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Article

Trade-offs between release number and fish size for Chinook Salmon hatchery programs

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Abstract

Objective: **Salmon populations have been declining over the past several decades, and recent studies have found that hatchery-reared fish are returning to spawn as adults at a smaller size and at younger ages. Because of these declines and shifts in size and age at maturation, some spring Chinook Salmon *Oncorhynchus tshawytscha* hatcheries are struggling to reach their programmatic goals. This is compelling hatchery managers to rethink current rearing protocols. The goal of this investigation was to assess and compare the physiology and performance of fish reared under the standard protocol to those of fish reared under an alternative strategy.**

Methods: **A comparative study of juvenile spring Chinook Salmon was conducted at the Round Butte Hatchery/Pelton Ladder facility near Madras, Oregon, across five brood years. The standard rearing practice was compared to an alternative protocol, and we applied a unique experimental design whereby fish density (biomass per unit water volume) between the treatments was similar but the size of the individual fish and the number of fish per rearing vessel varied. The different rearing regimes yielded two treatments: (1) Big–Low: fish reared to a larger body size, with fewer fish per raceway (standard protocol) and (2) Small–High: fish reared to a smaller body size, with more individual fish per raceway (alternative protocol). Fish were evaluated for various prerelease (size, energetics, smolt development, and early male maturation) and postrelease (smolt out-migration travel time, adult returns to Bonneville Dam, and age at return) metrics.**

Results: **Prior to release, significant physiological differences between the Big–Low and Small–High treatments were observed for some smolt quality indicators (size, condition factor, and percent solid) but not all indicators (gill Na^+, K^+-ATPase). Despite these differences, the Small–High treatment did not appear to be physiologically compromised by being reared to a smaller body size with twice the number of fish. Postrelease travel time downstream to Bonneville Dam was faster for the Big–Low treatment. Proportionately, the standard production (Big–Low) treatment produced significantly more younger (age-2 and age-3) adult males, but returns were not significantly different for age-4 males and females compared to the alternative (Small–High) protocol. After adjusting for numbers of fish released, returns for all age-classes were higher in the Small–High treatment, suggesting that fish production goals could potentially be reached by rearing more small fish.**

Conclusions: **In this comparative hatchery-scale experiment, fish from the alternative rearing strategy generally outperformed fish from the standard hatchery practice. Given the unpredictability and influence of a variety of postrelease variables on survival, hatcheries may want to consider the trade-offs between altering fish size and/or fish abundance within the constraints of density (total biomass) limits for rearing vessels (tanks, raceways, etc.). This study highlights the benefits of periodically examining standard rearing practices to ensure that they are meeting desired hatchery performance goals and objectives.**

Keywords: adult returns, Chinook Salmon, density, hatchery, minijacks, size

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Lay Summary

A hatchery-scale experiment was conducted to compare standard rearing practices to an alternative protocol. The alternative method of rearing larger numbers of small fish appears to improve hatchery production by yielding an increase in the number of fish returning as well as a more diverse adult age structure.

Introduction

Declining salmon populations are well documented, and mortality has been attributed to a variety of different causes, including but not limited to river and ocean conditions (McCormick et al., 2009; Peterson et al., 2014; Scheuerell et al., 2009; Sharma et al., 2013), predation (Duffy & Beauchamp, 2008; Evans et al., 2012; Sebring et al., 2013), dam passage (Algera et al., 2020), and disease (Dietrich et al., 2011). Furthermore, as mature adults, hatchery-reared salmon are returning from the ocean to spawn at a smaller size and at younger ages (Ohlberger et al., 2018; Oke et al., 2020). These declines and shifts are forcing hatchery managers to question whether current hatchery rearing practices are appropriate for reaching their production goals and conservation objectives (Oregon Department of Fish and Wildlife, 2017).

In salmon hatchery programs, smolt size-at-release targets are selected to optimize performance and survival, but they may not have the intended outcome. The "bigger smolt is a better smolt" paradigm is supported by literature demonstrating that larger juveniles (smolts) have a greater probability of survival to adulthood (Brown et al., 2013; Evans et al., 2014; Faulkner et al., 2019; Hager & Noble, 1976; Martin & Wertheimer, 1989; J. Tipping, 1986; J. M. Tipping, 1997, 2011; Zabel & Williams, 2002). However, not all research supports this paradigm; other research focused on size at release has found that the strategy of rearing and releasing larger smolts often produces more younger mature males (more age-2 "minijacks" and age-3 "jacks") and fewer of the more desirable older adults (age-4 and age-5 mature males; Bosch et al., 2023; Feldhaus et al., 2016; Gallinat et al., 2023; Harstad et al., 2018; Larsen et al., 2013). These studies highlight the need to consider trade-offs associated with rearing and releasing larger fish when choosing size-at-release targets.

Rearing density is an important metric for salmon hatcheries, and rearing guidelines are developed to maximize production without compromising fish health and welfare. Studies assessing the effects of rearing density on fish are numerous, with some showing negative effects when density is increased (Banks & LaMotte, 2002; Kavanagh & Olson, 2014; Martin & Wertheimer, 1989; Olson & Paiya, 2013; Schreck et al., 1985; Sveen et al., 2018) and others demonstrating little to no effect (Araújo-Luna et al., 2018; Clarke et al., 2013; Ewing & Ewing, 1995; Soderberg & Meade, 1987). Rearing density studies commonly employ one of two different experimental designs: (1) manipulating the total number of fish in the rearing vessel (Araújo-Luna et al., 2018; Banks & LaMotte, 2002; Clarke et al., 2013; Schreck et al., 1985; Sveen et al., 2018; see Figure 1A) or (2) manipulating the size of the individual fish (Clarke et al., 2014; Martin and Wertheimer, 1989; see Figure 1B). Regardless of the design, manipulation of density in these studies results in a change in the overall total biomass within each of the experimental rearing vessels. A third, less-explored method for altering fish production would be to simultaneously alter fish numbers and size while keeping the density (total biomass) of the experimental rearing vessels equivalent (Figure 1C). This third design seeks to maximize fish production by reducing fish size and increasing the number of fish in a rearing vessel while maintaining a constant density.

Although the literature on the effects of smolt size at release or rearing density alone is comparatively extensive, to our knowledge very few—if any—studies have aimed to vary fish size and the number of fish reared while keeping overall biomass relatively equivalent. Intuitively, if fish are reared to a smaller size at release, the total biomass in a rearing vessel is also reduced, increasing the space per individual or providing additional space to possibly rear more individual fish. If the physiological quality of the juvenile fish is not compromised, the strategy of rearing more small fish could potentially increase the number of returning adults per rearing vessel. Furthermore, several studies have demonstrated that releasing smaller smolts may lead to a shift in age structure toward more desirable older adult age-classes (Bosch et al., 2023; Feldhaus et al., 2016; Gallinat et al., 2023; Harstad et al., 2018; Larsen et al., 2013) and may even improve the number of overall adult returns (Clarke et al., 2013; Martin & Wertheimer, 1989; Young et al., 2021).

In studies conducted at the Round Butte Hatchery/Pelton Ladder facility on the Deschutes River, Oregon, researchers assessed smolt quality, early male maturation, and survival of spring Chinook Salmon *Oncorhynchus tshawytscha* and were able to demonstrate that fish reared at this facility have higher adult returns than other Columbia River hatchery spring Chinook Salmon (Beckman et al., 1999, 2017; D. Spangenberg et al., 2014). Additionally, D. Spangenberg et al. (2014) found that Chinook Salmon from the Hood River, Oregon, that spent a majority of the rearing process at the Round Butte Hatchery/Pelton Ladder facility had a higher smolt-to-adult return than Hood River Chinook Salmon reared at either Parkdale Fish Hatchery (West Fork Hood River, Oregon) or Carson National Fish Hatchery (NFH; Wind River, Washington). The study also revealed that Hood River Chinook Salmon outperformed Deschutes River Chinook Salmon that were reared in the same location, although fish were released from different locations and at different times on the Hood and Deschutes rivers, respectively. Lastly, D. Spangenberg et al. (2014) found that Deschutes River Chinook Salmon reared at the Round Butte Hatchery/Pelton Ladder facility had a higher propensity for early male maturation compared to Hood River Chinook Salmon. The difference was attributed in part to the difference in average size at release between Deschutes River Chinook Salmon (31-g body weight; 142 mm fork length [FL]) and Hood River Chinook Salmon (18-g body weight; 118 mm FL).

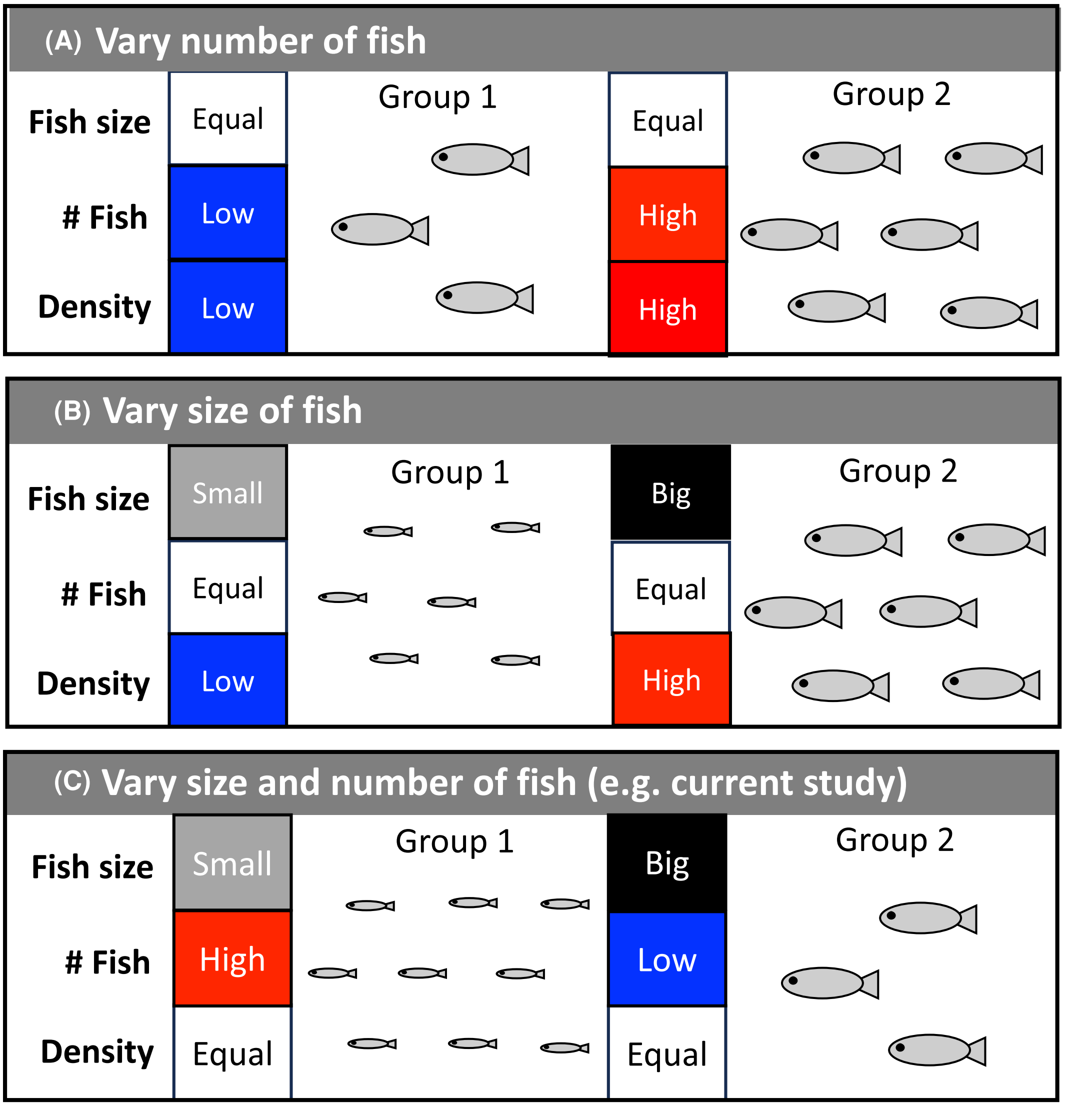

Figure 1 Illustration of types of fish rearing studies that (A) vary the number of fish of equal size, (B) vary fish size while keeping the number of fish equal, or (C) vary both fish size and the number of fish. The subsequent effects on rearing density (biomass/volume) are also shown.

Based on these past studies, an alternative strategy was tested at the Round Butte Hatchery/Pelton Ladder facility, with fish reared to a smaller body size and increasing the number of fish per rearing vessel. The hypothesis was that the alternative strategy would improve smolt-to-adult returns and shift the adult demographics to produce fewer of the smaller, younger (age-2 and age-3) adults and more of the larger, older (age-4 and age-5) adults. The overall objective of this research was to optimize rearing strategies for this hatchery program and provide insights for application to other regional spring Chinook Salmon hatchery programs throughout the Pacific Northwest.

Methods

Study location and experimental design

This experiment was conducted over 5 years (adult fish brood years [BYs] 2016–2020) at Round Butte Hatchery (river kilometer [rkm] 177) and Pelton Ladder (rkm 161), both located on the Deschutes River (measured from the confluence with the Columbia River). This facility was constructed in 1972 to mitigate barriers to salmon migration and habitat loss caused by the construction of the Pelton–Round Butte Hydroelectric Project (Figure 2) on the Deschutes River near Madras, Oregon. The hatchery manages a spring Chinook Salmon supplementation program that primarily provides fishing and harvest opportunities.

Each year, food ration manipulation was used to create two different size-at-release treatments categorized as “Big” (8 fish per pound [fpp] or ~60 g) and “Small” (15 fpp or ~30 g). In addition to differences in size, treatment groups also differed in the number of fish reared per vessel and were classified as either “Low” (~85,000 fish/vessel) or “High” (~150,000 fish/vessel). The Small treatment group (hereafter, “Small–High treatment”) on average had about 66.7% (range = 51.4–81.9%) more fish than the Big treatment group (hereafter, “Big–Low

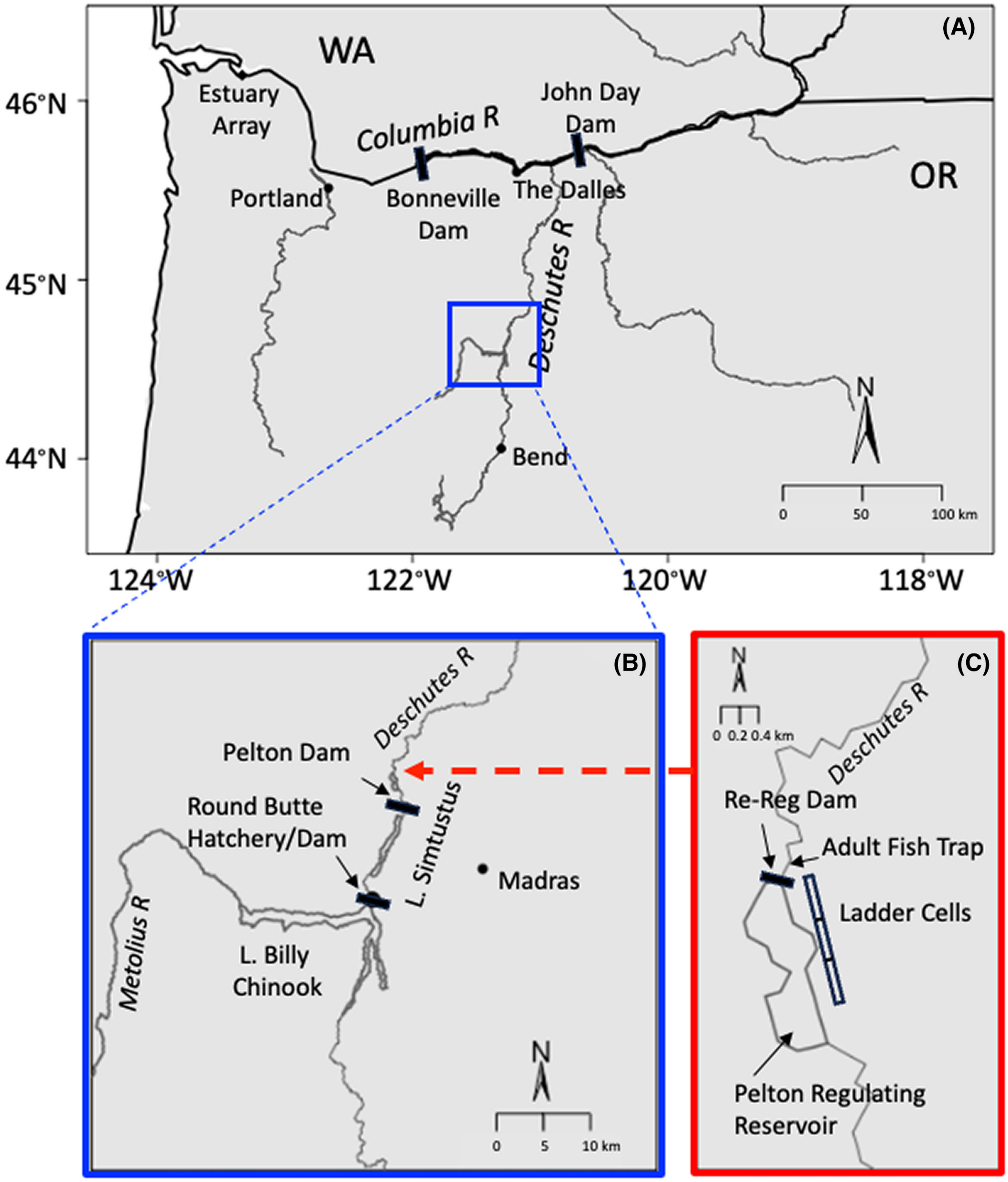

Figure 2 Maps of (A) the Deschutes River, Oregon, and (B), (C) the three dams associated with the Pelton–Round Butte Hydroelectric Complex (Round Butte, Pelton, and Reregulating dams), as well as the juvenile Chinook Salmon rearing sites at Round Butte Hatchery and the Pelton Ladder cells. Juvenile fish with PIT tags were detected downstream during out-migration at Bonneville Dam and the Columbia River estuary array. (Note: The ladder cells are not drawn to scale).

treatment"). Despite the size and abundance differences, the total biomass (e.g., kg/m^3) per treatment was relatively similar throughout the duration of the study (Table 1). Due to the configuration of Pelton Ladder (Figure 2), replication of both the Big–Low and Small–High treatment groups was not possible in any given BY. Managers opted to replicate the Small–High treatment during each year. In each BY, the different treatment groups were rotated randomly among the three ladder cells. Before release in the spring, a subset of the fish was tagged with PIT tags to allow for assessments of juvenile out-migration, adult returns to Bonneville Dam (the lowermost dam on the Columbia River; rkm 234), and adult age structure.

Fish source and hatchery rearing

Deschutes River spring Chinook Salmon adults were collected throughout their entire return period (May–August) and held until the time of spawning at the adult fish trap below the Pelton Reregulating Dam (rkm 161 on the Deschutes River; Figure 2C). Due to broodstock shortages in some years, additional adults were sourced from the nearby Warm Springs Hatchery, located on a Deschutes River tributary that is approximately 15 km from Round Butte Hatchery (Figure 2A). Adults were spawned over several weeks from late August to mid-September. Fish were typically crossed at a 1:1 (female : male) ratio; however, in some cases a 1:2

Table 1 Number of PIT-tagged Chinook Salmon released, total release numbers, size at release (fork length [FL], weight [WT], and fish per pound [FPP]), and total biomass per ladder cell (CELL) for each size treatment (TREAT) and each brood year (BY) of this study. Brood year 2018 release sizes are missing from our data, as COVID-19 travel restrictions prevented us from collecting this information in 2020. Abbreviation is as follows: NA = not available.

BY	CELL	TREAT	Number of PIT tags released	Total release number	Mean FL (mm)	Mean WT (g)	FPP	Biomass (kg)[b]
2016	Lower (1)	Small–High	4,762	150,749	131.5	25.5	17.8	4,328
	Middle (2)	Big–Low	4,911	83,610	150.0	40.0	11.3	3,416
	Upper (3)	Small–High	4,943	153,412	139.0	29.5	15.4	5,155
2017	Lower (1)	Small–High	4,950	148,377	135.4	28.7	15.8	5,060
	Middle (2)	Small–High	4,981	148,670	138.2	30.4	14.9	5,032
	Upper (3)	Big–Low	4,986	86,643	157.2	48.0	9.5	3,970
2018	Lower (1)	Big–Low	4,879	90,416		COVID		2,929
	Middle (2)	Small–High	4,916	152,051		COVID		4,338
	Upper (3)	Small–High	4,880	151,740		COVID		4,413
2019	Lower (1)	Small–High	4,966	138,239	137.4	30.3	15.0	4,645
	Middle (2)	Big–Low	4,790	84,359	161.7	51.3	8.8	5,102
	Upper (3)	Small–High	4,954	132,711	144.2	34.4	13.2	4,269
2020	Lower (1)	Small–High	1,966	[a]	NA	NA	NA	
	Middle (2)	Small–High	4,897	126,995	131.9	24.2	18.8	2,866
	Upper (3)	Big–Low	4,914	83,887	161.3	50.3	9.0	3,964

[a] The Small treatment fish were intermixed with fish overwintered at Fall River Hatchery for BY 2020.

[b] Biomass was calculated using fish weight at release reported in the Regional Mark Information System (Regional Mark Processing Center, 2024).

(female : male) ratio was used to ensure that all eggs were fertilized. Depending on the number and age structure of the returning males, the hatchery limited the spawning of age-3 males (jacks) to 10% or less when possible.

Embryos were incubated at Round Butte Hatchery (Figure 2B) in vertical Heath stacks (MariSource, Burlington, Washington). Water supplied for incubation was UV filtered and mixed from different sources (well and surface) to control temperatures (range = 5.6–12.8°C) and ensure that the hatch timing of embryos from various spawning dates was synchronized. Embryos hatched in late October, and the alevins remained in their incubation trays until they had absorbed enough of their yolk sac to reach the "button-up" stage of development. At this time (end of December), salmon fry were transferred to indoor circular rearing tanks, where they were reared in UV-sterilized water at a constant temperature of 10 ± 1°C. In March, at a size of approximately 1.5 g (300 fpp), the fry were transferred to outdoor concrete raceways. Later that year (mid-November), fish were transferred to the Pelton Ladder (Figure 2C) for final rearing until their release the following spring. Fish were released from the ladder cells in early April.

Fish were fed a diet from one of two manufacturers: either Bio-Oregon (Longview, Washington) or EWOS (Surrey, British Columbia, Canada). A monthly size census was conducted to adjust the feed ration. The daily ration was calculated based on current fish size using standardized recommendations provided by the feed manufacturers; to ensure the health and welfare of the fish, the ration never fell below 0.8% of body weight per day. Feeding commenced 1–2 d after the fish were placed into the indoor circular tanks. At this stage, the treatment groups had not been established and fish were fed ad libitum every 15–30 min. In the spring, fish were transferred to outdoor raceways and were fed a medicated feed for approximately 28 d. Once the prophylactic treatment was complete, the differential feeding regimes were implemented to create the Big–Low and Small–High treatment groups.

Over the course of the experiment, depending on the BY, various pathological agents (i.e., *Ichthyobodo necatrix* and *Renibacterium salmoninarum*) were a concern. Different courses of action were taken to treat an existing condition or to apply a prophylactic measure (Supplementary Table 1 [see online Supplementary Material]).

Sample collection

Fish from each BY were sampled (with exceptions for some measures noted in Supplementary Table 2) four times (October, January, February, and March/April) prior to smolt release for a variety of smolt quality indicators (FL; weight; Fulton's condition factor [*K*]; gill Na^+, K^+-ATPase activity; whole-body percent solid; and early male maturation). Samples were collected at Round Butte Hatchery or at Pelton Ladder depending on the time of year. To collect a random sample, fish were either dipnetted out of a raceway (Round Butte Hatchery) or captured from a ladder cell by using a cast net (Pelton Ladder). For the first three sampling points, we conducted a census of 200 fish/treatment (with some noted exceptions in January and February for BY 2019; Supplementary Table 2). From the random sample of fish for each treatment, the first 175 fish (75 fish for January–February of BY 2019) were lightly anesthetized in a buffered solution of tricaine methanesulfonate (MS-222; Argent Chemical Laboratories, Redmond, Washington) and measured for FL to the nearest 1 mm and for body weight to the nearest 0.1 g. Fork length and weight (g) data were then used to calculate *K* using the following formula:

$$K=\left(\text{weight}/\text{FL}^3\right)\times 100{,}000.$$

An additional 25 fish were lethally sampled in a buffered solution of 0.05% MS-222. These fish were measured for size as described above, and tissue samples were obtained for the physiological assessments.

Gill filaments were removed and placed in a 0.05-mL tube containing a solution of sucrose, EDTA, and imidazole according to methods described by Zaugg (1982). Gill samples were frozen in a portable freezer at −20°C while in the field and then were transferred to a −80°C freezer for long-term storage prior to analysis. Whole fish bodies were labeled, placed into individual zip-top plastic bags, and kept at −20°C until processing for percent solid.

At the final sampling point, just prior to smolt release in April, 300 fish/treatment were captured and lethally sacrificed, and size metrics and tissue samples were collected and processed (as described above) at the Pelton Ladder. In addition, the fish's caudal peduncle was severed, blood was collected into a heparinized Natelson tube, and the blood was then transferred to a 0.4-mL polyethylene tube (VWR Scientific, Radnor, Pennsylvania). Phenotypic sex was determined for each individual by visual examination of the gonads. Female blood was discarded. Individual male blood samples were centrifuged for 5 min at $3{,}000\times g$ to separate out the plasma, which was then pipetted into a labeled 0.5-mL microcentrifuge tube. Plasma samples were stored at −20°C while in the field and then at −80°C until they were analyzed for evidence of precocious male maturation via quantification of plasma 11-ketotestosterone (11-KT) levels (see the *Laboratory Analysis* section).

Laboratory analysis

Gill Na⁺, K⁺-ATPase

Gill Na^+, K^+-ATPase activity has been used in numerous studies as an indicator of smolt development in Chinook Salmon (Beckman et al., 1999; Franklin et al., 1992; D. Spangenberg et al., 2014). Gill tissue collected from the field was processed and Na^+, K^+-ATPase activity was measured according to McCormick (1993). All values are reported in $\mu\text{mol PO}_4\cdot\text{mg protein}^{-1}\cdot\text{h}^{-1}$.

Whole-body percent solid

Whole-body moisture content has been shown to be inversely related to whole-body lipid in salmonids (Peters et al., 2007; Shearer, 1994; Trudel et al., 2005). Thus, the proportion whole-body solid (i.e., inverse of the proportion whole-body moisture) can be used as a surrogate for approximating whole-body lipid and making relative comparisons (D. K. Spangenberg et al., 2023). Percent solid was determined by thawing previously frozen fish samples and cutting them into small pieces (~0.5 cm^3). Fish pieces were placed in a preweighed aluminum pan and dried in an oven at 104°C to a consistent weight (~48 h). Wet and dry weights were then used to calculate the percent solid using the following formula:

$$\text{Whole-body solid }(\%)=\left(\text{dry weight}/\text{wet weight}\right)\times 100.$$

11-Ketotestosterone

For this study, the maturation status of males maturing at age 2 (versus nonmaturing males) was determined by measuring the levels of 11 Ketotestosterone (11-KT) in the plasma collected from fish prior to release in the spring. Plasma 11-KT levels were measured in the laboratory using an enzyme-linked immunosorbent assay adapted from the method of Cuisset et al. (1994) and applied according to the method of Larsen et al. (2004). Similar to previous studies, an 11-KT level of 0.8 ng/mL was used as a threshold for maturation; males with 11-KT values above this level were considered to be maturing, whereas males with 11-KT below this level were considered immature (Harstad et al., 2014; Larsen et al., 2004).

PIT tagging and detections

In each year of the study, about 5,000 fish/treatment were PIT-tagged in the fall—October or November, depending on the BY (Table 1). Fish were released in April, and the total number of fish released varied between BYs but was about 85,000 for the Big–Low treatment and about 150,000 for the Small–High treatment (Table 1).

Juvenile and adult PIT tag detections were queried through the Columbia River Data Access in Real Time website (www.cbr.washington.edu/dart) to determine travel time and adult return rates (Table 2) to Bonneville Dam. Travel time was calculated as the mean number of days traveled from release at Pelton Ladder to Bonneville Dam for each combination of treatment and year. Adult return rates were calculated by dividing the number of PIT-tagged fish detected as returning to the adult fish ladders at Bonneville Dam by the number of PIT-tagged fish that were released for each combination of treatment, year, and adult age-class.

Data analysis

Seasonal profiles of smolt quality: Size, condition factor, percent solid, and Na⁺, K⁺-ATPase

Linear regression models were run for each sampling date for FL, *K*, and Na^+, K^+-ATPase. Percent solid was analyzed using fractional logistic regression to accommodate proportional data (bounded by 0, 1). Brood year (categorical variable) was included as a fixed effect in each model to account for differences between years.

Table 2 Proportion of Chinook Salmon released that were detected as returning to Bonneville Dam for each brood year (BY), feed treatment (TREAT), cell position (CELL), and age-class for the juveniles released from Pelton Ladder during this study.

BY	TREAT	CELL	Age 2	Age 3	Age 4
2016	Small–High	Lower	0.00042	0.00021	0.00126
	Big–Low	Middle	0.00163	0.00020	0.00041
	Small–High	Upper	0.00142	0.00020	0.00061
2017	Small–High	Lower	0.00000	0.00000	0.00020
	Small–High	Middle	0.00040	0.00000	0.00060
	Big–Low	Upper	0.00100	0.00040	0.00040
2018	Big–Low	Lower	0.00123	0.00123	0.00471
	Small–High	Middle	0.00183	0.00142	0.00407
	Small–High	Upper	0.00307	0.00328	0.00881
2019	Small–High	Lower	0.00242	0.00181	0.00362
	Big–Low	Middle	0.00856	0.00313	0.00459
	Small–High	Upper	0.00787	0.00222	0.00686
2020	Small–High	Lower	0.00000	0.00035	0.00069
	Small–High	Middle	0.00020	0.00020	0.00041
	Big–Low	Upper	0.00142	0.00061	0.00041

Minijacks

Logistic regression analysis of individual male maturation status (0 = immature, 1 = maturing as a minijack) was used to compare the proportion of minijacks. Both feed treatment and BY were analyzed as categorical predictors.

Energetics versus minijacks

Fractional logistic regression models were used to predict minijack (proportion) estimates from the seasonal population means of FL, *K*, and percent solid (*N* ranged from 8 to 11). Brood year was again included in the models as a categorical predictor variable.

Juvenile out-migration

Travel time of individual PIT-tagged fish from release at Pelton Ladder to the juvenile bypass facility at Bonneville Dam was determined via linear regression analysis, with feed treatment, cell position, and year of release (shown as corresponding BY) all treated as categorical predictors of travel time. Cell position and BY were included in the models to account for out-migration environmental factors (river flow and temperature) and water quality differences among upper, middle, and lower cells across different years.

Adult returns (return rate and age at return)

Fractional logistic regression models were used to test whether feed treatment was a significant predictor of detections of age-2–4 PIT-tagged fish returning to Bonneville Dam. Predictions for each age-class (age 2, 3, or 4) were calculated in three separate models. The categorical variables of cell position and BY were included in each model to test and correct for any differences in PIT tag return rates among the rearing cells at Pelton Ladder. Brood year was included in the model to account for interannual variation in ocean entry conditions that may impact smolt survival.

Marginal predictions from the fractional logistic regression models described above were used to calculate mean age at return. The PIT tag return rate for each age-class was then converted to the proportion of the total returns ([return rate for each age-class]/[total PIT tag returns]) for each treatment. Next, the proportion of the total return for each age-class was multiplied by the age-class (2, 3, or 4) and then summed to achieve estimates of mean age at return.

Expanded returns (estimated numbers per cell)

The proportion of PIT tag returns was expanded to reflect the possible numbers of returns produced per ladder cell instead of being a per capita estimate. This was necessary because the number of fish reared per cell differed depending on which treatment was in the cell. More fish were reared in the cells for the Small–High treatment (~150,000 versus ~85,000; see Table 1) to maintain equal density (based on biomass) per rearing cell. The expanded adult return estimates were calculated by multiplying the proportion of PIT tag returns by the total number of fish that were released as smolts for each group. Estimated margins were derived from linear regression models that included feed treatment, cell position, and BY as categorical predictors.

All statistical analyses were conducted using STATA version 15.1 (StataCorp, College Station, Texas), and figures were created using GraphPad Prism version 10.2.3 (GraphPad Software, Boston, Massachusetts).

Results

Prelease assessment

Size and energetics

Across all BYs, the differential feeding treatments (Big versus Small) created consistent differences in mean FL throughout the rearing process (Figure 3A; Supplementary Table 3). On average, the Big–Low group was 14.2 mm larger than the Small–High group in October–February and then was 20.8 mm larger just prior to release in April (Supplementary Table 2). Condition factor was not significantly different between treatments in October; however, the Big–Low treatment diverged from the Small–High treatment by January of each year, with the Big–Low treatment having a higher mean *K*. Those differences became more pronounced by the time of release in April (Figure 3B; Supplementary Table 3). Percent solid was significantly higher in the Big–Low treatment at all sampling points (Figure 3C; Supplementary Table 3). Both feed treatments showed a decreasing trend in *K* and percent solid from October to April.

Smoltification

Both treatment groups smolted, as evidenced by increased gill Na^+, K^+-ATPase activity prior to release in April (Na^+, K^+-ATPase levels $> 2\ \mu mol\ PO_4 \cdot mg\ protein^{-1} \cdot h^{-1}$), and no

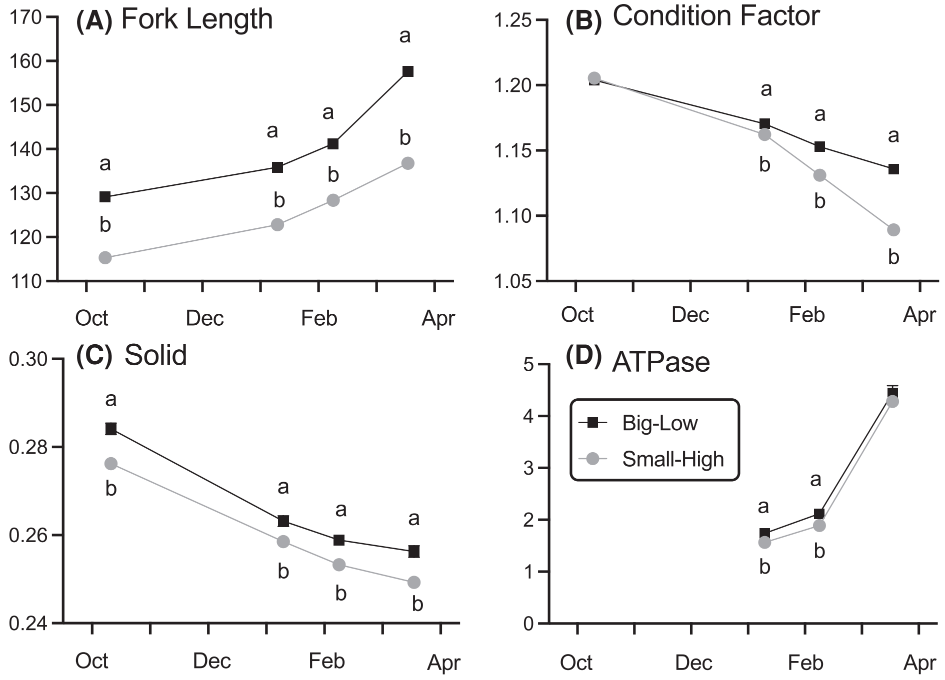

Figure 3 Mean values of the seasonal smolt quality indicators measured during rearing of juvenile Chinook Salmon at Round Butte Hatchery and the Pelton Ladder acclimation facility for brood years 2016–2020: (A) fork length (mm); (B) condition factor; (C) proportion solid; and (D) gill Na^+, K^+-ATPase activity ($\mu mol\ PO_4 \cdot mg\ protein^{-1} \cdot h^{-1}$). Different lowercase letters signify statistical differences between size treatments (Small–High and Big–Low) for seasonal comparisons in each panel ($P < 0.05$). Error bars represent the SE associated with predicted margins but are too small to see for most symbols. See Supplementary Table 3 for statistical models for each panel.

significant difference was observed between the Big–Low and Small–High treatment groups just prior to release (4.45 versus 4.28 $\mu mol\ PO_4 \cdot mg\ protein^{-1} \cdot h^{-1}$, respectively; Figure 3D; Supplementary Table 3). During January and February, the Big–Low treatment had relatively low Na^+, K^+-ATPase activity, but the values were significantly higher than those of the Small–High treatment (Figure 3D; Supplementary Table 3).

Early male maturation

The percentage of male fish maturing precociously (assessed prior to release) varied approximately threefold between treatments, with averages of 10.9% and 29.6% in the Small–High and Big–Low treatments, respectively (odds ratio = 3.6; Figure 4B; Supplementary Table 4).

Brood year differences and relationship between energetics and early male maturation

There were significant BY differences in the magnitude of the measured smolt quality indicators across years (Supplementary Table 3), but the seasonal differences and the differences between feed treatments were consistent. Furthermore, the proportion of minijacks for both feed treatments varied across years (Figure 4C; Supplementary Table 4). Fractional logistic regression models were used to test the relationships between seasonal smolt quality measures (FL, *K*, and percent solid) and subsequent minijack proportions independent of feed treatment. Fork length was a consistent predictor of minijack proportions across all dates (October–April; Figure 5; Supplementary Table 5). Percent solid was also a significant predictor of minijack proportions when measured in October ($z = 8.18$, $P < 0.001$), but this relationship was no longer present by January or thereafter. Condition factor showed no relationship to minijack proportions throughout the investigation (Figure 5; Supplementary Table 5).

Postrelease performance

Juvenile out-migration

Mean travel time varied between the Big–Low and Small–High treatments, with the Big–Low group having a significantly faster travel time to Bonneville Dam than the Small–High group (13.9 versus 15.5 d, respectively; $t = -10.91$, $P < 0.001$; Figure 6A; Supplementary Table 6). Brood year and cell position were also significant predictors of travel time (Figure 6B and C; Supplementary Table 6). The longest travel times were observed for out-migrating fish in 2019 and for fish reared in the lowest cell at Pelton Ladder.

Adult return rates and age at return

Adult returns (as quantified by the number of PIT tag detections/total tags released) varied by the age at return for the treatments (Table 2). The Big–Low treatment had higher returns of age-2 and age-3 fish but equal or lower age-4 adult returns than the Small–High treatment (Figure 7; Supplementary Table 7). The odds of maturing and returning at age 2 were 1.9 times higher for the Big–Low treatment than for the Small–High treatment ($z = 6.69$, $P < 0.001$). The odds of maturing and returning at age 3 were 1.43 times higher for the Big–Low treatment than for the Small–High treatment ($z = 2.04$, $P = 0.041$; Supplementary Table 7). These results highlight a shift in the age at return between the two

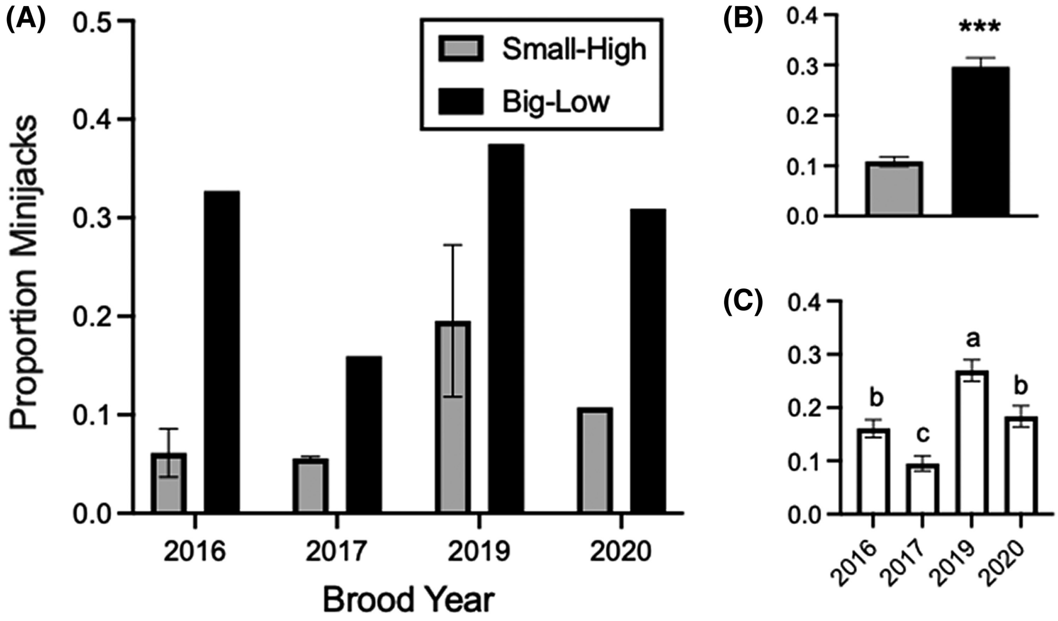

Figure 4 Age-2 (minijack) maturation estimates among male Chinook Salmon: (A) raw data, (B) marginal predictions from a logistic regression model that included feed treatment (Small–High or Big–Low) as a categorical variable, and (C) marginal predictions from a logistic regression model that included brood year as a categorical variable. Error bars represent 1 SE (the Big–Low treatment has no error bars due to the lack of replication within a given year). Different lowercase letters signify statistical differences between bars in each panel ($P < 0.05$). See Supplementary Table 4 for statistical models for each panel. $^{***}p < 0.001$.

treatments. When the age composition of the returns for each treatment was examined, the mean age at return was greater for the Small–High treatment, which had a higher proportion of adults returning as age-4 fish (Figure 7B).

Cell position and BY also had significant effects on the proportion of returns to Bonneville Dam. The fish reared in the upper cell position had higher return numbers across all age-classes, and fish reared in the lowest cell had lower adult return rates, especially for the age-2 fish (Figure 8; Supplementary Table 7). Brood year also had a significant effect on returns across all age-classes, with the highest returns observed for BYs 2018 and 2019 (release years 2020 and 2021; Figure 8; Supplementary Table 7).

Expanded returns (estimated numbers per cell)

The aforementioned return estimates are per capita estimates. As different numbers of fish were reared and released from the different feed treatments, it is also useful to examine the returns expanded by the release numbers for each treatment, cell, and BY. Per capita adjusted returns reflect rearing capacity differences between the Small–High and Big–Low treatments, with a greater number of fish returning per rearing cell in the Small–High treatment for all age-classes (Figure 9), particularly for age-4 returns. Approximately 49 more age-2 fish, 53 more age-3 fish, and 232 more age-4 fish returned from the Small–High treatment compared to the Big–Low treatment (Supplementary Table 8).

Discussion

In this study, an alternative rearing strategy (more small fish) was compared to the standard rearing protocol (fewer large fish) at the Round Butte Hatchery/Pelton Ladder facility, and juvenile smolt quality and adult returns and demographics were assessed. Prior to release, we observed physiological differences between the two treatments (Big–Low and Small–High) for most metrics (i.e., size, *K*, and percent solid) but not all of them (i.e., gill Na^+, K^+-ATPase). After release, juvenile out-migration time was slightly higher for the Small–High group. The proportion of returning adults was significantly higher in the Big–Low treatment for age-2 and age-3 males but was not significantly different for age-4 males and females compared to the Small–High treatment. However, the Small–High treatment outperformed the Big–Low treatment in terms of total adult returns, as more smolts were released per rearing vessel from the Small–High treatment. Moreover, the mean age at return from the Small–High treatment was shifted toward larger, older fish.

Trade-offs between size, survival, and age at maturity

Previous studies of both Chinook Salmon (James et al., 2023) and Sockeye Salmon *O. nerka* (Koenings et al., 1993) have suggested that there may be a size-to-survival threshold; once the threshold is exceeded, increases in body size no longer confer a higher survival. In fact, exceeding this threshold may have deleterious consequences, as the rearing of larger smolts could increase the proportions of undesirable precocious males and shift the age at return for both sexes toward younger adults (Gallinat et al., 2023). Determining size-at-release targets for Chinook Salmon hatchery programs becomes a balancing act between optimizing for smolt survival and age at return. In the current investigation, trade-offs between size, survival, and age at maturity were evident. The Big–Low treatment had

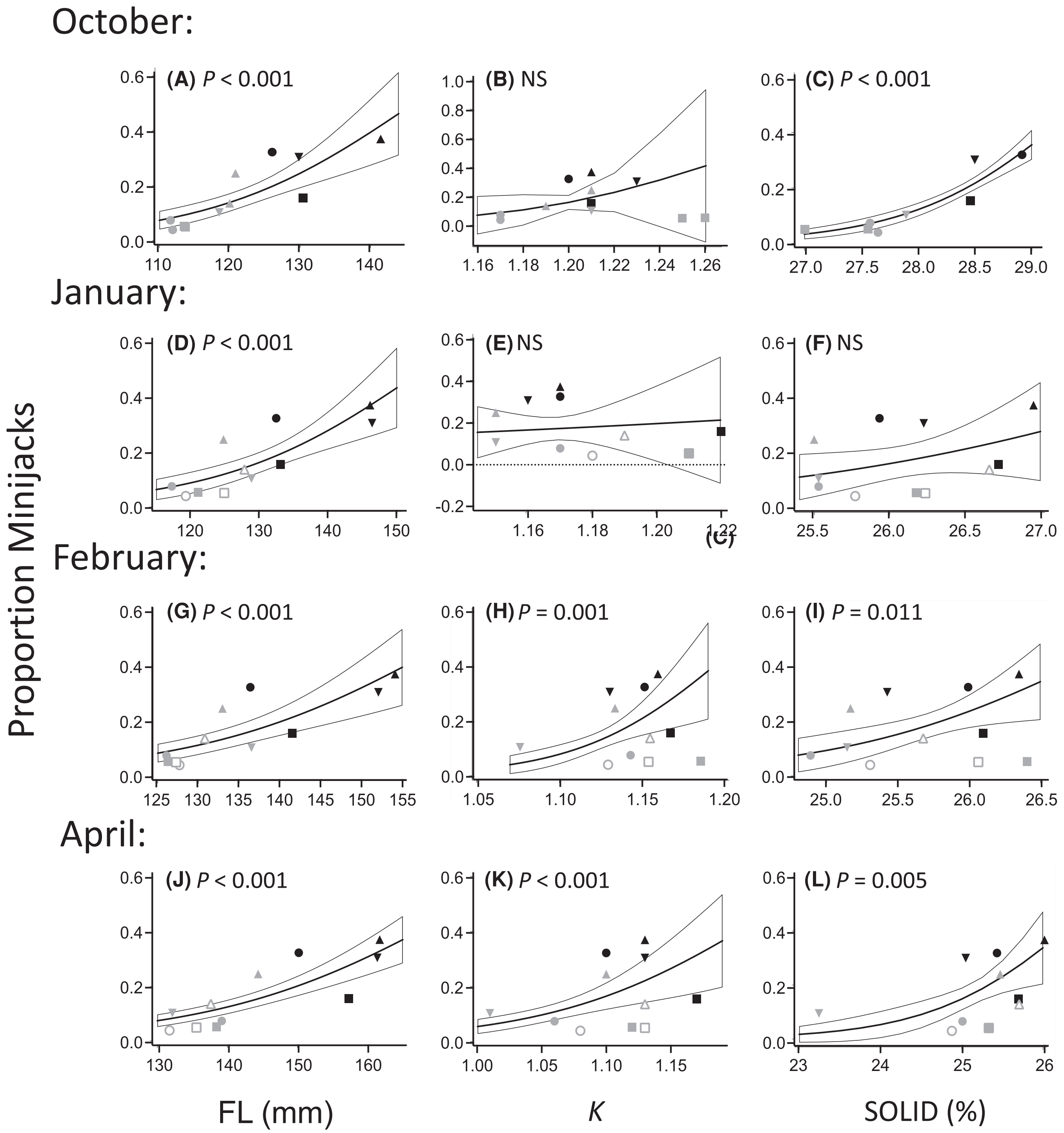

Figure 5 Relationships between the size (fork length [FL]) or energetic status (condition factor [*K*] or percent solid) of Chinook Salmon in (A)–(C) October, (D)–(F) January, (G)–(I) February, and (J)–(L) April and the proportion of minijacks (determined via 11-Ketotestosterone levels in April) across brood years (BYs). Each data point represents a population mean shown in Supplementary Table 2. The trend line and 95% CIs are from fractional logistic regression models shown in Supplementary Table 5. Symbols and shading represent the following: circles = BY 2016, squares = BY 2017, triangles = BY 2019, upside-down triangles = BY 2020, black = Big–Low treatment, gray = Small–High treatment, and open symbols = cell 1 at Pelton Ladder. Abbreviation is as follows: NS = not significant.

higher overall return rates than the Small–High treatment, but the Big–Low treatment also had a greater tendency to produce undesirable age-2 males. Gallinat et al. (2023) found similar trade-offs when they categorized Tucannon River (Washington) spring Chinook Salmon from eight BYs into five size-groups ranging from <120 mm to ≥180 mm. Smaller smolts had reduced survival, and larger smolts matured earlier at either age 2 or age 3. Ultimately, the intermediate-sized smolts (with FLs ranging from 140 to 159 mm) provided the optimum size for that hatchery program.

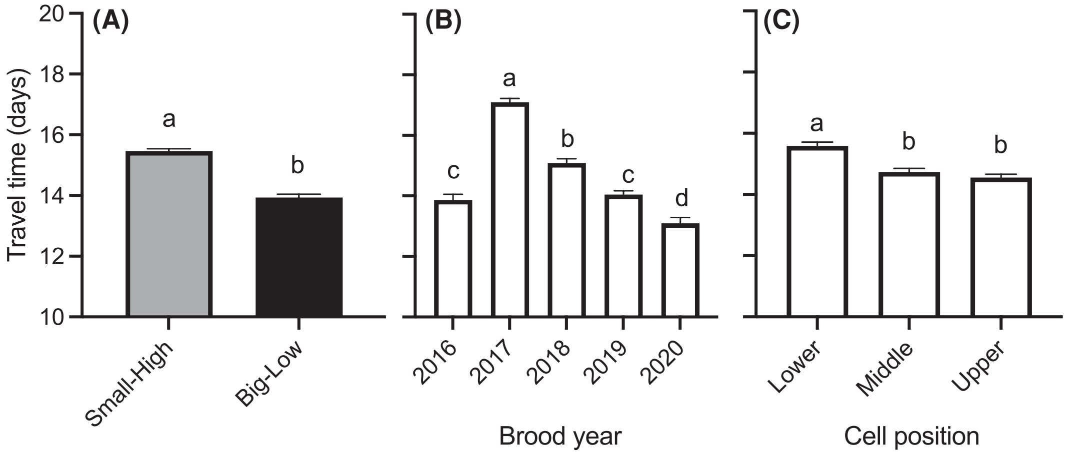

Figure 6 Differences in mean travel time (d) from Pelton Ladder to Bonneville Dam for out-migrating juvenile Chinook Salmon. The linear regression model included (A) feed treatment, (B) brood year, and (C) cell position at Pelton Ladder as predictor variables. Error bars represent 1 SE. Different lowercase letters signify statistical differences between bars in each panel ($P < 0.05$). See Supplementary Table 6 for statistical models for each panel.

Common to many hatchery size and survival experiments is the use of terms such as "large" and "small," both of which are relative and impede attempts to compare results from different studies. Feldhaus et al. (2016) examined data from Lookingglass Hatchery, Oregon, over 10 BYs and found no significant differences in smolt-to-adult survival or smolt-to-adult return between "large" and "small" Chinook Salmon smolts. They noted that in some studies (Bilton et al., 1982; Martin & Wertheimer, 1989; Morley et al., 1996), the smolts that were considered big were actually of similar size to the "small" smolts in their study. We found similar nomenclature discrepancies when comparing fish in this study to those in other studies. For example, smolt size (FL) from our Small–High treatment (131–144 mm) overlapped more in size with the large smolts (129–148 mm) of Feldhaus et al. (2016) than smolts from our Big–Low treatment (150–167 mm). When compared to smolts from the Gallinat et al. (2023) study, neither the Small–High treatment nor the Big–Low treatment aligned with the smallest (<120 mm) or largest (>180 mm) smolts from that study; rather, both of our treatments overlapped with two different intermediate size ranges. Our Small–High treatment spanned both the 120–139-mm and 140–159-mm ranges, and our Big–Low treatment spanned both the 140–159-mm and 160–179-mm ranges. Given the relativity of size designations such as "large" and "small," one must consider and compare the actual size of fish to draw meaningful conclusions.

Fish density

At Pacific salmon hatcheries, the density (biomass) limit for the rearing vessels is dictated by the unique infrastructure and environmental conditions that exist at a specific hatchery facility. If a hatchery is interested in increasing adult returns but has reached its maximal density capacity (i.e., no additional fish can be reared), alternative strategies could be considered. In the current investigation, two treatments were compared: Standard production of approximately 85,000 fish reared to a size target of about 8 fpp (~57 g) versus approximately 150,000 fish reared to a size target of about 15 fpp (~30 g). Both treatments were at a similar density (total biomass), but they varied in how that biomass was allocated between size and number of individual fish. The Small–High treatment fish outperformed their Big–Low counterparts by returning more older adults. Feldhaus et al. (2016) recognized a similar trade-off in size versus number of fish for the Imnaha River (Oregon) hatchery program. Based on the mean smolt-to-adult survival rates calculated for their large and small smolts, Feldhaus et al. (2016) predicted that if they reared and released 85,000 small smolts at 20 g (~23 fpp) instead of 50,000 large smolts at 34 g (~13 fpp) from each raceway, an additional 334 adult Chinook Salmon would return to the Columbia River. These studies highlight that if fish density (total biomass per rearing vessel) is a limiting factor, experimenting with different combinations of fish size and fish numbers could be an effective strategy to optimize production.

Challenges and limitations with multiyear hatchery-scale experiments

Conducting large-scale hatchery experiments over multiple BYs provides useful insights, but there are some caveats. In this study, infrastructure and layout were noted barriers to creating an optimal experimental design. At the Pelton Ladder, three cells were available for rearing fish; therefore, replication of both treatment groups was not possible within a given BY. This spatial restriction limited our ability to make some statistical inferences. Additionally, the ladder cells were inline and connected with barriers in between—meaning that fish could not pass between the screened cells, but the water did flow sequentially through them. This created an "upstream versus downstream" effect rather than an optimal isolated "tank" experimental design. We did not test water quality in this experiment, but there was a clear and consistent cell effect that can most likely be attributed to the uppermost cell having the highest water quality and the furthest downstream cell having the lowest water quality. Within treatment groups, juvenile smolt out-migration time was significantly slower for the lowest cell compared to the upper two ladder cells (Figure 6C), and the uppermost

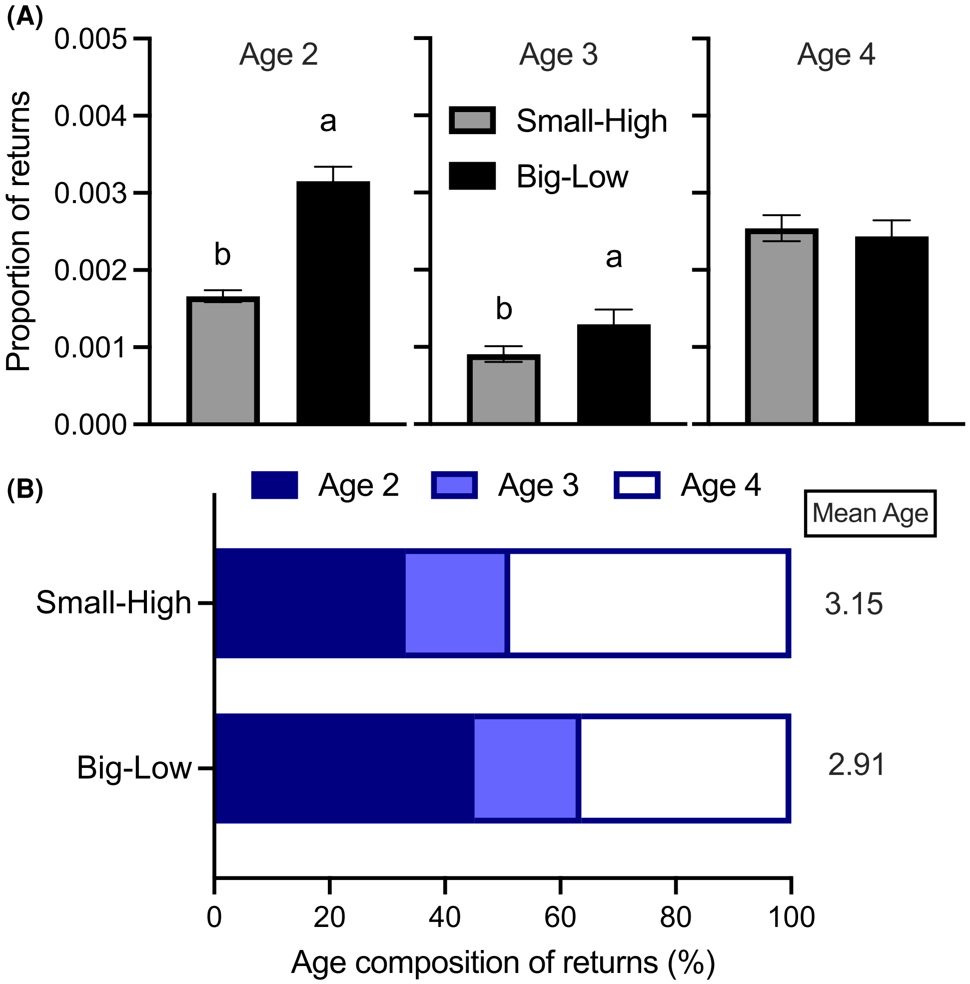

Figure 7 (A) Marginal predictions of the proportion of Chinook Salmon released that were detected as returning at age 2, 3, or 4 to Bonneville Dam on the Columbia River for the feed treatments (Small–High or Big–Low). Different lowercase letters signify statistical differences between bars in each panel ($P < 0.05$). Error bars represent 1 SE. (B) Age composition of the fish that returned from each feed treatment based on the estimates from panel A is shown. See Supplementary Table 7 for a statistical summary of fractional logistic regression models.

cell consistently had the highest adult returns (Figure 8). Treatment groups were rotated amongst the ladder cells in each BY, and this position-specific factor remained consistent within treatments (Big–Low or Small–High) after accounting for interannual variability and feed treatment (Figure 8). Interannual variability and relatively low adult returns over the period of this work also contributed to analytical challenges. Finally, this experiment was conducted over several years, some of which were during the COVID-19 global pandemic. This unprecedented situation presented additional challenges and limitations with respect to data and sample collection and resulted in some data gaps. Despite these acknowledged limitations and data gaps, we still identified important trends and conclusions that were consistent with previously published literature.

Hatchery-scale experiments can offer insights into how different variables (smolt quality, water quality, interannual and intra-annual variability, etc.) can affect survival and adult demographics. Although hatcheries are not built to be experimental laboratories, as aging infrastructure is replaced, thought and consideration can be given to developing new infrastructure that accommodates the ability to conduct small-scale hatchery experiments. This capacity could enable hatcheries to test and optimize different rearing regimes to meet production goals. In the face of future environmental uncertainties, having infrastructure that can accommodate various rearing regimes will allow programs to remain flexible and adaptive.

Management implications

Most hatcheries select a single size target and rear fish to a similar size with very little variation within or between years, with the hope that the selected size optimizes survival. However, survival can be affected by a variety of biotic and abiotic factors, such as release timing (James et al., 2023; Morley et al., 1996), freshwater conditions (Bosch et al., 2023; Crozier & Zabel, 2006; National Research Council, 2004), ocean conditions (Mueter et al., 2002; Peterson et al., 2006), dam passage (Muir et al., 2001; Sigourney et al., 2015), and predators (Duffy & Beauchamp, 2008; Emmett & Krutzikowsky, 2008; Hostetter et al., 2012). The influence of these factors can vary in space and time within a given year and between years, meaning that the optimal size in a certain year may not be the optimal size in the following year.

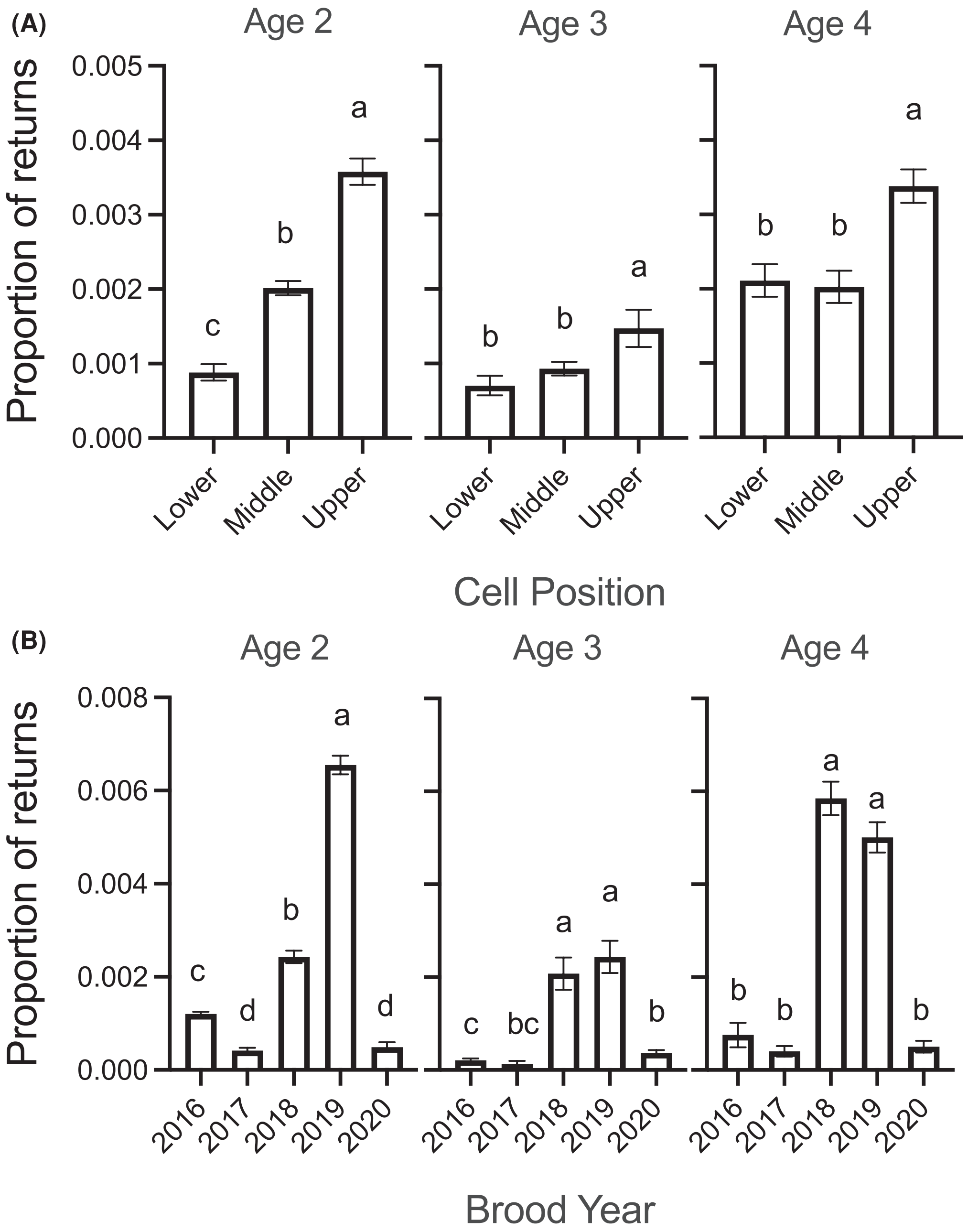

Figure 8 Marginal predictions of the proportion of Chinook Salmon released that were detected as returning at age 2, 3, or 4 to Bonneville Dam on the Columbia River for the following variables: (A) Pelton Ladder cell position and (B) brood year. Different lowercase letters signify statistical differences between bars in each panel ($P < 0.05$). Error bars represent 1 SE. See Supplementary Table 7 for a statistical summary of fractional logistic regression models.

To mitigate this uncertainty, hatchery programs may opt to hedge their bets and release fish of various sizes and/or abundances to maximize survival—if they are able. In this study, the Big–Low treatment group had a higher per capita adult return rate, especially with younger age-classes (ages 2 and 3); however, because more fish were released from the Small–High treatment, there was a trend for the smaller fish to have higher returns at all age-classes. We only assessed two different treatments based on fish size and numbers, but there are various other combinations that could be tested, assuming there is sufficient broodstock to increase production. We recognize that this might not always be the case. The present study provides some initial insights into a potentially new rearing strategy for hatcheries: rearing and releasing fish of varying sizes and numbers per vessel to mitigate for any postrelease uncertainties.

Finally, this study connects to a larger body of research—conducted episodically over the past 35 years on the Deschutes and Hood rivers—that is unique in the literature. In these studies, physiological assessment of juvenile spring Chinook Salmon at hatchery facilities in or near these basins was used to link smolt quality to postrelease performance and adult survival (Beckman et al., 1999, 2017; D. Spangenberg et al., 2014; D. K. Spangenberg et al., 2015). Over time, hatchery managers altered their rearing protocols based on the results

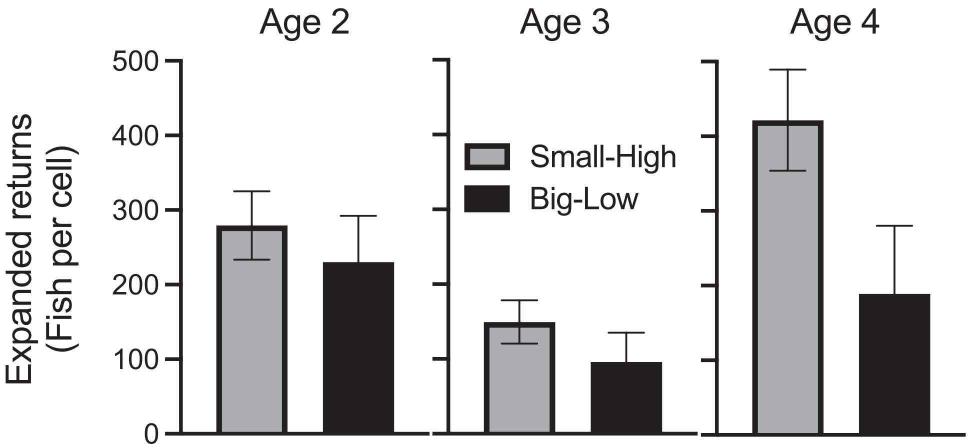

Figure 9 Estimated number of Chinook Salmon returning per rearing cell (Pelton Ladder) for the feed treatments (Small–High or Big–Low). The per capita estimates (proportion returns; Figure 7A) were expanded by multiplying by the number of fish released from each cell for each treatment and brood year, as more fish were reared in and released from Small treatment cells. Error bars represent 1 SE. See Supplementary Table 8 for statistical models for each panel.

from these studies. For example, Beckman et al. (1999) compared fish reared at three different locations (Round Butte Hatchery, Pelton Ladder, and Warm Springs Hatchery) and found that spring growth rate had a greater effect on juvenile out-migration time than release size. In a subsequent study (D. Spangenberg et al., 2014), Hood River spring Chinook Salmon were reared at three different hatchery facilities (Parkdale Fish Hatchery [Hood River, Oregon], Carson NFH [Wind River, Washington], and the Round Butte Hatchery/Pelton Ladder facility [Deschutes River, Oregon]) to assist managers in determining where to rear their excess production. The study found that Hood River fish reared at the Round Butte Hatchery/Pelton Ladder facility outperformed fish that were reared at the other facilities (D. Spangenberg et al., 2014). A second assessment compared Hood River fish to Carson NFH fish and found that stock (Hood River versus Carson NFH), temperature, and growth rates led to higher rates of precocious male maturation in Hood River fish than in Carson NFH fish (Beckman et al., 2017; D. Spangenberg et al., 2014; D. K. Spangenberg et al., 2015). Based on these findings, hatchery managers were able to adjust location and rearing protocols to optimize production. Overall, this study represents a culmination of the previous work, as it directly tested the viability of releasing smaller smolts within a direct hatchery production context.

Conclusions

Salmon survival and age at return are determined by numerous factors, some of which are within the control of hatchery managers and some of which are not. Fish size and density are two variables that managers can manipulate and control to maximize production. This study compared the standard rearing protocol at the Round Butte Hatchery/Pelton Ladder facility to an alternative strategy of rearing smaller smolts but in greater numbers while maintaining a similar biomass in each of the standard rearing cells. Standard production (Big–Low) smolts tended to return at higher rates but also returned at younger age-classes. The alternative rearing strategy (Small–High) produced fewer minijacks, returned a greater number of fish at all age-classes, and shifted the mean age at return to older adults. This study highlights the trade-offs between size, survival, and age at maturation in spring Chinook Salmon. Through experimental manipulations of size and fish abundance, hatchery managers can develop strategies to optimize production and reach their objectives. Furthermore, if production allows, managers may consider rearing and releasing smolts of varying size and abundance combinations—a bet-hedging strategy that may prove to be effective in the face of stochastic environmental variability.

Supplementary Material

Supplementary material is available at *North American Journal of Aquaculture* online.

Data Availability

The data that support the findings of this study are available in the Dryad Digital Repository (Harstad et al., 2026), and PIT tag data are available from Columbia River Data Access in Real Time (https://www.cbr.washington.edu/dart).

Ethics Statement

Fish were reared in accordance with the Oregon Department of Fish and Wildlife Fish Health Policy (OAR 635-007-0965) and Hatchery Management Policy (OAR 635-007-0544).

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Conflicts of interest

The authors declare no conflicts of interest.

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