Transactions of the American Fisheries Society, 2026, **00**, 1–17
https://doi.org/10.1093/tafafs/vnag015
Published: 14 May 2026
Feature Article

Reducing feeding frequency and dietary lipid during hatchery rearing increases adult age at recovery in Chinook Salmon

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Abstract

Objective: Age of maturation in Chinook Salmon *Oncorhynchus tshawytscha* is phenotypically plastic, influenced by both genotype and environmental factors. Salmon hatchery programs often rear fish under accelerated growth regimes using high-lipid diets that can result in younger age at maturity, including increased prevalence of age-2 males (minijacks). In the first phase of this investigation (previously published), we demonstrated that minijack prevalence could be decreased by up to 65% through a combination of reduced feeding frequency and dietary lipid. The goal of the second phase of this investigation was to report on the dietary treatment effects on (1) juvenile travel time and apparent river survival, (2) adult recovery rates and demography, and (3) the relationship between the prevalence of minijacks and adult recovery.

Methods: Juvenile Umatilla River hatchery fall Chinook Salmon were reared at Bonneville Hatchery, Oregon, under four dietary treatments across four replicate rearing cohorts. The dietary treatments included two feeding frequencies (standard [fed 7 d/week] and reduced [fed 4 d/week]) and two dietary lipid levels (standard [18%] and reduced [12%]) in a 2 × 2 factorial design. The fish were differentially implanted with coded wire tags according to treatment, and some of the fish were tagged with passive integrated transponder tags. The downstream passive integrated transponder tag detections at John Day Dam were used to determine juvenile travel time and river survival. The coded wire tags were used to determine adult recoveries in the marine and freshwater environment. The recovery data were analyzed within the context of significantly variable ocean conditions over the course of the four ocean entry years.

Results: The downstream travel time of the out-migrating juveniles was significantly affected by the dietary treatments, with the smallest treatment fish traveling slower (mean travel time = 68.2 d) than the largest treatment fish (mean travel time = 45.2 d). However, juvenile downstream survival to John Day Dam was not statistically different between treatments. Dietary treatment had a significant effect on total adult recovery. More adult fish (ages 4–6) were recovered from the low feeding frequency–low dietary lipid treatment (0.51%) than from the high feeding frequency–high dietary lipid treatment (0.42%) over the four ocean entry years. In addition, despite being smaller at release, this treatment produced older and larger adults (mean age at recovery = 4.46 years) than were produced by the largest smolts at release (mean age at recovery = 3.72 years). However, interannual variation in the ocean conditions had a more substantial effect on adult recovery than did any hatchery-rearing regime.

Received: September 25, 2025. **Revised:** January 29, 2026. **Accepted:** March 5, 2026

***Conclusions*: The results of this investigation provide insights for customizing feeding regimes to reduce precocious male maturation while increasing overall adult size, recovery rates, and age at recovery in salmon hatchery programs within the context of variable ocean conditions.**

Keywords: adult recovery, age at maturation, Chinook Salmon, diet manipulation, growth, hatchery, ocean conditions

Lay summary

Reduced feeding frequency and dietary lipid in hatchery Chinook Salmon decreased early male maturation and increased the recovery of larger, older adults. These findings provide insight into how variations in juvenile rearing have far-reaching effects on adult recovery for hatchery programs.

Introduction

State, federal, and tribal hatcheries release over 60 million juvenile Chinook Salmon *Oncorhynchus tshawytscha* into the Columbia River basin annually. The goals for these programs include providing significant contributions to adult harvest and/or natural spawning (i.e., supplementation) in addition to meeting hatchery broodstock needs. Since the first salmon hatcheries were implemented in the Columbia River in the 1880s (Lichatowich, 1999), many advances have been made in fish culture. Methods have been developed to control disease, reducing both in-hatchery and postrelease mortality (Wedemeyer, 2002). In addition, artificial feeds have been developed, leading to improvements in fish health and growth efficiency. Despite these advances, abundance, productivity, and marine survival of Chinook Salmon populations have decreased over the past few decades (Atlas et al., 2023; Crozier et al., 2021; James et al., 2023). In addition, several recent studies have shown that over the past several decades, both hatchery and wild adult salmon are returning at smaller sizes and younger ages, which can have negative biological, ecological, and economic implications (Lewis et al., 2015; Malick et al., 2023; Ohlberger et al., 2018; Oke et al., 2020).

Several influential studies have demonstrated that increased smolt size is correlated with improved survival (Bilton, 1984; Clarke & Shelbourn, 1985; Holtby et al., 1990; Martin & Wertheimer, 1989; Zabel & Achord, 2004). Accordingly, the current paradigm for many hatchery programs is that “bigger is better,” based primarily on the premise that smaller smolts are more susceptible to predation (Sogard, 1997). However, higher growth rates in culture and larger size may induce an alternative life history pathway in which males initiate maturation early at age 2 (minijacks) and migrate only short distances downstream before initiating upstream migration to their natal headwaters (Beckman & Larsen, 2005; Larsen et al., 2010; Pearsons et al., 2023) or bypass smolting and simply remain in freshwater (Larsen et al., 2004, 2006, 2013). In addition, current high-lipid feeds that are designed to promote high growth rates for salmon aquaculture may also promote early male maturation (Shearer & Swanson, 2000; Silverstein et al., 1998). Relatively high rates of minijacks have been found in some current hatchery populations, with potential consequences for the return of full-size anadromous males (Harstad et al., 2014, 2018; Larsen et al., 2019; Spangenberg et al., 2014, 2015). Within and among hatcheries, larger fish (or those containing higher levels of body fat) are more likely to initiate early male maturation than smaller, leaner fish (Harstad et al., 2023; Larsen et al., 2006; Madeiros et al., 2018; Spangenberg et al., 2014, 2015). Given these trade-offs, it stands to reason that the optimal size at release for juvenile Chinook Salmon is still unclear.

The uncertainty about relationships among smolt size, juvenile and adult survival, and early male maturation has generated interest in collectively revisiting the interplay among these factors. In addition, there is some interest in discerning the effect of reducing adiposity on early male maturation. Recently, (in phase 1 of the current study) we examined the effects of varying feeding frequency and dietary lipid content on growth, release size, and minijack maturation in a hatchery-scale production experiment (see Harstad et al., 2023) with Umatilla River (Oregon, USA) fall-run Chinook Salmon (mature adults return to freshwater in the fall). Smolt size at release in Harstad et al. (2023) varied by treatment, and minijack maturation (enumerated prior to smolt release) was more prevalent in the larger smolts. For phase 2 of this hatchery-scale dietary treatment study, conducted over four consecutive ocean entry years (OEYs), we report herein on adult returns. Specifically, we examine (1) the effect of dietary treatment on juvenile out-migration metrics, travel time, and apparent survival; (2) the effect of dietary treatment on adult recovery rate and age at recovery in the context of annual variation in ocean conditions; and (3) the relationship between in-hatchery minijack prevalence and adult recoveries. The results of this phase of the study provide new and useful insights into the design of rearing regimes for hatchery Chinook Salmon in the Columbia River and other Chinook Salmon hatchery programs.

Methods

Experimental design and study location

This study is the second phase of a 2 × 2 factorial design study. Phase 1 was previously reported in Harstad et al. (2023) and documented the effects of varying dietary treatments (feeding frequency and lipid content) on the energetics and minijack production for experimental groups of yearling fall Chinook Salmon that were reared at the Bonneville Hatchery and released into the Umatilla River. This hatchery program is located in northeastern Oregon (Figure 1) and produces fall Chinook Salmon for marine and freshwater fisheries, tribal harvest, and hatchery broodstock.

The four dietary treatments were combinations of standard and reduced feeding frequencies (7 d/week vs. 4 d/week) and standard and reduced dietary lipid content (18% vs. 12%). The standard 18% dietary lipid feed (BioClark) was

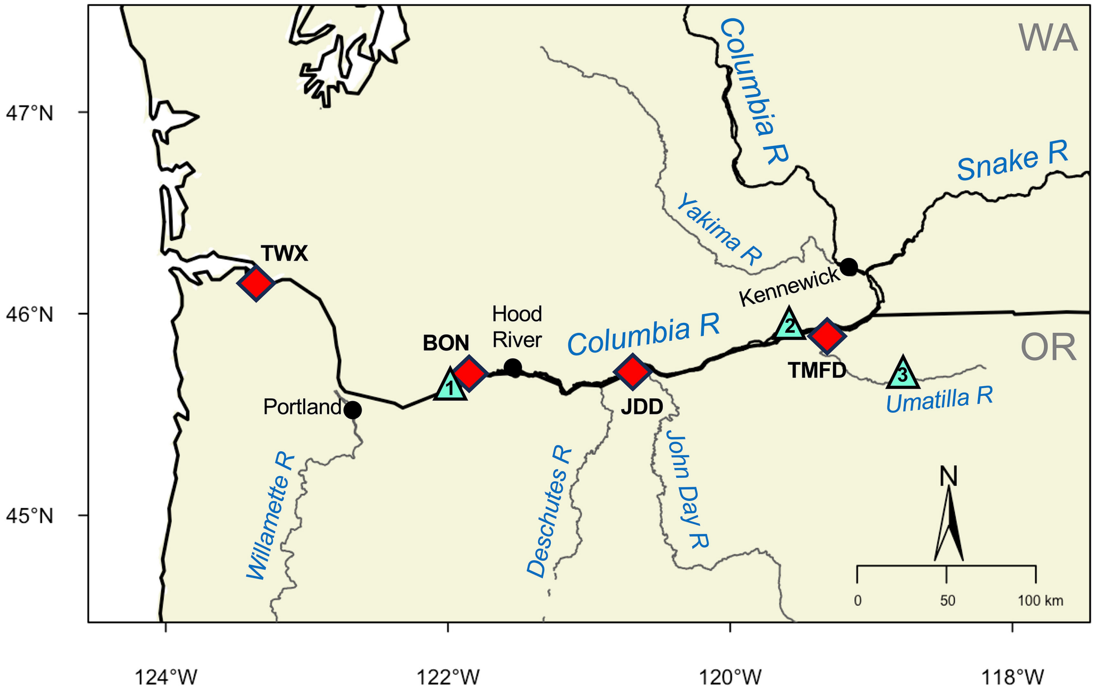

Figure 1 Rearing and passive integrated transponder tag interrogation sites for the Umatilla River fall Chinook Salmon hatchery program in northern Oregon. The rearing sites (aqua triangles) are as follows: 1 = Bonneville Hatchery, 2 = Umatilla and Irrigon hatcheries, and 3 = Pendleton Acclimation Facility (river kilometer [rkm] 465.090 [numbers to the left of the decimal are the kilometers upstream from the base of the Columbia River, numbers to the right of the decimal are the kilometers upstream from the mouth of the Umatilla River). The interrogation site abbreviations (red diamonds) are as follows: TWX = estuary towed array (rkm 75); BON = Bonneville Dam (rkm 234); JDD = John Day Dam (rkm 347); TMFD = Three Mile Falls Dam (rkm 465.005).

manufactured by Bio-Oregon, and the reduced 12% dietary lipid feed was a special formulation of the Abernathy Salmon Diet manufactured by Rangen, Inc. These commercially available diets contain comparable minimum levels of protein (47% vs. 45%, respectively; Harstad et al., 2023). The amount of feed provided per day adhered to the feed manufacturer's recommendations based on fish size and water temperature; however, fish from the different dietary treatments received varying amounts of feed per week. Specifically, the 4-d/week treatments were fed the recommended daily ration of 4 d/week rather than the standard protocol of 7 d/week. The differences in the amount of feed that was fed per week for each treatment increased over time as the size differences between the treatments became more pronounced (see Harstad et al., 2023).

The four dietary treatment combinations (4 d/week and 12% dietary lipid content [4d-12%], 4 d/week and 18% dietary lipid content [4d-18%], 7 d/week and 12% dietary lipid content [7d-12%], and 7 d/week and 18% dietary lipid content [7d-18%]) were applied from March through December during hatchery rearing, with all of the fish subsequently being fed the standard, 7d-18%, treatment over the winter months and until smolt release the following spring. This experimental feeding design differs from typical size-at-release rearing protocols, where feeding and growth is relatively constant across the juvenile rearing period until the time of release. Placing all of the fish on the standard feed protocol (fed 18% lipid diet, 7 d/week) after autumn can help increase the size and condition factor of the fish prior to smolt release. The experiment was carried out over four replicate rearing cohorts (OEYs 2012–2015). The fry were placed into ponds the year after the adults were spawned and then reared in the hatchery for approximately 1 year. The fish were released the following spring as age-1+ smolts after approximately 1 month of acclimation at Pendleton Acclimation Facility. See Harstad et al. (2023) for a detailed description of juvenile fish rearing for this study.

In the present study, we examine the performance of the fish from the four dietary treatments after the smolts were released from the acclimation site (Figure 1). Our previous investigation (Harstad et al., 2023) reported the prevalence of minijacks that were produced during hatchery rearing (assessed just prior to smolt release) in each dietary treatment for each year of the study. In addition, energetic indices (including fish size) were measured at several points during juvenile rearing and correlated with minijack prevalence (Harstad et al., 2023). The data for minijack prevalence and fish size from phase 1 of this study are also included in the current study, and their relationships to juvenile out-migration and adult metrics are examined.

Fish release and tagging

The release dates (from Pendleton Acclimation Facility) for the fish that were used in this study ranged from February 27 to March 8 across years. On average, approximately 97,000 fish were released annually for the standard dietary treatment (7d-18%; see Table 1). For the other treatments, the annual release numbers ranged from 37,000 to 52,000 fish (Table 1).

Table 1 Total numbers of fish released and numbers of fish with coded wire tags (CWTs) and passive integrated transponder (PIT) tags released for each dietary treatment (4 d/week and 12% dietary lipid content [4d-12%], 4 d/week and 18% dietary lipid content [4d-18%], 7 d/week and 12% dietary lipid content [7d-12%], and 7 d/week and 18% dietary content [7d-18%]) and ocean entry year (OEY), including mean fish size and minijack prevalence prior to hatchery release.

OEY	Dietary treatment	Tag code (CWT)	Tag ID (PIT)	Total # fish released	Number of CWTs released	Number of PIT tags released	Fish size (mm)[a]	Minijacks (%)[b]
2012	4d-12%	090490	OUR-2011-264-LFR	46,626	45,937	1,487	108.3	35.9
2012	4d-18%	090489	OUR-2011-264-HFR	50,751	50,751	1,493	118.2	69.4
2012	7d-12%	090491	OUR-2011-265-LFN	47,325	45,148	1,489	143.6	59.1
2012	7d-18%	090492	OUR-2011-263-STD	90,936	90,390	1,987	143.5	65.3
2013	4d-12%	090656	OUR-2012-262-LFL	37,227	36,855	1,161	98.0	28.1
2013	4d-18%	090655	OUR12263.HFL	51,031	50,725	1,487	114.3	50.3
2013	7d-12%	090654	OUR12263.LFH	50,420	50,017	1,493	121.7	50.3
2013	7d-18%	090657	OUR12262.STD	89,745	89,027	1,960	147.1	54.0
2014	4d-12%	090686	OUR13303.LFL	36,548	35,555	904	93.3	6.6
2014	4d-18%	090685	OUR13303.HFL	54,331	52,836	977	105.9	4.9
2014	7d-12%	090684	OUR13304.LFH	50,877	49,466	995	147.4	33.3
2014	7d-18%	090683	OUR13304.STD	104,872	104,283	999	161.9	59.1
2015	4d-12%	090868	OUR14303.LFL	28,925	28,925	959	95.7	7.0
2015	4d-18%	090866	OUR14304.HFL	50,494	50,393	995	102.9	19.4
2015	7d-12%	090867	OUR14303.LFH	35,771	35,771	988	121.6	14.6
2015	7d-18%	090869	OUR14304.STD	103,895	103,895	1,999	140.7	46.4

[a] Fork length was measured in February just before fish were moved to the Pendleton Acclimation Facility.
[b] Produced during juvenile hatchery rearing. Females were omitted from this estimate (see Harstad et al., 2023 for details).

Fish from each dietary treatment were implanted with coded wire tags (CWTs), with an implant rate of 95.4% to 100% across years. A subset of fish from each dietary treatment was also implanted with passive integrated transponder (PIT) tags each year for approximately 1–3% of the total fish released (range: 977–1,999 fish per treatment; Table 1). The release numbers of PIT- and CWT-tagged fish were obtained from the Columbia River DART (Data Access in Real Time; see Columbia Basin Research, 2022) and the Regional Mark Information System (RMIS; see Regional Mark Processing Center, 2022) databases, respectively. The total fish release numbers were also obtained from RMIS.

Data collection

Passive integrated transponder tag detections

We queried PIT tag detections at John Day Dam using the Columbia River DART database to estimate travel time. The values for travel time (from Pendleton Acclimation Facility to John Day Dam; travel distance = 208 km) were calculated as the mean number of days that were traveled by the fish from each dietary treatment and year combination. Apparent juvenile downstream migration survival was estimated from the PIT tag detections at several interrogation sites (John Day Dam, Bonneville Dam, Estuary Array; see Figure 1) via Cormack–Jolly–Seber modeling using the online analysis tools on the Columbia River DART website. We are reporting on detections at John Day Dam instead of Bonneville Dam because detections at the Estuary Array were too low in some years to determine apparent survival.

Coded wire tag recoveries

The estimates for adult recovery were determined from the CWT recovery information that was obtained from the RMIS database, which included both marine fishery recoveries and freshwater recoveries in the Columbia River and its tributaries (Table 2). Most of the CWT recoveries were from the Columbia River, and these recoveries were split between freshwater fisheries and broodstock collection. Because providing both marine and freshwater opportunities is a major goal of this harvest program and a substantial portion of the CWT recoveries also came from the marine environment, we included all of the CWT recoveries, not just those that were considered escapement to the Umatilla River (i.e., smolt-to-adult return), to capture a more complete picture of the potential survival and estimated age structure of this population. Thus, we are effectively reporting smolt-to-adult survival (i.e., SAS; presented as "CWT recovery rate" throughout), defined as the proportion of smolts with CWTs that survive to be taken in

Table 2 Recovery estimates for coded wire tags (shown as a percentage of coded-wire-tagged fish that were released) from marine and freshwater environments by ocean entry year (OEY) and age at recovery. The estimated number of coded wire tag recoveries were obtained from the Regional Mark Information System database (Regional Mark Processing Center, 2022). The values are shown as percentages here but were analyzed as proportional data. Dietary treatments are as follows: 4 d/week and 12% dietary lipid content (4d-12%), 4 d/week and 18% dietary lipid content (4d-18%), 7 d/week and 12% dietary lipid content (7d-12%), and 7 d/week and 18% dietary content (7d-18%).

		Age						Environment	
OEY	**Dietary treatment**	**2**	**3**	**4**	**5**	**6**	**All**	**Marine**	**Columbia River**
2012	4d-12%	0.0000	0.0002	0.0056	0.0042	0.0003	0.0103	0.0036	0.0067
	4d-18%	0.0002	0.0013	0.0054	0.0038	0.0005	0.0113	0.0040	0.0073
	7d-12%	0.0002	0.0005	0.0058	0.0034	0.0003	0.0103	0.0030	0.0073
	7d-18%	0.0024	0.0010	0.0060	0.0026	0.0001	0.0121	0.0033	0.0088
	2012 means	0.0007	0.0007	0.0057	0.0035	0.0003	0.0110	0.0034	0.0075
2013	4d-12%	0.0000	0.0001	0.0023	0.0028	0.0003	0.0055	0.0017	0.0038
	4d-18%	0.0001	0.0002	0.0034	0.0023	0.0001	0.0062	0.0024	0.0037
	7d-12%	0.0002	0.0004	0.0026	0.0018	0.0001	0.0051	0.0021	0.0030
	7d-18%	0.0015	0.0011	0.0028	0.0018	0.0001	0.0072	0.0020	0.0053
	2013 means	0.0005	0.0005	0.0028	0.0022	0.0001	0.0060	0.0020	0.0039
2014	4d-12%	0.0000	0.0000	0.0013	0.0014	0.0000	0.0027	0.0009	0.0018
	4d-18%	0.0000	0.0003	0.0000	0.0002	0.0000	0.0005	0.0003	0.0003
	7d-12%	0.0001	0.0002	0.0019	0.0010	0.0000	0.0032	0.0012	0.0021
	7d-18%	0.0012	0.0002	0.0016	0.0012	0.0000	0.0042	0.0010	0.0032
	2014 means	0.0003	0.0002	0.0012	0.0009	0.0000	0.0027	0.0008	0.0018
2015	4d-12%	0.0000	0.0004	0.0012	0.0006	0.0000	0.0022	0.0006	0.0017
	4d-18%	0.0000	0.0000	0.0007	0.0005	0.0000	0.0013	0.0005	0.0007
	7d-12%	0.0000	0.0003	0.0005	0.0005	0.0000	0.0013	0.0003	0.0009
	7d-18%	0.0000	0.0000	0.0002	0.0002	0.0000	0.0004	0.0000	0.0003
	2015 means	0.0000	0.0002	0.0007	0.0004	0.0000	0.0013	0.0004	0.0009

marine or freshwater fisheries, plus those returning to spawning grounds or hatcheries (Independent Scientific Advisory Board, 2025). But, our presentation of CWT recovery rate is also not typical of SAS reporting, as we split the recoveries by age-at-return designations (ages 2–3 and ages 4–6) instead of lumping all of the age-classes together to distinguish the age-classes that are considered to be precocial maturation (ages 2–3) from the other adult age-classes (4–6).

Specifically, the CWT recovery rate for ages 2–3 for each release group was calculated by dividing the sum of estimated CWTs recovered at ages 2–3 by the number of released CWT fish, and the CWT recovery rate for ages 4–6 for each release group was calculated by dividing the sum of estimated CWTs recovered at ages 4–6 by the number of released CWT fish. Tag recoveries in the RMIS database are expanded based on the proportion of the catch that is sampled in fisheries data or other data expansions that are done by the reporting agency. We used the estimated CWT estimate as is from RMIS. This may underestimate the absolute magnitude of survival to adulthood for each release group but should provide robust estimates for the purpose of comparing the dietary treatments within each year of the study.

Comments on data

We note that we are reporting on recovery age, not age at maturation. Fish that are recovered in marine fisheries may either be immature (mature in some subsequent year) or maturing (returning to freshwater to spawn that year). Fish that are recovered in freshwater are assumed to be maturing in that given recovery year. Our analysis compares recovery age between treatments; therefore, we infer differences in age of maturation for fish between treatments but we do not report on actual age at maturation.

It should also be noted that in the present investigation, minijacks were enumerated after smolt release using CWT recovery data, but these estimates are not equivalent to those reported in the first phase of this investigation (Harstad et al., 2023) prior to smolt release. Comparing and contrasting minijack prevalence under these two different measures is of interest for understanding whether or how the different methods of quantifying minijacks might be related.

Data analysis

All of the figures and statistical analyses were completed using a combination of STATA/IC version 15.1 (StataCorp LLC) and GraphPad Prism version 10 (GraphPad Software). Statistical significance was set at $\alpha = 0.05$. The levels of factor variables within the statistical models were compared using the posttest commands "test" and "lincom" in STATA.

Juvenile out-migration

The estimates for travel time from release at Pendleton Acclimation Facility to John Day Dam were analyzed using linear regression models. The dietary treatment and OEY effects were assessed using a two-way ANOVA model including both as predictor variables. Fish size at the time that the fish were moved from the hatchery to the acclimation site (i.e., February fork length [FL]) from Harstad et al. (2023) was assessed as a covariate in an additional ANCOVA model including OEY or alone in a simple linear regression model for travel time.

Juvenile survival during out-migration was assessed using Cormack–Jolly–Seber estimates that were generated in the Columbia River DART website (Columbia Basin Research, 2022). These estimates were then analyzed using fractional logistic regression models ("fracreg" command in STATA, using a logit link function), as these estimates are proportional data (outcome values are bounded by 0, 1). The factor variables, dietary treatment, and OEY were assessed as predictor variables, with the continuous variable February FL (note that to avoid collinearity, dietary treatment and February FL were never included as predictor variables in the same models).

Coded wire tag recovery rate

We used fractional logistic regression models to assess several variables that could affect the recovery rate of adults that were assessed via CWTs. These variables included the four dietary treatments, OEY, February FL, minijacks produced during hatchery rearing, travel time and apparent survival to John Day Dam, and ocean conditions at the time that out-migrating juveniles reached the marine environment. Note that we analyzed CWT recovery rate as a proportion but present the results as a percentage in the figures for ease of interpretation.

To assess ocean entry conditions, we used the rank data that are compiled annually (since 1998) by the National Marine Fisheries Service based on several climate, physical, and biological indicators that could affect the survival of juvenile salmon in the northern California Current (see National Marine Fisheries Service, 2022 for details). Each category is ranked from lowest to highest relative to other years (years reported herein, 1998–2021). A mean rank of indicators is calculated to give an overall trend assignment, with lower ranks reflecting "good" conditions and higher ranks reflecting "poor" conditions.

Age at recovery

To further examine the effect of dietary treatment on the CWT recovery profiles of specific age-class (ages 2, 3, 4, 5, and 6 binned separately), we used generalized ordered logit regression ("gologit2" command in STATA) because age-class is an ordered categorical variable. Age of the fish at the time of CWT recovery was analyzed by location (marine environment, in the Columbia River, and all recoveries combined). Linear regression models were then used to calculate the mean age at recovery for each dietary treatment across the marine environment, Columbia River, and all recoveries combined.

Outlier analyses

Because we suspected that the CWT recovery rate for ages 4–6 that were fed with the 4d-18% treatment in OEY 2014 was uncharacteristically low, we tested each OEY separately for outliers using the Grubb's test and also looked at the distance that each treatment data point was from the mean for each OEY (see Supplementary Figure 1, panels A and B [see online Supplementary Material]; Supplementary Table 1 [see online Supplementary Material]). Because the 4d-18% data point for within OEY 2014 was determined to be a statistical outlier, we omitted this data point from the statistical analyses involving all CWT recovery rates reported herein. This same data point (4d-18%, OEY 2014) was also uncharacteristically low for the prevalence of minijacks, assessed prior to smolt release (Supplementary Figure 1, panel C). We used the linear regression model (minijack prevalence = February FL + dietary lipid + OEY; $N = 15$, omitting the suspected outlier, 4d-18%) to examine the relationship between minijack prevalence and size for the dietary lipid treatments separately, as lipid has an effect on this relationship (Supplementary Table 1; no interaction was observed between size and lipid treatment). The differences between the predicted and observed values (shown in Supplementary Figure 1, panel D; Supplementary Table 1) were then analyzed using the Grubb's test and confirmed that the 4d-18% data point for minijack prevalence was a statistical outlier (Supplementary Table 1). Therefore, we also omitted this data point from any of the analyses that involved values for the prevalence of minijacks prior to smolt release.

Results

Juvenile out-migration

Travel time

The dietary treatments did affect the downstream travel time of the out-migrating juveniles for the 208-km travel from Pendleton Acclimation Facility to John Day Dam. On average, the fish that were fed with the standard diet (7d-18%) and the 7d-12% diet traveled to John Day Dam in fewer days (45.2 and 47.6 d, respectively) than did those that were fed with the 4d-18% diet (60.1 d) and the 4d-12% diet (68.2 d; Figure 2A; Supplementary Table 2). There was some variation in mean travel time depending on OEY, with OEY 2013 requiring the most days to arrive at John Day Dam (Figure 2B). Overall, mean fish size prior to hatchery release (February FL) was inversely correlated with travel time ($t = -7.48$, $P < 0.001$; Figure 2C; Supplementary Table 2).

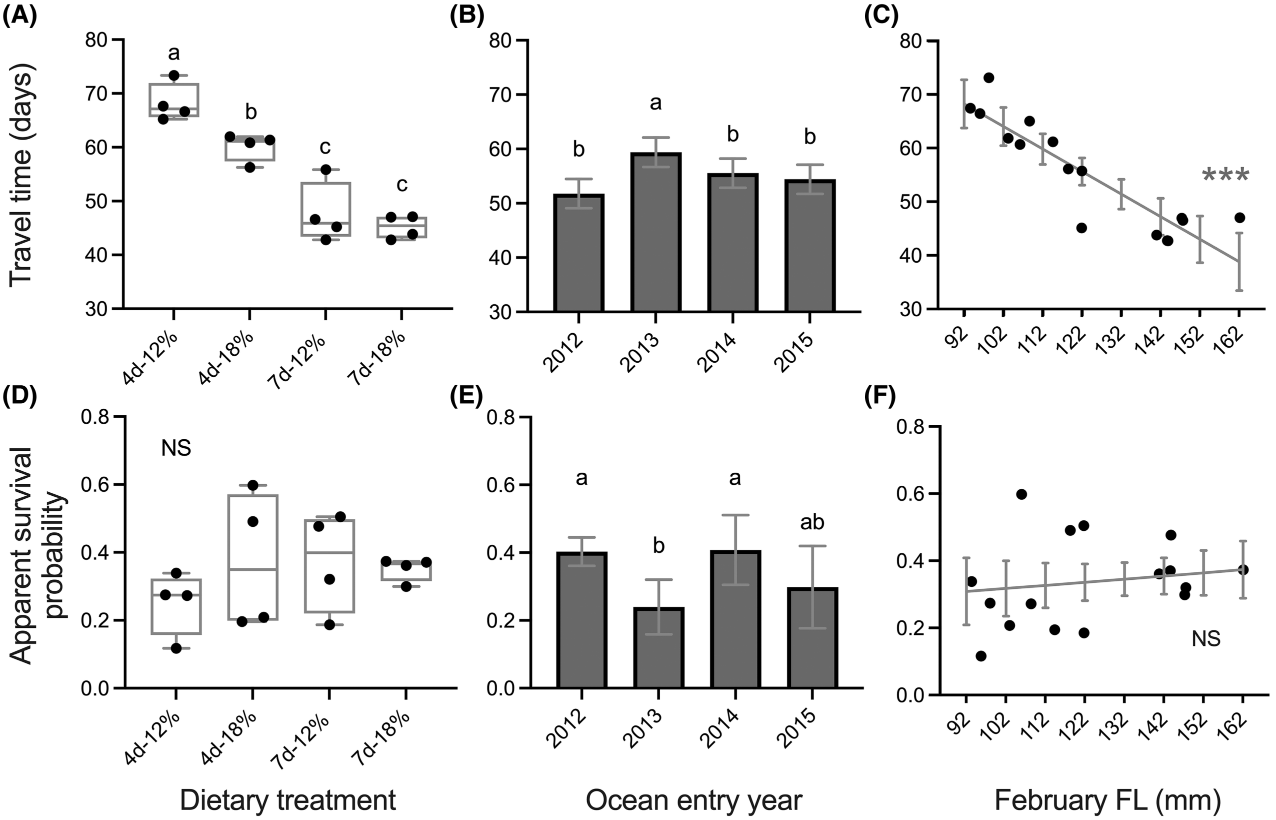

Figure 2 Juvenile out-migration metrics (i.e., travel time [*d*] and apparent survival [Cormack–Jolly–Seber estimates]) to John Day Dam between (A, D) dietary treatments (4 d/week and 12% dietary lipid content [4d-12%], 4 d/week and 18% dietary lipid content [4d-18%], 7 d/week and 12% dietary lipid content [7d-12%], and 7 d/week and 18% dietary content [7d-18%]) and (B, E) ocean entry years and their relationship with (C, F) February fork length (FL) for each dietary treatment/ocean entry year combination just prior to moving the fish to the Pendleton Acclimation Facility. The different lowercase letters represent significant differences following the analyses (see Supplementary Table 2 for more details). Model 1 corresponds with panels A and B, Model 3 corresponds with panel C, Model 4 corresponds with panels D and E, and Model 5 corresponds with panel F ($N = 16$ in all of the analyses). Panels A and D are min/max box plots and mean values for each year, panels B and E show mean values and 95% CIs, and panels C and F show the predicted margins and 95% CIs with mean values for each dietary treatment each year (***$P < 0.001$; NS = no statistical difference).

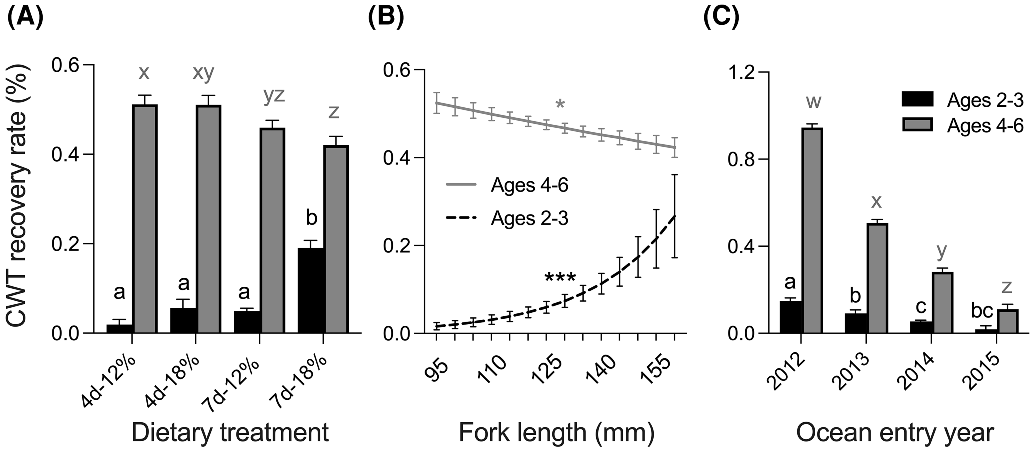

Figure 3 Coded wire tag (CWT) recovery rates by (A) dietary treatment (4 d/week and 12% dietary lipid content [4d-12%], 4 d/week and 18% dietary lipid content [4d-18%], 7 d/week and 12% dietary lipid content [7d-12%], and 7 d/week and 18% dietary content [7d-18%]) and their relationship with (B) February fork length and (C) CWT recovery rates by ocean entry year (OEY), for ages-2–3 and ages-4–6 Chinook Salmon. The different lowercase letters represent significant differences following the analyses (see Supplementary Table 3 for more details). The lowercase black letters compare ages-2–3 CWT recoveries, and the gray letters compare ages-4–6 CWT recoveries. Panels A and C were generated from fractional logistic regression models including TREAT (treatment) and OEY as predictive variables. Panel B was generated from fractional logistic regression models including February fork length and OEY as predictive variables ($N = 15$ in all analyses because the 4d-18% treatment from OEY 2014 was omitted). The error bars indicate standard error of the mean (*$P < 0.05$; ***$P < 0.001$).

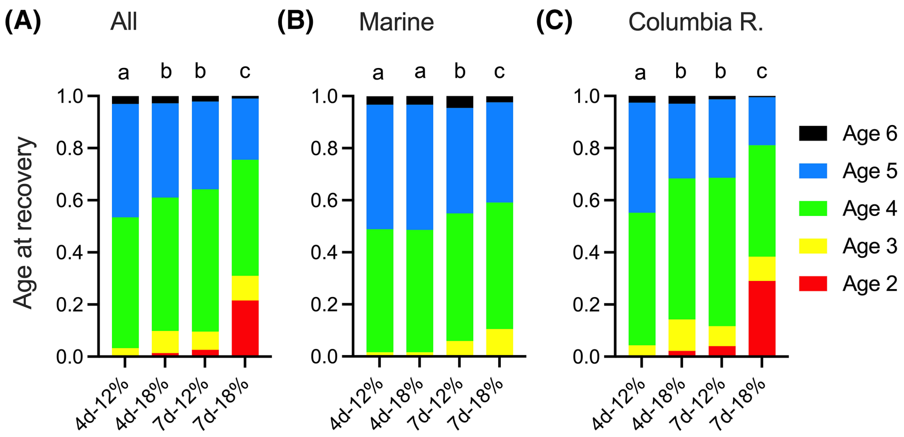

Figure 4 Mean age-at-recovery profiles for each dietary treatment (4 d/week and 12% dietary lipid content [4d-12%], 4 d/week and 18% dietary lipid content [4d-18%], 7 d/week and 12% dietary lipid content [7d-12%], and 7 d/week and 18% dietary content [7d-18%]) from recovered coded wire tags: (A) all recoveries combined ($N = 4{,}918$), including (B) the marine environment ($N = 1{,}512$) and (C) the Columbia River ($N = 3{,}407$), across the 4 years of this study. The different lowercase letters represent significant differences between dietary treatments from the generalized ordered logit regression models (see Supplementary Table 4). Data for the 4d-18% treatment from ocean entry year 2014 were omitted.

Table 3 Mean age at recovery for each dietary treatment (TREAT; 4 d/week and 12% dietary lipid content [4d-12%], 4 d/week and 18% dietary lipid content [4d-18%], 7 d/week and 12% dietary lipid content [7d-12%], and 7 d/week and 18% dietary content [7d-18%]) across all ocean entry years (OEYs; 2012–2015) for each recovery location—all recoveries (marine and Columbia River combined), the marine environment, and the Columbia River. Mean age at recovery was the predicted margin for each treatment from the linear regression: Recovery age = TREAT + OEY (see Supplementary Table 5 for details of statistical models). The different letters within each column represent significant differences between dietary treatments.

Dietary treatment	All recoveries	Marine	Columbia River
4d-12%	4.46 z	4.53 z	4.43 z
4d-18%	4.31 y	4.53 z	4.18 y
7d-12%	4.26 y	4.44 z	4.17 y
7d-18%	3.72 x	4.33 y	3.51 x

Apparent survival

The dietary treatments showed no consistent statistically significant effect on the average apparent survival of juveniles to John Day Dam (Figure 2D). There were year differences in apparent survival probability (Figure 2E; Supplementary Table 2), with lower survival estimates in OEY 2013 than in OEYs 2012 and 2014 (0.240 vs. 0.403 and 0.408, respectively). Finally, the mean February FL of the dietary treatment groups prior to release had no significant influence on the apparent probability of survival to John Day Dam (Figure 2F; Supplementary Table 2).

Adult (CWT) recovery

Coded wire tag recovery rate

The dietary treatments and February FL had significant but opposite effects on the CWT recoveries for ages 2–3 and ages 4–6. The CWT recoveries for ages 2–3 were greatest for the standard (7d-18%) fish relative to all of the other treatments (Figure 3A; Supplementary Table 3), and we observed a positive relationship between mean February FL and the CWT recovery rate for ages 2–3 across treatments (Figure 3B; Supplementary Table 3). For ages 4–6, the highest estimates of recoveries were for the smaller treatment groups (4d-12% and 4d-18%; Figure 3A; Supplementary Table 3) and a negative relationship was found between February FL and CWT recovery rate for ages 4–6 (Figure 3B; Supplementary Table 3). Ocean entry year was also a significant predictor of CWT recovery rate for all ages (Figure 3C; Supplementary Table 3); CWT recovery rates were highest for OEY 2012 and decreased each subsequent year of this study.

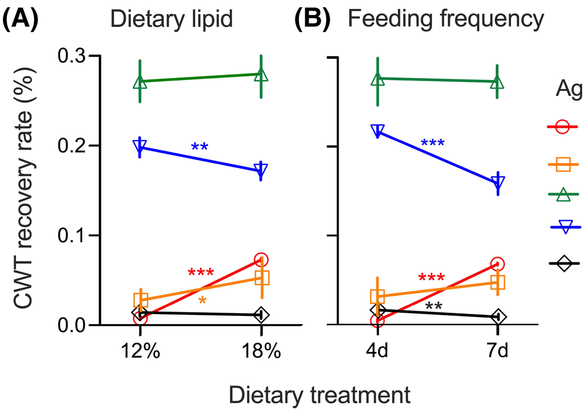

Figure 5 Estimated marginal mean coded wire tag (CWT) recovery rates (%) for each age at recovery. Panel A compares the effects of dietary lipid and panel B compares the effects of days that the fish were fed each week. The error bars represent 95% CIs (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; see Supplementary Table 6 for statistical details).

Age at recovery

We observed significant differences in the age-at-recovery demographics across dietary treatments based on CWTs

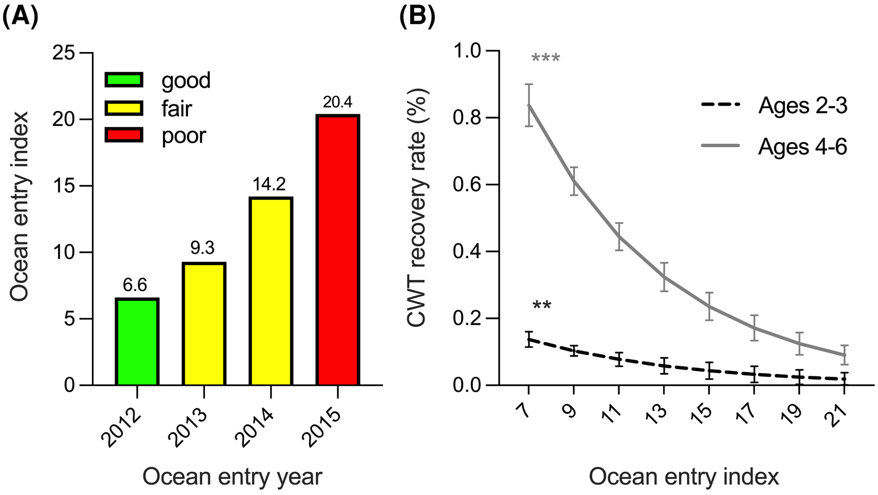

Figure 6 (A) Ocean entry condition for the 4 years of this study and (B) its predicted relationship with ages 2–3 and ages 4–6 coded wire tag (CWT) recovery estimates. The ocean entry condition index values and condition categories (good, fair, poor) were obtained in March 2022 (compiled rankings of years 1998–2021) from the National Marine Fisheries Service (2022). The model predictions for panel B are from the fractional logistic regression models that are shown in Supplementary Table 7. The error bars represent the 95% CIs (**$P < 0.01$; ***$P < 0.001$).

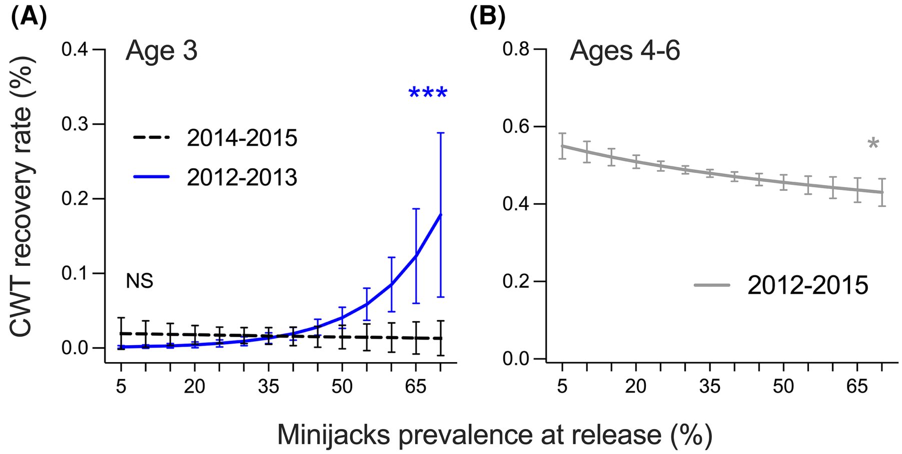

Figure 7 Relationship between minijack prevalence among males (%) during hatchery rearing and (A) age-3 and (B) ages-4–6 coded wire tag (CWT) recovery rates. The error bars are 95% CIs. Ocean entry years (OEYs) 2012–2013 were analyzed separately from OEYs 2014–2015 for age-3 CWT recoveries because the relationship changed in later years (*$P < 0.05$, ***$P < 0.001$; see Supplementary Table 8 for statistical summaries).

(Figure 4; Supplementary Table 4). Overall, the 4d-12% treatment had the highest estimated mean age at recovery (4.46 years) and the 7d-18% treatment had the lowest estimated mean age at recovery (3.72 years; Figure 4A; Table 3). The 7d-18% treatment had the highest recovery rate for age-2 fish (21.5% vs. 0.1–2.7%) and the lowest recovery rate for age-5 fish (23.5% vs. 33.6–43.4%; Figure 4A). Overall, age 4 was the most frequently observed age-class, followed by age 5 (44.4–55.4% vs. 23.5–43.5%; Figure 4A–C).

Differences in age at recovery were found depending on where the fish were recovered. The fish that were recovered in the marine environment (harvest) had a mean age of 4.40 years versus 3.91 years for those that were recovered from the freshwater environment (combination of harvest, broodstock, and any natural spawners). Age-2 fish were not observed in the CWTs that were recovered from the marine environment, and age-3 fish were recovered at lower rates in marine environments than in freshwater (Figure 4B and C; Table 3).

Feeding frequency and dietary lipid effect on age at recovery

Both dietary lipid and feeding frequency had an effect on age at recovery (Figure 5A and B; Supplementary Table 6). Both the standard dietary lipid level (18%) and standard feed frequency (7 d) increased the frequency of age-2 fish and decreased the frequency of age-5 fish. The standard lipid treatment also increased the frequency of age-3 fish. Finally, reducing feeding frequency to 4 d increased the recovery of age-6 fish.

Ocean entry condition effect

The ocean entry conditions varied across the 4 years of this study (Figure 6), with "good" ocean entry conditions in OEY 2012, "fair" ocean entry conditions in OEYs 2013 and 2014,

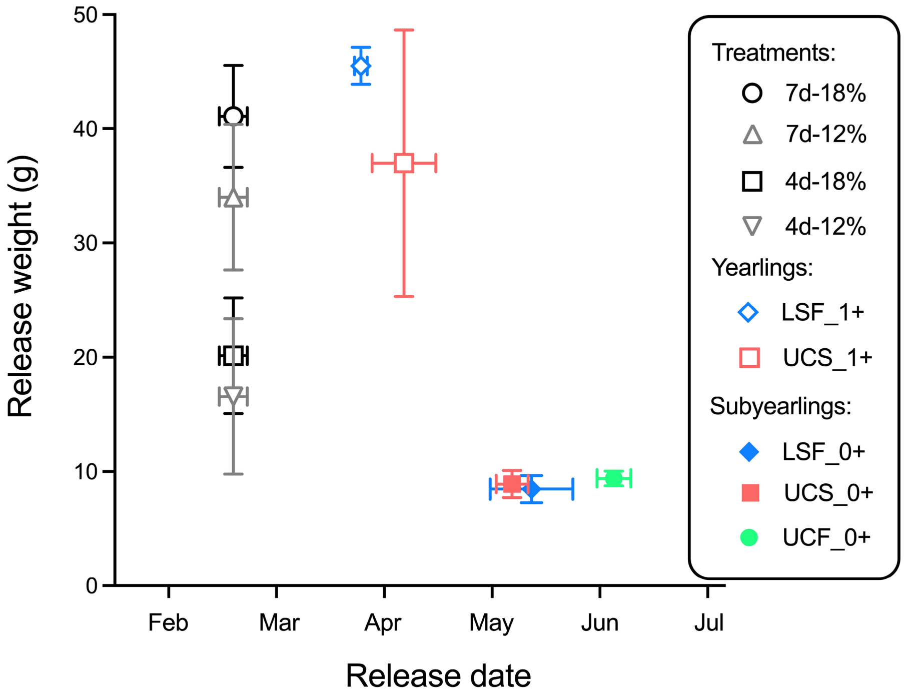

Figure 8 Size at release (g) by hatchery release timing for this experiment in contrast to other summer- and fall-run Chinook Salmon hatchery populations in the upper Columbia and lower Snake rivers. The error bars represent 1 SD. The release dates and size-at-release data were obtained from the Regional Mark Information System database (Regional Mark Processing Center, 2022) for all groups for the ocean entry year 2012–2015 releases. Dietary treatments are as follows: 4 d/week and 12% dietary lipid content (4d-12%), 4 d/week and 18% dietary lipid content (4d-18%), 7 d/week and 12% dietary lipid content (7d-12%), and 7 d/week and 18% dietary content (7d-18%). Abbreviations are as follows: UCS = upper Columbia summer Chinook Salmon; UCF = upper Columbia fall Chinook Salmon; LSF = lower Snake fall Chinook Salmon.

and "poor" ocean entry conditions in OEY 2015. These ocean entry conditions were highly predictive of the CWT recovery rates for both ages-2–3 and ages-4–6 fish (Figure 6; Supplementary Table 7). The CWT recovery rates decreased with poorer ocean entry index values for both age-classes.

Effect of hatchery minijack prevalence

For age-3 recoveries, there was a positive relationship with minijack prevalence in the first 2 years of the study, during which ocean entry conditions were better and there were higher CWT recovery rates. In OEYs 2014–2015, this relationship was no longer significant (Figure 7A; Supplementary Table 8) when recovery rates were very low overall. For recoveries of ages 4–6, we observed an overall negative trend between minijacks produced and CWT recoveries across years (Figure 7B; Supplementary Table 8). It should be noted that minijack recovery is not equivalent to minijack production in the hatchery (Supplementary Figure 2).

Discussion

This investigation clearly demonstrates that early hatchery rearing has profound effects on both total recovery and age at recovery in fall Chinook Salmon. The first phase of this study, reported in Harstad et al. (2023), was designed to assess the effects of varying dietary treatments during hatchery rearing on the prevalence of minijacks in yearling fall Chinook Salmon. That study found significant minijack prevalence in all of the treatment groups across the 4 years of the study (up to 60% of males in some groups), but fewer minijacks were observed when feeding frequency and/or dietary lipid content were reduced. The current investigation focused on the abundance and age of adult fish that either recovered in fisheries or returned to hatcheries or natural spawning areas from the dietary treatments reported in Harstad et al. (2023). Our most surprising result, reported herein, was that a similar number of older/larger fish (i.e., ages 4–6) was recovered across all of the dietary treatment groups, with slightly higher recoveries observed for the reduced dietary treatment groups and the highest recoveries for the "most extreme" 4d-12% treatment. These findings call into question a singular focus on survival to adulthood across all age-classes combined (i.e., SAS) for the assessment of hatchery-rearing programs and suggest that hatchery production strategies that focus on producing larger smolts might benefit by reducing their size-at-release targets. Our results suggest that hatchery-rearing regimes can be specifically designed to increase the age of returning adult Chinook Salmon. More broadly, this study reveals a series of interactions among dietary treatment, recovery rate, age at recovery, and ocean entry conditions that defy simple conclusions and deserve further exploration and discussion.

Recoveries, survival, and age structure

A simple change in perspective produced perhaps the most profound insight from this study. Examining the total recovery of all fish of all ages combined (i.e., SAS) does not lead to the same conclusions as focusing on the recovery of older and larger fish (ages 4–6). Based on this perspective, we found that significantly more older/larger fish were recovered from the reduced feeding frequency and dietary lipid (4d-12%)

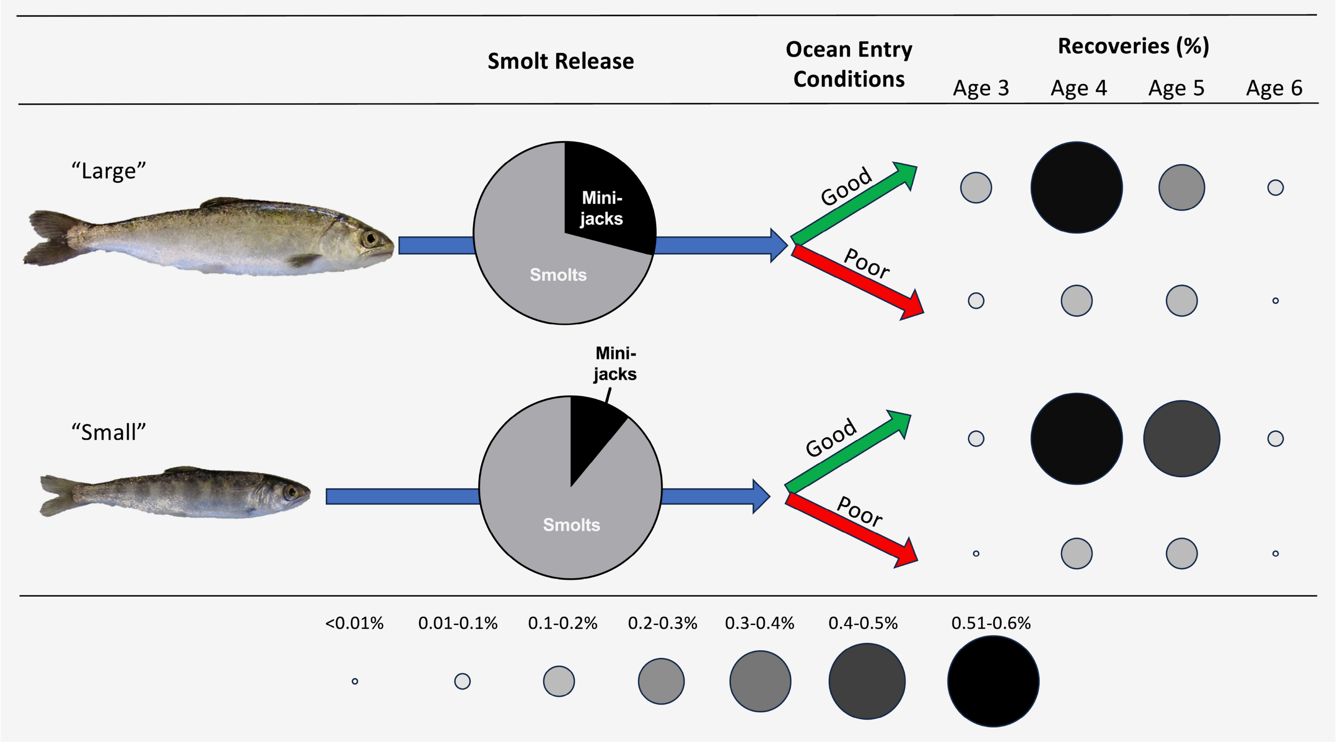

Figure 9 Examples of minijack prevalence (percentage of all fish that were released as smolts, including females) during juvenile rearing and resulting coded wire tag recoveries by adult age for two of the release years (ocean entry year [OEY] 2012 = good year; OEY 2014 = poor year) and two of the dietary treatments ("Large" = standard 7 d/week and 18% dietary treatment; "Small" = 4 d/week and 12% dietary treatment) under differing ocean entry conditions. The green arrows represent a good OEY, and red arrows represent a poor OEY.

treatment than from the standard feeding frequency and dietary lipid (7d-18%) treatment over the four rearing cohorts. Conversely, significantly more younger/smaller (ages 2–3) fish were recovered from the standard 7d-18% treatment. Intermediate results were found from the intermediate dietary treatments. Perhaps counterintuitively, more high-value (i.e., older/larger) fish were recovered from the groups of the smallest fish that were released. From the perspective of potential value to the fishery and broodstock collection efforts, smolts from the standard dietary treatment were not of optimal size, as they tended to return at a higher frequency as younger/smaller adults. Furthermore, the age distribution within the ages 4–6 recovery group was not even; the smallest smolts produced a higher proportion of age-5 and age-6 adults (except for OEY 2014, which was nearly equivalent across all treatments except for the outlier, 4d-18%) than the larger standard dietary treatment. Therefore, there were differences within the older/larger recovery group (ages 4–6) in the distributions of fish ages and sizes between dietary treatments.

Relationships between survival and adult abundance may appear to be relatively straightforward. However, for salmon species with more complex life histories, like Chinook Salmon, one must consider age of maturation within the context of adult abundance. A minijack (age-2 male) is technically an adult but too small to merit harvest, and its value for adult spawning is equivocal. Consequently, we chose to discriminate recoveries by age and then bin the fish into two groups: "younger/smaller" (ages-2–3 fish; primarily males) and "older/larger" (ages-4–6 fish; males and females). Historically, this distinction of returns by age has not been common in the literature, in part because the variation in age of maturity is greater in Chinook Salmon (ranging from age 1 to 7) than in many other salmon species. This discrimination of recoveries by age is based on the premise that Chinook Salmon of different ages have different inherent biological and management values. It also reflects that age of maturation is plastic and that varying hatchery practices may alter the proportion of recovered fish in these different age-classes.

Tags and inferences regarding sex

Sex is not routinely assessed when fish that are tagged with CWTs are inspected in fisheries, and similarly, the passive detection of PIT tags does not provide any data on the sex of returning adults. Therefore, we have limited understanding of if (and how) age at recovery varies between males and females in this study. However, we are relatively certain that all of the recovered age-2 fish were minijacks and almost all of the age-3 fish were jacks (males as opposed to age-3 females [i.e., jills]; see Supplementary Figure 3). Given our limited information on male and female occurrence by age, we have little ability to generate inferences about the effects of juvenile rearing on adult sex ratios or the fecundity of returning females. However, we do know that juvenile rearing has a profound effect on the prevalence of age-2 maturing males, suggesting that there must be an effect on the occurrence of older maturing males based on the simple fact that if a male matures at age 2, it is lost from the pool of fish that might mature at an older age. Additional insights could be attained by examining the effects of varied juvenile rearing on the size and age of female fish, as shown in Malick et al. (2023).

Implications for the timing and physiology of maturation

More broadly, our results demonstrate that there is a strong environmental component to determining age of maturation in Chinook Salmon. Variation in life history traits, such as age at maturation, are commonly ascribed to genetic by environmental interactions (Roff, 1996; Stearns, 1992). Historically, the genetic component of this process has been a common research focus (Barson et al., 2015; Carlson & Seamons, 2008; Gjerde, 1984; Hankin et al., 1993; Lepais et al., 2017; McKinney et al., 2021; Sinclair-Waters et al., 2020). Our results directly suggest that environmental factors during juvenile rearing may affect the subsequent maturation schedule of hatchery-reared Chinook Salmon adults 1 to 5 years after hatchery release independently of broadscale genetic differences. This result is similar to other recent reports that suggest that variation in age at maturation of hatchery and naturally reared fish from genetically similar populations is due to differences in their juvenile rearing environments (Carvalho et al., 2023; Chen et al., 2023) and variation of growth/fish size within the rearing environment (Bosch et al., 2023). Given that we did not conduct any genetic analysis, we are limited in our ability to thoroughly explore this genetic by environmental interaction. In addition, we recognize that we assessed age at recovery and not age at maturation due to our inclusion of potentially immature fish that were harvested in the ocean within our analysis of recoveries. Nonetheless, age at recovery is a conservative estimate of age at maturation and this estimate varied significantly among treatments. A large step forward in managing Chinook Salmon production hatcheries could be achieved by fully exploring the environmental drivers of age at maturation and then designing rearing strategies that optimize age at maturation to provide fish to fisheries, spawning grounds, and hatchery broodstock collection efforts.

Much of the current literature on genetic by environmental interactions and the initiation of maturation focuses on the "trigger" for maturation in the fall, a full year prior to spawning (Larsen et al., 2006; Rowe et al., 1991; Shearer & Swanson, 2000; Silverstein et al., 1998; Thorpe et al., 1998). These studies demonstrate that some combination of larger body size, growth rate, and body adiposity in the autumn triggers maturation in the following year as compared with smaller, slower growing, and lower adiposity fish (Shearer & Swanson, 2000; Silverstein et al., 1998). Our results suggest that these same physiological factors have effects that last well beyond the initiation of maturation in the following year and that these factors seem to influence the tendency of a fish to mature 1–5 years later. The physiological mechanisms that are responsible for these potential long-term effects on age at maturation are unclear and beyond the scope of the current investigation, but they deserve further research.

Is juvenile out-migration predictive of adult recovery?

In this investigation, our observation and assessment of smolt migration rate and postrelease riverine survival provided little insight into subsequent adult recoveries (see Supplementary Figure 4). Our results documented differences in migration time and found that faster migration did not predict greater recoveries of ages 4–6 fish, nor was there any relationship with downstream smolt survival and ages 4–6 recoveries. This is a bit disquieting because decisions on hatchery practices are sometimes made based on differences in smolt travel time and river survival due, in part, to the protracted time frame (years) that is required for adult recoveries to be realized. Fisheries managers should exercise caution when evaluating and implementing changes to juvenile rearing programs in the absence of adult recovery information.

Implications of smolt size on survival to adulthood

Current hatchery practices are highly influenced by a series of studies in the 1980s that suggested that large smolts returned as adults in higher proportions than smaller smolts (Bilton, 1984; Bilton et al., 1982; Fagerlund et al., 1989; Martin & Wertheimer, 1989). Similarly, Tipping (2011) demonstrated that larger smolts survived better than smaller smolts across several different hatchery programs. Nelson et al. (2019) described how hatchery release size increased with time through the 1980s to the 2010s for hatchery Chinook Salmon that inhabited Puget Sound, presumably in response to these studies.

In a current review of Canadian Chinook Salmon hatchery releases, James et al. (2023) found that larger smolts at release had higher juvenile-to-adult survival rates than smaller smolts. But this size advantage only lasted up to a release size range of 14–18 g for yearling Chinook Salmon. James et al. (2023) suggest that there may be a threshold above which additional increases in size no longer improve smolt survival. For context, this suggested optimal size range (14–18 g) is much smaller than the average release size of yearling Chinook Salmon smolts in the upper Columbia and Snake River basins (ranging from ~25 to 48 g; see Figure 8); however, optimal release size may vary geographically. Other recent studies have suggested that increased smolt size may not always confer higher survival (Beckman et al., 1999, 2017; Bosch et al., 2023; Feldhaus et al., 2016; Gallinat et al., 2023; Harstad et al., 2018). Finally, a recent study of wild Chinook Salmon from the Snake River basin (Bond et al., 2024) found a positive relationship between smolt size and marine survival only up to a size of ~12 g (FL data reported by Bond et al., 2024 was converted here to grams for comparison using the length–weight relationship established in Harstad et al., 2023), above which the relationship was equivocal. Our results further reinforce these recent studies that question whether larger smolts always survive at a higher rate than smaller smolts.

Context on smolt size

Differences among studies that have examined variation in smolt size and survival may arise from a lack of precision in the definitions of differences in size. As currently applied, the attributes of "large" and "small" are qualitative and contextual. Within a specific experiment, the terms are useful to distinguish treatments, but they do not provide direct information about actual size and how actual size relates to other data in the literature or the size of naturally produced smolts. For example, within the current experiment, the smolts that were produced might be considered comparatively small (16.6 g, 4d-12% treatment) or large (41.1 g, 7d-18% treatment; Figure 8). In reality, none of the treatment groups produced fish that were particularly small when compared with other summer/fall Chinook Salmon hatchery smolts in the interior Columbia River basin (Figure 8). In addition, the large smolts in this experiment were actually "standard"—that is, they were the normal target size for this stock of fish that are reared at these facilities (Clarke et al., 2011). In contrast, naturally rearing summer/fall Chinook Salmon in either the Snake River or upper Columbia River basins often smolt and migrate to the ocean as underyearling fish, a year earlier and an order of magnitude lighter than standard hatchery fish (Connor & Tiffan, 2012). In this context, our large smolts were not large in comparison to average hatchery yearling smolts and our small fish were quite large in comparison to naturally produced fish. In fact, our small fish were larger than hatchery releases of subyearling Chinook Salmon in the region (Figure 8). This example demonstrates that one must consider actual size when comparing and evaluating "size-at-release" studies and place smolt size within a larger geographic and biological framework, including the size of naturally produced fish rather than simply comparing the relative attributes of isolated experimental groups.

Ocean conditions and adult demography

This investigation clearly demonstrated that variation in the marine environment had a larger effect on adult recovery than did variation in the smolt-rearing strategy. Ages 4–6 CWT recoveries across rearing cohorts varied by 8.6-fold across the 4 years of our study but varied by only 1.2-fold across the four dietary treatments. Certainly, it is not novel to find variation in ocean survival; marine effects on salmon survival are well established (Beamish et al., 2000; Hare et al., 1999; Johnson, 1988). Of particular importance, OEY 2015 had the highest ocean entry index rating (i.e., poorest ocean conditions for salmon survival) since this ranking system began in 1998. The anomalous ocean conditions that year have been shown in subsequent research to negatively affect the prey that are consumed in coastal waters by juvenile Chinook Salmon, leading to the prediction of poor returns for this cohort (Daly et al., 2017). On average, differences in dietary treatment resulted in <18% variation in ages 4–6 CWT recoveries between the 4d-12% and 7d-18% dietary treatment groups. This fact adds support for the point that varying hatchery-rearing strategies can never fully mitigate poor ocean conditions. Interannual variation in the marine environment weakened the power of our experiment to clearly demonstrate consistent differences among the dietary treatments. In particular, as we did not have the rearing capacity to replicate treatments within years, we were unable to evaluate whether there was an interaction among dietary treatments and marine conditions across rearing cohorts. Simply, we could not demonstrate whether or how marine conditions may interact with smolt size to alter recoveries in different years. Nonetheless, it appears that ages 4–6 CWT recoveries did not vary widely across dietary treatments, even under the poor marine conditions for OEY 2015 (see Figure 9). Even in poor ocean entry conditions, the smallest smolts still had the highest ages 4–6 recoveries. Thus, despite expectations, these observations suggest that larger smolts did not have greater survival during poor ocean years over the range of smolt sizes that we produced for this study (see Figure 9).

Several recent articles have highlighted the effects of varying maturity schedules on natural marine mortality and/or marine harvest rates of Chinook Salmon and the consequences of differing maturation schedules with respect to this mortality (Carvalho et al., 2023; Chen et al., 2023; Satterthwaite, 2023). In essence, the longer that fish reside in the ocean prior to maturation, the greater the rates of either harvest and/or natural mortality. This relationship is best captured by directly quoting Carvalho et al. (2023, p. 937):

> Given the tradeoff that stems from earlier maturation, future research and management . . . should consider the implications of different mechanisms that can alter age structure of a population. Changing adult natural mortality rates will likely have minimal impacts on a population that exhibits early maturation because fish return before they are exposed to additional mortality or before most of the adult population can benefit from reduced mortality. On the other hand, if maturation rates are delayed and the population has high age structure diversity, changing natural mortality rates will have a greater impact as fish will experience the increase or decrease in mortality as they remain in the ocean.

The data that we present here add to the growing recognition of varying maturation schedules and the consequences of that variation for harvest management. Although increasing mean age at maturation can increase ocean residence time, thus increasing the total number of ocean mortalities, the net benefit is more recoveries at older age-classes. In addition, our results clearly suggest that managers may alter the length of marine residence (age of maturation) by altering early rearing in the hatchery. If or how marine environmental variation influences age of maturation in Chinook Salmon is largely unexplored, as there are relatively few research efforts comparing the physiological assessment of immature and maturing Chinook Salmon that are captured at sea. However, Siegel et al. (2017, 2018) report correlations between sea surface temperature, early marine growth, and age of maturation for two populations of western Alaska Chinook Salmon based on scale increments that were collected from maturing adults. These data reinforce our findings that varying size/growth of juvenile Chinook Salmon has subsequent effects on age of maturation regardless of whether the variation in growth occurs in freshwater or in the ocean.

Considerations for assessing Chinook Salmon hatchery-rearing strategies and goals

Reducing the incidence of early male maturation (by implementing one of the more restricted dietary regimes) among hatchery-reared Chinook Salmon appears to generate a number of positive outcomes. Fewer younger/smaller adults (ages

2–3) are produced, and more older/larger adults (ages 4–6) return. These results are not solely due to reduced numbers of age-2 males; rather, there appears to be an overall shift in the age of maturation toward older age-classes when employing more restricted dietary regimes during the hatchery phase, although this appears to be dependent on ocean conditions (Figure 9). Also, reducing smolt size could allow hatcheries to increase the number of smolts that they produce, as rearing space is often a limiting factor (Spangenberg et al., 2026).

The benefits of reduced feeding are probably not universal across hatchery programs but may be most applicable to programs that release relatively large yearling smolts. A first step toward evaluating whether a program could benefit from altering juvenile rearing might be to assess minijack prevalence at release to establish a baseline scope for change. More broadly, hatchery programs might consider a greater focus on age structure for returning adults (both age and size) and balance the potential trade-offs between both natural (i.e., predation, disease) and harvest-associated marine mortality. Managers might consider varying juvenile rearing and observing whether there is correlated variation in the age structure of returning adults and then reevaluate the program goals to incorporate the size and age of returning fish. However, evaluations must be considered within the context of varying ocean conditions and the effects of natural marine mortality with respect to years of ocean residence (Carvalho et al., 2023; Satterthwaite, 2023). Reducing marine mortality at the expense of increasing numbers of younger/smaller returning adults might be more advantageous in some situations.

Perhaps most important is developing an understanding of the effects of variation in juvenile rearing strategies on the subsequent life history trajectories of maturing fish. The effects of variation in juvenile rearing are manifested throughout the entire life history of a fish, and the subsequent variation in adult characteristics (i.e., survival; size and age at maturation) are of primary importance for many management evaluations.

Supplementary material

Supplementary material is available at *Transactions of the American Fisheries Society* online.

Data availability

Data are available from the corresponding author upon reasonable request.

Ethics statement

There were no ethical guidelines applicable to this study.

Funding

Bonneville Power Administration under project numbers 2002-031-00 and 1990-005-00, with administrative support by Brady Allen, Timmie Mandish, Deborah Docherty, and Verl Miller.

Conflicts of Interest

The authors report no conflicts of interest. Brian R. Beckman holds the position of associate editor for *Transactions of the American Fisheries Society* and has not peer reviewed or made any editorial decisions for this article.

Acknowledgments

We thank the Bonneville Hatchery staff for fish rearing; Will Cameron, Mark Suchy, and Keith Curnutt (Oregon Department of Fish and Wildlife, Umatilla Hatchery Monitoring and Evaluation) for their instrumental work of fish tagging and sampling; Ann Gannam (U.S. Fish and Wildlife Service, Abernathy Fish Technology Center) and David Brock (Rangen, Inc.) for helpful advice on choosing and manufacturing a low-lipid feed; and Joseph Feldhaus and Wayne Wilson (Oregon Department of Fish and Wildlife) for assisting with CWT database interpretation. In addition, we would like to thank the reviewers for the constructive comments that improved this manuscript.

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