Age at return and size at PIT-tagging analyses.*—The mean age of return for tagged fish from CWT and PIT tag datasets was compared via a paired *t*-test. We compared size at PIT tagging (FL, mm) by age at return using one-way ANOVAs with Tukey's multiple comparisons tests. We did this analysis on each release group that was tagged late enough to have notable variation in size (SD > 6 mm, Table 3); this omitted two release groups (Similkameen BY 2009 and Carlton BY 2009) that were tagged prior to mid-September. The effect of juvenile size (standardized as the percent deviation from mean FL within each release group) on probability of return for each age-class was tested using logistic regression analysis. Standardized length was calculated as

$$\text{Standardized length} = (X_{ij} - \overline{X}_i)/\overline{X}_i \cdot 100$$

where $\overline{X}_i$ is the mean FL for a release group *i* and X_{ij} is the FL of each individual *j* within release group *i*; this was calculated for individuals within each release group separately. For each age-class analyzed, standardized length of individual fish that returned at that age-class was compared to fish that returned at older age-classes (examples: standardized length of individual fish that returned at age 2 was compared to standardized length of individual fish that returned at ages 3-6; standardized length of individual fish that returned at age 3 was compared to standardized length of individual fish that returned at ages 4-6; etc.). For the returns at older age-classes, the younger age-classes were excluded from analysis because they had previously left the ocean environment and where no longer part of the ocean population that could undergo this physiological "decision" to mature and return to the Columbia River. This approach was more intuitive than using a multinomial logistic regression as separate logistic regression analyses allowed us to test this relationship with size separately for each age at return. Also, analyses were stratified by season of tagging (fall vs. spring) to see if size during these periods also influenced age at return.

<A>RESULTS

<B>Seasonal Growth

Seasonal growth profiles varied from fish among different hatchery programs (Figure 3a). Similkameen and Chelan Falls fish were reared to larger sizes in October (15-20 g) compared to Carlton and Dryden fish (approximately 10 g). With the exception of Chelan Falls fish, the trend reversed during the winter months, and by time of release, the groundwater winter-reared fish were larger (Carlton averaged 49.1 g, Dryden averaged 43.5 g) than the surface water winter-reared fish at Similkameen (mean = 29.7 g). The winter growth rates reflect this same trend. The Dryden and Carlton fish experienced significantly higher winter growth rates (~0.9% weight gain/day) than fish reared at Similkameen (~0.4% weight gain/day) that experienced the lowest winter temperatures (Figure 3b). These differences in winter growth rates are also reflected in the deviation in size at release from target release sizes across programs (ΔWT, Table 2). Similkameen fish were on average smaller than target size across BYs (ΔWT = -15.8 g), whereas Dryden (ΔWT = -2 g) and Carlton fish (ΔWT = +3.7 g) weights were close to target size. Chelan Falls release groups had the highest average size at release (ΔWT = +8.6 g).

<B>Size, Winter Growth and Minijack Rates

The prevalence of minijacks among males ranged from 4% to 45% across release groups (Table 2) and there were significant differences between hatchery programs for the probability of males maturing as minijacks across years (likelihood ratio [LR] $\chi^2 = 97.05$, df = 3, $N = 2112$, $P < 0.001$; Figure 4a). Overall minijack rates were the highest among the Carlton males (groundwater winter rearing) and lowest among the Similkameen males, which experienced the coldest winter rearing temperatures. Minijack rate was positively correlated with winter SGR ($R^2 = 0.32$, $P = 0.04$; Figure 4b) but was not correlated with October size ($R^2 = 0.06$, $P = 0.45$; Figure 4c) or size at release ($R^2 = 0.25$, $P = 0.08$; Figure 4d).

<B>Survival Estimates

Survival to adulthood varied across hatchery programs and BYs (Figure 5, Table 3). Overall, the release groups that overwintered at their acclimation sites (Similkameen and Chelan Falls) trended toward higher survival estimates based on both the CWT and PIT tag data (Figure 5a, Table 3). Regression of SAS with the categorical predictor variables, program and BY, found both program ($F_{3,\,7} = 7.94$, $P = 0.012$) and BY ($F_{3,\,7} = 9.71$, $P = 0.007$) to be significant predictors of survival (Table 4, Model 3). Similkameen fish had the highest survival, threefold higher than the SAS for Dryden and Carlton (Figure 5b). Also, fish from even-numbered BYs demonstrated a three- to fourfold higher survival than fish from odd-numbered BYs across all programs (Figure 5c). Although there were differences in the magnitude of survival estimates derived from PIT tag and CWT data (Table 3), these estimates were highly correlated ($R^2 = 0.98$, $P < 0.0001$).

<B>Predicting Survival (SAS)

Nine regression models were compared for their ability to predict SAS (Table 4). Predictors included BY, program, winter-rearing water source (surface vs. groundwater), mean weight at release and minijack rate. Due to the even/odd BY survival pattern noted previously (Figure 5c), including BY with the other predictors reduced AIC values compared to models without BY (Table 4). The models with program or winter water source, in combination with BY, were the best predictors of SAS and were approximately equivalent ($R^2 = 0.88$, AIC = 16.7 vs. $R^2 = 0.83$, AIC = 18.1; Table 4). Within these models, the predictor variables of hatchery program ($F_{3,\,7} = 7.94$, $P = 0.012$) and water source ($F_{1,\,9} = 17.92$, $P = 0.002$) were both significant. The linear predictions of SAS demonstrate that fish from hatchery programs on cooler surface water during winter rearing (Similkameen and Chelan Falls) experienced higher survival to adulthood (Figure 6a&b) than those reared on groundwater. There were no significant interactions ($P < 0.05$) between BY and other variables (hatchery program, water source, weight or minijack rate; data not shown).

We examined the relationship between survival to adulthood and the attributes of the fish from each release group, minijack rate and size at release. Minijack rate trended towards a negative relationship with SAS but was not significant ($F_{1, 11} = 2.17$, $P = 0.169$; Table 4). When BY was included in the regression model, minijack rate became a significant predictor of survival to adulthood (Wald test: $t = -3.05$, $P = 0.016$; Figure 6c, Table 4). Including BY also increased the magnitude of the negative slope between minijack rate and SAS (β = -0.044 vs. β = -0.027; Table 4). Mean weight at release was not a significant predictor of adult return ($F_{1, 12} = 3.56$, $P = 0.084$; Table 4), even in combination with BY (Wald test: $t = -1.85$, $P = 0.098$; Figure 6d, Table 4).

<B>Age at Return

The relative abundance of adult returns for each age-class varied by hatchery program and BY in both the PIT tag and CWT datasets (Table 5). Minijacks, because of their small size, are seldom recovered in the fisheries, enumerated returning to hatcheries, or counted on spawning grounds and are missing from the CWT database. Because of this, CWT returns provided a contrasting view of the age of freshwater return compared to PIT tag returns (Figure 7). This size/age-class bias in detection of CWT fish created a significant difference in the maturation schedules (i.e. the proportion of fish returning at each age-class for a hatchery program) generated for the two tag types (paired *t*-test: $t_6 = 5.05$, $P = 0.002$; Figure 7) with an average age at return ± SE of 3.3 ± 0.21 and 4.29 ± 0.05 years for PIT tag and CWT estimates, respectively. The PIT tag data demonstrate that most "adult" returns for Carlton (Figure 7a) and Dryden (Figure 7b) programs were age-2 fish (minijacks) that migrated below Bonneville Dam and were detected ascending the adult fish ladder approximately two months after hatchery release (date of return data not shown). Maturation schedules for Chelan Falls and Similkameen fish, which overwintered on surface water, also included age-2 returns but at much lower relative frequencies (26% and 15% of the returns respectively; Figure 7c-d) than found for Carlton and Dryden fish (62% and 54% of the returns respectively; Figure 7a-b). When minijacks were removed from this comparison, mean age at return was similar for these two tag types (CWT = 4.32, PIT = 4.28; paired t-test: $t_6 = 1.103$, $P = 0.31$). Although overall survival rates varied significantly between BYs, the relative pattern of age at return (%) within BYs remained relatively consistent (Table 5, Figure 7).

<B>Age at Return and Size at PIT Tagging

Examining the relationship between size of fish at PIT tagging and subsequent return data clearly demonstrates that size during freshwater rearing influences the age of maturation and return across all age-classes (Figure 8). Fish that returned at age 2 tended to be larger as juveniles than fish that returned at subsequent age-classes (Figure 8). This trend was apparent in all release groups that were PIT-tagged in mid-September or later.

Logistic regression analysis of standardized fish length at PIT tagging also showed an effect of juvenile size on age of maturation. The probability of return at age 2 was highly influenced by standardized length for both fall (LR $\chi^2 = 52.3$, df = 1, $N = 959$, $P < 0.001$) and spring (LR $\chi^2 = 138.7$, df = 1, $N = 592$, $P < 0.001$) tagged fish (Figure 9, Table 6) with larger juveniles within a release group having higher probability of returning at age 2. Odds ratios show that a 1% increase in standardized length increases the odds of returning at age 2 by 6-9% (Table 6). Similar trends were observed for probability of returning at age 3 and age 4, but odds ratios (Table 6) and slopes of logistic regression curves (Figure 9) were reduced compared to age 2, indicating that the effect was of a smaller magnitude for these age-classes.

<A>DISCUSSION

We found striking differences in age of return and survival to adulthood among genetically similar groups of yearling upper Columbia River basin summer Chinook Salmon that were raised under different hatchery rearing regimes. This investigation clearly demonstrated that variation in acclimation strategies significantly altered the seasonal thermal regimes fish were exposed to and consequently altered the associated seasonal growth profiles of the fish. Fish from hatchery programs that overwintered on cooler ambient surface water temperatures had reduced winter growth compared to fish from programs reared through the winter on the much warmer groundwater. These environmental differences induced significant differences in rate of early male maturation, age at adult return and survival (SAS) among these groups of summer Chinook Salmon.

<B>Rearing Environment and Minijack Production

Summer Chinook Salmon juveniles from programs that overwintered on groundwater had significantly higher incidences of age-2 male maturation at hatchery release than juveniles from programs that overwintered on cooler surface water. The fact that minijack rates were significantly correlated with winter growth rate suggests that winter growth may be an important component of the physiological “decision” to mature in these fish. To our knowledge, this is the first report on drivers for early male maturation for yearling summer-run Chinook Salmon. Previous studies on spring-run Chinook Salmon have suggested a critical “maturation initiation” period in summer-autumn of each year when the maturation decision is made for the following autumn (Silverstein et al. 1998; Shearer and Swanson 2000; Campbell et al. 2003; Larsen et al. 2006). In the current investigation, winter growth rate had a stronger relationship with minijack rate than autumn size (mid-October) suggesting that the maturation decision may be delayed in summer Chinook Salmon compared to spring Chinook Salmon in keeping with their inherently later seasonal spawn timing. Similar to the aforementioned studies in spring Chinook Salmon, our data clearly demonstrate that growth in the hatchery during critical seasonal periods can significantly affect rates of precocious male maturation.

A consequence of producing a high proportion of minijacks in different release groups is that SAS was negatively correlated with minijack rate. This trend was also observed by Beckman et al. (2017) in Hood River (located in Oregon, Figure 1) spring Chinook Salmon populations that were reared under different hatchery conditions across several BYs. The production of male Chinook Salmon that mature at age 2 in this semelparous species automatically lowers potential “adult” return rates as they have already reached their single opportunity to reproduce and therefore don’t return as full-size anadromous adults.

<B>Rearing Environment and Survival (SAS)

This study demonstrated nearly a threefold difference in adult return rates across hatchery programs that are within close geographical proximity in the upper Columbia River basin. Surprisingly, fish from the program with the highest mean SAS (Similkameen) also had the longest migration distance for both outmigrating smolts and returning adults. In addition, fish from the Similkameen program had the greatest number of hydroelectric dams (nine) to pass in each migration direction. This suggests that differences in the quality of smolts released may play a more significant role in SAS than previously appreciated. Our data suggests rearing strategies can affect survival to adulthood, and highlights how optimizing rearing strategies could improve adult return. Since genetic diversity between the stocks is limited (Kassler et al. 2011), differences in adult return are presumed to have resulted predominantly from environmental rearing differences between hatchery programs rather than genotypic differences between stocks. The most apparent environmental difference between these programs results from their strategy for early hatchery rearing (size in the fall) and timing of transfer to surface water acclimation sites. Thus, our data suggests that early hatchery rearing can have a profound effect on fish attributes that ultimately impacts SAS.

One of the most common fish attributes measured is size at release. Studies on how smolt size affects post-release survival in Chinook Salmon have provided somewhat varying results. Some investigations have found a positive relationship between smolt size at release and survival to adulthood in both yearling spring Chinook Salmon (Martin and Wertheimer 1989; Claiborne et al. 2011; Beckman et al. 2017) and subyearling fall Chinook Salmon (Connor et al. 2004). Additionally, Zabel and Achord (2004) found higher rates of survival in larger wild juvenile spring Chinook Salmon from the Snake and Columbia River basins. In contrast, other studies have found no effect of juvenile size at release on survival to adulthood (Miller et al. 2013; Feldhaus et al. 2016) or on survival following early ocean entry (Claiborne et al. 2014). Interestingly, the relationship between size at release and SAS was negative in the current investigation. The Similkameen fish were consistently the smallest at release but had the highest SAS. Clarke et al. (2012) had similar results in a hatchery program of yearling spring Chinook Salmon (from the Umatilla River, Oregon, Figure 1) reared on different combinations of groundwater and surface water. They found that release groups that were transferred from groundwater to their acclimation sites for rearing on surface water in either November or January experienced different rearing environments. Fish that were not transferred until January experienced warmer winter-rearing temperatures and higher growth, but paradoxically lower survival to adulthood than fish transferred in November (Clarke et al. 2012). Taken together, these two studies suggest that factors beyond size-selective mortality, such as early male maturation, can drive differences in adult return rates from different Chinook Salmon hatchery programs.

<B>Ocean Conditions and Survival (SAS)

One unexpected observation in this study was the odd/even BY pattern of survival across all programs with fish from even-numbered BYs (even BY fish also out-migrate in even years) having nearly threefold higher survival rates than those from odd BYs. Maturation schedules are relatively consistent across BYs even as total returns vary severalfold (Table 5, Figure 7). This may indicate that some factor(s) shortly after ocean entry influence survival as all age-classes of return are affected equally (in contrast to conditions affecting survival at older age-classes that would only affect the later returning age-classes). Fish from these yearling summer Chinook Salmon programs enter the ocean in May-June of each year and typically migrate northward (Weitkamp 2010; Teel et al. 2015). The timing of their ocean entry and early migration coincides with the return of adult Pink Salmon *O. gorbuscha* to the Fraser River in Canada and the Puget Sound in odd years. No adult Pink Salmon return to these areas in even years. The presence of high abundances of adult Pink Salmon in odd years has been correlated with reduced prey abundance and reduced growth and survival of other salmon stocks in the Bering Sea and North Pacific (Shiomoto et al. 1997; Sugimoto and Tadokoro 1997; Ruggerone and Nielsen 2004; Springer and van Vliet 2014). We suggest that it is possible that in odd years the juvenile Chinook Salmon from this study encountered reduced prey availability as they migrated northwards off the Canadian Coast due to feeding by adult Pink Salmon returning to their natal streams to spawn. A broader examination of the return rates for yearling summer Chinook Salmon in the upper Columbia River, along with closer examination of ocean conditions, such as the Pacific Decadal Oscillation, are needed to validate this hypothesis and are beyond the scope of this paper.

<B>Rearing Environment and Age at Return

This study demonstrated that growth during the first 1+ year in culture (approximately 18 months) has a significant impact on the age of maturation in yearling hatchery summer Chinook Salmon. We demonstrated that within PIT-tagged release groups, the largest individuals at the time of tagging had the greatest probability of returning at younger ages, regardless of whether they were tagged in the fall or spring. This indicates that early rearing effects on size and growth can persist through several annual maturation decision windows in fish that did not mature during previous window(s).

One caveat of using PIT tag detections at Bonneville Dam for age at return analyses is that gender-specific data are not available. Sex ratios are often skewed toward females in age-4+ adult Chinook Salmon due to the maturation of males at younger ages (Healey 1991). The mixed gender in the age 4-6 PIT tag detections may be diluting our ability to detect size effects in our statistical analyses, particularly for older age-class returns. This may also explain why mean size at tagging is higher for age-4 returns than for age-3 returns for Dryden BYs 2008-2009 (Figure 8c&d).

Previous studies have shown that growth during freshwater rearing affects the age at which Chinook Salmon mature and return to spawn in both wild (Ruggerone et al. 2009; Tattam et al. 2015) and hatchery-reared populations (Martin and Wertheimer 1998; Ewing and Ewing 2002; Clarke et al. 2012; Feldhaus et al. 2016). Salmonid fishes have evolved in environments with strong seasonal variation in temperature and food availability and their physiologically driven life history decisions are responsive to seasonal patterns in energy stores and growth. Beckman et al. (1999, 2017) and Larsen et al. (2006) characterized the catabolic and anabolic phases naturally-rearing spring Chinook Salmon experience in rivers and referred to this dynamic as the "wild fish template". It stands to reason that when fish experience warmer winter temperatures (i.e. ~14°C October-January) and the accelerated growth that accompanies such conditions, that maturation schedules may also be advanced. Taken together, the findings from this and previous studies demonstrate the profound long-term impacts early rearing and especially unseasonably high growth rates can have on influencing the demography of a given hatchery program.

<B>Minijack Production vs. Age 2 Returns

The number of minijacks returning to Bonneville Dam represents a subset of the number of minijacks estimated at hatchery release (Larsen et al. 2004; Beckman and Larsen 2005). In addition to potential detection biases of the PIT tag readers for smaller fish (Burke et al. 2006), there are several other factors that can influence the number of minijacks returning to Bonneville Dam. (1) Not all minijacks leave natal streams and some minijacks display partial downstream migration (Beckman and Larsen 2005, Larsen et al. 2010). (2) Mortality of juvenile salmon after hatchery release (e.g. predation, dam turbine mortality) also affects the rate of minijacks that return to Bonneville Dam. Previous work by Beckman and Larsen (2005) has shown that PIT tag detections of Yakima River spring Chinook Salmon (located in Washington, Figure 1) minijacks are much lower than numbers generated by 11-KT surveys of yearling males just prior to smolt release. Minijack detection rates at Bonneville Dam were approximately 0.05% - 0.4% of tagged fish released. Minijack rates from 11-KT analysis prior to release produced minijack rates of 15-33% of the release population. There is a magnitude discrepancy between these two metrics, but they were nonetheless positively correlated (Beckman and Larsen 2005). Although the detection of minijacks returning to Bonneville Dam cannot be used as a substitute for enumeration of minijacks at the hatchery, they can indicate that there are substantial numbers of minijacks originating from a given hatchery program.

<B>CWT and PIT Tags Tell Unique, but Complementary Stories

CWTs and PIT tags have served valuable roles in fisheries management for decades, most notably in the Snake and Columbia River basins. In the current investigation, we used results from both tag types, as the information provided may be both confirmatory (results agree) and complementary (the two tag types may provide different information). We found higher adult return rates were estimated via PIT tag detections at the Bonneville Dam adult ladders compared to rates estimated from CWTs reported in the RMIS database (Table 3). However, these data are confirmatory as we found a high correlation between the two tag types. It is also interesting to note that CWT and PIT tags tell very different stories about age at return besides differing in their estimates of survival. The CWT database is essentially missing any indication of the numerous fish that migrate as smolts and return precociously as minijacks for these summer Chinook Salmon programs. The PIT tag data complements the CWT data as it illuminates a different age-class of returning fish. We encourage others to employ data from both tag types when comparing results from different hatchery programs.

<B>Management Implications

Overwinter rearing conditions and resulting differences in winter growth rates have important implications for hatchery Chinook Salmon. Deviations from the “wild fish template” can significantly alter the maturation schedule of male Chinook Salmon. This investigation demonstrated that producing larger fish for release, via higher winter growth, also produced more precocious males, reduced age of return and did not increase overall survival to adulthood. In fact, the program that had the longest migration distance and smallest mean size at release had the highest survival estimates. A challenge going forward will be to design rearing regimes that avoid unseasonably warm rearing temperatures in the winter or to develop a strategy to manipulate rations in a manner that reduces winter growth without compromising fish health. This study found that fish overwintered on cooler surface water had reduced winter growth, but this may not be feasible for all hatchery programs. Our results strongly suggest that by optimizing winter-rearing strategies, hatchery programs could improve the survival and age structure in yearling summer Chinook Salmon.

<A>ACKNOWLEDGMENTS

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LIST OF FIGURES

Figure 1. Map of the upper Columbia River basin showing the central rearing facility (Eastbank Hatchery, open circle symbol) and acclimation sites (numbered triangles) used to rear yearling summer Chinook Salmon juveniles and major dams (black bars) encountered during juvenile outmigration and adult return. 1 = Similkameen Pond, 2 = Carlton Pond, 3 = Chelan Falls, 4 = Dryden Pond.

Figure 2. Temperature profiles for **(A-B)** groundwater winter-rearing hatchery programs (DRY = Dryden, CARL = Carlton) and **(C-D)** surface water winter-rearing programs (CHF = Chelan Falls, SIM = Similkameen). The arrows represent the time of transfer from Eastbank Hatchery to subsequent acclimation sites where fish were released in April as yearling smolts. To be consistent across this and all figures to follow, the visual scheme for hatchery program is: grey = surface water winter rearing; black = groundwater winter rearing; solid lines/bar/symbols = DRY and CHF; dashed lines or open bars/symbols = CARL and SIM.

Figure 3. **(A)** Mean weight (g) during hatchery rearing and **(B)** winter specific growth rate (SGR, % weight gain/day) for October through April for each release). Brood years were used as replicates. Error bars = SE. Different letters represent a statistical difference in one-way ANOVAs with Tukey's multiple comparisons test ($\alpha = 0.05$).

Figure 4. **(A)** Mean minijack rate among males for each hatchery program (error bars = SE, different letters represent significant differences between hatchery programs [$\alpha = 0.05$] from logit model: Maturation = $\beta_0 + \beta_1$[program], likelihood ratio [LR] $\chi^2 = 97.05$, df = 3, $N = 2112$, $P < 0.001$, Pseudo $R^2 = 0.04$); and relationship of each release group's minijack rate with **(B)** winter specific growth rate (SGR [% weight gain/day], slope = 27.1, $R^2 = 0.32$, $P = 0.04$), **(C)** size in October (slope = -0.75, $R^2 = 0.06$, $P = 0.45$), and **(D)** size at release (slope = 0.55, $R^2 = 0.25$, $P = 0.08$) based on simple linear regression. Dashed lines = 95% CI around regression line. Symbol key: grey open = SIM, grey closed = CHF, black open = DRY, black closed = CARL, circle = BY 2006, square = BY 2007, triangle = BY 2008, diamond = BY 2009.

Figure 5. **(A)** Percent survival (SAS) based on estimated CWT recoveries for brood years 2006-2009 for summer Chinook Salmon that underwent winter rearing on either groundwater or surface water and the marginal effects of **(B)** program and **(C)** brood year on the linear prediction of survival (Model: SAS = $\beta_0 + \beta_1$[program] + β_2[brood year], $F_{6, 7} = 8.86$, $N = 14$, $P = 0.006$, $R^2 = 0.88$). Error bars = SE. Different letters represent a statistical difference ($\alpha = 0.05$).

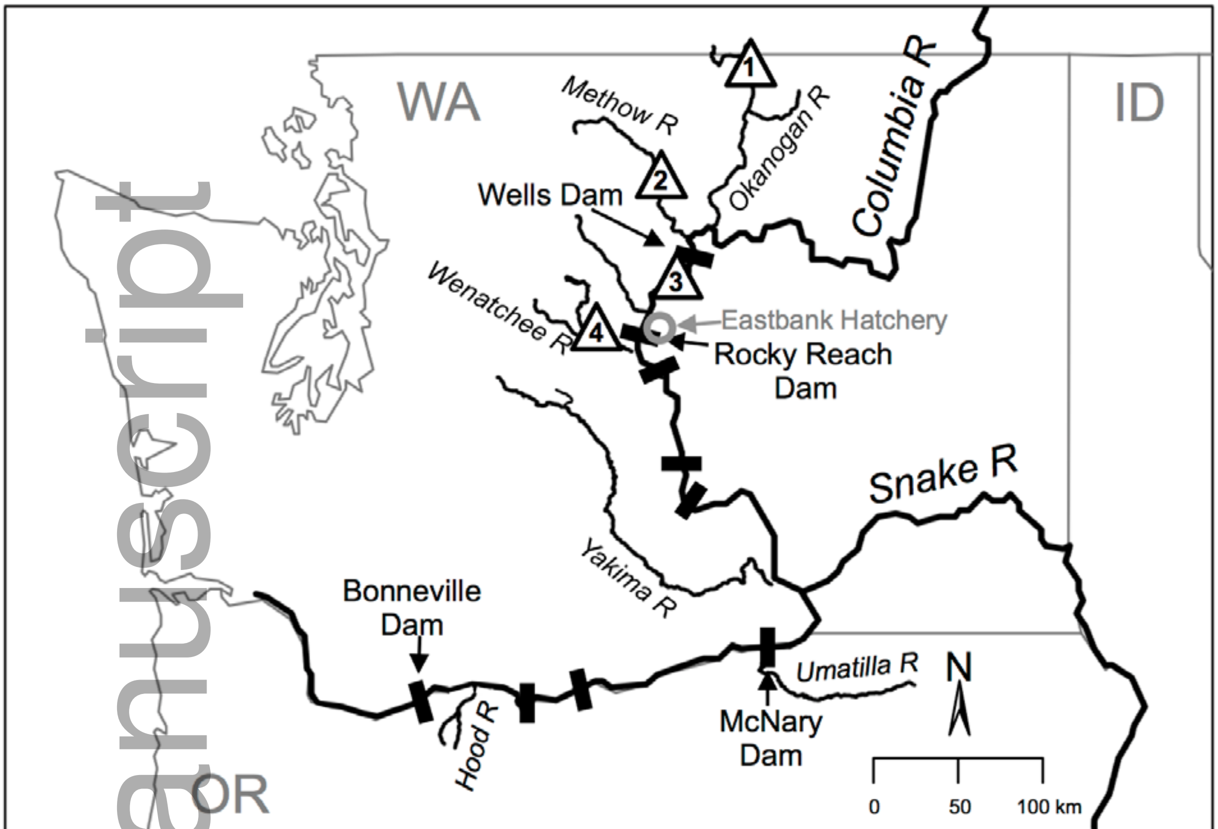
Figure 6. Linear prediction of SAS and marginal effects of **(A)** program + brood year, **(B)** winter water source + brood year, **(C)** minijack rate + brood year, and **(D)** weight +

brood year. Linear predictions are based on models 3, 5, 7 & 9 from Table 4. Error bars = SE of predicted values.

Figure 7. Percent of total returns by age-class based on PIT tag detections at Bonneville Dam **(A-D)** and CWT recovery estimates from the RMIS database **(E-H)** for each hatchery release group. Brood years as replicates. Error bars = SE. See Methods for notes on different biases for each tag type.

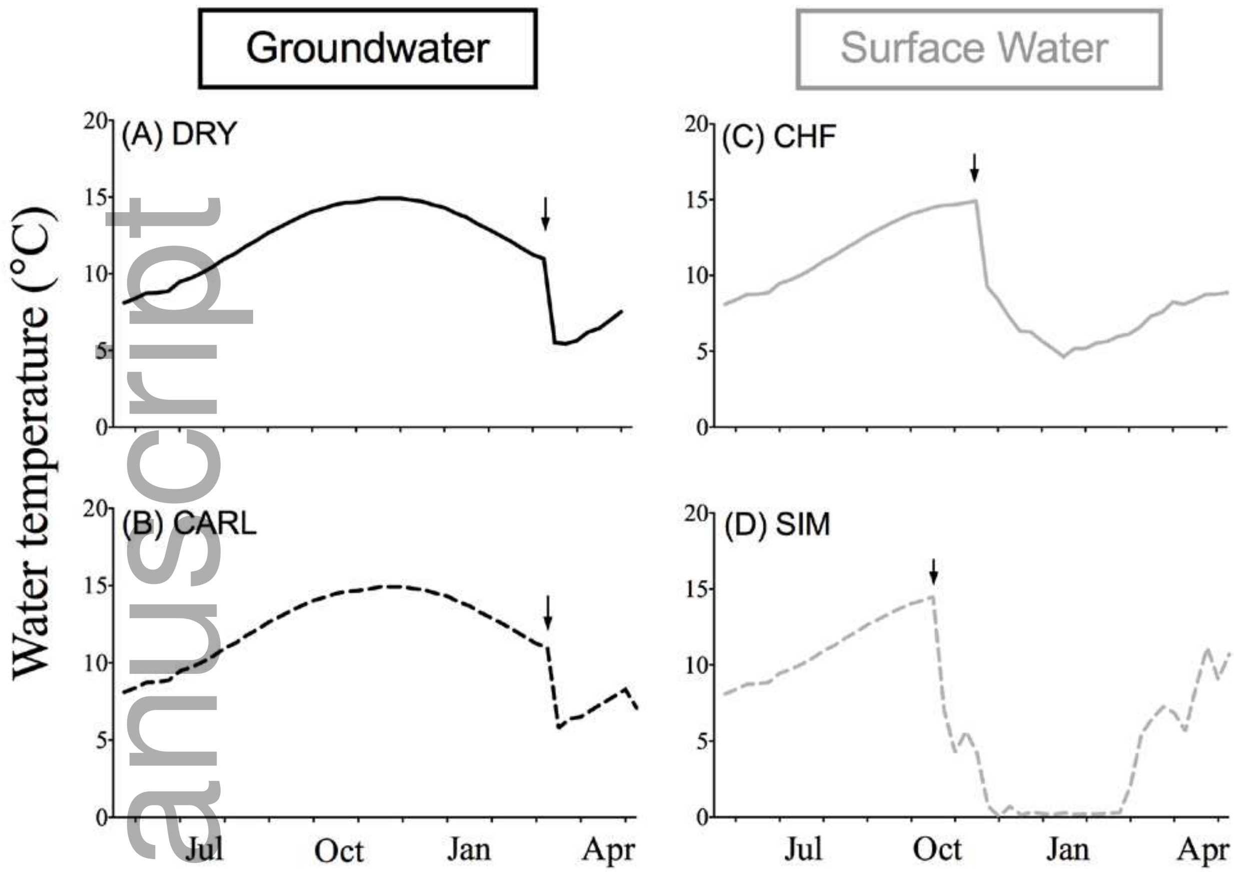
Figure 8. Mean size at tagging by age at return for the hatchery release groups that were PIT tagged during the fall **(A-C)** or spring **(D-E)** in this study (brood years 2006 – 2009). PIT-tagging dates and mean size at tagging for release groups are given in Table 3. Similkameen BY 2009 and Carlton BY 2009 were omitted from this figure due to low variation (SD) in size at tagging (≤ 6 mm) and early time of tagging (beginning of September or earlier). Numbers within bars are number of PIT tagged fish detected returning to Bonneville Dam for each age-class. Different letters represent a statistical difference in one-way ANOVAs with Tukey's multiple comparisons test ($\alpha = 0.05$). Error bars = SE.

Figure 9. Predicted probability of return (p) for age-class (2 – 5) for fish PIT tagged **(A)** during the fall at age 1, or **(B)** during the spring at age 1+ based on logistic regression models with standardized fork length at tagging (percent deviation from the mean length for individual fish; each release group was calculated separately) as the predictor variable. Return data contains both male and female fish that were PIT tagged. Higher age-class return analyses excluded those that had matured and returned at a younger age-class (see Table 6).



814

815 FIGURE 1



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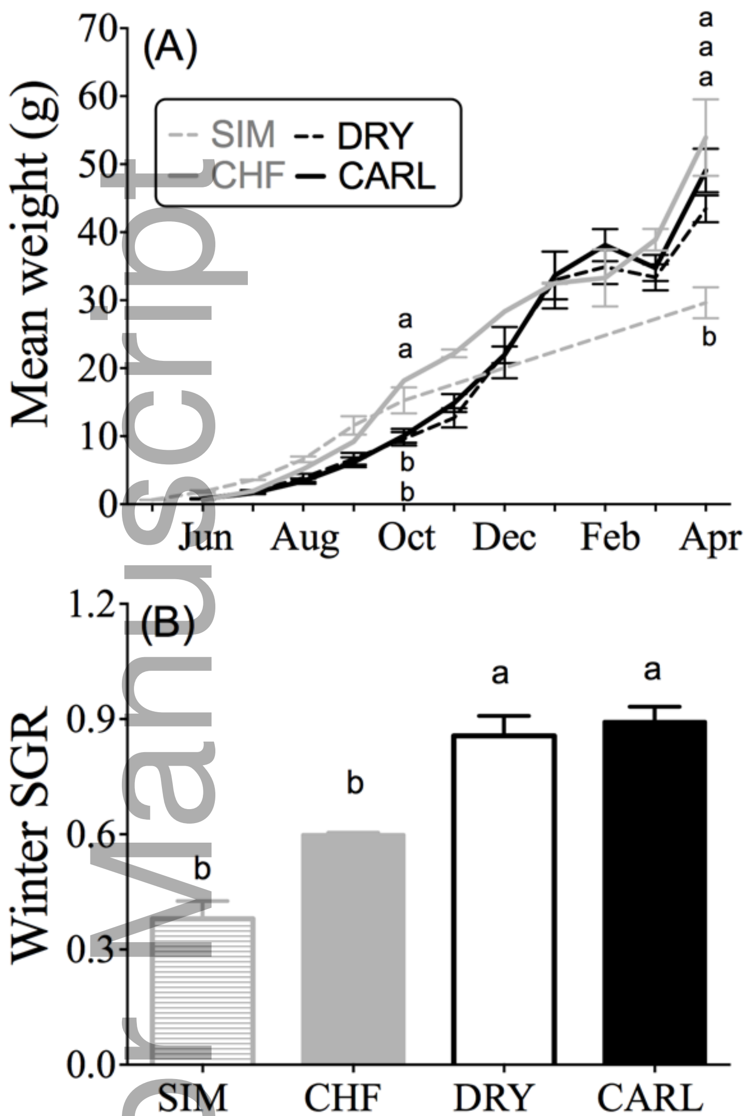
817 FIGURE 2



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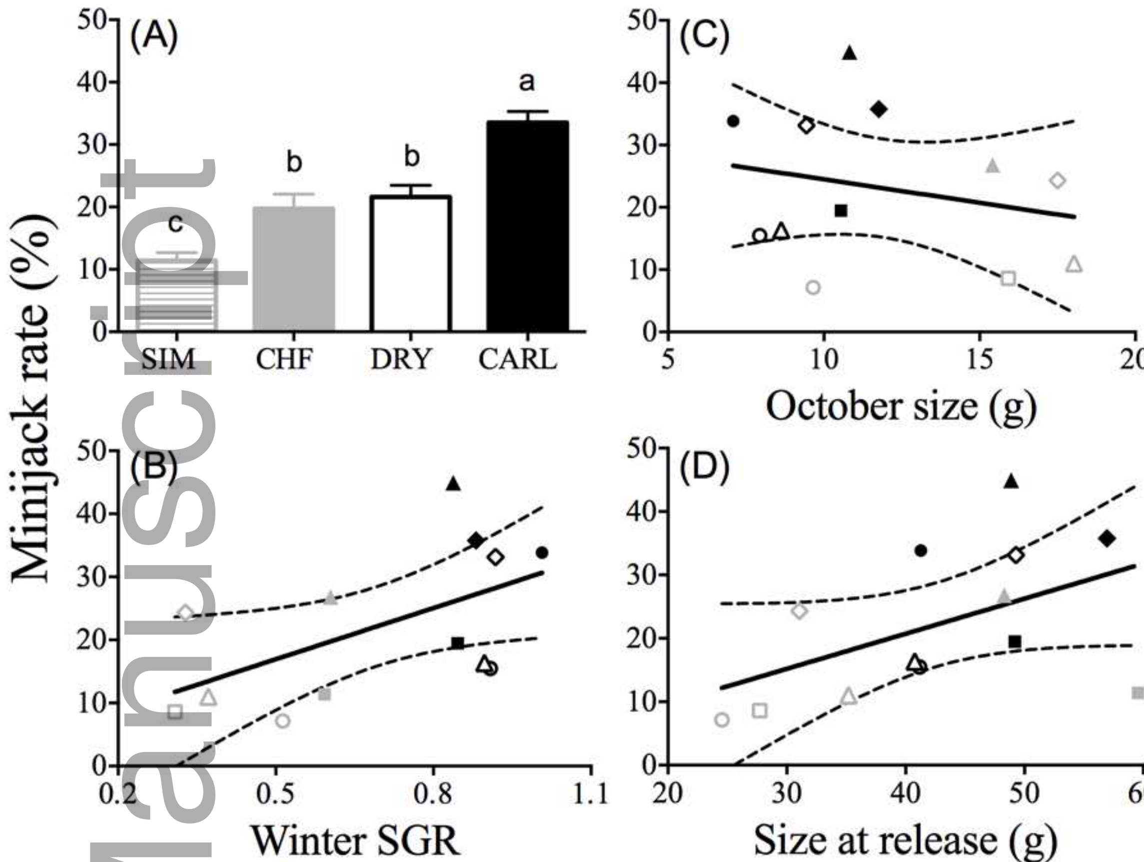
819 FIGURE 3



820

821 FIGURE 4

822

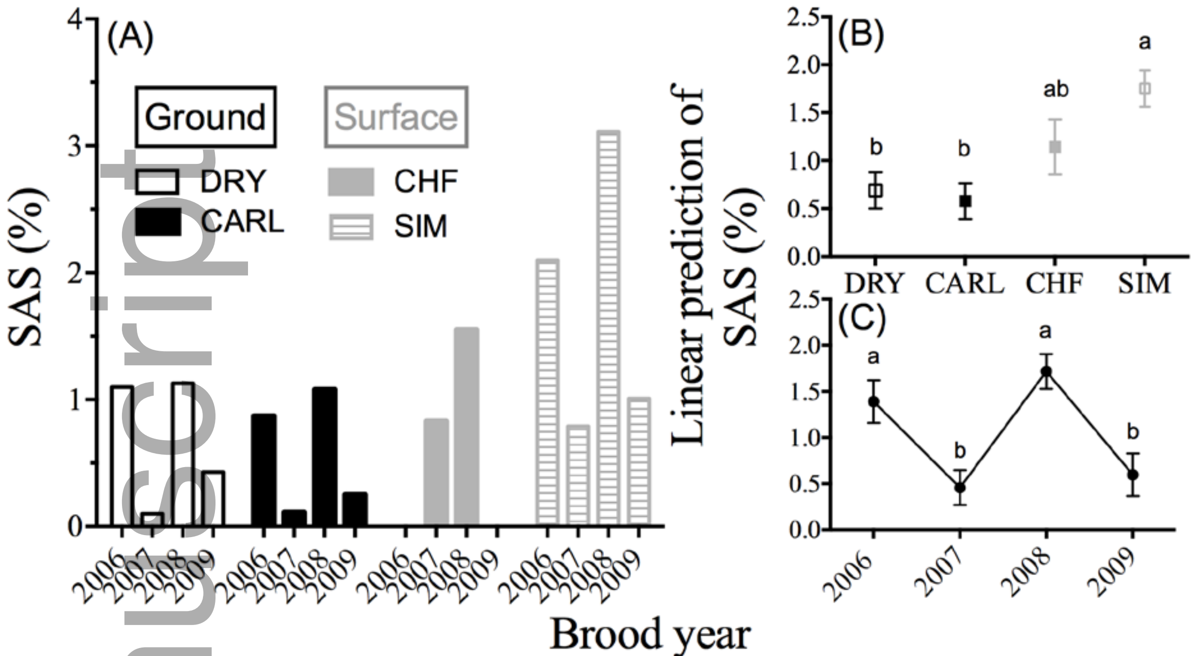
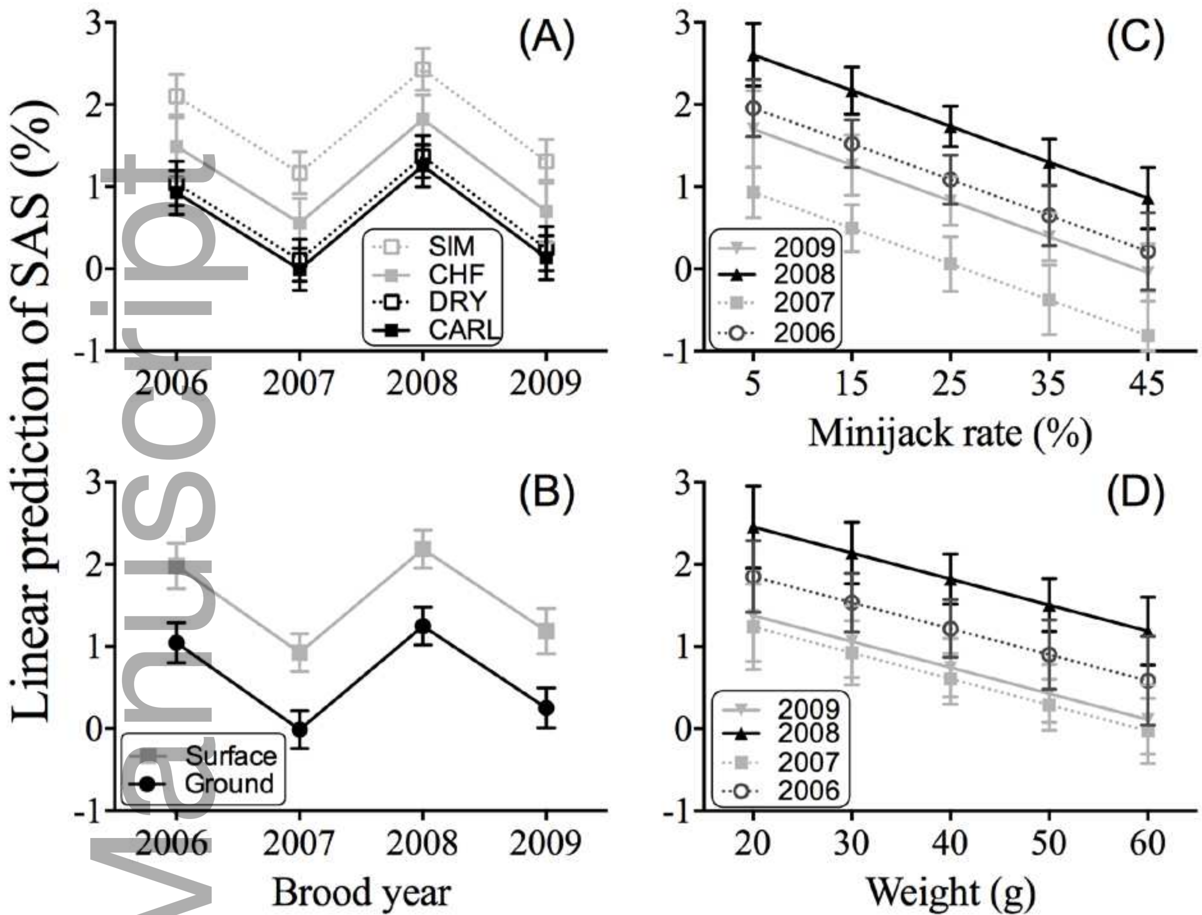
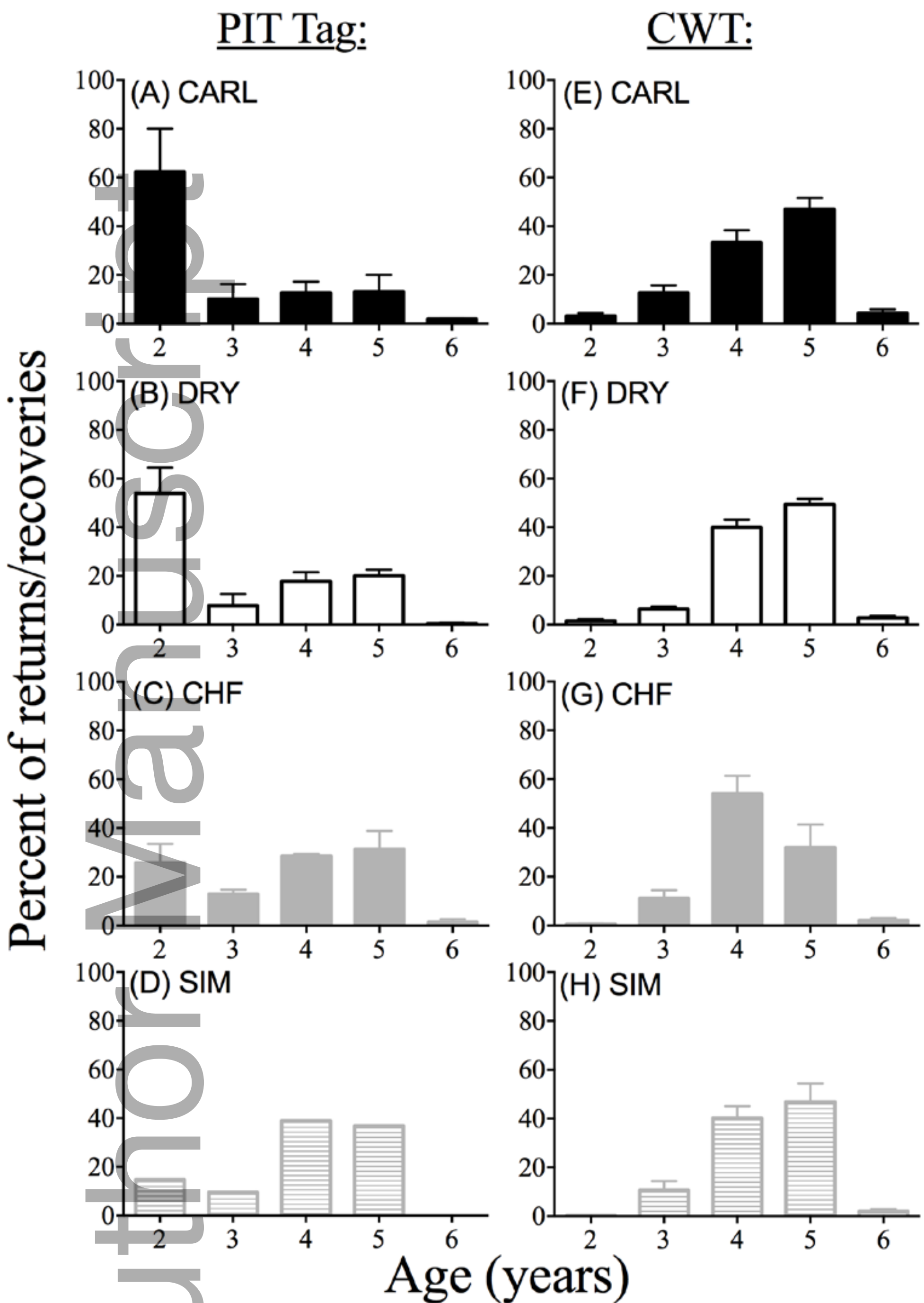

(A)
Ground
Surface
DRY
CARL
CHF
SIM
SAS (%)
0
1
2
3
4
2006
2007
2008
2009
Brood year
(B)
Linear prediction of SAS (%)
0.0
0.5
1.0
1.5
2.0
2.5
b
b
ab
a
DRY
CARL
CHF
SIM
(C)
a
b
a
b
2006
2007
2008
2009

FIGURE 5



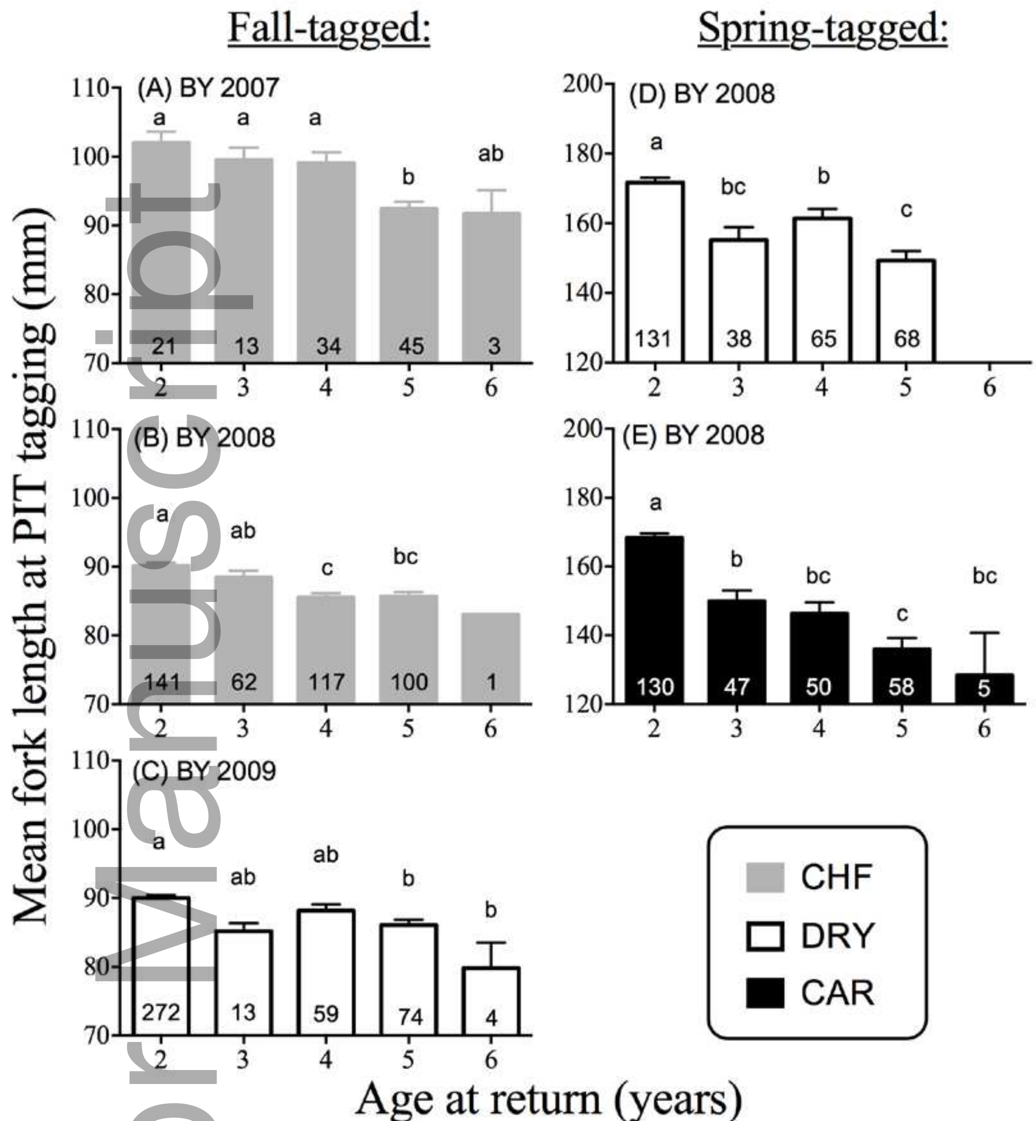
(A)
(B)
(C)
(D)
Linear prediction of SAS (%)
SIM
CHF
DRY
CARL
Surface
Ground
2009
2008
2007
2006
Brood year
Minijack rate (%)
Weight (g)

FIGURE 6



829

830 FIGURE 7



Fall-tagged:
Spring-tagged:
(A) BY 2007
(B) BY 2008
(C) BY 2009
(D) BY 2008
(E) BY 2008
Mean fork length at PIT tagging (mm)
Age at return (years)
CHF
DRY
CAR

FIGURE 8

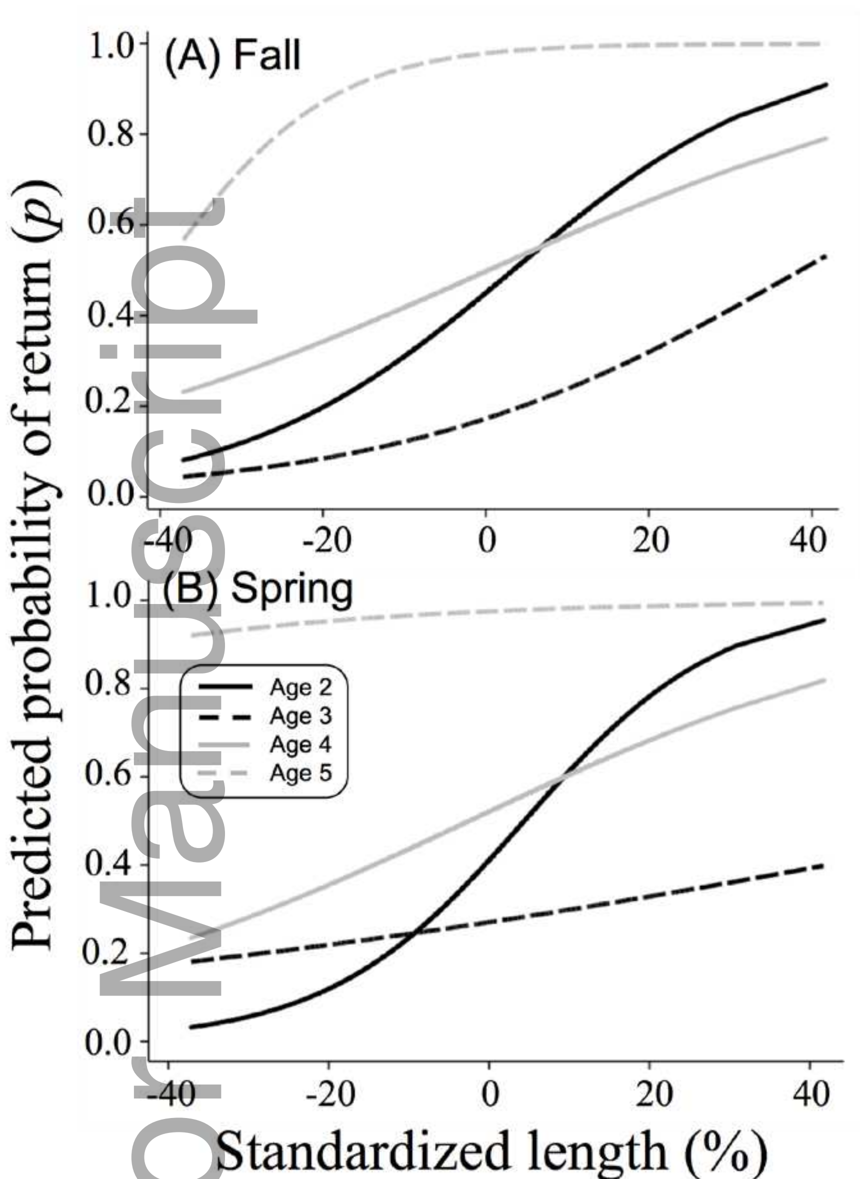


FIGURE 9

TABLE 1. Hatchery stock, brood years (BYs) sampled, acclimation site and release locations of the upper Columbia River basin yearling summer Chinook Salmon hatchery programs. Fish from all hatchery programs began their juvenile rearing at Eastbank Hatchery, located near Wenatchee, Washington and continued rearing there until acclimation (expect for CHF BY 2007, see footnote). The river kilometer (RKM) designation provides the RKM location on the Columbia River, followed by the RKM location for the primary tributary and the RKM location for a secondary tributary (if applicable) separated by period(s).

Program code	Hatchery program[a]	Hatchery Stock	BY	Ponding month	Acclimation site	Month transferred to acclimation site	Release river (RKM)
DRY	Wenatchee Summer Chinook	Wenatchee	2006-2009	June	Dryden Pond	late Feb/early Mar.	Wenatchee R (754.026)
CHF	Upper Middle Columbia Mainstem Summer Chinook	Wells	2007-2008	June	Chelan Falls, Net Pens[b]	late Nov.	Chelan R (810.000)
CARL	Methow Summer Chinook	Methow-Okanogan	2006-2009	June	Carlton Pond	late Feb/early Mar.	Methow R (843.058)
SIM	Okanogan Summer Chinook	Methow-Okanogan	2006-2009	May	Similkameen Pond	late Oct/early Nov.	Similkameen R (858.119.008)

[a] Hatchery program names listed above are from the Columbia River hatchery reform project report (HSRG 2009). For ease, we refer to these programs by their acclimation site throughout this article.

[b] BY 2007 Chelan Falls fish spent Nov.-Feb. at Turtle Rock facility (RKM = 765) prior to acclimation at Chelan Falls.

TABLE 2. Minijack evaluation brood year (BY), sample date, fork length (FL, mm), weight (WT, g), coefficient of variation (CV, %), condition factor (*K*), sample size and minijack rates (among males) from assessment of each hatchery program just prior to smolt release. ΔWT is the difference between weight at release and the target size of 45.4 g.

Program code	BY	Sample date	FL (mm)	CV, FL	WT (g)	CV, WT	ΔWT (g)	*K*	CV, *K*	*N*	Minijacks (%)
DRY	2006	4/17/08	154.8	18.3	41.2	54.4	-4.2	1.01	8.1	300	15.5
	2007	4/8/09	150.0	23.3	42.5	66.6	-2.9	1.07	8.5	300	4.1

	2008	4/6/10	152.3	18.0	40.8	51.4	-4.6	1.04	7.8	299	16.3
	2009	4/13/11	162.1	13.1	49.3	40.5	3.9	1.09	6.5	302	33.2
CHF	2007	4/29/09	168.5	16.8	59.6	46.3	14.2	1.14	7.9	226	11.4
	2008	4/27/20	153.9	23.0	48.3	78.2	2.9	1.06	18.9	299	26.8
CARL	2006	4/8/08	154.0	17.5	41.3	55.2	-4.1	1.02	7.2	300	33.9
	2007	4/15/09	158.1	23.0	49.2	65.8	3.8	1.04	9.4	294	19.5
	2008	4/13/10	163.3	13.7	48.9	38.9	3.5	1.05	6.6	299	44.9
	2009	4/12/11	169.8	15.8	57.0	45.1	11.6	1.07	7.5	300	35.8
SIM	2006	4/16/08	126.2	11.9	24.6	35.8	-20.8	1.17	5.6	300	7.1
	2007	4/14/09	133.5	11.5	27.7	33.6	-17.7	1.12	6.3	300	8.6
	2008	4/14/10	140.9	11.7	35.2	35.6	-10.2	1.20	6.0	300	11.0
	2009	4/13/11	137.5	12.4	31.1	35.7	-14.3	1.14	5.4	299	24.3

TABLE 3. Number of CWT and PIT tagged fish released each brood year (BY) for each population of yearling Summer Chinook Salmon, resulting smolt-to-adult survival (SAS) and smolt-to-adult return (SAR) estimates, and date and size at PIT tagging (mean FL and SD). SAS is based on CWT recoveries reported in RMIS database CWT summary report and includes harvest in addition to escapement. SAR is based on PIT tag detections of returning fish at Bonneville Dam (RKM = 234) on the Columbia River. Any age-2 recoveries and detections were removed from these SAS and SAR estimates.

							Size at PIT tagging	
Program code	BY	#CWT released	SAS (%)	#PIT tags released	SAR (%)	PIT-tagging dates	Mean FL (mm)	SD (mm)
DRY	2006	931,880	1.10	0				
	2007	453,699	0.10	0				
	2008	859,387	1.13	10,035	1.70	3/1/10 - 3/3/10	153.7	22.3

	2009	828,871	0.43	29,930	0.50	9/7/10 - 9/23/10	85.9	6.8
CARL	2006	417,795	0.87	0				
	2007	426,194	0.11	0				
	2008	373,246	1.08	10,094	1.59	2/16/10 - 2/18/10	145.0	22.9
	2009	239,621	0.25	5,020	0.20	9/1/10 - 9/2/10	78.4	6.0
CHF	2007	53,130	0.83	9,940	0.96	9/15/08 - 9/26/08	92.4	8.2
	2008	98,137	1.55	11,070	2.53	9/14/09 - 9/30/09	86.1	7.5
SIM	2006	597,276	2.10	0				
	2007	508,473	0.79	0				
	2008	341,120	3.11	0				
	2009	522,296	1.01	5,089	1.59	7/26/10 - 7/28/10	69.5	4.8

TABLE 4. Comparison of regression models predicting smolt-to-adult survival (SAS). Models are listed from the broadest predictor variable, brood year (BY), to descriptors of rearing (hatchery program [PROGRAM] and winter-rearing water source [ground vs. surface, WATER]), to fish attributes (minijack rate [MJ] and mean weight at release [WT]). BY was added to regression models with program, water source and fish attributes and was significant within these models (**P* < 0.05). Interactions with BY were tested but none were significant (data not shown). Beta (β) is the correlation coefficient for the continuous predictor variables, MJ and WT.

Model	Predictor variable(s)	*N*	df	*F*	*P*	R^2	AIC	ΔAIC	β MJ	β WT
1	BY	14	3, 10	3.17	0.072	0.49	31.5	14.8		
2	PROGRAM	14	3, 10	2.22	0.149	0.40	33.7	17.0		
3	BY, PROGRAM	14	6, 7	8.86	0.006	0.88	16.7	0.0		
4	WATER	14	1, 12	6.38	0.027	0.35	30.9	14.2		

5	BY, WATER	14	4, 9	10.88	0.002	0.83	18.1	1.4		
6	MJ	13	1, 11	2.17	0.169	0.16	31.6	14.9	-0.027	
7	BY, MJ	13	4, 8	5.83	0.017	0.74	22.2	5.5	-0.044*	
8	WT	14	1, 12	3.56	0.084	0.23	33.2	16.5		-0.037
9	BY, WT	14	4, 9	3.80	0.045	0.63	29.0	12.3		-0.032

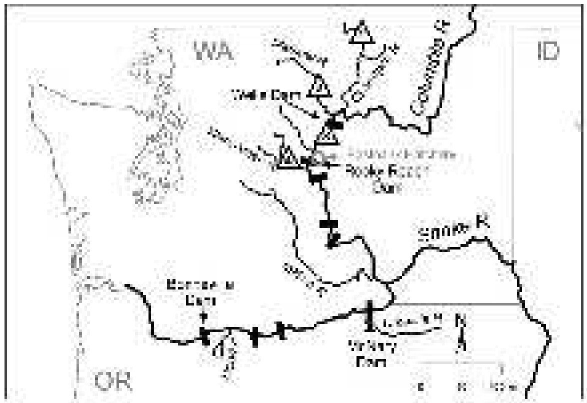
TABLE 5. Survival estimates by age class at return of upper Columbia summer Chinook Salmon for brood years (BYs) 2006-2009. SAR estimates are percent of PIT tagged fish release that were detecting returning to Bonneville Dam (RKM 234 on Columbia River). SAS estimates (based on CWT data) are minimum percent recoveries for each age class from RMIS database.

		SAR (%, based on PIT tags)						SAS (%, based on CWTs)						
BY	Program code	Age 2	Age 3	Age 4	Age 5	Age 6	Total	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Total
2006	CARL							0.02	0.07	0.33	0.43	0.04	0.00	0.89
	DRY							0.01	0.07	0.41	0.59	0.03	0.00	1.11
	SIM							0.00	0.09	0.79	1.18	0.04	0.00	2.10
2007	CARL							0.00	0.01	0.02	0.06	0.01		0.11
	CHF	0.21	0.13	0.34	0.45	0.03	1.17	0.01	0.07	0.39	0.35	0.03		0.84
	DRY							0.00	0.00	0.04	0.05	0.01		0.10
	SIM							0.00	0.04	0.24	0.47	0.04	0.00	0.79
2008	CARL	1.29	0.47	0.50	0.57	0.05	2.87	0.00	0.16	0.47	0.43	0.01		1.08
	CHF	1.27	0.56	1.06	0.90	0.01	3.80	0.01	0.23	0.96	0.35	0.02		1.56
	DRY	1.31	0.38	0.65	0.68	0.00	3.01	0.00	0.08	0.55	0.49	0.02		1.13
	SIM							0.01	0.63	1.66	0.81	0.01		3.12
2009	CARL	0.80	0.04	0.08	0.06	0.02	1.00	0.02	0.05	0.09	0.10	0.01		0.27
	DRY	0.91	0.04	0.20	0.25	0.01	1.41	0.00	0.03	0.17	0.21	0.01		0.43
	SIM	0.28	0.18	0.73	0.69	0.00	1.87	0.00	0.13	0.40	0.47	0.01		1.01

TABLE 6. Model summaries for predicted probability of return (p) for age classes 2-5 for fish PIT tagged **(A)** during the fall at age 1, or **(B)** during the spring at age 1+ based on logistic

regression models with standardized fork length at tagging, (FL-mean)/mean × 100, as the predictor variable. These model summaries correspond with the predicted probabilities illustrated in Figure 9. LR = likelihood ratio; OR = odds ratio. This analyses did not include CARL BY 2009 & SIM BY 2009 as they were PIT tagged in July-early September and had very little variation in size at tagging.

		Model					Predictor		*N*, by age class				
Model	Response variable	*N*	df	LR χ^2	*P*	Pseudo R^2	OR	*z*	Age 2	Age 3	Age 4	Age 5	Age 6
A) Fall-Tagged:													
1	*p*, Age 2	959	1	52.3	0.000	0.04	1.06	7.0	434	88	210	219	8
2	*p*, Age 3	525	1	7.9	0.005	0.02	1.04	2.8		88	210	219	8
3	*p*, Age 4	437	1	6.9	0.009	0.01	1.03	2.6			210	219	8
4	*p*, Age 5	227	1	3.5	0.063	0.05	1.10	1.8				219	8
B) Spring-Tagged:													
5	*p*, Age 2	592	1	138.7	0.000	0.17	1.09	9.9	261	85	115	126	5
6	*p*, Age 3	331	1	2.6	0.104	0.01	1.01	1.6		85	115	126	5
7	*p*, Age 4	246	1	15.3	0.000	0.05	1.03	3.8			115	126	5
8	*p*, Age 5	131	1	1.1	0.300	0.03	1.03	1.0				126	5



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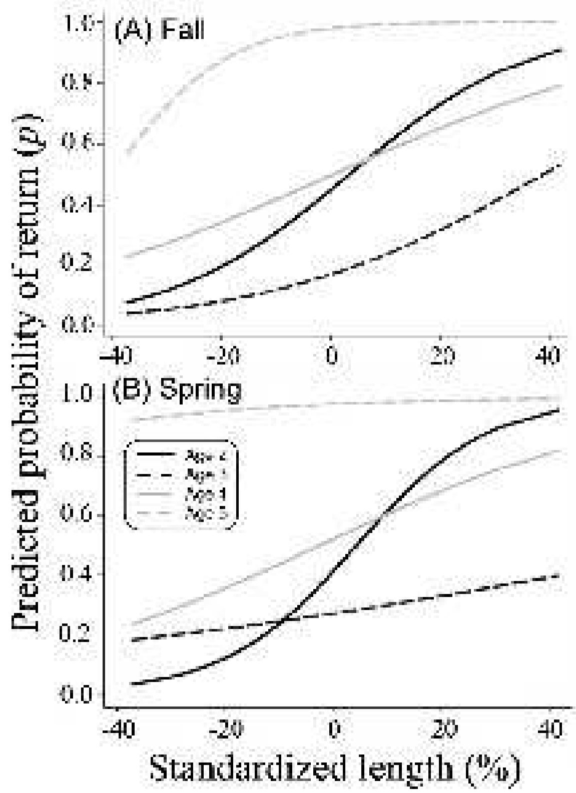

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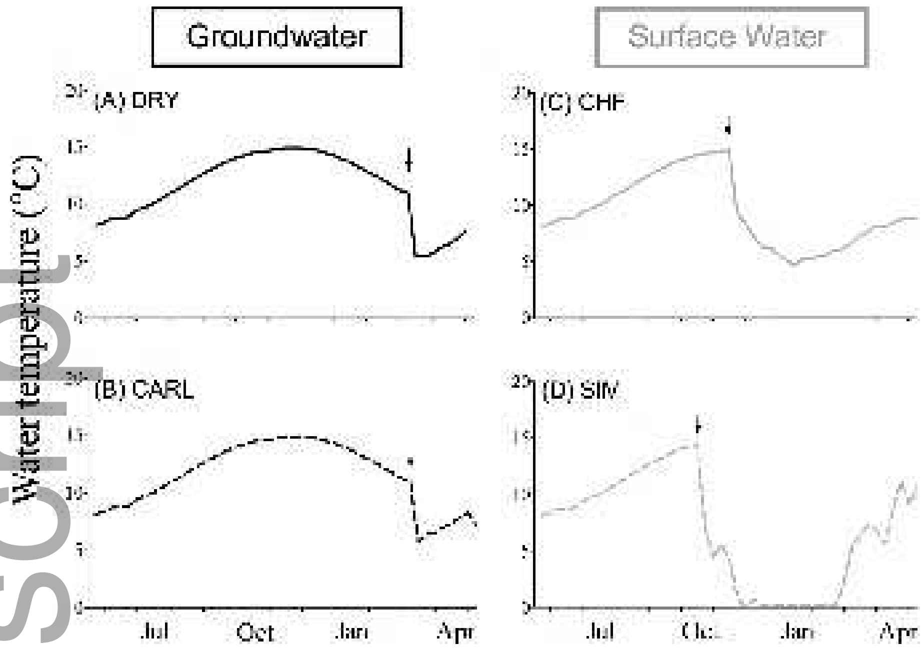

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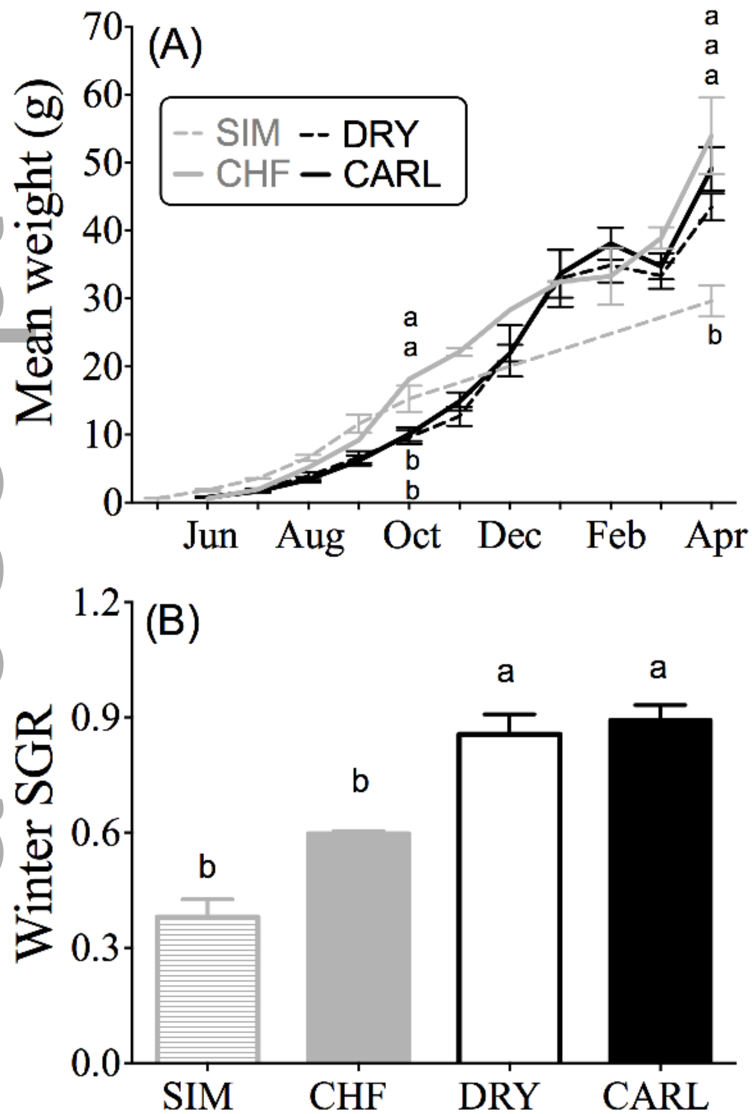

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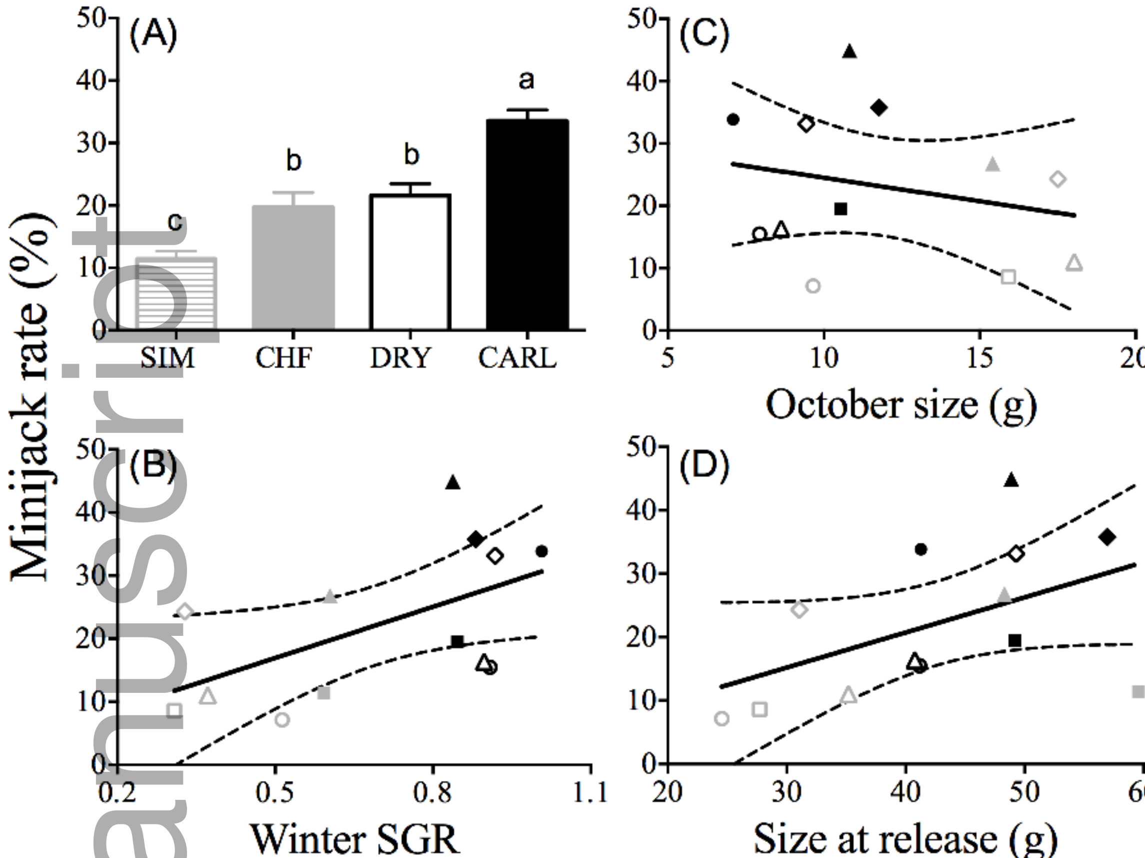

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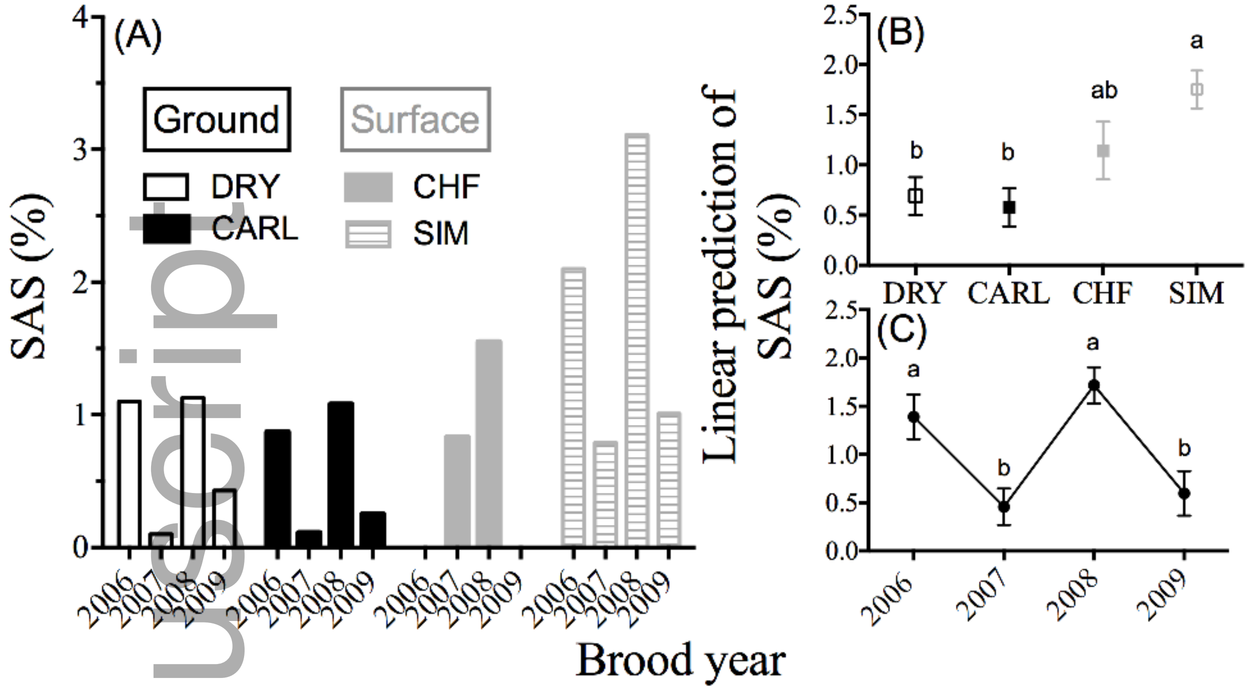

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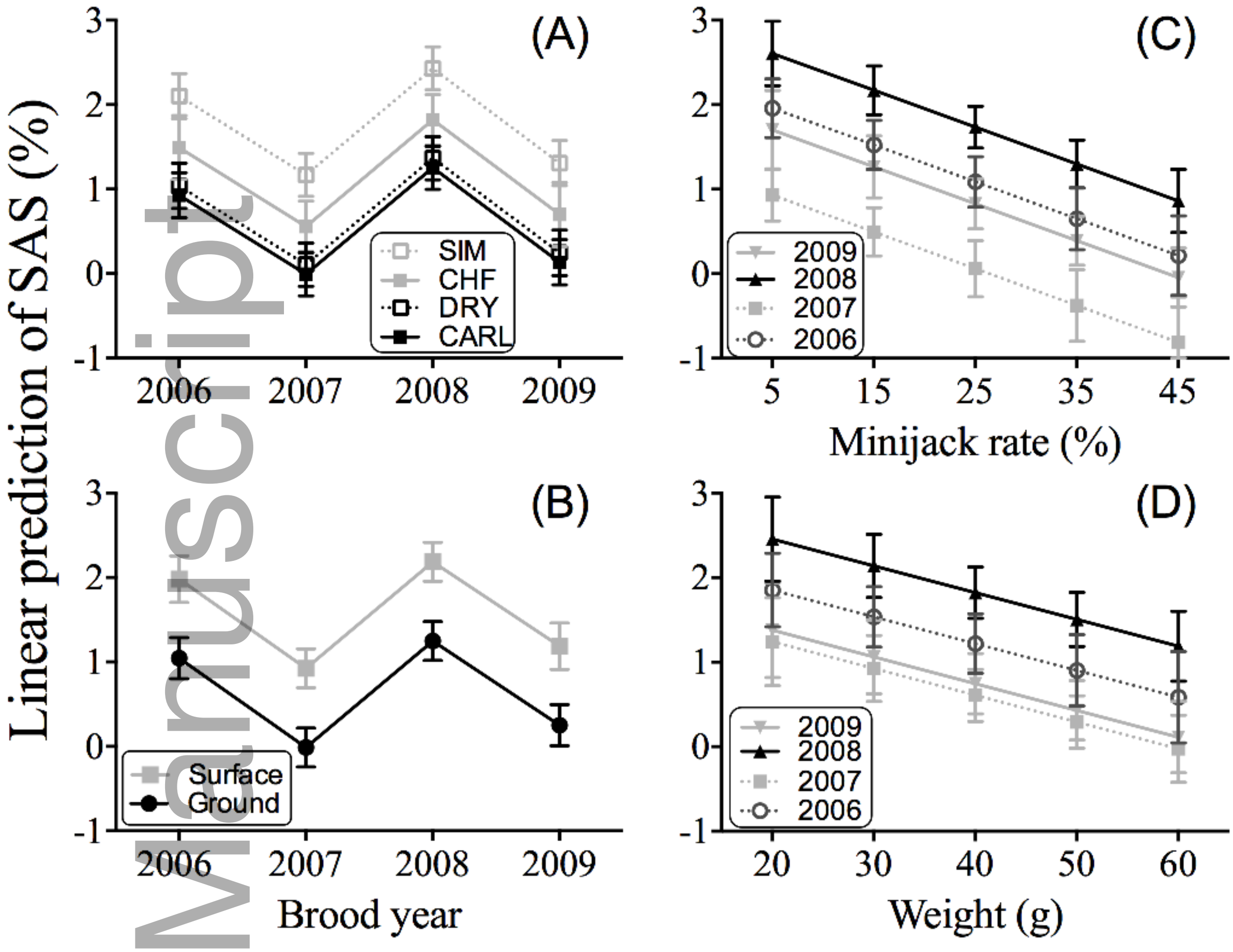

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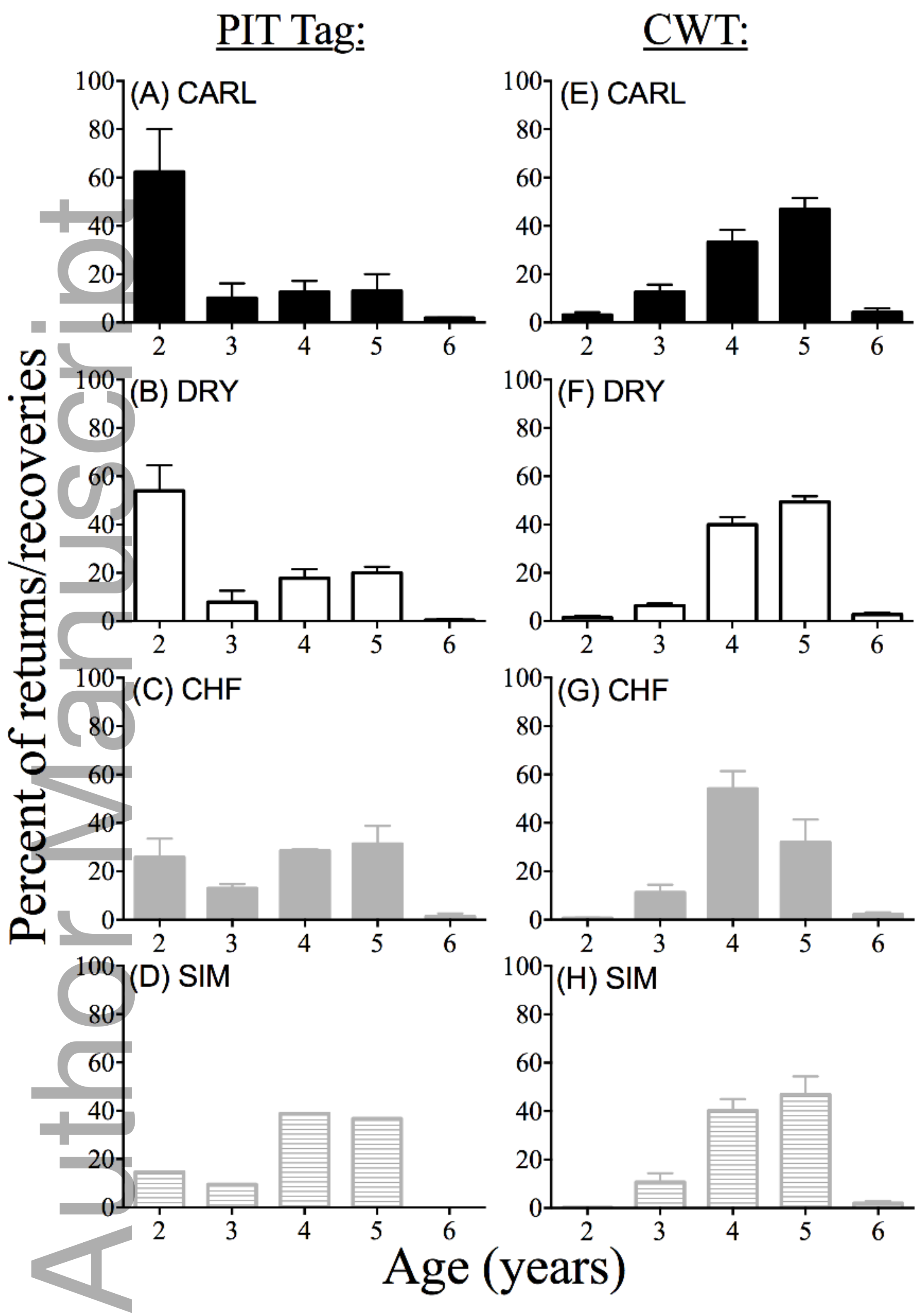

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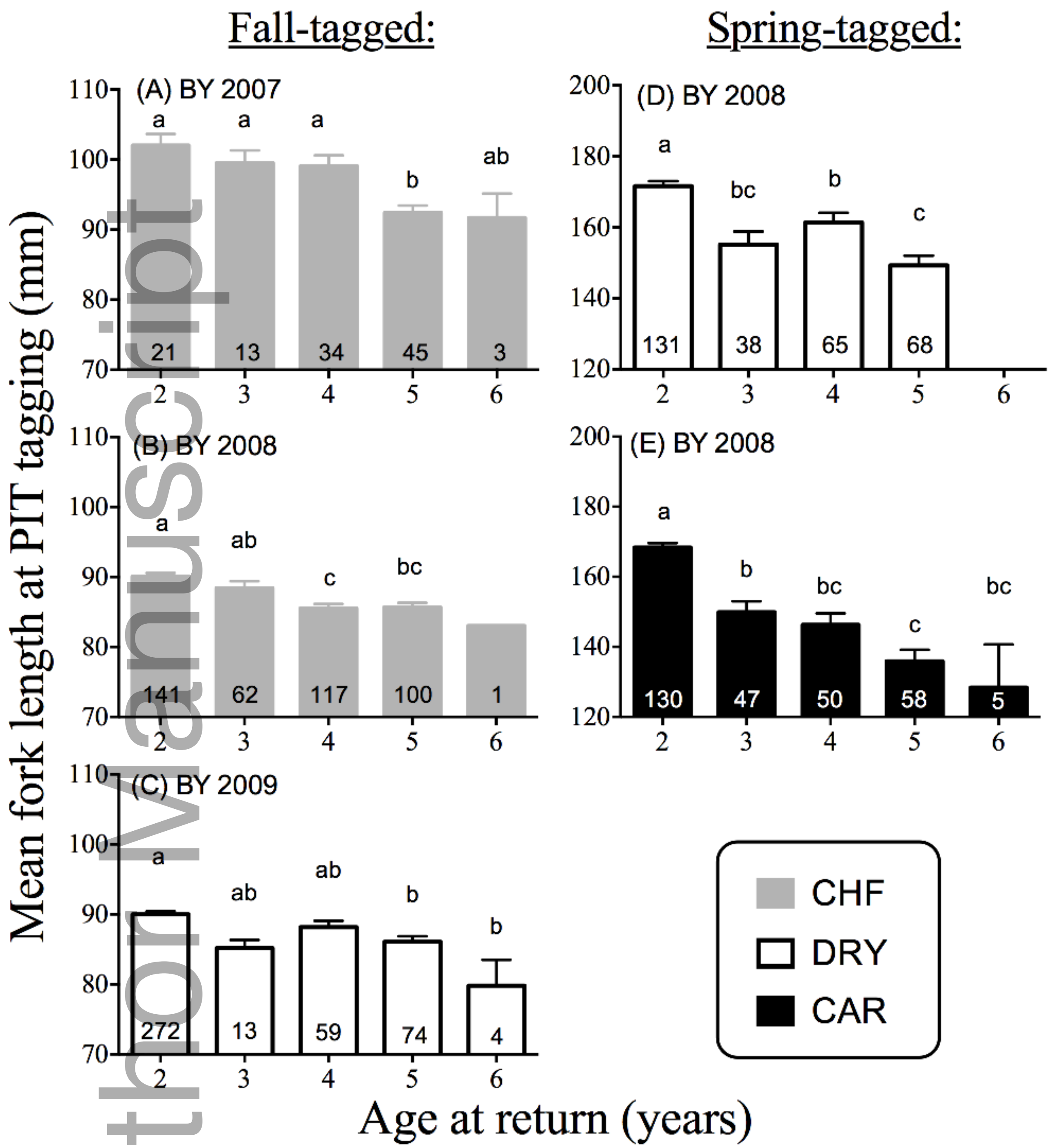

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