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ARTICLE

The Influence of Size at Release on Performance of Imnaha River Chinook Salmon Hatchery Smolts

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Abstract

Ten brood years (BYs 1988–1990 and 1992–1998) of spring–summer Chinook Salmon *Oncorhynchus tshawytscha* smolts that were reared at Lookingglass Fish Hatchery (Oregon) and released from the Imnaha River Weir and Acclimation Facility were evaluated to determine whether size at release affected juvenile migration survival, smolt-to-adult survival (SAS) rate, smolt-to-adult return (SAR) rate, production efficiency, age composition, straying rate, or harvest rate. Smolts were marked with adipose fin clips and were tagged with coded wire tags (all BYs) and PIT tags (BYs 1992–1998). For BYs 1992–1998, the out-migration survival rate to Lower Granite Dam (LGD) on the Snake River was greater for large smolts (30–38 g) than for small smolts (18–23 g). This juvenile survival difference did not translate to an adult survival difference, as the total (ages 3–5) and adult (ages 4–5) SAR and SAS rates did not differ between large and small smolts. Straying rates were less than 0.02% and harvest rates were less than 0.05% for both treatments, and we found no significant differences between groups. Total production efficiency (number of mature salmon/10 kg of smolts released) was greater for small smolts than for large smolts but not significantly so. Small smolts produced significantly more (~10%) age-5 females than did large smolts. Treatments (smolt size at release) did not differ in sex ratio or the age composition of male returns. Because broodstock availability limited production in 5 of the 10 years, we also compared size at release within standard-density (14.8–22.2 kg/m^3) and low-density (2.2–8.6 kg/m^3) rearing years. At standard density but not at low density, juvenile survival to LGD was significantly greater for large smolts than for small smolts. Adult and total SAR and SAS rates, total production efficiency, and straying rates did not differ between standard-density and low-density rearing years. Harvest rate of the small smolts was significantly greater than that of the large smolts at low density but not at standard density. We found no performance benefit in rearing large Chinook Salmon smolts instead of small smolts.

Pacific salmon *Oncorhynchus* spp. production losses in the Columbia River basin are often attributed to a combination of overfishing, habitat loss, and operation of hydropower dams on the Columbia and Snake rivers (Lichatowich 1999). Fish hatcheries constitute the most widely recognized and controversial tool that is used to mitigate for this lost salmon production. Although there are numerous hatchery programs in the Pacific Northwest, their role in providing harvest opportunities and slowing or reversing the declines in natural salmon populations is constantly scrutinized and debated (Flagg and Nash 1999; Flagg et al. 2000; Ruckelshaus et al. 2002; Brannon et al. 2004; Chilcote et al. 2011; Trushenski et al. 2014). To be successful, hatchery programs (1) must be proactive and monitor the benefits and risks of aquaculture practices to determine juvenile rearing strategies that maximize survival rates and (2) must also cope with localized facility limitations (e.g., rearing space, water resources, broodstock availability, and operating costs), competing management objectives, and conservation concerns.

One metric that is easily manipulated in the hatchery environment is the size of salmon smolts. Although “large” and “small” are ambiguous terms, studies have shown that larger juvenile Chinook Salmon *O. tshawytscha* smolts have a greater survival rate than smaller smolts when reared in either a hatchery (Bilton 1984; Martin and Wertheimer 1989; Morley et al. 1996) or a

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natural environment (Zabel and Achord 2004; Monzyk et al. 2009). Juvenile fish size also serves as a limiting factor for hatcheries when space is limited. To raise larger smolts, hatchery managers must choose either to raise fewer smolts or to rear smolts at higher densities. However, increases in rearing density have been shown to decrease postrelease survival in salmon (Banks 1994; Ewing and Ewing 1995; Barnes et al. 2013).

Early evaluations of the Imnaha River spring–summer Chinook Salmon supplementation program, which began with brood year (BY) 1982, identified several failures in meeting program goals and revealed conflicting management objectives (Carmichael et al. 1990; Carmichael and Messmer 1995). First, the program was failing to meet the annual mitigation goal of returning 3,210 hatchery Chinook Salmon to the Lower Snake River Compensation Plan (U.S. Fish and Wildlife Service) mitigation area (i.e., the Snake River basin above Lower Granite Dam [LGD]). The program was also struggling to meet broodstock collection needs for continued hatchery supplementation. More concerning was evidence that hatchery-origin Chinook Salmon were maturing at an earlier age than natural-origin individuals, thus failing to meet a program objective that the life history characteristics of hatchery fish should mimic those of natural Chinook Salmon.

Therefore, the goal of this study was to determine whether manipulating the size of spring Chinook Salmon smolts reared at Lookingglass Fish Hatchery (LFH; Oregon Department of Fish and Wildlife [ODFW]) and released into the Imnaha River could assist the hatchery program in better meeting its various objectives. We examined 10 BYs of Imnaha River Chinook Salmon to compare the following performance metrics between large smolts (30–38 g [12–15 fish/lb]) and small smolts (18–23 g [20–25 fish/lb]): (1) juvenile survival rate to LGD, (2) juvenile travel time to LGD, (3) the smolt-to-adult return (SAR) rate, (4) harvest rate, (5) straying rate, (6) the smolt-to-adult survival (SAS) rate, (7) total production efficiency, (8) age composition, and (9) size (FL) at maturity. For each performance metric, we tested the hypothesis that there was no difference between large and small smolts. We also took advantage of an unplanned decrease in rearing density to test for performance differences between size treatments under standard rearing densities and low rearing densities.

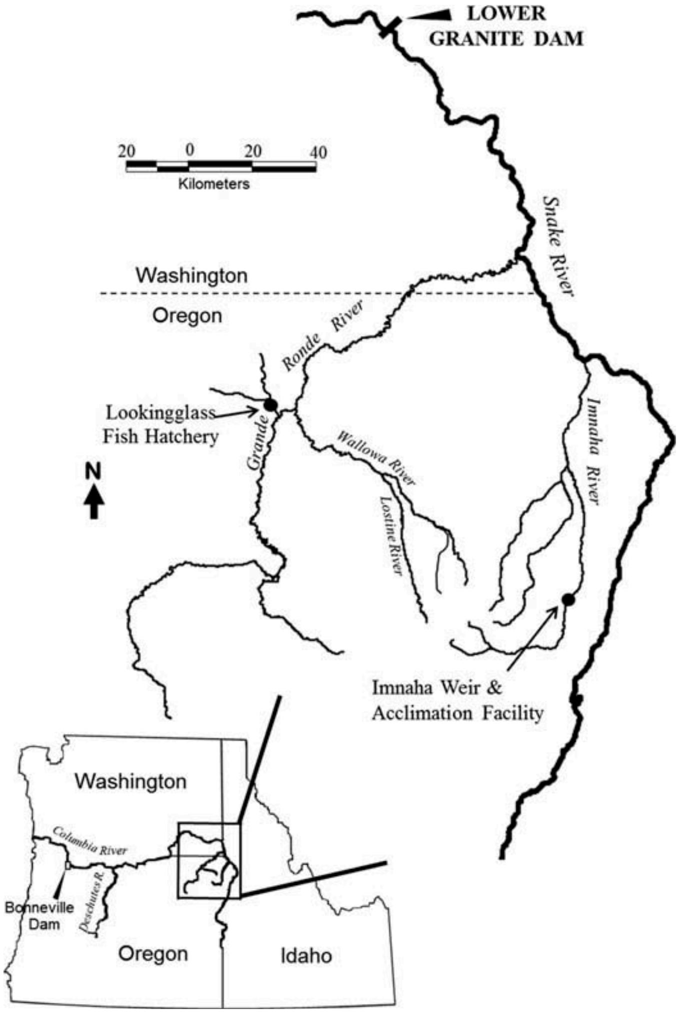

FIGURE 1. Map of the Grande Ronde and Imnaha River basins, Oregon–Washington, showing locations of the Imnaha River Weir and Acclimation Facility and the Lookingglass Fish Hatchery, where Chinook Salmon were reared.

METHODS

Fish and facilities.—The Chinook Salmon smolts used for this study were part of the Imnaha River production and were the offspring of hatchery- and natural-origin adults collected at the Imnaha River Weir and Acclimation Facility (IMNAHW), which is located at river kilometer (rkm) 85.3 on the Imnaha River (Figure 1). Adult Chinook Salmon were trapped at IMNAHW from June through early September, and some were retained for broodstock. Chinook Salmon egg incubation and juvenile rearing occurred at LFH, which is located on Lookingglass Creek, a tributary of the Grande Ronde River (rkm 138) in northeastern Oregon. Hatchery- and natural-origin Chinook Salmon were spawned together, and the eggs used to produce the smolts came from a common pool of eggs. Size differences between treatments were achieved by manipulating the incubation temperature, early rearing temperature, and feeding rates. In all other aspects, the fish were treated identically from the time of egg collection through the time of release. All eggs were incubated in well water, and the swim-up fry were placed into indoor, Canadian-style troughs. When fry reached approximately 1–2 g, they were transferred to outdoor concrete raceways (30.5 m long × 3 m wide × 1 m deep; 91.5 m^3), where they were reared for about 1 year. Yearling smolts were transported from LFH to IMNAHW on approximately March 1–15 and were held in an acclimation pond for up to 30 d before being released.

Experimental treatments were conducted with paired releases of large and small smolts from BYs 1988–1990 and 1992–1998. Both the size targets and rearing densities for large and small smolts changed over the course of this study (Table 1). For BYs

TABLE 1. Release metrics and total returns (ages 3–5) of large and small smolts from standard-density and low-density rearing years for Imnaha River hatchery Chinook Salmon, brood years (BYs) 1988–1990 and 1992–1998.

BY	Smolt size	Raceway number	Target mean weight (g)	Actual mean (SD) weight (g)	Mean rearing density (kg/m^3)	Mean (SD) FL (mm) at release	Total PIT tags	Percent with CWT	Total smolts released	Total returns (ages 3–5)
Standard-density rearing years										
1988	Large	12	38	36.5 (6.0)	22.0	141 (8.6)	NA	99.0	51,669	301
		13		35.5 (6.8)	21.7	141 (9.1)		99.0	52,013	346
	Small	14	23	25.1 (4.6)	21.7	124 (9.7)	NA	77.0	73,337	654
		15		24.4 (5.5)	21.8	124 (7.5)		74.0	76,018	652
1989	Large	16	30	29.8 (13.3)	18.1	135 (15.8)	NA	81.0	51,557	111
		17		28.0 (13.3)	18.7	132 (16.3)		72.0	56,848	137
	Small	14	23	20.5 (3.1)	19.2	121 (5.5)	NA	54.0	79,654	207
		13		20.5 (3.2)	19.2	121 (5.6)		54.0	79,611	189
1990	Large	17	38	41.4 (24.2)	21.6	148 (24.6)	NA	98.0	44,346	32
		18		40.2 (24.8)	21.4	146 (26.1)		100.0	45,256	43
	Small	15	23	21.3 (3.6)	21.8	123 (6.4)	NA	99.0	87,102	16
		16		21.6 (3.6)	21.8	123 (6.5)		99.0	85,796	17
1992	Large	14	30	29.8 (8.5)	18.3	129 (12.1)	498	95.0	52,075	18
	Small	15	18	17.6 (2.7)	17.4	112 (5.8)	497	98.0	84,013	112
		16		18.9 (3.4)	18.7	113 (6.2)	500	96.0	83,900	31
1993	Large	13	30	26.1 (4.2)	15.4	129 (5.9)	499	99.0	50,222	87
		14		25.8 (3.7)	14.8	129 (6.9)	498	97.0	48,723	177
	Small	9	18	20.4 (3.4)	18.7	120 (6.8)	499	99.0	77,952	164
		16		20.4 (3.4)	17.9	120 (6.8)	499	99.0	72,959	90
Low-density rearing years										
1994	Large	3	30	25.5 (3.7)	4.1	129 (7.5)	710	99.0	13,839	53
		4		27.9 (10.6)	4.6	130 (10.0)	716	96.0	13,890	14
	Small	6	18	23.3 (4.3)	6.3	124 (7.9)	1,061	99.0	22,915	10
		7		22.3 (5.7)	6.0	124 (8.7)	1,005	97.0	22,840	5
1995	Large	6	30	30.7 (5.1)	3.6	133 (7.0)	2,772	98.0	9,896	110
		7		32.9 (5.0)	2.6	136 (9.0)	1,773	97.0	6,613	85
	Small	3	18	22.6 (3.8)	3.4	123 (7.0)	3,446	99.0	12,834	179
		4		20.1 (2.8)	5.1	118 (6.0)	5,387	96.0	21,568	176
1996	Large	1	30	29.3 (6.1)	2.4	135 (9.3)	1,504	95.0	6,997	54
		2		30.2 (6.2)	5.0	133 (7.7)	3,012	90.0	14,022	95
		3		31.7 (4.1)	5.2	132 (7.4)	3,039	94.0	14,171	107
	Small	4	18	19.9 (2.5)	2.2	121 (5.5)	2,029	95.0	9,494	53
		5		20.0 (2.7)	4.5	120 (5.6)	3,973	95.0	19,056	289
		6		19.6 (2.7)	2.2	121 (6.2)	2,047	90.0	9,513	93
				19.9 (3.0)	4.6	118 (6.0)	4,223	94.0	19,874	204
1997	Large	10	30	28.9 (3.8)	3.8	132 (9.2)	496	89.0	13,395	277
		11		28.5 (5.4)	5.4	132 (10.5)	499	88.0	13,997	167
		13		27.8 (5.6)	5.6	133 (8.3)	499	91.0	13,442	267
		15		27.9 (8.6)	8.6	132 (9.9)	501	87.0	14,871	205
	Small	8	18	18.5 (2.6)	2.6	117 (5.7)	4,988	95.0	22,385	663
		9		18.7 (3.5)	3.5	119 (6.0)	4,988	93.0	21,787	562
1998	Large	7	30	27.0 (6.9)	6.9	129 (8.2)	2,182	96.0	18,894	488
		10		29.9 (6.5)	6.5	130 (8.7)	2,042	91.0	17,590	464
	Small	4	18	21.3 (3.4)	3.4	120 (6.7)	2,149	98.0	18,624	512
		5		21.1 (4.4)	4.4	120 (6.4)	2,164	95.0	18,618	508
		16		21.9 (3.8)	3.8	120 (7.1)	2,117	97.0	18,633	335

1988–1990, the target size for small smolts was 23 g (20 fish/lb), and the target for large smolts was either 30 g or 38 g (15 or 12 fish/lb). For BYs 1992–1998, targets were 30 g (15 fish/lb) for large smolts and 18 g (25 fish/lb) for small smolts.

Rearing raceways at LFH were designed to rear Chinook Salmon smolts to 23 g (20 fish/lb) at a density of 15–22 kg/m^3. Rearing densities were 44,000–87,000 smolts/raceway (14.8–22.2 kg/m^3) for BYs 1988–1993 and were less than 23,000 smolts/raceway (2.2–8.6 kg/m^3) for BYs 1994–1998. Therefore, both the large smolt size and the rearing densities for BYs 1988–1993 represented the normal/standard production for Chinook Salmon smolts reared at LFH. For BYs 1994–1998, smolt rearing densities decreased by about 75% due to low adult returns and the resulting reduced availability of adults that could be collected for broodstock. For clarity, we use the terms "standard density" for BYs 1988–1993 and "low density" for BYs 1994–1998.

Juvenile Chinook Salmon were routinely examined for disease by ODFW fish health specialists. A raceway was removed from these analyses if it was identified as containing smolts infected with bacterial kidney disease (BKD), which affects juvenile survival and performance and is a common illness at Pacific Northwest salmon hatcheries (Fryer and Lannan 1993; Sandell et al. 2015). Brood year 1991 was entirely excluded from this study due to high BKD mortality of those juveniles at LFH. The replicate raceway of large smolts from BY 1992 (49,682 coded-wire-tagged and adipose fin-clipped smolts) was also removed from analysis due to BKD.

In the February prior to release, a random sample of smolts from each raceway was measured to the nearest FL (mm; N = 250) and weighed (g; N = 50). We used the FL and weight data to calculate Fulton's condition factor (K; Anderson and Neumann 1996).

Smolt survival and travel time to Lower Granite Dam.—We used 12-mm, full-duplex PIT tags to estimate smolt outmigration survival to LGD for BYs 1992–1998 (BYs 1988–1990 were not PIT-tagged). Between October and February (22–156 d prior to release), a random sample of juveniles was dipnetted from each raceway, and a PIT tag was implanted into each fish. Juvenile survival from release to LGD was estimated by using the PIT tags. The number of PIT tags per raceway ranged from 496 to 5,387 (0.59% to 27.5% of the total number of fish released). The unit of study was raceway rather than individual smolt, so we did not use the FL and weight data from individually PIT-tagged smolts. Travel time (d) from IMNAHW to LGD (rkm 173) was calculated as the difference between the release date and the first detection date at LGD. The probability of smolt survival from IMNAHW to LGD was calculated by using a Cormack–Jolly–Seber multiple mark–recapture model (Cormack 1964; Jolly 1965; Seber 1965) in PitPro version 4.19 (www.cbr.washington.edu). For each release year (i.e., migration year; 1994–2000), we looked for PIT tag detections (recapture events) at LGD, Little Goose Dam (rkm 113), and Lower Monumental Dam (rkm 42) on the lower Snake River and at John Day Dam (rkm 347) and Bonneville Dam (rkm 234) on the lower Columbia River. Any PIT tags that were not detected at LGD but were detected at a downstream location were used for survival analyses but not for travel time analyses.

Total survival.—Fish from each raceway used in this study were differentially tagged with coded wire tags (CWTs) and were marked with adipose fin clips. Estimated numbers of hatchery salmon from each CWT group were summarized from the Regional Mark Information System's (RMIS) CWT recovery database (www.rmpc.org), which provides recoveries expanded for sampling rates at each recovery location. Except for CWTs that were recovered in the Imnaha River basin, we used the expanded CWT recoveries reported from the RMIS database to estimate straying and harvest rates. For Imnaha River basin CWT recoveries, we used CWTs that were recovered from weir collections and spawning ground recoveries to estimate the number of hatchery adults for each CWT group based on the total escapement and sampling rate. All CWT data were adjusted for tag loss and the coded-wire-tagged proportion of each cohort. The CWT application rate ranged from 54.0% to 99.0%. We estimated CWT loss by randomly checking 300–500 individual smolts per raceway to assess the presence–absence of a CWT; this was done approximately 8 months after CWT implantation and approximately 1–3 months prior to release. The SAR, harvest, straying, and SAS rates were calculated by using the estimated numbers of age-3, age-4, and age-5 Chinook Salmon recovered from each CWT group divided by the number of smolts released from that CWT group. The SAR rate represented the percentage of total expanded CWTs from a tagging group that returned to the mouth of the Imnaha River. Harvest rate was the percentage of the total expanded CWTs that were recovered in sport fisheries, commercial fisheries, or tribal fisheries in the ocean, Columbia River, or Snake River. No sport fisheries or tribal fisheries were open in the Imnaha River during the return years 1995–2003. We defined straying rate as the percentage of total expanded CWTs that were recovered from locations outside of the direct migration route to the Imnaha River. This is a maximum straying rate because fish sampled outside of the migratory path must be killed to recover CWTs, so the ultimate destination of those fish is unknowable. The SAS rate was calculated as the sum of the harvest, straying, and SAR rates. Total return rate was the sum of age-3–5 returns. Jacks were defined as age-3 returns; the adult return rate was the sum of age-4 and age-5 returns.

Total production efficiency.—We used total production efficiency as a metric to compare the production of returned mature Chinook Salmon between treatment groups. This metric (expressed as the number of mature returns produced per 10 kg of smolts released) was the expanded number of age-3–5 returns (i.e., the same number used to calculate the SAS rate) divided by the mean weight (g) of smolts at liberation and multiplied by 10,000. Total production efficiency is useful when discussing whether treatments are beneficial for a hatchery program's return goals.

Age composition, sex composition, and length at maturity.—Age composition was calculated for each BY based on the sum of expanded CWT recoveries. To compare sex composition, sex-specific age composition, and FL at maturity, we used unexpanded CWT recoveries of Chinook Salmon collected in the Imnaha River basin (i.e., at IMNAHW or during spawning ground surveys). For this analysis, we required a minimum of 20 recoveries per CWT release group; this requirement limited our analysis of sex composition and sex-specific age composition between large and small smolts to six BYs (1988–1989, 1993, and 1995–1998). Smolt size and the size at age of adult hatchery returns were compared with those of natural-origin Imnaha River Chinook Salmon. For natural-origin individuals, BY was estimated by first collecting and aging scale samples from natural-origin fish collected in the Imnaha River basin and then subtracting the scale age from the recovery year. Fork length (mm) was measured from Chinook Salmon that were recovered as carcasses on the spawning grounds and from fish that were collected for hatchery broodstock.

Data analysis.—We used raceway as the experimental unit for data analyses. Juvenile and adult survival rates, total production efficiency, harvest rates, straying rates, and age composition data were logit transformed (Warton and Hui 2011). Data were analyzed using simple linear regression and ANOVA techniques. Two-way ANOVA (with smolt size as the fixed effect and BY as the random effect) was used to test the null hypothesis that treatment groups did not differ in juvenile survival or travel time from IMNAHW to LGD (i.e., a mixed-effects model). We used the same model and null hypothesis to test for differences in adult and total SAR rates, adult and total SAS rates, harvest rates, straying rates, total production efficiency, age composition, and length at return for each age-class. To test for potential density-related differences between smolt treatments and to ensure that any observed treatment effects were not confounded by differing release numbers from the standard-density and low-density rearing years, we first analyzed all 10 BYs and then repeated the analyses for each of the standard-density and low-density rearing years.

All statistical analyses were performed in R version 3.2.0 (R Development Core Team 2015). Mixed-effects models were analyzed with the R package "nlme" (Pinheiro et al. 2015). The Shapiro–Wilk test (Royston 1982) was used to evaluate the assumption of normality; Levene's test (Fox 2008) was used to determine whether the variance was homogeneous across groups. Assumptions of equal variance were met for all comparisons. Statistical tests were considered significant at P-values less than 0.05.

RESULTS

The actual mean weights achieved for Chinook Salmon smolts during the study differed from the target smolt weights. Actual mean weights ranged from 26 to 41 g for large smolts and from 18 to 25 g for small smolts (Table 1). At the time of release, the mean FL of large smolts ranged from 129 to 147 mm, and the FL of small smolts ranged from 113 to 124 mm. Values of K ranged from 1.2 to 1.4 for large smolts and from 1.1 to 1.3 for small smolts.

Smolt Survival and Travel Time to Lower Granite Dam

Without accounting for density, mean juvenile survival from release at IMNAHW to LGD was significantly greater for large smolts (mean ± 1SE = 66.6 ± 1.5%) than for small smolts (64.1 ± 1.5%; ANOVA: $F_{1,\ 25} = 4.46$, $P = 0.045$; Figure 2). During the two standard-density rearing years in which PIT-tagged juveniles were available for analysis (BYs 1992 and 1993), the mean survival rate to LGD was significantly greater for large smolts (67.7 ± 3.6%) than for small smolts (60.7 ± 2.9%; ANOVA: $F_{1,\ 4} = 18.85$, $P = 0.012$). During the low-density rearing years, there was no significant difference in survival between large smolts (66.3 ± 1.8%) and small smolts (65.2 ± 1.7%; ANOVA: $F_{1,\ 20} = 1.02$, $P = 0.105$).

Smolt releases from the acclimation facility did not occur on the same day every year. There was a difference of 26 d between the earliest smolt release (March 16, 1999) and the latest smolt

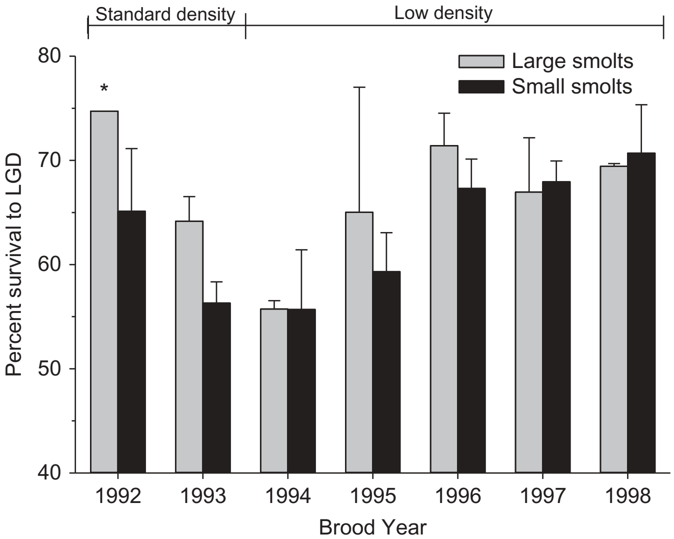

FIGURE 2. Mean (±2SE) survival rate of PIT-tagged large and small Chinook Salmon smolts from the Imnaha River Weir and Acclimation Facility (the release site) to Lower Granite Dam (LGD) on the Snake River for standard-density rearing years (brood years [BYs] 1992–1993) and low-density rearing years (BYs 1994–1998). Large smolts from BY 1992 (indicated with an asterisk) were reared in only one raceway.

release (April 11, 1994). Earlier releases resulted in longer mean travel times for both large smolts ($r^2 = –0.883$, $P < 0.001$) and small smolts ($r^2 = –0.921$, $P < 0.001$). Mean travel time from release at IMNAHW to LGD ranged from 22 to 56 d, and the median arrival day at LGD ranged from April 27 to May 10. Within a given release year, the mean difference in travel time between large-smolt and small-smolt releases ranged from 1 to 7 d. After accounting for juvenile migration year, there was no significant difference in mean travel time (d) between large-smolt and small-smolt releases (ANOVA: $F_{1,\ 31} = 0.425$, $P = 0.519$). Mean juvenile survival to LGD was not explained by mean travel time for either large smolts (ANOVA: $F_{1,\ 14} = 0.127$, $P = 0.727$) or small smolts ($F_{1,\ 15} = 2.031$, $P = 0.175$).

Total Survival

Over the 10 BYs examined, the mean adult SAR rate for large smolts (mean ± SE = 0.65 ± 0.13%) was lower than that of small smolts (0.73 ± 0.16%), but the difference was not statistically significant (ANOVA: $F_{1,\ 34} = 0.25$, $P = 0.623$; Table 2). Similarly, the total SAR rates did not differ between large smolts (mean ± SE = 0.85 ± 0.17%) and small smolts (0.92 ± 0.20%; ANOVA: $F_{1,\ 34} = 1.20$, $P = 0.282$). Mean SAR and SAS rates observed for BYs 1989–1990 and 1992–1994 were less than half the mean rates observed for BYs 1988 and 1995–1998.

For both adult and total SAS rates, mature Chinook Salmon that were produced from large smolts had lower mean return rates than those produced from small smolts (Table 2; Figure 3). Over the entire study, harvest rates ranged from 0% to 0.20%, and straying rates ranged from 0% to 0.06%. Mean harvest rate of mature fish that were produced from large smolts (mean ± SE = 0.02 ± 0.01%) was significantly less than the mean harvest rate of those produced from small smolts (0.03 ± 0.011%; ANOVA: $F_{1,\ 34} = 4.81$, $P = 0.035$). Mean straying rate was similar between mature Chinook Salmon that were produced from large smolts (mean ± SE = 6.000 ± 0.003%) and those that were produced from small smolts (0.007 ± 0.002%; ANOVA: $F_{1,\ 34} = 1.84$, $P = 0.184$).

The calculations for mean SAR and SAS rates differed in that the SAS rates incorporated harvest and straying rates. After accounting for harvest and straying rates, we found that the mean adult SAS rates for Chinook Salmon produced from large smolts (mean ± 1SE = 0.68 ± 0.14%) were lower than those from small smolts (0.76 ± 0.17%) but not significantly so (ANOVA: $F_{1,\ 34} = 0.19$, $P = 0.665$). After accounting for jack (age-3) returns, we found no significant difference (ANOVA: $F_{1,\ 35} = 1.17$, $P = 0.287$) in mean total SAS rates from large smolts (0.88 ± 0.17%) and small smolts (0.96 ± 0.21%).

When these analyses were repeated for the standard-density (BYs 1988–1993) and low-density (BYs 1994–1998) rearing years, there was no change in the adult SAS, total SAS, adult SAR, total SAR, total production, or straying rate results (Table 2). Mean adult and total SAR and SAS rates for large smolts remained lower than those of small smolts in both the standard-density and low-density rearing years, and the differences remained statistically nonsignificant ($P \geq 0.278$). Similarly, mean straying rates remained greater for large smolts in both the standard-density and low-density years, and again there was no statistically significant difference. During the standard-density years, mean harvest rates of large and small smolts were identical (mean ± SE = 0.001 ± 0.001%). Mean harvest rates for both treatment groups increased for smolts released during the low-density rearing years and were significantly lower for mature individuals produced from large smolts (mean ± SE = 0.038 ± 0.011%) than for those produced from small smolts (0.048 ± 0.018%; ANOVA: $F_{1,\ 20} = 5.14$, $P = 0.035$).

Total Production Efficiency

Mean total production efficiency was lower for large smolts (mean ± SE = 3.0 ± 0.6 mature fish/10 kg of smolts released) than for small smolts (4.7 ± 1.0 mature fish/10 kg of smolts) over the entire course of the study; however, after accounting for BY variation, the difference was not statistically significant (ANOVA: $F_{1,\ 34} = 1.58$, $P = 0.218$; Table 2). None of the differences between treatment groups was statistically significant within either the standard-density or low-density rearing years; mean total production efficiency of small smolts was 44% greater than that of large smolts from the standard-density rearing years and was 60% greater than that of large smolts from the low-density years.

Age and Sex Composition

Over the entire study, age-3 returns (jacks) comprised 24.4 ± 3.9% (mean ± 1SE) of the total returns produced from large smolts and 21.8 ± 3.4% of the returns produced from small smolts; however, this difference was not significant (ANOVA: $F_{1,\ 34} = 1.86$, $P = 0.182$; Figure 4). The mean percentage of returns at age 4 did not differ between large smolts (mean ± 1SE = 63.4 ± 3.6%) and small smolts (62.7 ± 3.8%; ANOVA: $F_{1,\ 34} = 0.52$, $P = 0.474$); likewise, the percentage of returns at age 5 was not significantly different between large smolts (12.2 ± 2.7%) and small smolts (15.5 ± 3.7%; ANOVA: $F_{1,\ 34} = 0.03$, $P = 0.871$). The same pattern in mean age composition between large and small smolts was observed for both the standard-density and low-density rearing years.

For BYs with a sufficient number of CWT recoveries (BYs 1988–1989, 1993, and 1995–1998), males (all ages) that were produced from large smolts comprised 62.1 ± 3.4% (mean ± 1SE) of the CWT recoveries in the Imnaha River basin, and males that were produced from small smolts comprised 63.5 ± 2.6% of the CWT recoveries; the difference was not significant (ANOVA: $F_{1,\ 28} = 0.353$, $P = 0.557$). For the same BYs, the mean percentage of age-4 females produced from large smolts (mean ± 1SE = 80.9 ± 6.8%) was significantly greater than that produced from small smolts (71.3 ± 8.8%), and the mean percentage of age-5 females produced from large smolts (19.0 ± 6.8%) was significantly less than that produced from small smolts (28.7 ± 8.8%; ANOVA: $F_{1,\ 6} = 16.3$, $P = 0.007$; Figure 4). Among returning males that were released as large

TABLE 2. Return rate metrics and age composition (means with SE in parentheses) for large and small Chinook Salmon hatchery smolts that were reared at Lookingglass Fish Hatchery and released into the Imnaha River (SAR = smolt-to-adult return rate to the mouth of the Imnaha River; SAS = smolt-to-adult survival rate to the mouth of the Columbia River; total production efficiency = total return of ages 3–5 produced per 10 kg of smolts released; adult = ages 4–5; total = ages 3–5). The *F*-statistic and *P*-value from the mixed-effects model are shown for all brood years (BYs 1988–1998), standard-density rearing years (BYs 1988–1993), and low-density rearing years (BYs 1994–1998).

Metric	Large smolts	Small smolts	$F_{1,\ 34}$	*P*
All years (BYs 1988–1998)				
SAR adult	0.654 (0.129)	0.727 (0.160)	0.25	0.623
SAR total	0.846 (0.165)	0.920 (0.196)	1.20	0.282
Harvest rate	0.022 (0.008)	0.028 (0.011)	4.81	0.035
Straying rate	0.012 (0.003)	0.007 (0.002)	1.84	0.184
SAS adult	0.679 (0.135)	0.756 (0.170)	0.19	0.665
SAS total	0.881 (0.173)	0.955 (0.207)	1.17	0.287
Total production efficiency	3.019 (0.618)	4.659 (1.043)	1.58	0.218
Age 3 (%)	24.4 (3.9)	21.8 (3.4)	1.86	0.182
Age 4 (%)	63.4 (3.6)	62.7 (3.8)	0.52	0.474
Age 5 (%)	12.2 (2.7)	15.5 (3.7)	0.03	0.871
Standard-density rearing years (BYs 1988–1993)[a]				
SAR adult	0.223 (0.069)	0.230 (0.085)	0.04	0.847
SAR total	0.264 (0.073)	0.273 (0.102)	0.84	0.376
Harvest rate	0.001 (0.001)	0.001 (0.001)	1.85	0.197
Straying rate	0.007 (0.002)	0.004 (0.001)	1.17	0.299
SAS adult	0.229 (0.070)	0.236 (0.087)	0.01	0.910
SAS total	0.271 (0.075)	0.279 (0.103)	0.78	0.393
Total production efficiency	0.850 (0.215)	1.225 (0.408)	0.61	0.448
Age 3 (%)	26.8 (7.8)	23.3 (6.3)	2.66	0.127
Age 4 (%)	53.8 (6.0)	56.0 (4.4)	0.59	0.457
Age 5 (%)	19.4 (5.0)	20.6 (6.0)	0.01	0.914
Low-density rearing years (BYs 1994–1998)[b]				
SAR adult	0.952 (0.171)	1.109 (0.226)	0.26	0.613
SAR total	1.249 (0.213)	1.417 (0.267)	0.39	0.537
Harvest rate	0.038 (0.011)	0.048 (0.018)	5.14	0.035
Straying rate	0.016 (0.005)	0.009 (0.003)	1.25	0.278
SAS adult	0.991 (0.179)	1.157 (0.241)	0.27	0.612
SAS total	1.302 (0.223)	1.475 (0.284)	0.41	0.528
Total production efficiency	4.521 (0.807)	7.300 (1.447)	0.95	0.343
Age 3 (%)	22.7 (3.9)	20.6 (3.9)	0.29	0.594
Age 4 (%)	70.0 (3.5)	67.9 (5.5)	0.19	0.665
Age 5 (%)	7.3 (2.4)	11.5 (4.5)	0.11	0.747

[a] For BYs 1988–1993, the *F*-statistic df = 1, 13.

[b] For BYs 1994–1998, the *F*-statistic df = 1, 20.

and small smolts, there was no significant difference in sex-specific age composition for age-3–5 returns (ANOVA: all $F_{1,\ 6} \leq 1.60$, all $P \geq 0.255$).

Fork Length at Maturity

We found no significant differences in mean FL of age-3–5 returns that were produced from large and small smolts (Figure 5). Mean FL was 566 ± 2.8 mm (mean ± 1SE) for age-3 adults produced from large smolts and 569 ± 2.5 mm for those produced from small smolts (ANOVA: $F_{1,\ 588} = 0.09$, $P = 0.767$). Mean FL was 784 mm for age-4 adults produced from both large smolts and small smolts (ANOVA: $F_{1,\ 1{,}073} = 0.11$, $P = 0.738$). Fork length was 924 ± 4.5 mm (mean ± 1SE) for age-5 adults produced from large smolts and was 935 ± 4.0 mm for age-5

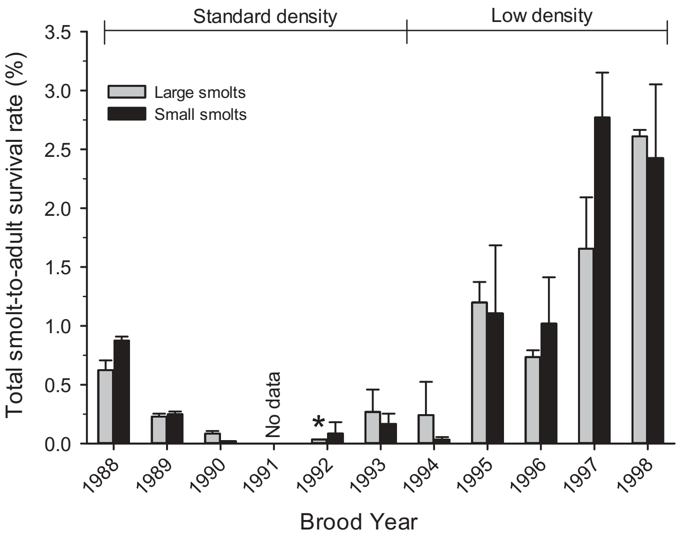

FIGURE 3. Mean (±2SE) total smolt-to-adult survival rates for large and small Chinook Salmon smolts released from the Imnaha River Weir and Acclimation Facility for standard-density rearing years (brood years [BYs] 1988–1990 and 1991–1993) and low-density rearing years (BYs 1994–1998). Large smolts from BY 1992 (indicated with an asterisk) were reared in only one raceway.

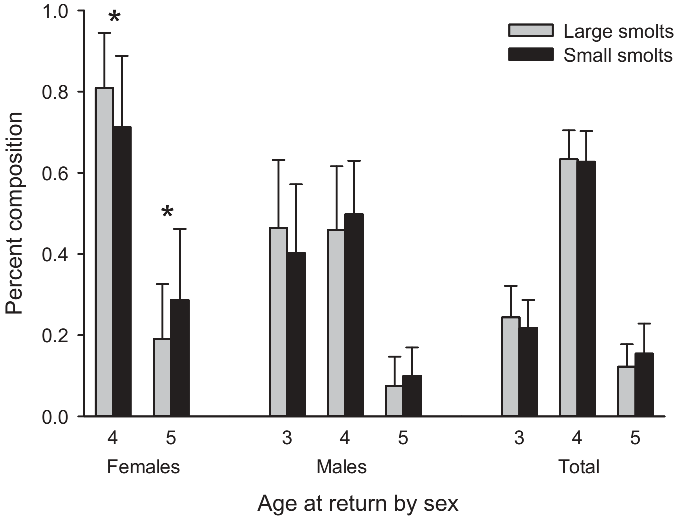

FIGURE 4. Mean (±2SE) age composition of female (ages 4–5), male (ages 3–5), and total (ages 3–5) hatchery Chinook Salmon that returned to the Imnaha River after being released as large or small smolts. Asterisks indicate a significant difference between large smolts and small smolts ($P < 0.05$).

adults produced from small smolts (ANOVA: $F_{1,\ 387} = 1.67$, $P = 0.197$). Across ages, FL was 751 ± 135 mm (mean ± 2SE) for adults produced from large smolts and 750 ± 140 mm for adults produced from small smolts (ANOVA: $F_{1,\ 2{,}070} = 0.43$, $P = 0.511$). For reference, the FLs of naturally produced adults were 557 ± 4.0 mm (mean ± 1SE) at age 3; 761 ± 1.0 mm at age 4; and 914 ± 1.5 mm at age 5.

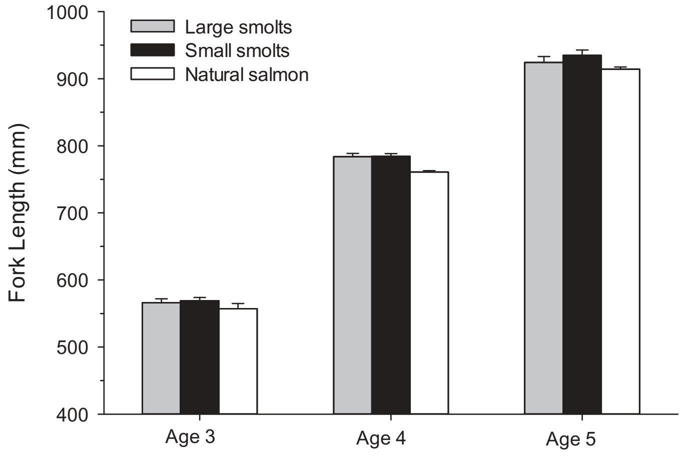

FIGURE 5. Mean (±2SE) FL of age-3–5 hatchery Chinook Salmon returning to the Imnaha River after being released as large or small smolts; and mean FL of naturally produced Chinook Salmon returning to the Imnaha River (brood years 1988–1990 and 1992–1998).

DISCUSSION

Overall, our results indicated that small Chinook Salmon smolts performed as well as or better than large smolts, but we found few meaningful differences in the measured performance metrics between smolt sizes. Total survival rates (ages 3–5), adult survival rates (ages 4–5), and total production efficiency did not differ between large and small smolts. For both of the treatment (size at release) groups, the SAR rate, SAS rate, and total production efficiency varied through time, with neither treatment group having consistently higher rates.

These results contrast with prior findings that adult return rates of hatchery Chinook Salmon can be improved by releasing larger smolts (Bilton 1984; Martin and Wertheimer 1989; Morley et al. 1996). However, a cursory examination of “large” versus “small” smolts is misleading, and a closer inspection of absolute smolt size allows our results to be reconciled with those of prior studies. In our study, mean annual weights ranged from 26.0 to 41.4 g for large smolts and from 18.3 to 24.8 g for small smolts; the mean annual difference in weight was 9.7 g (range of differences = 3.9–19.2 g). In contrast, for the Bilton (1984) study, small juvenile Chinook Salmon were 3.6 g and large juveniles were 12.6 g. Morley et al. (1996) released small juvenile Chinook Salmon at a weight of 3.0 g and large juveniles at 16.2 g. Martin and Wertheimer (1989) classified small Chinook Salmon as weighing 9.7–10.3 g and large individuals as weighing 28.2–31.8 g. All three studies reported that releases of larger juveniles resulted in higher return rates than releases of smaller juveniles. The large juveniles examined by Bilton (1984) were closer in size to the small smolts studied by Martin and Wertheimer (1989), which in turn were about half the size of the small smolts we examined. The large smolts studied by Martin and Wertheimer (1989) were larger than the large smolts released by Bilton (1984) and Morley et al. (1996) but were similar in size to the smallest of our large smolts.

By comparison, Hatch et al. (2014) reported that natural-origin Chinook Salmon smolts emigrating from the Imnaha River between 1994 and 2010 had mean weights of 10.6–14.1 g and mean FLs of 99–110 mm—nearly 33% smaller than the small Imnaha River hatchery smolts we studied. Similarly, natural-origin Chinook Salmon smolts that emigrated from the John Day River, Oregon, between 2000 and 2009 had a mean length of 98–110 mm (Tattam et al. 2015). The current size target for spring Chinook Salmon smolts reared at LFH is 21–23 g; this target is substantially smaller than those for other ODFW hatchery programs, which release spring Chinook Salmon smolts ranging from 30 to 57 g (ODFW, unpublished data; hatchery management plans available at www.dfw.state.or.us/fish/hatchery). Spring Chinook Salmon from Washington Department of Fish and Wildlife hatcheries are released at mean weights of 30–57 g and mean FLs of 145–195 mm (Tipping 2011); spring and summer Chinook Salmon smolts from Idaho hatcheries are released at mean weights of 21.6–30.4 g (Chris Sullivan, Idaho Department of Fish and Game, personal communication). Although the mean release size of hatchery-reared spring Chinook Salmon smolts is variable, even the small hatchery-reared smolts are large in comparison with naturally reared spring Chinook Salmon smolts.

Because Imnaha River hatchery smolts are at the upper end of the size spectra previously studied, it is possible that both our large and small smolts exceeded a threshold beyond which survival benefits associated with increased size are asymptotic or even decreasing. Indeed, Koenings et al. (1993) suggested a size-threshold hypothesis for Sockeye Salmon *O. nerka*; they found that SAR rates increased with smolt size until the smolts reached 90 mm, but beyond that size there was no added survival benefit. The lack of significant survival differences between large and small Imnaha River hatchery smolts suggests that we may have reached a similar size threshold, but further study will be required to test this hypothesis.

There is uncertainty about rearing density effects on SAR and SAS rates for Chinook Salmon, as positive, negative, and null relationships have all been reported (Ewing and Ewing 1995). Unlike the study by Banks (1994), our study was not designed to directly test for a density effect. In this study, the shift in rearing density resulted from a lack of broodstock availability, which affected smolt rearing numbers; thus, the density comparison was not a planned treatment effect, and the lower densities were not paired with standard densities. We originally planned to terminate the study after BY 1991. However, preliminary study results at the time were inconclusive, and in terms of achieving production goals, there was no apparent benefit to rearing larger smolts and no apparent detriment to rearing smaller smolts. Therefore, hatchery managers decided to rear and release both large and small smolts at reduced densities through BY 1998. Because the two rearing densities were not used concurrently, it was impossible to directly test the effect of rearing density on SAR or SAS rates. We hypothesized that if density was an important factor contributing to survival rates, we would see a shift in the SAR rate or SAS rate between the two rearing densities wherein one treatment group would consistently return at a higher rate under one density but not the other. The important finding from our study was that after accounting for BY, the SAR and SAS rates exhibited no statistically significant differences between treatment groups when the data were analyzed in aggregate (all 10 BYs) or under either of the two rearing densities. Therefore, we conclude that even under two different rearing densities, there was no benefit to rearing larger smolts.

In our study, four of the five lowest return survival rates were observed for BYs in which the smolts were reared at standard density. Although impossible to disprove, the standard rearing density at LFH is unlikely to explain the low SAR rates observed for BYs 1988–1993. First, Chinook Salmon smolts were being reared at LFH according to the density standards for which LFH was designed. Second, the general pattern of low SAR rates in the late 1980s and early 1990s, followed by a steady increase through BY 1998, was also observed in other Snake River spring and summer Chinook Salmon populations and has been attributed to regional-scale, oceanic, or climatic conditions (Williams et al. 2001; Scheuerell and Williams 2005). Beckman et al. (1999) reported low SAR rates for three Deschutes River hatchery spring Chinook Salmon populations from BYs 1988–1990. Another possible explanation for BY variation is fishery exploitation. However, mean harvest rates comprised less than 6.5% of the SAS rates for any given BY. Similarly, straying rates of Imnaha River adults were no greater than 0.02%, which is important because it suggests that this hatchery population exhibits minimal spawning interactions with other Chinook Salmon populations. Overall, neither the harvest exploitation rate nor the straying rate provides a convincing argument for explaining the low adult survival rates.

We observed no statistically significant differences between smolt treatment groups in terms of sex composition or the age composition of male returns; however, we did find significant differences in the proportion of females that returned at ages 4 and 5. On average, release groups of small smolts returned 10% more age-5 females than did release groups of large smolts. From a broodstock collection perspective, this is an important finding for the simple reason that older females have greater fecundity (Beacham and Murray 1993; Eddy et al. 2014).

We also did not find any size differences among hatchery adults produced from large and small smolts, and the hatchery adults were comparable in size to naturally produced adults (Figure 5). Furthermore, when compared to adult returns from naturally produced smolts, a greater proportion of hatchery Chinook Salmon (both treatments) always returned at age 3, and a lower proportion returned at age 5 (ODFW, unpublished data). However, even without a difference in the overall size of returning adults, the ecological consequences of differing size at maturity or age at maturity must not be taken lightly. Because age at maturity and size at age are heritable (Hankin et al. 1993; Carlson and Seamons 2008; Kinnison et al. 2011) and because selection on size or other phenotypic traits can occur unintentionally in hatchery environments (Hankin et al. 2009), allowing hatchery adults to spawn in nature provides an opportunity for the exchange of heritable traits with natural-origin adults.

The Imnaha River Chinook Salmon population is unique in northeast Oregon in that historically more than 50% of its females matured at age 5 (ODFW, unpublished data). However, the percentage of age-5 natural-origin returns to the Imnaha River has been decreasing since supplementation began and has averaged less than 30% for the last 10 complete BYs. Although there is concern that the size at maturity and age at maturity of returning hatchery adults can influence the age structure of naturally produced Chinook Salmon, evidence exists that the sizes of naturally produced Chinook Salmon smolts also influence age at maturity (Scheuerell 2005). For example, Tattam et al. (2015) reported that for naturally reared Chinook Salmon smolts in the John Day River, the probability of maturing at age 3 increased with smolt length, and the probability of maturing at age 5 was inversely related to smolt condition factor. Perhaps releasing Imnaha River hatchery smolts that are closer in size to naturally produced smolts would reverse the declining trend in age-5 returns.

The trend toward a younger age at return for larger hatchery smolts is well known and has been documented previously (Bilton 1984; Martin and Wertheimer 1989; Claiborne et al. 2011). Although our study showed a slight trend toward returning at a younger age for the large smolts, the mean age composition of adults did not significantly differ between large and small smolts. Even within BYs, there was little difference: relative to small smolts, the large smolts produced a greater percentage of age-3 returns for 6 of 10 BYs; a greater percentage of age-4 returns for 5 of 10 BYs; and a greater percentage of age-5 returns for 4 of 10 BYs. Importantly, we were unable to quantify differences in minijack rates between the large- and small-smolt treatments, so our conclusions about age at return are limited to ages 3–5. This younger age at return may be another indication that we have reached an asymptote of the benefit from releasing larger smolts.

Data on the survival of PIT-tagged smolts from IMNAHW to LGD offer additional insight into our lack of a statistically significant smolt-size treatment effect. The variation in hatchery smolt survival from release to LGD among BYs (or smolt out-migration years) was greater than the variation between large and small smolts. We found no significant difference between treatment groups in terms of mean travel days to LGD, and there was no relation between mean travel time and survival to LGD. This suggests that annual variation in juvenile survival to LGD was more important than any variation due to the smolt sizes we tested.

The size of juvenile migrants is an important covariate for understanding juvenile survival to an endpoint such as LGD (e.g., Zabel 2002; Monzyk et al. 2009); however, other factors, including stream temperature and flow (Zabel 2002; Sykes et al. 2009) or the growth rate immediately prior to migration (Beckman et al. 1998), may be just as important. Rather than focusing on rearing the hatchery smolts to a specific size target so as to maximize juvenile survival, it might be more beneficial to understand how the juvenile survival rate, SAR rate, and SAS rate are influenced by (1) hatchery practices that affect the growth rate prior to release (Spangenberg et al. 2014); (2) the timing of release; (3) the usage of acclimated, volitional, or direct stream releases; and (4) the release location. By doing so, we may be able to increase the SAS rate and improve the age composition of returning adults. Thus, concerns about juvenile release-size targets that increase survival to LGD but do not increase the adult return rates or reduce the jack or minijack rates may be a waste of time and effort.

During the present study, a mean of 17 million smolts were collected at Columbia and Snake River dams each year and were transported (primarily in barges) to release locations below Bonneville Dam (Buchanan et al. 2006). A percentage of those transported smolts originated from the Imnaha River, which is separated from the Pacific Ocean by eight hydropower dams. This is important because we could not examine juvenile survival rate differences between the large- and small-smolt treatment groups downstream of LGD relative to the migration experience (i.e., run of the river versus transported). For example, the estimated annual in-river migrant survival probability for Snake River spring–summer Chinook Salmon smolts from LGD to the Bonneville Dam tailrace during smolt out-migration years 1993–1999 ranged from 31% to 59% (Williams et al. 2001); comparable survival estimates for barged smolts were nearly 100% (Budy et al. 2002; McMichael et al. 2011). Because arrival time at LGD was similar for large and small hatchery smolts, we assume that the two treatment groups were subjected to similar annual transportation or migration experiences below LGD, but we do not know whether they had similar survival rates from LGD to the Pacific Ocean. Therefore, results from this study may not be directly comparable with the results of other studies that have occurred during different transportation or hydropower operating scenarios.

We found no evidence that the rearing and release of larger-sized hatchery Chinook Salmon smolts into the Imnaha River increased either production efficiency or survival relative to the release of smaller hatchery smolts, which are still about 33% larger than natural-origin Imnaha River smolts. Total production efficiency is a useful metric for scaling the results relative to the production of returning adults per raceway (i.e., the mass of juveniles released) and is particularly useful for comparing hatchery programs with adult return goals. When the management goal is to increase the number of returning adult salmon from space-limited, egg-rich environments like hatcheries, managers strive to optimize survival based on the inverse relationship between the number of smolts produced and the size of smolts produced. Even if survival is lower for smaller hatchery smolts, it is possible to return a greater number of adult salmon from a raceway of smaller smolts relative to a raceway of larger smolts simply because a greater number of small smolts can be reared and released per raceway. Based on the smolt sizes compared in our study, this seems to be the case. For example, LFH could maintain a similar raceway density (e.g., 1,700 kg of fish/raceway) by rearing either 50,000 large smolts (34 g) or 85,000 small smolts (20 g). Based on our mean total SAS rates for large smolts (0.881%) and small smolts (0.955%), the additional 35,000 small smolts released from each raceway would result in 334 additional mature Chinook Salmon returning to the Columbia River over the number of mature returns that would be produced by a raceway of large smolts. These additional 334 returns would consist of approximately 66 age-3 fish, 206 age-4 fish, and 62 age-5 fish.

Overall, our findings contradict the simplistic paradigm that larger Chinook Salmon smolts provide greater adult returns than do smaller smolts. Although maximizing survival rates remains an important management objective, the optimization of smolt size in relation to an optimal hatchery rearing density and size at release so as to maximize survival rates may not be a simple panacea for achieving all hatchery program objectives. We emphasize that hatchery management goals should not ignore the evolutionary consequences of salmon aquaculture practices (Carlson and Seamons 2008; Carlson et al. 2011). Although long-term, site-specific studies and monitoring of hatchery rearing and release protocols are challenging and costly, such studies provide valuable information that should be used to advance and adapt each hatchery program.

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