



Effects of volitional emigration timing and smolt size on survival and age-at-return in a Pacific salmon hatchery population

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Abstract Many Pacific salmon populations are returning from sea at younger ages and smaller sizes. Hatchery culture, management practices, and environmental factors influence juvenile release size and emigration timing, which in turn affect important demographic characteristics in returning adults. We analyzed data from approximately 345,000 tagged spring Chinook Salmon juveniles exiting Cle Elum Supplementation and Research Facility (Yakima River, Washington, USA) acclimation sites over thirteen brood years (2002–2014), evaluating smolt size, emigration timing, river flow, juvenile survival, and age-at-return. We observed a relationship between size and volitional exit timing of smolts from acclimation sites, with larger fish tending to emigrate earlier than smaller fish. Early emigration was also

coincident with lower river flows near acclimation sites. Later emigration timing was correlated with an increase in apparent survival of juveniles to Bonneville Dam (500–530 km downstream of acclimation sites), but also with a lower rate of survival to return from sea. In general, for juveniles successfully emigrating downstream of Bonneville Dam, age-at-return increased with decreasing juvenile fish size and later emigration timing. Our results support a growing body of evidence that hatchery practices may result in larger smolts that tend to return at younger ages. Given the biological and economic consequences of younger age-at-maturation, methods to reverse this trend should be further explored and implemented.

Keywords Acclimation · Aquaculture · Demography · Ecology · Management · Productivity

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Introduction

Over the past century, hundreds of hatchery programs have been implemented throughout the Pacific Northwest to compensate for declines in the abundance of salmon populations including Chinook Salmon (*Oncorhynchus tshawytscha*; Lichatowich 1999; Waples et al. 2007). Although hatchery programs vary and typically have a combination of management objectives, a consistent goal is to increase the number of returning adults to provide harvest opportunities (subsistence, ceremonial,

commercial, and recreational), while meeting escapement objectives for continued health of the population. An additional goal is to mitigate for lost production and productivity as habitats are increasingly altered to serve the needs of growing human populations (Lackey 2001; Waples et al. 2009; Hartman et al. 2020). Examples of variables in hatchery operations and management that can be adjusted to optimize fish survival include broodstock selection (Hankin et al. 2009; Winsor et al. 2021), incubation temperature (Winsor et al. 2021), feed ration and concomitant growth rates (Beckman et al. 1999, 2017; Larsen et al. 2006; Spangenberg et al. 2014; Winsor et al. 2021), rearing density (Banks 1994; Beckman et al. 1999), raceway water flow (Banks 1994) and temperature (Spangenberg et al. 2014), number of juvenile fish released (Paquet et al. 2011), release size and timing (Irvine et al. 2013), acclimation (Dittman et al. 2010; Rosenberger et al. 2013), and, in some cases, migration pathways (Ward et al. 1997). All of these variables must be managed within the context of a series of complex interactions with the natural environment that may be unique to a given species, population, and river system.

In addition to regional declines in salmon productivity, evidence from recent studies in both natural and hatchery origin fish indicates that adults are returning to spawn at younger ages and smaller sizes (Lewis et al. 2015; Ohlberger et al. 2018; Oke et al. 2020). The potential anthropogenic and natural factors responsible for these changes are not fully understood, but are an active area of investigation because of their importance to salmon population demographics, sustainability, ecosystem dynamics, and fisheries (Ohlberger et al. 2020; Oke et al. 2020). In both the natural and hatchery environments, older, larger females are typically more effective breeders due to higher fecundity (Knudsen et al. 2008; Ohlberger et al. 2020; Oke et al. 2020), and in the natural environment, larger males are more effective competitors for breeding opportunities (Fleming and Gross 1994; Schroder et al. 2010, 2012). Additionally, older, larger fish increase biomass in natal streams as they contain more marine-derived nutrients that are important to maintaining primary productivity and overall ecosystem health (Bilby et al. 1998, 2003; Oke et al. 2020). Finally, larger fish are more desirable in subsistence, cultural, commercial, and recreational

fisheries (Fenberg and Roy 2008; Zhou et al. 2010; Lubich et al. 2021).

Intraspecific trait variation is important to community ecology and dynamics (Bolnick et al. 2003, 2011). For example, variations in size, spatial distribution, and ability to tolerate extreme environmental conditions can allow a species to better exploit available habitats or continue to thrive under less than ideal conditions. Understanding the extent to which management protocols and environmental factors in a hatchery culture setting may influence juvenile size, emigration timing, and size and age at maturity is important for optimizing hatchery operations for both the quantity and the quality (e.g., traits such as size and age) of adults they ultimately produce. Studies in natural and hatchery origin fish have shown that larger juveniles often have a higher probability of surviving to adulthood (Zabel and Williams 2002; Tipping 2011; Brown et al. 2013; Evans et al. 2014; Faulkner et al. 2019). However, larger smolts have also been associated with younger age at maturity (Tipping 2011; Larsen et al. 2013; Harstad et al. 2014; Tattam et al. 2015). A study of artificially reared juvenile Coho Salmon (*O. kisutch*) in British Columbia, Canada, found a significant interaction between size and timing of releases with more age-3 male (common name: jack) production compared to older age classes observed from early release of large juveniles (> ~20 g in April; Bilton et al. 1982). Similarly, Tattam et al. (2015) observed a correlation between emigration timing and age-at-maturity in a wild Chinook Salmon population from the John Day River in northeast Oregon. While earlier releases in the Bilton et al. (1982) study were correlated with younger age-at-maturity, wild juveniles in the John Day River (Tattam et al. 2015) that were tagged later in the spring (later emigrants) had higher probability of maturing at age-4 rather than age-3.

The emigration timing of hatchery-released juveniles and river conditions (e.g., water temperature and flow) during emigration are among many factors affecting downstream survival, size and age at maturity, and adult return rates. Flow manipulations in impounded systems like the Columbia River that change the timing, duration, or magnitude of temperature and flow regimes may impact growth rates (Dunnigan and Terrazas 2021) and in the spring can significantly affect the emigration of salmonid smolts. Increased natural flows (e.g., spring freshets)

encourage emigration, reduce travel times, and can improve survival of juvenile Chinook Salmon (Connor et al. 2003; Sommer et al. 2005; del Rosario et al. 2013; Takata et al. 2017). Warmer water temperatures, potentially indicative of drought conditions, have been associated with earlier emigration (Sykes et al. 2009). However, juvenile survival can be reduced when fish emigrate during periods of lower flows or warmer water temperatures as energetic costs increase, and these conditions may also result in longer travel times increasing exposure to predation and other mortality risks (NRC 2004; Pandit et al. 2017; Keefer et al. 2018). Previous studies have demonstrated that arrival timing to the estuary may be related to survival to adulthood (Zabel and Williams 2002) and juvenile fish that emigrate past Bonneville Dam (rkm 233; the furthest downstream dam) on the Columbia River from early to mid-May have been reported to survive at rates 4–50 times greater than those arriving in mid-June (Scheuerell et al. 2009).

Taken together, these factors illustrate the importance of using life-cycle analyses (e.g., Beckman et al. 1998, 2017; Harstad et al. 2018) to empirically evaluate and better understand the interrelationships between smolt size at release, smolt development, emigration timing, and ecosystem dynamics (e.g., freshwater, estuary, and marine conditions) and their effects on survival and adult demography. The widespread use of passive integrated transponder (PIT, Biomark, Boise, ID) tag technology (Prentice et al. 1990; Connolly et al. 2008; www.ptagis.org) and PIT-tagging programs has facilitated analyses of juvenile and adult migration and survival, habitat use, and fishery management practices (Greenberg and Giller 2000; O'Donnell et al. 2010; Thiem et al. 2013). In the Columbia River Basin, PIT tags have allowed insights into specific components of the life history of individual salmon including downstream survival and travel time through the emigration corridor as well as comparative studies of release groups and survival to adult return (McCann et al. 2022).

The Cle Elum Supplementation and Research Facility (CESRF; rkm 297) on the Yakima River, Washington, is relatively unique in its ability to facilitate the type of life-cycle investigation described above, thereby providing insights that might allow hatcheries, including the CESRF, to be adaptively managed to better meet overall program objectives. We studied detection histories from over 344,000

PIT-tagged CESRF spring Chinook Salmon spanning thirteen brood years (2002–2014; juvenile migration years 2004–2016; return/spawn years 2004–2019) and conducted post hoc analyses (stated as null hypotheses) to evaluate how present hatchery management protocols impact overall program results:

H_0 (1): volitional exit date of juveniles from the acclimation and release sites was independent of acclimation site, smolt size, and river flow near acclimation sites,

H_0 (2): apparent survival of juvenile emigrants at downstream detection sites was independent of acclimation site, smolt size, and volitional exit date, and

H_0 (3): smolt-to-adult return (SAR) and age-at-return were independent of smolt size, acclimation site, and volitional exit date.

Materials and methods

Study area and CESRF facilities

The Yakima River, located in south central Washington State, is a tributary to the Columbia River (Fig. 1). Since the establishment of the CESRF in 1997, the Yakama Nation has been collaborating with the Washington Department of Fish and Wildlife (WDFW) and other regional and national fishery management agencies to monitor and evaluate a hatchery supplemented population of spring Chinook Salmon in the upper Yakima River (the portion upstream of Roza Dam, rkm 206; Fig. 1; Fast et al. 2015). Each year fish are spawned and reared at the central hatchery facility in Cle Elum, WA (CESRF, Fig. 1; Knudsen et al. 2006; Fast et al. 2008). After approximately ten months of rearing (in October and November), fish are marked and then later transported from the CESRF (as yearling presmolts the following January or February) to three acclimation sites located at Easton (ESJ) 25 km upstream of the CESRF, Clark Flat (CFJ) 25 km downstream of the CESRF, and Jack Creek (JCJ) on the Teanaway River 27 km upstream from its confluence with the Yakima River (rkm 287; Fig. 1). Fish are reared using a combination of well and river water while at the CESRF, but once fish are moved to acclimation sites only river water is used, as the intent is to “imprint” the fish to

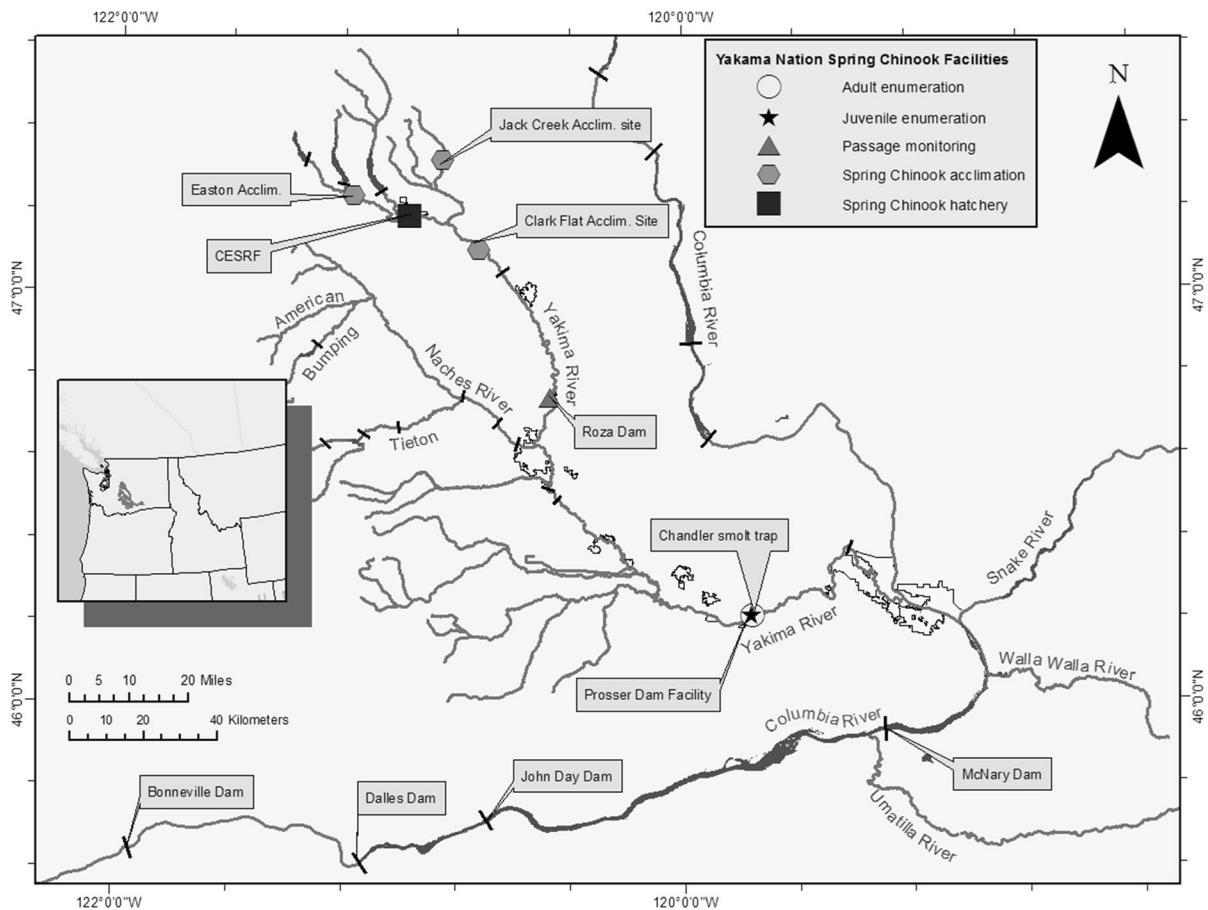


Fig. 1 Map of the study area showing the Yakima and lower Columbia River basins, Cle Elum Supplementation and Research Facility (CESRF), spring Chinook Salmon acclima-

tion sites (Easton, Jack Creek, Clark Flat), and downstream Yakima and Columbia River dams (map courtesy of Paul Huffman, Yakama Nation Fisheries, retired)

these sites so that returning adults will home to these portions of the river system and “integrate” with the natural spawning population (Dittman et al. 2010; Fast et al. 2015). Target release for the CESRF program is 810,000 smolts at 15 fish per pound (30.2 g per fish).

Marking and PIT-tag detection

An annual average of 777,000 CESRF spring Chinook Salmon were released during this study period, including a subset of approximately 40,000 PIT-tagged fish (range 4.7–6.2%, mean 5.2% of each annual release). Tagged fish were distributed across all rearing raceways and acclimation sites, with site allocation based on overall experimental

needs (Fast et al. 2008; Bosch 2019). PIT-tag codes allowed individual fish to be identified by brood year, acclimation site, and raceway of release. Fork lengths were taken from all fish at the time of PIT tagging, but weights were collected for only a small subsample ($N = 12, 113$; 3.5% of N for length-sampled fish) of individual PIT-tagged fish in a quality control exercise subsequent to tagging. PIT codes, fish lengths, and other release information were submitted annually to the PIT Tag Information System (PTAGIS; <http://www.ptagis.org>) database maintained by the Pacific States Marine Fisheries Commission (PSMFC). The PSMFC has also installed and maintained automatic PIT-tag detectors (with passive detection capability for both juvenile and adult fish) at several locations throughout

the Columbia (e.g., Bonneville, McNary, and John Day Dams) and Yakima river systems (including the ESJ, JCJ, and CFJ acclimation sites). Thus, the PTAGIS database contains historical release and detection data for all Columbia River Basin PIT-tagged fish.

We queried the PTAGIS database in March and December 2019 to retrieve and enumerate PIT-tag detections of all spring Chinook Salmon marked at the CESRF that were released and subsequently detected volitionally exiting the acclimation sites (brood years 2002–2014; emigration years 2004–2016). For each fish detected at release, we also retrieved both downstream and upstream (return years 2004–2019) PIT-tag detection data at all monitoring locations (dams) downstream of the acclimation sites (Fig. 1). We assumed fish migrated past a given dam if a PIT tag was detected at or downstream (juvenile migrants), and at or upstream (returning fish), of that dam. Data were evaluated for interannual consistency and anomalies (described further below). Records deemed to be anomalous were excluded from statistical analyses (further explained in text following table), leaving a total of more than 344,000 unique PIT-tagged fish that were analyzed in this study (Table 1).

Statistical analyses

Volitional exit timing (day of year a fish was detected migrating out of the acclimation sites (ED)), smolt size at release (fork length (FL)), acclimation site (Ac.Site), and daily average river flow (cubic feet per second (cfs)) near each acclimation site during the emigration period (Ac.RF; <https://www.usbr.gov/pn/hydromet/yakima/>) were considered critical parameters for purposes of this study. Volitional exit (including fish forced from acclimation sites upon closure of the sites) occurred between March 9 and May 16 annually (68 days). Fish with exit dates outside of this range were excluded from the analyses. On average, fork length at time of PIT tagging in October–November was approximately 93.5% of fork length when fish were sampled randomly at the acclimation sites in March at the beginning of volitional release (Bosch 2019). As noted earlier, the total sample size for weights of individual PIT-tagged fish was only 3.5% of the sample size for length-sampled fish. Therefore, we used fork length at PIT tagging as a surrogate for smolt size at release in this study. Smolt sizes less than 75 or greater than 149 mm were considered outliers (<0.15% of all fish estimated to have been released) and were excluded from the analyses.

Table 1 Passive integrated transponder (PIT) tag information for juvenile Cle Elum Supplementation and Research Facility (CESRF) spring Chinook Salmon smolts used in this study: number of fish detected exiting acclimation sites (Clark Flat (CFJ), Easton (ESJ), and Jack Creek (JCJ)) and all sites

combined; mean fork lengths (FL (mm)) and weights (WT (grams)) of fish at tagging; and number of detections at or downstream of Bonneville Dam (BON), for brood years 2002–2014 (juvenile emigration years 2004–2016)

| Year | CFJ | ESJ | JCJ | Total | FL | WT ¹ | BON |
|-------|--------|---------|---------|---------|-------|-----------------|--------|
| 2002 | 4349 | 6448 | 6495 | 17,292 | 106.7 | 13.9 | 246 |
| 2003 | 4340 | 6467 | 6513 | 17,320 | 106.1 | 13.7 | 236 |
| 2004 | 4330 | 6440 | 4369 | 15,139 | 97.6 | 12.1 | 521 |
| 2005 | 8731 | 12,931 | 13,110 | 34,772 | 109.2 | 14.8 | 1081 |
| 2006 | 3845 | 5833 | 5876 | 15,554 | 108.7 | 16.5 | 422 |
| 2007 | 7871 | 11,679 | 11,663 | 31,213 | 108.9 | 15.2 | 1726 |
| 2008 | 7786 | 11,684 | 11,680 | 31,150 | 106.3 | 15.2 | 1750 |
| 2009 | 7821 | 11,610 | 8927 | 28,358 | 111.5 | 17.5 | 360 |
| 2010 | 7667 | 11,575 | 11,720 | 30,962 | 108.9 | 17.0 | 1066 |
| 2011 | 7636 | 11,478 | 11,654 | 30,768 | 108.0 | 16.1 | 672 |
| 2012 | 7599 | 11,498 | 11,654 | 30,751 | 109.7 | 17.1 | 678 |
| 2013 | 7733 | 11,503 | 11,642 | 30,878 | 112.3 | 14.9 | 754 |
| 2014 | 7651 | 11,334 | 11,518 | 30,503 | 113.1 | 18.1 | 1181 |
| Total | 87,359 | 130,480 | 126,821 | 344,660 | 108.2 | 15.6 | 10,693 |

¹From subsample of fish; see text

The spring Chinook Salmon program at the CESRF consists of integrated (16 raceways) and segregated (2 raceways) production (we refer readers to Mobrand et al. 2005 and Fast et al. 2015 for additional information regarding integrated and segregated hatchery production); only integrated program releases were included in this study. In brood years 2002 through 2004, one-half of the fish were subjected to a slower growth feed regime (Larsen et al. 2013) resulting in reduced size at release for these fish. The slower growth fish from these brood years were excluded from the analyses. In brood year 2006, one-half of the fish were fed an EWOS® diet; for interannual consistency, fish fed this diet were excluded from the analyses.

To evaluate hypotheses 1 and 3, we used mixed-effects linear regression (Zuur et al. 2009; Gosselin et al. 2018) to model the effects of fixed variables (e.g., ED, Ac.Site, FL, and Ac.RF) and two-way interactions between variables, with brood year (BY) as a random variable, on ED (H_01) and SAR (H_03). For H_03 , we assumed the underlying error distribution was binomial and used a logit link in the model (McCullagh and Nelder 1989). Ac.Site was considered a factor with 3 levels; it could have been considered a random variable, but there were only three of them and possible differences between them could be useful for management. BY was considered random since the included years were a “sample” of all possible years and we were not interested in making inference for individual years.

We first fit the largest model denoted as

$$H_01 : ED \sim Ac.Site + FL + Ac.RF + Ac.Site * FL + Ac.Site * Ac.RF + FL * Ac.RF + (1|BY) + error,$$

$$H_03 : SAR \sim Ac.Site + FL + ED + Ac.Site * FL + Ac.Site * ED + FL * ED + (1|BY) + error,$$

where “~” denotes “as a function of,” “*” denotes interaction, (1|BY) denotes that BY was random with respect to the intercept term (i.e., the result is that predicted ED curves based on other variables would have BY = 13 “parallel” curves for the years), and the error term was assumed to be normally distributed. Inference based on the fixed variables therefore was evaluated by averaging over BYs. Note that FL and Ac.RF were standardized (i.e., subtract the overall

mean and divide by the overall standard deviation) so that parameter coefficients would be on the same scale; means and predictions were back-transformed to the original scale.

Next, we fit the suite of models that were subsets of this largest model. We omitted subset models where an interaction was included but each of the pertinent main effects were not. We compared models using Akaike’s Information Criterion (AIC; Burnham and Anderson 2002). We chose the “best” model as the one with minimum AIC. If multiple models were close to the minimum, we chose the most parsimonious as “best” (e.g., FL + Ac.RF in one and only FL in another), unless they contained different types of variables (e.g., FL in one model and ED in another) in which case we model-averaged them (Burnham and Anderson 2002). These analyses were done in R (R Core Team 2021) and used the lme4 package (v1.1–26; Bates et al. 2015).

Additional information, evaluations, and analyses specific to each hypothesis were as follows.

H_0 (1): volitional exit date of juveniles from the acclimation and release sites was independent of acclimation site, smolt size, and river flow near acclimation sites.

We used analysis of variance (ANOVA) to test whether annual trends in mean smolt size, volitional exit date, and river flow near acclimation sites varied by acclimation site and brood year.

H_0 (2): apparent survival of juvenile emigrants at downstream detection sites was independent of acclimation site, smolt size, and volitional exit date.

To evaluate factors affecting juvenile survival from Ac.Site to Bonneville Dam (BON; rkm 234; Fig. 1), we used a mark-recapture method, the Cormack-Jolly-Seber model (CJS; Cormack 1964; Jolly 1965; Seber 1965). The CJS model allows separate estimation of the probability of apparent survival, defined as the product of the probability of true survival and study area fidelity (Lebreton et al. 1992) between time t and $t + 1$ or between dam 1 and dam 2, as well as recapture (or detection) probability (Cormack 1964; Jolly 1965; Seber 1965; Conner et al. 2020). This model has been commonly used within the Columbia River

Basin to estimate survival rates for juvenile anadromous fish species (Skalski et al. 1998; Smith et al. 2002; Conner et al. 2020; Tiffan et al. 2021; McCann et al. 2022). The mark-recapture model used an encounter history for each fish, denoted “1” (released) and as “0” (not detected) or “1” (detected) at each of two detection sites: (1) BON either at the juvenile fish bypass system (PTAGIS code=BOJ) or through the corner collector (PTAGIS code=BCC) and (2) downstream of BON, via estuary PIT trawl (Ledgerwood et al. 2004) or on East Sand Island avian bird colonies (Evans et al. 2016). Thus, there were four possible detection histories: “100,” “101,” “110,” and “111,” to denote acclimation site exit detection and combined detection at and downstream of BON.

Using detection histories for each cohort, we estimated survival probability from acclimation site exit to BON for each Ac.Site (CFJ, ESJ, and JCJ) and for each BY (2002 to 2014), for a total of 39 combinations. We chose variables ED and FL as covariates to include in these models. All BY data were pooled within detection histories, and we included a series of explanatory models with and without covariates using RMark (Laake 2013; Cooch and White 2018). We tested “goodness of fit” of competing models by estimating the variance inflation factor (\hat{c}) for the largest model using the median \hat{c} test in program MARK (Cooch and White 2018). All subsequent models were corrected for overdispersion ($\hat{c} > 1.0$). Models were again evaluated using quasi-AIC scores (QAIC_c), resulting in selection of the model with the minimum QAIC_c (Burnham and Anderson 2002). We further estimated the apparent survival probability (from acclimation site to Bonneville Dam) using the best model to illustrate how the covariates affect survival rate and detection or recapture rate.

H_0 (3): smolt-to-adult return (SAR) and age-at-return were independent of smolt size, acclimation site, and volitional exit date.

We calculated SAR of PIT-tagged fish detected leaving each Ac.Site to adult return to Bonneville Dam for each brood year release in the study. Bonneville Dam was selected to maximize the number of fish available for this analysis. Note that we present SAR as a percentage, while modeling was based on proportions (i.e., SAR/100). Note further that these analyses and this investigation were designed only to address

the null hypothesis as stated; McNary-to-McNary and Bonneville-to-Bonneville SARs for individually PIT-tagged CESRF fish detected at juvenile emigration and adult return at these dams are available in McCann et al. (2022). For age-at-return analyses, we could only include PIT-tagged fish which were detected returning upstream at Bonneville Dam (2072 total PIT detections for all brood years and acclimation sites combined). Brood year was subtracted from year of upstream passage detection to determine age. Returning fish were categorized as age-2 (minijacks or <1-ocean year), age-3 (jacks, 1-ocean), age-4 (2-ocean), and age-5 (3-ocean). For the entire 13-year dataset, only 19 and 24 fish returned at ages 2 and 5, respectively (each age class representing only 1.2% of all returning fish). Therefore, we combined age-2 and age-3 and age-4 and age-5 fish into categories as age2&3 and age4&5 and repeated the modeling analysis detailed above substituting “age4&5” for “SAR”.

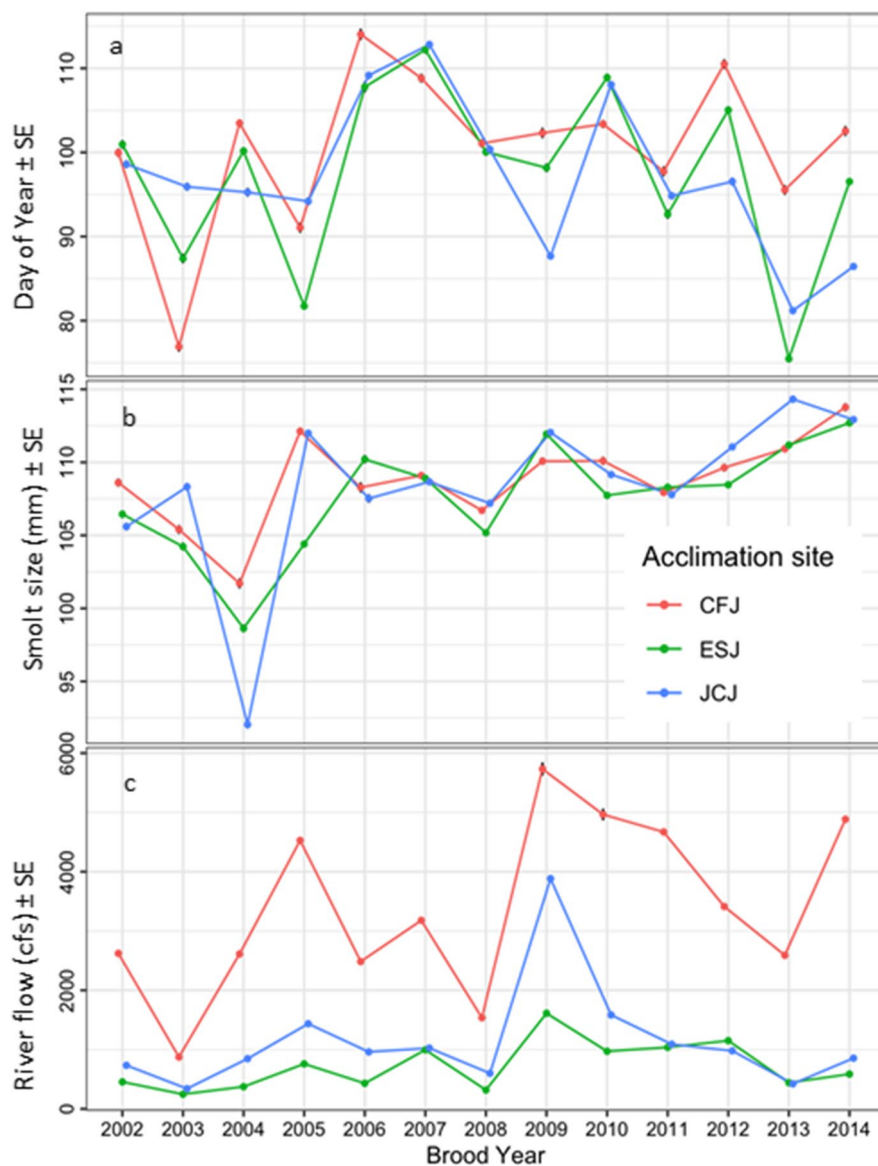
Results

H_0 (1): volitional exit date of juveniles from the acclimation and release sites was independent of acclimation site, smolt size, and river flow near acclimation sites.

We observed a slight variation in mean volitional exit date by acclimation site among brood years (Fig. 2a; Online Resource Fig. S1). The mean exit dates for JCJ, ESJ, and CFJ were April 7 (day of year 97.0 ± 2.5), April 7 (97.5 ± 3.0), and April 10 (100 ± 2.6), respectively; the differences were not significant (ANOVA: $F_{2,36} = 0.51$, $P = 0.61$). When all data were pooled, the median and mean exit dates were April 9 and April 7 (day of year 100 and 98.0 ± 1.5 , mean \pm SE), respectively, demonstrating a slight tendency of fish to exit earlier in the volitional emigration period than later.

Smolt size averaged over all brood years and acclimation sites was 109.0 ± 0.67 mm (mean \pm SE), and differences among acclimation sites were not significant (Fig. 2b; CFJ: 109.0 ± 0.85 mm; ESJ: 108.0 ± 1.06 mm; and JCJ: 108.0 ± 1.50 mm; ANOVA: $F_{2,36} = 0.28$, $P = 0.76$). However, we observed a linear trend of increasing smolt size over time for all sites combined ($r^2 = 0.33$; $P < 0.01$) and for each acclimation site (CFJ: $r^2 = 0.33$, $P = 0.04$; ESJ: $r^2 = 0.46$, $P = 0.01$; JCJ: $r^2 = 0.31$, $P = 0.05$).

Fig. 2 Mean annual volitional exit date (day of year) (a), smolt size (fork length (mm)) (b), and river flow (cfs) near the acclimation sites (c), by acclimation site and brood year



River flow averaged over all brood years and acclimation sites was 1750 ± 248 cfs (mean \pm SE) during the volitional emigration period (Fig. 2c). River flow near CFJ was over four times greater (3392 ± 405 cfs) than flow near ESJ (722 ± 113 cfs) and was three times greater than flow near JCJ (1135 ± 249 cfs). There was no increasing linear trend over time for the overall river flow ($r^2=0.04$, $P=0.21$), nor for any of the acclimation sites (CFJ: $r^2=0.24$, $P=0.09$; JCJ: $r^2=0.01$, $P=0.71$; ESJ: $r^2=0.15$, $P=0.19$).

The relationship between exit date and smolt size ranged from -0.37 to $+0.17$. Slopes were negative

and significant for most brood years (Fig. 3a; Online Resource Fig. S2a), indicating that larger smolts tended to exit the acclimation sites earlier than smaller smolts. Similarly, slopes of the relationship between volitional exit date and river flow near the acclimation sites ranged from -0.05 to $+0.33$. The majority of slopes were positive (Fig. 3b; Online Resource Fig. S2b), indicating that smolts tended to exit later with increasing river flow. Among the several models we used to evaluate how much variation in exit date was explained by smolt size and river flow near the acclimation sites, the best fit model included

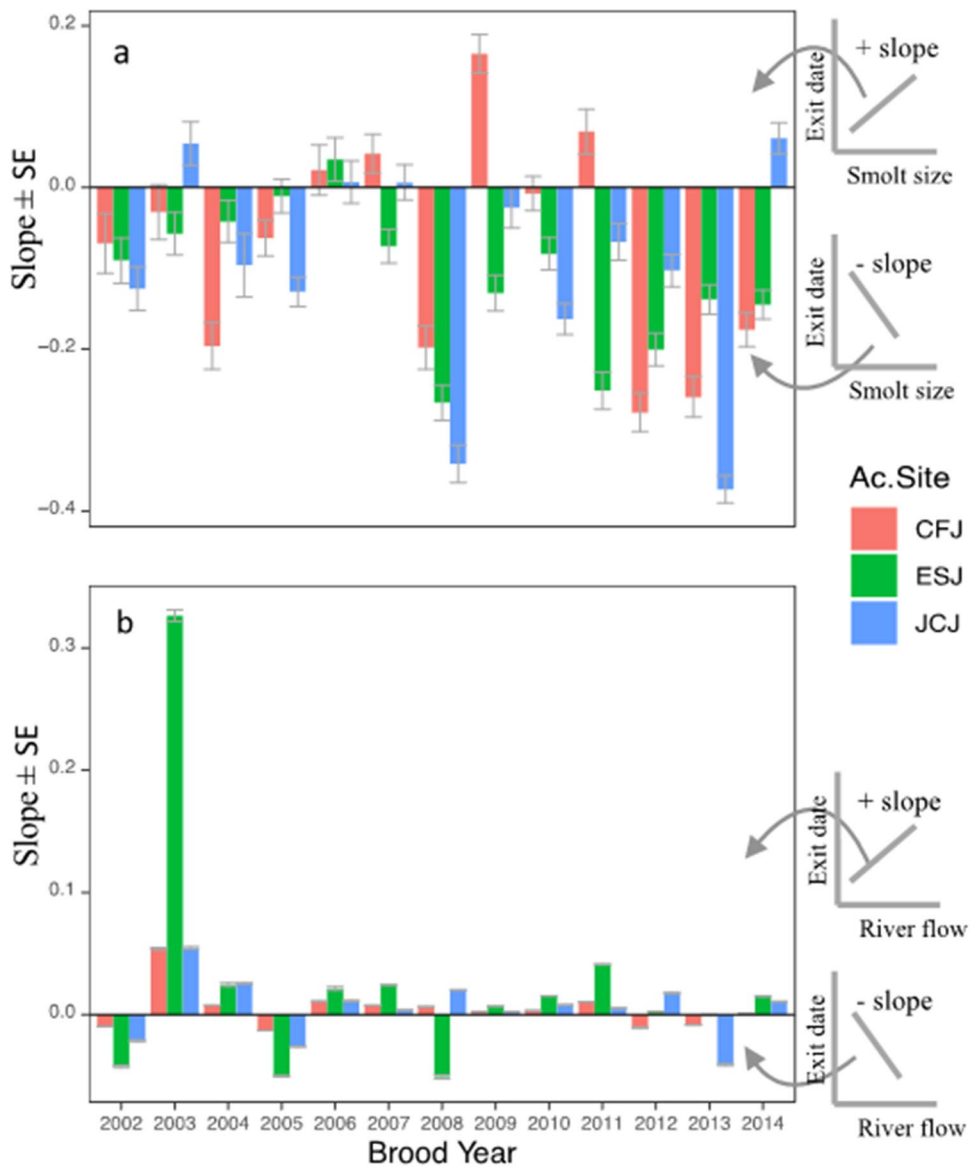


Fig. 3 Slope of the relationship between volitional exit date and smolt size (a) and between volitional exit date and river flow (b) for each brood year and acclimation site (see Online Resource Fig. S2). Insets illustrate slopes between the variables

all variables, which explained nearly 25% of the variation (Table 2). Therefore, estimated exit date must be viewed in context with river flow and smolt size, but independent of acclimation site. We have used standardized variables in our modeling so that model coefficients are on the same scale. Therefore, we can say that the relationship between smolt size and exit date (i.e., negative slope around -0.2 implies later exit dates for smaller fish) is opposite to that of river

flow and exit date (i.e., positive slope around $+0.02$ implies later exit dates at higher flows). Furthermore, the nearly 10 times larger coefficient for the smolt size relationship implies smolt size has a much larger impact than river flow on exit date.

At CFJ, predicted exit date increased over a range of several weeks from early April to mid-May as river flow increased across its range for both smaller (20th percentile FL = 102 mm) and larger (80th percentile

Table 2 Ranking and statistical parameters of candidate linear mixed-effects models for predicting exit date (ED) based on acclimation site (Ac.Site), smolt size (FL), and river flow near each acclimation site (Ac.RF), with brood year (BY) as a random effect

| Model configuration | df | AIC | Δ | R^2c |
|---|-----------|------------------|----------|--------------|
| ED ~ Ac.Site + FL + Ac.RF + Ac.Site*FL + Ac.Site*Ac.RF + FL*Ac.RF | 10 | 2,925,220 | 0 | 0.255 |
| ED ~ Ac.Site + FL + Ac.RF + Ac.Site*FL + Ac.Site*Ac.RF | 9 | 2,925,333 | 113.1 | 0.254 |
| ED ~ Ac.Site + FL + Ac.RF + Ac.Site*Ac.RF + FL*Ac.RF | 8 | 2,925,415 | 194.3 | 0.222 |
| ED ~ Ac.Site + FL + Ac.RF + Ac.Site*FL + FL*Ac.RF | 8 | 2,936,359 | 11,138.6 | 0.254 |

Note: df is degrees of freedom, delta (Δ) is the difference of each model from the model with minimum AIC, and R^2c is the proportion of variance explained by both the fixed and random factors; “+” denotes an additive model and “*” denotes an interaction. The model with the lowest AIC score is considered to be the best model, which has been shown in bold. All models also include term (1BY) for random intercept by BY. Other models were not supported

FL = 116 mm) fish (Online Resource Fig. S3). At ESJ, the pattern in predicted exit date was nearly identical but with substantially lower flows than at CFJ. However, at JCJ, predicted exit date increased by only one week relative to increasing river flow across its range, regardless of smolt size.

At CFJ, predicted exit date slightly increased in the first week of April as smolt size increased and river flow was low (20th percentile, 1669 cfs), but when river flow was high (80th percentile, 4945 cfs), predicted exit date slightly decreased in the second week of April as smolt size increased (Online Resource Fig. S4). At ESJ and JCJ, predicted exit date decreased by about one week as smolt size increased, all in the first half of April regardless of river flow. One minor nuance was at ESJ where predicted exit date occurred in the first week in April at low river flow.

H_0 (2): apparent survival of juvenile emigrants at downstream detection sites was independent of acclimation site, smolt size, and volitional exit date.

Average apparent survival probability from acclimation site to Bonneville Dam (with data pooled for all brood years) was $21.85 \pm 0.80\%$ (mean \pm SE) and with minor variation among acclimation sites (Fig. 4). The highest average survival was for fish exiting CFJ ($25.10 \pm 1.66\%$) with slightly lower average survival for the other two sites (ESJ: $21.15 \pm 1.30\%$; JCJ: $20.39 \pm 1.35\%$). Average survival among brood years showed little difference; the high apparent survival for brood year 2004 fish exiting ESJ was likely an outlier as it was based on just 3 re-detections below Bonneville Dam.

Among the 69 additive and interactive models evaluated, the survival model that had an interaction between acclimation site, exit date, and smolt size

had the lowest QAICc (Table 3; Online Resource Table S1). However, only exit date had an effect on detection. The model predicted that, among fish exiting earlier, smolts that were smaller in size had lower survival probability compared to larger smolts (Fig. 5). Among fish that exited later, survival probability increased at greater rates for smaller smolts relative to larger smolts, with survival probability for smaller smolts actually exceeding that of larger smolts among fish exiting latest from the CFJ site. Fish from CFJ had the highest survival probability regardless of smolt size.

H_0 (3): smolt-to-adult return (SAR) and age-at-return were independent of smolt size, acclimation site, and volitional exit date.

Observed SARs fluctuated between brood years (Fig. 6), beginning at approximately 0.5% for the first four BYs, then increasing threefold to over 1.5% for BY 2006, before declining to between 0.5% and 1.0% for brood years 2007 to 2014. SARs were generally similar among acclimation sites although CFJ had a higher SAR estimate in 9 of 13 years (Fig. 6).

The model including all variables was the best model (Table 4). Predicted SAR from this model showed increasing SAR for CFJ from around 0.3 to 1.7 for early-migrating fish (20th percentile ED = 77) over the range of smolt sizes, while for later emigrating smolts (80th percentile ED = 116) SAR increased from 0.3 to 0.6 (Fig. 7). This pattern was quite similar for all acclimation sites, although the predicted SAR for larger smolts exiting earlier at ESJ and JCJ was not quite as great as predicted SAR for larger smolts from the CFJ site.

Conversely, the best model showed predicted SAR decreased during the emigration period for

Fig. 4 Estimates of apparent juvenile survival probability from acclimation site to Bonneville Dam by brood year and acclimation site (CFJ, ESJ, and JCJ)

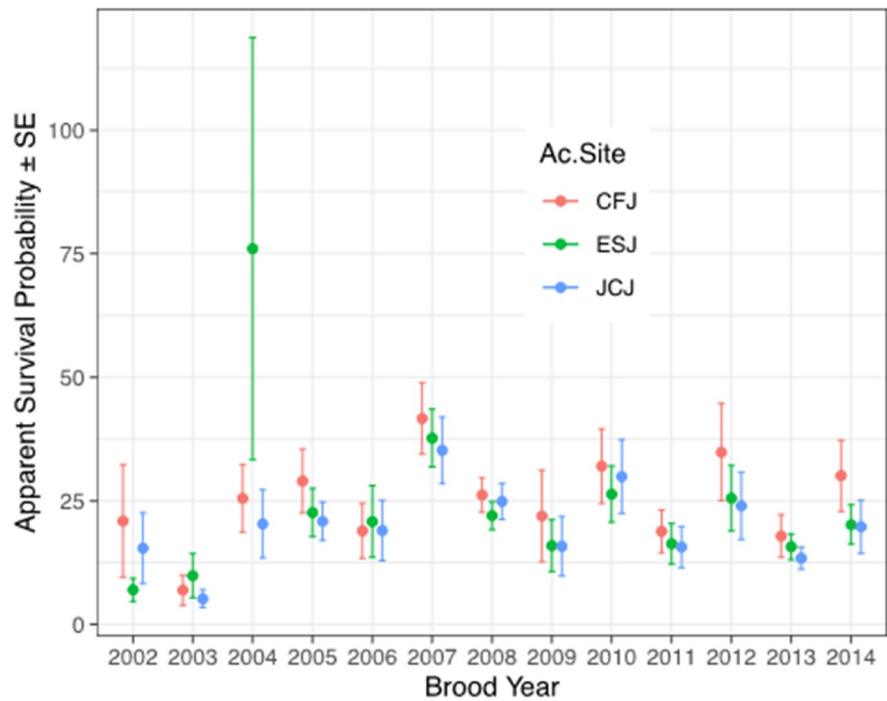


Table 3 Ranking and statistical parameters of candidate CJS models for predicting survival (φ), detection or recapture probability (p), considered as constant (1) or varied with detection site (\sim dam), acclimation site (Ac.Site), exit day (ED), and smolt size (FL)

| Model configuration | <i>K</i> | QAICc | Δ | Wt |
|--|-----------|-----------------|-------------|-------------|
| $\varphi(\sim \text{dam} * \text{Ac.Site} * \text{ED} * \text{FL}) p(\sim \text{dam} * \text{ED})$ | 28 | 78,767.6 | 0.00 | 0.86 |
| $\varphi(\sim \text{dam} * \text{FL} * \text{ED}) p(\sim \text{Ac.Site} + \text{ED})$ | 12 | 78,772.2 | 4.57 | 0.09 |
| $\varphi(\sim \text{dam} * \text{FL} * \text{ED}) p(\sim \text{Ac.Site} + \text{FL} + \text{ED})$ | 13 | 78,773.4 | 5.72 | 0.05 |
| $\varphi(\sim \text{dam} * \text{FL} * \text{ED}) p(\sim \text{Ac.Site} + \text{FL})$ | 12 | 78,778.4 | 10.76 | 0.00 |
| $\varphi(\sim \text{dam} * \text{ED}) p(\sim \text{dam} * \text{Ac.Site} * \text{ED} * \text{FL})$ | 28 | 78,781.1 | 13.45 | 0.00 |
| $\varphi(\sim \text{dam} * \text{ED}) p(\sim \text{Ac.Site} + \text{FL} + \text{ED})$ | 9 | 78,781.6 | 13.94 | 0.00 |
| $\varphi(\sim \text{dam} * \text{FL} * \text{ED}) p(\sim \text{dam} * \text{Ac.Site} * \text{ED} * \text{FL})$ | 32 | 78,782.5 | 14.83 | 0.00 |
| $\varphi(\sim \text{dam} * \text{ED}) p(\sim \text{Ac.Site} + \text{FL})$ | 8 | 78,784.6 | 17.00 | 0.00 |
| $\varphi(\sim \text{dam} * \text{FL} + \text{ED}) p(\sim \text{dam} * \text{Ac.Site} * \text{ED} * \text{FL})$ | 29 | 78,785.5 | 17.90 | 0.00 |
| $\varphi(\sim \text{dam} * \text{Ac.Site} * \text{ED} * \text{FL}) p(\sim \text{dam} * \text{FL} + \text{ED})$ | 29 | 78,790.2 | 22.55 | 0.00 |

Note: *K* represents the number of parameters used in the model, delta (Δ) is the difference of each model from the model with minimum QAIC_c, and Wt represents the weight of the model; “+” denotes an additive model, and “*” denotes an interaction. The model with the lowest QAIC_c score is considered to be the best model, shown in bold. Information for all 69 models evaluated are given in Online Resource Table S1

all smolt sizes (Fig. 8). Again, the pattern was fairly similar between acclimation sites. For CJF, predicted SAR decreased from around 0.75 to 0.4 over the season for smaller smolts (20th percentile FL = 102 mm) but from 1.0 to 0.4 for larger smolts (80th percentile FL = 116 mm). For ESJ, these decreases were 0.5 to 0.4 and 0.75 to 0.4 for smaller

and larger smolts, respectively. For JCJ, they were 0.7 to 0.2 and 0.9 to 0.2 for smaller and larger smolts, respectively (Fig. 8).

In general, predicted SAR from acclimation site smolt release to Bonneville Dam adult return increased for larger smolts and more so for those emigrating earlier. Also, predicted SAR decreased for smolts emigrating

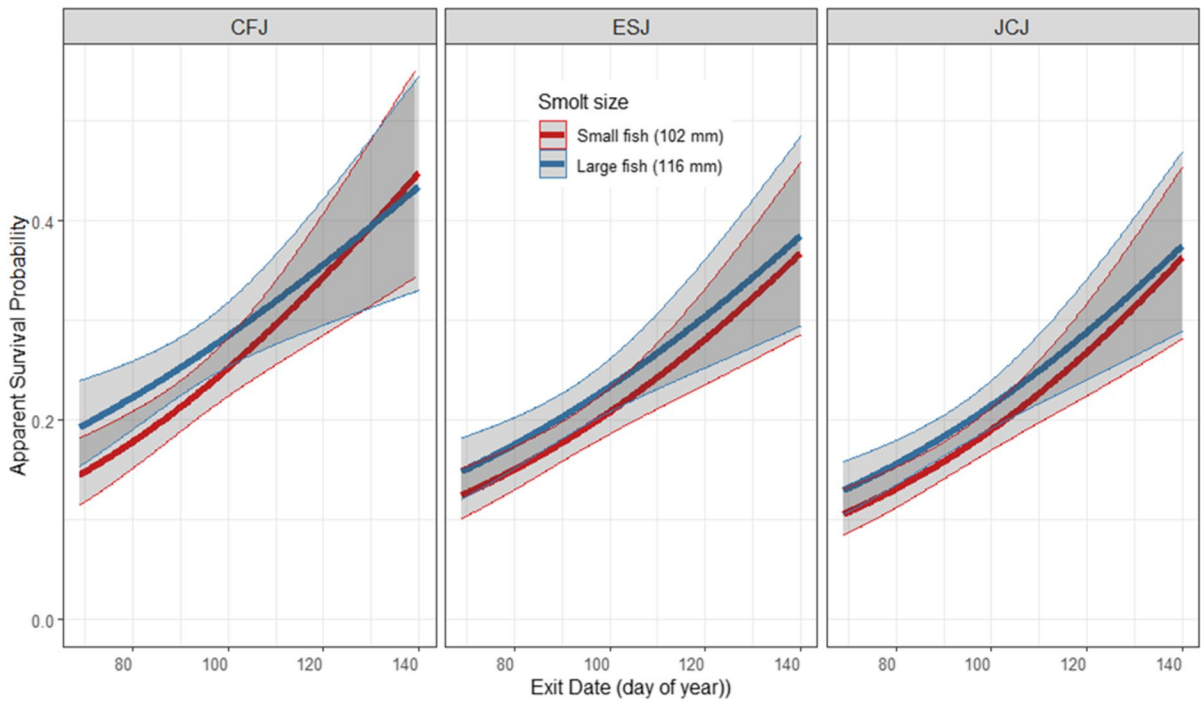
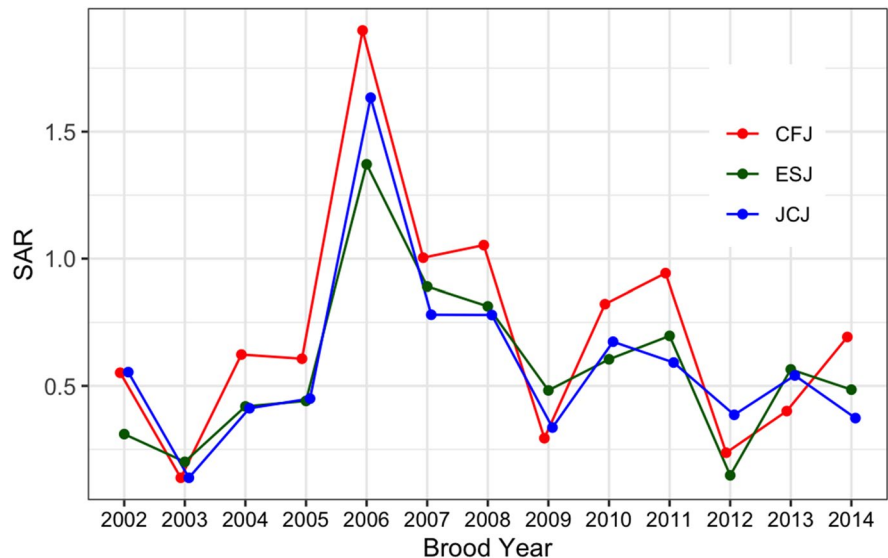


Fig. 5 Predicted apparent survival probability (acclimation site to Bonneville Dam) of small (20th percentile FL=102 mm) and large (80th percentile FL=116 mm)

smolts as a function of exit date based on the best CJS model (Table 3). The shaded area is the standard error of the predicted mean

Fig. 6 Estimated smolt-to-adult return (SAR) for PIT-tagged CESRF fish by brood year and acclimation site. SAR is the percentage of fish exiting as juveniles from acclimation sites (CFJ, ESJ, and JCJ) and returning to Bonneville Dam as mature fish (after 0 to 3 years in the Pacific Ocean)



later in the season and was the lowest among larger smolts emigrating later. The relationship between SAR and smolt size was stronger than with emigration timing. Patterns were fairly similar across acclimation sites.

Based on tag detections at Bonneville Dam, the percentage of age-4 and age-5 returning adult fish varied across acclimation sites and brood years (Fig. 9). We observed no differences between

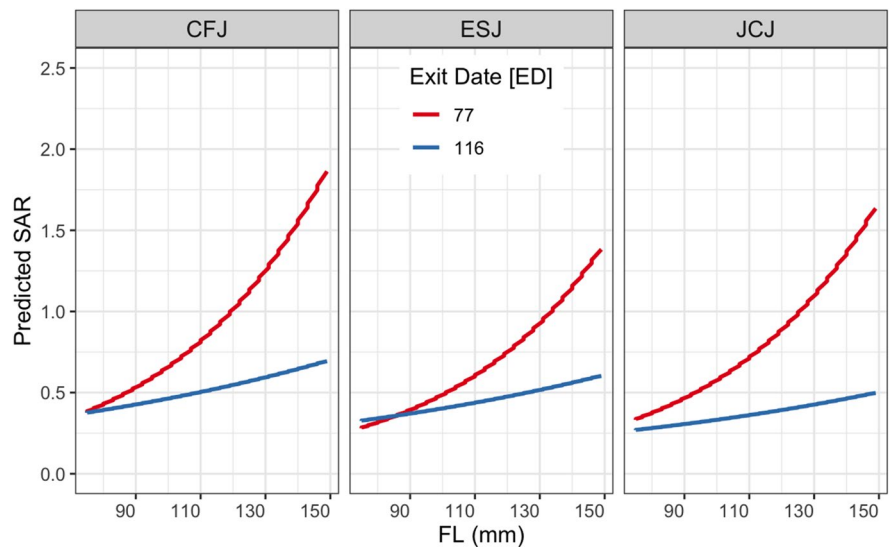
Table 4 Ranking and statistical parameters of candidate mixed-effects linear regression models for predicting SAR from acclimation site (Ac.Site) smolt release to Bonneville

Dam adult return based on Ac.Site, exit day (ED), and smolt size (FL) with brood year (BY) as a random effect

| Model configuration | df | AIC | Δ | R^2_c |
|---|----------|-----------------|----------|--------------|
| SAR ~ Ac.Site + FL + ED + Ac.Site*FL + Ac.Site*ED + FL*ED | 10 | 24,792.7 | 1.3 | 0.121 |
| SAR ~ Ac.Site + FL + ED + Ac.Site*FL + Ac.Site*ED | 9 | 24,796.4 | 5.0 | 0.121 |
| SAR ~ Ac.Site + FL + ED + Ac.Site*FL + FL*ED | 8 | 24,799.1 | 7.7 | 0.118 |
| SAR ~ Ac.Site + FL + ED + Ac.Site*ED + FL*ED | 8 | 24,791.4 | 0 | 0.121 |
| SAR ~ Ac.Site + FL + ED + Ac.Site*ED | 7 | 24,795.3 | 3.9 | 0.120 |
| SAR ~ Ac.Site + FL + ED + FL*ED | 6 | 24,797.4 | 6.0 | 0.118 |
| SAR ~ Ac.Site + FL + ED | 5 | 24,802.2 | 10.8 | 0.118 |

Note: df is degrees of freedom, delta (Δ) is the difference of each model from the model with minimum AIC, and R^2_c is the proportion of variance explained by both the fixed and random factors; “+” denotes an additive model, and “*” denotes an interaction. The model with the lowest AIC score is considered to be the best model, shown in bold. All models also include term (1|BY) for random slope by BY; other models were not supported

Fig. 7 Predicted smolt-to-adult return percentage (SAR) using the best model (Table 4) by acclimation site (CFJ, ESJ, and JCJ), smolt size (FL), and 20th and 80th percentile exit day of the year (ED, 77 and 116, respectively)



acclimation sites, but there was a general trend toward younger age-at-return over time. Modeling to estimate predicted age-at-return showed the strongest support for our candidate model that included emigration timing, smolt size, and their two-way interaction (Table 5). Therefore, inference from the best model can be made pooling data across acclimation sites. For all PIT-tagged CESRF juveniles successfully emigrating below Bonneville Dam, detections for fish returning from marine waters indicated that age-at-return increased with decreasing smolt size and with later emigration from acclimation sites (Fig. 10).

The predicted age4&5 percentage of all returning fish increased from approximately 60% to 90% over the course of the emigration period for smaller smolts (20th percentile FL=102) and from 55 to 80% for larger smolts (80th percentile FL=116) (Fig. 11a). Conversely, the predicted age4&5 percentage decreased from approximately 80% to 35% as smolt size increased earlier in the emigration period (20th percentile ED=77) and from approximately 95% to 25% as smolt size increased with later emigration (80th percentile ED=116) (Fig. 11b). The smolt size relationship with return age was stronger than the emigration timing relationship.

Fig. 8 Predicted smolt-to-adult return percentage (SAR) using the best model (Table 4) by acclimation site (CFJ, ESJ, and JCJ), exit day of year (ED), and 20th and 80th percentile smolt size (FL, 102 mm and 116 mm, respectively)

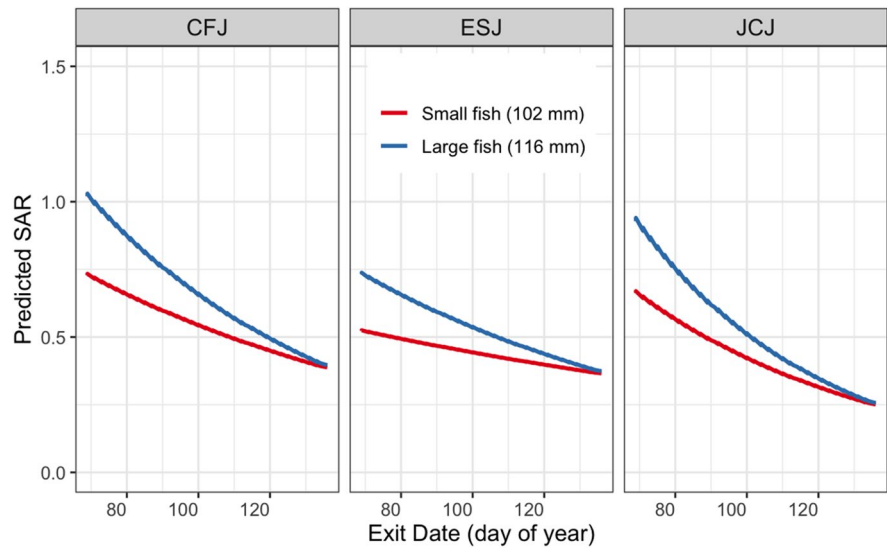
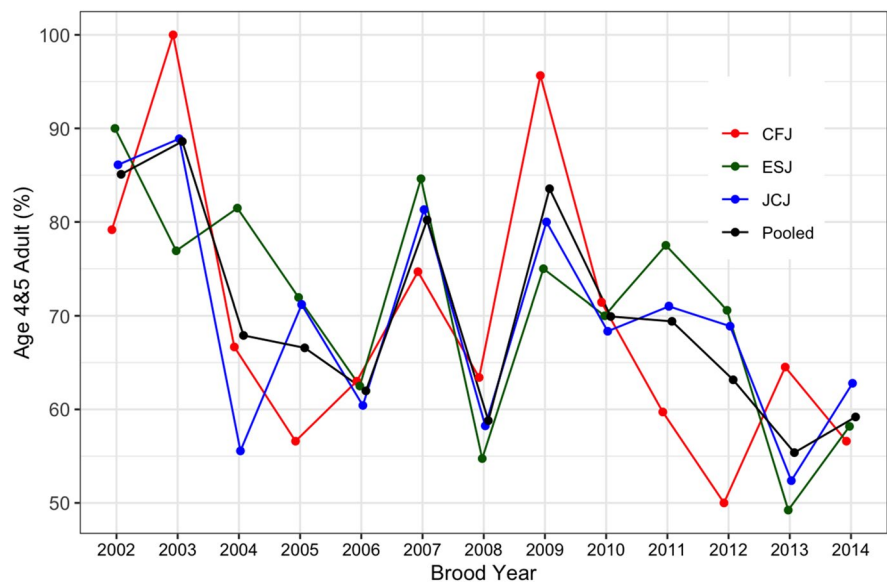


Fig. 9 Predicted age4&5 adults (2–3 years in the Pacific Ocean; as a percentage of all returning fish) using the best model (Table 5) by brood year (BY) and acclimation site (CFJ, ESJ, JCJ, and pooled for all 3 acclim sites combined)



Discussion

We observed several dependencies among emigration timing (volitional exit date), smolt size, and river flow near acclimation and release sites, in relation to juvenile survival probability, smolt-to-adult return, and age-at-return. Therefore, all of the tested null hypotheses would be rejected. Our results support and extend previously reported findings that

size of juvenile salmon at emigration is an important factor affecting emigration timing (Beckman et al. 1998) and life history patterns (Larsen et al. 2004, 2013, 2019; Harstad et al. 2018), particularly age-at-maturity (Bilton et al. 1982; Tattam et al. 2015; Harstad et al. 2018). These results also support previous work indicating that seasonal growth rates in juvenile salmon (Beckman et al. 1999, 2017; Larsen et al. 2006, 2019) and demography of

Table 5 Ranking of candidate mixed-effects linear regression models for predicting returning age-4 and age-5 fish from acclimation site (Ac.Site) smolt release to Bonneville Dam based on Ac.Site, exit day (ED), and smolt size (FL)

| Model configuration | df | AIC | Δ | R^2c |
|---|----------|---------------|------------|--------------|
| Age ~ Ac.Site + FL + ED + Ac.Site*FL + Ac.Site*ED + FL*ED | 10 | 2461.7 | 8.2 | 0.168 |
| Age ~ Ac.Site + FL + ED + Ac.Site*FL + Ac.Site*ED | 9 | 2466.3 | 12.8 | 0.154 |
| Age ~ Ac.Site + FL + ED + Ac.Site*FL + FL*ED | 8 | 2458.9 | 5.4 | 0.168 |
| Age ~ Ac.Site + FL + ED + Ac.Site*ED + FL*ED | 8 | 2458.1 | 4.6 | 0.168 |
| Age ~ Ac.Site + FL + ED + Ac.Site*FL | 7 | 2462.4 | 8.9 | 0.154 |
| Age ~ Ac.Site + FL + ED + FL*ED | 6 | 2455.1 | 1.6 | 0.167 |
| Age ~ Ac.Site + FL + ED | 5 | 2459.3 | 5.8 | 0.154 |
| Age ~ FL + ED + FL*ED | 4 | 2453.5 | 0.0 | 0.166 |
| Age ~ FL + ED | 3 | 2457.7 | 4.2 | 0.152 |

Note: df is degrees of freedom, delta (Δ) is the difference of each model from the model with minimum AIC, and R^2c is the proportion of variance explained by both the fixed and random factors; “+” denotes an additive model, and “*” denotes an interaction. The model with the lowest AIC score is considered to be the best model, shown in bold. All models also include term (1BY) for random intercept by BY; other models were not supported

returning fish (e.g., size and age) should be important considerations in developing management goals for artificial production facilities (Ohlberger et al. 2020; Oke et al. 2020).

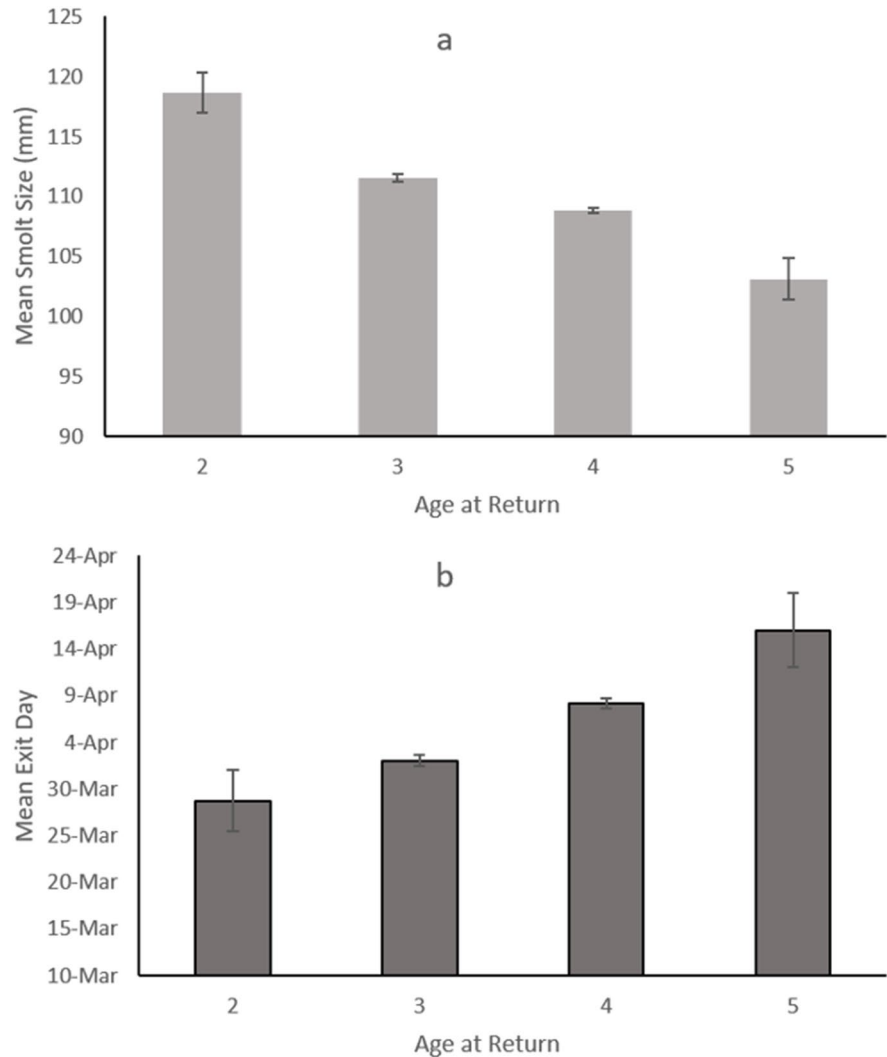
In this investigation, larger fish volitionally exited acclimation sites earlier than smaller fish. This finding is consistent with previous studies documenting that larger spring Chinook Salmon smolts tended to move downstream earlier than smaller smolts (Beckman et al. 1998; Zabel and Achord 2004). Beckman et al. (1998) reported that movement patterns were most closely related to growth rates and associated smolt development, including increased gill Na⁺/K⁺-ATPase activity, during the spring period preceding emigration (e.g., corresponding to time spent at acclimation sites in this investigation). With the exception of putative precociously maturing males (see discussion below), this investigation provides further evidence that larger smolts may tend to undergo the physiological, morphological, and behavior changes associated with smoltification earlier and emigrate earlier than smaller smolts.

River flow has been shown to influence downstream migration timing and survival of salmonid smolts (McCormick et al. 1998; Connor et al. 2003). Our analyses suggested that lower river flows near the acclimation sites may lead to earlier emigration timing. Sykes et al. (2009) found that accumulated thermal units, rather than river flow, was the parameter that best explained downstream migration timing for Chinook Salmon smolts in a river system that is

flow-controlled, similar to the Yakima River. In the upper watersheds of the Yakima River system, flow and water temperature are greatly affected by winter snowpack. Emigration timing in our study was correlated with winter snowfall at Snoqualmie Pass (about 48 km west of Cle Elum, WA) with the two earliest emigration years associated with the lowest winter snowfall and the latest emigration year associated with the highest snowfall (Washington State Department of Transportation). The warmer water associated with lower flows (less snowpack) may have played a role in advancing physiological changes and inducing earlier emigration observed in this study, as even a small difference of 1–2 °C can result in a significant increase in accumulated thermal units.

We observed generally low survival (20–25%) of juveniles released from all three acclimation sites to Bonneville Dam. This compares with estimated 1999–2020 mean hatchery-origin yearling Chinook Salmon juvenile survival values of approximately 30.5% for Snake and 36.7% for Upper Columbia River fish from release to Bonneville Dam (Widener et al. 2021). All species of both natural- and hatchery-origin Yakima River juvenile salmon experience substantial survival bottlenecks due to factors such as emigration timing, flow management, and predation with earlier emigrating fish tending to have better survival from release to McNary Dam than fish emigrating from late May through July (Blodgett et al. 2022). Factors limiting salmon survival in the Yakima River Basin are being addressed through implementation

Fig. 10 Mean juvenile smolt size (a) and exit day (b) by age-at-return for CESRF fish returning to Bonneville Dam (whiskers represent SE), $N = 19, 650, 1379,$ and 24 for ages 2 through 5, respectively



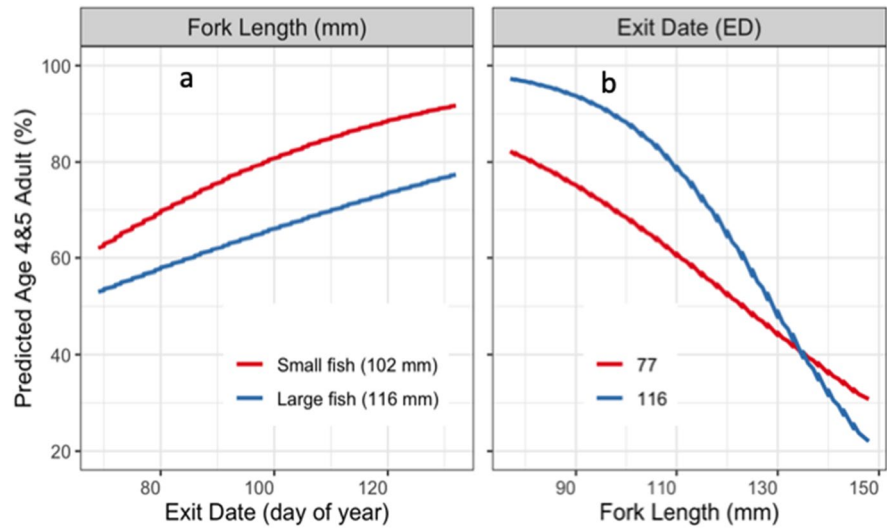
of the Yakima River Basin Integrated Plan (USBOR 2011).

We observed that larger smolt size was associated with better apparent survival, based on detections of both juveniles and returning fish at Bonneville Dam for CESRF spring Chinook Salmon. However, while larger smolts tended to emigrate earlier in our study, we also found that earlier emigrating juveniles demonstrated lower survival probability to Bonneville Dam than did later emigrants, regardless of smolt size. In addition, both the largest and earliest emigrating smolts returned at younger ages (age-2 minijack and age-3 jack males) as opposed to age-4 and age-5 (males and females). The lower juvenile survival probability for earlier emigrants might be partially

explained by the fact that these fish experience a longer exposure period to predation and other potential mortality risks (NRC 2004; Pandit et al. 2017; Keefer et al. 2018). Regardless of emigration timing, smaller smolts may experience greater predation risk due to slower speed in avoiding predators (Hasegawa et al. 2021), while larger smolts also experience substantial predation vulnerability due to factors such as caloric content (Werner et al. 1983), predator size (Barnes et al. 2010), or visibility (Forsman and Appelqvist 1998).

It is also possible that many of the larger, earlier emigrating juveniles in our study were precociously mature males. Larsen et al. (2004) found high rates (average ~40% of all males released over 10 years)

Fig. 11 Predicted age4&5 adults (2–3 years in the Pacific Ocean; as a percentage of all returning fish) using the best model (Table 5) by **a** acclimation site exit day (ED), for the 20th (102 mm) and 80th (116 mm) percentile smolt sizes (FL), and **b** smolt size (FL), for the 20th (77) and 80th (116) percentile exit days (ED); data pooled across acclimation sites



of precocious male maturation in the CESRF population. Precocious maturation (at age-1 or age-2) is a known life-history strategy for male salmonids, whereby fish remain in headwater spawning areas and use their small size and agility to gain spawning opportunities (commonly referred to as “sneaking”) with anadromous females (Fleming 1996). Other studies have demonstrated that a significant proportion of the maturing minijack Chinook Salmon produced by the CESRF (Larsen et al. 2013) and other Columbia Basin hatchery programs (Zimmerman et al. 2003; Beckman and Larsen 2005; Beckman et al. 2017; Harstad et al. 2014, 2018) migrated significant distances downstream (including beyond Bonneville Dam) in the spring in a “smolt-like” manner (Larsen et al. 2010) and then were redetected shortly afterwards moving upstream in an apparent attempt to migrate back to their headwater rearing areas. Tag detection histories indicate that survival of these migrating minijacks is very low, representing a significant loss to anadromous adult (age-3, age-4, and age-5) male production (Beckman and Larsen 2005). Thus, precocial maturation among the larger or earlier emigrating smolts in this study may have contributed to the younger age-at-maturity distributions we observed for these fish.

This investigation clearly demonstrates the challenges associated with developing size-at-release targets for hatchery programs, specifically as they pertain to the survival advantages of releasing larger smolts. As observed in previous investigations (Zabel

and Williams 2002; Zabel and Achord 2004; Beckman et al. 2017; Poirier and Olson 2017), we found that larger smolts produced more returning adults. However, we also found that these same larger juveniles tended to return more age-2 minijacks and age-3 jacks and fewer of the larger, more desirable age-4 and age-5 fish. In contrast, we observed that smaller juveniles generally emigrated later and had lower apparent survival both as juveniles and returning fish to Bonneville Dam, but returned a greater abundance of older age classes. Tattam et al. (2015) studied PIT-tagged wild Columbia River Chinook Salmon from 10 successive cohorts and found similar relationships between smolt length and age-at-return (larger smolts had increased probability of age-3 maturation) and between later emigration and older age-at-return. Poirier and Olson (2017) reviewed literature on sub-yearling and yearling hatchery release strategies for Columbia River fall Chinook Salmon and reported a similar finding: the larger yearlings generally returned at younger average ages and often returned as minijacks and jacks at a much higher frequency than did the smaller subyearling releases. Finally, in a study of artificially reared Coho Salmon, Bilton et al. (1982) found that jack (age-2) returns were maximized with earlier releases of larger smolts.

Results from this investigation and several previous studies highlight a paradox for yearling Chinook Salmon hatchery programs that endeavor to rear smolts to a size that optimizes downstream survival and smolt development for early ocean rearing and

growth, while minimizing early male maturation (Larsen et al. 2006, 2013; Spangenberg et al. 2014; Beckman et al. 2017; Harstad et al. 2018). A recurring theme from all these studies, as described in Larsen et al. (2013), is that high growth rates, most notably in the first autumn–winter of rearing, create a population composed of high proportions of both large smolts and minijacks. In contrast, lower autumn feeding rates create a high proportion of relatively small smolts but a lower proportion of minijacks and jacks. Subsequent high growth rates in the spring tend to increase smolt release size and improve smolt development. This feeding regime is sometimes referred to as “the wild fish template” as it more closely mimics development patterns observed in naturally rearing fish (Beckman et al. 2000). More recently, this phenomenon was investigated at a production scale in upper Columbia River hatchery summer Chinook Salmon populations (Harstad et al. 2018). They found that colder water reduced winter growth resulting in smaller fish size at juvenile migration but that smaller smolts returned at older age-classes than did larger smolts. Further, the release group that consisted of the smallest fish and migrated the greatest distance returned as adults at the highest rate with older fish comprising more of the return than observed for other treatment groups (Harstad et al. 2018).

In the Yakima River Basin, the American River (elevation 843 m for spawning and rearing areas) has the coldest water temperatures (<https://www.usbr.gov/pn/hydromet/yakima/>), and spring Chinook Salmon from this subbasin demonstrate the oldest average age-at-return (Bosch 2019). For spring Chinook Salmon in the Upper Yakima River Basin that were part of this study, the JCJ (elevation 790 m) and ESJ (661 m) acclimation sites generally experienced colder water temperatures than the CFJ (499 m) site (<https://www.usbr.gov/pn/hydromet/yakima/>), and fish returning from these uppermost acclimation sites had slightly increased probabilities of returning at older ages. Fish from CFJ, which were larger at release and had a shorter migration distance, returned at higher rates, although with a slightly younger age distribution, a result consistent with previous findings (Tipping 2011; Larsen et al. 2013; Faulkner et al. 2019). These findings are also consistent with Spangenberg et al. (2014) and Beckman et al. (2017) who reported that the same stock of fish may respond differently to the unique environmental conditions

of a different hatchery rearing environment and that these differences may in turn influence developmental physiology and life history pathways that affect smolt-to-adult return rates and the demography of returning adults.

A recent analytical model of 60 years of data from several, primarily natural origin Pacific salmon, stocks in Alaska found significant declines in size of returning adults in recent decades (Oke et al. 2020). They concluded that the decline was primarily driven by a shifting age structure toward younger ages in response to climate change and competition at sea. Thus, even in wild populations, a demographic shift toward smaller, younger fish may present significant impacts to species viability. Hatchery programs that release larger smolts that tend to return at younger ages may further amplify these demographic trends. From a management perspective, the extent to which these trends in both hatchery and wild fish may be reversed is a daunting prospect given the reliance on improved marine environmental conditions. However, there may be immediate opportunities to affect change in the freshwater environment by modifying culture and release strategies for hatchery fish.

Results from this investigation of CESRF spring Chinook Salmon may have general utility for many salmon hatchery programs throughout the Columbia Basin and broader Pacific region. While each program has unique hatchery (water temperature, density, ration, etc.) and tributary (elevation, geology, hydrology, habitat) characteristics, many regional watersheds share enough similarities that hatchery fish may experience many common factors in the freshwater migration and marine environment. Therefore, results from this study may provide useful general insights on optimal sizes and release timing for further refinement at the program level to optimize adult returns and demography. Strategies for altering size at release targets include manipulation of incubation temperature to adjust emergence and pond timing (Winsor et al. 2021), juvenile growth modulation via ration and temperature manipulation (Larsen et al. 2006; Spangenberg et al. 2014; Harstad et al. 2018; Winsor et al. 2021), photoperiod manipulation (Beckman et al. 2007; Imsland et al. 2014; Foss et al. 2020), and the use of partial reuse aquaculture systems (PRAS) for improved environmental control throughout rearing (Willard and Murauskas 2019). Furthermore,

whether with protracted volitional release or a single release event, timing of juvenile releases may be calibrated to optimize adult returns based on PIT-tag histories as employed in this investigation. While declines in size and age at maturity of hatchery salmon stocks present significant ecological and socioeconomic consequences to population resilience and stock recovery, results from this investigation demonstrate that even modest adjustments to rearing and release strategies could prove effective in mitigating this trend.

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Data availability Data used in this study are available at [pta-gis.org](https://www.cbfish.org), [cbfish.org](https://www.cbfish.org) (see <https://www.cbfish.org/Document.mvc/Viewer/P186823>), and by contacting the corresponding author.

Declarations

Ethics approval Ethical approvals were not applicable to the present study.

Conflict of interest The authors declare no competing interests.

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