Transactions of the American Fisheries Society 135:1567–1577, 2006

DOI: 10.1577/T05-246.1

[Article]

The Effect of Moderately Increased and Variable Raceway Flow Rates on Juvenile Physiology, Survival, and Adult Return of Hatchery-Reared Chinook Salmon

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Abstract.—Increasing hatchery raceway flow to a rate similar to that seen in nature exercises salmon in the expectation that improving swimming ability will result in better survival. However, insufficient water prevents most hatcheries from fully simulating natural stream currents. We examined the effect of moderate and seasonally variable flow rates (0.25–0.75 body lengths/s) on growth and physiology of juvenile Chinook salmon *Oncorhynchus tshawytscha* and their ability to withstand acute stress, survive downstream migration, and return as adults. Changes in salmon growth, condition, and hematocrit followed similar patterns and did not substantially vary between treatments or cohorts. Patterns of change in plasma glucose levels were also similar for each treatment. Hepatosomatic index was higher in the 1994 cohort than in the 1995 cohort and in the exercised salmon. Liver glycogen levels were higher in the 1995 cohort. Plasma glucose and cortisol levels increased after stress and were greater in the control. Hematocrit decreased following stress but did not differ between cohorts or treatments. Hepatosomatic index decreased following stress and was higher in the 1994 cohort. Liver glycogen levels did not change following stress or between treatments but were greater in the 1995 cohort. Downstream survival did not vary between cohorts or treatments. Migration time did not vary between treatments, but the 1995 cohort migrated more quickly. Harvest and stray rates were very low and did not vary between cohorts or treatments. Hatchery return, total return, and total survival rates did not vary between treatments, but the 1995 cohort had greater survival. A greater percentage of the exercised salmon returned at age 3 than was the case for the control salmon. Our results provide little evidence that rearing Chinook salmon under a moderately increased and seasonally variable flow regime confers any benefit to the salmon over that derived from a steady, low flow rate.

Improving the survival of hatchery-reared salmon and the rate at which they return as adults to the target stream or hatchery is a primary objective of salmon fishery and hatchery managers. To improve survival in nature, hatcheries often strive to better simulate natural conditions. There are several points in the presmolt life history phase of hatchery-reared salmon at which management actions and environmental modifications may be implemented to improve the likelihood of achieving these objectives. One method is to increase the flow rate in raceways to a rate similar to that in nature. Increased raceway flow to 1–2 body lengths (BL) per second exercises the salmon and has been shown to improve growth, food conversion, and endurance in various salmonids (Besner and Smith 1983; Leon 1986; Houlihan and Laurent 1987; Christiansen et al. 1992; Jorgensen and Jobling 1993). This is done under the hypothesis that improving swimming ability may improve their performance in natural stream conditions, therefore improving survival during smolt migration and resulting in better survival to adulthood.

As with any change in hatchery management protocols, the benefits of rearing and releasing salmon under more natural conditions must be weighed against the increased cost of those activities. Increasing flow through raceways is likely to increase the cost of rearing salmon. Additionally, limited water availability may not allow an increase to 1–2 BL/s. However, the benefits of an increased return rate may outweigh these costs. These issues are of particular importance when one is dealing with populations listed under the U.S. Endangered Species Act, such as those of Chinook salmon *Oncorhynchus tshawytscha* in the Grande Ronde and Imnaha rivers of northeastern Oregon.

We report the results of an experiment to examine the effect of moderate and seasonally variable flow rates to exercise juvenile Chinook salmon. Specifically, we examined their growth and physiology and their ability to withstand acute stress, survive to downstream migration locations, and return as adults when reared under raceway flows greater than those normally used at Lookingglass Fish Hatchery, in the Grande Ronde River basin of northeast Oregon.

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Received October 11, 2005; accepted May 18, 2006
Published online November 30, 2006

Methods

Hatchery and fish.—Lookingglass Fish Hatchery (LFH) is located on Lookingglass Creek in northeastern Oregon 3.7 km upstream from where it flows into the Grande Ronde River, a tributary of the Snake River. Fish released from LFH migrate 850 km downstream to the ocean, passing eight main-stem hydroelectric dams on the Snake and Columbia rivers.

Rapid River stock spring Chinook salmon were reared from eggs at and released from LFH during 1994–1996 (1994 cohort) and 1995–1997 (1995 cohort). These fish were part of the LFH production for those cohorts and came from 49 females and 45 males in 1994 and 52 females and 135 males in 1995. No effort was made to ensure equal representation from each family group in each raceway. The number of fish per experimental (exercise and control) raceway was lower than normal production, but reducing the water level in the raceways by half to increase current velocity made final rearing density similar to that of production raceways at LFH (about 17 kg/m^3). The fish were fed by hand several times per day at a daily rate (amount of feed/gram body weight) that varied (based on water temperature) from 0.1% during the winter to 1.8% in August and was the same for control and exercise raceways. The number of smolts released from each raceway ranged from 34,225–38,962, and mortalities ranged from 1.3% to 4.4% from the time that the fish were coded-wire-tagged to release.

We used well water for early rearing and unfiltered Lookingglass Creek water when the Chinook salmon were stocked into outdoor raceways in the spring following hatching. Outdoor raceways at LFH are 30.5 m $\times$ 3 m and 1 m deep (95 m^3), but we reduced water depth to 0.5 m to increase current velocity. Rearing density (Piper et al. 1982) in control raceways increased from 1.7 kg/m^3 at the beginning of the experiment (May) to 17.6 kg/m^3 at the time of release in the following spring. In the experimental raceways, density ranged from 2.35 to 17.8 kg/m^3. Loading density (Westers 2001) in the control raceways increased from 0.08 to 0.37 kg·L^{-1}·min^{-1} from May to April. Loading density in the exercised raceways ranged from 0.06 in May to 0.27 kg/Lpm in January and at release was 0.13 kg/Lpm.

We used four raceways for each cohort, creating two replicates for each cohort and treatment. We sampled the fish by walking from the upstream to the downstream end of the raceway, which scared the fish to the lower end, where they became sufficiently concentrated to scoop out with a dip net the few fish needed for each sample. These fish were immediately taken inside and killed by lethal dose of tricane methanesulfonate (MS-222), unless they were to be used for the stress test. All statistical tests were considered to be significant at $\alpha = 0.05$.

Exercise protocol.—We exposed the parr to one of two protocols for flow rate of water through the outdoor rearing raceways. We held control salmon at a consistent relative water velocity of approximately 0.2 BL/s, the standard flow rate for LFH (Figure 1). Relative water velocity in the exercised raceways varied seasonally, ranging from 0.25 BL/s during winter to 0.75 BL/s, which is the maximum possible at LFH during low-flow periods in late summer and winter. Flow rate was decreased to a relative velocity of 0.2 BL/s around 1 July of each year during coded wire tagging. Inflow rates and current velocities in the raceways were adjusted as the fish grew to maintain the appropriate relative water velocities for the control and experimental protocols. In the control raceways, inflow ranged from 965 to 2,237 L/min, and current velocity ranged from 1.02 to 2.37 cm/s; in the exercised raceways the ranges were 965–6,294 L/min and 1.02–6.66 cm/s. Experimental treatments were applied from May through the following March–April, when the salmon were released. Mean size at smoltification was 22.5 g and neither mean length, weight, nor condition factor (K) varied between cohorts, treatment groups, or raceways ($P \geq 0.132$).

Juvenile growth and physiology.—We sampled the parr periodically throughout the rearing cycle: July (1995 cohort only), November, and every 2 weeks during prerelease smoltification (February to March or April). For sampling periods in which we did not conduct stress sampling, we collected 12 salmon from one of the replicate raceways for each treatment. For those dates on which we did conduct stress tests, we collected eight salmon from each replicate raceway (16/treatment) for time 0 samples. For these analyses, we used only the time 0 samples for the raceways that were sampled for all sampling periods.

We measured length and weight from each Chinook salmon, calculated its K, and collected blood samples for determining hematocrit and plasma glucose levels. We also collected and weighed the liver for measurement of liver glycogen level and calculation of hepatosomatic index (HSI = [liver weight/body weight]·100). We sent blood and liver samples to Biotech Research Consultants, Corvallis, Oregon, for analysis. Plasma glucose was measured by mixing the sample with glucose oxidase and peroxidase in 0.1 M citrate buffer (pH 4.2), and color was developed by addition of 2,2′-azino-bis(3-ethylbenzthiazoline-6-sulphonic acid). Liver glycogen was measured by precipitating all proteins and glycogen with ethanol, then dissolving the protein in boiling KOH. Glycogen

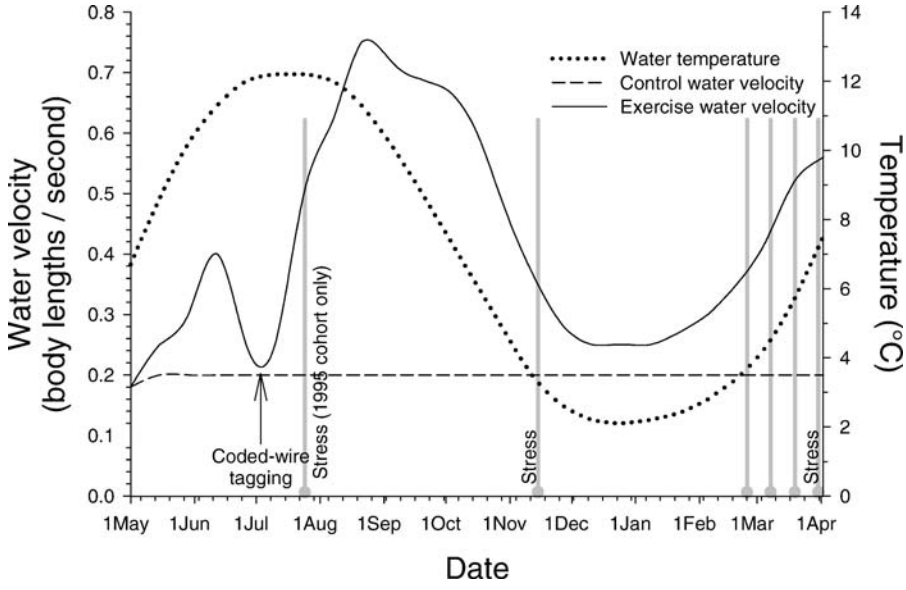

FIGURE 1.—Experimental design for evaluation of moderate, seasonally variable flow rate effects on Chinook salmon physiology, smolt survival, and adult return rates at Lookingglass Fish Hatchery, Oregon. Vertical lines indicate dates of physiological and stress sampling.

was then precipitated by adding 66% ethanol overnight at 4°C. After washing and drying, the glycogen was dissolved in water and assayed by the method of Dubois et al. (1956) using glucose as a standard. We compared the means of somatic and physiological variables for each sampling date between treatment groups via a three-way analysis of variance (ANOVA), where cohort, treatment, and sample date were independent variables. We used regression of mean values for each sampling date to look for trends over time (Sokal and Rohlf 1981).

Juvenile stress physiology.—We conducted stress tests in July (1995 cohort only), November, and April, in which we sampled eight fish from each raceway (16 per treatment) for a prestress sample (time 0) and an additional eight Chinook salmon from each raceway for the poststress sample (stress). We stressed the salmon by holding them in a net out of water for 30 s and then held them for 2 h in a covered and aerated 19-L bucket before sacrificing for measurements and tissue samples. We collected the same set of somatic and physiological samples and measurements as for the parr physiology monitoring and analyzed the tissue samples in the same manner. We collected additional blood samples for measuring plasma cortisol levels via an homogeneous enzyme-linked immunosorbent assay test (Biotech Research Consultants, Corvallis, Oregon). We compared means of somatic and physiological variables for each sampling date between treatment groups using a four-way ANOVA with cohort, treatment, sample date, and raceway as independent variables (Sokal and Rohlf 1981).

Survival and adult returns.—All smolts released were adipose fin-clipped to identify them as hatchery-reared and were marked with unique coded wire tags (CWTs) to identify raceway and treatment. Additionally, we individually marked approximately 900 parr (1994 cohort) and 3,500 parr (1995 cohort) from each raceway with passive integrated transponder (PIT) tags for estimation of downstream migration timing and survival. At the time of normal seaward migration, we released the smolts directly into Lookingglass Creek to migrate to the ocean and return as adults to LFH. We examined adult returns from each treatment and cohort over the period of 1997–2000. Snouts containing CWTs were collected in ocean and freshwater fisheries, from carcasses recovered on spawning grounds in Lookingglass Creek and as strays in other streams, and from adults returning to LFH (some were captured at Lower Granite Dam and transported to LFH). For collections in which subsamples were collected (i.e., fisheries and some spawning ground surveys), we expanded the number of tags recovered to estimate the total number of adults recovered within each group.

We calculated migration time as the number of days required for a PIT-tagged smolt to travel from LFH to Lower Granite Dam. We released the 1994 cohort on 4

TABLE 1.—Mean (SD in parentheses) length, weight, condition factor, plasma glucose, plasma cortisol, liver glycogen, hematocrit, and hepatosomatic index (HSI) of the 1994 cohort of juvenile Chinook salmon reared under control and exercised (increased-flow) growth regimes at Lookingglass Hatchery, Oregon.

	9 Nov 1995		20 Feb 1996		5 Mar 1996		19 Mar 1996		29 Mar 1996	
Variable	Control	Exercise	Control	Exercise	Control	Exercise	Control	Exercise	Control	Exercise
Length (mm)	111.5 (6.19)	119.5 (8.11)	123.6 (9.21)	118.8 (6.50)	119.3 (7.51)	121.1 (7.56)	121.7 (6.62)	130.5 (7.81)	130.1 (12.37)	127.1 (4.58)
Weight (g)	15.70 (2.468)	19.78 (4.146)	21.85 (4.366)	18.65 (3.341)	18.87 (3.712)	20.08 (3.828)	20.22 (3.681)	21.88 (4.322)	24.73 (8.052)	23.10 (2.753)
Condition factor	1.13 (0.089)	1.15 (0.035)	1.14 (0.057)	1.10 (0.051)	1.10 (0.085)	1.12 (0.052)	1.11 (0.046)	0.98 (0.115)	1.10 (0.082)	1.12 (0.036)
Glucose (ng/mL)	62.5 (11.17)	63.1 (13.36)	71.4 (14.88)	69.7 (9.39)	53.2 (6.76)	52.5 (13.02)	56.5 (8.90)	64.0 (11.68)	88.0 (11.26)	59.3 (13.44)
Hematocrit	39.3 (3.11)	38.8 (3.69)	42.4 (3.83)	39.8 (4.32)	37.6 (4.52)	36.2 (4.86)	40.4 (2.71)	41.9 (3.99)	36.0 (2.78)	38.0 (4.34)
HSI	1.76 (0.302)	1.78 (0.167)	1.70 (0.230)	1.67 (0.246)	1.62 (0.282)	1.57 (0.267)	1.67 (0.206)	1.68 (0.119)	1.56 (0.200)	1.74 (0.233)
Liver glycogen (mg/g)	22.1 (11.10)	23.3 (6.08)	10.9 (6.06)	11.8 (6.98)	5.3 (3.22)	3.9 (2.27)	3.8 (1.97)	4.6 (2.09)	4.8 (1.33)	4.5 (1.37)

April 1996 and the 1995 cohort on 7 April 1997. We also estimated survival indices based on PIT tag observations of smolts at lower Snake and Columbia river dams and of coded-wire tags recovered in the commercial, sport and tribal harvests, at the hatchery weir and on the spawning grounds. We defined smolt survival rate as the percentage of PIT-tagged smolts that survived to Lower Granite Dam (i.e., they were detected at one of the lower Snake and Columbia River dams).

We estimated survival to Lower Granite Dam for each raceway using the Cormack–Jolly–Seber survival probability calculated in the SURPH 2.1 program (Lady et al. 2001). This method accounted for the probability of detection when calculating the probability of survival (detection probability = capture probability × survival probability). Harvest rate is the percentage of all CWTs recovered that were recovered in commercial, sport, or tribal fisheries in the Columbia River. Hatchery return rate is the percentage of all CWTs recovered at the LFH weir plus those recovered on spawning ground surveys in Lookingglass Creek. Stray rate is the percentage of all CWTs recovered that were recovered on spawning ground surveys in streams other than Lookingglass Creek. Smolt-to-adult survival (SAR) is the percentage of coded-wire-tagged salmon released that were recovered as returning adults in freshwater. Lastly, we examined age composition of the returning cohort: the percentage that each age-class in the total return to the hatchery weir and from spawning ground surveys. We transformed survival rates and age composition data using an arcsine transformation (Krebs 1999) and compared differences in migration timing and survival using a three-way ANOVA with cohort, treatment, and raceway as independent variables (Sokal and Rohlf 1981).

Results

Juvenile Growth and Physiology

Changes in fish growth and condition followed similar patterns for the exercised and control groups and did not substantially vary between treatment groups or cohorts (Tables 1, 2). Mean length and weight of each treatment and cohort generally increased, and mean K generally decreased from November to March and April ($P \leq 0.041$); however, the weights for the exercised 1995 cohort ($P = 0.075$) did not change over time, and K for the exercised 1994 cohort ($P = 0.160$) did not change over time. Mean length and weight did not vary among cohorts or treatments ($P \geq 0.127$). Condition factor did not vary among treatments ($P = 0.145$) but was higher in the 1994 cohort than in the 1995 cohort ($P = 0.024$). Mean plasma glucose levels varied among cohorts and sampling dates ($P < 0.001$), but there were no trends in their change over time for any treatment or cohort ($P \geq 0.283$). Patterns of change in mean plasma glucose levels were similar for each treatment, levels being low in March and high in April ($P \leq 0.015$). The 1994 cohort had higher mean plasma glucose levels than the 1995 cohort. Mean hematocrit levels were lower in the 1995 cohort than in the 1994 cohort and also varied among sampling dates ($P \leq 0.024$). Mean hematocrit did not change significantly from November to March and April in the 1994 cohort ($P \geq 0.100$) but decreased in both treatment groups of the 1995 cohort ($P \leq$

TABLE 2.—Mean (SD in parentheses) length, weight, condition factor, plasma glucose, plasma cortisol, liver glycogen, hematocrit, and hepatosomatic index (HSI) of the 1995 cohort of juvenile Chinook salmon reared under control and exercised (increased-flow) growth regimes at Lookingglass Hatchery, Oregon.

	19 Nov 1996		20 Feb 1997		6 Mar 1997		20 Mar 1997		4 Apr 1997	
Variable	Control	Exercise	Control	Exercise	Control	Exercise	Control	Exercise	Control	Exercise
Length (mm)	112.8 (3.01)	113.1 (3.48)	124.5 (6.71)	117.1 (5.88)	123.2 (6.07)	117.9 (5.18)	127.8 (8.71)	120.9 (9.10)	126.3 (5.15)	127.9 (7.95)
Weight (g)	16.24 (2.129)	15.60 (1.546)	20.51 (3.452)	17.50 (3.145)	20.37 (3.164)	17.61 (2.544)	23.01 (4.803)	19.50 (4.391)	21.30 (2.825)	23.64 (5.120)
Condition factor	1.13 (0.118)	1.07 (0.024)	1.05 (0.053)	1.08 (0.056)	1.08 (0.040)	1.07 (0.046)	1.09 (0.055)	1.08 (0.054)	1.05 (0.036)	1.11 (0.074)
Glucose (ng/mL)	54.2 (6.58)	52.1 (4.66)	51.0 (12.32)	47.3 (13.91)	46.6 (12.45)	41.8 (9.84)	60.2 (7.44)	72.8 (12.27)	54.1 (14.78)	52.0 (11.11)
Hematocrit	43.3 (2.42)	44.3 (4.27)	38.5 (5.00)	38.8 (3.93)	35.9 (5.11)	34.2 (4.80)	35.4 (4.46)	38.9 (6.01)	35.9 (3.48)	36.5 (2.88)
HSI	1.54 (0.106)	1.40 (0.220)	1.43 (0.123)	1.53 (0.186)	1.55 (0.220)	1.78 (0.171)	1.61 (0.211)	1.79 (0.198)	1.51 (0.136)	1.70 (0.214)
Liver glycogen (mg/g)	25.4 (9.86)	44.6 (11.77)	15.3 (5.18)	21.6 (15.27)	32.0 (16.47)	33.8 (27.14)	28.5 (15.08)	34.0 (8.18)	18.3 (10.15)	15.7 (4.72)

0.002). Mean HSI varied among cohorts, treatments, and sampling dates ($P \leq 0.022$), being higher in the 1994 than the 1995 cohort and in the exercised than control treatment. The pattern of change in HSI over the sampling period differed between cohorts but was similar between treatment groups within cohorts. There was no trend in change in HSI from November to March and April for either cohort or treatment ($P \geq 0.069$). Mean liver glycogen levels were higher in the 1995 cohort than the 1994 cohort and differed among sampling dates ($P < 0.001$). Mean liver glycogen levels decreased over time in each treatment of the 1994 cohort ($P < 0.001$), but not in the 1995 cohort ($P = 0.085$). In the 1995 cohort, we found a decreasing trend from summer to spring, when mean liver glycogen levels increased in each group during March 1997 ($P < 0.001$).

Juvenile Stress Physiology

Size and condition of the sampled fish were similar between treatment groups, time 0 and stress samples, and raceways ($P \geq 0.165$; Tables 3, 4). Both mean length and K were greater in the 1994 cohort ($P \leq 0.005$). Both mean plasma glucose and cortisol levels increased after stress and were greater in the control salmon ($P \leq 0.049$). Mean plasma glucose levels were

TABLE 3.—Mean (SD in parentheses) length, weight, condition factor, plasma glucose, plasma cortisol, liver glycogen, hematocrit, and hepatosomatic index (HSI) of the 1994 cohort of juvenile Chinook salmon reared at Lookingglass Hatchery, Oregon, under control and exercised (increased-flow) growth regimes and sampled before (time 0) and 2 h after experiencing 30 s of stress.

	9 Nov 1995				29 Mar 1996			
	Control		Exercise		Control		Exercise	
Variable	Time 0	Stress	Time 0	Stress	Time 0	Stress	Time 0	Stress
Length (mm)	109.4 (8.19)	111.8 (7.72)	117.9 (6.95)	112.1 (5.89)	126.4 (11.60)	124.8 (7.98)	128.4 (8.56)	123.1 (6.57)
Weight (g)	15.21 (2.308)	16.18 (3.289)	19.13 (3.618)	16.09 (2.747)	22.90 (6.899)	21.53 (4.224)	24.12 (4.893)	21.04 (3.662)
Condition factor	1.17 (0.191)	1.14 (0.056)	1.15 (0.054)	1.13 (0.048)	1.11 (0.062)	1.10 (0.080)	1.13 (0.047)	1.12 (0.034)
Glucose (ng/mL)	61.0 (10.80)	83.7 (8.95)	57.4 (12.35)	89.8 (10.73)	81.9 (14.53)	135.2 (18.72)	69.9 (16.19)	105.7 (27.60)
Cortisol (ng/mL)	24.3 (18.47)	197.5 (51.40)	27.2 (18.13)	176.1 (55.90)	56.7 (22.90)	239.3 (70.11)	73.7 (34.75)	206.3 (68.62)
Liver glycogen (mg/g)	23.9 (11.62)	19.5 (10.15)	25.9 (7.77)	22.4 (13.64)	3.7 (1.60)	3.3 (2.68)	3.9 (1.24)	4.1 (1.98)
Hematocrit	38.8 (4.09)	40.4 (3.77)	38.2 (3.43)	42.1 (3.87)	36.4 (4.53)	31.6 (2.96)	37.4 (4.29)	31.3 (3.86)
HSI	1.81 (0.342)	1.63 (0.198)	1.84 (0.159)	1.64 (0.228)	1.66 (0.231)	1.48 (0.169)	1.68 (0.201)	1.44 (0.167)

TABLE 4.—Mean (SD in parentheses) length, weight, condition factor, plasma glucose, plasma cortisol, liver glycogen, hematocrit, and hepatosomatic index (HSI) of the 1995 cohort of juvenile Chinook salmon reared at Lookingglass Hatchery, Oregon, under control and exercised (increased-flow) growth regimes and sampled before (time 0) and 2 h after experiencing 30 s of stress.

	19 Nov 1996				4 Apr 1997			
	Control		Exercise		Control		Exercise	
Variable	Time 0	Stress	Time 0	Stress	Time 0	Stress	Time 0	Stress
Length (mm)	116.5 (5.47)	117.1 (6.01)	116.2 (5.62)	117.3 (7.73)	129.1 (6.21)	128.3 (6.97)	125.6 (7.54)	124.9 (6.31)
Weight (g)	17.97 (2.808)	18.38 (2.886)	17.31 (2.968)	18.62 (4.040)	22.86 (3.539)	22.93 (4.248)	21.71 (4.783)	21.11 (3.209)
Condition factor	1.13 (0.088)	1.14 (0.044)	1.09 (0.038)	1.13 (0.046)	1.05 (0.043)	1.08 (0.066)	1.08 (0.086)	1.08 (0.046)
Glucose (ng/mL)	56.6 (7.16)	82.6 (12.45)	54.3 (5.76)	81.0 (6.74)	59.1 (14.25)	92.7 (23.61)	63.8 (24.56)	85.7 (18.95)
Cortisol (ng/mL)	103.7 (35.86)	272.5 (35.35)	98.1 (52.87)	235.5 (56.72)	124.0 (45.90)	229.4 (33.43)	102.9 (33.99)	246.0 (44.18)
Liver glycogen (mg/g)	44.6 (11.77)	29.0 (20.15)	30.6 (14.48)		15.3 (8.15)		15.2 (8.75)	
Hematocrit	40.8 (9.06)	40.5 (2.79)	43.5 (4.31)	40.3 (8.64)	36.3 (2.85)	34.1 (3.20)	35.3 (3.07)	34.1 (2.58)
HSI	1.53 (0.120)	1.46 (0.273)	1.41 (0.200)	1.48 (0.211)	1.49 (0.144)	1.49 (0.159)	1.60 (0.197)	1.54 (0.206)

greater in the 1994 cohort, and mean cortisol levels were greater in the 1995 cohort ($P < 0.001$). Mean plasma glucose and cortisol levels were higher in the later (March and April) samples than in the earlier (November) samples, except for cortisol in the 1995 cohort, which did not vary between sampling dates ($P \geq 0.05$). Mean hematocrit decreased following stress, being lower in the later samples for each cohort ($P \leq 0.015$), but did not differ between cohorts or treatments ($P \geq 0.132$). Hematocrit varied between the two raceways for the exercise group ($P = 0.034$), but not the control raceways ($P \geq 0.05$). Mean HSI decreased following stress and was higher in the 1994 cohort ($P < 0.001$). Mean HSI also varied with sampling date ($P < 0.001$), but only in the 1994 cohort, the early sample having a higher mean HSI. The HSI also varied between the two raceways for the control group ($P = 0.033$), but not the exercise raceways ($P \geq 0.05$). Mean liver glycogen levels did not change following stress or between treatments ($P \geq 0.095$). However, mean liver glycogen levels were greater in the 1995 cohort and in the earlier samples ($P < 0.001$).

Survival and Adult Returns

Survival of smolts to Lower Granite Dam did not vary between cohorts, treatment groups, or raceways ($P = 0.269$). Detection rates were very similar between cohorts and treatments, ranging from 58.7% to 60.7%. Migration time to Lower Granite Dam did not vary between treatments ($P = 0.183$) but did vary between cohorts and raceways ($P < 0.001$). The 1994 cohort reached Lower Granite Dam in a mean of 23.4 d; the 1995 cohort mean was 20.7 d. This 3-d difference in migration timing was probably caused by the later discharge peak in 1996 (24 April) versus 1997 (20 April) and, while statistically significant, is unlikely to have been biologically significant because detection rates at the dam did not significantly differ. Raceway 16, which was used for the 1994 cohort exercised group and the 1995 cohort control, had a slower mean migration time (22.1 d) to Lower Granite Dam than the other three raceways (21.1–21.3 d), but again, this difference is unlikely to have been biologically significant. There was an interaction between cohort and raceway ($P = 0.014$) but not between treatment and cohort ($P = 0.984$).

Harvest and stray rates were generally low, ranging from 0% to 6.3% except for one control raceway of the 1994 cohort, in which 4 of 19 recoveries (21.1%) were from Chinook salmon that had strayed (Table 5). The majority of the adults (78.9–100%) from each raceway returned to Lookingglass Creek. Harvest, hatchery return, and stray rates did not vary between cohorts, treatments, or raceways ($P \geq 0.116$). Mean SAR varied with cohort ($P = 0.002$), but not between treatments or raceways ($P \geq 0.091$). The 1995 cohort survived at a much higher rate than the 1994 cohort; only 51 CWTs (0.04%) were recovered from the 1994, but 568 (0.39%) were recovered from the 1995 cohort. Of the control salmon, a mean of 0.26% of the releases were recovered; of those, 91.3% returned to Lookingglass Creek, 6.3% were strays, and 2.5% were captured in the harvest. A mean of 0.23% of the exercised salmon

TABLE 5.—Number of Chinook salmon smolts released with coded wire tags (CWTs), percent of passive integrated transponder tags detected at and estimated survival rate to Lower Granite Dam, harvest hatchery returns, straying rates, and number and rate of survival from smolt to adult for each cohort (1994 and 1995) and raceway of Chinook salmon reared under an exercise or control growth regime at Lookingglass Fish Hatchery, Oregon.

Experimental group and raceway	CWTs released	Dam recoveries		Recoveries						Smolt-to-adult survival	
				Harvest		Hatchery		Stray			
		Percent	Survival	*N*	Rate	*N*	Rate	*N*	Rate	*N*	Rate
1994 cohort											
Control											
Raceway 15	34,379	44.0	0.58	0	0	15	78.9	4	21.1	19	0.055
Raceway 17	32,997	47.0	0.63	1	6.3	15	93.8	0	0	16	0.048
Total or average	67,376	45.5	0.61	1	2.9	30	85.7	4	11.4	35	0.052
Exercise											
Raceway 14	33,902	45.0	0.56	0	0	10	100	0	0	10	0.029
Raceway 16	33,534	46.6	0.62	0	0	6	100	0	0	6	0.018
Total or average	67,436	45.8	0.59	0	0	16	100	0	0	16	0.024
1995 cohort											
Control											
Raceway 17	37,340	45.4	0.63	2	1.4	138	97.2	2	1.4	142	0.380
Raceway 16	36,310	41.9	0.57	3	2.1	136	95.1	4	2.8	143	0.394
Total or average	73,650	43.7	0.60	5	1.8	274	96.1	6	2.1	285	0.387
Exercise											
Raceway 14	36,172	43.8	0.59	2	1.2	157	97.5	2	1.2	161	0.445
Raceway 15	37,156	41.0	0.59	1	0.8	117	95.9	4	3.3	122	0.328
Total or average	73,328	42.4	0.59	3	1.1	274	96.8	6	2.1	283	0.387

were recovered, of which 98.4% returned to the hatchery, 1.1% strayed, and 0.5% were captured in fisheries.

Age composition of the returning adults varied between treatment groups but only for the age-3 adults ($P = 0.014$), for which the return rates were 9.6% for exercised salmon and 1.5% for controls (Table 6; Figure 2). Age composition did not vary between cohorts or raceways ($P \geq 0.096$), but there was an interaction between treatment and cohort for the age-3 salmon ($P = 0.032$). Mean percentage of exercised salmon returning at ages 4 (88.4%) and 5 (1.9%) did not differ from those of the control salmon (93.2% and 5.4%, respectively; $P \geq 0.496$).

TABLE 6.—Number of Chinook salmon released with coded wire tags (CWTs), number recovered at age, and age composition of returning adults for each cohort (1994 and 1995) reared under an exercise or control growth regime at Lookingglass Fish Hatchery, Oregon.

Experimental group and raceway	CWTs released	Age 3		Age 4		Age 5	
		N	Percent	*N*	Percent	*N*	Percent
1994 cohort							
Control							
Raceway 15	34,379	0	0.0	14	93.3	1	6.7
Raceway 17	32,997	0	0.0	14	93.3	1	6.7
Total or average	67,376	0	0.0	28	93.3	2	6.7
Exercise							
Raceway 14	33,902	1	10.0	9	90.0	0	0.0
Raceway 16	33,534	1	16.7	5	83.3	0	0.0
Total	67,436	2	13.3	14	86.7	0	0.0
1995 cohort							
Control							
Raceway 17	37,340	6	4.3	128	89.9	8	5.8
Raceway 16	36,310	2	1.5	137	96.3	4	2.2
Total or average	73,650	8	2.9	265	93.1	12	4.0
Exercise							
Raceway 14	36,172	8	5.1	145	89.8	8	5.1
Raceway 15	37,156	8	6.8	111	90.6	3	2.6
Total or average	73,328	16	6.0	256	90.2	11	3.8

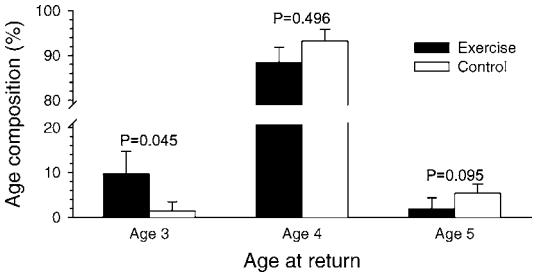

FIGURE 2.—Mean + SD percent of total adult Chinook salmon returns from the 1994 and 1995 cohorts reared under control or exercise (increased-flow) growth regimes at Lookingglass Fish Hatchery, Oregon, and returning at ages 3–5.

Discussion

We found few differences between exercised and control Chinook salmon, most notably a difference in age composition of returning adults. The raceway flow rate to which the exercised fish were exposed may not have been sufficient to induce physiological changes in these salmon.

Juvenile Growth and Physiology

Somatic and physiological changes during the juvenile growth and smoltification periods did not substantially vary between treatment groups. Patterns of change were similar between treatment groups, although the magnitude of change sometimes differed. However, the patterns of change were not always similar between cohorts. The few differences in size between groups on a given sampling period are unlikely to have affected physiological results.

Growth and swimming endurance have been shown to be promoted by exercise (Hochachka 1961), maximum growth occurring at a continuous exercise rate of 1–1.5 BL/s (Besner and Smith 1983; Davison 1989) and the greatest food conversion rate at 1.0 BL/s (Jorgensen and Jobling 1993). Houlihan and Laurent (1987) reported an increase in the rates of both protein synthesis and degradation in rainbow trout *O. mykiss* and attributed increased growth to a proportionately greater rate of protein synthesis in fish exercised at 1.0 BL/s. In our study, we were able to attain a maximum flow of only 0.75 BL/s and found no difference in growth between treatments.

Plasma glucose has been shown to both increase and decrease after a period of exercise (Wendt and Saunders 1973; Johnston and Moon 1980; Woodward and Smith 1985; Nielsen et al. 1994). Plasma glucose levels normally increase leading up to smoltification, then decrease during smoltification (Woo et al. 1978; Sweeting et al. 1985; Virtanen 1987). Our salmon seemed to have been more influenced by changes due to smoltification because both the exercised and control salmon displayed an initial decrease in plasma glucose during late winter followed by an increase in April, although none of the changes were large. These salmon were released in March and April, so samples could not be collected through the entire smoltification process.

Davie et al. (1986) found no change in the hematocrit or hemoglobin of exercised rainbow trout. In both of our cohorts, hematocrit fluctuated similarly during the smoltification period but did not show an increasing or decreasing trend. Hematocrit is expected to increase during smoltification (Stefansson et al. 1989), but Virtanen (1987) reported an increase in hematocrit during the winter followed by a decrease during smoltification. It may be that smoltification-related changes in hematocrit occurred in our salmon after they were released.

Liver physiology changes during smoltification (Blake et al. 1984; Bradley and Rourke 1984; Johanning and Bradley 1989; McCormick and Bern 1989) and liver glycogen levels and HSI decrease as salmon become increasingly active (Woo et al. 1978; Sheridan et al. 1983, 1985; Virtanen 1987; Plisetskaya et al. 1988; Cowley et al. 1994; Hoffnagle 1994). Additionally, HSI increases in association with periods of low activity (Boujard and Leatherland 1992). Therefore, we would expect that exercised salmon would have low HSI. Liver glycogen and HSI levels varied similarly between treatments within cohorts but not between cohorts; however, we saw no differences between treatments, which leads us to conclude that a flow rate of 0.75 BL/s is insufficient to induce this level of energy expenditure.

Juvenile Stress Physiology

An increase in plasma glucose and cortisol levels is an indicator of stress in fish, as shown in a variety of salmonids (Woodward and Smith 1985; Barton et al. 1986; Barton and Iwama 1991). Plasma cortisol levels also rise during smoltification (Specker and Schreck 1982; Langhorne and Simpson 1986). Plasma glucose and cortisol levels increased following stress, but there were no consistent differences between treatment groups and no difference in change of plasma cortisol levels over time.

Hematocrit, HSI, and liver glycogen displayed no consistent trends following stress or between treatment groups. It is likely that 2 h following the stress event or the amount of stress (30 s in a net) were insufficient to illicit a response in hematocrit or HSI. Hochachka (1961) reported that following stress (5 min of being chased), trained trout had used more of their available muscle glycogen and recovered their muscle and liver

glycogen more quickly. In our case, it appears that little liver glycogen was used but our stressor was for a shorter period and probably involved less physical exertion.

Survival and Adult Returns

We found no benefit of exercise to either downstream migration timing (arrival at Lower Granite Dam), downstream migration survival (detection at Lower Granite Dam), return rates, or smolt-to-adult survival. Wendt and Saunders (1973) reported an increase in smolt-to-adult survival rate in Atlantic salmon *Salmo salar* exercised at velocities greater than 2.0 BL/s for 2–12 months before release. Evenson and Ewing (1993) found no benefit in adult return rate of 1 h of exercise daily for the month before release in steelhead (anadromous rainbow trout). However, this may not have been a sufficient amount of exercise, as may have been the case in our study.

A greater proportion of the exercised Chinook salmon than control fish returned at age 3. If this was truly caused by the exercise regime, then this is an undesirable result because hatchery salmon tend to return at a younger age than natural salmon and considerable effort has been expended by hatchery managers to prevent this. Although a greater proportion of the exercised salmon in both cohorts returned as jacks (13.5% versus 0% in 1994; 6% versus 2.5% in 1995), the greater length and weight of the exercised 1994 cohort in the autumn preceding smoltification may explain the larger difference in the 1994 cohort and the overall result (Tables 1, 2). Maturing salmon tend to be larger at an early age, and size appears to be the primary factor affecting early maturation in salmon, although smaller salmon with a high fat content may also mature early (Silverstein et al. 1998). Shearer and Swanson (2000) showed endocrinological and histological evidence that maturation in males was initiated approximately a full year before spawning. Restricting feeding during fall and spring (Hopkins and Unwin 1997) and favoring muscle growth over fat accumulation (Silverstein et al. 1999) can reduce the rate of precocial maturation in salmon. It may be that the low level of exercise to which we subjected the exercised salmon was high enough to increase appetite but not so high as to prevent fat accumulation. Also, the smaller size of the exercised 1995 cohort may have been indicative of underfeeding. We do not have jack return data for natural chinook salmon in the Grande Ronde River basin for those cohorts. However, mean percentage of salmon returning at age 3 (all males) for three natural Grande Ronde populations was 5.3% for the 1997–2001 cohorts. So, it is likely that the jack rate for the salmon in our study (mean = 5.6%) was similar to that of the 1994 and 1995 cohorts of natural Chinook salmon in this river basin.

Conclusions

Our results provide little evidence that rearing Chinook salmon under a seasonally variable flow regime of 0.25–0.75 BL/s provided any benefit to the salmon over a steady flow of 0.2 BL/s. In fact, the most significant results documented the exercised salmon returning at a younger age than the controls, opposite of what managers would like to see.

The literature provides information on improved return rates for salmon reared under a presmolt exercise regime but recommendations differ. Besner and Smith (1983) suggested that a long-term low-velocity exercise regime might improve swimming ability in coho salmon *O. kisutch* and therefore improve survival. The lowest velocity that they tested was 1 BL/s, higher than we were able to achieve. Wendt and Saunders (1973) reported an increase in smolt-to-adult survival rate in Atlantic salmon exercised at high velocities (2.0 BL/s). Kiessling et al. (1994) studied postsmolt Chinook salmon in saltwater and concluded that improvements in growth reported in the literature may have resulted from behavioral changes caused by increased flow rather than exercise per se. They concluded that a low swimming speed (0.5 BL/s) combined with a maximum food ration was the most cost-effective protocol for raising postsmolt Chinook salmon. However, this will result in earlier maturation of males, as seen in this study and reported for Grande Ronde Chinook salmon reared in a captive broodstock program (Hoffnagle et al. 2003). Jorgensen and Jobling (1993) reported that exercise may have reduced agonistic activity and improved the rate of fin-wound healing but did not improve osmoregulatory activity during smoltification. Further studies may be warranted for Chinook salmon reared at LFH, but a greater number of replicates (raceways and cohorts) will be required to better evaluate this moderate and seasonally variable growth regime. The flows rates provided to the exercise groups at LFH were the maximum attainable at the facility, so it appears that we cannot improve survival of Chinook salmon reared at Lookingglass Fish Hatchery by simply increasing flow over the standard flow rate employed there. Therefore, if flow rates cannot be increased to at least 1 BL/s, it appears that keeping them at a lower level is more beneficial and cost effective.

Acknowledgments

We thank Timothy A. Whitesel and Steven J. Parker for getting these studies started. We also appreciate the able assistance of the hatchery crew at Lookingglass

Fish Hatchery for rearing the salmon we evaluated and those surveyors who recovered snouts on spawning ground surveys. Deb Eddy helped immensely with retrieval of auxiliary data. Scott Pattrerson assisted with the fish culture descriptions and calculations. This study was funded by the U.S. Fish and Wildlife Service, Lower Snake River Compensation Plan.

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