INFORMATION REPORTS Number 2005-02

FISH DIVISION Oregon Department of Fish and Wildlife

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

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on Juvenile Physiology, Survival and Adult Return

of Hatchery-reared Chinook Salmon Oncorhynchus tshawytscha

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April 2005

Funds supplied by:

Lower Snake River Compensation Plan, U.S. Fish and Wildlife Service

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Abstract

To improve post-release survival in nature, salmon hatcheries have begun to better simulate natural conditions, such as increasing the flow rate in raceways to a rate similar to that seen in nature. This "exercises" the salmon in the expectation that improving swimming ability will improve their survival during smolt migration, resulting in better survival to adulthood. We examined the effect of variable moderate flow rates (0.25-0.75 body lengths per second) on growth and physiology of juvenile chinook salmon Oncorhynchus tshawytscha and their ability to withstand acute stress, survive downstream migration and return as adults. Over the 5-8 month sampling period, mean length, weight and condition factor increased similarly in both the exercised and control groups. Mean plasma glucose levels were similar in each treatment group and peaked in early spring of each year. Hematocrit did not vary in a consistent trend for either treatment group or cohort. Hepatosomatic index (HSI) decreased in the 1994 cohort control group and increased in the 1995 cohort exercised group. In both cohorts, liver glycogen levels decreased through the winter and continued to decline in the 1994 cohort while in the 1995 cohort there was a significant peak in liver glycogen levels in each group during March 1997. Following stress, mean plasma glucose and cortisol levels increased, mean hematocrit varied inconsistently, mean HSI generally decreased, mean CSI decreased inconsistently in the 1995 cohort and mean liver glycogen level did not change. Mean survival of smolts to Lower Granite Dam did not vary between treatment groups with detection rates ranging narrowly from 58.7-60.7%. Mean percentage of adults returning at age 3 was higher for exercised salmon than for controls and a higher percentage of controls returned at age 5 than exercised salmon. Mean smolt-to-adult survival rate varied significantly between cohorts but there was no difference in mean survival rate between treatment groups. Variation within cohorts was greater between the exercised raceways than the controls, indicating that additional years of study are needed to compensate for large differences in survival between cohorts to make any conclusions regarding differences between treatments. Our results provide little evidence that rearing chinook salmon under a moderately increased and seasonally variable flow regime provided any benefit to the salmon over a steady low flow.

Introduction

Improving 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. Additionally, it is imperative to reduce the rate of straying of hatchery-reared salmon into streams without hatchery supplementation in order to maintain the genetic integrity of native populations. This is particularly true when the hatchery stock is non-endemic, as was the case for the Rapid River Chinook salmon reared at Lookingglass Fish Hatchery (LFH).

Several points in the pre-smolt life history of hatchery-reared salmon may be managed and modifications implemented in order to improve the likelihood of achieving these management objectives. To improve survival in nature, the trend in salmon hatcheries is to better simulate natural conditions. One method is to increase the flow rate in raceways to a rate similar to that seen in nature. Increased raceway flow "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 and may not be possible if water is limited. However, the benefits of an increased return rate, due to improved imprinting and/or smolt-to-adult survival rate, may outweigh these costs. These issues are of particular importance when dealing with ESA-listed populations.

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

Methods

Hatchery and fish

Lookingglass Fish Hatchery is located 3.7 km upstream from the mouth of Lookingglass Creek which flows into the Grande Ronde River at river kilometer (RK) 137, a tributary of the Snake River in northeast Oregon at RK 270 (Figure 1). Fish released from LFH migrate 850 km downstream to the ocean, through eight mainstem dams on the Snake and Columbia rivers.

Rapid River stock spring Chinook salmon were reared from eggs at and released from LFH. We used well water for early rearing and unfiltered Lookingglass Creek water when the salmon were stocked into outdoor raceways in the spring following hatching. We conducted exercise treatments during 1995-1996 (1994 cohort) and 1996-1997 (1995 cohort). Four raceways were used for each cohort, creating two replicates for each cohort and treatment. All statistical tests were considered to be significant at α =0.1



Figure 1. Grande Ronde and Imnaha river basins in northeast Oregon and location of Lookingglass Fish Hatchery.

Exercise protocol

The parr were exposed to one of two protocols for flow rate of water through the outdoor rearing raceways. Control salmon were held at a consistent current velocity of approximately 0.2 body lengths / second (BL/s), the standard flow rate for LFH (Figure 2). Water velocity in the exercised raceways varied seasonally, ranging from 0.25 BL/s during winter to 0.75 BL/s in late summer, the maximum allowable at LFH. Water flow into the raceways was regulated to increase current velocity as the fish grew and reached a maximum of 105 L/s.. The experimental period ranged from November (1994 cohort) or July (1995 cohort) through the following March/April, when the salmon were released. Mean size at smoltification was 22.5 g and did not vary between treatment groups or cohorts (Table 1).

Juvenile growth

Parr were sampled periodically throughout the rearing cycle: July (1995 cohort, only), November and every two weeks prior to release during smoltification (February - March/April). At each sampling period, we measured length and weight from the sampled individuals and calculated condition factor (K). We compared mean length, weight and K for each sampling date between treatment groups using a t-test and for trends over time by ANOVA and regression (Sokal and Rohlf 1981).



Figure 2. Experimental design for evaluation of moderately increased raceway flow rates at Lookingglass Fish Hatchery. Vertical lines indicate dates of physiological and stress sampling.

Table 1. Target and actual mean weight of control and exercised Chinook salmon smolts released from Lookingglass Fish Hatchery, 1994 and 1995 cohorts.

		Со	ntrol	Exer	rcised
Cohort	Cohort Release date		Actual mean weight (g)	Target weight (g)	Actual mean weight (g)
1994	4 APR 1996	22.7	22.2	22.7	22.7
1995	6 APR 1997	22.7	23.3	22.7	21.9

Juvenile physiology

At each sampling period, length and weight were measured for each fish, blood samples were collected for measurement of hematocrit and plasma glucose and cortisol levels, and the liver collected for measurement of liver glycogen level and weighed for calculation of hepatosomatic index (HSI = liver weight / body weight * 100). Means of physiological variables for each sampling date were compared between treatment groups using a t-test and for trends over time by ANOVA and regression (Sokal and Rohlf 1981).

Juvenile stress physiology

Twice (1994 cohort) or three times (1995 cohort), a stress test was conducted in which a sample of 8-10 fish from each treatment was sampled immediately before and two hours after being stressed by being held in a net out of water for 30 seconds. The same set of samples and measurements were collected from the stress-tested salmon in addition to the heart being collected and weighed for calculation of cardiosomatic index (CSI = heart weight / body weight * 100). Means of physiological variables, length, weigh and condition factor (K) were compared between treatment groups and pre- vs. post-stress samples on a given sampling date using a t-test (Sokal and Rohlf 1981).

Survival and adult returns

All smolts released were fin-clipped to identify them as hatchery-reared and smolts in each raceway were marked with unique coded-wire tags to identify treatments. Additionally, approximately 900 parr (1994 cohort) and 5,000 parr (1995 cohort) from each raceway were individually marked with PIT tags for estimation of downstream migration timing and survival. At the time of normal seaward migration, the smolts were released directly into Lookingglass Creek to migrate to the ocean and return to LFH. Adult return data were collected over the period of 1997-2000. Snouts containing coded-wire tags were collected in ocean and freshwater fisheries, from carcasses recovered on spawning grounds in the target stream and other streams (strays) and from adults returning to LFH (some were captured at Lower Granite Dam and transported to LFH). For collections in which subsamples were collected (fisheries and some spawning ground surveys), expansions of the number of tags recovered were made to estimate the total number of adults returning within each group.

Migration timing was the time required for a PIT-tagged smolt to reach Lower Granite Dam. The 1994 cohort was released on 4 April 1996 and the 1995 cohort was released on 7 April 1997. We compared survival rates between experimental groups by PIT tag observation of smolts at Lower Granite Dam and of adults captured at the hatchery weir, in the harvest and as strays. We also compared total smolt-to-adult survival and age composition of adults returning to northeast Oregon. Survival rate is the percentage of released tags recovered to a given point (e.g., Lower Granite Dam or hatchery) or from all sources (fisheries, strays and returning to LFH) for adult survival rate. Age composition of the returning cohort is the percentage that each age class comprises of the total returning to the hatchery weir, recovered on spawning ground surveys in Lookingglass Creek or as strays. Mean survival rates and age composition data were transformed using an arcsine transformation (Krebs 1999). Differences in migration timing and survival between treatments were tested using a two-way ANOVA with treatment and cohort as independent variables (Sokal and Rohlf 1981).

Results and Discussion

We found few differences between exercised and control 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 differences in these salmon.

Juvenile growth

Fish growth, as measured by length, weight and K, followed similar patterns for the exercised and control groups but did not substantially vary between treatment groups (Figures 3-5). Mean size of each treatment and cohort increased over the sampling period ($P \le 0.0569$), except the 1994 cohort exercised group (P=0.1890), which were generally larger than the controls, though only significantly so on 9 November 1995 (length and weight; $P \le 0.0036$) and 19 March 1996 (length; P=0.0069). Mean weight of the control group was larger than that of the exercised group on 20 February 1996 (P=0.0570). In the 1995 cohort, the control salmon were larger in both length and weight ($P \le 0.0753$) on 20 February, 6 March and 20 March 1997. Condition factor varied little over the sampling period and the only group with a significant change was the 1994 cohort control salmon, in which K decreased (P=0.0569). Condition factor also varied little between groups. The only differences were in the 1994 cohort where mean K was greater for the control salmon on 20 February 1996 (P=0.0748) and on 19 March 1996 (P=0.0010), when the sampled exercised salmon included five individuals with K ≤ 0.92 .

Growth and swimming endurance have been shown to be promoted by exercise (Hochachka 1961), with maximum growth 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 growth, if anything, was inhibited by the exercise regime. Data for calculation of food conversion were only sporadically recorded and showed no trends in variation seasonally or between treatments. Davison (1989) pointed out that feeding rate is important when comparing exercised to unexercised fish. When fish are fed to satiation, exercise does appear to promote growth (Leon 1986). However, studies using smaller rations resulted in similar growth rates between exercised and control groups (Hochachka 1961; White and Li 1985; Woodward and Smith 1985).

Juvenile physiology

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

Each treatment group showed peaks in plasma glucose during early spring of each year ($P \le 0.0151$; Figure 6). However, mean plasma glucose levels showed no trend over time ($P \ge 0.3090$) for either group or cohort and patterns of change were similar in each treatment group with few differences for any date. For the 1994 cohort, the exercise group had a greater mean than the control group on 19 March 1996 (P=0.0950) while the control group had a higher mean plasma glucose level on 29 March 1996 (P=0.0401). For the 1995 cohort, the control group had a higher mean plasma glucose level on 25 July 1996 (P=0.0060) and the exercised salmon had a higher mean plasma glucose level on 20 March 1997 (P=0.0067).

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



Figure 3. Mean (± 1 SD) fork length (mm) of juvenile Chinook salmon reared under control and exercised (increased flow) growth regimes, 1994 and 1995 cohorts. Note: '*' indicates a significant difference between control vs. exercise salmon for a given sampling date. *=P<0.1; **=P<0.05.



Figure 4. Mean (± 1 SD) weight (g) of juvenile Chinook salmon reared under control and exercised (increased flow) growth regimes, 1994 and 1995 cohorts. Note: '*' indicates a significant difference between control vs. exercise salmon for a given sampling date. *=P<0.1; **=P<0.05.



Figure 5. Mean (± 1 SD) condition factor (K) of juvenile Chinook salmon reared under control and exercised (increased flow) growth regimes, 1994 and 1995 cohorts. Note: '*' indicates a significant difference between control vs. exercise salmon for a given sampling date. *=P<0.1; **=P<0.05.



Figure 6. Mean (± 1 SD) plasma glucose level (ng/mL) of juvenile Chinook salmon reared under control and exercised (increased flow) growth regimes, 1994 and 1995 cohorts. Note: '*' indicates a significant difference between control vs. exercise salmon for a given sampling date. *=P<0.1; **=P<0.05.

1994). Plasma glucose levels normally increase leading up to smoltification then decrease during smoltification (Woo et al 1978; Sweeting et al 1985; Virtanen 1987). In each year of our study, 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/April so samples could not be collected through the entire smoltification process.

Hematocrit did not vary in a consistent trend ($P \ge 0.1984$) for either treatment group or cohort (Figure 7). Also, there was only one date on which hematocrit varied between treatment groups: mean hematocrit of the exercised group was higher than that of the control group in the 1995 cohort on 25 July 1996 (P=0.0070).

Davie et al (1986) found no change in hematocrit or hemoglobin of exercised rainbow trout. In both cohorts, hematocrit fluctuated similarly during the smoltification period. Hematocrit is expected to increase during smoltification (Stefansson et al 1989) due to changes in respiratory capacity (Higgins 1985) caused by changes in hemoglobin (Koch 1982) and swelling of erythrocytes (Soivio and Nikinmaa 1981). Virtanen (1987) reported an increase in hematocrit during the winter followed by a decrease during smoltification.

Hepatosomatic index varied over time but inconsistently between cohorts (Figure 8). In the 1994 cohort, HSI decreased in the control group (P=0.0301) but not in the exercised group (P=0.1027). For the 1995 cohort, HSI increased in the exercised group (P=0.0569) but not in the control group (P=0.2877). The pattern of change in HSI differed between cohorts but was similar between groups within cohorts. In the 1994 cohort, each group had its highest mean level on 9 November 1995 and its lowest on 5 March 1996, although these changes were statistically significant only in the exercised group (P=0.0133). In the 1995 cohort, each group had its lowest mean HSI on 25 July 1996 and each had a peak in HSI on 20 March 1997, although this was significant only in the exercised group (P<0.0001). There were no pairwise differences in mean HSI on any sampling date for the 1994 cohort (P \ge 0.6032). For the 1995 cohort, HSI was higher in the control salmon on 19 November 1996 (P=0.0501) and for the exercised salmon on 6 March, 20 March and 4 April 1997 (P \le 0.0921).

Liver glycogen level decreased over time in each treatment and cohort ($P \le 0.0665$), except the 1995 cohort control group (P=0.1799; Figure 9). In the 1994 cohort, there was a consistent decrease in liver glycogen level. In the 1995 cohort, the trend was decreasing from summer to spring, when mean liver glycogen levels increased in each group during March 1997 (P<0.0001). There was only one pairwise difference in liver glycogen level between groups: the 1995 cohort control group had a higher mean liver glycogen level on 19 November 1996 (P=0.0208).

Liver physiology changes during smoltification (Blake et al 1984; Bradley and Rourke 1984; Johanning and Bradley 1989; McCormick and Bern 1989). Decreases in liver glycogen and fatty acid synthesis and an increase in glycogen and fatty acid use cause a decrease in liver glycogen levels and HSI during smoltification (Woo et al 1978; Sheridan et al 1983; 1985; Virtanen 1987; Plisetskaya et al 1988; Cowley et al 1994). We observed that liver glycogen and HSI levels varied similarly between treatments and within cohorts but not between cohorts. Hepatosomatic index increases in association with periods of low activity (Boujard and Leatherland 1992) and HSI decreases during smoltification, as salmon become increasingly active (Hoffnagle 1994). Therefore, we would expect that exercised salmon would have low HSI. We saw no difference in liver glycogen or HSA between treatments and may conclude that a flow rate of 0.75 BL/s is insufficient to induce this level of energy expenditure.



Figure 7. Mean (± 1 SD) hematocrit of juvenile Chinook salmon reared under control and exercised (increased flow) growth regimes, 1994 and 1995 cohorts. Note: '*' indicates a significant difference between control vs. exercise salmon for a given sampling date. *=P<0.1; **=P<0.05.



Figure 8. Mean (± 1 SD) hepatosomatic index (HSI) of juvenile Chinook salmon reared under control and exercised (increased flow) growth regimes, 1994 and 1995 cohorts. Note: '*' indicates a significant difference between control vs. exercise salmon for a given sampling date. *=P<0.1; **=P<0.05.



Figure 9. Mean (± 1 SD) liver glycogen level (mg/g) of juvenile Chinook salmon reared under control and exercised (increased flow) growth regimes, 1994 and 1995 cohorts. Note: '*' indicates a significant difference between control vs. exercise salmon for a given sampling date. *=P<0.1; **=P<0.05.

Juvenile stress physiology

Size and condition of the sampled salmon were usually similar between treatment groups and between Time \emptyset and Stress samples (Figures 10 and 11). Size within each group varied and was reflected in occasional size differences between treatment groups during a given sampling period and between pre- and post-stress sampling within treatment groups. However, K differed only once and patterns of change in physiological indices were similar between treatment groups and unlikely to have been affected by small size differences of the sampled salmon. Mean length and weight did vary (P<0.0036) between the treatment groups on the Time \emptyset sample on 9 November 1995 (1994 cohort) and for the Stress sample on 25 July 1996 (1995 cohort). Between samples, mean length and weight decreased (P<0.0805) for the exercised salmon on 9 November 1995 and 29 March 1996 (1994 cohort) and increased for the control salmon on the 25 July 1996 sample (1995 cohort). Mean condition factor never varied between treatment groups during a sampling period (P>0.1459) and only varied between pre- and post-stress samples on 19 November 1995 (cohort) when K was lower (P=0.0099) in the exercised salmon sampled prior to stress than in those sampled following stress (Figure 12).

The 1995 cohort control group sampled on 25 July 1996 showed no change in plasma cortisol levels. Mean plasma glucose level varied ($P \ge 0.0401$) between treatment groups only for the Time Ø samples on 29 March 1996 (1994 cohort) and 25 July 1996 (1995 cohort; Figure 13). Mean plasma glucose levels varied between treatment groups at the Stress sample for both of the 1994 cohort samples ($P \le 0.0919$) with the exercised salmon having higher mean levels on 9 November 1995 and the control salmon having higher mean levels on 29 March 1996. Mean plasma glucose levels increased after stress for each treatment in all samples ($P \le 0.0088$).

Following stress, mean plasma cortisol levels increased in all treatments and samples



Figure 10. Mean (± 1 SD) length (mm) of juvenile Chinook salmon reared under control and exercise (increased flow) growth regimes and sampled before (Time Ø) and 2 hours after (Stress) 30 seconds of stress, 1994 and 1995 cohorts. Note: '+' indicates a significant difference between control vs. exercise pairs for a given sampling date. '*' indicates a significant difference between Time Ø and the Stress sample within a treatment group. One symbol indicates P<0.1, two symbols indicate P<0.05, three symbols indicate P<0.01, four symbols indicate P<0.001, five symbols indicate P<0.0001.



Figure 11. Mean (± 1 SD) weight (g) of juvenile Chinook salmon reared under control and exercise (increased flow) growth regimes and sampled before (Time \emptyset) and 2 hours after (Stress) 30 seconds of stress, 1994 and 1995 cohorts. Note: symbols are as for Figure 10.



Figure 12. Mean (± 1 SD) condition factor (K) of juvenile Chinook salmon reared under control and exercise (increased flow) growth regimes and sampled before (Time \emptyset) and 2 hours after (Stress) 30 seconds of stress, 1994 and 1995 cohorts. Note: symbols are as for Figure 10.



Figure 13. Mean (± 1 SD) plasma glucose (ng/mL) of juvenile Chinook salmon reared under control and exercise (increased flow) growth regimes and sampled before (Time \emptyset) and 2 hours after (Stress) 30 seconds of stress, 1994 and 1995 cohorts. Note: symbols are as for Figure 10.

(P<0.0001) except for one sampling group (Figure 14). Cortisol levels in the 25 July 1996 sample (1995 cohort) for the control group did not vary between the Time \emptyset and Stress samples (P=0.5478). Mean plasma cortisol levels varied between treatment groups at Time \emptyset only for the 25 July 1996 sample (1995 cohort; P<0.0001). However, cortisol levels in this group were initially high which may have been evidence of an earlier stressful event in that group (e.g., these salmon are reared in outdoor ponds and it is possible that a predator, such as an otter or mink, had been present the previous night). Mean plasma cortisol levels varied between treatments for the Stress samples on 25 July and 19 November 1996 (1995 cohort; P<0.0384).

Plasma glucose and cortisol levels increased following stress but there were no consistent trends in differences between treatment groups. An increase in plasma glucose and cortisol levels is an indicator of stress in fish and has been 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). Our Time \emptyset results show no difference in change of plasma cortisol levels over time but we did not follow the salmon through the entire smoltification process, as they were released in April. Barton et al (1985) reported an increase in cortisol stress response (difference between resting and post-stress cortisol levels) over the period of smoltification. In our study, the magnitude of change in mean cortisol level in salmon sampled in November vs. those sampled in March/April was similar in both cohorts.

Mean hematocrit varied (P=0.0070) between treatment groups only at Time \emptyset on 25 July 1996 (Figure 15). Mean hematocrit increased in the exercised salmon following stress on 19 November 1996 (1995 cohort; P=0.0055) but decreased (P<0.0019) following stress in both the exercised and control salmon in the 29 March 1996 sample (1994 cohort). Mean hematocrit was also lower (P=0.0542) in the control salmon sampled following stress on 4 April 1997 (1995 cohort).

Mean HSI decreased ($P \le 0.0788$) following stress in both treatment groups and on each sampling date for the 1994 cohort but did not vary ($P \ge 0.3634$) for the 1995 cohort (Figure 16). Mean HSI varied between treatment groups at Time Ø on 19 November 1996 and 4 April 1997 (1995 cohort; $P \le 0.0921$).

Mean CSI did not change ($P \ge 0.2411$) following stress for the 1994 cohort (Figure 17). However, mean CSI decreased following stress in the 1995 cohort control group on 19 November 1996 (P=0.0811) and in the exercised group on 25 July 1996 and 4 April 1997 (P=0.0598). Mean CSI varied (P=0.0167) between treatment groups only for the post-stress sample on 19 November 1996 (1995 cohort).

Mean liver glycogen level did not change ($P \le 0.2750$) in the 1994 cohort (Figure 18). Mean liver glycogen level varied between treatment groups at Time Ø in the 1995 cohort on 25 July and 19 November 1996 ($P \le 0.0601$).

Hematocrit, HSI, CSI and liver glycogen displayed no consistent trends in variation following stress or between treatment groups. It may be that two hours following the stress event and/or the amount of stress (30 seconds in a net) were insufficient to illicit a response in hematocrit, CSI or HSI. Hochachka (1961) reported that exercised rainbow trout had characteristics that more closely resembled those seen in wild rainbow and cutthroat trout O. *clarki*, having more hemoglobin and greater CSI, than unexercised trout. Also, following stress (5 minutes of being chased), trained trout had used more of their available muscle glycogen and recovered their muscle and liver glycogen more quickly.



Figure 14. Mean (± 1 SD) cortisol (ng/mL) of juvenile Chinook salmon reared under control and exercise (increased flow) growth regimes and sampled before (Time Ø) and 2 hours after (Stress) 30 seconds of stress, 1994 and 1995 cohorts. Note: symbols are as for Figure 10.



Figure 15. Mean (± 1 SD) hematocrit of juvenile Chinook salmon reared under control and exercise (increased flow) growth regimes and sampled before (Time \emptyset) and 2 hours after (Stress) 30 seconds of stress, 1994 and 1995 cohorts. Note: symbols are as for Figure 10.



Figure 16. Mean (± 1 SD) hepatosomatic index (HSI) of juvenile Chinook salmon reared under control and exercise (increased flow) growth regimes and sampled before (Time \emptyset) and 2 hours after (Stress) 30 seconds of stress, 1994 and 1995 cohorts. Note: symbols are as for Figure 10.



Figure 17. Mean (± 1 SD) cardiosomatic index (CSI) of juvenile Chinook salmon reared under control and exercise (increased flow) growth regimes and sampled before (Time \emptyset) and 2 hours after (Stress) 30 seconds of stress, 1994 and 1995 cohorts. Note: symbols are as for Figure 10.



Figure 18. Mean (± 1 SD) liver glycogen (mg/g) of juvenile Chinook salmon reared under control and exercise (increased flow) growth regimes and sampled before (Time Ø) and 2 hours after (Stress) 30 seconds of stress, 1994 and 1995 cohorts. Note: symbols are as for Figure 10.

Survival and adult returns

Mean survival of smolts to Lower Granite Dam did not vary (P=0.9386) between treatment groups (Table 2). Detection rates were very similar between cohorts and treatments, ranging from 58.7-60.7%. Migration timing to Lower Granite Dam did not vary between treatments (P=0.6811) but did vary between cohorts (P<0.0001; Figure 19). The 1994 cohort reached Lower Granite Dam in a mean of 23.6 days while the 1995 cohort took only a mean of 20.6 days. There was no interaction between treatment and cohort (P=0.2748).

Table 2. Number of PIT-tagged Chinook salmon smolts in the exercised and control treatment groups released from Lookingglass Fish Hatchery and percent detected at Lower Granite Dam, 1994 and 1995 cohorts.

	1994	cohort	1995 cohort			
Treatment	PIT tags released	Percent detected	PIT tags released	Percent detected		
Exercise	3,565	58.7	19,790	59.0		
Control	2,989	60.7	20,237	59.8		



Figure 19. Percent and cumulative percent of PIT-tagged Chinook salmon, reared under control and exercised (increased flow) growth regimes and released from Lookingglass Fish Hatchery, reaching Lower Granite Dam in 1996 (1994 cohort) and 1997 (1995 cohort). Note: 2 control (0.05%) and 4 exercised (0.10%) 1995 cohort smolts were captured between 20 May - 11 June.

Mean survival rate varied with cohort (P=0.0001), as only 51 CWTs were recovered from the 1994 cohort while 568 were recovered from the 1995 cohort (Table 3; Figure 20). Mean return rates for the 1995 cohort were as much as sixteen times higher than those of the 1994 cohort. There was no difference (P=0.3226) in mean survival rate between treatment groups (Figure 20) and no significant interaction between variables (P \ge 0.3041). Control Chinook salmon were recovered at a mean rate of 0.22%; 0.21% at the hatchery weir, 0.004% in the harvest and 0.007% as strays. Exercised Chinook salmon were recovered at a mean rate of 0.21%; 0.20% at the hatchery weir, 0.002% in the harvest and 0.004% as strays.

Age composition of the returning adults varied between treatment groups (Table 4; Figure 21). Mean percentage of adults returning at age 3 was higher (P=0.0026) for exercised salmon (9.6%) than for controls (1.5%). Age 3 age composition did not vary between cohorts (P=0.5218) and there was an interaction between treatment groups and cohort (P=0.0126). At age 4, mean percentage of exercised salmon (88.4%) did not differ (P=0.1108) from that of the control group (93.2%), nor between cohorts (P=0.5149 and there was no interaction (P=0.4542). A higher percentage (P=0.0101) of control salmon returned at age 5 (5.4%) than exercised salmon (1.9%) and a higher percentage (P=0.0843) of salmon returned at age 5 from the 1995 cohort (3.9%) than the 1994 cohort (3.3%). There was a significant interaction between

Cohort,	CWTa	Hatchery		Harvest		Stray		Total	
raceway	released	Ν	%	Ν	%	Ν	%	Ν	%
1994									
Control									
15	34,379	15	0.044	0	0.000	4	0.012	19	0.055
17	32,997	<u>15</u>	0.045	<u>1</u>	0.003	0	0.000	<u>16</u>	0.048
Total/Mean	67,376	30	0.045	1	0.002	4	0.006	35	0.052
Exercise									
14	33,902	10	0.029	0	0.000	0	0.000	10	0.029
16	33,534	6	0.018	<u>0</u>	0.000	<u>0</u>	0.000	<u>6</u>	0.018
Total/Mean	67,436	16	0.024	0	0.000	0	0.000	16	0.024
1995									
Control									
17	37,340	138	0.370	2	0.005	2	0.005	142	0.380
16	36,310	136	0.375	3	0.008	4	0.011	143	0.394
Total/Mean	73,650	274	0.372	5	0.007	6	0.008	285	0.387
Exercise									
14	36,172	157	0.434	2	0.006	2	0.006	161	0.445
15	37,156	117	0.315	<u>1</u>	0.003	4	0.011	122	0.328
Total/Mean	73,328	274	0.374	3	0.004	6	0.008	283	0.387

Table 3. Number released and survival rates for each cohort and raceway of Rapid River Chinook salmon reared under an exercise or control growth regimes at Lookingglass Fish Hatchery, 1994 and 1995 cohorts.



Figure 20. Mean (± 1 SD) hatchery, harvest, stray and total survival rates (percent of total released) of Chinook salmon reared under control and exercise (increased flow) growth regimes and released from Lookingglass Fish Hatchery in 1996 (1994 cohort) and 1997 (1995 cohort).

treatment and cohort for ages 3 and 5 (P=0.0106).

Wendt and Saunders (1973) reported an increase in smolt-to-adult survival rate in Atlantic salmon exercised at velocities greater than 2.0 BL/s for 2-12 months prior to release. Evenson and Ewing (1993) found no benefit in adult return rate of one hour of exercise daily for the month prior to release in steelhead *O. mykiss*. 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 salmon than control salmon returned at age 3. If this was caused by the exercise regime, then this is an undesirable result. Although a greater proportion of the exercised salmon in both cohorts returned as jacks (13.5% vs. 0% in 1994; 6% vs. 2.5% in 1995), the greater length and weight of the 1994 cohort exercised salmon in the autumn preceding smoltification may explain the larger difference in the 1994 cohort and the overall result (Figures 3 and 4). 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). 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. Shearer and Swanson (2000) showed endocrinological and histological evidence that maturation in males was initiated approximately a full year prior to spawning. 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 1995 cohort exercised salmon may have been indicative of underfeeding.

The evaluations of survival and age composition suffered from large variation between

Cohort,			•				-	
experimental group,	CWTs	CWTs Age 3		Aş	Age 4		Age 5	
raceway	released	Ν	%	Ν	%	Ν	%	
1994								
Control								
15	34,379	0	0.0	14	93.3	5	6.7	
17	32,997	<u>0</u>	0.0	14	<u>93.3</u>	<u>2</u>	6.7	
Total/Me	ean 67,376	0	0.0	28	93.3	7	6.7	
Exercise								
14	33,902	1	10.0	9	90.0	0	0.0	
16	33,534	<u>1</u>	16.7	5	83.3	<u>0</u>	0.0	
Total/M	ean 67,436	2	13.3	14	86.7	0	0.0	
1995								
Control								
17	37,340	6	43	128	89 9	8	58	
16	36 310	2	1.5	137	96.3	4	2.0	
Total/M	ean 73.650	<u>=</u> 8	$\frac{1.5}{2.9}$	$\frac{157}{265}$	<u>93 1</u>	$\frac{1}{12}$	$\frac{2.2}{4.0}$	
Exercise	eun 75,000	0	2.9	200	<i>yyyiii</i>	12	1.0	
14	36 172	8	51	145	89.8	8	51	
15	37,156	8	6.8	111	90.6	3	2.6	
Total/Me	ean $\frac{37,130}{73,328}$	$\frac{6}{16}$	$\frac{6.0}{6.0}$	$\frac{111}{256}$	$\frac{90.0}{90.2}$	$\frac{-5}{11}$	$\frac{2.0}{3.8}$	

Table 4. Number released and age composition of returning adults for each cohort and raceway of Rapid River Chinook salmon reared under an exercise or control growth regimes at Lookingglass Fish Hatchery, 1994 and 1995 cohorts.

cohorts and replicates in some parameters, particularly in the exercise groups, which may have masked significant differences between treatments. For example, a similar number of tagged smolts were released for each cohort (134,812 for the 1994 cohort vs. 145,978 for the 1995 cohort) but low survival in the 1994 cohort resulted in only 51 tag recoveries (0.04%; 16 from the exercised group and 35 from the control), whereas 568 tags (0.4%) were recovered for the 1995 cohort. Variation between replicates was greater within the exercise raceways than the control raceways. Additional years of study to compensate for large differences in survival between cohorts would benefit these analyses. We were unable to conduct additional years of study because of changes in hatchery operations resulting from program direction changes.

Management Recommendations

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.



Figure 21. Mean (± 1 SD) percent of total adult Chinook salmon reared under control and exercise (increased flow) growth regimes that returned to Lookingglass Fish Hatchery at ages 3, 4 and 5, 1994 and 1995 cohorts. Note: '*' indicates a significant difference between control vs. exercise salmon for a given age, **=P<0.05; ***=P<0.01.

The literature provides information on improved return rates for salmon reared under a presmolt exercise growth regime but recommendations differ. Besner and Smith (1983) suggested that a long-term low velocity exercise regime might improve swimming ability and, therefore, improve survival. 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 post-smolt 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 post-smolt Chinook salmon. However, this will result in earlier maturation of males, as is reported for 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 evaluate this growth regime. The flows rates provided to the exercise groups at LFH were the maximum attainable at the facility. Therefore, it appears that we cannot improve survival of Chinook salmon reared at Lookingglass Fish Hatchery by increasing flow over the standard flow rate employed there.

Acknowledgments

We acknowledge the able assistance of the hatchery crew at Lookingglass Fish Hatchery for rearing these salmon and those surveyors who collected snouts on spawning ground surveys. Deb Eddy helped immensely with retrieval of auxiliary data. This study was funded by the U.S. Fish and Wildlife Service, Lower Snake River Compensation Plan.

References

- Barton, B. A., C. B. Schreck, R. D. Ewing, A. R. Hemmingsen and R. Patiño. 1985. Changes in plasma cortisol during stress and smoltification in coho salmon, *Oncorhynchus kisutch*. General and Comparative Endocrinology 59:468-471.
- Barton, B. A., C. B. Schreck and L. A. Sigismondi. 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile chinook salmon. Transactions of the American Fisheries Society 115:245-251.
- Barton, B.A., and G.K. Iwama. 1991. Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. Annual Review of Fish Diseases 1: 3 26.
- Besner, M. and L. S. Smith. 1983. Modification of swimming mode and stamina in two stocks of coho salmon (*Oncorhynchus kisutch*) by differing levels of long-term continuous exercise. Canadian Journal of Fisheries and Aquatic Sciences 40:933-939.
- Blake, R. L., F. L. Roberts and R. L. Saunders. 1984. Parr-smolt transformation of Atlantic salmon (*Salmo salar*): activities of two respiratory enzymes and concentrations of mitochondria in the liver. Canadian Journal of Fisheries and Aquatic Sciences 41:199-203.
- Boujard, T. and J. F. Leatherland. 1992. Circadian pattern of hepatosomatic index, liver glycogen and lipid content, plasma non-esterified fatty acid, glucose, T₃, T₄, growth hormone and cortisol concentrations in *Oncorhynchus mykiss* held under different photoperiod regimes and fed using demand feeders. Fish Physiology and Biochemistry 10:111-122.
- Bradley, T. M. and A. W. Rourke. 1984. An electrophoretic analysis of plasma proteins from juvenile *Oncorhynchus tshawytscha* (Walbaum). Journal of Fish Biology 24:703-709.
- Christiansen, J. S., Y. S. Svendsen and M. Jobling. 1992. The combined effects of stocking density and sustained exercise on the behaviour, food intake, and growth of juvenile Arctic charr (*Salvelinus alpinus* L.). Canadian Journal of Zoology 70:115-122.
- Cowley, D. J., M. A. Sheridan, T. L. Hoffnagle, A. J. Fivizzani, B. A. Barton and C. D. Eilertson. 1994. Changes in lipid metabolism and plasma concentrations of thyroxine, cortisol and somatostatin in land-locked chinook salmon, *Oncorhynchus tshawytscha*, during smoltification. Aquaculture 121:147-155.
- Davie, P. S., R. M. G. Wells and V. Tetens. 1986. Effects of sustained swimming on rainbow trout muscle structure, blood oxygen transport, and lactate dehydrogenase enzymes: evidence for increased aerobic activity of white muscle. Journal of Experimental Biology 237:159-171.
- Davison, W. 1989. Training and its effects on teleost fish. Comparative Biochemistry and

Physiology 94A:1-10.

- Evenson, M. D. and R. D. Ewing. 1993. Effect of exercise of juvenile winter steelhead on adult returns to Cole River Hatchery, Oregon. Progressive Fish-Culturist 55:180-183.
- Higgins, P. J. 1985. Metabolic differences between Atlantic salmon (*Salmo salar*) parr and smolts. Aquaculture 45:33-53.
- Hochachka, P. W. 1961. The effect of physical training on oxygen debt and glycogen reserves in trout. Canadian Journal of Zoology 39:767-776.
- Hoffnagle, T. L. 1994. Smoltification and imprinting in introduced, land-locked chinook salmon (*Oncorhynchus tshawytscha*). Doctoral dissertation, University of North Dakota, Grand Forks.
- Hoffnagle, T. L., R. W. Carmichael and W. T. Noll. 2003. Grande Ronde Basin spring Chinook salmon captive broodstock program, project status report, 1 October 1995-31 December 2002. Prepared for Bonneville Power Administration, Portland, Oregon. Northeast Region fish Research and Development, Oregon Department of Fish and Wildlife, La Grande.
- Hopkins, C. L. and M. J. Unwin. 1997. The effect of restricted springtime feeding on growth and maturation of freshwater-reared chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). Aquaculture Research 28:545-549.
- Houlihan, D. F. and P. Laurent. 1987. Effects of exercise training on the performance, growth, and protein turnover of rainbow trout (*Salmo gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences 44:1614-1621.
- Johanning, K. M. and T. M. Bradley. 1989. Plasma protein changes in Atlantic salmon (Salmo salar) during parr-smolt transformation. Comparative Biochemistry and Physiology 92B:555-560.
- Johnston, I. A. and T. W. Moon. 1980. Exercise training in skeletal muscle of brook trout (*Salvelinus fontinalis*). Journal of Experimental Biology 87:177-194.
- Jorgensen, E. H. and M. Jobling. 1993. The effects of exercise on growth, food utilisation and osmoregulatory capacity of juvenile Atlantic salmon, *Salmo salar*. Aquaculture 116:233-246.
- Kenaston, K. R., R. B. Lindsay and R. K. Schroeder. 2001. Effect of acclimation on the homing and survival of hatchery winter steelhead. North American Journal of Fisheries Management 21:765-773.
- Kiessling, A., P. Gallaugher, H. Thorarensen, A. Kolok, J. G. Eales, R. Sweeting, B. Gong, B. A. Mckeown, B. Dosanjh, A. P. Farrell and D. Higgs. 1994. Influence of sustained exercise and endurance training on growth, muscle physiology, cardiovascular parameters, and plasma levels of metabolic hormones of seawater adapted all-female chinook salmon. Pages 300-305 *in* D. Mackinlay, editor, Proceedings of the International Fish Physiology Symposium. Vancouver, B.C.
- Koch, H. J. A. 1982. Hemoglobin changes with size in the Atlantic salmon (*Salmo salar* L.). Aquaculture 28:231-240.
- Krebs, C. J. 1999. Ecological methodology, second edition. Addison Welsey Longman, Inc., Menlo Park, CA.
- Langhorne, P. and T. H. Simpson. 1986. The interrelationship of cortisol, gill (Na+K) ATPase and homeostasis during the parr-smolt transformation of Atlantic salmon (*Salmo salar* L.). General and Comparative Endocrinology 61:203-213.

- Leon, K. 1986. Effect of exercise on feed consumption, growth, food conversion, and stamina of brook trout. The Progressive Fish-Culturist 48:43-46.
- McCormick, S. D. and H. A. Bern. 1989. *In vitro* stimulation of Na⁺K⁺-ATPase activity and ouabain binding by cortisol in coho salmon gill. American Journal of Physiology 256:R707-R715.
- Nielsen, M. E., L. Boesgaard, R. M. Sweeting, B. A. McKeown and P. Rosenkilde. 1994.
 Plasma levels of lactate, potassium, glucose, cortisol, growth hormone and triiodo-Lthyronine in rainbow trout (*Oncorhynchus mykiss*) during exercise at various levels for 24 h. Canadian Journal of Zoology 72:1643-1647.
- Plisetskaya, E. M., P. Swanson, M. G. Bernard and W. W. Dickhoff. 1988. Insulin and coho salmon (*Oncorhynchus kisutch*) during the part to smolt transformation. Aquaculture 72:151-164.
- Shearer, K. D. and P. Swanson. 2000. The effect of whole body lipid on early sexual maturation of 1+ age male chinook salmon (*Oncorhynchus tshawytscha*). Aquaculture 190:343-367.
- Sheridan, M. A., W. V. Allen and T. H. Kerstetter. 1983. Seasonal variations in the lipid composition of steelhead trout, *Salmo gairdneri*, associated with the parr-smolt transformation. Journal of Fish Biology 23:125-134.
- Sheridan, M. A., N. Y. S. Woo, and H. A. Bern. 1985. Changes in the rates of glycogenesis, glycogenolysis, lipogenesis and lipolysis in selected tissues of the coho salmon (*Oncorhynchus kisutch*) associated with parr-smolt transformation. Journal of Experimental Zoology 236:35-44.
- Silverstein, J. T., K. D. Shearer, W. W. Dickhoff and E. M. Plisetskaya. 1998. Effects of growth and fatness on sexual development of chinook salmon (*Oncorhynchus tshawytscha*) parr. Canadian Journal of Fisheries and Aquatic Sciences 55:2376-2382.
- Silverstein, J. T., K. D. Shearer, W. W. Dickhoff and E. M. Plisetskaya. 1999. Regulation of nutrient intake and energy balance in salmon. Aquaculture 177:161-169.
- Soivio, A. and M. Nikinmaa. 1981. The swelling of erythrocytes in relation to the oxygen affinity of the blood of the rainbow trout, *Salmo gairdneri* Richardson. Pages 101-119 *in* A. D. Pickering, editor. Stress and fish. Academic Press, London.
- Sokal, R. R. and F. J. Rohlf. 1981. Biometry, second edition. W. H. Freeman, New York.
- Specker, J. L. and C. B. Schreck. 1982. Changes in plasma corticosteroids during smoltification of coho salmon, *Oncorhynchus kisutch*. General and Comparative Endocrinology 46:53-58.
- Stefansson, S. O., G. Naevdal and T. Hansen. 1989. The influence of three unchanging photoperiods on growth and parr-smolt transformation in Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 35:237-247.
- Sweeting, R. M., G. F. Wagner and B. A. McKeown. 1985. Changes in plasma glucose, amino acid nitrogen and growth hormone during smoltification and seawater adaptation in coho salmon, *Oncorhynchus kisutch*. Aquaculture 45:185-197.
- Virtanen, E. 1987. Correlations between energy metabolism, osmotic balance and external smolt indices in smolting young salmon, *Salmo salar* L. Annales Zoologici Fennici 24:71-78.
- Wendt, C. A. G. and R. L. Saunders. 1973. Changes in carbohydrate metabolism in young Atlantic salmon in response to various forms of stress. Pages 55-82 *in* M. W. Smith and W. M. Carter, editors. The International Atlantic Salmon Symposium 1972.

International Atlantic Salmon Foundation Special Publications Series 4. International Atlantic Salmon Foundation, New York.

- White, J. R. and H. W. Li. 1985. Determination of the energetic cost of swimming from the analysis of growth rate and body composition in juvenile chinook salmon (*Oncorhynchus tshawytscha*). Comparative Biochemistry and Physiology 81A:25-33.
- Woo, N. Y. S., H. A. Bern and R. S. Nishioka. 1978. Changes in body composition associated with smoltification and premature transfer to seawater in coho salmon (*Oncorhynchus kisutch*) and king salmon (*O. tshawytscha*). Journal of Fish Biology 13:421-428.
- Woodward, J. J. and L. S. Smith. 1985. Exercise training and the stress response in rainbow trout, *Salmo gairdneri* Richardson. Journal of Fish Biology 26:435-447.