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IDENTIFICATION OF THE SPAWNING, REARING, AND MIGRATORY REQUIREMENTS OF FALL CHINOOK SALMON IN THE COLUMBIA RIVER BASIN

Annual Report 1996

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ANNUAL REPORT 1996 – 1997

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Hanford Reach Columbia River


Hells Canyon Snake River

USGS

U.S. FISH & WILDLIFE SERVICE

BONNEVILLE POWER ADMINISTRATION

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EXECUTIVE SUMMARY

This report summarizes results of research activities conducted in 1996 and 1997, and in years prior. The majority of the chapters have been submitted to professional journals for peer-review publication. The findings in these chapters represent the efforts of both this project and the collaboration between this project and other researchers working on fall chinook salmon. These chapters communicate significant findings that will aid in the management and recovery of fall chinook salmon in the Columbia River basin. In addition to being published here, we feel that peer-review publication will add to the credibility of our research results, and make them more widely available to the community.

Aerial and underwater redd-search techniques were used to monitor fall chinook salmon spawning in the mainstem Snake River in 1996. Redd searches were conducted in the mainstem Snake River between the head of Lower Granite Dam and Hells Canyon Dam. The number of redds counted in 1996 was the second highest since annual searches began in 1986. A total of 113 redds were observed—71 during aerial searches, and 42 during underwater searches. Redds were documented in three areas where spawning had not been previously documented. The use of both aerial and underwater search techniques have greatly increased the accuracy of redd counts in recent years.

Fall chinook spawning below the four dams on the lower Snake River was documented in a collaborative between this project and Battelle Pacific Northwest Laboratory. Underwater redd searches were made in areas suitable for spawning, as determined by a GIS, below Lower Granite, Little Goose, Lower Monumental, and Ice Harbor dams from 1993-1996. Relatively few redds were found below Lower Granite and Little Goose dams, one redd was located below Ice Harbor, and no redds were found below Lower Monumental Dam. Redds were generally found in 4-8 m of water, over cobble substrate, and were located adjacent to the outfall flow from juvenile fish bypass systems. Tailrace spawning accounted for about 12% of the mainstem redds in 1993 and 1994, but their relative contribution to the Snake River population was less in subsequent years and when we included tributary spawning. This manuscript was submitted to the Transactions of the American Fisheries Society to be published as a paper and is currently in press.

Chapter three represents a collaborative effort between this project and the Idaho Power Company in developing equipment for use in underwater redd searches. Two underwater video camera carriers were designed by modifying hydraulic sounding weights

and suspension equipment normally used for stream gauging. Both carriers were suspended from the bow of a boat, and used in water up to 13 m deep with velocities up to 3 m/s. Each system has its own advantages and disadvantages, but both were used to successfully find deepwater redds in a large flowing river. This manuscript was submitted to the North American Journal of Fisheries Management to be published as a Management Brief, and is currently in press.

Substrate quality necessary for successful fall chinook salmon incubation and emergence was evaluated using field samples and laboratory experiments. Substrates from selected spawning areas in Hells Canyon of the Snake River contained 1.2 to 8.5% fines <0.85 mm. Laboratory emergence experiments indicated that fine sediments in Snake River spawning areas are not deleteriously affecting emergence success of fall chinook salmon. This is the thesis work of a University of Idaho master's candidate that was supported by this project.

Factors affecting the detection rates of PIT-tagged juvenile fall chinook salmon at Lower Granite Dam on the Snake River were evaluated for the years 1992 to 1995. Rearing subyearling fall chinook salmon were PIT tagged and subsequently detected at Lower Granite Dam to provide an index of survival. Detection rate was positively related to mean summer flow, and negatively related to maximum summer water temperature. Results in this chapter support summer flow augmentation as a beneficial interim recovery measure for enhanced survival of subyearling chinook salmon in the Snake River. This information was recently published in a paper in the North American Journal of Fisheries Management.

Knowing the racial origin of PIT-tagged juvenile chinook salmon in the Snake River is critical to managing ESA-listed fall chinook salmon. Genetic techniques were used to separate fall and spring race fish. Mixed-race samples of juvenile chinook salmon were analyzed to genetically identify racial origin of individuals. Allozyme allele frequency differences between Snake River spring race and fall race chinook salmon were so large that our estimates of racial composition of annual samples were very accurate. Paired genotypes for sMEP-1* and PGK-2* were particularly effective as discriminators. Results indicate that the natural Snake River fall chinook population has not had its genetic integrity compromised by Columbia River strays, and that Snake River fish are more closely aligned with Lyons Ferry Hatchery stock. This was a collaborative effort with the Washington Department of Fish and Wildlife, and a paper

containing this information has been submitted to Transactions of the American Fisheries Society.

The rearing characteristics and seaward migration of juvenile fall chinook salmon in the Snake River was evaluated using PIT tags. PIT-tagged juvenile fall chinook salmon were released in rearing areas of Hells Canyon and detected at Lower Granite Dam from 1992 to 1997. An average of 77% of tagged fish were detected at Lower Granite Dam in the six years of study. Time from tagging to detection was related to fork length at tagging and Julian day of release. Fish that were > 75 mm were more likely to be detected than fish < 75 mm. A model developed to forecast run timing at Lower Granite Dam predicted the median date of passage to be, on average, within 9.5 days of the observed median date of passage. This has been submitted as a paper to the North American Journal of Fisheries Management, and is currently in review.

The behavior of actively migrating juvenile fall chinook salmon in Little Goose Reservoir was described using radio telemetry. Radio-tagged juvenile fall chinook salmon were released in the Lower Granite Dam tailrace and detected in Little Goose Reservoir using fixed-site receivers. Fish usually had the fastest migration rates in the upper reservoir where water velocities were highest. Upon reaching the Little Goose forebay, migration rates were the slowest observed, and some fish traveled back upstream for various amounts of time, or were delayed in the forebay up to a week or more. This has been submitted as a paper to the North American Journal of Fisheries Management, and is currently in review.

We evaluated the physiological development, migratory behavior, and adult contribution of fall chinook salmon migrating past McNary Dam. Subyearling fall chinook salmon were freeze branded and coded-wire tagged at McNary Dam to determine travel time to John Day Dam and subsequent adult contribution. Multiple regression analyses showed that travel time was related to flow and fish size. Physiological development progressed with fish size, and early migrants may have a survival advantage over later migrants. Early migrants have contributed more adults than later migrants in two of the four years of study. This was submitted as a paper to the North American Journal of Fisheries Management, and is currently in review.

ACKNOWLEDGEMENTS

We thank individuals in the Idaho Department of Fish and Game, Idaho Power Company, U.S. Fish and Wildlife Service, Washington Department of Fish and Wildlife, U.s. Army Corps of Engineers, National Marine Fisheries Service, Nez Perce Tribe, and Fish Passage Center that assisted with the project activities. We extend special thanks to our colleagues at the Biological Resources Division and the Idaho Fishery Resource Office of the U.S. Fish and Wildlife Service for their assistance. Special thanks is extended to Rodney Garland for compiling, assistance in editing, and graphic design of this report. We gratefully acknowledge reviewers for the valuable comments and suggestions which we have incorporated into this report. We appreciate the assistance of Debbie Docherty, Project Manager, Bonneville Power Administration.

CHAPTER ONE

Fall Chinook Salmon Spawning Ground Surveys in the Snake River Upstream of Lower Granite Dam, 1996

by

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Introduction

Redd searches were conducted in 1996 as part of an ongoing effort to determine the number, timing, and location of fall chinook salmon *Oncorhynchus tshawytscha* spawning each year in the Snake River between the head of Lower Granite Reservoir and Hells Canyon Dam. Redd counts in this reach were first reported infrequently from 1959 to 1978 (Irving and Bjornn 1981, Witty 1988). Then in 1986, annual redd searches were started by an interagency team, and reported by the Washington Department of Fisheries (WDFW; Seidel and Bugert 1987, Seidel et al. 1988, Bugert et al. 1989-1991, and Mendel et al. 1992). In 1991, the U. S. Fish and Wildlife Service (USFWS) joined in conducting redd searches to help develop search techniques, and report search results (Connor et al. 1993; Garcia et al. 1994a, 1994b, 1996, 1997).

The objective of this report is to describe the number, timing, and location of fall chinook salmon spawning in the Snake River from 1991 to 1996. We present detailed information from searches conducted in 1996, and summarize data from 1991 to 1995. We include redd counts from searches conducted in the Snake River and tributaries from 1986 to 1990 for comparative analysis. Results from redd searches conducted cooperatively with the Idaho Power Company (IPC) are also reported.

Study Area

The study area consisted of the 162-km free-flowing reach of the Snake River between Asotin, Washington, and Hells Canyon Dam (Figure 1). We describe specific locations within this area using river kilometers (Rkm), and landmarks derived from U.S. Army Corps of Engineers navigation charts (COE 1990) and U.S. Geological Survey topographical maps. Based on differences in river flow and turbidity, the study area was divided into three river reaches (lower, middle, upper) delineated by the entry points of the Grande Ronde and Salmon Rivers (Figure 1). From 1991 to 1994, river flow remained relatively stable in all river reaches (Figure 2). In 1995, river flow in the upper reach remained stable through most of the work period, but varied considerably in the lower and middle reaches. In 1996, flows were relatively stable over all river reaches until 20 November. Turbidity was low (.2 Nephelometric Turbidity Units(NTU)), and roughly equal, in all river reaches when flows were low and stable. At higher, unstable, flows, turbidity was usually highest in the lower reach, and lowest in the upper reach.

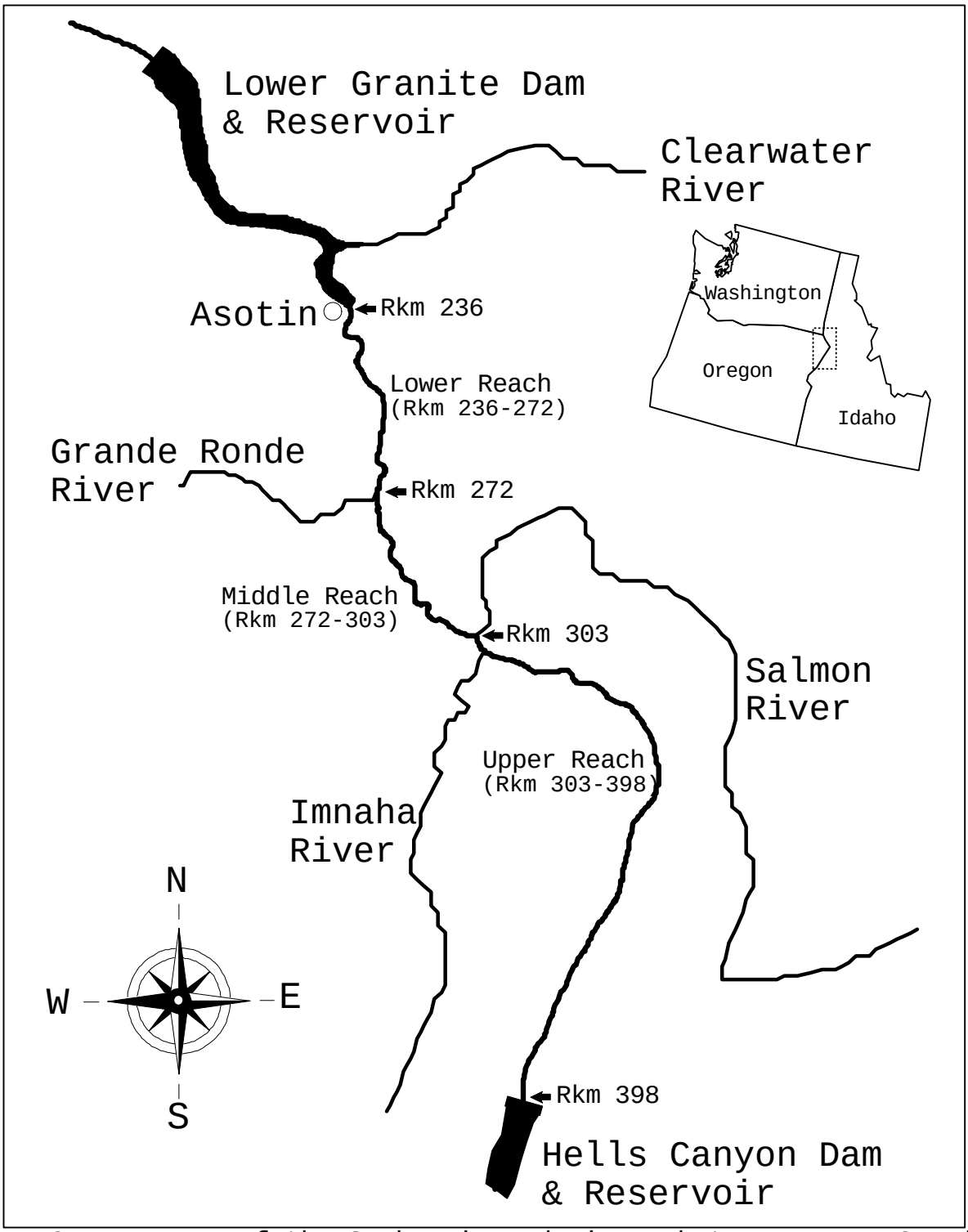

FIGURE 1.-Map of the Snake River drainage between Lower Granite and Hells Canyon dams. The boundaries of river reaches are delineated by arrows, and river kilometers (Rkm).

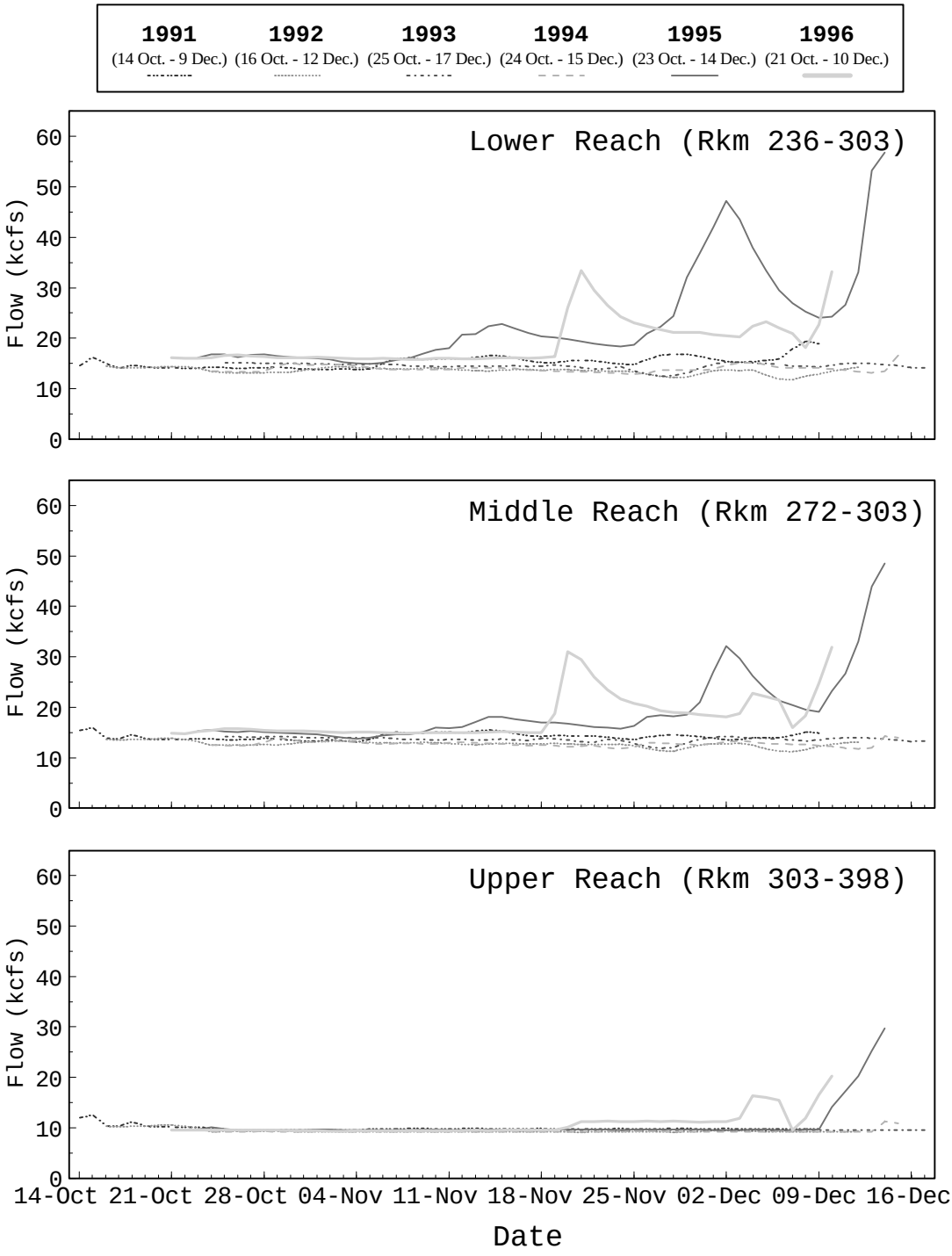

FIGURE 2.-Daily average discharge (kcfs) in the lower, middle and upper reaches of the Snake River during the work periods (shown in parentheses in the legend) from 1991 to 1996.

Methods

Aerial searches of the Snake River were conducted seven to eight times a year from 1991 to 1996 at weekly (6-8-d) intervals beginning in mid to late October. Due to high turbidity (>4 NTU), or poor flight conditions, portions of the study area were not searched on 3 of 8 flights in 1991, 2 of 8 flights in 1992, 4 of 7 flights in 1995, and 2 of 7 flights in 1996.

Each aerial search was conducted by two experienced observers who viewed the river bottom from a helicopter flown at an altitude of < 200 m. One observer tracked the progress of each flight using an aerial photo of the river, and when redds were observed, recorded the date, number of redds, and marked the position of the redds on the photo. The second observer recorded the number of new redds, the number of old redds that were first viewed on a previous flight but still visible, and the number and locations of areas that needed to be validated because they were either oddly shaped or could not be seen clearly. The second observer also made a sketch of each site for use on subsequent searches to track redd development.

Validating aerial observations involved examining potential redds from a boat, or using an underwater video camera. An area of disturbed bottom substrates was determined to be a redd if three of the following four conditions were met: a) adult fall chinook salmon were present, b) there was a defined pit and tailspill, c) bottom substrates were composed of 2.5-15-cm dominant particle size, and d) the area was greater than about half the size of an average fall chinook salmon redd (0.5 x 17 m^2 (Chapman et al. 1986) = 8.5 m^2). Redds were validated by at least one of the two persons that observed the potential redd from the air.

Underwater searches were conducted from 1991-1996 in areas too deep to allow detection from the air. In 1991 and 1992, underwater observations were made by the USFWS using methods developed by Swan (1989) that involved direct observation of the river bottom by scuba divers (Connor et al. 1993; Garcia et al. 1994a). From 1993-1996, the USFWS and IPC conducted underwater searches using a video system consisting of a DC-powered 8-mm video recorder, waterproof camera, 110° lens, 20-m camera cable, and at least one monitor. The submersible camera was either enclosed in an aluminum sheath mounted on a 34-kg lead weight, or attached to an aluminum frame mounted between two 13-kg lead weights, and could be adjusted 45° to 90° down from horizontal (Groves and Garcia, *In press*). The camera was suspended from a boat using a wire rope passed through a roller on the bow, and

attached to a sounding reel with a depth indicator mounted in the boat cabin.

Searches using underwater video were conducted by passing the camera over the river bottom in a zigzag pattern, with each pass ending about 10 m upriver of the previous pass. From 1993 to 1995, we used natural features along the shore to judge the distance between passes. In 1996, we determined this distance by placing a rope constructed of different-colored 10-m sections along the shoreline. The distance between the camera and river bottom, and the angle of the camera, was adjusted to maximize the amount of viewable area without losing our ability to observe details of the bottom substrates. If a redd was observed, the distance between passes in the search pattern was reduced by half (5 m), and the entire area was searched at least one more time.

Observations of redds were recorded on video tape, and when large groups of redds were found, redd coordinates were recorded using an electronic surveying equipment. Coordinates were used to plot the position of redds observed on each search so that redd positions could be reviewed along with the video to determine the total number of redds at each spawning location. In areas where redds overlapped, and could not be identified individually, the perimeter of the redd group was surveyed, and the overall area divided by 17 m^2 to estimate the total number of redds in the group based on the average size of fall chinook salmon redds observed in the Columbia River (Chapman et al. 1986).

Underwater searches were limited to areas > 3-m deep with a dominant bottom substrate particle size (Bovee 1982) ranging from 2.5 to 15-cm diameter (Raleigh et al. 1986). In 1991 and 1992, a few pilot searches were conducted to develop search techniques (Table 1). Then, from 1993 to 1996, the USFWS and IPC attempted to annually search 89 deepwater areas (21 in the lower reach, 20 in the middle reach, and 48 in the upper reach) known to fit the criteria. The number of areas searched each year varied, however (Table 2), due to periods of high turbidity (>4 NTU), and equipment failures.

We assessed the accuracy of redd counts by examining fish to redd ratios (Dauble and Watson 1997). This involved using the number of adult fall chinook salmon counted in the Lower Granite Dam fish ladder (COE 1987-1996), and relating passage of fish at the dam to the redds counted upriver. A fish/redd ratio

TABLE 1.-Number of different areas in the Snake River searched using underwater video in 1996. Areas are grouped by investigator and year (Connor et al. 1993; Garcia et al. 1994, 1996, 1997; Groves and Chandler 1996).

	Areas searched by year					
Investigator	1991	1992	1993	1994	1995	1996
U.S. Fish and Wildlife Service	1	3	5	38	21	32
Idaho Power Company	0	0	45	38	21	15
	1	3	50	76	42	47

TABLE 2.-The number of areas searched for fall chinook salmon redds using underwater cameras in the Snake River, 1993 to 1996.

Reach	Number of known patches of 2.5-15 cm bottom substrates	Number of areas searched by year			
		1993	1994	1995	1996
Lower	21	17	18	0	13
Middle	20	14	17	3	7
Upper	48	19	41	39	27
Totals	89	50	76	42	47

of 2:1 was expected, assuming each adult female fall chinook salmon constructs one redd, and the female/male ratio was 1:1. Although useful for our purposes, this 2:1 ratio is only an approximation since female fall chinook salmon may dig more than one redd (Scott and Crossman 1973), and the sex ratio of Snake River fall chinook salmon can vary from year-to-year (Mendel, WDFW, personal communication). To calculate meaningful fish/redd ratios upriver of Lower Granite Dam, we had to account for redds observed in Snake River tributaries (Table 3). In addition, we had to account for the portion of fish that travel downriver of the dam after being counted in the fish ladder. We assumed this portion to be 30% annually, although it has been reported to be as high as 37.5% (Mendel and Milks 1997).

Results

The number of redds counted in 1996 was the second highest since annual searches began in 1986 (Table 4). A total of 113 redds were observed, 71 during aerial searches (Table 5), and 42 during underwater searches (Table 6). Redds were observed in three areas where spawning had not been previously documented (Tables 6 and 7), compared to an average of 4 (range, 2-8) areas from 1991 to 1996. The number of redds counted during underwater searches in 1996 comprised 37% of the overall redd count, compared to 21-53% contributed from 1993 to 1996.

The fish/redd ratios from 1993 to 1996 averaged 3.4:1 (range, 3.0-3.9:1). This average is larger than the expected value (2:1), but is a considerable improvement over the average fish/redd ratio (6.3:1; range, 4.9-7.6) for the preceding five years (1987-1992). At least two factors contributed to the improved accuracy reflected in reduced fish/redd ratios. First, the use of underwater searches, which accounted for an average of 22% (range, 12-31%) of all redds counted upriver of Lower Granite Dam from 1993 to 1996, and second, increased search effort in Snake River tributaries (Table 2).

Spawn timing varied each year based on redd counts from aerial searches (Figure 3). The spawning period occurred within a 4 to 8 week period each year. The date of intitial spawning differed by as much as 2 weeks, and the date of the end of spawning differed by as much as 4 weeks. Peak spawning ranged within a 4-week period. In general, spawning started by late October, peaked from early to mid November, and ended by mid December.

TABLE 3.-The number of fall chinook salmon redds counted, and aerial searches performed, in the Grande Ronde, Clearwater, Imnaha, and Salmon rivers (B.D. Arnsberg, Nez Perce Tribe, personal communication; USFWS, unpublished data).

Year	Redd counts	Number of Searches
1987	7	4
1988	23	5
1989	11	5
1990	8	4
1991	8	14
1992	35	20
1993	92	32
1994	53	32
1995	44	17
1996	93	25

TABLE 4.-Number of fall chinook salmon redds counted in the Snake River by search method and year, 1986-1996. Data sources and methods for collecting data from 1986-1990 can be found in Garcia et al. (1996). No underwater searches were conducted from 1986-1990.

Search Method	Year										
	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
Aerial	7	66	64	58	37	46	47	60	53	41	71
Underwater						5	0	67	14	30	42
Totals	7	66	64	58	37	51	47	127	67	71	113

TABLE 5.-New fall chinook salmon redds counted in 1996 during aerial searches of the Snake River. Counts are presented by river kilometer (Rkm), landmark, and date. Complete searches covered from Asotin, Washington (Rkm 235), to Hells Canyon Dam (Rkm 398). An empty cell indicate areas not searched on the corresponding day.

		New redds counted by date							
Rkm	Landmark	21-Oct	28-Oct	04-Nov	11-Nov	19-Nov	25-Nov	02-Dec	totals
244.4	Ten Mile Canyon	0	0	3	1	0	-	0	4
245.2	Big Bench Point	0	0	1	2	0	-	0	3
266.9	Match Line	0	0	2	1	0	-	0	3
272.9	Up. G. Ronde Range No. 1	0	0	0	1	0	-	0	1
277.6	Deer Head Rapids	0	0	0	3	0	-	0	3
289.0	Cougar Bar Range No. 4	0	5	0	3	0	-	0	8
307.0	Eureka Bar	0	0	0	1	0	0	0	1
311.2	Divide Creek Site	0	2	0	0	0	0	0	2
312.1	Big Canyon Range	0	1	1	0	0	0	0	2
319.9	Robinson Gulch	0	3	2	1	0	0	0	6
330.5	Copper Creek-to-Getta Creek	0	2	0	0	0	0	0	2
334.4	Lookout Creek Range	0	2	1	0	0	0	0	3
334.7	Forest Boundary	0	2	6	1	0	0	0	9
343.2	Lower Pleasant Dam Site	0	1	0	0	0	0	0	1
343.5	Rapid No. 127	0	0	1	0	0	0	0	1
351.9	Kirby Range No. 2	0	4	0	3	0	0	0	7
352.4	Middle Kirby Rapids No. 137	0	1	0	1	0	0	0	2
352.9	Kirby Range No. 5	2	0	0	0	0	0	0	2
379.2	Hat Creek	0	2	5	0	-	0	0	7
387.0	Granite Creek-to-Rocky Bar	0	0	1	0	-	0	0	1
387.3	Rocky Bar Site	0	1	0	0	-	0	0	1
391.8	Chimney Bar	0	0	0	2	-	0	0	2
		2	26	23	20	0	0	0	71

TABLE 6.-Number of fall chinook salmon redds counted in the Snake River during underwater searches. Data are presented by river kilometer (Rkm), landmark, and year, 1991-1996 (Garcia et al. 1997). A dash (-) indicates no search was conducted at the corresponding river mile.

		Year					
Rkm	Landmark	1991	1992	1993	1994	1995	1996
261.3	Captain Johns Creek	5	0	0	0	-	2
266.5	Billy Creek	-	-	28	0	-	0
267.4	Fisher Range	-	-	11	0	-	0
267.7	Lower Lewis Rapids	-	-	21	0	-	0
289.0	Cougar Bar[a]	-	-	2	8	25	33
311.8	Big Canyon Creek	-	-	1	0	0	0
312.3	Zig Zag Creek	-	-	-	5	0	0
318.9	Camp 71 site	-	-	-	-	-	2
320.8	Trail Gulch	-	-	1	0	0	5
341.4	Davis Creek	-	-	-	0	2	0
352.0	Kirby Range No. 2	-	-	-	-	3	0
358.5	Suicide Point	-	-	3	0	0	0
381.3	Lower Dry Gulch	-	-	-	1	0	0
	Totals	5	0	67	14	30	42

[a] At Rkm 289.0, ten redds were estimated to fit within an area of overlapping redds in 1995, and 14 in 1996.

TABLE 7.-Number of fall chinook salmon redds counted in the Snake River during aerial searches, 1986 to 1996. Counts are presented by river kilometer (Rkm) and year.

	Year										
Rkm	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
238.6	0	0	0	0	1	0	0	0	0	0	0
239.4	0	0	0	1	0	0	0	0	0	0	0
239.9	0	0	0	1	0	2	0	1	0	0	0
243.8	0	0	0	0	0	0	0	2	0	0	0
244.4	0	0	1	0	0	0	0	0	0	3	4
245.2	0	13	15	23	16	0	7	3	5	0	3
252.5	0	0	0	1	0	0	0	0	0	0	0
252.9	0	0	0	0	1	0	0	0	0	0	0
253.3	2	0	0	0	0	0	0	0	0	0	0
257.0	0	0	0	0	0	0	3	0	0	0	0
259.0	0	0	0	0	0	0	7	11	0	3	0
261.3	0	0	2	1	2	15	11	1	0	0	0
262.3	0	3	0	0	0	0	0	0	0	0	0
262.7	0	0	0	0	2	0	0	0	0	0	0
264.5	0	2	0	0	0	0	0	0	0	0	0
265.0	0	0	0	2	1	0	0	0	1	0	0
265.8	0	0	5	0	0	0	0	2	3	0	0
266.0	0	0	0	0	0	0	0	2	0	0	0
266.3	0	4	0	0	0	0	0	0	0	0	0
266.9	0	2	14	0	0	1	3	9	0	0	3
267.4	0	0	0	0	0	0	0	6	0	0	0
267.9	0	0	0	0	0	6	0	0	0	0	0
271.4	0	0	0	0	0	0	0	5	6	3	0
272.9	0	0	0	1	0	0	0	0	0	1	1
277.6	0	1	0	0	0	0	0	0	0	0	3
279.8	0	1	0	0	0	0	0	0	0	0	0
284.0	0	0	0	0	0	0	0	0	0	1	0
286.9	0	0	0	0	0	0	0	0	1	0	0
287.9	0	0	0	1	0	0	0	0	1	0	0
289.0	0	0	0	0	0	0	0	4	5	2	8
305.7	0	0	0	0	0	0	0	0	0	1	0
305.9	0	0	0	0	0	0	0	0	1	0	0
307.0	0	1	5	0	2	5	1	0	0	0	1
308.4	2	2	4	0	0	0	0	0	0	0	0
311.2	0	0	0	5	2	0	0	0	2	0	2
311.7	0	4	0	0	0	0	6	1	2	1	0
311.8	0	0	0	0	0	0	0	0	1	1	0
312.1	0	2	0	0	3	0	0	1	2	4	2
312.3	0	0	2	0	2	0	0	0	0	0	0

(Table 7. Continued)

Rkm	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
315.4	0	0	3	0	0	0	0	0	2	0	0
315.7	0	1	0	0	0	0	0	0	0	0	0
319.9	0	5	0	3	2	7	3	0	6	1	6
328.4	0	1	0	0	0	0	0	0	0	0	0
330.3	0	0	0	0	0	3	0	0	0	1	0
330.5	0	1	0	0	0	0	0	0	0	0	2
332.1	0	1	4	0	0	1	2	1	0	2	0
334.4	0	0	1	0	0	0	0	0	0	0	3
334.5	0	0	2	0	0	0	0	0	0	0	0
334.7	0	0	0	1	0	0	0	0	0	2	9
337.4	0	1	0	0	0	0	0	0	0	0	0
340.9	0	0	0	0	0	0	0	2	0	0	0
343.2	0	0	0	2	0	0	0	0	0	0	1
343.5	0	0	0	0	0	0	0	0	0	0	1
343.8	0	0	0	0	1	0	2	0	0	0	0
345.1	0	0	0	0	0	0	0	1	0	0	0
345.5	0	2	0	0	0	0	0	0	0	0	0
347.7	0	0	0	0	0	0	0	0	1	0	0
349.6	0	0	0	0	0	0	1	3	0	1	0
350.4	0	0	0	1	0	0	0	0	0	0	0
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351.9	0	0	0	0	0	0	0	0	0	1	7
352.4	0	0	0	0	0	0	0	0	0	3	2
352.9	0	0	2	0	0	0	1	0	3	0	2
358.3	0	0	0	1	0	0	0	0	0	0	0
358.5	2	3	0	0	0	0	0	0	0	0	0
358.6	0	0	0	3	0	0	0	0	1	0	0
359.1	0	0	0	0	0	0	0	0	3	3	0
359.9	0	0	1	0	0	0	0	0	0	0	0
378.3	0	0	0	0	0	0	0	0	0	1	0
379.2	0	4	0	3	0	0	0	0	5	2	7
379.7	1	1	2	1	0	0	0	0	0	0	0
380.9	0	1	0	0	0	0	0	0	0	0	0
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383.9	0	2	0	2	0	0	0	0	0	1	0
387.0	0	6	0	0	0	0	0	0	0	0	1
387.3	0	0	0	3	0	6	0	0	0	0	1
391.5	0	1	0	1	0	0	0	0	0	0	0
391.8	0	0	0	0	0	0	0	0	0	0	2
393.6	0	0	0	1	2	0	0	0	0	0	0
395.3	0	0	0	0	0	0	0	0	0	2	0
396.6	0	0	1	0	0	0	0	0	0	0	0
	7	66	64	58	37	46	47	60	53	41	71

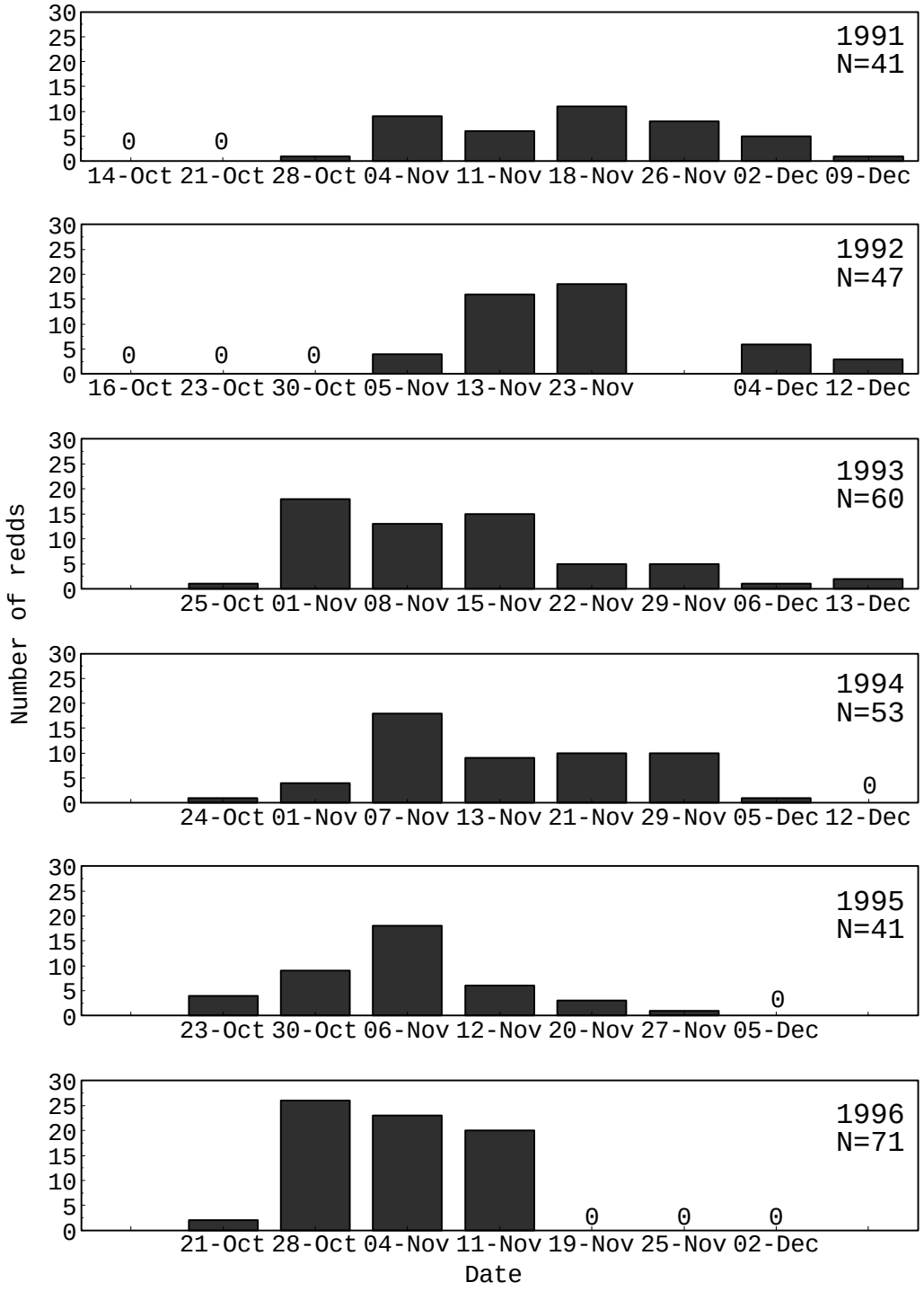

FIGURE 3.-Number of fall chinook salmon redds counted by search date in the Snake River during aerial searches, 1991-1996. Bars are aligned by weeks of the year. Zeros indicate searches were conducted but no redds were observed.

Since 1986, redds have been observed at 81 discrete spawning areas during aerial searches from Rkm 238.6 to Rkm 396.6 (Table 6). From 1993 to 1996, redd distribution (redds/km) varied between river reaches (Figure 4), but overall, averaged 0.82 redds/km in the lower and middle reaches, and 0.37 redds/km in the upper reach. The highest concentration of redds observed annually (1993-1996) within a continuous 2-km reach ranged from 22-62% of the corresponding total annual redd count.

Discussion

Aerial redd counts show consistently low numbers in the Snake River over the past ten years. Aerial redd counts ranged from 41 to 71 in the four years of our study (1993-1996), and from 37 to 66 in the preceding six consecutive years (1987.1992). Redd counts recorded prior to 1986 are of limited use for comparison with later counts because the searches were not well documented, or too few searches were conducted to provide useful information on population size (e.g., a single search in 1986).

We observed variability in the timing and location of fall chinook salmon spawning in the Snake River. A high degree of variability is common for observations of a small population made over a relatively short period (Ott 1993). The variability we observed, and the continued use of new spawning sites, supports previously reported evidence that spawning habitat availability is not limiting the population at this time (Connor et al. 1994).

The purpose of our work was to determine the number, timing, and location fall chinook salmon spawned in the Snake River using redd counts. We were able to accomplish this by modifying established aerial search methods, and developing an underwater search technique in cooperation with the Idaho Power Company. Annual redd searches using combined aerial and underwater search techniques are the best approach for indexing the population of fall chinook salmon in the Snake River at this time. Redd searches should continue until a better, more efficient, approach is developed, tested, and proven.

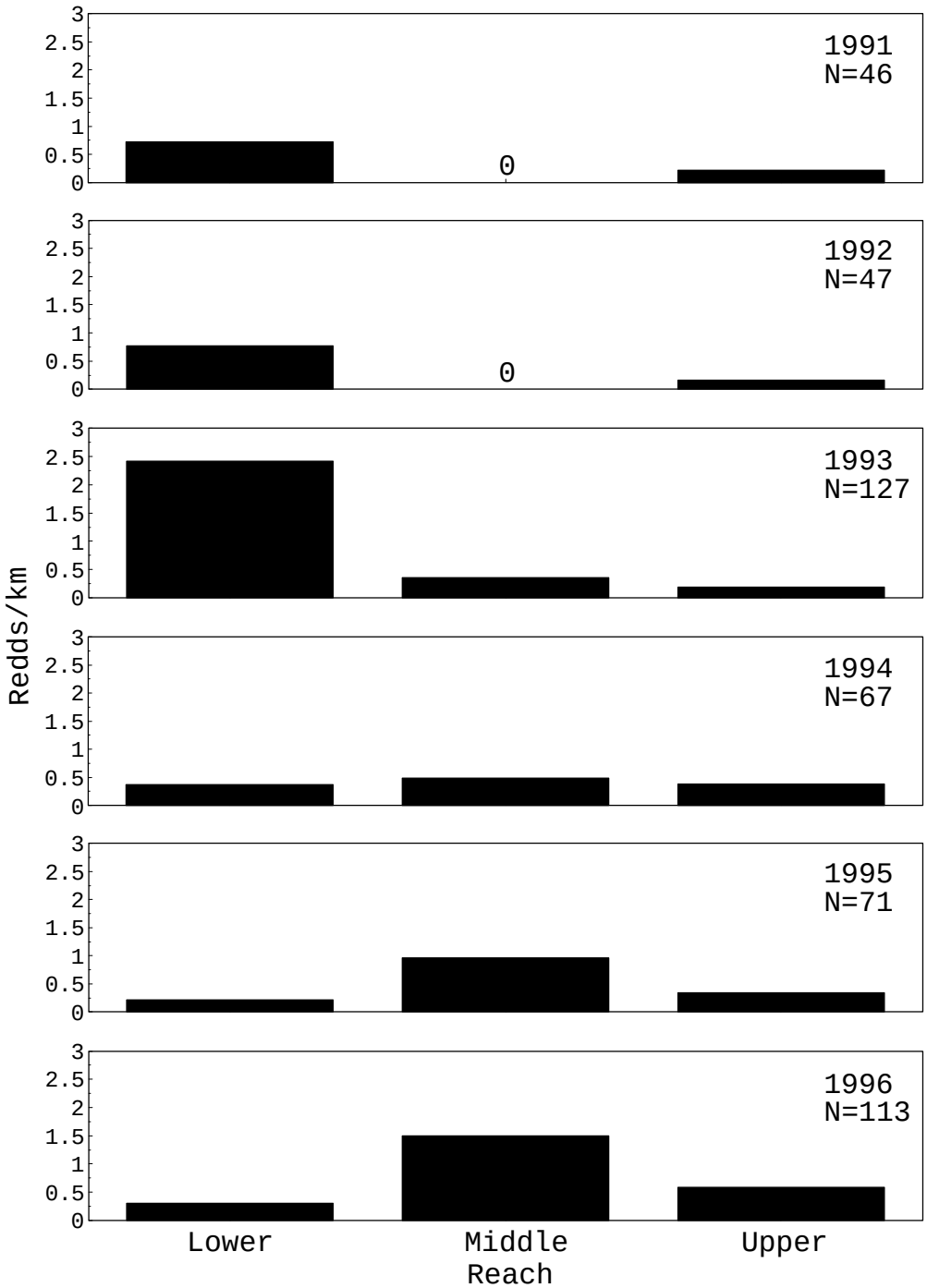

FIGURE 4.-Distribution (redds/km) of fall chinook salmon redds observed in the Snake River during aerial and underwater searches, by reach and year, 1991-1996.

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CHAPTER TWO

Fall Chinook Salmon Spawning Downstream Of Lower Snake River Hydroelectric Projects

by

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Introduction

Historically, fall chinook salmon spawned in the mainstem Snake River from its confluence with the Columbia River to its headwaters near Shoshone Falls, Idaho, a distance of approximately 1,000 km (Gilbert and Evermann 1892); Fulton 1968; Figure 1). Since 1975, following construction of the Hells Canyon Dam and the four lower Snake River hydroelectric dams, mainstem spawning was apparently restricted to the Hells Canyon Reach (river km 236-397; Horner and Bjornn 1979). All other riverine habitat, except for a short distance downstream of mainstem hydroelectric projects, was blocked or inundated.

Snake River fall chinook salmon populations were recently listed under the Endangered Species Act (NMFS 1992), resulting in focused studies on their habitat requirements in the Hells Canyon Reach (Connor et al. 1993). This listing also required the U.S Army Corps of Engineers (Corps) to evaluate potential impacts of mainstem dam operations on Snake River salmon. There was anecdotal evidence that fall chinook salmon spawned in the tailrace area downstream of two lower Snake River dams. For example, Bennett et al. (1983, 1993) captured subyearling chinook salmon in Little Goose reservoir before collection of downstream migrants in the juvenile collection facility at Lower Granite Dam. Salmon embryos, believed to be fall chinook salmon, were discovered downstream of Lower Monumental Dam during dredging operations in February 1992 (Kenney 1992). High fallback rates and holding patterns of adults during the spawning season (Mendel et al. 1992, 1994), also provided evidence that fall chinook salmon spawned downstream of some lower Snake River hydroelectric facilities.

The objective of this study was to search for and characterize fall chinook salmon, *Oncorhynchus tshawytscha*, spawning sites in areas immediately downstream of the four lower Snake River dams (Lower Granite, Little Goose, Lower Monumental, and Ice Harbor; Figure 1). This information was needed to minimize impacts of in-channel construction activities on fall chinook salmon and has important implications related to future operation of lower Snake River hydroelectric projects, including assessment of reservoir drawdown.

Methods

Because the tailraces were large, we limited our searches to locations where physical habitat conditions were similar to areas fall chinook salmon spawn. The areas we searched were identified

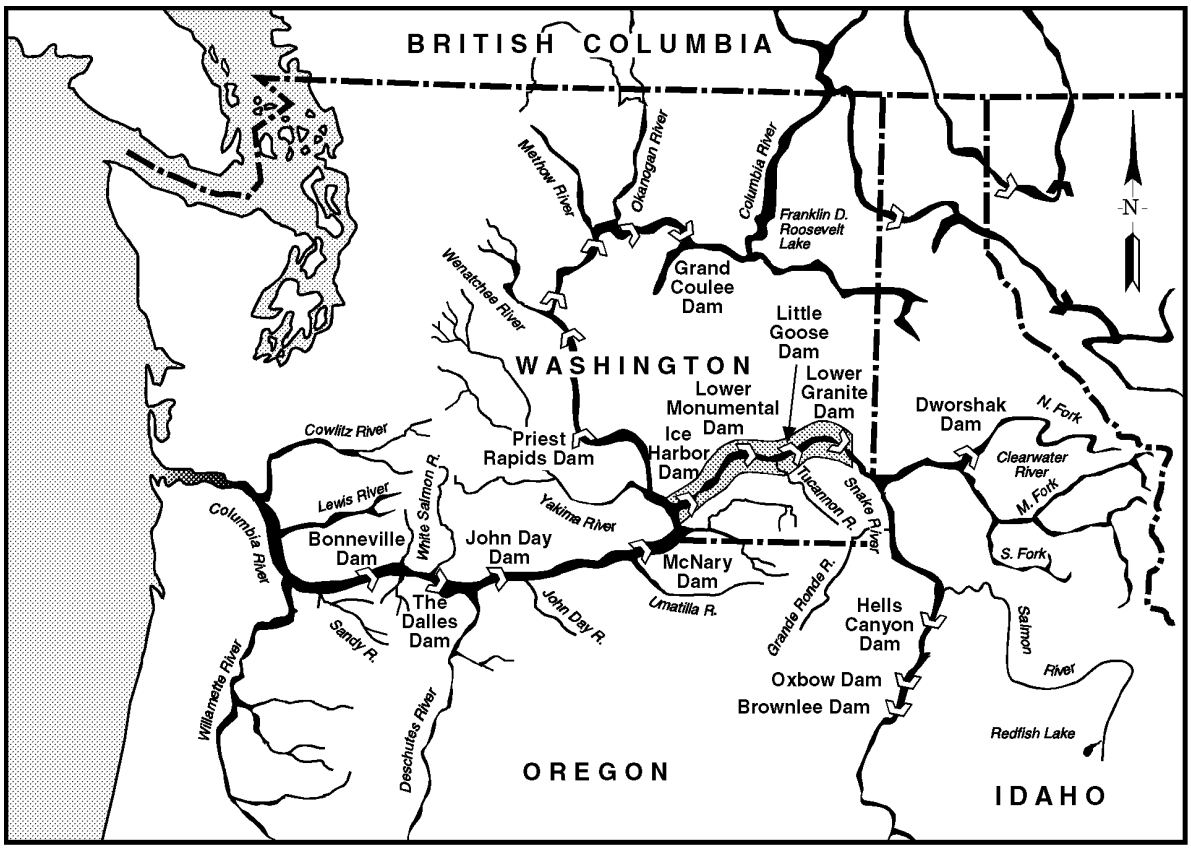

FIGURE 1.-Location of Lower Snake River hydroelectric projects within the Columbia River watershed.

using a Geographic Information System (GIS-Intergraph) that contained baseline data on river channel bathymetry (30-cm contours), near-bed velocity, and dominant substrate collected by a Corps contractor in 1993. Ranges for velocity (0.6-1.8 m/sec), depth (7.6 m below base water-surface elevation), and substrate (0.2-30 cm diameter), found at fall chinook spawning sites, were summarized from measurements taken in the Snake River (Connor et al. 1993; Groves 1993), the mainstem Columbia River (Chapman 1943; Burner 1951; Chambers 1955; Chapman et al. 1983; Swan et al. 1988; Giorgi 1992), and from other large river systems (Thompson 1972; Smith 1973; Hamilton and Buell 1976; Bovee 1978; Neilson and Banford 1983; Bell 1986). The value for slope (<20%) was based on a >80% frequency distribution of Snake River (W.P. Connor, U.S. Fish and Wildlife Service, personal communication) and Hanford Reach redds (Swan et al. 1988). Maps were produced showing areas where these physical habitat ranges overlapped (search areas) for a distance of 2 km downstream of each project. The substrate characteristics of each search area were validated using underwater video. Areas where substrate composition was outside the size range common to fall chinook salmon spawning were not searched. The search area downstream of Ice Harbor Dam was estimated to be 121,810 m^2 in 1993, revised to 158,520 m^2 in 1994, based on additional substrate data. The search areas downstream of Lower Monumental, Little Goose, and Lower Granite dams were 18,380 m^2, 15,450 m^2, and 44,260 m^2, respectively.

Redd searches were conducted using an underwater video system mounted on a double carrier (Groves and Garcia, in press) and deployed from a boat. The camera was aimed 90^o down from horizontal and passed 0.6 -1.3 m over the river bottom at regular intervals (e.g., 7.5-30 m), providing a view path of 1.5 -4.2 m^2. Search patterns were established by first setting a reference cross section that bisected each search area (e.g., CP1-see example survey area; Figure 2) using a laser transit (Leitz/ Sokkisha Set 2 Electronic Total Station) or a Global Positioning System (GPS; Trimble Pro XL). A series of paired wooden stakes were set up parallel to the reference cross section and served as navigation aid. Mid-river marker buoys were also positioned to delineate search area boundaries. The distance between the transect intervals was least for areas thought to have highest potential for spawning (based on substrate characteristics), and for proposed construction sites. Boat position was recorded during each search using a GPS, providing accuracy of $\pm$ 2 m following differential correction.

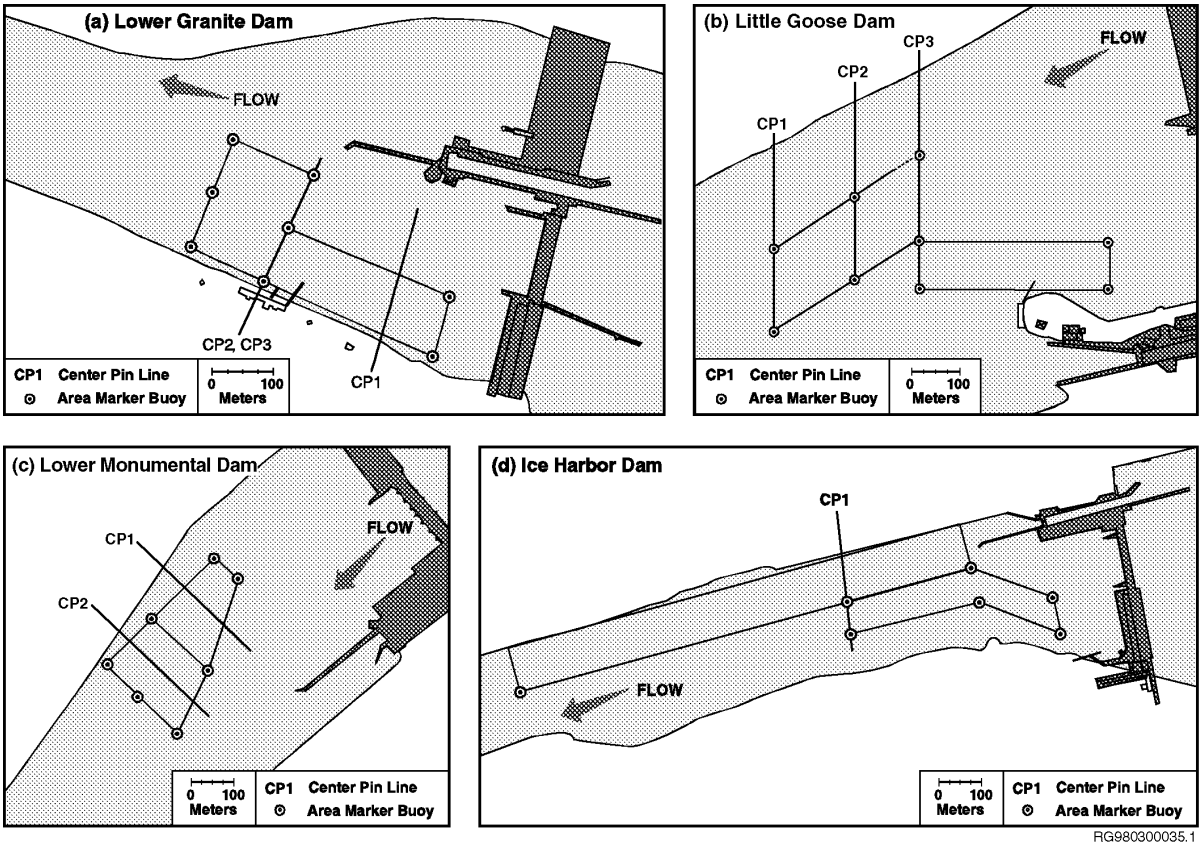

FIGURE 2.-Location of designated search areas, including reference cross-sections, downstream of the four lower Snake River projects.

Spawning surveys were conducted from mid-November through January or following the peak redd construction period for fall chinook salmon (Connor et al. 1993; Dauble and Watson 1997). Most surveys were conducted between 1000 and 1500 hours to take advantage of optimal ambient light conditions. We added an infrared light source in 1996 to provide non-intrusive illumination and to extend the survey period during winter hours. Effective searches could only be conducted when water turbidity was < 4 Nephelometric Turbidity Units (NTU), providing a visibility of approximately 30 cm. Redds were mainly identified by changes in background contrast, bed elevation, or substrate composition. After a redd was located, multiple GPS readings were taken to record its location. Weighted markers (4 cm diameter x 60 cm long rebar) with numbered flagging were dropped from the boat to mark individual redds. These markers helped relocate redds during subsequent surveys. All stored images were reviewed in the laboratory to confirm redd sightings.

Water velocities at individual redd locations were measured using a Marsh McBirney Flow-Mate model 2000 portable flow meter. The sensor was attached to the camera sled platform and obtained a near-bed velocity measurement about 35-40 cm above the substrate. Water depths were measured using a digital echo sounder. The depth and velocity measurements represented a "point-in-time" measurement and changed according to operating conditions (e.g., discharge, spill) at the dam. For example, tailwater elevation differed by as much as $\pm$ 1 m during the spawning period.

Results

We searched 7 to 11% of each search area in 1993, 2 to 10% in 1994, 3 to 11% in 1996, and 9% (two projects) in 1997. No surveys were conducted in 1995 because of project spilling and high turbidity. The general characteristics of each search area varied. For example, the area downstream of Ice Harbor Dam where redds might be found encompassed most of the channel cross section, including the navigation channel and area downstream of the powerhouse. However, we concluded from our video surveys that the area downstream of the powerhouse was the only location having substrate and flow conditions suitable for spawning. For example, the navigation channel had low potential for spawning because past dredging activities had removed much of the alluvium. Dominant substrate in the search area downstream of Lower Monumental Dam was highly variable, ranging from gravel to boulder. It was evident that substrate and depth characteristics in this survey area had also been altered by past dredging activities. In contrast, much of the defined search area

downstream of both Little Goose and Lower Granite dams had superficial substrate and flow characteristics that appeared suitable for spawning.

During the four years of surveys, we found evidence that fall chinook salmon spawned downstream of three of the four lower Snake River projects (Table 1). Lower Granite Dam had the highest redd totals, but Little Goose had the highest frequency of use. At both projects, redds were located on the powerhouse side of the dam tailrace and near a high-volume discharge from the juvenile bypass outfall. All redds found at Little Goose Dam occurred within the splash zone of the bypass outfall, while those downstream of Lower Granite Dam occurred immediately downstream of the bypass outfall. The single redd found at Ice Harbor Dam in 1996 was near a support piling of the newly constructed juvenile bypass outfall. No redds or evidence of disturbed gravel were found within any the designated search areas surveyed downstream of Lower Monumental Dam.

We estimated the total spawning area (including inter-redd distance) downstream of Lower Granite Dam in 1993 and 1994 was 2,560 m^2 (Figure 3). The spawning area downstream of Little Goose Dam was more localized and encompassed only about 580 m^2 for all survey years (Figure 4). The actual amount of habitat used for spawning was only 5.8 and 3.1% of the area identified by GIS at Lower Granite and Little Goose dams, respectively.

The depth of water over redds downstream of Lower Granite Dam ranged from 4.0 to 6.0 m (mean depth 6.7 m), and near-bed velocities ranged from 0.4 to 0.7 m/sec. Depth of redds downstream of Little Goose Dam was similar, ranging from 4.5 to 8.1 m (mean depth 6.6 m) and near-bed velocities ranged from 0.3 to 0.4 m/sec.

Discussion

Our observations confirmed that small numbers of fall chinook salmon spawn in the mainstem Snake River downstream of the Hells Canyon Reach. Thus, some spawning has now been documented downstream of each of the four lower Snake River hydroelectric dams. The occurrence of redds in tailrace areas explains some of the apparent interdam loss of adult fall chinook salmon, a loss previously attributed to between-project mortality (reviewed in Dauble and Mueller 1993). Redds found downstream of lower Snake River dams did not represent a significant proportion

TABLE 1.- Annual redd totals for lower Snake River hydroelectric projects based on underwater video surveys conducted in 1993, 1994, 1996, and 1997. No surveys were conducted at Ice Harbor and Lower Monumental dams in 1997.

Survey year	Ice Habor	Lower Monumental	Little Goose	Lower Granite
1993	0	0	4	14
1994	0	0	4	5
1996	1	0	4	0
1997	-	-	1	0

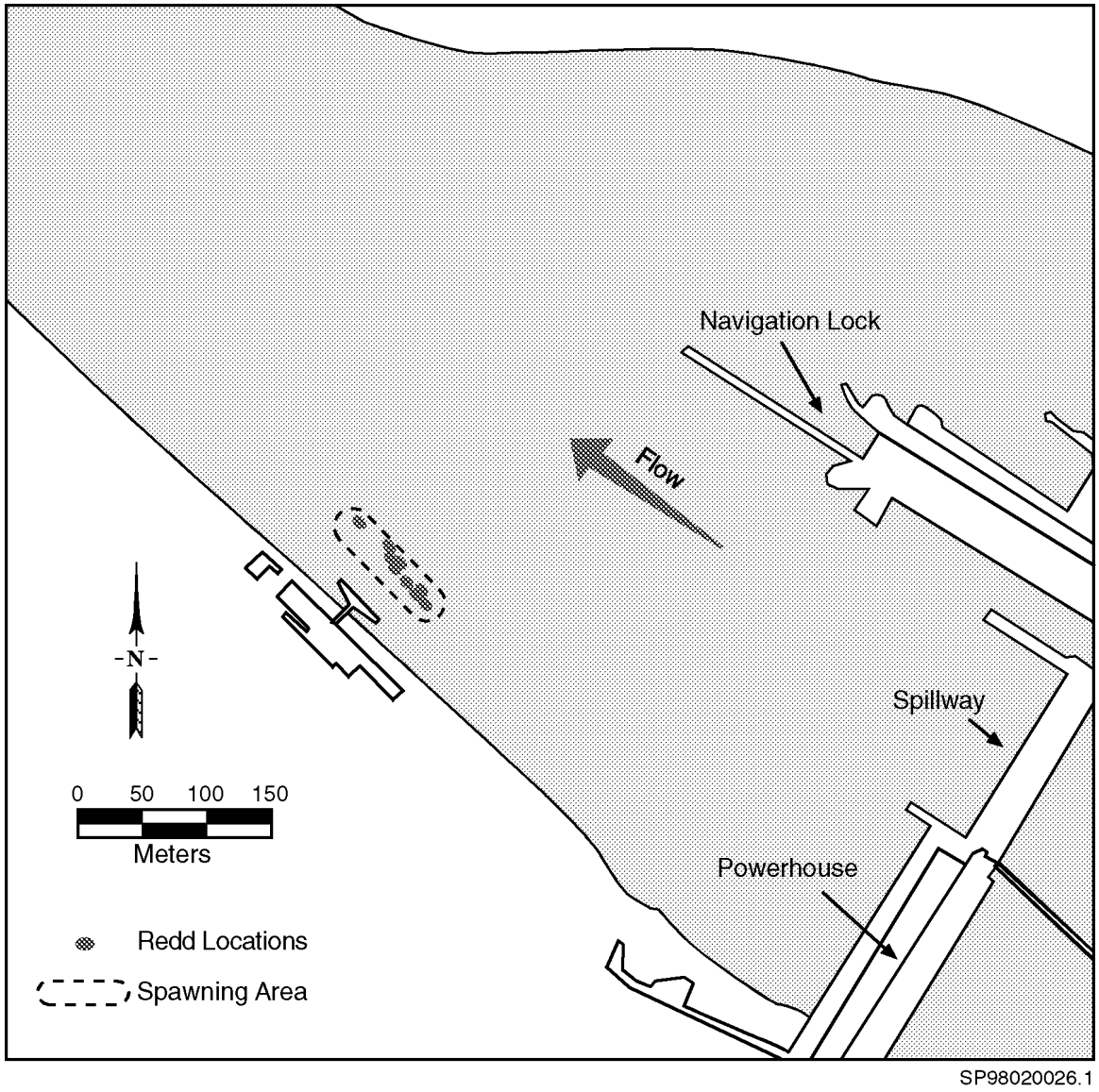

FIGURE 3.-Fall chinook salmon spawning area and principal project features downstream of Lower Granite Dam.

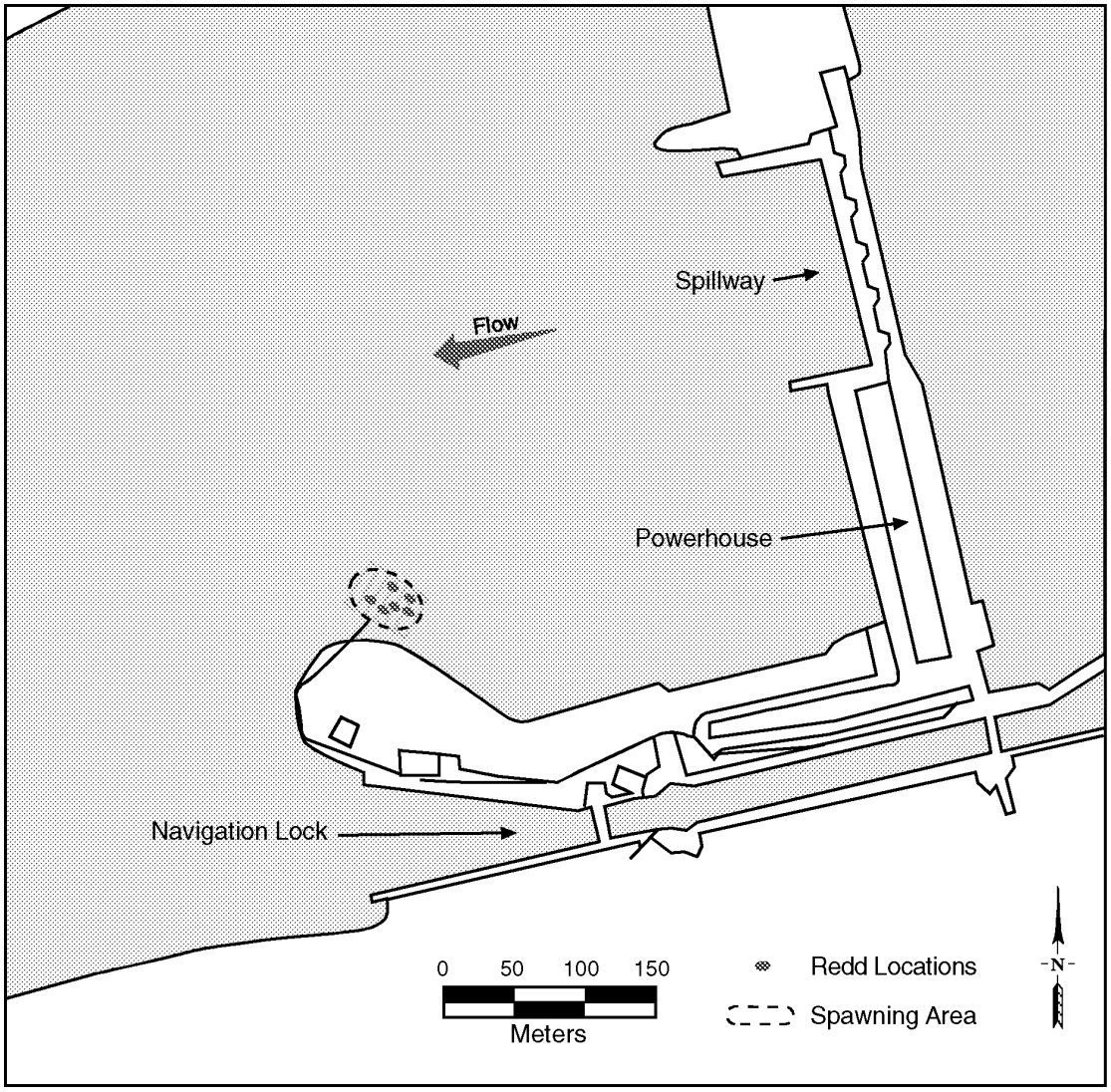

FIGURE 4.-Fall chinook salmon spawning area and principal project features downstream of Little Goose Dam.

of production relative to other areas in the Snake River system during our survey years. Although tailrace spawning accounted for about 12% of the mainstem Snake River redds in 1993 and 1994, spawning was more limited in 1996 and 1997. The relative importance of these tailwater spawning sites to Snake River fall chinook salmon populations is less when tributary use is considered (Groves and Chandler 1996).

Fidelity toward spawning areas appeared high during our survey years, but temporal use patterns were irregular. Thus, it was difficult to determine whether fall chinook salmon returning to these areas existed as "satellite" populations or if the tailraces served as convenient locations for some upstream migrant adults to spawn. Nonetheless, irregular use of defined spawning sites in the tailwater areas is consistent with use patterns in other parts of the Snake River. For example, Groves and Chandler (1996) reported that frequency of use for fall chinook spawning sites in the Hells Canyon Reach ranged from 9 to 77% for the 50 sites they monitored from 1986 to 1995.

Although suitable spawning habitat (based on physical characteristics) appeared present throughout much of the Little Goose and Lower Granite tailraces, redds were found only in the area immediately adjacent to outfall flows. This suggests that the flow patterns, overhead turbulence, nearby structures, and/or that pheromones or other odors from the juvenile fish facility, may attract migrating adult salmon. Redd locations also may have been influenced by powerhouse operations. Locations in the Mid-Columbia River where spawning sites occur downstream of the powerhouse include Wanapum (Rogers et al 1988; Horner and Bjornn 1979), Rock Island (Horner and Bjornn 1979), and Wells dams (Giorgi 1992). Operational variables, such as the relative amount of discharge through the powerhouse, influences both substrate size and mobility, key spawning habitat variables.

The primary purpose of our GIS-based habitat evaluation was to effectively direct initial search efforts. Because the range of physical habitat values used for model input was wide, we did not try to quantify available spawning habitat. However, Parsley and Beckman (1994) applied GIS technology, in conjunction with the Physical Habitat Simulation System (PHABSIM; Bovee 1982) to quantify rearing habitat for juvenile white sturgeon. Thus, this tool can be refined to provide predictions of potential or available habitat. We also found that GIS was useful for linking across two or more spatial data sets. For example, we used GIS to develop cross-section profiles for individual redds that showed their location relative to channel morphology and velocity vectors.

To our knowledge, underwater video technology was not used for locating salmon redds before 1992. However, this technology is now routinely used in the Snake and Columbia rivers to characterize spawning habitat and to search for redds (Garcia et al 1994; Groves and Chandler, in press). We used underwater video to locate fall chinook salmon redds at depths ranging to 9 m. This value compares to a redd depth limitation of 3-4 m for aerial surveys conducted under similar conditions of visibility (Dauble and Watson 1997). Searches with the video camera have advantages over other underwater techniques commonly used to verify salmonid spawning locations, such as SCUBA, in terms of increased coverage, safety, and documentation.

Our studies show that operation of existing hydroelectric facilities in the lower Snake River has created physical habitat conditions suitable for spawning by fall chinook salmon. These conditions appear to exist for only short distances downstream of most projects. It was previously documented (Parsley and Beckman 1994) that dam tailrace areas provide vestigial, though highly regulated, riverine habitat for other important Columbia River fish species such as white sturgeon. Thus, any proposed operations for hydroelectric facilities, such as reservoir drawdown, spilling, and altered outfall flows, need to be carefully evaluated to ensure that potential impacts to important fish species are minimized. Additionally, future recovery planning for listed fall chinook salmon (NMFS 1995) should consider the relative importance of this riverine habitat to remaining mainstem and tributary populations.

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CHAPTER THREE

Two Carriers Used to Suspend an Underwater Video Camera from a Boat

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Introduction

Remotely operated underwater video cameras (UVC's) can be used to make observations in areas that are otherwise impractical to reach (Helfman 1983). The types of carriers used by fishery biologists to place and move UVC's through the water have varied with study objectives and work environments. Existing literature concerning UVC's was limited to use in lentic systems, over relatively homogeneous substrates. To observe lake trout *Salvelinus namaycush* spawning grounds in water 2–9 m deep, Nester and Poe (1987) housed an UVC in a stainless steel case and suspended it from a boat on polyvinyl chloride (pvc) pipe up to 8 m long. Bergstedt and Anderson (1990) attached an UVC to a sled made of pvc pipe and towed it behind a boat in water 3–8 m deep to observe bricks they had distributed over a sandy lake bottom. Edsall et al. (1993) used an UVC housed in a remotely operated vehicle to observe burbot *Lota lota* residing over a variety of bottom substrates at depths to 42 m.

The need to locate chinook salmon *Oncorhynchus tshawytscha* spawning grounds and redds, and to characterize substrate types for habitat mapping and modeling in a large river, created a challenge for deployment of an UVC that could not be met using existing carriers designed for lentic conditions. For example, we required a carrier that could be suspended from a boat, operated in water 3–13 m deep with velocities up to 3 m/s without being subjected to excessive drag, maneuvered over potentially damaging substrate types, and adjustable to allow the camera to rotate from 0° to 90° (down from horizontal). We developed and tested two lotic UVC carriers and a deployment system by modifying hydraulic sounding weights and equipment normally used for stream gaging.

Methods

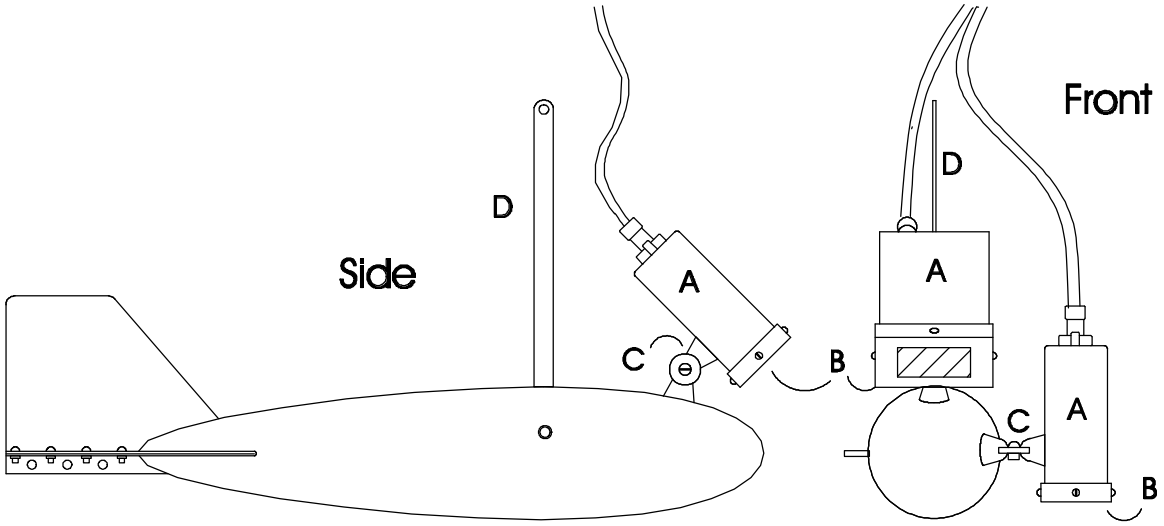
We built two types of UVC carriers, one using a single 34 kg hydraulic sounding weight (single carrier), and the other using two 11 kg sounding weights (double carrier). Both carriers were designed to accommodate a Sony WPC140 waterproof housing containing a series HVM camera with a 110° lens. The camera and housing were connected to a DC-powered 8 mm video recording system by 20 m of camera cable. Real-time observations were made possible by connecting the video recording system to an independent black and white monitor having a 23 cm diagonal screen. The carriers were tested and used separately by different crews and at different river locations. Each UVC carrier was suspended from a boat by a 3 mm diameter metal cable that passed through a roller on the bow, and attached to a U. S.

Geological Survey (USGS)-type sounding reel with a calibrated depth indicator. The carriers were attached to the suspension cable using a prefabricated stainless steel hanger bar and a USGS type B connector.

The single carrier consisted of an aluminum casing (4.8 mm thickness) attached near the nose of the sounding weight using two universal brass heads (modified from electrical tool extensions) (Figure 1). One brass head was attached to the bottom of the aluminum case, and the other was embedded into the nose of the hydraulic weight. Each brass head was equipped with interlocking teeth that allow the protective case to be positioned at various angles between 0° and 90° down, relative to horizontal. The aluminum casing was left fully open at the front, and an opening was cut into the back plate in order to allow video coaxial cable connections. The plastic waterproof camera housing was placed into the aluminum protective case from the front, and was held in place by a face plate that was attached using four 9.7 mm machine screws.

For the double carrier, two sounding weights were welded together with an aluminum framework (6.4 mm thickness), and two of the hydraulic fins were replaced with a single connecting plate (Figure 2). The stainless steel hanger bars were drilled to fit a 9.7 mm diameter course-thread stainless steel rod covered with two aluminum tubes (12.7 mm diameter, 3.2 mm wall thickness). The two aluminum covering tubes provided support and centered the small hanger bar. An additional aluminum frame was used with the double carrier to provide extra protection for the camera when it was set at 45° and 90° down from horizontal.

Modifications to both carriers provided for the use of two cameras in combination, one oriented forward at 45° down from horizontal and another set at 90° down from horizontal. On the single carrier the second camera was attached to either side of the weight using a duplicate of the nose mount and the protective aluminum case (Figure 1, front view). A bracket was used to add the second camera to the double carrier (Figure 2, side view). We used this arrangement to help detect subtle differences in contrast and relief of substrates when searching for redds, and for referencing video segments to calibrated images during substrate analyses.



Single-weight carrier

FIGURE 1.-Side and front views of the single carrier, showing the aluminum case (A), removable face plate (B), universal brass mounting heads (C), and hanger bar (D). The side view shows a single camera set facing forward at about 45° down from horizontal. The front view shows two cameras angled down by 45° and 90° from horizontal.

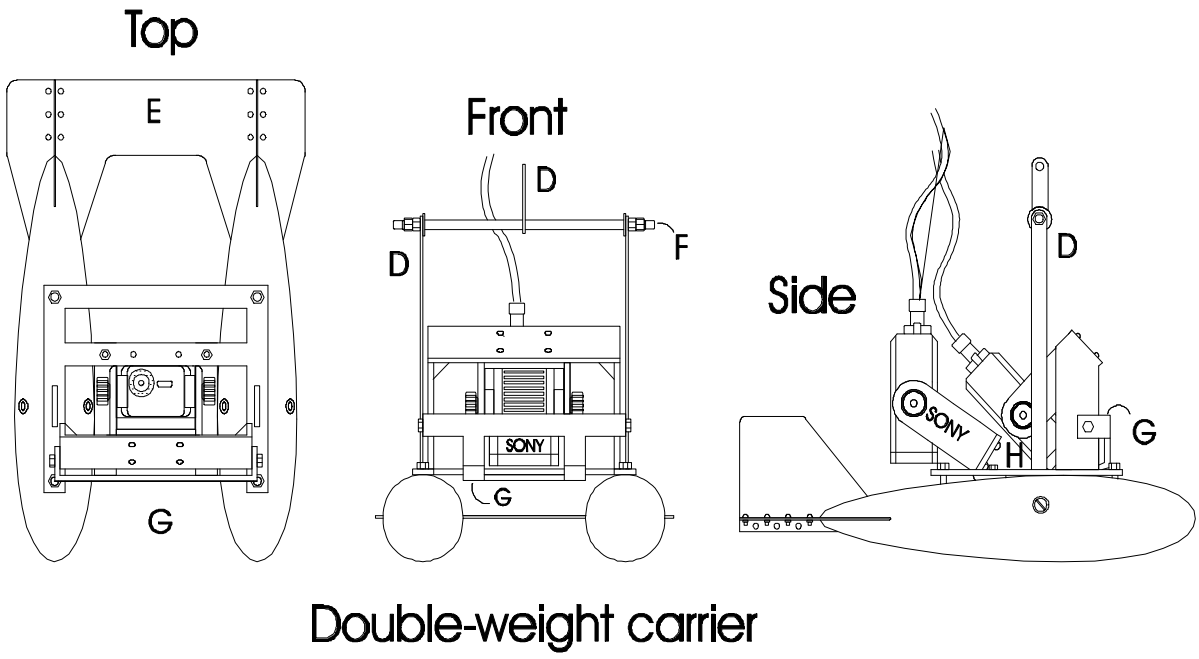


FIGURE 2.-Top, front, and side views of the double carrier showing hanger bar (D), connecting plate (E), cross bar (F), protective carriage (G), and mounting plate (H). The top and front views show a single camera set at 90° down from horizontal. The side view shows two cameras angled down from horizontal by 45° and 90°.

Results and Discussion

We successfully used the two UVC carriers to remotely observe and measure substrates and search for chinook salmon redds over a wide range of depth and velocities in a large river (Groves 1993, Garcia et al. 1994, Groves and Chandler 1996). Each carrier design had unique features, and both were used to depths of 13 m, and where velocities approached 3 m/s. The single carrier provided less camera protection, tended to wobble at higher velocities (> 1 m/s), but offered less drag. The double carrier provided a greater degree of camera protection and stability in all flow ranges (to about 3 m/s), but created drag that pulled the carrier under the boat when operated in water > 3 m deep with velocities > 1 m/s.

Both carriers were damaged by collision with large boulders at least once while working in areas having erratic turbulence due to high water velocity and jutting bottom substrates. Damage to the single carrier was limited to the aluminum case, and was due to repeated impact with large boulders. We recommend using a stainless steel case for increased protection of the camera. The hanger cross bar on the double carrier was bent once after the carrier lodged between two boulders and excessive force was needed to extract it. In all instances, the waterproof camera housing remained intact, and we believe that risk of damage could be minimized with increased operator experience.

Our designs could be used as presented, or modified to fit other camera types and water conditions. For example, during underwater video observations of habitat use, a Marsh-McBirney (Model 2000) velocity meter was attached to measure velocity at specific heights above redds. Also, our current method of moving the UVC up and down through the water column relies on a manually operated winch; it is possible that an electric winch system could be used to reduce muscle strain. Additionally, water drag on the video cable can be a nuisance, resulting in excessive cable bowing downstream under the boat. This problem can be an obvious disaster in a propeller operated craft. We overcame this obstacle by running the video cable through a type of friction braking bar commonly used for technical mountaineering and rappelling. Finally, strong lighting around the monitor face can result in glare that degrades the video picture during real-time observations. We overcame this problem by placing an extended protective hood around the monitor. The hood was made of light plywood, painted flat black inside and extended out from the face of the monitor by approximately 30 cm.

Each carrier system proved successful in allowing us to deploy and maneuver an underwater camera in a large river having moderately high water velocities. These designs have also been adopted by other agencies attempting similar studies downstream of hydroelectric projects in the lower Snake and Columbia Rivers (Dauble et al. 1994).

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CHAPTER FOUR

Evaluation of Substrate Quality For Incubation of Fall Chinook Salmon Embryos in the Snake River

by

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Introduction

Concern over the low abundance of Snake River fall chinook salmon *Oncorhynchus tshawytscha* culminated in 1991 when the National Marine Fisheries Service was petitioned to list this stock under the 1973 Endangered Species Act (ESA; NMFS 1992). Recovery efforts for fall chinook salmon are limited by the lack of understanding of life history requirements.

Successful natural reproduction of Snake River fall chinook salmon could be limited by the quality of spawning gravel. Fall chinook salmon spawn in the free-flowing reach of the Snake River between river kilometers (RKMs) 235 and 398 (Garcia et al. 1994). Cursory surveys have shown that 12 natural spawning locations have been important from 1987 through 1994. Some physical features of these 12 spawning locations have been described using Instream Flow Incremental Methodology (Connor et al. 1993) and limited substrate analysis.

A complex mixture of sediment sizes in combination with certain hydraulic conditions are required to provide an ideal spawning environment for chinook salmon (Reiser and Bjornn 1979) although the mixture of sediment sizes for optimum salmon survival is not clear (Platts et al. 1979). Chapman et al. (1986) reported that the substrate used by spawning fall chinook salmon at Vernita Bar in the Columbia River contained a high proportion (32-35%) of cobble and large gravel (> 75 mm) with a smaller proportion of fines (< 0.85 mm, 4.3-5.8%).

High concentrations of fine sediments can create detrimental effects during salmonid egg and fry development (Meehan and Swanston 1977). Excessive amounts of fine sediment in the spawning substrate can decrease permeability and water velocity to incubating embryos (Lotspeich and Everest 1981). Decreased flow through the substrate reduces oxygen availability to embryos and slows removal of metabolic wastes that may be toxic to embryos (Iwamoto et al. 1978). Also, entrapment of fry occurs when fine sediments are lodged in substrate interstices that prevent emergence (Phillips 1975). The purpose of this project was to describe the composition of gravel in the Snake River between Rkms 245.1 and 398, and to assess effects of the substrate composition on the incubation success of fall chinook salmon. The objectives were to (1) characterize the spawning substrate at 12 previously identified fall chinook salmon spawning locations and (2) estimate incubation success of fall chinook salmon embryos in artificial redds using substrate representative of the 12 study locations.

Study Area

The free-flowing reach of the Snake River extends from Hells Canyon Dam (RKM 398) to the upstream end of Lower Granite Reservoir (RKM 235) near Asotin, Washington. Twelve spawning sites within the free-flowing reach, previously identified from redd counts (Connor et al. 1993), were sampled to assess substrate composition (Figure 1). Riffles, glides, lateral gravel bars, and runs all within deep and shallow locations were associated with the spawning locations. Four of the 12 locations, RKMs 245.1, 257.1, 259, and 261.3, were sampled to assess substrate composition during 1994 and the remaining eight locations, RKMs 249, 254.7, 267, 277.6, 312.7, 343.7, 349.6, and 352.9 were sampled during 1995.

Methods

Substrate Composition

Substrate at eight of 12 known spawning sites was sampled by freeze-core or dome suction sampling whereas four sites were sampled by video analysis due to high flow conditions. Ten random substrate samples were collected at each of eight of the 12 previously identified spawning sites. Site maps, created from underwater videos, with locations of suitable-sized spawning substrate, were obtained for each study site (Connor et al. 1994). A numbered grid was placed over the site maps and 10 random numbers were selected that corresponded to potential sampling locations. Substrate sampling locations were identified by SCUBA divers from lead lines marked at 10-m intervals extended perpendicular to the current. SCUBA divers descended to the appropriate sampling locations and used a modified dome suction sampler (Gale and Thompson 1975) to collect substrate in water > 1.2 m deep. The dome suction sampler consisted of a transparent acrylic hemisphere (dome; measured 30.2 cm in diameter x 25.4 cm in height) with two 15 cm diameter holes cut on adjacent sides of acrylic dome. The diver’s arm was inserted through one hole, covered with overlapping neoprene to prevent fine sediments from escaping, and large substrate from inside the sampler was placed by the diver into a collection bag attached to the other hole. An additional 1.9 cm hole into the dome facilitated mounting a bilge pump (powered by an attached 12-volt battery) to vacuum fine sediments into a separate collection bag. The dome was mounted to the top of a serrated stainless steel band (measured 30.5 mm x 30.5 cm high) that permitted easier penetration into coarse substrates.

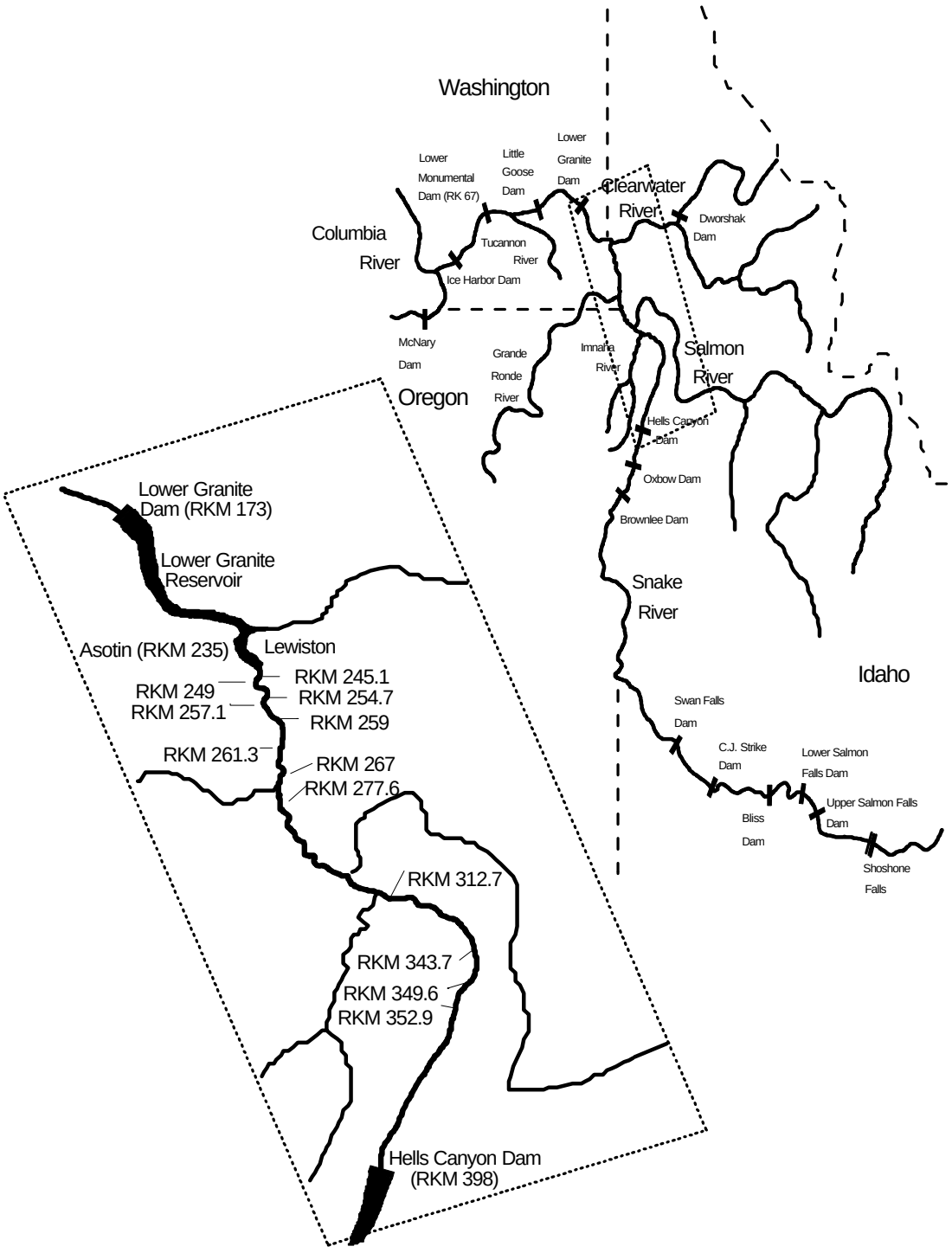


FIGURE 1.-Map of Snake River drainage and specific sampling locations (river kilometer, RKM, 245.1 to 352.9) for fall chinook salmon spawning gravel.

A modified, tri-tube, freeze-core sampler (Everest et al. 1980), fueled by liquid CO_2, was used to sample substrate in water < 1.2 m deep. We used a diamond-shaped, galvanized deflector (0.5 x 0.9 x 1.4 m high) to divert water flow and enhance freezing of the substrate. Extracted cores were placed on a subsampler, heated, sorted into three strata (stratum 1 = 0-10.16 cm, stratum 2 = 10.16-20.3 cm, stratum 3 = 20.3-30.5 cm; Everest et al. 1980), and placed into labeled collection bags.

Substrate samples were transported to the University of Idaho, dried, and shaken through U.S. standard sieves with mesh sizes of 0.25, 0.85, 2.0, 3.35, 4.75, 6.4, 9.5, 12.5, 20, 50, and 75 mm. Dry weight from each sieve was used to calculate the mean particle size distribution of each sample.

Gravel quality indices used to predict salmonid incubation success are generally classified as one of two types: (1) the proportion of a substrate sample smaller than a given size (percent fines) or, (2) a measure of central tendency of the entire particle distribution (Young et al. 1991). We chose fines < 0.85 and < 6.4 mm with central tendency measures of geometric mean particle size (d_g) and Fredle index (f_i) for comparison with results from similar experiments (McNeil and Ahnell 1964; Bjornn 1969; McCuddin 1977; Shirazi and Seim 1979; Tappel and Bjornn 1983; Young et al. 1991; Arnsberg et al. 1992). Geometric mean particle size was calculated as:

$$d_g = d_1^{w1} \times d_2^{w2} \times \ldots d_n^{wn} ;$$

where d = mean particle diameter captured by a sieve, and w = decimal fraction by weight of particles retained by a given sieve. The Fredle index was calculated as:

$$f_i = d_g \div S_o;$$

where d_g = geometric mean, $S_o = \sqrt{d_{84} \div d_{16}}$ the sorting coefficient, d_{84} and d_{16} = weight of particles at which 84% or 16% (one standard deviation) of the sample is finer (Kondolf 1988).

The percentages of substrate < 0.85 mm and < 6.4 mm for each sample were normalized by arcsine transformation for comparison by analysis of variance (Ott 1984). We examined mean particle size distribution at each location by plotting the data on a logarithmic scale. Substrate samples from fluvial systems have particle size distributions close to lognormal (Shirazi and Seim 1979; Tappel and Bjornn 1983). Fredle index numbers were log

transformed ($f_t = \sqrt{fi + 0.375}$) for normality (Ott 1984). A general linear model (GLM) of analysis of variance (SAS 1989) was used to statistically compare ($P < 0.05$) vertical stratification within and among each freeze-core sample.

We used the National Institutes of Health digital image processing procedure (Kemeny et al. 1993) for analysis of surface substrate videos collected by the U.S. Fish and Wildlife Service at four sites (RKMs 249, 254.7, 267, and 277.6) because the water was too deep (> 3 m) and fast for either freeze-core or dome suction sampling. Sampling sites were selected from the video tapes using the criteria of dominant and subdominant substrate < 15.24 cm and > 1.00 cm from which 25 random snapshots, per site, were taken with a Macintosh 7200/100 computer using the Photoshop image software.

Substrate particles shown in the snapshots were manually outlined with the free-hand utility tool of the software. The computer measured the area, major axis (the longest portion of the particle), and minor axis (shortest portion of the particle) of each particle. Areas containing fine particles (< 6.4 mm) were combined into an outlined image, and the area of these images were calculated for the total amount of fines in the photograph. Particles were then placed into sieve sizes of < 6.4, 6.4, 9.5, 12.5, 20, 50, and 75 mm based on the formula: $D = 1 \div \sqrt{2} \left[\sqrt{1 + (c \div b)^2}\right] \times b$; where D is the sieve opening, b is the major axis, and c is the minor axis of the particle being measured (Church et al. 1987). Percentages of each sieve size were determined by the sieve area divided into the total area measured in the image. Particle size distribution was computed at each site and graphically presented.

Emergence Success

Eight spawning substrate compositions that encompassed the range of substrates in known spawning areas of the Snake River, were chosen to simulate effects on fall chinook salmon embryos. Forty-eight troughs (121.9 cm length x 30.5 cm wide x 30.5 cm deep) were filled 25 cm high with eight gravel-sand mixtures (Figure 2). Six replicates of each gravel and sand mixture were weighed and combined by hand to obtain the eight target compositions (Table 1) and were randomly placed into separate troughs.

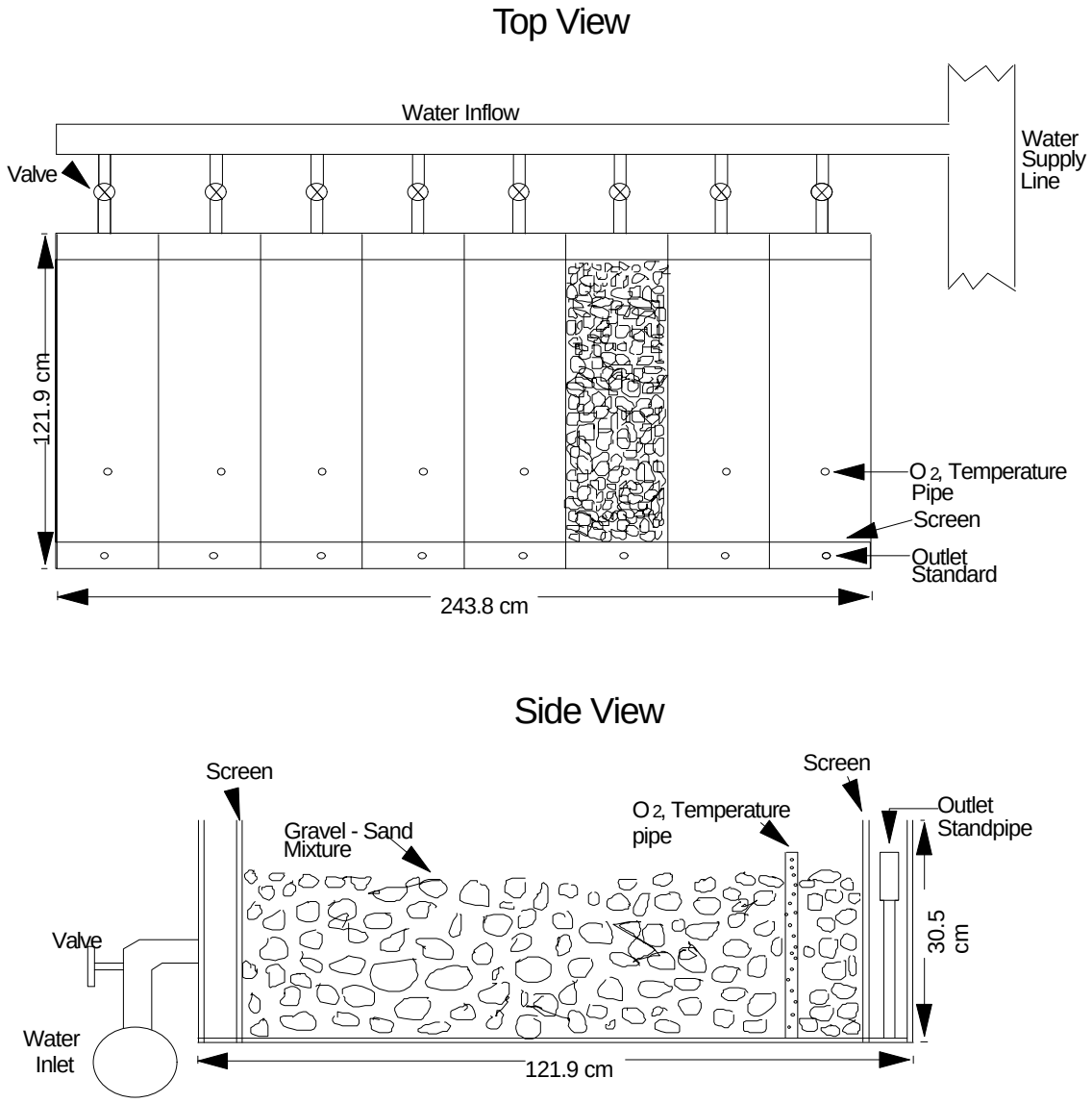


FIGURE 2.-Diagram of troughs used to estimate emergence success of fall chinook salmon embryos in various substrate compositions.

TABLE 1.-Substrate composition (%) used to assess embryo incubation success of fall chinook salmon in the laboratory during 1995 and 1996.

	< 6.4 mm			> 6.4 < 25 mm			> 25 mm		
	Planned	Measured		Planned	Measured		Planned	Measured	
Composition		1995	1996		1995	1996		1995	1996
1	0	2	2	75	72	80	25	26	18
2	8	11	9	70	72	77	22	17	14
3	12	26	13	81	68	83	7	6	4
4	16	23	19	75	73	75	9	4	6
5	20	29	23	65	66	67	15	5	10
6	26	28	27	70	69	70	4	3	3
7	30	32	32	54	60	57	16	8	11
8	35	36	36	65	62	64	0	2	0

Eyed fall chinook embryos from Bonneville Fish Hatchery, Bonneville, Oregon, were used for the trough experiment in 1995. Three holes placed near the inflow, middle, and outflow of each trough were dug 25 cm deep into the gravel, simulating egg pockets. Two Whitlock/Vibert (W-V) boxes, each filled with 50 embryos and trough substrate, were placed in two of the holes and 50 embryos were placed in the bottom of the third hole. All embryos were gently covered with trough substrate.

In 1996, fall chinook gametes (eggs from three females and milt from five males) obtained from Lyons Ferry Hatchery, Washington, were brought to the University of Idaho laboratory where they were fertilized and water hardened. One hundred fifty embryos were placed in troughs similar to the 1995 procedures although only one W-V box, filled with 50 embryos and substrate, was used for each trough assessing incubation success, prior to emergence. During both years, 100 embryos each were placed in three Heath Tray incubators to monitor handling mortality (controls) of the embryos.

Chilled, unchlorinated, recycled tap water flowed laterally through the troughs. Flows through the troughs were regulated by ball valves and determined by gradient differences between the inflow and outflow sources. A 2% gradient was maintained where possible. Dissolved oxygen was measured with a YSI model 57 meter (Yellow Springs Instruments, Yellow Springs, Ohio) in perforated PVC pipe (20 cm long x 1.8 cm diameter) placed in the middle of each egg pocket nearest the outflow (9.78 mg/L = 100% saturation). Water temperatures were recorded hourly with a RTM 2000 meter (Ryan Tempmentor, Ryan Instruments, Redmond, Washington).

As fry emerged, they were removed from the troughs with suction devices or small nets, placed in sample bags, and preserved in 10% formalin. After being preserved for more than 21 days, fry were blotted dry, weighed to the nearest 0.1 mg, and measured for total length (0.5 mm; Rombough 1985). Survival was calculated as the percentage of fry that emerged, transformed by arcsine (Ott 1984) and compared among substrate compositions using polynomial regression analysis (SAS 1989).

Substrate samples from the inflow, middle, and outflow of the trough were taken with a 15.24 cm McNeil sampler (McNeil and Ahnell 1964) at the conclusion of the fry emergence. Substrate samples were dried, shaken through U.S. standard sieves (0.25, 0.5, 0.85, 2.0, 3.35, 4.75, 6.4, 9.5, 12.5, 20, 50, and 75 mm), and weighed. Percent fines (< 0.85 and < 6.4 mm), geometric mean particle size, and Fredle index were calculated similarly to the

substrate samples collected in the Snake River. Least squares means (SAS 1989; $P < 0.05$) were used to determine if differences in substrate composition occurred between troughs. Differences in the mean indices of substrate composition and the corresponding percent emergence were compared by *t*-test ($P < 0.05$). Samples containing less than 5 % fines < 0.85 mm were considered large diameter substrate (LDS), whereas, samples containing more than 10% fines < 0.85 mm were considered small diameter substrate (SDS).

Results

Substrate Composition

Differences in particle size distribution of substrates sampled in water > 1.2 m deep were observed (Figure 3). Substrate from RKMs 245.1, 261.3, and 343.7 contained significantly higher percentages of small (< 2.0 mm) particles ($P < 0.049$) than those sampled at other locations whereas RKMs 259, 312.7, 349.6, and 352.9 contained higher percentages of larger (> 6.4 mm) particles. Substrate sampled with the dome suction sampler at RKM 257.1 was generally > 15.24 cm and considered too large for spawning, and, thus was omitted from further analysis. Mean percent fine substrate particles < 0.85 mm was highest at RKM 245.1 (8.5%) and decreased upstream to a low at RKM 352.9 (1.16%; Table 2). Mean percent fine particles < 6.4 mm were also highest at RKM 245.1 (19.82%) and generally decreased upstream to a low at RKM 312.7 (7.51%). The geometric mean particle size and mean Fredle index values were highest at RKM 312.7 ($d_g = 39.86$ and $f_i = 18.32$) and lowest at RKM 245.1 ($d_g = 17.68$ and $f_i = 5.89$).

Substrate sampled by the freeze-core sampler at RKM 245.1 contained the lowest percent fines in stratum 1 (10.71%) and fines gradually increased with depth (Table 3). Percent fines between strata 1 and 2, and strata 1 and 3 were significantly different ($P < 0.009$), whereas those between strata 2 and 3 were not significantly different ($P > 0.914$). No significant difference in percent fines (< 0.85 mm) was found at Rkm 261.3 among strata. Geometric mean particle size and mean Fredle index decreased with depth at RKM 245.1 but remained similar among depths at RKM 261.3.

Data collected by image processing showed a higher abundance of particles < 6.4 mm at RKMs 254.7 and 277.6 than at RKMs 249

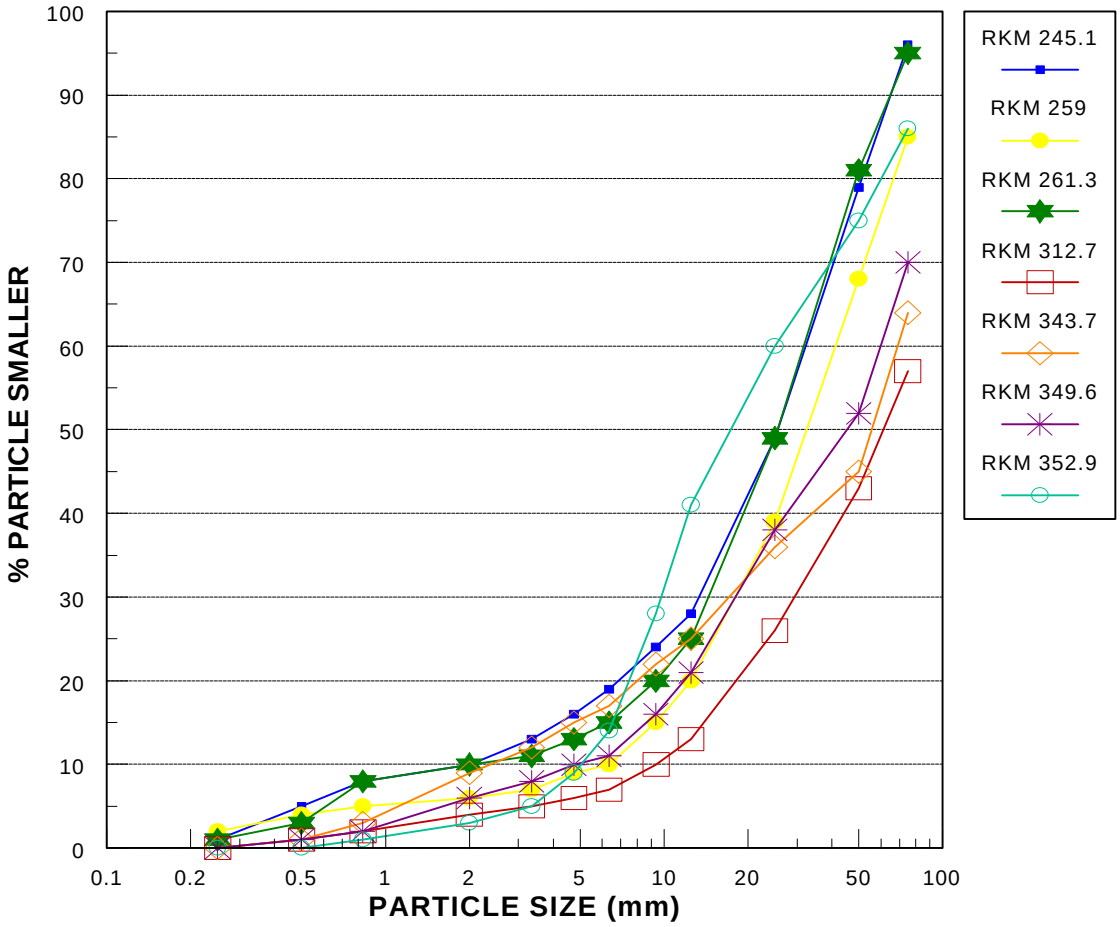


FIGURE 3.-Mean particle size distribution (log base 10) of substrate sampled from fall chinook salmon salmon locations in the Snake River during 1994 and 1995.

TABLE 2.-Mean quality indices of substrate sampled in > 1.2 m of water during 1994 and 1995 between river kilometers 245.1 and 352.9 in the Snake River.

Location	n	Percent fines		Geometric mean diameter (mm)	Fredle index
		< 0.85 mm	< 6.4 mm		
245.1	10	8.50 (4.9)[1]	19.82 (10.2)	17.68 (6.4)	5.89 (3.5)
259	9	5.03 (3.9)	9.67 (6.8)	26.94 (9.7)	11.28 (6.6)
261.3	10	7.84 (2.2)	15.31 (2.8)	18.62 (3.4)	6.57 (1.8)
312.7	10	2.27 (1.6)	7.51 (4.0)	39.86 (9.1)	18.32 (7.9)
343.7	10	3.06 (0.77)	16.94 (3.9)	28.45 (5.7)	8.15 (4.1)
349.6	10	2.23 (1.1)	11.02 (3.6)	29.87 (6.2)	10.84 (3.9)
352.9	10	1.16 (0.81)	13.58 (6.5)	19.97 (6.2)	6.85 (1.6)

[1] = standard deviation

TABLE 3.-Mean quality indices of substrate sampled in < 1.2 m of water during 1994 at river kilometers 245.1 and 261.3 in the Snake River (gravel depth; stratum 1 = 0-10.16 cm, stratum 2 = 10.16-20.3 cm, stratum 3 = 20.3-30.5 cm).

Location	n	Percent fines < 0.85 mm strata			Geometric mean diameter (mm) strata			Fredle index strata		
		(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)
245.1	4	10.71	16.00	17.10	15.02	10.90	8.28	4.13	1.58	1.18
261.3	3	10.74	9.75	7.13	12.57	13.68	17.20	4.01	3.19	3.94

Common line represents no significant difference.

and 267. Random locations at RKMs 249 and 267 contained a larger proportion of surface substrates > 30 mm (Figure 4).

Emergence Success

No significant difference ($P > 0.74$) in W-V box incubation success was observed at hatching in 1996 (early pulls; 35 days after planting) among the eight gravel compositions. Overall mean survival (adjusted relative to hatchability of 81.4%) was 65.3% and the mean survivals ranged from 56.2 to 78.7%.

Four substrate compositions from the trough experiment in 1995 were evaluated for incubation and emergence success (Table 4). Substrate compositions 3 and 4 (category C) and 5, 6, 7, and 8 (category D) were combined because no statistical differences ($P > 0.122$) in gravel compositions were found. Eight compositions were evaluated from the trough experiment associated with incubation success in 1996; all compositions contained statistically different ($P < 0.0001$; Table 4) quantities of particles < 6.4 mm.

We found an inverse relationship between percent fines (< 0.85 mm and < 6.4 mm) and survival to emergence of the four gravel-sand mixtures in 1995 (90 days = December 1994 to February 1995) and in 1996 (144 days = November 1995 to March 1996) with the eight gravel-sand mixtures. The adjusted mean percent survival to emergence in the test trough with 2% fines < 6.4 mm was 78.5% in 1995, and 61.5% in troughs with 1.8% fines < 6.4 mm in 1996 (Figure 5). The best fitting model to describe the relationship between survival (y) to emergence of fall chinook salmon based on the 1995 data were the geometric mean particle size (x), where: $y = -0.685 + 0.204x - 0.006x^2$ ($r^2 = 0.63$). Emergence in substrates with geometric mean < 5 mm was zero, increased rapidly to 10 mm, and remained similar at larger mean sizes (Figure 6). In 1996, the best model that described emergence survival was using percent fines < 0.85 mm (x), where: $y = 61.97 - 3.029x$ ($r^2 = 0.49$). Fry survival is linear and decreases rapidly as percent fines (< 0.85 mm) increase.

Year comparisons of percent fines (<0.85 and <6.4 mm), geometric mean particle size, and Fredle index showed no significant difference between years ($P = 0.7525$, LDS and $P = 0.2157$, SDS). Variances associated with mean indices between 1995 (2.24 LDS and 3.88 SDS) and 1996 (2.30 LDS and 3.85 SDS) were alike indicating similar substrate characteristics between years. However, mean emergence success between the years were

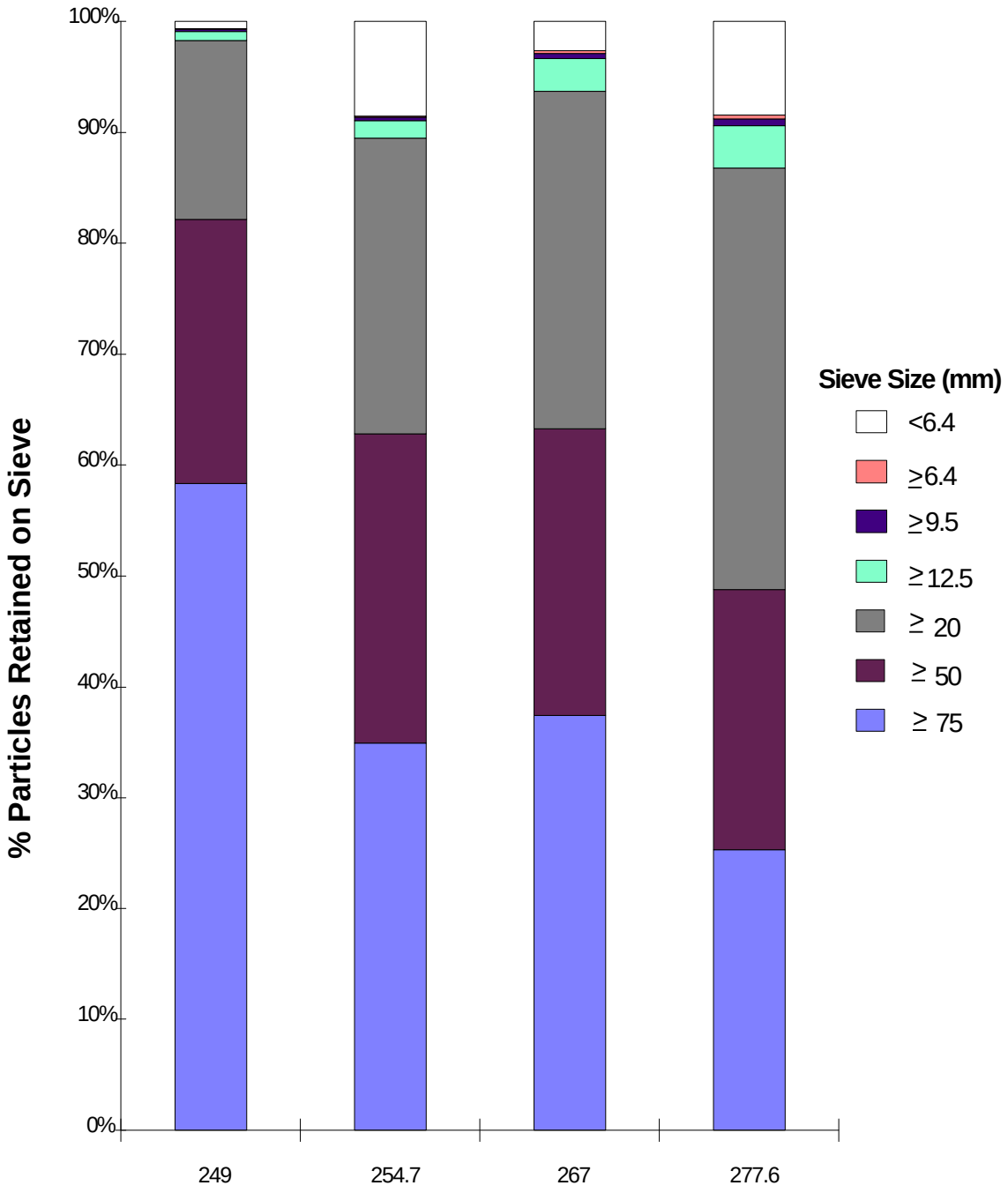
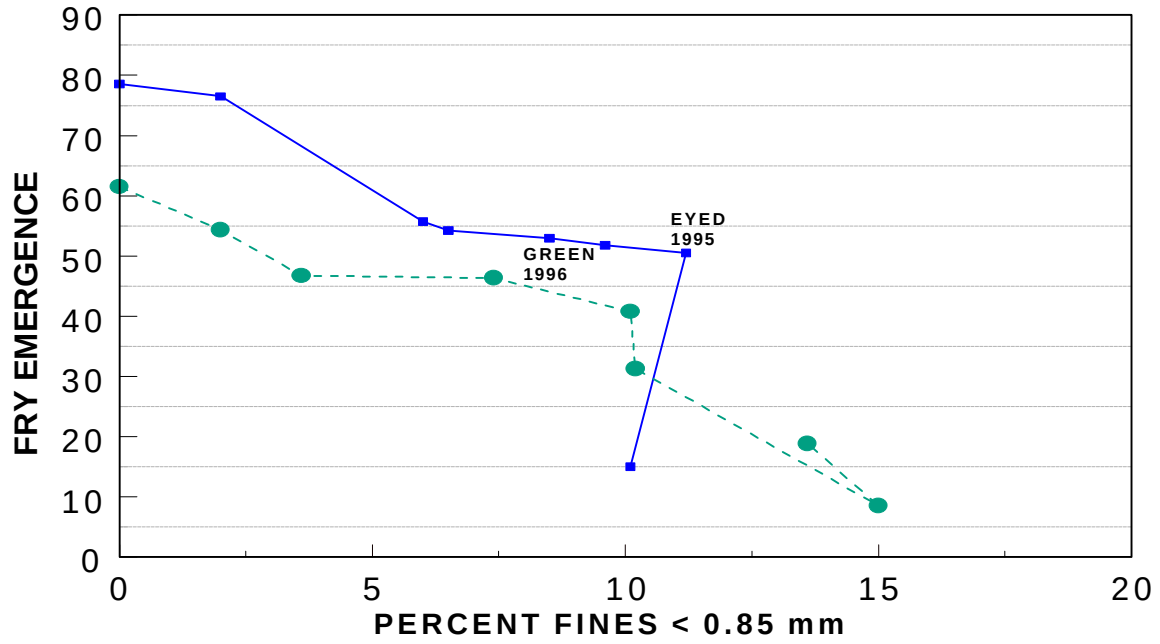


FIGURE 4.-Substrate compositions sampled at river kilometers 249, 254.7, 267, and 277.6 of the Snake River using NIH image during 1995.

TABLE 4.-Mean egg survival to emergence, length, weight, and number of fall chinook salmon from substrate compositions in experimental troughs during 1995 (eyed eggs) and 1996 (green eggs).

Composition	n	Fines < 0.85 mm	Fines < 6.4 mm	Geometric mean	Fredle index	Percent survival	Length (mm)	Weight (mg)
1995 eyed eggs								
A	6	0.1	2	17.8	9.9	78.5 (4.4)[1]	32.8 (5.6)	391 (80.7)
B	6	2.2	11	13.5	7.0	76.5 (5.7)	31.6 (5.9)	377 (140)
C	12	6.1- 6.5	23 - 26	8.4 - 8.6	3.9 - 4.0	55.0 (13.9)	32.1 (5.8)	375 (80.6)
D	24	8.5 - 11.2	28 - 35	6.5 - 7.7	2.0 - 3.0	41.5 (20.8)	31.2 (5.9)	359 (82.5)
1996 green eggs								
1	6	0.0	1.8	16.6	9.5	61.5 (18.8)	34.5 (4.7)	416 (92.7)
2	6	2.0	8.6	13.4	7.5	54.3 (12.8)	34.4 (5.0)	394 (95.7)
3	6	3.6	13.0	10.9	6.1	46.7 (12.8)	35.0 (3.8)	392 (86.9)
4	6	7.4	18.6	9.3	4.5	46.4 (12.6)	36.2 (4.0)	425 (95.0)
5	6	10.2	23.2	8.5	2.9	40.8 (17.9)	36.0 (4.5)	413 (90.0)
6	6	10.2	27.5	7.4	2.6	31.3 (20.5)	36.4 (2.7)	417 (82.0)
7	6	15.0	32.5	6.6	1.4	8.6 (11.9)	35.0 (5.5)	432 (113)
8	6	13.7	36.3	5.8	1.5	19.0 (18.5)	36.1 (3.2)	400 (93.3)

[1] = standard deviation



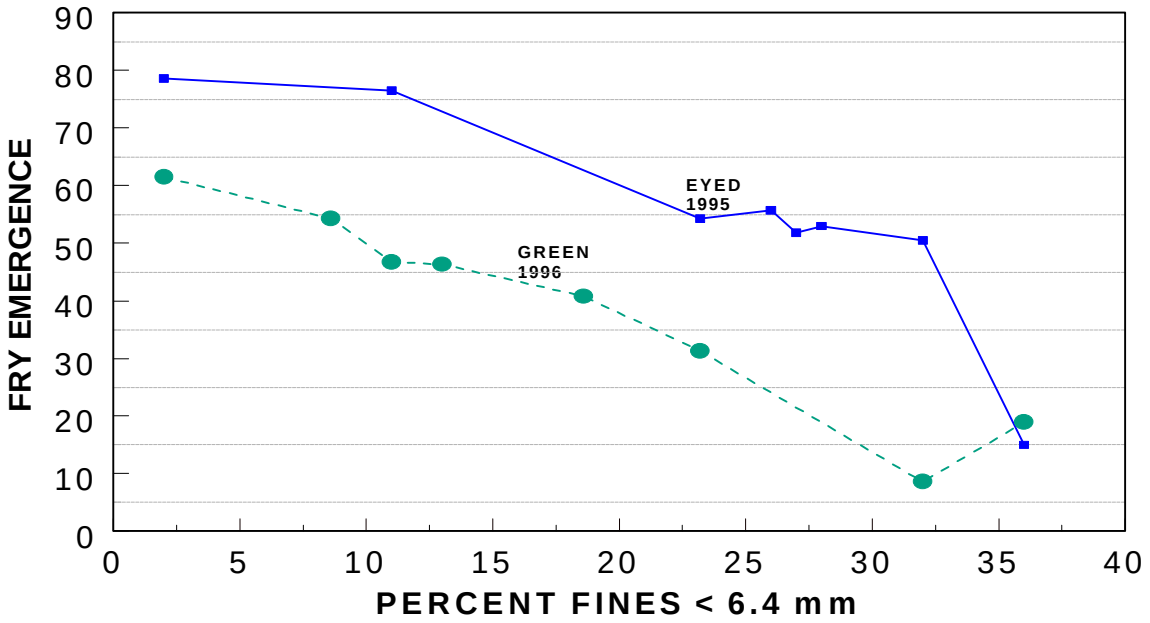


FIGURE 5.-Adjusted mean percent fry that emerged from experimental troughs in 1995 (eyed embryos) and 1996 (green eggs).

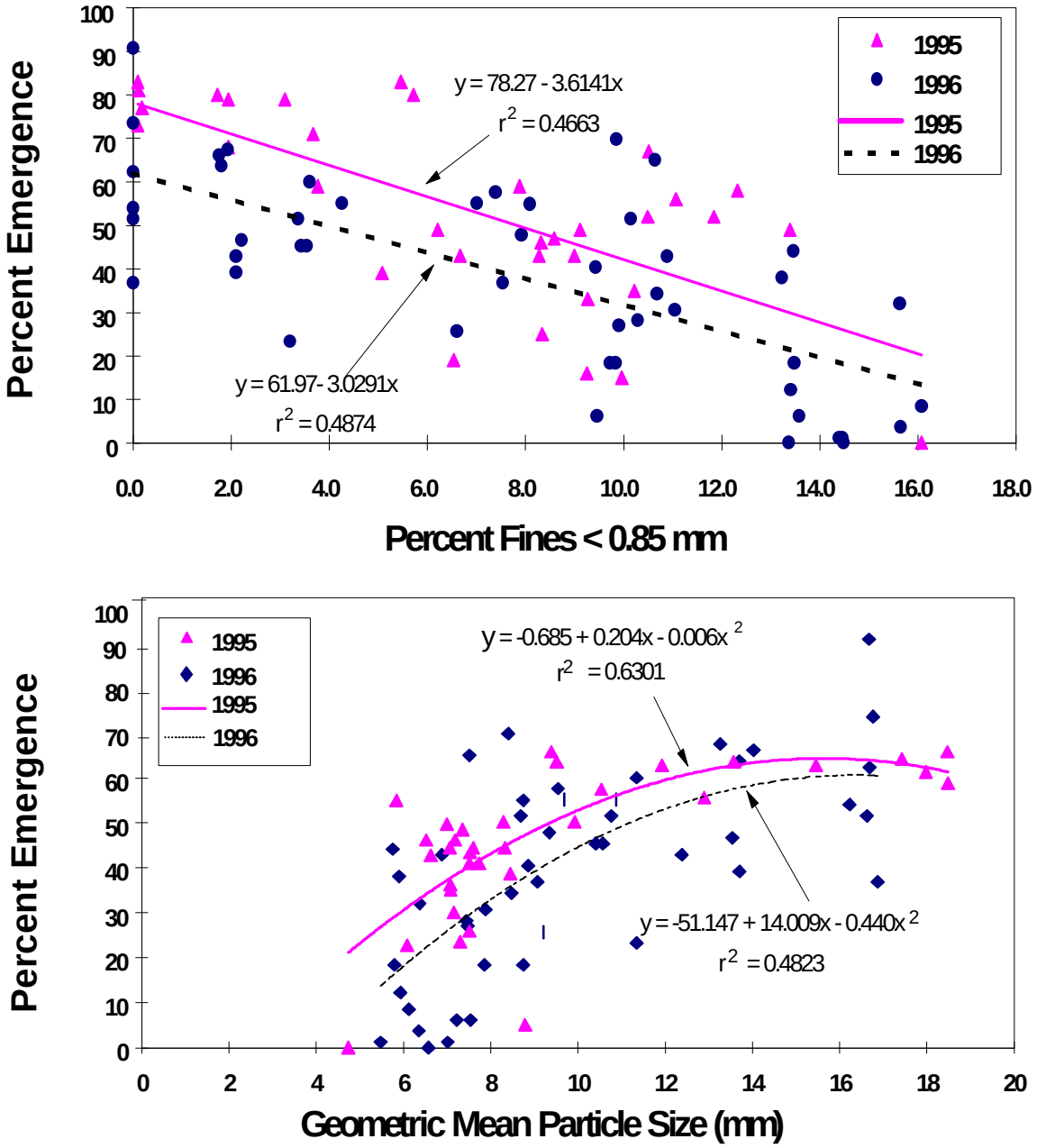


FIGURE 6.-Relationship between survival to emergence of fall chinook salmon, fine sediment < 0.85 mm, and the geometric mean substrate particle, size in experimental troughs during 1995 and 1996.

significantly different (P = 0.0005 LDS, and P = 0.0141 SDS) as higher percent of eyed eggs emerged (75% LDS, 46% SDS) than did green eggs (54% LDS, 23% SDS). Variances associated with mean percent emergence were similar among the eyed eggs in 1995 (429) versus green eggs in 1996 (408) using SDS, whereas variances for mean percent emergence of green eggs (238) was four times that of eyed eggs (54) using LDS.

Mean length and weight of emerging fall chinook salmon fry were not affected by the amount of sediment in the substrate. No significant differences in mean weight (P > 0.42) and length (P > 0.65) were found among the substrate compositions in either year (Table 4). Dissolved oxygen concentrations in all test troughs in both years were > 9 mg/L (92% saturation) throughout the study and did not decrease with increased amounts of fine sediments. Average water temperature in the troughs in 1995 was 11.2 ^{o}C and ranged from 7.9 to 16.6 ^{o}C and in 1996 averaged 9.5 ^{o}C and ranged from 5.9 to 15.7 ^{o}C. Apparent velocities in 1996 ranged from 0.95 cm/s in troughs with 0% fines < 0.85 mm to 0.06 cm/s in troughs with 13.7% fines < 0.85 mm (Table 5). Estimates of apparent velocities in 1995 were not representative because of a mechanical error.

Discussion

Comparison of the substrate composition from the area sampled in the Snake River with that of several commonly used indices of spawning gravel quality indicated that the substrate did not contain sufficiently high fines to adversely affect emergence success. Sampling location RKM 245.1 had the highest percent fines < 0.85 mm (8.5%) and < 6.4 mm (19.8%) but our results from the trough experiments suggested that no significant decrease in emergence success would occur. Substrate samples from other locations suggested that emergence success of fall chinook salmon should not be inhibited by the substrate composition.

Overall spawning substrate quality in the free-flowing reach of the Snake River has changed little from the early 1990s. The percent fines < 0.85 mm at RKMs 245.1 and 261.3 sampled by the freeze-core sampler (15.2% and 9.2%, respectively) were similar to those found at these locations (15.6% and 7.2%) by Arnsberg et al. (1992). Our strata profile showed an increase in finer particles with depth at RKM 245.1 and uniform quality at RKM 261.3 whereas Arnsberg et al. (1992) found uniform quality of all three strata from RKMs 245.1 and 261.3. Streamflow data in the Snake River taken from the USGS gage station near Anatone,

TABLE 5.-Mean apparent velocities in 1996 from experimental troughs filled with different substrate compositions.

Composition	Fines < 0.85 mm	Fines < 6.4 mm	Apparent Velocity (cm/s)
1	0.0	1.8	0.95
2	2.0	8.6	0.66
3	3.6	13.0	0.47
4	7.4	18.6	0.45
5	10.2	23.2	0.20
6	10.2	27.5	0.12
7	15.0	32.5	0.09
8	13.7	36.3	0.06

Washington, (U.S. Geological Survey, 1992-94) showed relatively low flows in 1992 (annual mean = 511.2 m^3/sec), increasing in 1993 (annual mean = 956.1 m^3/sec), and decreasing in 1994 (mean flow = 596.4 m^3/sec). Both studies, Arnsberg et al. and ours, were sampled during low water years (1992 and 1994) where smaller sediment probably settled and accumulated in these spawning areas consequently showing similar characteristics between years. Upstream dams act as sediment traps allowing limited fine sediment deposition downstream (Goldman and Horne 1983). Our study supports this by reason of no major tributaries to the Snake River between Hells Canyon Dam and the Imnaha River. Comparing our study locations sampled above the Imnaha River to those sampled downstream the Grande Ronde River (Table 2); showed fines < 0.85 mm at RKMs 312.7, 343.7, 349.6, and 352.9; significantly less ($P < 0.026$) than downstream locations at RKMs 245.1, 259, and 261.3. An increase in fine sediment (< 0.85 mm) below the Grande Ronde River probably originates from runoff of three major tributaries; the Imnaha, Salmon, and Grande Ronde rivers.

Chapman (1988) states that the salmonid redd in a stream begins as a pocket from which the female has removed fines and small gravels. Several researchers (Burner 1951; McNeil and Ahnell 1964; Chapman 1988; Garrett 1995) have noted that conditions in the egg pocket and the surrounding redd have less fine particles than the neighboring gravel. Many studies (Bjornn 1969; Koski 1975; McCuddin 1977; Tappel and Bjornn 1983), including ours, have shown an inverse relationship between the amount of fine sediments and salmonid survival to emergence. We estimated fall chinook survival to emergence simulating substrate found in the Snake River prior to spawning. Our estimates of fry survival are probably lower than would naturally occur because salmonids modify substrate composition during redd construction that was not simulated in the trough experiments. Garrett (1995) reported significant intrusion of fines during the incubation period of kokanee *Oncorhynchus nerka* in the North Fork of the Payette River, Idaho. However, low ambient sediment levels in the Snake River probably would limit fine sediment intrusion during the incubation period of fall chinook salmon.

The NIH image processing procedure proved to be a fast and inexpensive tool in analyzing surface substrate. However, due to high water we were unable to compare NIH image with other sampling methods. This comparison needs pursuing in order to validate whether a correlation exists between the substrate surface and substrate particles below the surface.

Differences in emergence success between years were related to egg development. In 1995, eyed embryos were used, compared to fertilizing the eggs immediately prior to placement in 1996. Although estimates of emergence success were corrected for fertility effects based on survivals in the hatching trays, we believe the differences between years were probably the result of handling green eggs versus using eyed eggs. In 1996, zero fines < 0.85 mm were found in six troughs, and adjusted emergence success was 61.5%. We believe that more representative estimates of emergence success at the various substrate compositions during 1996 should probably be increased by approximately 20% to 30% to accommodate for green egg handling differences. Although incubation success was lower in 1996, several factors could have contributed to lower emergence success. One possible factor could be formalin, used to check *Saprolegnia* growths, that was applied in treating both the troughs and the control trays. A possible synergistic reaction between the substrate and formalin, not accounted for in the control trays, could have been toxic to the embryos.

Another possible element that may have contributed to the large variances in the LDS was the gravel mixing and distribution in the troughs. Dry gravel compositions were weighed and combined together in homogeneous mixtures (Table 1) before planting the chinook eggs. However, fine sediment (< 6.4 mm) apparently shifts and settles when flowing water is added to the dry mixture. The shifting and settling possibly created areas where the percentage of fines concentrated more in some areas than in other areas of the trough. Gravel excavation after fry emergence in troughs containing 20% fines < 6.4 mm revealed areas of loosely packed gravel interspersed in more densely packed gravel-sand mixtures. If fry in the LDS substrate fortuitously located the loosely packed gravel then percent emergence probably would have been higher than if shifting and settling did not occur.

Bjornn and Reiser (1991) and Chapman (1988) indicate that fine sediments < 0.83 to 0.85 mm may not seriously impair embryo survival unless they comprise more than 6% to 10% of the substrate composition. We saw about a 20% decrease in emergence success as particles < 0.85 mm increased from 2% to 6%. Bjornn (1969) and McCuddin (1977), in trough studies similar to ours, found that no deleterious effects occurred on embryo survival until fines < 6.4 mm comprised 20% to 25% of the substrate composition. In both years of our study, as the percent fines (< 6.4 mm) increased beyond 10%, emergence success declined. Tappel and Bjornn (1983) reported embryo survival was about 90% when the Fredle index was > 5, whereas their embryo survival

decreased when the Fredle index was < 5. Our 1995 results concur with their estimate of survival.

Our results were similar to those reported from other laboratory and field experiments in that as percent fines increase in the sediment fry survival decreases. Our substrate samples show that spawning gravel in the Snake River has relatively low amounts of fine sediment above the Imnaha River and significantly higher amounts of fines below the Grand Ronde River. If these samples are representative of the overall substrate composition and fall chinook salmon can select substrates with lower composition fines, we suspect that Snake River fall chinook salmon will select spawning sites further upstream of the Grand Ronde River. Our hypothesis is supported by the U.S. Fish and Wildlife Service aerial redd surveys from RK 235 to Hell Canyon Dam (Garcia 1993). Their data collected between 1993-1996 showed redd numbers increasing upstream of the Salmon River compared to pre-1993 redd numbers (A.P. Garcia, personal communication).

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CHAPTER FIVE

Detection of PIT-tagged Subyearling Chinook Salmon at a Snake River Dam: Implications for Summer Flow Augmentation

by

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Introduction

Spring, summer, and fall chinook salmon *Oncorhynchus tshawytscha* are indigenous to the Snake River basin and were listed as threatened under the Endangered Species Act (ESA)(USFWS 1988) in 1992 (NMFS 1992). Spring and summer chinook salmon juveniles migrate seaward from headwater tributaries of the Snake River primarily as yearlings in spring (Chapman and Bjornn 1969; Achord et al. 1996). Fall chinook salmon emigrate as subyearlings primarily in summer (Thompson 1974). Although some spring and summer chinook salmon fry are washed downstream from headwater tributaries into the Snake River, the majority of subyearling chinook salmon which rear in the Snake River and migrate seaward in summer are fall chinook salmon.

High mortality and delays in seaward migration of juvenile chinook salmon caused by dams in the Snake and Columbia rivers (Park 1969; Raymond 1979, 1988) contributed to ESA listing of Snake River chinook salmon. Summer flow augmentation was initiated in 1991 to enhance survival and mitigate for migration delays. The National Marine Fisheries Service embraced the concept of summer flow augmentation in the proposed recovery plan (NMFS 1995) and recommended an average flow of 1,416 to 1,558 m^3/s at Lower Granite Dam (Figure 1) from 21 June to 31 August. Because the recommended flows are higher than natural runoff, summer flow augmentation became a necessity. We conducted our study to provide an index of survival for subyearling chinook salmon to Lower Granite Dam, and to relate this index to effects of summer flow augmentation on Lower Granite Reservoir flow and water temperature.

Study Area

Releases of water from U.S. Bureau of Reclamation reservoir projects and Brownlee Reservoir in the Snake River basin, and Dworshak Reservoir in the Clearwater River basin (Figure 1), provided summer flow augmentation to Lower Granite Reservoir from 1992 to 1995. Water released from the U.S. Bureau of Reclamation projects was ultimately passed through Brownlee Reservoir and the Hells Canyon Complex (Figure 1). Hells Canyon Complex regulates Snake River reservoir flows into the Snake River, but not water temperature. Hells Canyon Complex is referred to hereafter as being the source of flow augmentation from Snake River reservoirs. Dworshak Dam has multilevel selector gates for temperature regulation of water released from Dworshak Reservoir into the Clearwater River.

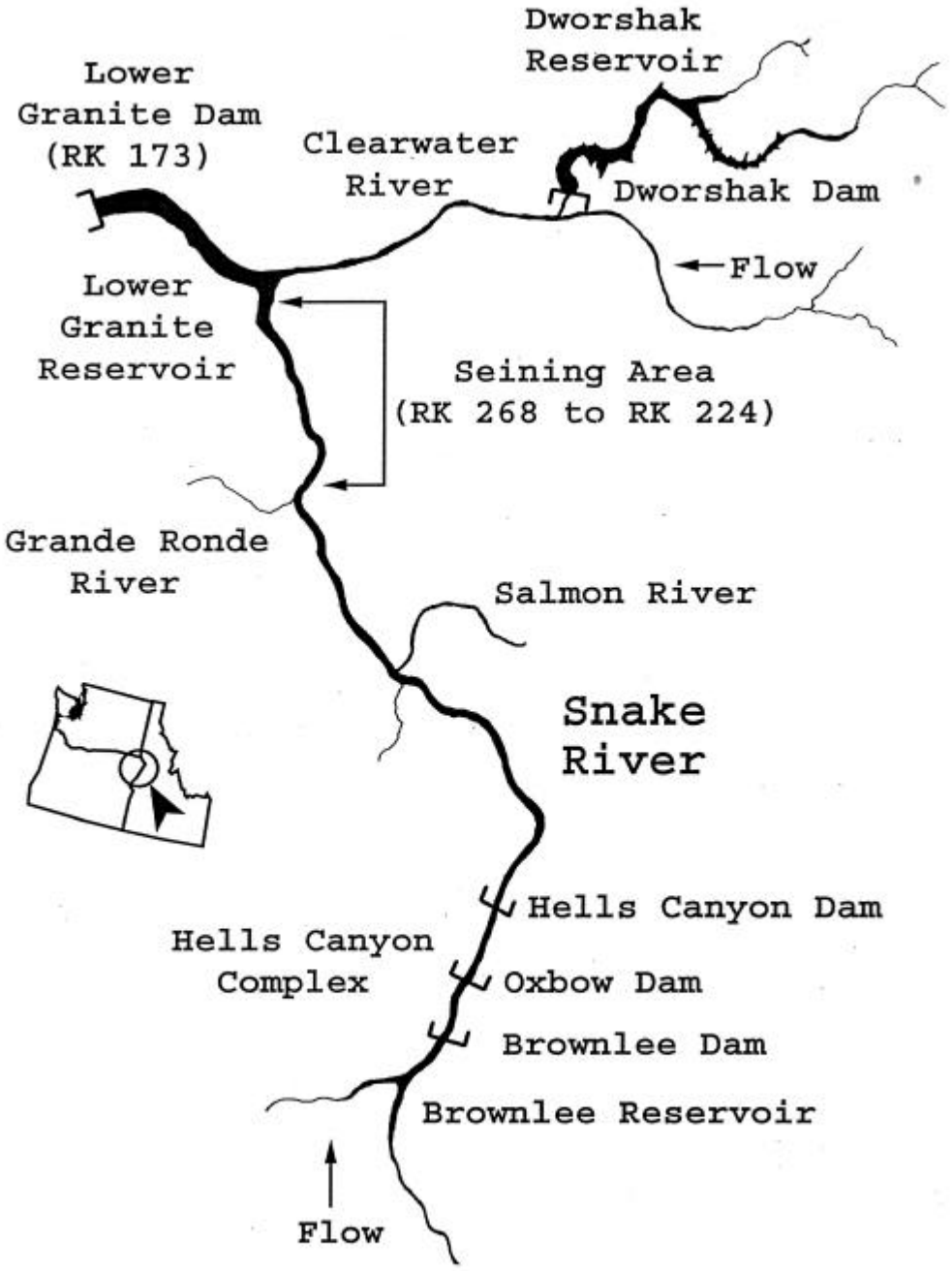

Figure 1.-Study area from 1992 to 1995 including locations of the seining area, rivers, reservoirs, and dams.

Seaward migrating subyearling chinook salmon pass through Lower Granite Reservoir (Figure 1). Lower Granite Reservoir is approximately 51 km long and has a surface area of 3,602 ha, a mean depth of 17 m, and a maximum depth of 42.1 m (Chipps et al. 1997). Lower Granite Reservoir was maintained at minimum operating pool elevation of 240.5 m above mean sea level during the subyearling chinook salmon emigration from 1992 to 1995.

Lower Granite Dam, located at river kilometer (RK) 173 on the Snake River (Figure 1), has six turbine intakes and eight spillways. Less than 1% (mean = 0.8 $\pm$ 0.08%) of the water passing Lower Granite Dam was routed over the spillways between 21 June and 31 August from 1992 to 1995. During this time period nearly all fish were routed to the powerhouse where a portion of fish were collected by submersible traveling screens. Detailed figures and descriptions of submersible traveling screens and juvenile fish bypass facilities at selected Columbia River basin dams are given by Gessel et al. (1991). Between 1992 and 1994, all six turbine units at Lower Granite Dam were equipped with standard length (6 m) screens. In 1995, experimental extended length (12 m) screens were installed in one turbine intake which could have increased fish guidance efficiency (i.e., % of fish collected by submersible traveling screens) and the recovery rate of marked fish. Collected fish were routed through the fish bypass system where they were electronically scanned for Passive Integrated Transponders (PIT) tags (Prentice et al. 1990*a*).

Methods

We beach seined subyearling chinook salmon along the Snake River between RK 268 and RK 224 (Figure 1). Seining started in April and was done weekly until water temperature neared 20^{o}C or catch neared zero. The seine had a weighted multistranded mudline, 0.48 cm mesh, and was 30.5 m x 1.8 m with a 3.9 m^3 bag. Each end of the seine was fitted with a weighted brail attached to 15.2 m lead ropes. The seine was set parallel to shore from a boat and hauled straight into shore.

Captured subyearling chinook salmon were placed in a 94.6 L aerated live-well treated with 100 g of NaCl and 12.5 mL of Polyaqua^{TM}. Fish were anesthetized in 18.9 L of oxygenated water containing a 10 mg/L to 26 mg/L tricane solution, 0.5 gm of $NaHCO_{3,}$ and 2.5 mL of Polyaqua^{TM}. We PIT tagged (Prentice et al. 1990*b*) all subyearling chinook salmon $\geq$ 60 mm fork length. We released PIT-tagged subyearling chinook salmon after a 15 min recovery in 18.9 L of oxygenated water treated with 20 g of NaCl and 2.5 mL of Polyaqua^{TM}.

We monitored water temperature in Lower Granite Reservoir at RK 178. Water temperature profiles in Lower Granite Reservoir indicate that data collected at RK 178 largely provides representative water temperatures for at least the lower two thirds of the reservoir (Bennett et al. 1997). Cooler water from the Clearwater River mixes with the warmer Snake River water in the upper 10 to 15 km of the reservoir. Three thermographs were positioned vertically on a rope approximately 5 m, 20 m and 30 m below the water surface at RK 178. We also placed a thermograph downstream of Hells Canyon Dam (Figure 1) to measure water temperature exiting Hells Canyon Complex. All thermographs recorded water temperature hourly. Daily average water temperature and flow data for Dworshak Dam, and daily average flow data for Lower Granite Dam, were provided by the U. S. Army Corps of Engineers. Daily average flow data for the Hells Canyon Complex, gaged at Hells Canyon Dam, were supplied by the U. S. Geological Survey.

Annual detection rates were calculated by dividing the number of PIT-tagged subyearling chinook salmon detected at Lower Granite Dam by the total number of subyearling chinook salmon PIT tagged. Annual mean flows for Lower Granite Reservoir were calculated using Lower Granite Dam flow data collected daily between 21 June and 31 August (i.e., mean summer flow). We used hourly water temperature data, recorded by the thermograph 20 m below the surface of Lower Granite Reservoir, to calculate daily mean water temperatures for the days 21 June to 31 August. We selected the 20-m depth because subyearling chinook salmon must sound to at least 20 m to pass Lower Granite Dam and fish could descend to this depth to avoid warm surface water. The maximum daily mean water temperature for each year (i.e., maximum summer water temperature) was then selected as an index of summer water temperature in Lower Granite Reservoir.

A Pearson correlation coefficient (SYSTAT 1994) was calculated to test the strength of association between mean summer flow and maximum summer water temperature. The effects of mean summer flow and maximum summer water temperature were tested separately on log(e) transformed detection rates using ordinary least-squares linear regression (SYSTAT 1994). We calculated 95% simultaneous confidence intervals (SYSTAT 1994) for the regressions.

Results

Mean summer flows in Lower Granite Reservoir between 21 June and 31 August in 1992 and 1994 (i.e., dry years) were low and maximum summer water temperatures were high (Table 1). In contrast, 1993 and 1995 (i.e., average water years) were characterized by average summer flows and relatively cool maximum summer water temperatures. Detection rates in dry years were lower than those in average water years (Table 1).

Mean summer flows and maximum summer water temperatures were highly correlated (r = -0.999). A multiple regression approach using both variables was therefore inappropriate. Separate regressions using mean summer flow and maximum summer water temperature as independent variables, and detection rate as the dependent variable, revealed significant relations. Mean summer flow was positively related to detection rate (Figure 2; n = 4; intercept = 0.80591; slope = 0.00166; r^2 = 0.993; P = 0.003). Maximum summer water temperature was negatively related to detection rate (Figure 2; n = 4; intercept = 11.90610; slope = -0.42520; r^2 = 0.984; P = 0.008).

Summer flows and summer water temperatures in Lower Granite Reservoir are largely regulated by releases from Hells Canyon Complex and Dworshak Reservoir. When water releases from Hells Canyon Complex and Dworshak Reservoir coincided from 1992 to 1995, they made up 45.2% to 96.1% of the total water volume through Lower Granite Reservoir. Summer flow augmentation from Hells Canyon Complex and Dworshak Reservoir markedly increased Lower Granite Reservoir flow in dry years (Figure 3), and dampened the rate of descent in the hydrograph in average water years (Figure 4).

Temperature of water released from Dworshak Reservoir from 1992 to 1995 ranged from 9.0^{o}C to 11.2^{o}C, while water released from Hells Canyon Complex ranged from 18.4^{o}C to 20.8^{o}C. The combination of cool water from Dworshak Reservoir, and relatively warmer water from Hells Canyon Complex, decreased Lower Granite Reservoir water temperature markedly in dry years (Figure 3). Isolating effects of flow augmentation on water temperature in average water years is difficult because of cooling effects of natural flows. However, flow augmentation in average water years appears to have moderated water temperatures in Lower Granite Reservoir (Figure 4).

TABLE 1.—Mean summer flow (m^3/s) and maximum summer water temperature(^oC) in Lower Granite Reservoir between 21 June and 31 August, 1992 to 1995, and detection statistics at Lower Granite Dam for subyearling chinook salmon PIT tagged in the Snake River between river kilometers 224 and 268.

Year	Mean summer flow (m^3/s)	Maximum summer water temperature (^oC)	Number		Detection rate (%)
			tagged	detected	
1992	539	23.9	725	37	5.1
1993	1,304	21.1	1,228	234	19.1
1994	744	23.3	2,212	186	8.4
1995	1,580	19.9	738	224	30.4

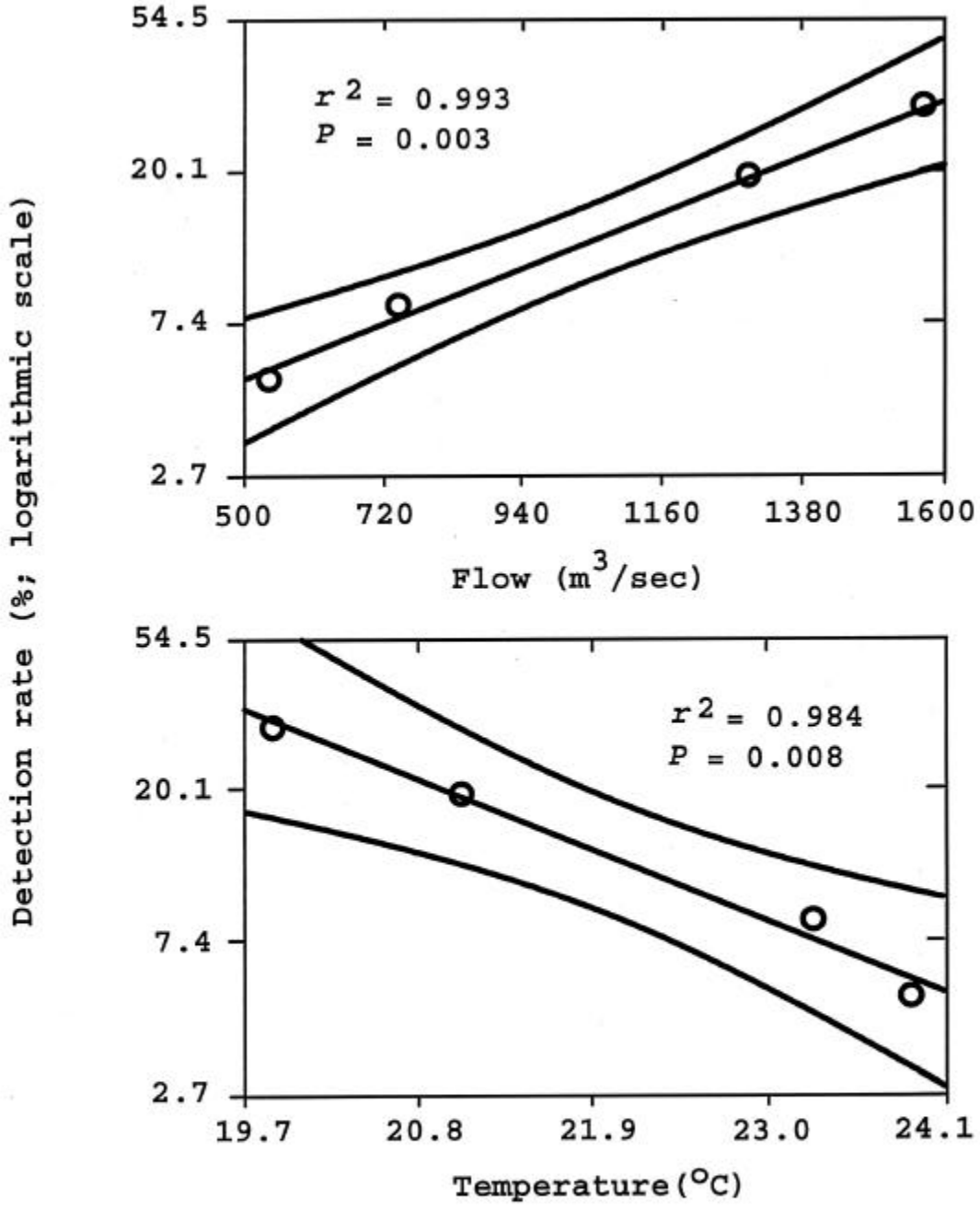

Figure 2.-The relations between mean summer flow (top) and maximum summer water temperature in Lower Granite Reservoir and detection rate of PIT-tagged Snake River subyearling chinook salmon from 1992 to 1995. Ninety-five percent simultaneous confidence intervals are also given

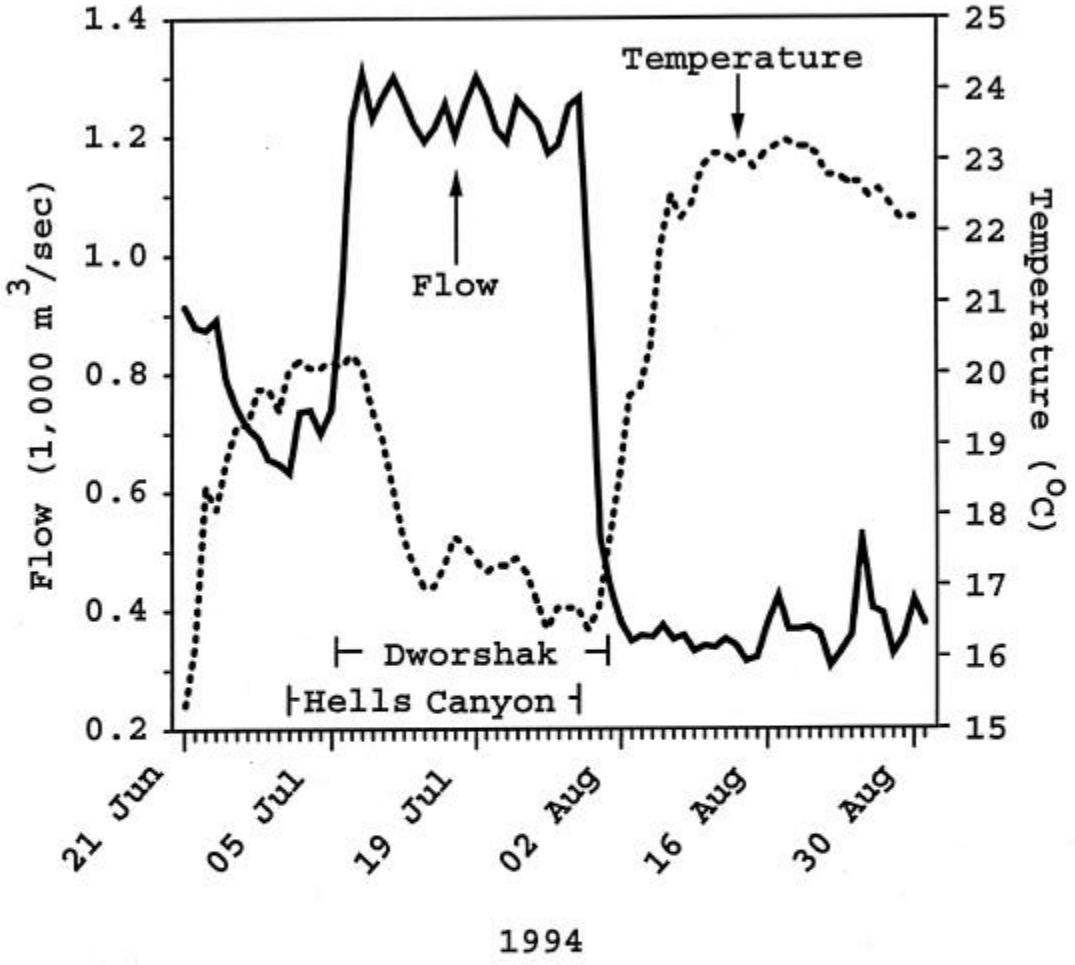

Figure 3.-Effects of summer flow augmentation on water flow and temperature measured in Lower Granite Reservoir in 1994, a dry water year. Time periods when flows were augmented using releases from Dworshak Reservoir and Hells Canyon Complex are indicated.

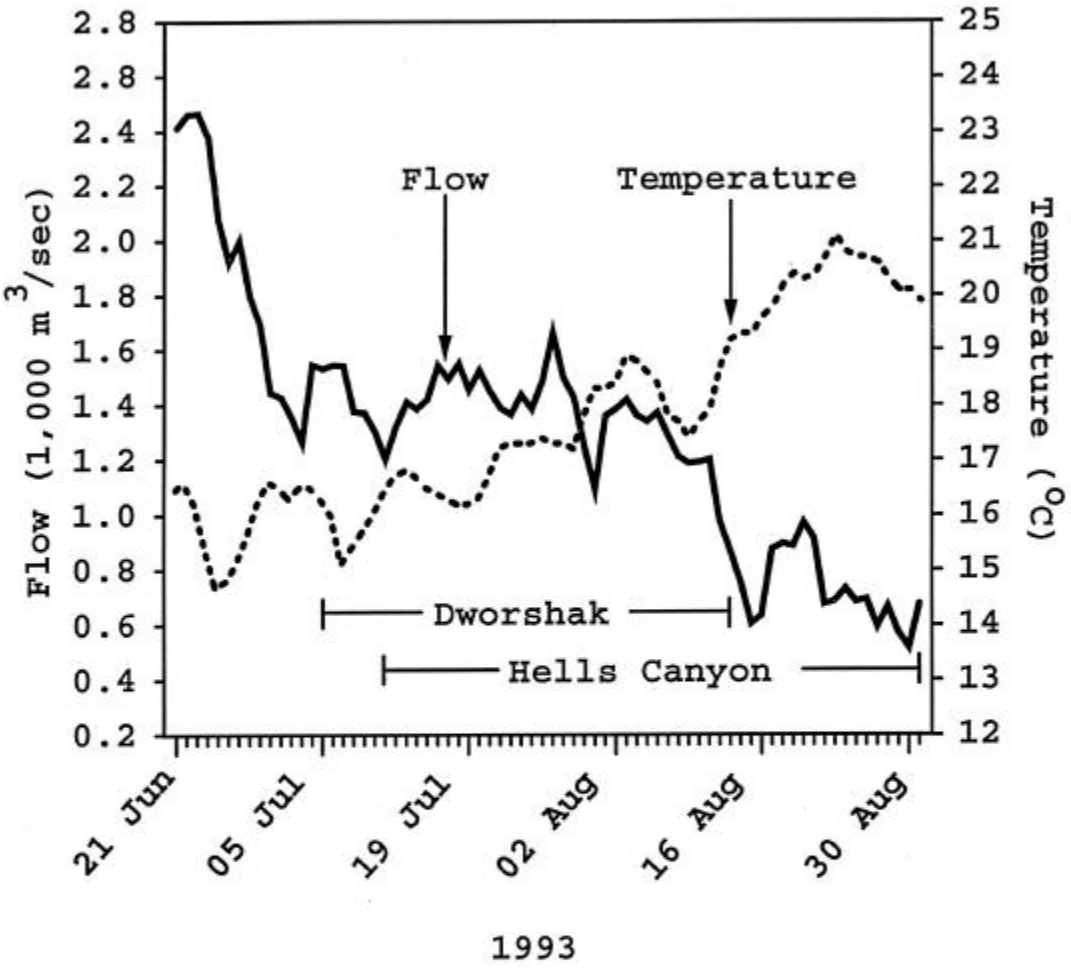

Figure 4.-Effects of summer flow augmentation on water flow and temperature measured in Lower Granite Reservoir in 1993, an average water year. Time periods when flows were augmented using releases from Dworshak Reservoir and Hells Canyon Complex are indicated.

Discussion

Detection rates of PIT-tagged subyearling chinook salmon provide indices of survival from 1992 to 1995 because most tagged fish that were not detected migrating seaward as subyearlings died upstream of Lower Granite Dam or traveled under the submersible traveling screens and by rotating turbine blades. Juvenile salmonids passing by turbine blades of Columbia River dams have been shown to die at rates of 11±2%(Schoeneman et al. 1961). The PIT-tagged subyearling chinook salmon that survived the turbine passage faced progressively warmer downstream Snake River reservoirs, passage delays, and mortalities at 1 to 7 additional dams.

Although Snake River mean summer flows and maximum summer water temperatures from 1992 to 1995 were highly correlated, we suspect that these variables act together to influence subyearling chinook salmon survival. Snake River flow may affect survival of seaward migrating subyearling chinook salmon in a number of ways. Delays in passage may occur in dry years compared to average water years. Such delays have been theoretically tied to disorientation of emigrants, increased exposure time to predators, reversal of smoltification, and disease (Park 1969; Raymond 1979; Berggren and Filardo 1993). Flow also affects survival by influencing water temperature. Water temperature in Lower Granite Reservoir has been shown to remain cooler for longer periods under higher flows than under lower flows (Anglea 1997). This phenomenon can be regulated by summer flow augmentation emphasizing cool water releases from Dworshak Reservoir.

Prior to ESA listing of Snake River chinook salmon, and before summer flow augmentation was implemented as a recovery measure, low flows with correspondingly higher water temperatures were probably lethal to subyearling chinook salmon in dry years. From 1992 to 1995, we PIT-tagged subyearling chinook salmon which reared and acclimated in water averaging 13.8°C prior to reservoir entry. Brett (1952) acclimated juvenile spring chinook salmon to 15°C water then transferred them to water ranging from 24°C to 28°C. Mortality in acclimated fish began at 24.1°C. Fifty percent of all juvenile chinook salmon reared in 25.0°C water died in 17 hours. In 1992, a dry year with little flow augmentation, mean daily water temperature 5 m below the surface of Lower Granite Reservoir was above the upper incipient lethal (24.3 to 25.2°C) for 5 consecutive days in late June prior to flow augmentation in July. This period of lethal water temperatures may have caused high mortality of PIT-tagged subyearling chinook salmon in Lower Granite Reservoir and

contributed to the low detection rate in 1992. In another dry year 1994, more cool water was released from Dworshak Reservoir than in 1992. Lower Granite Reservoir water temperatures remained below the upper incipient lethal throughout the summer in 1994 and the detection rate was 1.7 times higher than in 1992.

Water temperature may also influence survival of juvenile chinook salmon by affecting predation (Vigg and Burley 1991). Consumption of juvenile salmon by northern pikeminnow *Ptychocheilus oregonensis*, smallmouth bass *Micropterus dolomieu*, walleye *Stizostedion vitreum*, and channel catfish *Ictalurus punctatus* in John Day Reservoir was highest in July, concurrent with maximum summer water temperature (Vigg et al. 1991). Subyearling chinook salmon were prevalent in the diets of the above four prey species in August when predator and prey distributions in John Day reservoir overlapped (Poe et al. 1991). Anglea (1997) reported dramatically higher consumption rates of juvenile anadromous fishes by smallmouth bass in Lower Granite Reservoir between 1994 (dry year) and 1995 (average water year). Anglea.s consumption estimates for 1994 were high and comparable to those of Curet (1994), who examined subyearling predation by smallmouth bass in 1992, another dry year in Lower Granite Reservoir.

Management Implications

Our findings suggest that summer flow augmentation can benefit Snake River subyearling chinook salmon listed under ESA. Water released from Snake River reservoirs supplements Lower Granite Reservoir flow when seaward migrating subyearling chinook salmon are passing through Lower Granite Reservoir. Water released from Dworshak Reservoir can supplement Lower Granite Reservoir flow and decrease water temperature throughout the water column at depths available to pelagically emigrating subyearling chinook salmon (D. H. Bennett, University of Idaho, unpublished data). We conclude summer flow augmentation, especially cool water releases from Dworshak Reservoir, can increase subyearling chinook salmon survival by limiting thermally induced mortality in dry years and reducing predation under all flow conditions.

Research Needs

We acknowledge this paper was founded on four point estimates of detection rate, mean summer flow, and maximum summer water temperature. We suggest that researchers use replicate releases of PIT-tagged subyearling chinook salmon and a mark-recapture approach (Burnham et al. 1987) to provide precise

estimates of fish guidance efficiency and survival for comparison between and within years. We would have preferred this option, but it was unavailable between 1992 and 1994 because of technical and logistical limitations.

Replicate releases of PIT-tagged subyearling chinook salmon within each year would provide survival estimates for several groups of fish each exposed to different summer flows and summer water temperatures in Lower Granite Reservoir. If the mark-recapture study showed higher survival for fish released earlier in the summer, when flows are higher and water cooler, the argument for flow augmentation would be strengthened. If not, then factors other than summer flow and summer water temperature may be influencing subyearling chinook salmon survival.

Fish guidance efficiency may vary with changes in water flow and water temperature (Gessel et al. 1991). The logarithmic transformation of detection rate fit well in regression analyses because extended traveling screens probably increased fish guidance efficiency in 1995. However, we could not measure fish guidance efficiency to test for flow and temperature effects between years. A finding of increased fish guidance efficiency with higher flows and cooler temperatures would further support summer flow augmentation. A complete assessment of factors affecting fish guidance efficiency including the effects of smoltification (Giorgi et al. 1988) would strengthen future estimates of survival. Estimates of subyearling chinook salmon mortality for the period of near shore rearing were unavailable and should be obtained. A comprehensive study of the mechanics and timing of releasing water from Snake River reservoirs and Dworshak Reservoir would be especially informative since the temperature of water released from Dworshak Reservoir can be varied independent of flow.

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CHAPTER SIX

Identifying Genetic Race of Snake River Juvenile Chinook Salmon And Genetic Characterization of the Snake River Natural Fall Race Population

by

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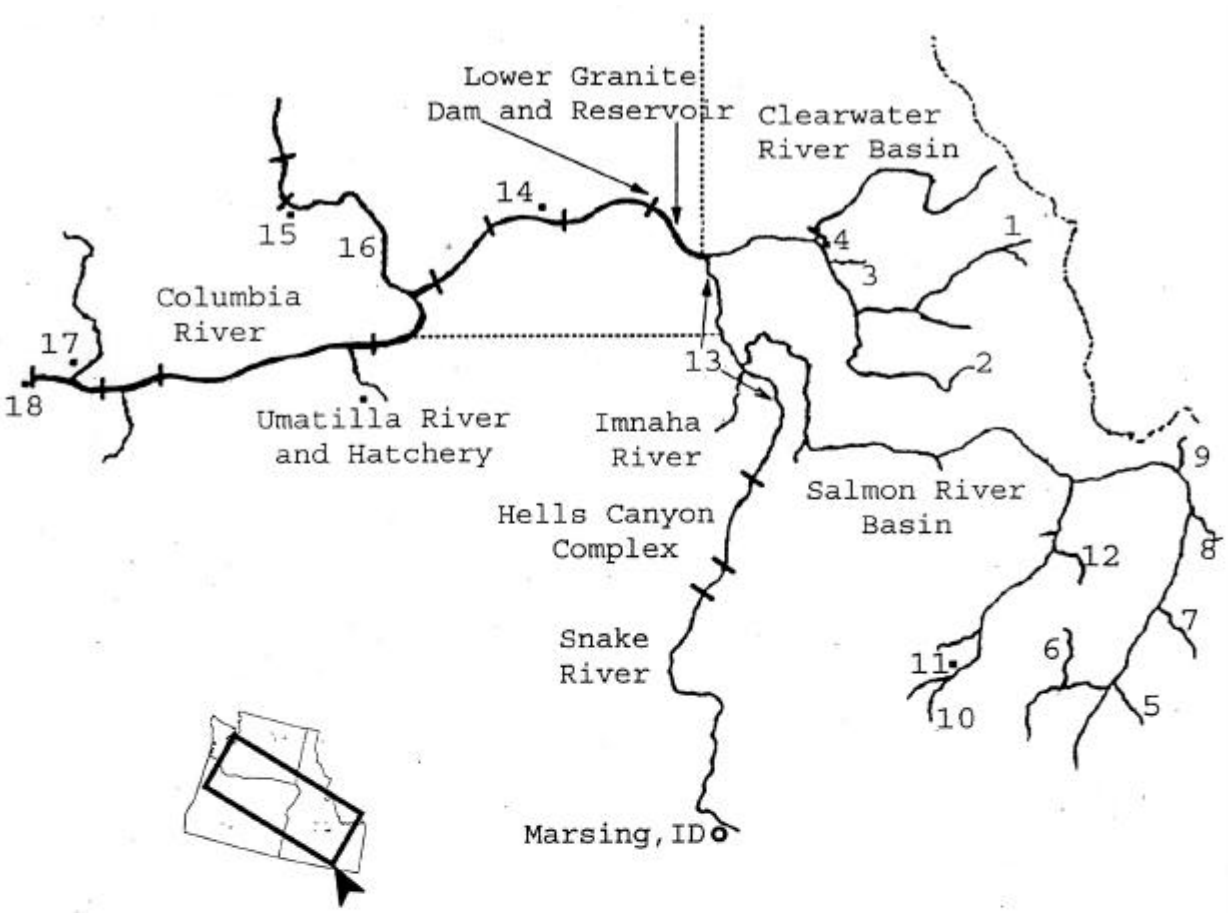
Introduction

The Snake River drainage basin is inhabited by groups of chinook salmon *Oncorhynchus tshawytscha* that historically have been delineated by the season adults enter freshwater and begin their spawning migration. These groups, known as spring-, summer- and fall-run, have declined precipitously in the last 30 years. All were given threatened status (NMFS 1992) under the Endangered Species Act (ESA; USFWS 1988). Data analysis during the ESA status review showed that Snake River chinook salmon formed two distinct biological lineages. Spring- and summer-run chinook were similar in many life history traits and in allozyme gene frequencies (Matthews and Waples 1991) and together were designated a single evolutionarily significant unit (ESU; Waples 1991). Fall-run chinook were strikingly divergent from the spring/summer-runs in genetic and other biological traits and were considered a separate ESU (Waples et al. 1991). Reproductive isolation appears virtually complete between Snake River spring/summer-run and fall-run chinook salmon and supports treating the two groups as separate biological races (Mayr 1970). Hereafter, we refer to Snake River spring/summer-run chinook salmon as spring race, and fall-run as fall race.

Our research focused primarily on fall race chinook salmon that spawned naturally in the Snake River. Historically, wild fall chinook salmon spawned throughout the Snake River from the Columbia River confluence to Shoshone Falls, Idaho (Fulton 1968), with a major spawning aggregation in the mainstem near Marsing, Idaho (Haas 1965; Irving and Bjornn 1981; Figure 1). Passage to this area was blocked by the completion of the Hells Canyon Complex of dams (1955-1967). Four dams allowing fish passage were built downstream of Hells Canyon between river km 173 and the Columbia River confluence by 1975. Available spawning habitat for fall chinook salmon was reduced to about 170 km of the mainstem between Hells Canyon Complex and Lower Granite Dam, to certain areas in Snake River tributaries, and to tail-races of the lower four dams (Irving and Bjornn 1981; Figure 1).

When Snake River fall race chinook salmon were petitioned for ESA listing, fishery managers had little information on how habitat changes had affected early life history or survival of wild fish. Data on attributes such as residence time and out-migration behavior were scant and were needed to guide recovery efforts. However, studying fall race juveniles in the field was complicated by the co-mingling of spring race juveniles in some areas and times. Research on life history of naturally spawned fall race juveniles required us to develop a method for



1. Crooked Fork Creek
2. Red River
3. Lolo Creek
4. Dworshak Hatchery
5. Herd Creek
6. West Fork Yankee Fork Creek
7. Pahsimeroi River
8. Lemhi River
9. North Fork Salmon River
10. Bear Valley Creek
11. Sawtooth Fish Hatchery
12. Camas Creek
13. Seining area for Snake River juveniles
14. Lyons Ferry Hatchery
15. Priest Rapids Hatchery
16. Hanford Reach
17. Little White Salmon Hatchery
18. Bonneville Hatchery

Figure 1.—Location of populations providing baseline genetic data, juvenile sampling sites, and other areas referred to in text.

determining the race of individuals captured during the study. We wanted to construct a model that would predict racial origin of fish based on size at age, which could be used throughout the juvenile's freshwater life (Connor et al. in preparation). We planned to use the genetic differentiation between Snake River fall and spring race chinook salmon as our major tool for identifying mixed-race juvenile samples, and for estimating race of individuals in these samples. Parameters from the genetically identified chinook salmon would be used to develop the model for classifying race of all juveniles from field data.

Genetic data for Snake River spring and fall race chinook salmon occurred as allele frequencies for allozyme (enzyme-encoding) gene loci, and had been collected for a variety of reasons, such as population delineation, hatchery evaluation, and mixed-stock fishery analysis (Bugert et al. 1991; Waples et al. 1993; Marshall 1996). We examined these data and found that large allele frequency differences at many loci existed between the spring and fall races, and that two loci, *sMEP-1** and *PGK-2**, stood out as particularly powerful for race discrimination. We expected multi-locus genotypes of juveniles sampled in-river to be highly informative. After assembling appropriate genetic baseline data, we planned to use maximum likelihood estimation (MLE) methods (Millar 1987; Pella and Milner 1987) to analyze spring and fall race composition of total juvenile samples. We believed that individuals could then be sorted by genotypes into prospective racial groups, and subjected to further MLE analysis to identify which juveniles (as a group) had the highest probability of being from either race. For each year of the project, we expected to identify a single group of fish that were progeny of naturally spawning fall race chinook salmon in the Snake River.

Fishery managers had great interest in using the estimated fall race juveniles for a genetic characterization of the naturally spawning Snake River population, which had not been available at the time of ESA listing. The only representation of the Snake River fall race gene pool was the population propagated at Lyons Ferry Hatchery by the Washington Department of Fish and Wildlife (WDFW; Figure 1). From inception in 1977, hatchery broodstock had been managed to preserve the genetic integrity of the Snake River fall race (Bugert et al. 1995). In the late 1980's, large numbers of fall-run chinook salmon from the Umatilla Hatchery (Figure 1) began to appear at Lyons Ferry Hatchery, prompting various remedial actions to prevent interbreeding of Columbia-origin and Snake River chinook salmon (Bugert et al. 1995). There was also evidence that Columbia-origin hatchery fish had been migrating to natural spawning areas

of the Snake River (Blankenship and Mendel 1994; LaVoy and Mendel 1996). Managers were concerned about potential negative genetic effects of these non-local hatchery strays on the wild population. Additionally, if the Lyons Ferry Hatchery population was to be used in supplementing natural Snake River production, it was important to know genetic relationships between contemporary wild, or natural spawners, and the Snake River gene pool as conserved in the hatchery.

In years where we succeeded in sampling and accurately identifying adequate numbers of naturally spawned Snake River fall race juveniles, we planned to use the samples as representatives of the annual adult spawner population. A variety of comparative statistical analyses using sample allele frequencies would be carried out to investigate relationships among sample years and address issues of genetic relationships with local and non-local hatchery populations. Due to past logistical problems in sampling adult spawners, we expected our estimated fall race juvenile samples to provide the first genetic characterizations of the natural Snake River population. These data would be valuable for choosing appropriate management actions aimed at recovering these threatened chinook salmon.

Methods

Juvenile Sampling

From 1991 to 1995, we sampled juvenile chinook salmon in the Snake River by beach seining as described in Connor et al. (in preparation). In our first year, we also received juveniles sampled with a mid-stream incline plane trap (river km 225), and collected juveniles that died in the Lower Granite Dam fish bypass system to ensure a large enough sample size for testing our genetic methods. We tagged juvenile chinook salmon that were seined or trapped with Passive Integrated Transponders (PIT tags) (Prentice et al. 1990). After PIT tagging, juveniles were released back into the river. We collected and sacrificed representative proportions of emigrating PIT-tagged juvenile chinook salmon at Lower Granite Dam for genetic analysis. Other PIT-tagged juveniles were sampled for biological data and released.

Laboratory Procedures

Field-sampled juveniles were kept on dry ice or in liquid nitrogen prior to storage in ultra-cold (-75^{o} C) freezers. We dissected four tissues, heart, liver, body muscle, and whole eyes, from each juvenile for electrophoretic allozyme analysis. We prepared tissue extracts and loaded gels as described in Shaklee and Varnavskaya (1994). Other procedures for horizontal starch gel electrophoresis and histochemical staining were similar to those described in Aebersold et al. (1987). We used four gel buffer systems to resolve most of the known variable allozyme systems in chinook salmon (Appendix 1). Our enzyme staining recipes were adaptations of those in Harris and Hopkinson (1976), except that we resolved formaldehyde dehydrogenase (FDHG) and superoxide dismutase (SOD) with recipes of Barman (1969) and Fevolden (1989), respectively.

We used several procedures to ensure accuracy of the interpretation and data entry of allelic genotypes. Many loci were analyzed in two or more tissues and with two different gel buffers to confirm allelic variation. All isozymes resolved on each gel slice were independently doubled-scored. Genotypic data were entered directly into computer files, and a computer program checked for discrepancies in genotypes from all sources of multiple scoring. When discrepancies could not be resolved immediately, samples were re-analyzed on other gels. Occasionally, allele mobility standards from other samples had to be used to verify rare alleles.

Compilation of baseline data

To do the genetic race identification of sampled juveniles, we assessed and compiled allozyme allele frequency data from chinook salmon populations that were potential contributors to natural production in the Snake River. Genetic data available for Snake River fall race chinook salmon consisted primarily of multiple annual samples from adult spawners at Lyons Ferry Hatchery (Bugert et al. 1991; WDFW unpublished data). Due to the occurrence of fall-run, upper Columbia River-origin, chinook salmon in Snake River spawning areas, we required baseline genetic data from appropriate Columbia populations (Bugert et al. 1991; Utter et al. 1995). Although no upper Columbia River fall-run chinook salmon populations are included at present in the Snake River fall race ESU, they share similarities in allozyme allele frequencies with the Snake River population, especially in contrast to the spring race (Waples et al. 1991). Hereafter, we usually refer to Columbia and Snake rivers fall-run chinook salmon as a single fall race to simplify descriptions of our work to genetically separate spring/summer- and fall-run juveniles in

the Snake River. We make no conclusions about inter-relationships of Columbia and Snake rivers populations. For spring race chinook salmon populations in Snake River tributaries (Salmon, Imnaha, Grande Ronde and Clearwater rivers) we found extensive, multiple-year genetic baseline data available (Waples et al. 1993; Marshall 1996). In total, we chose to use allele frequency data from 18 population samples as a baseline for our spring and fall race MLE mixture analyses (Table 1).

Comparing spring versus fall race allele frequencies, we saw that the loci *sMEP-1** and *PGK-2** had the relatively largest differences. Average allele frequencies for these two loci from the spring and fall race baseline data are presented in Table 2. The genetic divergence at these loci would not only be particularly useful for calculating mixed-race sample composition, but also for estimating the race of individuals. Given the race-specific pairing of *sMEP-1** and *PGK-2** allele frequencies, certain genotypes at both loci would be much more common in individuals from one group than another. All possible genotypic pairs and their frequencies as measured in the baseline samples are shown in Table 3. In general, 86% of Snake River spring race chinook salmon were identified by two genotype pairs or classes: *sMEP-1*bb/PGK-2*bb* and *sMEP-1*bb/PGK-2*ab*. Only 3% of upper Columbia- and Snake River-origin fall race chinook salmon were found in these two classes. The proportions of fall race fish in all nine *sMEP-1*/PGK-2** genotype classes were more widely distributed than those of the spring race. However, 87% of fall race chinook salmon occurred within five genotype classes compared to only 2% of spring race fish. An individual's *sMEP-1*/PGK-2** genotype served us as a foundation for sorting field-sampled juveniles by race.

Allele frequency variation at several other allozyme loci also showed great potential for estimating race composition within samples and for distinguishing race of individuals. For example, relatively high frequencies of *sIDHP-1*c*, *mMDH-2*b*, and *TPI-4*b* alleles occurred in spring race chinook salmon populations whereas they were nearly absent or at very low frequencies in fall race populations. The two races possessed relatively large allele frequency differences at the loci *sAH**, *mAH-4**, *sIDHP-2**, *MPI**, *PEP-LT**, and *sSOD-1**. The baseline data showed that some rare or very low frequency alleles (e.g., *sAAT-3*c*, *GPI-A*b*, *sIDHP-1*l*, *sIDHP-2*g*, *sIDHP-2*k*, *LDH-B2*b*, and *mSOD*b*) were exclusive to one race or the other. For all mixture analyses and genotypic sorting, we chose to use allele

Table 1. -Description of baseline samples of fall and spring race chinook salmon that provided population allele frequency data for genetic analyses. See Figure 1 for geographic locations.

River	Race	Population	N	Source
Snake, Clear-water	Spring	Crooked Fork Creek	102	Marshall 1996
		Red River	111	"
		Lolo Creek	99	"
		Dworshak Hatchery	302	"
Snake, Salmon	Spring	Herd Creek	103	Marshall 1996
		W.F. Yankee Fork Creek	105	"
		Pahsimeroi River	118	"
		Lemhi River	178	"
		N.F. Salmon River	136	"
		Bear Valley Creek	175	"
		Sawtooth Hatchery	290	"
		Camas Creek	106	"
Snake	Fall	Lyons Ferry Hatchery 1990-1991 tagged adults	200	Bugert et al. 1991; WDFW unpublished
		Lyons Ferry Hatchery 1992-1993 tagged adults[a]	192	WDFW unpublished

Table 1. -continued

River	Race	Population	N	Source
Upper Columbia	Fall	Hanford Reach	99	Utter et al. 1995
		Priest Rapids Hatchery	200	"
		Little White Salmon Hatchery	200	Bugert et al. 1991
		Bonneville Hatchery	200	"

[a] 1992 and 1993 Lyons Ferry Hatchery sample data were used together instead of combined with 1990 and 1991 samples because of unusual broodstock management that excluded all 1989 brood year adults from hatchery spawning (Bugert et al. 1995).

Table 2. -Mean allele frequencies and ranges for sMEP-1* and PGK-2* for populations of Snake and upper Columbia river fall race chinook salmon and Snake River spring race chinook salmon. Data were from baseline samples described in Table 1.

Locus allele	Mean frequency (range) fall race		spring race	
sMEP-1*				
*a	0.759	(0.716-0.782)	0.068	(0.005-0.136)
*b	0.241	(0.216-0.284)	0.932	(0.864-0.995)
PGK-2*				
*a	0.578	(0.547-0.608)	0.129	(0.051-0.240)
*b	0.422	(0.392-0.453)	0.871	(0.760-0.949)

Table 3. -Frequencies of paired genotypes for sMEP-1* and PGK-2* among all individuals sampled from populations of Snake and upper Columbia river fall race chinook salmon and Snake River spring race chinook salmon. Data were from baseline samples described in Table 1.

sMEP-1*/PGK-2* genotypes	Frequency of paired genotypes	
	fall race	spring race
*aa/aa	0.191	0.000
*aa/ab	0.285	0.002
*aa/bb	0.106	0.003
*ab/aa	0.117	0.002
*ab/ab	0.173	0.017
*ab/bb	0.071	0.094
*bb/aa	0.024	0.023
*bb/ab	0.022	0.191
*bb/bb	0.010	0.670

frequencies of 40 allozyme loci (including 3 isoloci; Appendix 2), which were available in all baseline samples, and which appeared most informative.

To gauge the strengths of our baseline data for distinguishing spring or fall racial origin, we ran two types of tests. First, we simulated race composition analyses by generating test samples from all baseline data, followed by MLE mixture analysis. Complete details on our simulation methods can be found in Shaklee (1991). We used sample sizes and baseline proportions in the simulations that could be expected from juvenile field sampling. Simulation results (Table 4) showed a very high level of accuracy in estimating proportions of the two races in a mixture. For our second test we had samples of individuals of known racial origin function as mixed samples of unknown origin, and conducted MLE mixture analyses with our baseline data set. We used samples (N=100) of Lyons Ferry Hatchery fall race juveniles from three different brood years (1990, 1991 and 1992), and Bear Valley Creek and Dworshak National Fish Hatchery spring race juveniles from two and one brood year(s), respectively. All three known fall race samples were estimated to be 100% fall race origin, and both spring race samples were estimated to be 100% spring race origin. Based on results of these trials, we assumed the baseline data set we constructed would perform well in estimating racial origins of Snake River juvenile chinook salmon.

Race analysis of field-sampled juveniles

For the entire juvenile sample of each year, we performed an MLE mixture analysis to estimate total relative proportions of spring and fall races. We compiled genotypes for juveniles from the 40 loci that were included in the baseline allele frequency data set. We used the MLE computer program of Milner et al. (1983) as modified by Millar (1987) to estimate contributions from each of the 18 baseline population samples. Estimated contributions were then summed and variances recalculated to produce final estimates of total spring race and fall race composition of the juvenile sample. Our MLE methods were identical to those described in Shaklee et al. (1990) for analyzing stock composition in Pacific salmon fisheries.

Mixture analysis results from each total sample were used to guide sorting of individuals into putative spring race or fall race groups. For example, if an annual sample of 100 fish was estimated to be composed of 10% spring race and 90% fall race

Table 4. -Results from MLE simulation analyses to test the accuracy of baseline data for estimating composition of mixed samples of Snake River fall and spring race chinook salmon.

		Fall race proportions		Spring race proportions	
Simulation	N	true	estimated (SD)	true	estimated (SD)
1	150	0.500	0.495 (0.05)	0.500	0.505 (0.05)
2	150	0.900	0.903 (0.02)	0.100	0.097 (0.02)
3	100	0.950	0.947 (0.03)	0.050	0.053 (0.03)

juveniles, we expected to find about 10 individuals (at least a number within the 95% confidence limits) whose genotypes were typical of the spring race. We sorted juveniles by genotypes as described below into two racial group subsamples. Each subsample was subjected to the same type of mixture analysis used on the original sample. Results for spring and fall race composition of each subsample directed further sorting needs and exchange of individuals between subsamples. This procedure continued iteratively until we had assembled two subsamples of juveniles that were estimated to be 100% of one race or the other.

Our initial sorting of total annual samples was based entirely on *sMEP-1*/PGK-2** genotypes of the juveniles. All fish with an *sMEP-1*/PGK-2** genotype of **bb/bb*, **bb/ab*, **bb/aa*, or **ab/bb* were grouped into a subsample of putative spring race chinook salmon. Fish with the five other *sMEP-1*/PGK-2** genotypes (Table 3) were grouped as a fall race subsample. As expected, this primary sorting rarely produced a mixture analysis result of 100% of either race for the two subsamples, but indicated the extent of further genotypic sorting needed. Subsequently, we focused on juveniles with *sMEP-1*/PGK-2** genotypes found at similar levels in both races (Table 3). For these juveniles, genotypes at other loci, particularly *mAH-4**, *sAH**, *GPIr**, *mIDHP-2**, *sIDHP-1**, *sIDHP-2**, *mMDH-2**, *MPI**, *PEP-LT**, *mSOD**, *sSOD-1**, and *TPI-4**, were used to group them in one subsample or the other. We further used multi-locus genotypes to sort juveniles with *sMEP-1*/PGK-2** genotypes that were shared at only a minor level between races (e.g., *sMEP-1*ab/PGK-2*ab*; Table 3). For guidance, we assumed that the number of fish from shared *sMEP-1*/PGK-2** genotype classes that should be sorted into either subsample depended on total sample mixture results. For example, the *sMEP-1*ab/PGK-2*bb* genotype occurred at very similar frequencies in spring and fall race populations. If a total sample was estimated to include 50% spring and 50% fall race juveniles, then we could expect to sort equal numbers of fish with the *sMEP-1*ab/PGK-2*bb* genotype into both racial subsamples.

We did no further multi-locus genotypic sorting once mixture analysis estimated that the putative spring race subsample was 100% spring-origin, and the putative fall race subsample was 100% fall-origin. At this point, the MLE analysis has calculated that frequencies of the 40-locus genotypes computed for each subsample have the highest probability of resulting from juveniles of one race. It has not estimated the racial origin of each juvenile in a subsample. We could have made two kinds of errors in genotypic sorting of individuals that would not be evident in final mixture analysis results. We may have misclassified fish possessing

genotypes rare for their race. A small percentage of genotypes were ambiguous for racial origin, and we may have mis-sorted these. In either case, the presence of juveniles with these genotypes would not have a large enough effect on subsample probabilities to alter an estimate of 100% single origin. For our purposes, we believed these errors were minor, and assumed that individuals in final subsamples were of the race estimated.

Genetic analysis of Snake River fall race juveniles

Each year's subsample of Snake River juveniles estimated to be 100% fall race chinook salmon was assumed to provide a genetic characterization of the previous year's natural spawner population. We tested all annual fall race samples for conformity of genotypic proportions to those expected under Hardy-Weinberg (HW) equilibrium. Hardy-Weinberg tests were expected to identify problems due to sorting by certain genotypic arrays. We did pair-wise tests of homogeneity of allele frequencies of annual samples with a log-likelihood ratio test and *G*-statistic (*G*-tests; Sokal and Rohlf 1981). Annual allele frequencies were used to investigate genetic relationships among juvenile brood years, and among juveniles and fall race populations at Lyons Ferry Hatchery (Snake River-origin) and from upper Columbia locations. For these comparative analyses, we computed genetic distances (Cavalli-Sforza and Edwards (1967) chord distance) between all samples with the BIOSYS-1 computer program (Swofford and Selander 1989). To visualize relationships, genetic distances were employed in cluster analyses using an unweighted pair-group method (Sneath and Sokal 1973), and in multidimensional scaling analyses (Lessa 1990) using BIOSYS-1 and the NTSYS-pc program (Rohlf 1994), respectively. We also used *G*-tests to identify significant differences in allele frequencies among fall race samples.

For regional comparative analyses, we used baseline allele frequency data from Snake River and upper Columbia fall race populations that had been compiled for mixture analyses (Table 1). As our study progressed, other pertinent genetic data became available from samples of the Lyons Ferry Hatchery population. We used allele frequency data from 1990 and 1992 brood year (BY) Lyons Ferry Hatchery juveniles, which were progeny of coded-wire tagged (CWT; known-origin) adults, and from 1994 CWT adult spawners (WDFW unpublished data). We also used genetic data from untagged adults sampled at Lyons Ferry Hatchery in 1990, which were estimated to contain a significant proportion of strays from Columbia River hatcheries and were not used as broodstock (Bugert et al. 1991). The proportions of various Columbia hatchery-origin fall-run chinook salmon passing above Lower Granite Dam in 1990 (potential natural spawners) were estimated to be similar to

proportions of strays seen at Lyons Ferry Hatchery (LaVoy and Mendel 1996). Thus, we thought the untagged 1990 Lyons Ferry Hatchery sample might act as a proxy for a genetic profile of 1990 Snake River natural spawners. Finally, we pooled genetic data for some samples to further explore relationships. Because these steps depended on outcomes of preceding analyses, we describe them in the results section.

Results

Estimating race

We sampled enough juveniles for genetic analysis in four years (1991, 1993, 1994, and 1995) of the Snake River chinook salmon life history study. For each annual sample, total sample size, estimated spring and fall race composition, and number of genotypically-sorted juveniles estimated to be 100% of either race, are presented in Table 5. Estimated proportions of spring and fall race juveniles in total samples varied widely among years. The number of individuals sorted by multi-locus genotypes into subsamples and estimated to be of either race was usually very close to the race proportions estimated in total samples. The relatively largest difference occurred in 1994, but numbers fell within the 95% confidence interval of estimated proportions (e.g., 28 fish (19.6%) were genotypically identified as spring race whereas 14.2% (3.2% SD) were predicted by the total sample mixture analysis). Although fall race subsample size was largest (143) in 1991, fall race juveniles made up the largest proportion of sampled fish in 1994 and 1995 (85.8% and 94.6%, respectively).

In 1991, most of the fish we collected using a beach seine were estimated to be fall race juveniles, whereas most collected mid-stream with an incline plane trap were estimated to be spring race. In 1993, we stopped using the incline plane trap for initial capture of juveniles, but spring race chinook salmon still dominated the composition of our genetic sample collected at Lower Granite Dam. Throughout our study virtually all yearling juveniles, aged by scale pattern analysis (Koo 1967), were genetically estimated to be spring race. This was expected given the spring race's freshwater life history pattern (Chapman and Bjornn 1969; Achord et al. 1996). However, we also estimated numerous subyearlings to be spring race-origin. Subsamples estimated as 100% fall race were composed entirely of subyearling juveniles.

Table 5. -Race estimation results for Snake River juvenile chinook salmon sampled at Lower Granite Dam in 1991, 1993, 1994, and 1995: estimated racial composition of total annual samples, and final number of fish in annual subsamples estimated to be 100% of either race.

		Race composition of total sample percent (SD)		Number of individuals estimated to be 100% (0 SD) of each race	
Year	Total N	fall	spring	fall	spring
1991	286	49.9 (3.1)	50.1 (3.1)	143	143
1993	154	37.5 (4.0)	62.5 (4.0)	59	95
1994	143	85.8 (3.2)	14.2 (3.2)	115	28
1995	119	94.6 (2.2)	5.4 (2.2)	111	8

We were always able to sort multi-locus genotypes into putative race subsamples and achieve 100% single race composition estimates for each pair. To obtain final subsamples, we usually only had to perform two or three iterations of multi-locus sorting and mixture analyses, following our primary sorting on *sMEP-1*/PGK-2** genotypes. We never found genotypes that were impossible from either race, given our baseline data set. Only rarely did we find fish with alleles not included in baseline allele frequencies. However, these alleles had been screened for and observed in at least one population of the region. These fish still could be sorted by their genotypes at all other loci and successfully included in subsamples estimated to be 100% of one race.

Genetic characterization of fall race juveniles

The four annual subsamples of estimated fall race juvenile chinook salmon were assumed to be progeny of natural spawners in the Snake River. They represented the 1990, 1992, 1993, and 1994 brood years, having parents who spawned in the year prior to sampling. Hereafter, we refer to the estimated fall race subsamples as fall race samples for simplicity. We employed these four samples in all analyses of genetic characteristics and relationships among populations. We acknowledge that some limitations may be posed by the small sample size (N=59) of the 1993 sample.

Allele frequencies at 40 loci for the four fall race juvenile samples are presented in Appendix 2. Generally, we found variant alleles at frequencies expected, given variability levels seen in baseline data for Lyons Ferry Hatchery and upper Columbia populations. We did observe a number of uncommon, or typically low frequency, alleles in every Snake River fall race juvenile sample. The *mIDHP-2*b* allele, rare in baseline data and absent in other Washington chinook salmon (Marshall et al. 1995), was present at approximately 2-3% in all years except 1993. We found the *sIDHP-2*g* allele in all years except 1995 (occurring at 3% in 1994), and *sIDHP-1*l* in the 1993 sample. One fish in the 1994 sample had an *LDH-B2*d* allele, which is very rare throughout the range of chinook salmon. We found one occurrence in 1991 of the *sSOD-1*e* allele, another allele rare in baseline populations and absent elsewhere. The most unusual variant was the *mMDH-2*d* allele, seen in 1991 and 1994 samples. This allele was not present in Lyons Ferry Hatchery or upper Columbia population sample data.

In each sample year, the total number of HW tests, and the number showing significant deviations from HW proportions, were as follows: 1991-17, 1; 1993-13, 1; 1994-15, 0; 1995-15, 1. The number of deviations per annual sample was close to that expected from random sampling error (5% of tests/sample would be significant). Also, in two years, the locus with HW deviations was *mAAT-2** and in both cases there was a deficiency of heterozygotes. This was most likely due to weak expression of the heterozygous phenotype *100/90* (**ac*) in juvenile tissues. Questionable phenotypes from gel scoring became genotypes with no data in final score files.

Hardy-Weinberg test results were a measure of confidence that our samples were random collections of fall race juveniles, and were plausible genetic characterizations of the Snake River fall race natural spawner population. Genotypic proportions at variable loci were typical of what one would expect in a relatively large, randomly mating population that did not include substantial numbers of fish from a genetically different population(s). Our genotypic sorting methods did not produce a group of fish biased towards particular genotypes. If any subyearling spring race juveniles were mistakenly included in the samples, they did not have a measurable effect. We thus were reasonably assured that comparative genetic analyses were appropriate.

We found significant differences ($P < 0.01$) in allele frequencies in all pair-wise *G*-tests ($N=6$) among the four fall race juvenile samples, except in one comparison. Allele frequencies of the 1991 and 1995 samples were not significantly different ($P > 0.10$). The number of variable loci participating in these tests ranged from 20 to 22. Some variable loci had to be excluded from *G*-tests. We did not use *mAAT-2** and *sSOD-2**, due to poor expression in juvenile tissues, *GPIr**, due to inability to detect heterozygotes, or *PEPB-1**, due to sex-linkage (A.R. Marshall, WDFW, unpublished data). A variety of individual loci showed significant differences ($P < 0.05$) within each *G*-test. No locus had significant differences within every test. We calculated the relatively largest differences in allele frequencies in the comparison of 1993 and 1994 samples. In this test, we found significant differences ($P < 0.05$) at ten loci, five of which included presence (at low frequencies) versus absence of alleles.

We started our regional comparative analysis using all four fall race juvenile samples individually and ten samples chosen from other fall race populations. We used genetic distances computed among these fourteen samples to produce the dendrogram

in Figure 2, and the multi-dimensional scaling (MDS) plot in Figure 3. In both cases, Snake River fall race juveniles showed similar relationships to each other and to other population samples. The 1991 (1990 BY) and 1995 (1994 BY) Snake River samples clustered together closely and grouped with several Lyons Ferry Hatchery samples. The 1993 (1992 BY) and 1994 (1993 BY) Snake River juvenile samples were well separated from each other and from all other samples. The 1993 and 1994 samples had, overall, the relatively largest genetic distance values computed. Viewing other relationships, the three upper Columbia fall race samples clustered together closely and the 1990 Lyons Ferry Hatchery untagged (presumed mixed-origin) adults sample grouped with them.

This analysis of genetic distances did not provide a definitive picture of relationships among Snake River naturally produced fall race juveniles, and the Lyons Ferry Hatchery and upper Columbia populations. The affinity of the 1991 (1990 BY) and 1995 (1994 BY) samples seemed reasonable since 1990 BY fish would have returned as four year-old spawners in 1994, and four year olds are often a dominant age class. We were concerned that the variability among our juvenile samples could obscure genetic relationships with other fall race populations of the region. Waples and Teel (1990) demonstrated that, for Pacific salmon populations, genetic drift due to small population size can cause relatively large fluctuations in allele frequencies among temporally-spaced juvenile samples. Combining temporal samples should provide a more precise description of population frequencies (Waples 1990). Also, we had been comparing single brood year samples to (in most cases) multi-brood year adult samples. We decided to combine the three consecutive juvenile samples, 1992, 1993 and 1994 BYs, which also were linked by the condition that the majority of the spawner escapement in each year (83%, 79%, and 68%, respectively) was estimated to be natural (non-hatchery) origin (LaVoy and Mendel 1996). At this point, we ignored temporal variation that might be due to genetic contributions from non-Snake River hatchery strays. We computed allele frequencies for the combined samples (Appendix 2) and used these along with those of the 1991 (1990 BY) sample alone for further comparative analyses.

We also pooled some other population samples to simplify the view of genetic relationships. We combined samples of fall race chinook salmon from Bonneville and Little White Salmon hatcheries because differences in allele frequencies were non-significant ($P > 0.05$), and there was a history of fish transfers between the

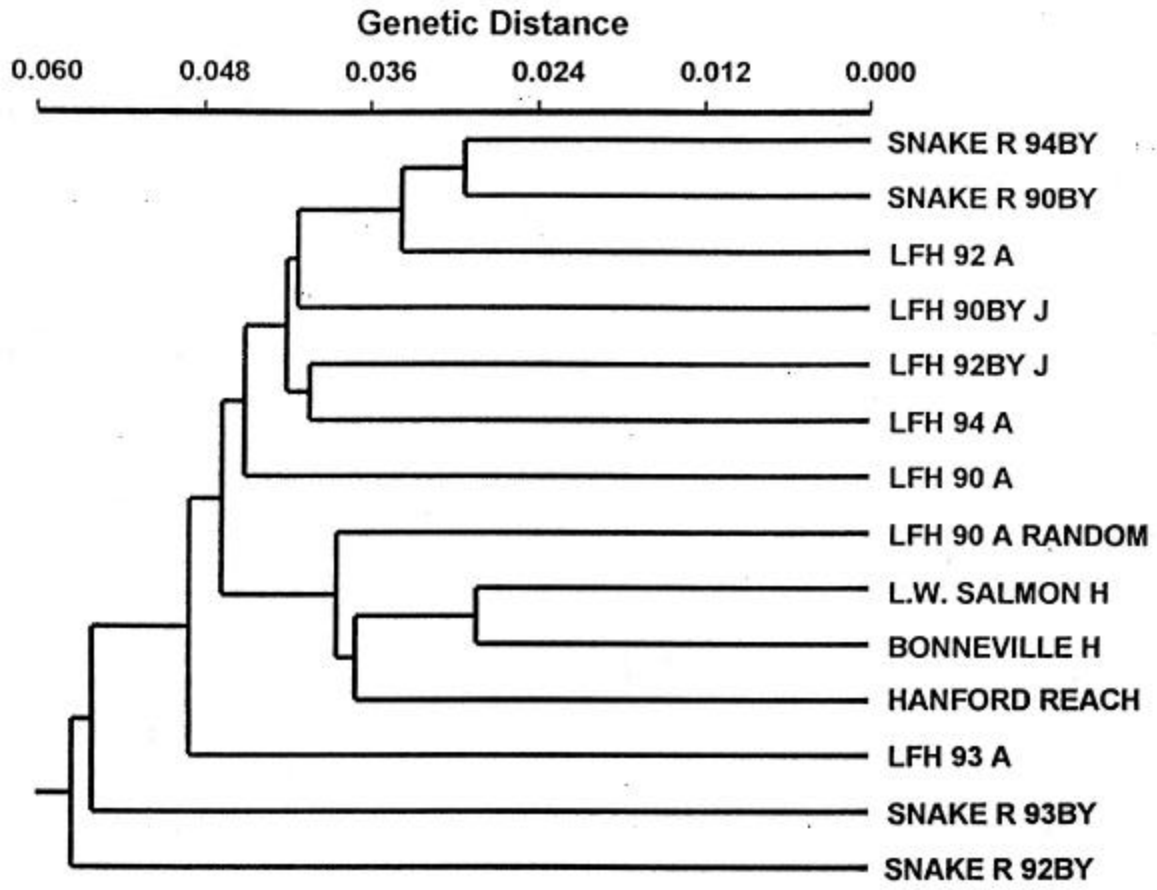


Figure 2.—Dendogram resulting from cluster analysis (unweighted pair-group method) of Cavalli-Sforza and Edwards (1967) chord genetic distances among 14 fall race chinook salmon population samples. Abbreviations: 90, 92, etc. = year of return (adults) or birth (juveniles); SNAKE R = Snake River natural fall race juveniles; LFH = Lyons Ferry Hatchery; L.W. Salmon = Little White Salmon; BY = brood year; A = adults; J = juveniles; H = hatchery.

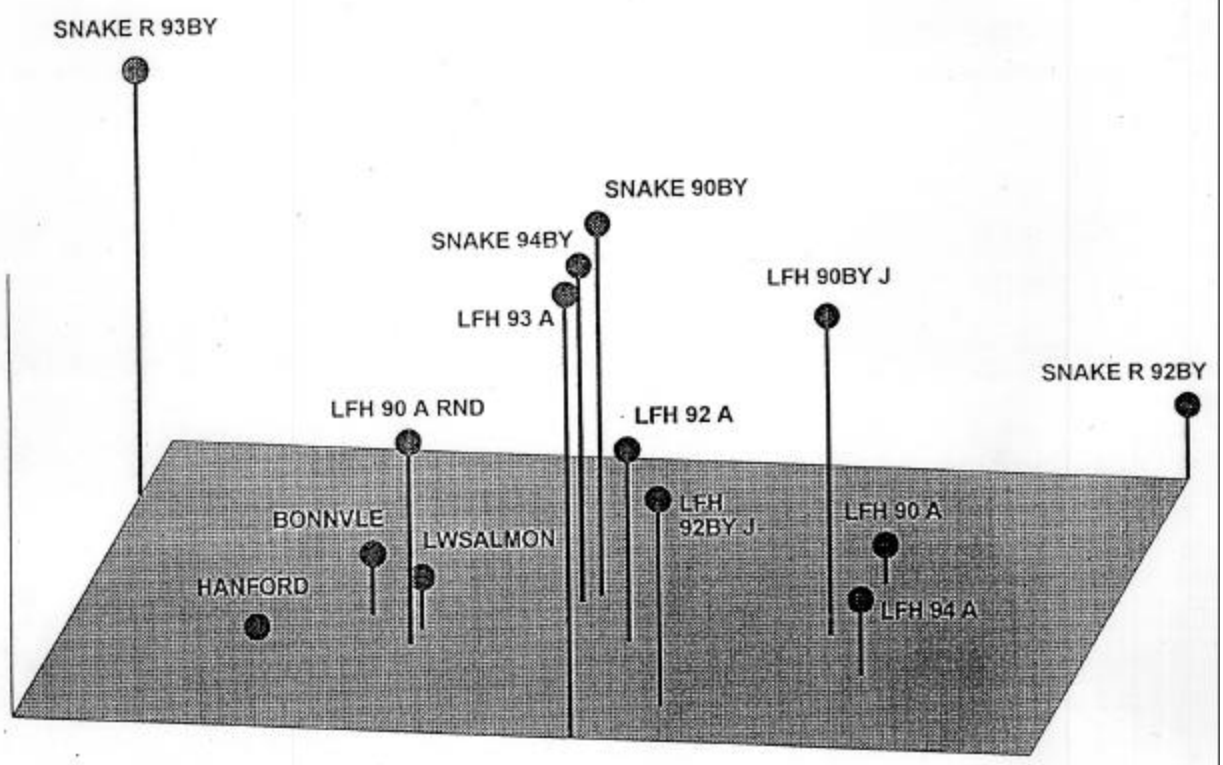


Figure 3.—Multidimensional scaling plot of Cavalli-Sforza and Edwards (1967) chord distances among 14 fall race chinook salmon population samples, with principal components analysis used as initial configuration. Abbreviations: 90, 92, etc. = year of return (adults) or birth (juveniles); SNAKE R = Snake River natural fall race juveniles; LFH = Lyons Ferry Hatchery; RND = random; LWSALMON = Little White Salmon Hatchery; BONNVLE = Bonneville Hatchery; HANFORD = Hanford Reach; BY = brood year; A = adults.

two. We pooled two pairs of Lyons Ferry Hatchery samples, 1990 tagged adults and their offspring (1990 BY juveniles), and 1992 tagged adults and offspring (1992 BY juveniles). Our end result was seven Snake and upper Columbia rivers fall race population samples for comparison with the two juvenile samples. We computed a new set of genetic distances among these nine samples.

A two-dimensional cluster analysis and a MDS plot of genetic distances among the nine samples are shown in Figures 4 and 5, respectively. In both, the combined Snake River 1992-1994 BY juveniles sample and the single 1990 BY sample cluster together most closely. In the dendrogram (Figure 4) these two cluster first with three of the known-origin Lyons Ferry Hatchery samples. They appear generally closer to, but distinct from, all known-origin Lyons Ferry Hatchery samples in the MDS plot (Figure 5). The two upper Columbia fall race samples and the 1990 Lyons Ferry untagged adults sample formed a separate cluster in both diagrams. In the MDS plot, the Snake River 1992-1994 BYs sample appeared in one dimension to be about midway between the upper Columbia and the Lyons Ferry Hatchery groupings. In another dimension ("height"), the combined juveniles sample appeared relatively distinct. The genetic distance between the two Snake River juveniles samples was smaller than distances computed between any pair of Lyons Ferry Hatchery samples.

We did find significant differences in allele frequencies overall (*G*-test; $P < 0.01$) between the combined Snake River 1992-1994 BYs fall race sample and the 1990 BY sample. Twenty-three loci were included in the test, and three individual loci (*GR**, *sIDHP-2**, *LDH-C**) showed significant differences ($P < 0.05$). Allele frequencies of the Snake River 92-94 BYs sample were also significantly different ($P < 0.01$) from those of the seven Lyons Ferry Hatchery and upper Columbia samples used in our second comparative analysis.

Discussion

Estimating race of field-sampled juveniles

Large allele frequency differences at many allozyme loci existed between fall race chinook salmon of either the Snake or upper Columbia rivers and spring race chinook salmon from the Snake Basin. Genetic distance values computed between these two groups have been some of the largest reported in comparative analyses of chinook salmon populations of the Pacific Northwest (Waples et al. 1991; Utter et al. 1995). Given this level of

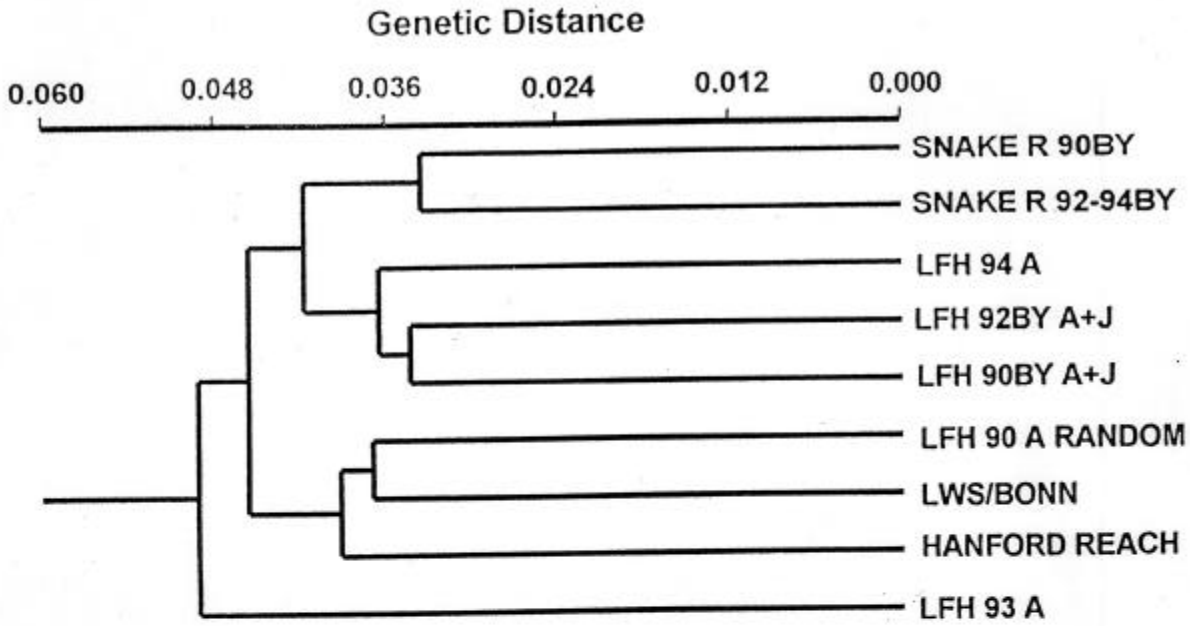


Figure 4.—Dendogram resulting from cluster analysis (unweighted pair-group method) of Cavalli-Sforza and Edwards (1967) chord genetic distances among nine fall race chinook salmon population samples. Abbreviations: 90, 92, etc. = year of return (adults) or birth (juveniles); SNAKE R = Snake River natural fall race juveniles; LFH = Lyons Ferry Hatchery; LWS/BONN = Little White Salmon and Bonneville Hatcheries; BY = brood year; A = adults; J = juveniles.

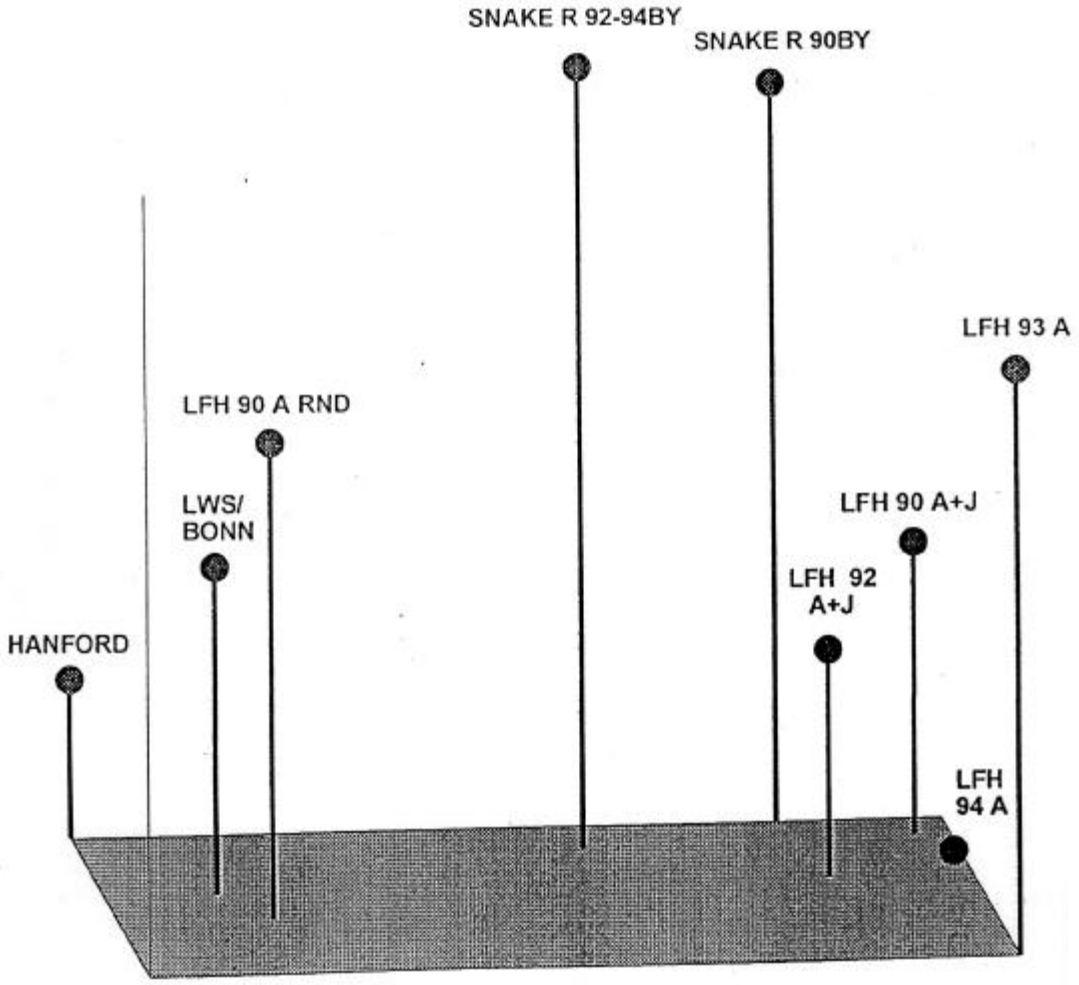


Figure 5.—Multidimensional scaling plot of Cavalli-Sforza and Edwards (1967) chord distances among nine fall race chinook salmon population samples, with principal components analysis used as initial configuration. Abbreviations: 90, 92, etc. = year of return (adults) or birth (juveniles); SNAKE R = Snake River natural fall race juveniles; LFH = Lyons Ferry Hatchery; RND = random; LWS/BONN = Little White Salmon and Bonneville hatcheries; HANFORD = Hanford Reach; BY = brood year; A = adults; J = juveniles.

genetic divergence, we were able to develop a method for determining race of Snake River juveniles sampled in the field. By compiling existing population allele frequency data we created a baseline data set for effective analysis of mixed race samples. Our simulations and tests with known-race samples showed that the baseline data performed extremely well in estimating spring and fall race contributions. We are confident we provided our colleagues (Connor et al. in preparation) with very accurate and precise assessments of the proportions of spring and fall race juveniles in their samples. We showed that although their sampling design targeted fall race juveniles, spring race fish were captured inadvertently in all years. This knowledge was essential to researchers investigating the natural life history of Snake River fall-race juvenile chinook salmon.

Of further importance was our ability to use the genetic divergence between races to estimate the racial origin of individuals. We correctly surmised that multi-locus genotypes would act as reliable identifiers of race. We discovered the value of using paired *sMEP-1** and *PGK-2** genotypes as a basic sorting tool. With genotype data for only these two loci, we could quickly and simply divide individuals into preliminary spring and fall race subsamples. Employing allelic variation from at least 12 other loci, we achieved further accuracy in genotypic sorting. The MLE mixture analysis results for our final subsamples detected no errors in race estimation among genotypically sorted individuals. Realistically, we probably did not correctly identify every juvenile by race. However, because errors were statistically inconsequential, we concluded that estimated fall race individuals could be used as true fall race juveniles for the life history study. Traits of these fish measured during their residence in the Snake River provided variables for a model developed to non-genetically classify race of every fish collected in the field (Connor et al. in preparation).

Special circumstances during the 1995 sampling period provided a blind test of our genetic methods. In 1994, fall race chinook salmon spawned in the Snake River above the confluence of the Imnaha River up to Hells Canyon Dam (Figure 1). There is no production of spring race chinook salmon upstream of the Imnaha River confluence. Juveniles were collected during the study in 1995 upstream of the Imnaha River, and thus were expected to be solely fall race origin. Information on collection site was not provided until we had completed all genetic analyses. It turned out that we had estimated all juveniles initially collected upstream of the Imnaha River (N=65) to be fall race-origin, and juveniles from below that location (N=50) to be of both races.

These results matched field sampling expectations, and further increased the credibility of our multi-locus sorting and mixture analysis procedures.

Genetic characterization of Snake River fall race chinook salmon

Given the statistical accuracy of our genetic identification methods, we believed that estimated fall race juveniles in each annual subsample represented progeny of fall race adults that had spawned naturally above Lower Granite Dam. Using each subsample as a representative sample of the total annual adult spawner population requires a review of possible sampling errors. Our annual samples of juvenile chinook salmon were comprised predominantly of juveniles that were PIT tagged after being captured in the Snake River with a beach seine. Sampling and tagging occurred over a distance of 185 kms, and a period of roughly 100 d, to ensure a broad representation of fish from different rearing areas and weekly age classes. Some fish were too small for tagging (< 60 mm fork length). However, these were probably not migratory, and had a good chance of later recapture at a size large enough to tag (W.P. Connor, USFWS, unpublished data). Our genetic samples eventually came from PIT tagged fish detected at Lower Granite Dam, after an extended period of rearing and migration. Overall, only 9% to 32% of tagged fish were detected, and only 24% to 65% of detected fish were collected for genetic analysis (W.P. Connor, USFWS, unpublished data). We have not identified any non-random factors affecting recapture at the dam. Sampling strategies generally appeared free of non-random errors. Final sample size of juveniles estimated to be fall race was probably the most important variable in how well we represented genetic characteristics of annual spawners.

We did find some significant variability in allele frequencies among our four annual samples of fall race juveniles. Small sample size in 1993 (1992 BY; N=59) may have been a source of some genetic heterogeneity among samples. We could have missed sampling some low frequency alleles in 1992 spawners. In other sample years, we did observe allelic variants that generally only occur at low frequencies in most chinook salmon populations. This gave us confidence that these samples represented the breadth of genetic diversity in annual spawners. Due to some rare alleles or genotypes occurring in more individuals per annual sample than might be expected, we considered the possibility of non-random sampling of family members. For a group of fall race juveniles sampled in 1994, we reviewed field data such as capture date and site, recapture date, growth rate, and back-calculated emergence date (W.P. Connor, USFWS, unpublished data), and did not observe patterns

that suggested kinship. Also, the recapture rate of less than 100% would help reduce sampling rate of siblings if any were captured and tagged together. Sample frequencies of rare alleles may indicate that allelic diversity in the wild population is still relatively broad.

An adequate interpretation of the genetic variability among annual juvenile samples also requires an understanding of conditions affecting each annual group of fall race spawners. In any population of chinook salmon, each year's spawners are unique because adults die after spawning, and proportions of several age classes among spawners can vary annually. These circumstances promote random changes in allele frequencies, or genetic drift, among brood years, which can be amplified by small population size. Identifying other sources of significant differences among brood year samples can be confounded by the effects of genetic drift (Waples and Teel 1990). We had estimates of the number of potential Snake River spawners from annual dam counts, but no estimates of actual spawners. Counts at Lower Granite Dam were relatively low (N=436) in 1990, but other study years had census numbers ranging from about 700 to nearly 1,000. We presume only some proportion of fish passing above the dam were successful spawners. If actual spawner numbers were quite a bit lower than dam counts as suggested by Blankenship and Mendel (1994), genetic drift may explain some of the variability seen among our juvenile samples.

Also essential for interpreting temporal genetic variability was knowledge of human activities that annually affected the origin of spawners passing above Lower Granite Dam. LaVoy and Mendel (1996) estimated the proportions of chinook salmon from three sources that comprised annual (1990-1995) groups of adults passed upstream of the dam (Table 6). Adults were identified as originating from natural (wild) spawners, Lyons Ferry Hatchery, or non-Snake River hatcheries, by using expanded CWT data. Lyons Ferry Hatchery-origin fish had been 100% marked since the 1989 brood year, and were intentionally removed at the dam starting in 1992 (Blankenship and Mendel 1994). Removal of other marked, hatchery-origin adults also began in 1992, but because marking rates were less than 100% for these fish (mostly from upper Columbia River hatcheries), not all hatchery-origin fish were prevented from passing above the dam. The National Marine Fisheries Service had requested removal of fall-run hatchery-

Table 6. -Origin of fall race chinook salmon escaping to spawning areas in the Snake River above Lower Granite Dam, as estimated by recoveries of marked fish at the dam (from LaVoy and Mendel, 1996). Hatchery numbers were estimated by expanding marked fish observations by juvenile marking rate. Total counts are actual counts at the dam's passage facility. "Jack" chinook salmon are males 56 cm or less in fork-length.

	Escapement - Number of Adults ("jacks" included)			
Year	Lyons Ferry Hatchery	Other Hatchery	Natural	Total
1990	221	114	101	436
1991	202	70	318	960[a]
1992	103	25	620	748
1993	43	167	777	987
1994	42	191	484	717
1995	0	285	379	664

Table 6. -continued

[a] The total 1991 count included "jacks", but they were not included in 1991 estimates of the three component groups.

origin chinook salmon to reduce effects on the genetic integrity of the wild population (Blankenship and Mendel 1994). This management action is reflected in changes among estimated relative proportions of the three sources of spawners (Table 6). Generally, Lyons Ferry Hatchery-origin fish decreased greatly, natural-origin fish increased in abundance, and other hatchery-origin fish fluctuated in relative proportions.

Genetic differentiation among the components of fall race adults that did spawn naturally would contribute to annual allele frequency variability among progeny. The magnitude of variation would depend on the degree of divergence and on component proportions. With genetic data for the Lyons Ferry and upper Columbia hatchery components, we can predict how spawners from these sources might effect allele frequencies of naturally produced progeny. Lyons Ferry Hatchery broodstock originated from the Snake River Wild Eggbank Program, and they were distinguishable from upper Columbia hatchery fall-run populations according to previous genetic analyses (Bugert et al. 1995). In 1990, 50% of adults escaping above Lower Granite Dam were estimated as Lyons Ferry Hatchery-origin. Four-year old progeny of these fish could have comprised much of the natural-origin spawner component (67%) in 1994 (Table 6). Two of our Snake River juvenile samples, 1990 and 1994 BYs, showed no significant differences in allele frequencies, and also had relatively small genetic distances from several Lyons Ferry Hatchery samples. We think it is reasonable to conclude that gene flow between this hatchery population and wild spawners has been substantial.

It is also plausible to expect that gene flow from non-Snake River hatcheries has occurred. The percentage of upper Columbia hatchery-origin fish in Snake River adult escapements has fluctuated widely (Bugert et al. 1991, 1995; LaVoy and Mendel 1996). We examined how their participation as spawners could have effected annual variability, especially the genetic heterogeneity of 1992 BY and 1993 BY juvenile samples. In 1992 and 1993, tagged Lyons Ferry Hatchery-origin adults were excluded from natural spawning, which minimized contributions from this gene pool, especially in 1993. Natural-origin chinook salmon comprised approximately 80% of the 1992 and 1993 spawner escapements (Table 6). We remind the reader that this is the Snake River spawner component we did not have genetic baseline data for, and were trying to estimate from our juvenile samples. Both 1992 and 1993 BY juveniles were divergent from all hatchery components, and generally showed no directional shifts in allele frequencies towards those of upper Columbia hatchery-origin chinook salmon. We believe these data show that genetic characteristics of remaining natural spawners were not heavily

affected by strays from upper Columbia hatcheries, and retained a level of diversity distinctive from hatchery gene pools.

We thought we would gain a more useful genetic profile of the natural Snake River fall race population by combining juvenile data from three consecutive brood years (1992 to 1994). By doing this, we had assumed that all temporal variability among juvenile samples was due to genetic drift and sampling error, not changes in genetic composition of annual spawners. This is probably not entirely accurate, but it did give us a characterization of the fish that actually reproduced successfully in important, available spawning habitat. The combined sample for the natural population retained its genetic distinctiveness relative to hatchery populations. Analyses did show that populations with closest genetic relationships were the Lyons Ferry Hatchery broodstocks. We interpret this association to indicate both that the Snake River fall race chinook salmon gene pool has been conserved at this Snake River hatchery, and that these hatchery-origin adults have contributed to natural production.

Management Implications

We believe the set of allele frequencies for the combined juveniles sample serves as a genetic baseline, characterizing the Snake River fall race during this time period. It can be used for monitoring and evaluating changes in the natural spawning population. We were encouraged to find the levels of genetic variability that we did, despite the often critically low annual population sizes of the past. We did not find evidence that straying of adults from upper Columbia hatcheries had irrevocably homogenized the genetic characteristics of Snake River fall race chinook salmon. A low level of detectable genetic effects should not, however, diminish concerns about potential negative impacts from these strays. Real and theoretical genetic effects of hatchery-origin salmonids on wild, or natural populations are reviewed and discussed in Hindar et al. (1991) and Campton (1995). In the Snake River, the largest problem has been a high incidence of Umatilla Hatchery-origin adults (upper Columbia fall-run stock), which is attributed to warm, low flows that discouraged adults from returning to the Umatilla River (Bugert et al. 1995). Management actions that have served, or could be added, to curtail this straying problem are still necessary to protect the genetic integrity of the Snake River fall race.

We think the genetic characterization from our juvenile samples indicates that the Snake River fall race natural spawning population represents an important genetic resource. Traits adapted to local conditions, which we did not assess, may also

characterize this resource. These were also general conclusions from a biological review following the ESA petition (Waples et al. 1991). Although the Lyons Ferry Hatchery population may be most closely related to the natural Snake River population, we recommend that use of hatchery fish to supplement natural production include plans to monitor effects. It will be very important to understand, for example, how well hatchery juveniles released into the river survive to return as spawners, and what their interactions with wild fish are as juveniles and adults. There is little knowledge of how supplementation might increase survival rates of naturally produced progeny. One of the keys to sustaining the genetic diversity of Snake River fall race chinook salmon is maintaining an abundance of natural, or wild spawners. Achieving this goes beyond hatchery practices, and includes resolving large problems of habitat alteration and degradation, as well as harvest issues. As progress is made in these areas, we believe the existing natural population has the capacity for recovery.

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CHAPTER SEVEN

Seaward Migration by Subyearling Chinook Salmon in the Snake River

by

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Introduction

The construction of four hydroelectric dams on the lower Snake River changed the free-flowing River into a series of reservoirs. High mortality and delays in seaward migration of juvenile chinook salmon *Oncorhynchus tshawytscha* are two consequences of impounding free-flowing rivers (Park 1969; Raymond 1979, 1988). These consequences were recognized in the late 1970's and Congress subsequently passed the Pacific Northwest Electric Power Planning and Conservation Act in 1980 (Public Law 96-501). One intention of this act was to foster a balance between hydroelectric power generation and flow needs of migrating anadromous salmonids.

The Columbia Basin Fish and Wildlife Program (NPPC 1987) was written in response to the Pacific Northwest Electric Power Planning and Conservation Act. This program led to the storage of reservoir water throughout the Columbia River basin for the purpose of augmenting flows during the spring when most anadromous salmonids migrate seaward. This water allocation was called the water budget.

From 1983 to 1992, the water budget did not include a flow allocation for summer-migrating subyearling fall chinook salmon. The water that was routinely released for power generation was expected to meet flow needs of juvenile fall chinook salmon during the summer months (Berggren and Filardo 1993). However, low natural runoff occurred during summer at the same time reservoirs were being refilled to replace water used for spring flow augmentation. This resulted in summer flows that were lower during the first several years of the water budget than occurred prior to its existence (Berggren and Filardo 1993).

Snake River fall chinook salmon continued to decline in abundance throughout the 1980's and were listed as threatened under the Endangered Species Act (ESA; USFWS 1988) in 1992 (NMFS 1992). After 1992, emphasis shifted from spring flow augmentation to summer flow augmentation (Giorgi et al. 1997*a*). In the proposed recovery plan the National Marine Fisheries Service recommended an average flow of 1,416 to 1,558 m^3/sec at Lower Granite Dam (Figure 1) from 21 June to 31 August (NMFS 1995).

In the Biological Opinion on the operation of the Columbia River power system and juvenile transportation program, the National Marine Fisheries Service called for the formation of a technical management team (NMFS 1994). The technical management team makes recommendations on dam and reservoir operations that

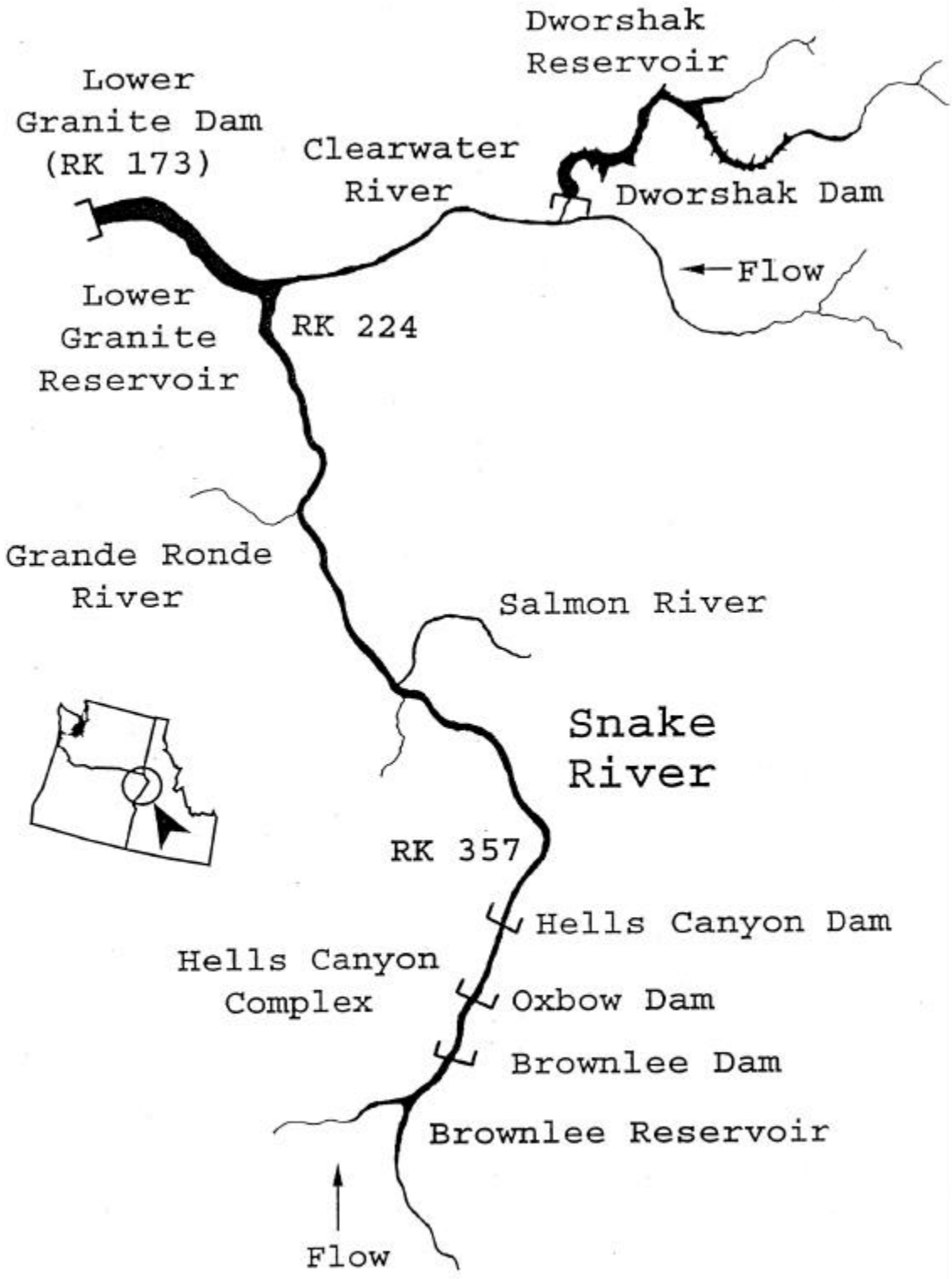

Figure 1.—The study area from 1992 to 1997 including the reach of the Snake River seined between RK 224 and RK 357, and major tributaries, and dams.

will optimize passage conditions for anadromous salmonids. Prior to the spring migration season the team develops a water management plan. This plan is then refined in-season as pertinent data becomes available.

We collected subyearling chinook salmon in the Snake River from 1992 to 1997 to provide fishery managers with data to help them assess and refine the water management plan. This paper provides a general description of seaward migration by subyearling chinook salmon in the Snake River, and presents an approach to forecast median date of passage at Lower Granite Dam.

Study Area

Chinook salmon spawn in the tributaries of the Snake River and in the mainstem. Snake River fall chinook salmon spawn primarily in the mainstem Snake River between Hells Canyon Dam and the upper end of Lower Granite Reservoir, and in the lower Grande Ronde and Clearwater rivers (Figure 1). Fall chinook salmon have an ocean-type life history (Healey 1991) and the juveniles migrate seaward primarily as subyearlings. Spring chinook salmon spawn in the headwaters of Snake River tributaries such as the Imnaha, Salmon, and Grande Ronde rivers (Figure 1). Some subyearling spring chinook salmon deviate from the typical stream-type (Healey 1991) life history and rear in the mainstem Snake River then migrate seaward as subyearlings during the summer with subyearling fall chinook salmon.

Subyearling chinook salmon, which were predominantly fall-race fish (W. P. Connor, U. S. Fish and Wildlife Service, unpublished data), were collected in the Snake River between RK 224 and 357 (Figure 1) from 1992 to 1997. Seaward migrating subyearling chinook passed through Lower Granite Reservoir (Figure 1) and by Lower Granite Dam. Physical features of Lower Granite Reservoir are described by Chipps et al. (1997) and Connor et. al (1998). Flows in Lower Granite Reservoir during the summer flow augmentation period averaged 539 m^3/s, 1,304 m^3/s, 744 m^3/s, 1,580 m^3/s, 1,623 m^3/s, and 2,007 m^3/s from 1992 to 1997, respectively. Lower Granite Dam is located at River km (RK) 173 on the Snake River (Figure 1). Fish bypass facilities and monitoring equipment used to detect marked fish at Lower Granite Dam are described by Gessel et al. (1991) and Prentice et al. (1990*a*).

Methods

Subyearling chinook salmon collection, handling, and tagging are described by Connor et al. (1998). Subyearling chinook salmon were collected with a beach seine and then were tagged with Passive Integrated Transponders (PIT tags)(Prentice et al. 1990*b*). The PIT-tagged fish were released where they were collected to resume rearing, dispersal, and eventual seaward migration. A subsample of PIT-tagged fish was detected in the fish bypass at Lower Granite Dam as described by Prentice et al. (1990*a*).

The subyearling chinook salmon outmigration was monitored at Lower Granite Dam by the Fish Passage Center (FPC) of the Columbia River Basin Fish and Wildlife Fish Authority from 1992 to 1997. Fish were collected between the hours of 0700 hours on day one to 0700 on day two. All fish collected by 0700 hours on day two were counted as passing Lower Granite Dam on day two. The FPC expanded the daily fish collection counts at Lower Granite dam, and then adjusted the counts for the proportion of water going through the powerhouse versus the spillway. These adjusted counts provide an index for the time of passage by Lower Granite Dam for the run at large. We compared the fish passage indices (FPC, unpublished data) to the PIT-tag detection data to determine how well PIT-tagged subyearling chinook salmon represented the run at large. We limited the comparison to the 21 June to 31 August summer flow augmentation period since this period is most relevant to flow management. The detection dates for PIT-tagged fish were standardized to the 0700 to 0700 hours collection period used by the FPC.

Time at large between PIT tagging and detection at Lower Granite Dam was calculated for each detected PIT-tagged subyearling chinook salmon. The resulting number is referred to hereafter as travel time, and is abbreviated when it is referred to in statistical models as TRVTIME. Predictor variables for travel time analysis included fork length at tagging, Julian date of release, and release location in RKs. The abbreviations FL, DATE, and RELRK are used when referring to regression coefficients. These variables were selected because they can be measured in the field at the time each fish was PIT tagged. We pooled data across years to increase the range of observations for both travel time and the predictor variables. Uniform random numbers were generated for each observation. We used 70% of the observations to build the model and reserved the remaining 30% for validation.

Least-squares multiple regression (SYSTAT 1994) was used to develop a travel time model from the estimation data. We started with the model: TRVTIME = β_0 + β_1(FL)+ β_2(DATE) + β_3(RELRK) + e. We plotted each predictor variable versus TRVTIME using year as the plotting symbol to see if pooling data over years was justified. The relationships did not change in a systematic way over years. We considered the coefficient of determination (R^2), t-tests for individual coefficients, and plots of residuals (Myers 1990) for candidate models in order to select the final prediction model for validation.

We validated the TRVTIME model derived from the estimation data set by predicting travel time for each fish in the validation data set. We calculated the mean square error (MSE) of the residuals (residual = actual - predicted travel time) using the validation data set and compared it with the MSE about the regression line for the estimation data set (SAS 1989). We also compared residual plots from the estimated model for both estimation and validation data sets. Finally, we estimated the regression coefficients for the TRVTIME model using the entire data set. Partial regression plots (SAS 1989) were used to interpret the regression coefficients of the final set of predictor variables.

The Kolmogorov-Smirnov two sample test (KS test; SAS 1989) was used to compare the release date and release fork length distributions for all fish beach seined and PIT tagged and for the subset of fish subsequently detected at Lower Granite Dam. These tests were used in the manner described by Giorgi et al. (1997*b*). The release dates and fork lengths compared were those of all fish released versus all fish that were released and detected at Lower Granite Dam. This test was intended to show if different sizes of fish, or fish released before or after certain dates, were more likely to survive the migration and be detected at Lower Granite Dam.

We tested three approaches for forecasting the median date of passage at Lower Granite Dam for the run at large. All three used the final TRVTIME model to make travel time predictions to Lower Granite Dam for each PIT-tagged fish. The predicted travel time was added to the date of release for each fish to forecast its detection date at Lower Granite Dam. The first approach was to forecast a passage date for every fish tagged within a year and then calculate a passage distribution. The passage distributions were only calculated between the dates of 21 June and 31 August to coincide with the summer flow augmentation period. The forecasted passage distributions were standardized within each year to account for differences in sample sizes among

years. After they were standardized, the forecasted passage distributions were pooled across years, and cumulative daily passage was calculated. The second approach was similar to the first, except we used results of the KS tests to select fish of a minimum fork length when forecasting passage dates. The third approach involved selecting a minimum fork length, and then a maximum release date, prior to forecasting passage date for each fish. The maximum release date was selected using KS test results.

The fish passage indices were also standardized within each year, and pooled, and then cumulative daily passage was calculated. The observed (i.e., from pooled fish passage indices) and forecasted cumulative daily passage distributions were plotted. By pooling the data across years we were able to select the approach that gave the best forecast of passage timing for the average year. We selected the final approach by comparing the observed and forecasted median dates of passage from the two cumulative daily passage distributions.

After selecting a forecasting approach, we applied it to each year separately. Observed (i.e., from each annual fish passage index) and forecasted passage distributions were calculated. Cumulative daily passage was calculated from the passage distributions, and then we compared the observed and forecasted medians within a year. This provided a general assessment of forecasting accuracy from year to year.

Results

Approximately 17% of the PIT-tagged subyearling chinook salmon that were released in the Snake River were detected at Lower Granite Dam from 1992 to 1997 (Table 1). Mean travel time during the 6 years averaged 45.5 d (SE = 0.70; range = 2.0 to 156 d). The mean migration rate was 3.3 km/d (SE = 0.12; range = 0.4 to 70.5 km/d). Fish, which were detected, were tagged and released from 6 April to 14 July at fork lengths ranging from 60 to 122 mm (Table 1).

Migratory Behavior and Timing

After they were PIT tagged, subyearling chinook salmon continued to rear and disperse downstream slowly as shown by the above travel times and by recapture data. We recaptured 6.1% (n = 64) of all fish tagged in 1992, 16.3% (n = 202) in 1993, 14.5% (n = 339) in 1994, 15.1% (n = 224) in 1995, 11.7% (n = 66) in

TABLE 1.—Numbers of subyearling chinook salmon that were PIT tagged in the Snake River (SNK) and later detected at Lower Granite Dam (LGR), and the range of predictor variables including Julian date of release (DATE), fork length at release (FL) and the River km where the fish were released, 1992 to 1997.

Year	PIT-tagged subyearlings		Range of predictor variables for detected fish		
	Numbers released in the SNK	Numbers detected at LGR	DATE (Julian)	FL (mm)	RK
1992	1,056	44	113-156	60-103	229-282
1993	1,237	234	117-195	60-122	224-266
1994	2,342	194	96-173	60-104	225-282
1995	1,481	479	116-187	60-116	226-361
1996	566	178	107-192	60-113	227-357
1997	651	126	119-191	60-108	225-357
All	7,333	1,255	96-195	60-122	224-361

1996, and 15.4% (n = 100) in 1997. The median number of days fish were at large between tagging and recapture was 5.5, 7.0, 8.0, 8.0, 7.0, and 7.0 d from 1992 to 1997, respectively (Figure 2). Some fish were recaptured numerous times over long time spans (e.g., five times over 56 d). In all years, recaptured fish did not travel downstream of initial capture sites, but some fish were captured upstream (n = 66; mean distance = 1.7±0.1 km) or downstream (n = 94; mean distance = 14.5±2.5 km; Figure 2).

The majority of PIT-tagged subyearling chinook salmon, and fish from the run at large, passed Lower Granite Dam during the 21 June to 31 August summer flow augmentation period. The percentages of PIT-tagged fish that past Lower Granite Dam during the summer flow augmentation period were 43% in 1992, 92% in 1993, 92% in 1994, 81% in 1995, 70% in 1996, and 83% in 1997. The percentages of the run at large that past Lower Granite Dam between 21 June and 31 August were 69%, 91%, 93%, 80%, 82%, and 68% from 1992 to 1997, respectively.

During the summer flow augmentation period, the dates of passage at Lower Granite Dam for PIT-tagged subyearling chinook salmon were generally similar to the those of the run at large (Figure 3). The onset, end, and peak dates of passage often occurred on similar days or on the same day (e.g., 1992, 1994, 1996). However, passage dates of the two groups of fish sometimes peaked on different days (e.g., 1993 and 1995) and the peak of one group was not always proportionate to that of the other (e.g., second peak in 1996). The passage distributions for tagged fish also included more dates with zero passage than did the passage distributions for the run at large (e.g., 1997).

Travel Time Modeling

The plot of residuals for the model, $TRVTIME = \beta_0 - \beta_1(FL) + \beta_2(DATE) + \beta_3(RELRK) + e$, which was made using the estimation data (n = 884), showed a classic megaphone shape indicating that the error variance increases with increasing values of mean TRVTIME. A $\log_e$ transformation of travel time solved this problem. The RELRK term was nonsignificant and was deleted from the model. The resulting candidate model, $\log_e(TRVTIME) = \beta_0 - \beta_1(FL) + \beta_2(DATE) + e$, was validated based on a comparison of the MSE of the residuals from the validation data (n = 371) set (MSE = 0.336) with the MSE of the estimation data set (MSE = 0.296; Myers 1990). The residual plots for both estimation and validation data sets had the same residual patterns.

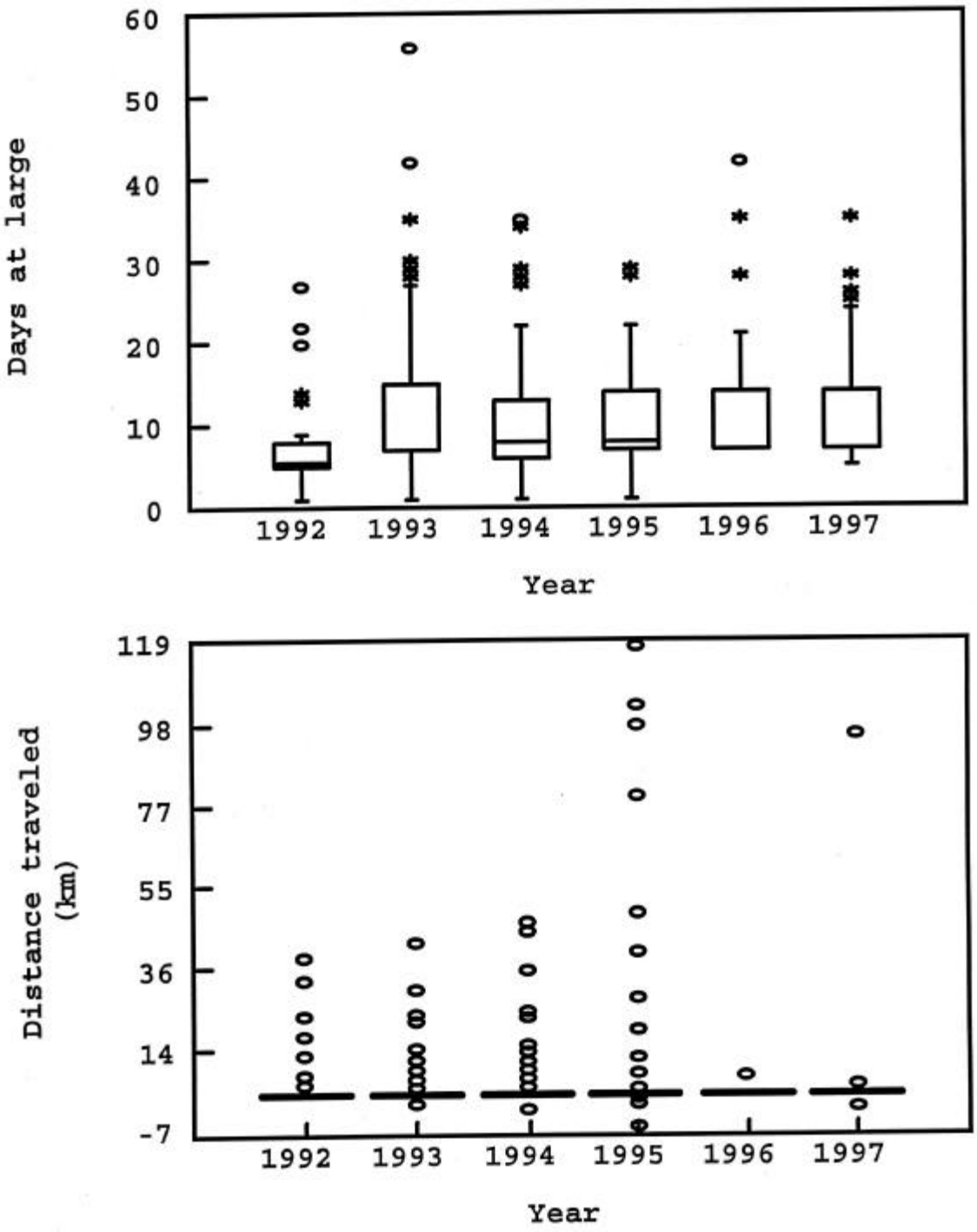

Figure 2.-Box plots showing the number of days PIT-tagged fish were at large in the Snake River between tagging and recapture, and the distance traveled (kms) by recaptured fish while at large, 1992 to 1997.

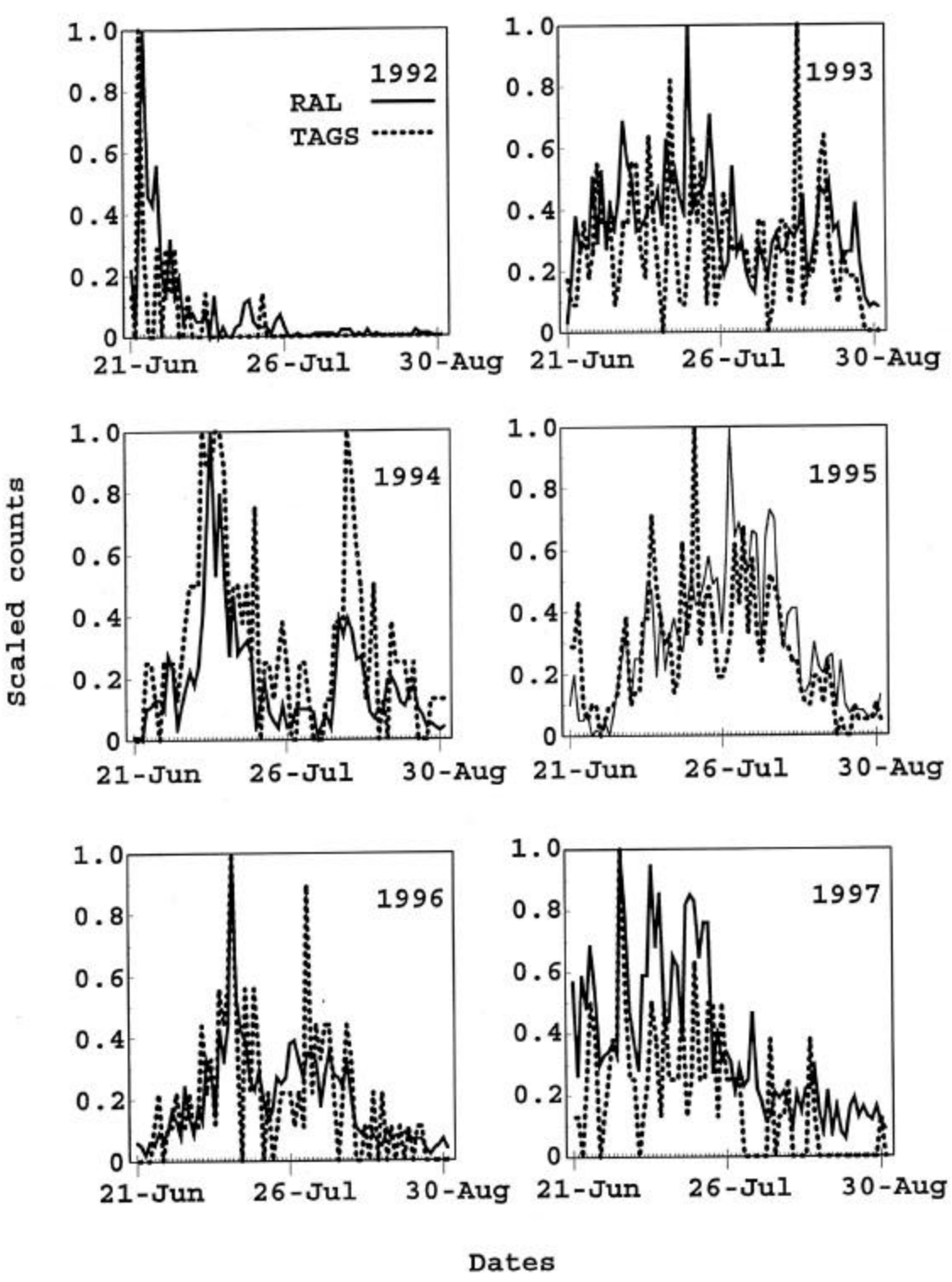

Figure 3.-Passage at Lower Granite Dam for the subyearling chinook salmon run at large (RAL)(Fish Passage Center, unpublished data) and for fish PIT tagged in the Snake River (TAGS), 1992 to 1997.

The final regression model based on the entire data set (n = 1,255) resulted in the model, log$e$ (TRVTIME) = 4.316054 - 0.034742(FL) + 0.013196(DATE)(Table 2). In this model, release date and fork length were significant and explained 39% of the variability in log$e$-transformed travel time (MSE = 0.307; P < 0.0001; R^2 = 0.39). For fixed release date, the relationship between travel time and fork length is negative (Figure 4). For every mm increase in fork length there is a 0.035 decrease in log$e$-transformed travel time. For fixed fork length, there is a positive relation between travel time and date (Figure 5). For every 1 d increase in release date, there is 0.132 increase in log$e$-transformed travel time (Figure 4).

Passage Forecasts

The cumulative distribution for fork length of all tagged fish differed significantly from the cumulative distribution for those detected at Lower Granite Dam at the P = 0.05 level of significance (Figure 5). Fish that were tagged at fork lengths $\leq$ 75 mm were less likely to survive migration to Lower Granite Dam than larger fish. The release date distribution of the subset of PIT-tagged subyearling chinook salmon that were detected at Lower Granite Dam did not differ significantly at the P = 0.05 level of significance from those released in the Snake River. There was a statistical difference at the P = 0.10 level of significance (Figure 5). Fish released on or after Julian date 172 (i.e., 21 June) were less likely to survive to Lower Granite Dam than fish released earlier.

The most accurate passage forecast at Lower Granite Dam for the run at large was made using fish that were > 75-mm fork length at tagging (n = 2,856)(Figure 6). The median date forecasted using this approach was 18 July, compared to the observed median for the run at large of 19 July. The forecast made using every fish that was PIT tagged (n = 7,333) resulted in a cumulative daily passage distribution that was consistently to the right (i.e., later) than that observed for the run at large (Figure 6). The forecasted median for this same approach was 23 July. Removing fish > 75-mm long, and which were released before Julian date 172 (n = 2,120), resulted in a forecasted median date of passage of 10 July and a distribution located to the left (i.e., earlier) of that observed for the run at large.

Passage forecasts made using fish > 75 mm at tagging were most accurate for the relatively lower flow years of 1992, 1993, 1994. For these years, the forecasted median date of passage was

TABLE 2.—Least-squares multiple regression results for log*e*-transformed travel time of subyearling chinook salmon that were PIT tagged in the Snake River and detected at Lower Granite Dam from 1992 to 1997. The predictor variables are Julian date of release (DATE), fork length at release (FL) and release location (RELKM).

Predictor variable	Regression coefficients	*T*-value	*P*-value	R^2
	Estimation models (*n* = 884)			
Constant	3.944186	15.653	0.000	0.408
DATE	0.014045	10.740	0.000	
FL	-0.034186	-24.052	0.000	
RELKM	0.000724	1.612	0.107	
Constant	4.181673	20.435	0.000	0.406
DATE	0.013774	10.611	0.000	
FL	-0.034246	-24.081	0.000	
	Final model (*N* = 1,255)			
Constant	4.316055	24.357	0.000	0.391
DATE	0.013196	11.537	0.000	
FL	-0.034742	-28.097	0.000	

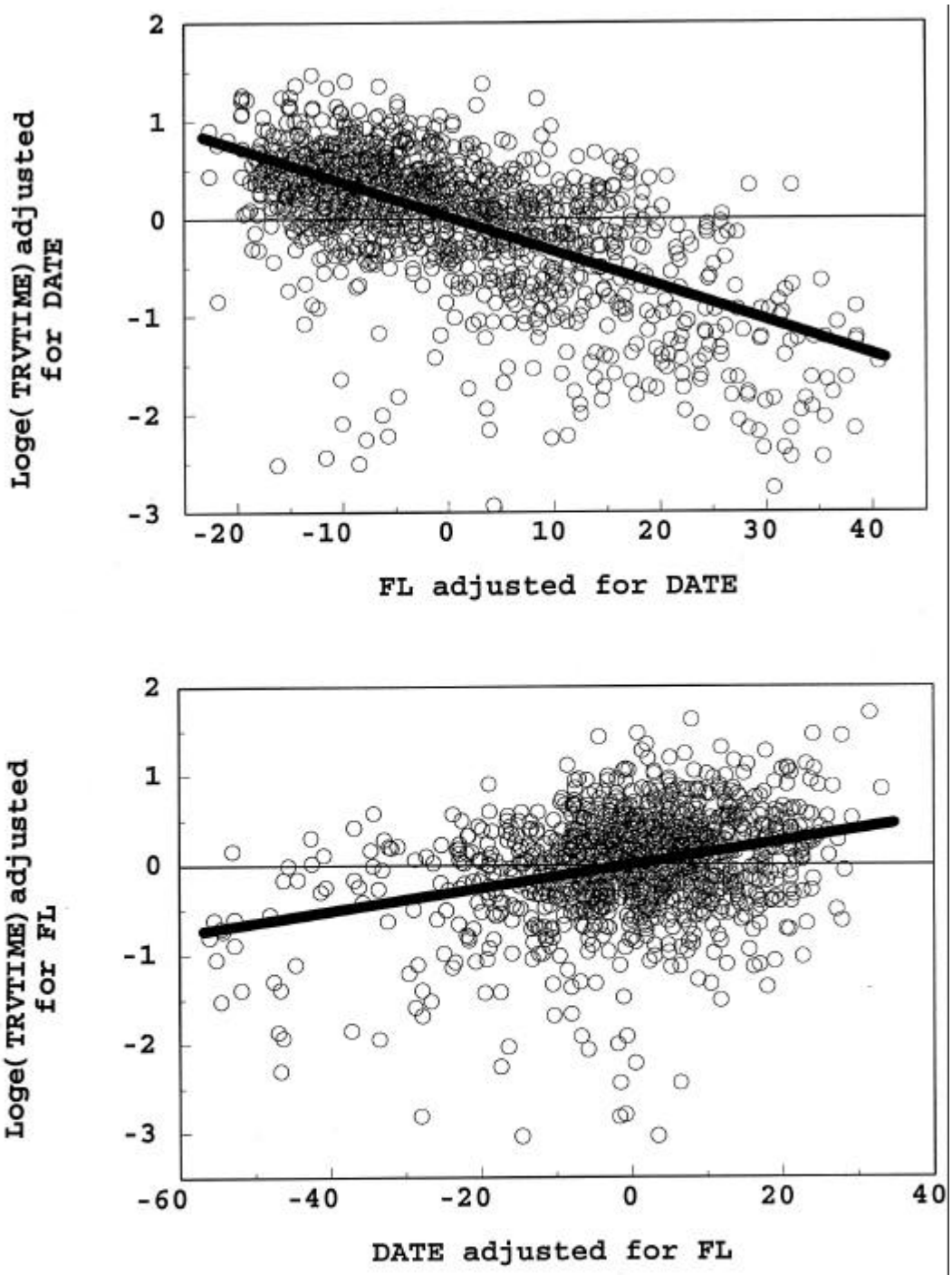

Figure 4.-Partial regression plots for the relation between travel time (TRVTIME) to Lower Granite Dam and fork length (FL) of subyearling chinook salmon after adjusting for the effects of release date (DATE)(Top), and for the relation between travel time and release date after adjusting for fork length effects (bottom).

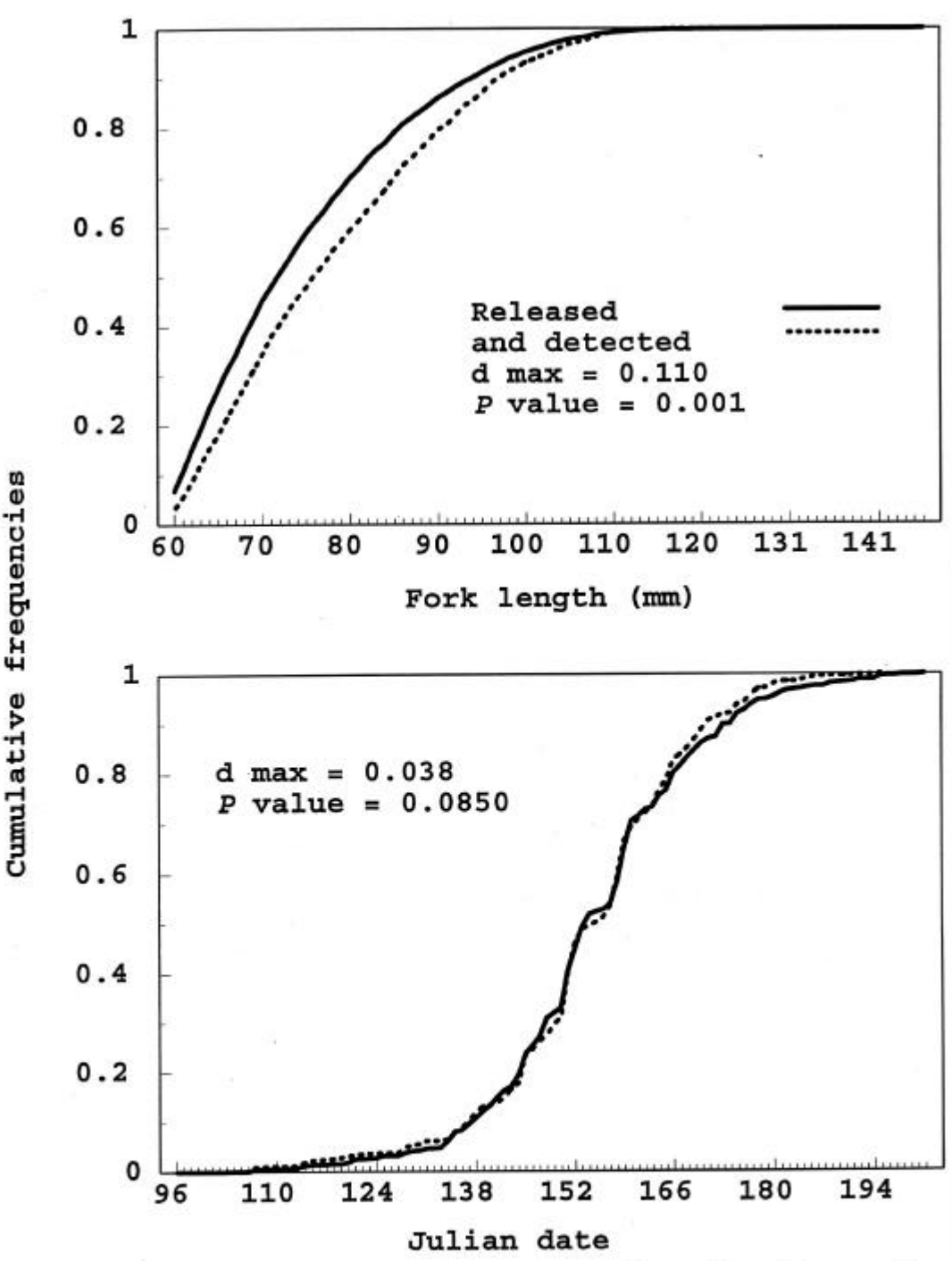

Figure 5.-Cumulative frequency distributions of fork length (mm)(Top) and release dates (Bottom) for subyearling chinook salmon that were PIT tagged and released in the Snake River, and which were PIT tagged released and detected at Lower Granite Dam, from 1992 to 1997. Location of maximum difference (d max) and P values for Kolomorov-Smirnov two sample tests are also given.

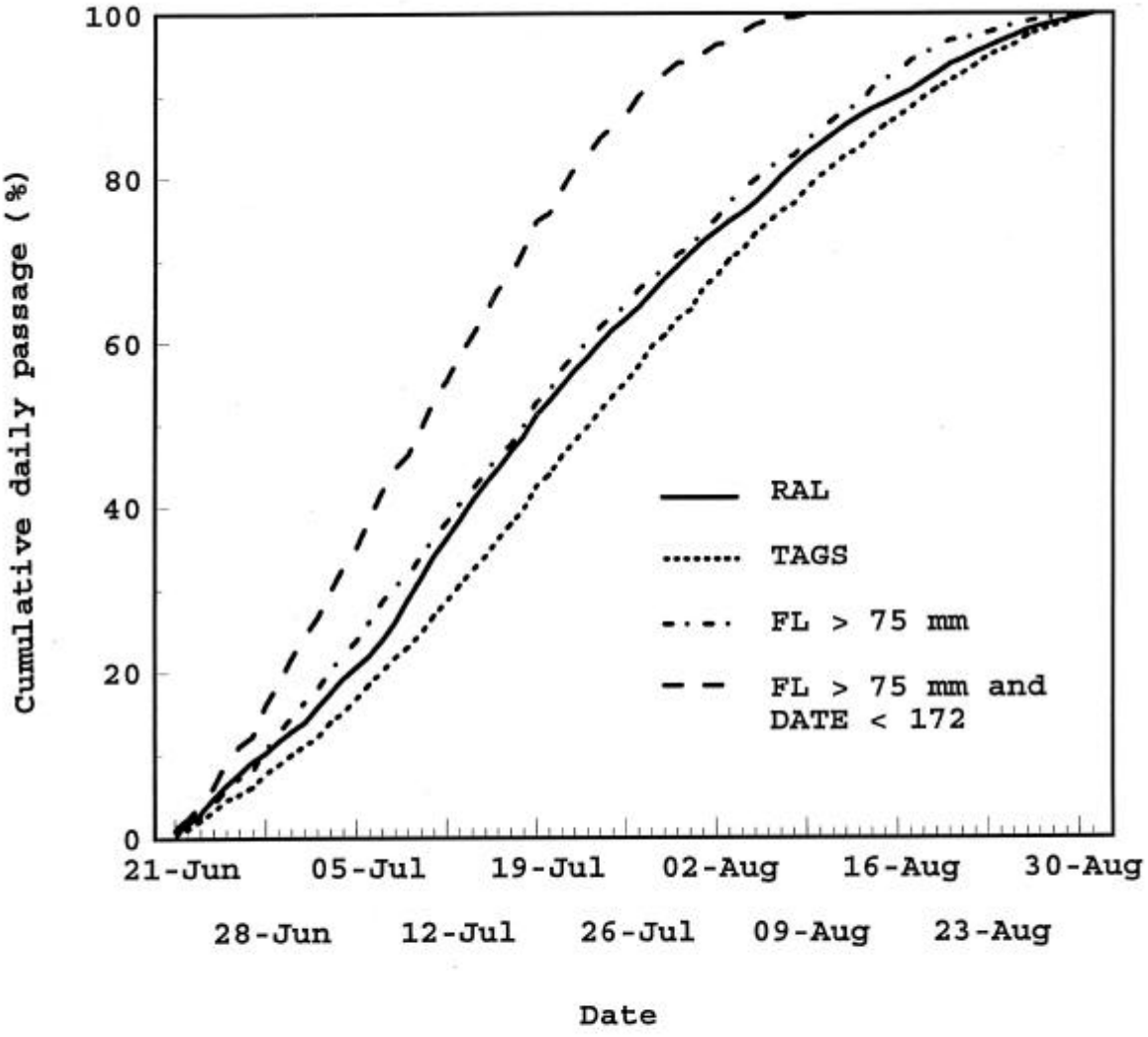

Figure 6.-Observed cumulative daily passage (Fish Passage Center, unpublished data) for the subyearling chinook salmon run at large (RAL) at Lower Granite Dam, and passage forecasts made for PIT-tagged fish using every PIT-tagged fish (TAG), PIT-tagged fish > 75 mm (FL > 75), and fish that were > 75 mm and tagged prior to Julian date 172 (FL > 75 and Date < 172), in the Snake River from 1992 to 1997.

within 8 d of that observed for the run at large (Table 3). Passage forecasts made for the relatively higher flow years of 1995, 1996, and 1997 were less accurate than those of lower flow years (Table 3). For example, in 1995 the observed and forecasted median dates of passage were 18 d apart.

Discussion

Migratory Behavior

Seaward migration by subyearling chinook salmon in the Snake River is a discontinuous process. During early rearing fish slowly dispersed downstream often lingering at specific nearshore sites. In the field we observed that decreasing flows accompanied by increasing water temperatures prompted subyearling chinook salmon to leave nearshore rearing areas. The number of fish we captured decreased markedly after water temperatures reached about 17°C. Similar behavior has been observed for subyearling chinook salmon in the Columbia River (Becker 1970, 1973; Rondorf 1990).

Subyearling chinook salmon become pelagic oriented after they leave the free-flowing Snake River and enter Lower Granite Reservoir. In 1992, Curet (1993) beach seined sampling stations in Lower Granite Reservoir over the same dates we sampled the Snake River. Patterns of subyearling chinook salmon catch in the River and in the reservoir were similar. Few fish were captured in nearshore areas after May. If the fish we captured in the River maintained a shoreline orientation and continued to disperse slowly downstream, catch would have continued in the reservoir into June. Additional data exists to substantiate pelagic migration behavior. From 1995 to 1997, subyearling chinook salmon were radio tagged at Lower Granite Dam and released downstream into the next reservoir. Radio-tagged fish followed the thalweg of the inundated river channel. This route led fish through the deepest and fastest available water (D.A. Venditti, personal communication).

When migrating in-reservoir, subyearling chinook salmon do not move consistently downstream. Approximately 22% of the radio-tagged fish released by Venditti moved back upstream once they reached the forebay (Venditti et al. In review). Approximately 4% of these moved 14 km. In Columbia River reservoirs, subyearling chinook salmon have been found to move upstream, or remain stationary, for long time spans (Sims and Miller 1982; Miller and Sims 1983). Breaks in downstream

TABLE 3.—Observed median passage dates at Lower Granite Dam for the subyearling chinook salmon run at large (Fish Passage Center, unpublished data), and the median dates that were forecasted using PIT-tag data collected in the Snake River, 1992 to 1997.

Year	Observed	Forecasted	Difference (days + or -)
1992	26-June	02-July	-6
1993	20-July	28-July	-8
1994	14-July	11-July	+3
1995	28-July	10-July	-18
1996	21-July	31-July	-10
1997	14-July	26-July	-12

progress, whether in reservoirs or free-flowing rivers, confound the development of regression models for predicting travel time. They offer a plausible explanation as to why our TRVTIME model only explained 39% of the observed variation in travel time to Lower Granite Dam.

Travel Time Modeling

This paper provides evidence that fork length and release date were significantly related to time travel time of subyearling chinook salmon. The effect of fork length was more significant than the effect of release date. These results parallel those reported for subyearling chinook salmon passing downstream in the Columbia River between Rock Island and McNary dams (Giorgi et al. 1997*b*). Giorgi et al. reported that the multivariate model log*e* (Migration rate) = -2.510 + 2.569(FL) - 1.286(DATE) significantly (P =0.000) explained 58.5% of the observed variation in migration rate (travel time/kms traveled). These same authors also found migration rate was influenced more by fork length (T-value = -28.097) than by release date (T-value = -9.087).

Subyearling chinook salmon that were PIT-tagged in the Columbia River migrated downstream markedly faster than fish tagged in the Snake River despite having to pass two additional dams. The mean rate of migration between Rock Island and McNary dams was 15.6 km/d (range = 0.8 to 59 km/d) for Columbia River fish (Giorgi et al. 1997*b*) compared a rate of 3.3 km/d (range = 0.4 to 70.5 km/d for Snake River fish. Subyearling chinook salmon in the Columbia River traveled 260 kms between release and detection compared to the average of 91 kms covered by Snake River fish. Zaugg et al. (1985) concluded that hatchery fall chinook salmon required a period of in-river migration to achieve maximum levels of smoltification and maximum migration rates. Fish in the Columbia River tagged by Giorgi et al. (1997*b*) may have migrated faster than Snake River fish because they migrated further. Additionally, Columbia River fish (mean = 100 mm; range = 62 to 167 mm) were larger than Snake River fish (mean 79 mm range = 60 to 122 mm) when they were tagged. In view of regression results in this paper, we conclude that fork length at tagging accounted for some of the difference in migration rates between fish of the two rivers.

Changes in habitat selection and levels of smoltification that occur as fish grow may partially explain the relation between subyearling chinook salmon fork length and travel time. Juvenile anadromous fish have been shown to move into faster

deeper water as they grow (Chapman and Bjornn 1969; Everest and Chapman 1972). Subyearling fall chinook salmon that were beach seined near shore in the Columbia River estuary were smaller and had lower levels of ATPase activity than fish captured in mid-River using purse seines (Zaugg et al. 1985). These same researchers hypothesized that horizontal distribution of migrating fall chinook salmon was dependent on fish size and the degree of smolt development. We propose that larger subyearling chinook salmon in the Snake River migrated faster than smaller fish because they occupied faster water and were more smolted.

Subyearling chinook salmon that were released later tended to have longer travel times than fish that were released earlier. These findings are similar to those reported for three other studies. A step-wise multiple regression was done for travel times of freeze-branded subyearling chinook salmon migrating between McNary and John Day dams. The resulting model was TRVTIME = -53.02 + 0.37(DATE)(R^2 = 0.47)(Giorgi et al. 1994). Using the same 1981-1983 data, and data from 1986 to 1988, Berggren and Filardo (1993) reported the multivariate model TRVTIME = -42.364 + 3,016.061($FLOW^{-1}$) + 0.133(DFLOW) + 0.165(DATE)(R^2 = 0.65). Where DFLOW was the absolute change in daily average flow over travel time days. Berggren and Filardo fixed the other variables and saw that DATE increased travel time as the summer season progressed. They explained that DATE accounted for a combined effect of flow and smoltification. The migration rate model of Giorgi et al. (1997*b*) we described earlier in this discussion, gave a regression coefficient for DATE of -1.286 also indicating a negative relation between release date and migration rate.

Release date is used in regression models as a surrogate for smoltification levels and flow. There was low correlation (n = 436; r = -0.186) between date of detection for subyearling chinook salmon and ATPase levels from 1993 to 1996 (K. F. Tiffan, personal communication) indicating that release date was not a surrogate for smoltification level in our study. As mentioned earlier, the distances migrated by fish we tagged were less than in Columbia River studies. Although larger Snake River fish were more smolted than smaller fish, it is likely that fish used in the Columbia River studies were more smolted than any fish we tagged.

Three studies provide evidence of flow effects on travel time that indicate that release date was a surrogate for flow in our TRVTIME model. Radio-tagged subyearling chinook migrated significantly faster through upstream reaches of Little Goose Reservoir than through downstream reaches (Venditti et al. 1997). These authors concluded that migration rate was indirectly

related to water velocity in the reservoir since water velocity was higher in the upper than in the lower reach. Berggren and Filardo (1993) showed that flow significantly increased travel times of subyearling chinook salmon through a Columbia River reservoir (refer to earlier discussion). The Multivariate model Migration rate = -16.750 + 2.496(FL) + 0.963(FLOW) accounted for 63% of the observed variation in migration rate for subyearling chinook salmon moving downstream between Rock Island and McNary dams (Giorgi et al. 1997*b*). When discussing this model Giorgi et al. discounted the significant effect of flow on the basis of poor predictive capability of the model. We submit that the low flows experienced by late migrating Snake River fish acted together with other independent variables to increase travel time.

Passage Forecasts

After the PIT-tagged subyearling chinook salmon left nearshore areas of the Snake River they passed Lower Granite Dam over a period of time similar to the run at large. This similarity indicated that beach seining provided catch data that was generally representative of the run at large. The differences in the passage distributions between PIT-tagged subyearlings and the run at large were likely the result of three factors. First, under the low levels of adult escapement between 1992 and 1997 sample sizes were limited by fish abundance. Secondly, beach seines were not equally efficient at capturing subyearling chinook salmon over the range of flows, water turbidities, and substrate conditions that we sampled. Even under comparatively high juvenile rearing densities and the simple habitat conditions in John Day Reservoir, beach seine capture efficiency for subyearling chinook salmon ranged from 0.41 to 0.96 (Parsely et al. 1989). Therefore, we may not have sampled fish in exact proportion to their availability, or over the exact time periods when the run at large was rearing. Thirdly, we did not sample every potential rearing site in the Snake River, and no fish were tagged the Grande Ronde and Clearwater rivers.

Differences between the forecasted and observed median dates of passage at Lower Granite Dam for subyearling chinook salmon within a year were also related to small sample sizes of detected fish and sampling biases. Among year differences in forecast accuracy (Table 3), on the other hand, may have been related to to subyearling chinook salmon survival. When forecasting run timing at Lower Granite Dam, we attempted to account for survival effects by selecting fish > 75 mm fork length. This minimum fork length criterion resulted in accurate run time forecasts for low flow years. Run forecasts for high flow years were less accurate

than for low flow years because the observed runs were more protracted than the forecasted runs. We hypothesize that differential survival between smaller and larger fish is less pronounced in high flow than in low flow years, and that this results in more protracted passage distributions in high flow years.

Implications for Management

Much written attention has been focused on the relation between migration rate of subyearling chinook salmon and flow (e.g., Miller and Sims 1984; Giorgi et al. 1990; Berggren and Filardo 1993; Giorgi et al. 1994; Giorgi et. al 1997*b*). This attention was well warranted. A main focus of the water budget was to expedite fish passage through reservoirs. Relating fish migration rate to flow, which is a surrogate for water particle travel time, was a logical first step.

New information suggests that the relation between water particle travel time and fish migration rate may not be the primary mechanism affecting subyearling chinook salmon survival. Detection rate of subyearling chinook salmon released in the Snake River and detected at Lower Granite Dam was found to be directly related to summer flow (n = 4; r^2 = 0.993; P = 0.003) and indirectly related maximum summer water temperature (n = 4; r^2 = 0.984; P = 0.008)(Connor et al. in press). Acknowledging small sample size (n = 4 years), and high correlation between flow and water temperature, these same authors argued that the summer flow augmentation decreased water temperature in Lower Granite Reservoir thereby reducing predation in all years, and limiting thermally induced mortality in low flow years.

To be effective, the water management plan must be shaped so that flow in Lower Granite Reservoir is augmented when subyearling chinook salmon are present. This paper confirms that the 21 June to 31 August summer flow covers the time period when the majority of subyearling chinook salmon are passing Lower Granite Dam. The range that was observed in the median dates of passage at Lower Granite Dam demonstrates a need for flexibility in the water management plan from year to year. This will be especially important during low flow years such as 1992 when subyearling chinook salmon past Lower Granite Dam early and flow averaged only 539 m^3/sec from 21 June to 31 August. We acknowledge that this paper did not provide an exact prediction of median date of passage at Lower Granite Dam for the subyearling chinook salmon run at large. It will, however, help the Technical Management Team to develop and refine the water

management plan, while providing researchers with a starting point for developing a more accurate predictive approach.

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CHAPTER EIGHT

Migratory Behavior and Forebay Delay of Radio-Tagged Juvenile Fall Chinook Salmon in a Lower Snake River Impoundment

by

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Introduction

Many Columbia River basin salmonid *Oncorhynchus* spp. stocks have declined to dangerously low population levels in recent history. Nehlsen et al. (1991) identified 76 stocks from this basin at some risk of extinction, and of these, 36 were high risk stocks. Currently, the Snake River fall chinook *O. tshawytscha* stock is listed as threatened under the Endangered Species Act (National Marine Fisheries Service (NMFS) 1992). Much of this decline has been attributed to mortality associated with passage through hydroelectric dams and impoundments (Raymond 1988).

The effect of hydroelectric development in the Snake and Columbia river basins on the migratory behavior of juvenile salmonids is of particular concern because dams are known to delay the migration timing and reduce the migration rates of these fish (Raymond 1969; Raymond 1979). Because of this delay, smolts now migrate during periods of reduced flow, elevated water temperature, and increased predation risk (Park 1969), and may experience lower survival than during preimpoundment conditions.

The life history of fall chinook salmon may make them more susceptible to the effects of migratory delay than other salmonids. Fall chinook salmon exhibit an ocean-type life history, and migrate to the ocean as subyearlings (Healy 1991). As such, they generally migrate later in the season, after releases from upstream storage reservoirs to improve in-river conditions for other juvenile salmonids have ended (Dauble and Watson 1997). Later migration also places them in the system when elevated water temperatures can lead to increased predation (Poe et al. 1991) and susceptibility to disease (Becker and Fujihara 1978).

Past studies have used the mark and recapture of freeze-branded fish (Raymond 1968; Park 1969; Bentley and Raymond 1976; Berggren and Filardo 1993; Giorgi et al. 1994) or passive integrated transponder (PIT; Prentice et al. 1990) tagged fish (Achord et al. 1996; Zabel and Anderson 1997) to describe juvenile salmonid passage and migratory behavior. These techniques permit large numbers of fish to be marked relatively quickly and inexpensively. However, it is impossible to identify specific locations between marking and recapture sites where migrational delays are occurring. Smith et al. (1993) recognized this limitation and recommended, "future research efforts be directed at improving the resolution of travel time estimates by measuring responses through shorter reaches of river."

Travel time through specific reservoir reaches can be estimated using radio telemetry, allowing investigators to identify areas where smolts experience inordinate migratory delays. The recent miniaturization of radio telemetry transmitters now allows researchers to tag smolts as small as 115 mm in fork length (FL). In this study, we used radio telemetry to describe the passage of naturally produced, fall chinook salmon smolts through three reaches of Little Goose Reservoir, Snake River, with particular emphasis on their behavior immediately upstream of the dam, in the forebay.

This research should prove useful to managers and policy makers involved in the recovery effort for the Snake River fall chinook salmon stock. We identified where smolts migrated relatively quickly, and where delay is occurred. It also provides additional insight into how smolts behave in large impoundments. A better understanding of this behavior, will maximize the benefit of strategies to improve survival, such as transportation, spill or surface bypass by allowing managers to target specific areas where problems are identified. Our objectives were to: 1) determine migration rates of juvenile fall chinook salmon through two reservoir reaches and the forebay, and 2) describe juvenile fall chinook salmon behavior while in the Little Goose Dam forebay.

Methods

Little Goose Reservoir is located on the lower Snake River in eastern Washington. The reservoir was created in 1970 with the completion of Little Goose Dam, and is approximately 60.3 km in length. Little Goose Dam is located at Snake River kilometer (Rkm) 112.7 upstream of Ice Harbor Dam (Rkm 15.6) and Lower Monumental Dam (Rkm 66.9). Lower Granite Dam (Rkm 173) is the only dam upriver of Little Goose Dam before the free-flowing Hells Canyon reach, where Snake River fall chinook salmon spawn naturally (Connor et al. 1993).

Field Procedures

Naturally produced juvenile fall chinook salmon were collected and fitted with radio transmitters at the Lower Granite Dam juvenile fish collection facility. Tagging took place between July 10-August 1, 1995; July 14-July 31, 1996; and July 14-August 6, 1997. Naturally produced juveniles were selected by Washington Department of Fish and Wildlife personnel by the absence of marks identifying all hatchery fall chinook salmon in the Snake River. Fish were at least 115 mm FL, and had no visible signs of injury or stress. Fish were anesthetized in a 100 mg/L solution of buffered tricaine methanesulfonate (MS-222),

measured to the nearest millimeter FL and weighed to the nearest 0.1 g. In 1995 and 1996, a radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA)[1] broadcasting on a unique frequency was then implanted gastrically using the technique of Burger et al. (1985). In 1997, transmitters utilizing coded technology (Lotek Engineering, Newmarket, Ontario, Canada), were surgically implanted in the fish's peritoneal cavity (Adams et al. 1998). After tagging, fish were allowed to recover in river water for approximately 24 h before release.

Changing transmitter type and implantation technique was done to increase the detection and long-term survival of radio-tagged fish. Coded technology permits up to 100 transmitters to be operated on the same frequency simultaneously while still allowing the identification of an individual animal. This greatly reduces scan time, thereby increasing detection probability through the increase in time spent monitoring each frequency. Additionally, laboratory studies suggest surgical implantation may increase the long-term survival of tagged fall chinook salmon smolts (Adams et al. 1998).

After release, fish movements were monitored by receivers connected to stationary antenna arrays (Figure 1). Arrays of antennas were located 14.4 km above Little Goose Dam at New York Island, on barges immediately upstream of Little Goose Dam, and along the face of the dam. Additional arrays were located at the Little Goose juvenile fish collection facility and on the shoreline approximately 1 km below the dam. Antenna arrays will be referred to as island, barge, dam and exit arrays. This configuration enabled us to calculate residence times and migration rates (km/d) for fish in the upper (45.9 km) and lower (14.4 km) reaches of the reservoir, the forebay (0.6 km), and to estimate the time fish spent in the forebay before passage. All antenna arrays used temporally synchronized data logging receivers (Lotek Engineering Inc., Newmarket, Ontario, Canada) and one to four Yaggi antennas with six or nine elements, which allowed detections from different receivers to be accurately time-sequenced.

Receivers in multiple-antenna arrays (barge and dam) were configured in a master-slave arrangement. In this system,

[1] Use of trade names does not imply endorsement by the U.S. Geological Survey or the United States Government.

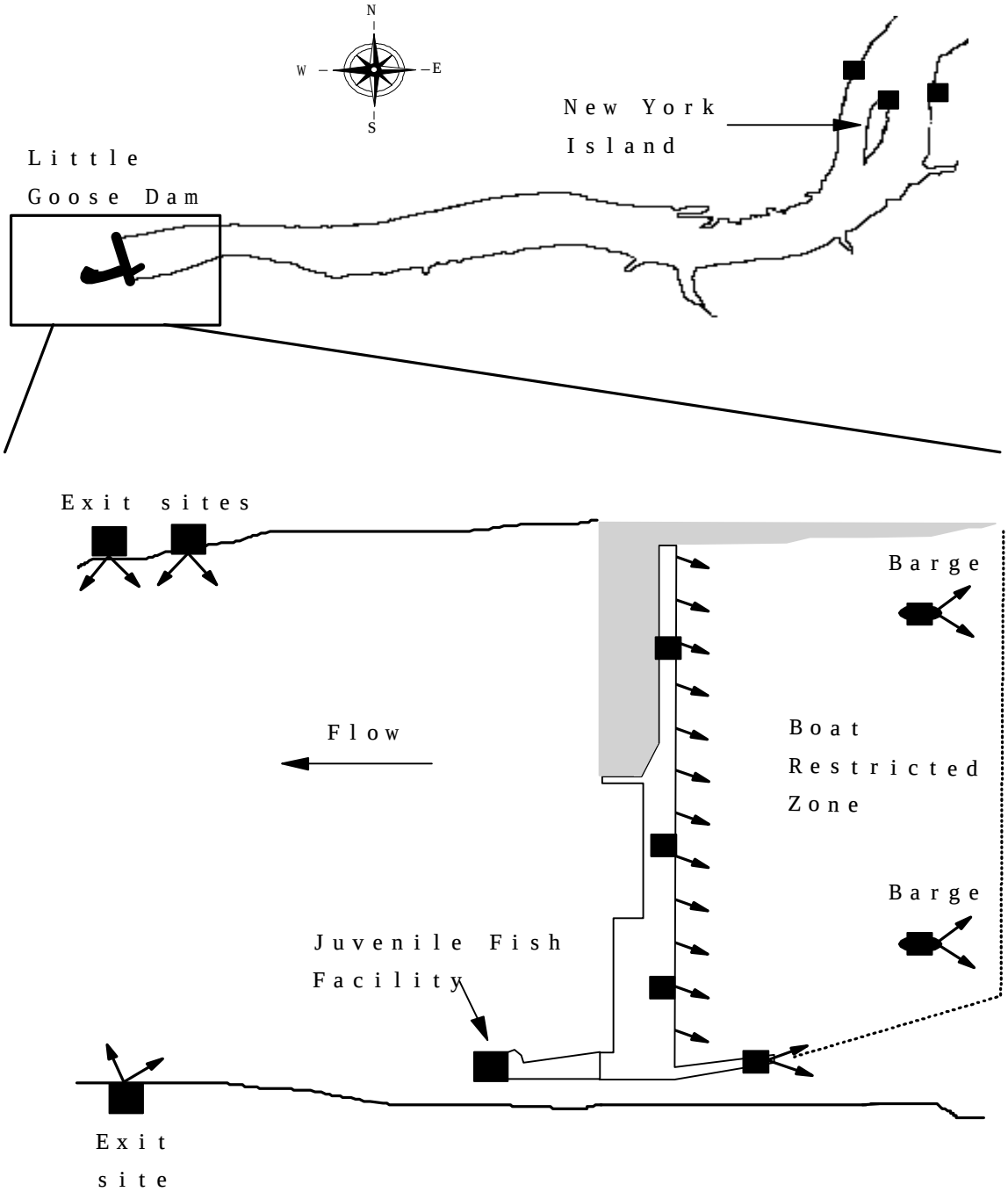

FIGURE 1.-Locations of fixed arrays of antennas used to monitor the movements of radio-tagged juvenile fall chinook salmon at New York Island and at Little Goose Dam during July-August 1995-1997. Squares represent radio receiver locations, and unlabeled arrows represent directional antennas.

receivers scanned each programmed frequency for 3 s, receiving signals from all antennas (master) simultaneously until a radio signal was detected. Receivers in 1995 and 1996, then recorded the date, time, frequency, signal strength, and beats-per-minute of the signal. In 1997, receivers recorded the date, time frequency (channel), code, and signal strength. The receiver then scanned each individual antenna (slaves) for an additional 3 s, recording the above information plus the slave antenna number if the signal was detected again. This configuration increased the accuracy and precision of location estimates, because directional properties of the antennas result in signal strength being highest on the antenna the transmitter was nearest.

Mean cross-sectional current velocity was estimated at three locations within the reservoir to describe the differences in water velocity between the reservoir and forebay. Water velocity information was collected using an acoustic Doppler current profiler, which determined water velocity in individual cells 1 m deep by 10 m long from the surface to approximately 85% of the water depth. Water velocities were collected, between July 31-August 7, 1997, along cross-sectional transects at the upper end of the reservoir (3.5 km below Lower Granite Dam), just below mid-reservoir (35 km below Lower Granite Dam), and in the Little Goose Dam forebay (0.5 km above Little Goose Dam). Water velocity data was collected within one week, and at times not differing by more than 1.5 h to minimize the effects of daily and seasonal flow variations.

Data Analysis

Data analysis consisted of arranging all detection records for an individual in chronological order creating a sequential record of each fish's location over time. From these records, residence time in the upper reach was calculated as the time from release to first detection at the island array. Residence time in the lower reach was the time between its initial detection at the island array and initial detection at either the barge or dam array. Forebay residence time was the time between initial detection at either the barge or dam array and the time of first detection at an exit array or its last detection at the barge or dam array if the fish was not detected at an exit array. Detection records were separated into "initial" and "subsequent" dam detections for analysis. An initial detection was defined for fish that had not been recorded at the dam previously, and were first detected at the barge array and then detected at the dam within 1 h. Detections not meeting these criteria were classified as subsequent. Detection records lasted from the time a fish first entered the radio-telemetry record at a barge or the

dam, and continued through its final detection prior to being absent from the telemetry record for > 1 h.

Detection records > 2 h in length were analyzed for duration and number of forebay crossings (laterally, longitudinally, and diagonally). The 2-h minimum record length was a compromise to include the maximum number of fish in the analysis while maintaining sufficient record length to describe their behavior. Movements per hour across the forebay were then calculated by dividing the total number of crossings by record duration.

A fish known to have reached the Little Goose Dam forebay was considered to have undertaken an upstream excursion when the following criteria were met: The fish was not detected at the dam or barge arrays for $\geq$ 1 h, and the detections ending and resuming the chronological sequence for that fish were at a barge or the navigation lock; or the fish was detected at the island array after it was known to have reached the dam, regardless of where the chronological record was broken or resumed. When an upstream excursion was detected we analyzed for duration, the number of excursions per individual, and whether or not the individual was detected at the island array.

Migration rates through the reservoir reaches and forebay residence times were compared between release groups using the nonparametric Kruskal-Wallis test, with significance assumed at $P < 0.05$. The nonparametric test was used because residence time and migration rate variables were not normally distributed in any year (Shapiro-Wilk W; $P < 0.05$). To approximate a nonparametric multiple range test of median migration rates and forebay residence times, we ranked the raw data and performed an analysis of variance on the rank scores. This procedure is equivalent to the Kruskal-Wallis test, and the *"F"* statistic calculated by the parametric procedure is often better than the c^2 approximation used in the Kruskal-Wallis test (SAS Institute 1990). A Tukey's Studentized Range Test (SRT) can then be calculated to interpret main effect differences (Heard et al. 1997).

The distribution of reservoir residence times for passive integrated transponder (PIT) tagged juvenile fall chinook salmon was compared graphically to that of radio-tagged individuals to determine if the two populations behaved similarly. PIT-tag detection data for Lower Granite, Little Goose, Lower Monumental, and McNary dams were accessed via the Columbia River DART (Data Acquisition in Real Time) site on the world wide web (University of Washington School of Fisheries; http://www.cqs.washington.edu/dart/dart.html). All PIT-tag detections at the dams of interest between June 1 and December 31 were downloaded for migration years 1995-1997, and then parsed to

include only hatchery fall chinook salmon. Hatchery fish were used because wild fish were not detected at multiple dams in sufficient numbers to allow meaningful analysis. Reservoir residence times, in days, were then computed for fish detected at multiple dams.

Results

A total of 405 juvenile fall chinook salmon were tagged with radio transmitters and released into Little Goose Reservoir. In 1995 and 1996, fish were released in six groups of approximately 20-25 fish, while in 1997, there were 13 releases of 8-26 fish (Table 1). The mean size of radio-tagged fish increased seasonally from 132 mm to 152 mm FL in 1995, 138 mm to 147 mm in 1996, and 127 mm to 146 mm g in 1997 (Table 1). Fish tagged in 1997 were significantly smaller than in 1995 or 1996 (Analysis of Variance; $P < 0.0001$). Tag retention during the 24-h recovery period was 100% in all years, but one tag failed during this time in 1995. Tagging mortality was 3.2% in 1995, 1.5% in 1996, and 2.5% in 1997.

The overall detection efficiency, percent of study fish detected, was 89%, 75%, and 90% of the fish released in 1995, 1996, and 1997, respectively. At the individual arrays during the three years of this study, detection efficiency ranged from 42% (1995, exit arrays) to 74% (1995, dam arrays). During the three study years, the island array detected 47%, 59%, and 67% of the fish released, and based on detections at the barge, dam, and exit arrays, 76%, 69%, and 75% were known to have reached the Little Goose Dam forebay (Table 2).

Water velocity decreased from the upper reservoir to the forebay. Mean cross-sectional velocities were 57 cm/s in the upper reservoir, 18 cm/s near mid-reservoir and 12 cm/s in the forebay.

TABLE 1.-Release dates, number (*N*) and mean (SD) fork lengths (mm) and weights (g) of radio-tagged juvenile fall chinook salmon released into Little Goose Reservoir during July-August 1995-1997.

Date	*N*	Length	(SD)	Weight	(SD)
		1995			
July 11	20	132	(9.5)	29.4	(6.0)
14	19	136	(10.9)	34.0	(8.2)
19	16	133	(12.4)	34.8	(8.8)
20	20	142	(8.4)	44.1	(8.4)
28	21	152	(6.0)	50.2	(6.5)
August 2	23	152	(8.4)	52.7	(7.2)
Overall	119	142	(12.4)	41.5	(11.5)
		1996			
July 16	25	138	(9.3)	33.0	(7.4)
19	25	143	(7.4)	39.0	(6.1)
23	19	144	(10.3)	41.3	(9.8)
26	20	143	(9.0)	38.1	(6.8)
30	19	148	(8.5)	42.7	(7.7)
August 2	20	147	(10.5)	42.5	(9.7)
Overall	128	144	(9.5)	39.1	(8.5)
		1997			
July 15	14	127	(3.8)	24.2	(2.9)
22	17	134	(5.5)	31.3	(4.1)
25	8	135	(7.6)	30.4	(5.2)
27	8	131	(5.0)	27.7	(3.6)
30	12	143	(5.4)	36.5	(4.1)
31	11	140	(9.5)	34.9	(7.5)
August 1	11	137	(9.4)	32.9	(5.9)
2	16	139	(9.9)	33.6	(6.3)
3	26	138	(8.5)	32.6	(5.9)
4	11	141	(6.5)	34.1	(4.8)
5	8	141	(10.1)	34.1	(8.1)
6	8	151	(4.2)	42.2	(4.8)
7	8	146	(5.0)	40.0	(5.4)
Overall	158	138	(9.0)	33.0	(6.7)

TABLE 2.-Detection efficiencies, as indicated by the percent of radio-tagged juvenile fall chinook salmon released that were detected, at the various radio telemetry antenna arrays located throughout Little Goose Reservoir during July-August, 1995-1997.

	Detection efficiencies (%)		
Array location	1995	1996	1997
Island	47.1	58.6	66.5
Barge	65.5	53.9	43.0
Dam	73.9	53.9	62.0
Exit	42.0	46.9	63.9
Dam/Barge/ Exit	75.6	68.8	75.3
Overall	89.1	75.1	89.9

Reservoir Migration

Residence time in the two reservoir reaches showed considerable variability, but were similar between years. Median residence time in the upper reach was 1.8 d in 1995 and 1996, and 2.3 d in 1997. Median residence in the lower reach was 1.0, 1. and 1.4 d in 1995, 1996, and 1997, respectively. Residence times ranged from 0.9 to 15.4 d in the upper reach, and from 0.1 to 10.0 d in the lower reach during the three years of study (Table 3).

Migration rates within the reservoir reaches did not differ between release groups, but fish moved faster through the upper reach than through the lower reach. The median migration rate of 26.0 km/d through the upper reach differed significantly from the rate of 14.9 km/d through the lower reservoir reach in 1995 (Wilcoxon 2-Sample Test; $P = 0.0002$). In 1996, the median migration rates of 24.8 km/d in the upper reach and 13.4 km/d in the lower reach were significantly different (Wilcoxon 2-Sample Test; $P = 0.0001$). In 1997, median migration rates were 20.2 km/d in the upper reach and 10.2 km/d in the lower, and again differed significantly (Wilcoxon 2-Sample Test; $P = 0.0001$; Figure 2).

Migration rates in the lower reservoir reach and in the forebay did not differ between the three years of study, but between year differences were detected in migration rates through the upper reservoir (Kruskal-Wallis; $P = 0.0002$). Tukey's SRT indicated radio-tagged juvenile fall chinook salmon migrated more slowly through the upper reservoir reach in 1997 than in either 1995 or 1996. Migration rates in the upper reach did not differ between 1995 and 1996.

Forebay Migration and Behavior

Initial dam detection records indicated juvenile fall chinook salmon generally entered the Little Goose Dam forebay along the north shoreline, and continued this approach until they were detected at the dam. Forty-eight, 18, and 20 fish met the initial detection requirements in 1995-1997, respectively, and were used to describe how juvenile fall chinook salmon approached the dam. Most (60%, 61%, and 90% in 1995-1997) entered the forebay at the northern barge, and continued their approach to the dam along the north shore, with 73%, 78%, and 70% being initially detected along the northern one-half of the dam during

TABLE 3.-Migration rates and residence times of radio-tagged juvenile fall chinook salmon in Little Goose Reservoir, 1995-7.

Quartile	Migration rate (km/d)			Residence time (d)		
	1995	1996	1997	1995	1996	1997
Lower Granite Dam to New York Island (Upper reach)						
Minimum	9.5	3.0	3.30	0.9	1.0	0.90
Quartile 1	19.3	19.60	15.0	1.3	1.2	1.60
Median	26.0	24.80	20.2	1.8	1.8	2.30
Quartile 3	36.4	37.80	29.1	2.4	2.3	3.10
Maximum	49.5	48.30	48.4	4.8	15.4	13.7
New York Island to Little Goose Dam (Lower reach)						
Minimum	1.5	1.4	1.8	0.2	0.3	0.1
Quartile 1	10.4	9.1	7.4	0.6	0.7	0.9
Median	14.9	13.40	10.2	1.0	1.1	1.4
Quartile 3	24.5	19.60	16.5	1.4	1.6	1.9
Maximum	63.6	44.70	102.4	9.6	10.0	8.1
Little Goose Dam forebay						
Minimum	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Quartile 1	0.3	0.3	0.3	0.3	0.3	0.3
Median	0.7	0.9	1.0	0.8	0.7	0.6
Quartile 3	2.3	2.3	2.3	2.2	1.7	1.6
Maximum	30.3	18.30	314.2	28.5	47.6	47.0[a]
Lower Granite Dam to Little Goose Dam forebay						
Minimum	4.9	3.7	3.7	1.2	1.3	1.8
Quartile 1	16.8	15.50	9.0	2.1	2.3	2.5
Median	20.1	20.20	17.9	3.0	3.0	3.3
Quartile 3	29.1	26.80	24.2	3.6	3.9	6.6
Maximum	50.0	46.30	32.4	12.4	16.3	16.3
Lower Granite Dam to Little Goose Dam exit						
Minimum	1.9	1.2	3.4	2.1	1.6	1.5
Quartile 1	9.9	9.2	10.0	3.4	2.8	3.2
Median	14.4	15.50	14.5	4.2	3.9	4.1
Quartile 3	17.6	21.20	18.6	6.2	6.5	6.0
Maximum	29.0	36.90	39.7	31.6	52.0	17.7

[a] Tags surgically implanted in 1997 did not allow removal for channel identification. Fish collected after September 1, 1997 were assumed to be from the last release group.

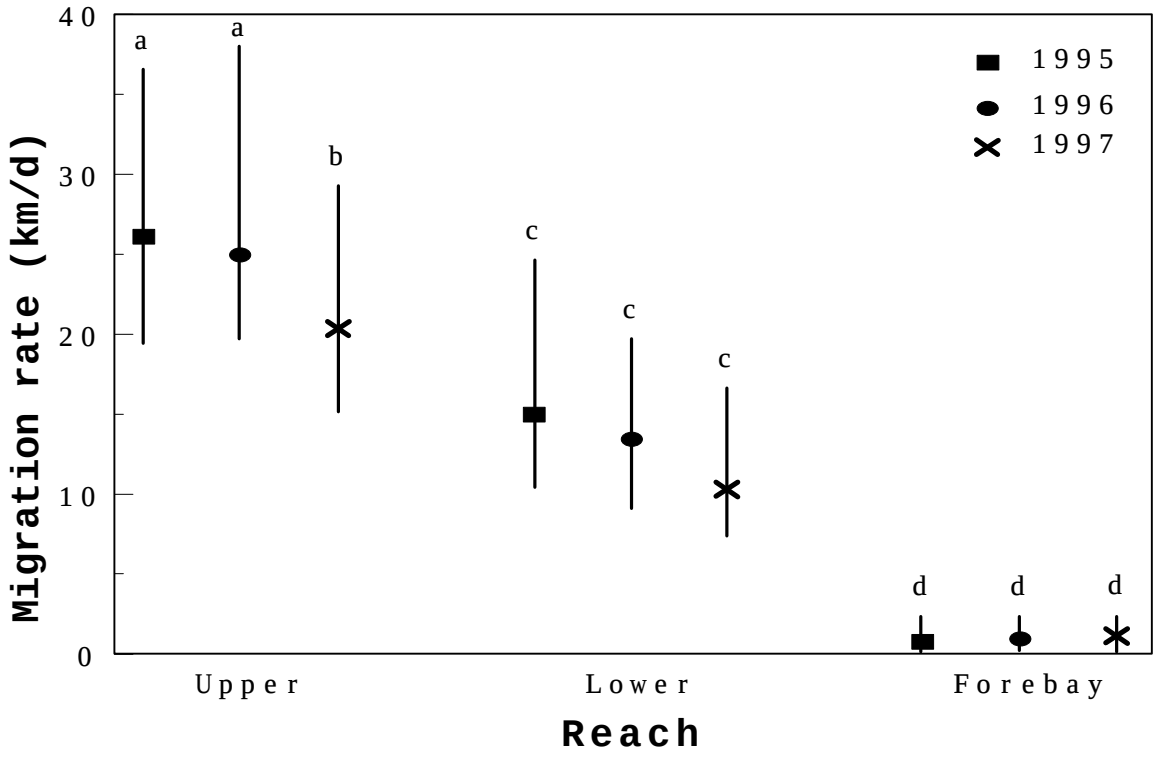

FIGURE 2.- Median migration rate (km/d) of radio-tagged juvenile fall chinook salmon through three reaches of Little Goose Reservoir. Bars extend to the first and third quartiles. Reaches were: upper, Lower Granite Dam to New York Island; lower, New York Island to the Little Goose Dam forebay; forebay, the upper extent of the boat restricted zone to exit gates below the dam. Dissimilar letters represent significant between year differences ($P < 0.05$).

1995-1997. Only four fish, one in 1995 and three in 1997, were known to have passed the dam during their initial detection record, resulting in simple entry and exit records.

Fish spent less time in the forebay than in either reservoir reach due to its short length (0.6 km), but migration rates through this section were the lowest observed. Median forebay residence times were 0.8, 0.7, and 0.6 d in 1995, 1996, and 1997 respectively. Median migration rates were 0.7, 0.9, and 1.0 km/d for the same period (Table 3; Figure 2). Migration rates through the forebay were variable and differed between release groups in 1995 (Kruskal-Wallis; $P = 0.0073$), but no differences were detected in 1996 or 1997 (Kruskal-Wallis; 1996, $P = 0.1790$; 1997 $P = 0.9958$). The migration rate of fish from release one, in 1995, (median 0.21 km/d) was significantly lower than those in releases three and six (medians 1.27 and 1.47 km/d, respectively) despite the general decline in river flow during the study period.

Detection patterns in the Little Goose Dam forebay exhibited a bimodal distribution. Peaks in the number of detections were observed early in the morning, between 0500 and 0600 hours, and then again in the evening, between 1800 and 2000 hours. The evening peak was generally the larger of the two peaks, and also had a longer duration (Figure 3). Peaks in the detection record did not appear related to mean hourly discharge at Little Goose Dam, where most flow exited through the turbines.

Two distinct behaviors were apparent in radio-tagged juvenile fall chinook salmon while in the Little Goose Dam forebay. The first consisted of repeated crosses of the forebay (Figure 4). A total of 276 detection records lasted $\geq$ 2 h, and were used in the analysis of fish behavior in the forebay; 116 records in 1995, 66 in 1996, and 94 in 1997. Radio-tagged smolts crossed the forebay between 0 and 21 times during each encounter with the dam (median 4, 4, and 3 crosses in 1995-1997, respectively). This resulted in fish crossing the forebay at a median rate of 0.97, 0.75 and 0.65 times per hour during the three years.

The second behavior pattern of radio-tagged juvenile fall chinook salmon in the forebay included numerous upstream excursions. Eighty-eight study fish made a total of 157 upstream excursions over the three years of study based on our criteria. In 1995, 34 fish made 65 excursions upstream with a median duration of 4 h 31 min (range, 1 h 2 min-170 h 30 min; 7.1 d).

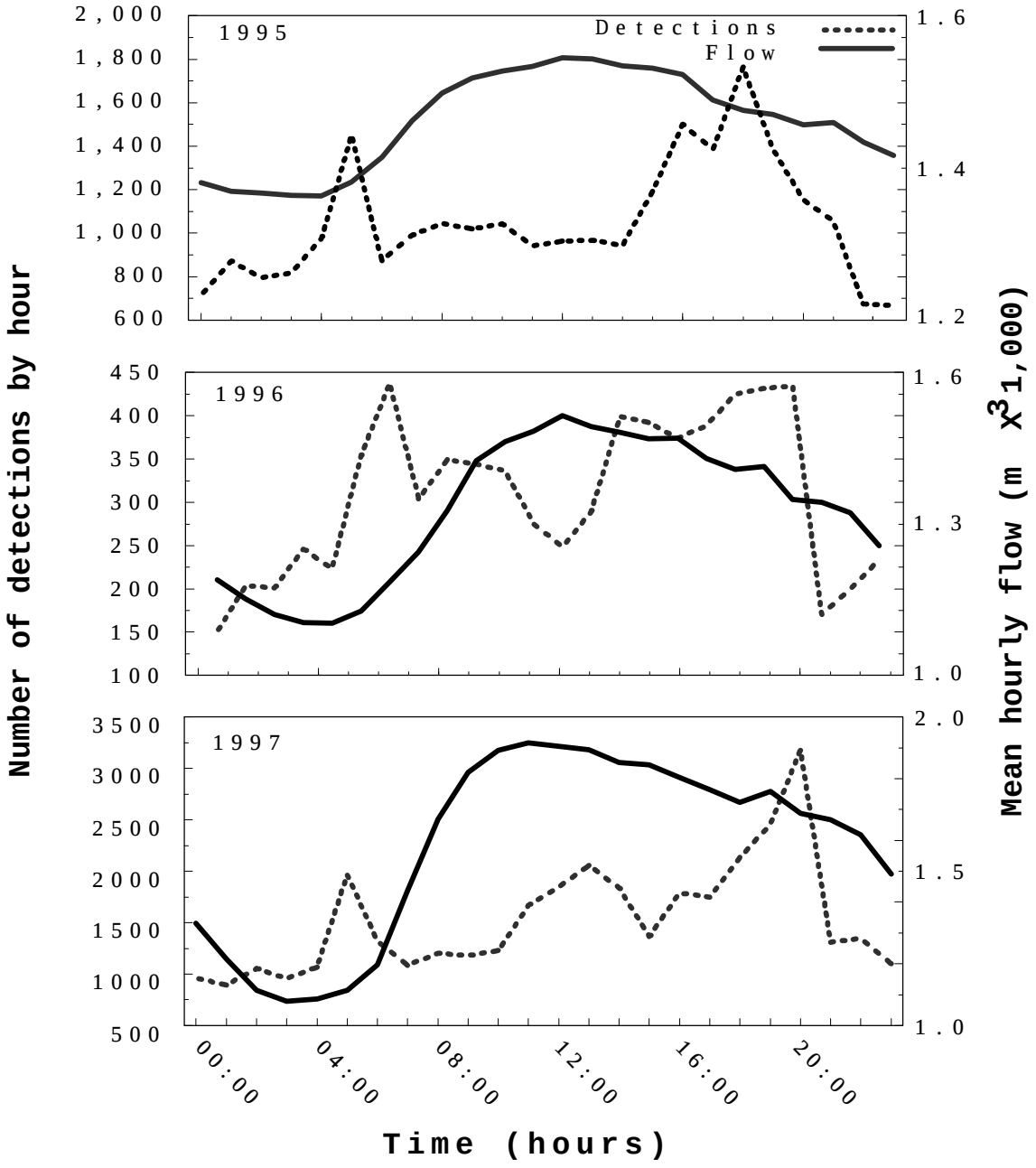

FIGURE 3.-Total number of detections over the entire study period versus mean hourly discharge at Little Goose Dam, July 11-August 24, 1995, July 17-August 26, 1996, and July 15-August 23, 1997.

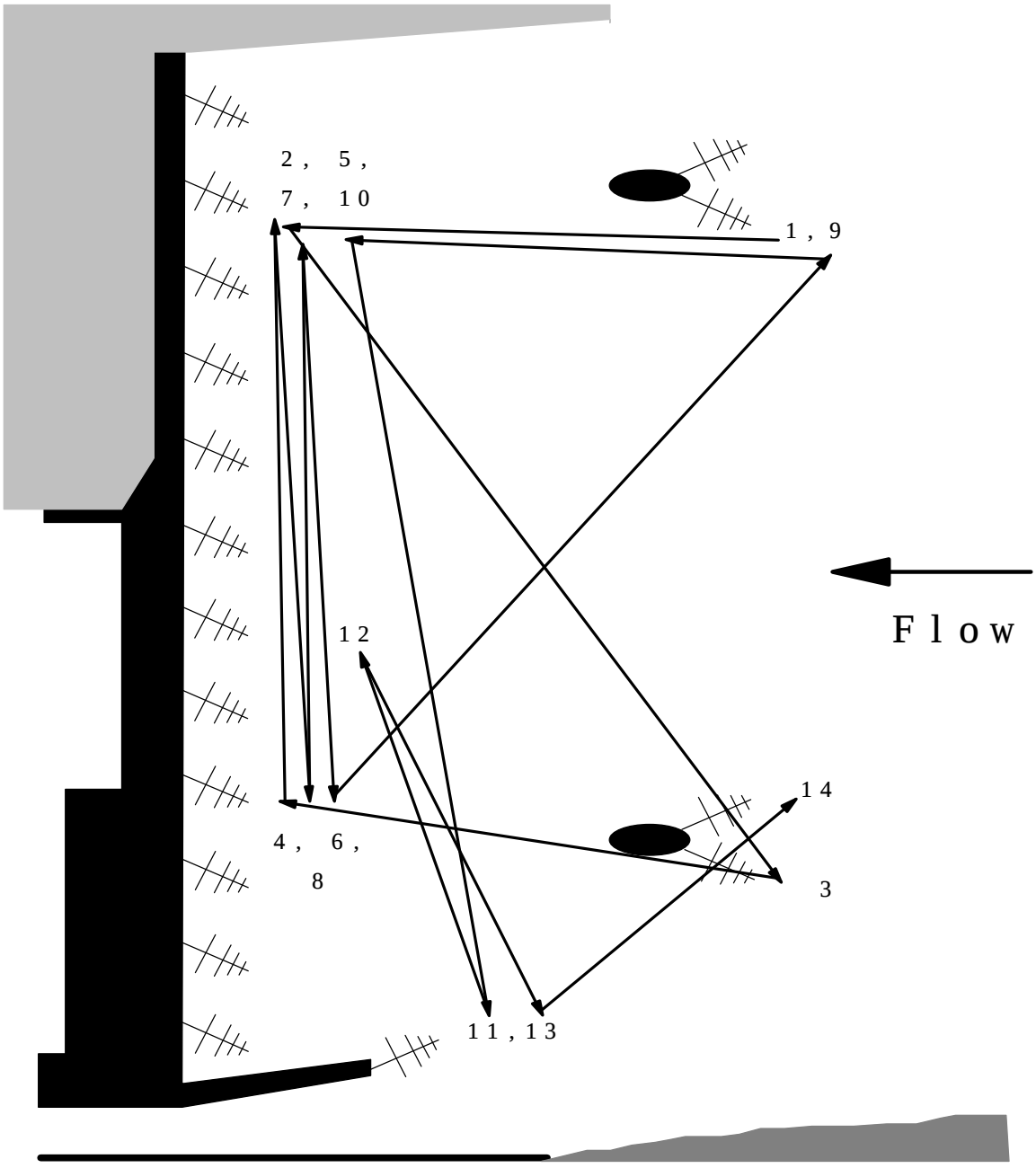

FIGURE 4.-Chronological order of 14 locations for an individual fish during its 9 h 55 min initial encounter with Little Goose Dam in 1995. This fish was collected 93 h 42 min later in the Little Goose Juvenile Bypass Facility.

Individual fish made up to six separate upstream excursions, and five traveled at least 14.4 km upriver and were detected at New York Island. Thirty fish undertook 61 upstream excursions in 1996, with a median of 4 h 56 min (range, 1 h 4 min-120 h 10 min; 5.3 d). Two fish made seven upstream excursions in 1996, and six returned to New York Island. Unlike 1995, when all fish traveling upstream to New York Island returned to the forebay telemetry record, two fish making upstream excursions to New York Island in 1996 were not detected later in the Little Goose Dam forebay. During 1997, 24 fish made 31 upstream excursions. Upstream excursions ranged from 1 h 12 min to 166 h 6 min (6.9 d), and had a median duration of 2 h 26 min. Four fish returned to New York Island, and of these, only one was later detected at Little Goose Dam.

Median residence times for fish passing through the forebay and lower reservoir reaches of Little Goose Reservoir combined were almost identical to the time spent in the upper reach, despite being only one-third as long. In addition, 93-100% of study fish passed through the upper reach within 5 d, but between 10% and 20% of study fish remained in the lower reservoir and forebay reaches for a period $\geq$ 7 d (Figure 5).

Plots of the reservoir residence time distributions of PIT-tagged fish were similar to those of radio-tagged smolts in Little Goose Reservoir. This suggested forebay delay may be occurring throughout the system. Most PIT-tagged juvenile fall chinook salmon passed through Little Goose Reservoir (60.3 km) and Lower Monumental Reservoirs (45.8 km) within approximately one week, but between 17% and 48% spent ten or more days in these reservoirs (Figure 6). PIT-tagged fish traveled relatively quickly through the 119 km between Lower Monumental Dam and McNary Dam (Columbia River Rkm 470), but despite this, 33%, 2%, and 15% took 40 or more days to migrate the 225 km between Lower Granite Dam and McNary Dam during 1995-1997 (Figure 6).

We determined the potential significance of behaviors such as crossing the forebay and upstream excursions that are likely to result in delays in downstream migration. If we assume the behavior of our radio-tagged fish was representative of the entire population migrating through Little Goose Reservoir then we can determine the importance of these findings. Using estimates of annual juvenile fall chinook salmon collection and fish guidance efficiency (FGE, the proportion of fish entering the powerhouse successfully guided into the bypass facility; Smith et al. 1997; NMFS unpublished data) at Little Goose Dam, we

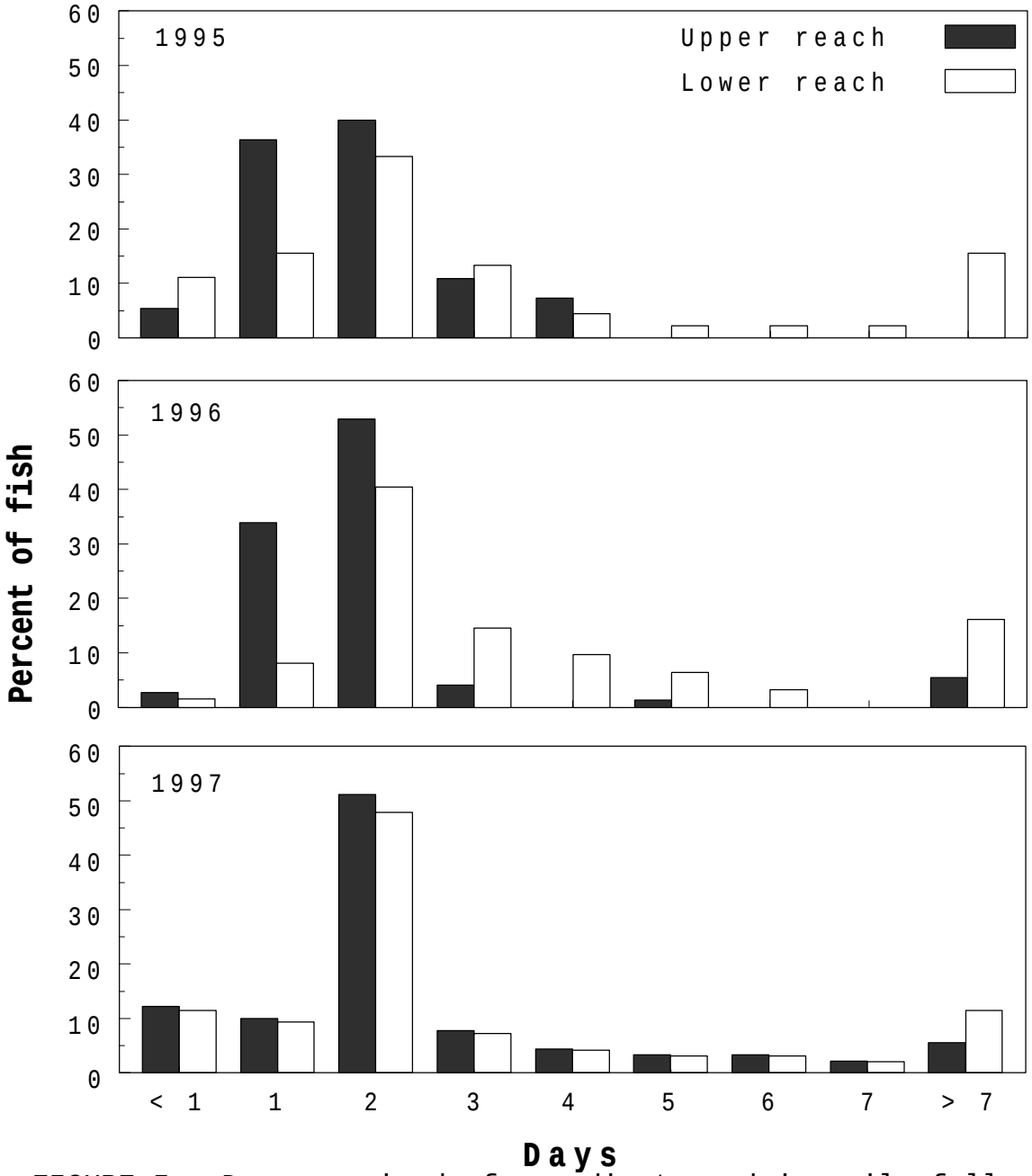

FIGURE 5.- Days required, for radio-tagged juvenile fall chinook salmon to migrate through the upper and lower reaches of Little Goose Reservoir in 1995, 1996, and 1997. The upper reach consisted of the 45.9 km from the Lower Granite Dam tailrace to New York Island. The lower reach was from New York Island to exit sites, and contained both the lower reservoir (14.4 km) and forebay reaches (0.6 km).

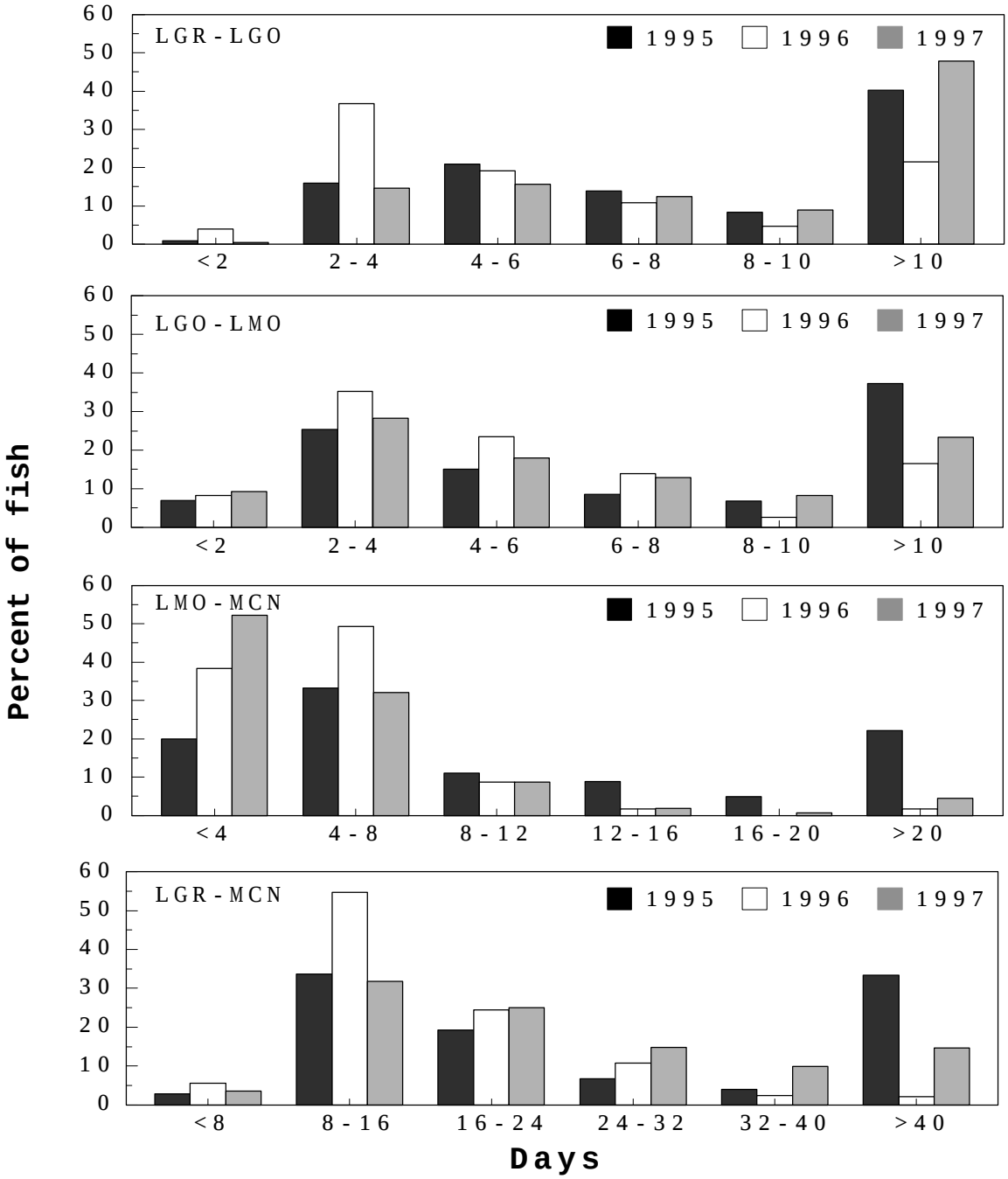

FIGURE 6.-Days required for PIT-tagged hatchery, juvenile fall chinook salmon to migrate from Lower Granite Dam (LGR) to Little Goose Dam (LGO), from Little Goose Dam to Lower Monumental Dam (LMO), from Lower Monumental Dam to McNary Dam (MCN), and from Lower Granite Dam to McNary Dam.

can expand the fraction of radio-tagged smolts which remained in the forebay $\geq$ 7 d to the total number of smolts which passed the dam. This expansion resulted in an estimated 6-13,000 smolts experiencing delays of this magnitude each year. In 1995, an estimated 46,000 juvenile fall chinook salmon passed Little Goose Dam (19,500 juvenile fall chinook salmon collected divided by the FGE of 0.424). This resulted in an estimate of 8,300 fish spending a week or more in the forebay area (46,000 smolts x 18% delayed; Figure 5). In 1996, collection and FGE estimates were 10,000 and 0.309 respectively, indicating approximately 6,100 smolts spent a week or more in the forebay (19% delayed; Figure 5). Collection, and FGE estimates for 1997 (60,000 and 0.529) indicate 13,600 smolts were delayed for a week or more in the forebay area (12% delayed).

Discussion

Radio telemetry proved to be an effective method for evaluating the migration rate and behavior of juvenile fall chinook salmon in Little Goose Reservoir. This approach was both efficient (75%-90% detected over three years) and provided additional information not supplied by traditional marking techniques (i.e., PIT tags or freeze brands). The additional resolution of radio telemetry also provided detailed information on individual fish behavior within multiple reaches of a single reservoir, and identified specific areas where seaward migrating smolts spent inordinate amounts of time.

Reservoir Migration

The reduced migration rate through the upper reach in 1997 was probably caused either by the smaller size of fish tagged in 1997, the change in tagging methodologies, or a combination of these factors. Giorgi et al. (1997) found size at PIT tagging to be the variable which explained the greatest amount of variation in juvenile fall chinook salmon migration rates in the Columbia River. Additionally, the swimming performance of wild Atlantic salmon smolts has been shown to be affected by surgical tagging but not by gastric implantation (Peake et al. 1997). This effect was apparently size related, as the migration rates of larger, hatchery Atlantic salmon smolts were not affected by either method.

We elected to switch to surgical implantation because of decreased growth associated with gastric implantation (Adams et al. 1998). We felt the potential for increased survival of these listed individuals warranted this change. However, in the future the selection of tagging methods will need to be more closely

examined and should depend on study objectives. While surgical implantation may provide increased long-term growth and survival, this method may also bias short-term migratory performance (Adams et al. 1998; Peake 1997). This may be especially true in studies using wild migrants, which are generally smaller than hatchery counterparts, and have higher tag to mass ratios (Peake 1997).

Residence times and migration rates of juvenile fall chinook salmon in Little Goose Reservoir indicated downstream migration was probably related to water velocity. Migration rates were lowest through the forebay, and highest in the upper reservoir during all three years of the study, which mirrored our water velocity measurements. Decreased migration rates in yearling chinook salmon are known to occur concurrently with decreased water velocity. Raymond (1968) documented a decrease in migration rate from 47 km/d to 13 km/d after fish entered the impounded waters of McNary Reservoir. Migration rates then returned to pre-impoundment levels (40 km/d) after reentering the free-flowing Columbia River below McNary Dam (this study was conducted prior to the completion of John Day Dam). Raymond (1969) also documented decreased migration rates in juvenile chinook salmon (probably spring race) between Ice Harbor Dam and The Dalles Dam from 18 km/d to 11 km/d after the completion of John Day Dam. Berggren and Filardo (1993) found flow to be the predictor variable which explained most of the variation in travel times for juvenile steelhead *O. mykiss*, yearling, and subyearling chinook salmon migrating in the Snake and Columbia rivers. Moser et al. (1991) also found the migration rates of coho salmon *O. kisutch* smolts to be "comparable with ambient current velocities". Fish moved rapidly downstream in areas of swift unidirectional current, but swam back and forth in the low velocity, reversing currents of the estuary. Among other genera of salmonids, Thorpe et al. (1981) reported the downstream displacement of Atlantic salmon *Salmo salar* smolts was related to surface currents, and their displacement was slightly faster than that of free-drifting drogues. We believe a similar relationship exists between water velocity and migration rates in juvenile fall chinook salmon. This relationship would explain the differences observed between the upper reach with relatively high velocity and the lower reaches with relatively low water velocities. One strategy to reduce residence time for seaward migrating smolts may be to increase lower reservoir and forebay water velocities.

Forebay Behavior

The bimodal nature of the daily number of detections may also be useful to managers trying to move fish more quickly through the system. During the times of peak activity, study fish were probably nearer the surface, and therefore more likely to be within the detection range of our equipment. Project operations which result in increased water velocity in the forebay (i.e., increased flow for power production, spill, or surface collector operation) may be particularly effective at these times.

We believe the forebay crossing and upstream excursions of study fish were also associated with reduced water velocity. Fried et al. (1978) found water current to be the main factor influencing the route and rate of outmigrating Atlantic salmon smolts, and Thorpe et al. (1981) reported the direction of Atlantic salmon smolt displacement and water movement to be significantly correlated. It is reasonable that seaward migrating Pacific salmon would also use water velocity as a guide through riverine systems. Upon entering an area of reduced water velocities, this mechanism could conceivably break down and the outmigrant would try to relocate the lost flow. We believe this "search pattern" was manifesting itself in the observed forebay crossing behavior. If, after a period of searching, the outmigrant was still unable to find the current to pass the obstruction (in this case into the juvenile collection facility or through the turbines), then an upstream excursion would allow the migrant to relocate the lost flow and make another attempt at passing. Park (1969) also suggests reduced reservoir flow probably delays smolts through disorientation. Fried et al. (1978) describes a similar situation where Atlantic salmon smolts entered shallow water, or when tidal influences caused current reversals. At these times smolts were reported to stop, mill about, or to begin swimming against the current.

We recognize the limitations of the criteria used to define upstream movements, but we feel there is sufficient evidence to indicate upstream excursions do take place. While it is possible some fish sounded and remained in the forebay during the time we considered an upstream excursion, it is equally possible other fish left and later returned to the forebay, after an upstream movement, without being detected at a barge. We have documented juvenile fall chinook salmon returning as far upstream as New York Island, and observed smaller scale upstream movements while mobile tracking from boats (unpublished data). Other researchers have also reported upstream movements of juvenile fall chinook salmon and steelhead trout (Giorgi et al. 1994; Adams et al.

1995). Unfortunately, the width of the reservoir downstream of New York Island, made additional fixed sites between the dam and island impractical.

Based on PIT-tag data, we believe the delays observed in the Little Goose Dam forebay occurred throughout the lower Snake River. Residence time histograms for PIT-tagged smolts migrating through impoundments between Lower Granite and McNary dams were very similar in shape as those of radio-tagged smolts in Little Goose Reservoir. Assuming PIT and radio-tagged smolts behaved similarly, this suggests a week or more of forebay delay was not uncommon in these reservoirs. Also, based on the similarity of the PIT-tag and radio-telemetry results, we feel information obtained from radio-tagged juvenile fall chinook is as applicable to the entire smolt population as is PIT-tag data.

Effect of Forebay Delay

Two deleterious conditions, predation and high water temperature, exist in the forebay, which may lead to substantial mortality among smolts with lengthy delays there. While median residence times of 0.6 d-0.8 d through the forebay may not be a substantial delay, 10-20% of radio-tagged fall chinook salmon remained in this area for $\geq$ 7 d, and represented a significant portion of the tagged population. Predation of out-migrating juvenile salmonids by northern pikeminnow *Ptychocheilus oregonensis* in John Day Reservoir is highest near the dams (Poe et al. 1991; Vigg et al. 1991). Poe et al. (1991) found juvenile salmonids comprised 66% of northern pikeminnow diet, by weight in the forebay of John Day Dam, compared to only 8% and 19% at two locations in the reservoir. Rieman et al. (1991) also reported northern pikeminnow predation on juvenile chinook salmon, above John Day Dam, was highest in July and August. Reducing the time smolts spend in the forebay would not only minimize predation risk, but also benefit them by moving them to the ocean sooner, via in-river migration or transportation. For example, had a radio-tagged fish which remained in the forebay 7 d been able to maintain the reduced migration rates observed in the lower reservoir reach, it would have traveled 71 to 104 km, placing it at approximately Ice Harbor Dam, only 16 km above the confluence of the Snake and Columbia rivers. Traveling at the rates observed in the upper reach would have placed the fish 141 to 182 km downstream, or approximately at McNary Dam. Had this fish been transported by truck it would have been released below Bonneville Dam 3 d or less after collection.

Relatively high water temperatures have also been observed in the Little Goose Dam forebay. Surface temperatures as high as 24.8^{o} C were observed in 1996, which is above the upper lethal

temperature for juvenile chinook salmon (Brett 1952). Mean weekly water temperatures in the forebay, in 1996, ranged between approximately 23^{o} C at the surface, and 20^{o} C at 20 m depth. The effects of long-term exposure to these temperatures on disease resistance, predator avoidance, and bioenergetic costs remain largely unexplored.

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CHAPTER NINE

Physiological Development and Migratory Behavior of Subyearling Fall Chinook Salmon in the Columbia River

by

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Introduction

Fall chinook salmon *Oncorhynchus tshawytscha* in the Columbia River have an ocean-type life history (Taylor 1990; Healy 1991). Fry emerge from spawning gravel in the spring, rear in nearshore areas for 2-3 months, then migrate to the ocean during their first summer of life as subyearlings. Their early life history is unique in that they rear in large main stem habitats (Dauble et al. 1989) rather than in tributaries or smaller coastal streams, as do other populations of fall chinook salmon (Reimers 1973; Taylor 1990; Huntington et al. 1996).

Because the Columbia River has been transformed into a series of reservoirs by hydropower development, migration conditions during the summer are characterized by decreasing flows and increasing temperatures. These conditions often become unfavorable to cold-water adapted salmon and may negatively influence migratory behavior and survival. In addition, hydroelectric dams have caused significant delays in migration timing and travel rates of juvenile salmonids (Raymond 1968, 1969, and 1979). Slower migration rates may result in decreased survival due to increased predation (Gray and Rondorf 1986; Poe et al. 1991) and susceptibility to disease at higher water temperatures (Becker and Fujihara 1978).

To mitigate for increased smolt travel times, fishery managers have provided additional flows during the spring and summer to enhance the outmigration of juvenile spring chinook salmon, steelhead *Oncorhynchus mykiss*, and subyearling fall chinook salmon (NPPC 1994). It is assumed that decreasing travel times will improve juvenile survival and ultimately adult returns. However, providing additional flow for juvenile migration is costly, and a flow-survival relationship adequate for defining flow requirements has yet to be clearly demonstrated (Calvin et al. 1996). A multi-year study from 1981 to 1983 examined the relation between flow and migratory behavior of subyearling fall chinook salmon and subsequent adult contribution, but failed to identify a relation between subyearling travel time between McNary and John Day dams and river flow (Sims and Miller 1982; Miller and Sims 1983, 1984; Giorgi et al. 1990; Giorgi et al. 1994). Giorgi et al. (1997) found that flow explained little of the variation in downstream migration rates of PIT-tagged subyearling chinook salmon in the mid-Columbia River, but flow and fork length accounted for 63% of the variation when combined. Berggren and Filardo (1993), using data from 1981-1983 and 1986-1988, showed that subyearling fall chinook salmon travel time between McNary and John Day dams was related to two flow variables and date. The date variable was used as a surrogate for a direct measure of smoltification, which

they concluded can help explain additional variation in travel times beyond flow-related variables alone.

Smoltification, the developmental process that prepares juvenile salmon for seawater entry and increases the disposition to migrate seaward, suggests that physiological processes are involved in juvenile chinook salmon migratory behavior. Zaugg (1989) showed that high gill Na^+/K^+ adenosine triphoshpatase (ATPase) activities were associated with decreased travel times in subyearling fall chinook salmon. The rise in gill ATPase activity during smoltification is also thought to prepare fish for seawater entry (Folmar and Dickhoff 1981). Osmoregulatory competence in seawater has been used to determine optimal time of release of hatchery fish (Clarke and Blackburn 1978; Clarke and Shelbourn 1985), and may represent a physiological preparation for migration (Hoar 1976). Smolt physiology has been studied in depth (Folmar and Dickhoff 1980; Wedemeyer et al. 1980; Hoar 1988) in part to identify smolt characteristics that will ensure high survival during both freshwater migration and seawater entry. These findings suggest that juvenile chinook salmon survival should be high for smolted individuals with fast travel times that arrive at the estuary at a time appropriate for successful seawater entry.

Although it is thought that reducing smolt travel times increases survival, subsequent adult returns provide a more comprehensive measure. Giorgi et al. (1990) found earlier migrating subyearling chinook salmon contributed more adults than later migrants. No physical or biological variable could be isolated to explain this phenomenon. In 1991, we initiated a multi-year marking study to resolve some of the questions regarding the importance of summer flow to subyearling fall chinook salmon travel times and adult contribution. The objectives were (1) to determine relations between subyearling fall chinook salmon travel times and physical variables such as flow, (2) describe the physiological development of subyearling fall chinook salmon during freshwater rearing and migration, and (3) determine the adult contribution from juvenile migrants.

Study Area

McNary Dam is located at river kilometer (rkm) 470 on the Columbia River, and is the first dam downstream of the confluence of the Snake and Columbia rivers (rkm 520). The Hanford Reach is a free-flowing section of the Columbia River that extends from the head of McNary pool (rkm 545) to Priest Rapids Dam (rkm 639). The Hanford Reach produces the majority of the wild subyearling

fall chinook salmon that migrate past McNary Dam. Priest Rapids State Fish Hatchery, located below Priest Rapids Dam, produces the largest component of the subyearling hatchery population that passes McNary Dam. John Day Dam is located down stream of McNary Dam at rkm 347.

Methods

Marking and Release

We marked subyearling fall chinook salmon at McNary Dam for travel time analysis and adult contribution from 1991 to 1994. Fish were collected from the juvenile fish facility, which uses submersible traveling screens to divert juvenile fish from the turbine intakes into gatewells and then to raceways (Matthews et al. 1986). Subyearling chinook salmon were anesthetized and marked with a coded-wire tag (CWT), or a combination of a CWT and a cold brand (Jefferts et al. 1963; Mighell 1969). The smolt migration was divided into early, middle, and late segments, which approximated the 10th, 50th, and 90th percentiles of subyearling chinook salmon passage at McNary Dam. Our goal was to mark 36,000 migrants during each segment of the outmigration for a total of 108,000 fish per year. Marking during each segment was further divided into three groups of 12,000 fish with a unique CWT for each group. During each day of marking, branded fish received a unique combination of character, location, and rotation. In 1994, some fish received a CWT only and could not be used in travel time estimates, but were marked to increase the number of fish to evaluate adult returns. Twenty-five to 100 fish were held each day for 48 h to measure delayed mortality and CWT loss. Fish surviving the delayed mortality test were transported down stream by barge or truck to prevent confounding of travel time estimates to John Day Dam.

Juvenile salmon were collected at John Day Dam using an air-lift pump on turbine 3B (Brege et al. 1990), and the brands on recaptured fish were recorded. One air-lift pump operated in 1991 and 1994, whereas two pumps were operated in 1992 and 1993, which doubled the sampling effort in those years. Recoveries of branded fish were adjusted for this difference in sampling effort.

Travel Time

Travel time of CWT groups was estimated to the nearest day by calculating the difference between the median date of release at McNary Dam and the median date of recovery at John Day Dam based on passage indices. A passage index is an expanded daily catch based on the amount of flow through the turbine sampling

unit, and is a relative measure of the total number of fish passing the dam. If the median date of recovery fell between days when no fish were recovered, the median was calculated by interpolation.

Travel times were calculated for fish groups marked with CWTs instead of branded groups because the number of recoveries within brand groups was often too low for reliable estimates. Berggren and Filardo (1993) recommended a minimum recovery sample size of 40 to obtain reliable travel time estimates. Travel times of CWT groups were further pooled to calculate and compare means from the early, middle, and late portions of the outmigration using analysis of variance (ANOVA; SAS 1994) for all years combined. Statistical significance was assumed at $P < 0.05$.

Stepwise multiple regression analysis was used to determine the relation between travel time of CWT groups and independent variables. Variables included mean flow, maximum flow, minimum flow, delta flow (maximum minus minimum), the reciprocals of these flow variables, mean temperature, median day of release, mean fork length, and mean gill ATPase activity. Reciprocal flow variables were included because they are functionally related to water velocity, which may be the primary stimulus of fish migratory behavior. Flow variables and temperatures at John Day Dam were averaged from the day after fish were released at McNary Dam through the median day of recovery at John Day Dam for each CWT group. All variables were $\log_e$ transformed to improve linearity and to reduce heteroscedasticity of residuals (Kleinbaum et al. 1987). Regression coefficients were standardized to evaluate the importance of each independent variable to subyearling fall chinook travel time (Lewis-Beck 1980). Since the independent variables used in multiple regression analyses had the potential of being collinear, we estimated the correlation coefficients between all variables. We also performed bivariate regressions to assess the effect of each variable on travel time.

Physiology

Seawater Challenges.-The osmoregulatory development of premigrant and actively migrating subyearling fall chinook salmon was evaluated using 24-h seawater challenges. Premigrants were collected biweekly from the Hanford Reach near Richland, Washington from mid April to the end of June in 1994 and 1995. Fish were collected with a beach seine and transported in 80-L plastic containers to the Columbia River Research Laboratory, Cook, Washington for acclimation and challenge. Actively

migrating fall chinook salmon were collected at McNary Dam to characterize the seawater adaptability of migrants during the early, middle, and late portions of the outmigration from 1992 to 1995. Fish were challenged in seawater at McNary Dam in 1992 and 1993, or transported and challenged at the Columbia River Research Laboratory in 1994 and 1995.

The general procedures of the seawater challenges followed those of Blackburn and Clarke (1987). Separate recirculating flow-through systems were used for challenged and control fish. The seawater system was composed of four to eight 80-L plastic containers that drained into a sump reservoir and a pump for recirculating the salt water. The freshwater control system was identical to the seawater system except only two to six containers were used. Each container held 10-15 fish, which were allowed to acclimate for 24 h prior to being challenged. Water chillers were placed in sump reservoirs to maintain water temperature at ambient river temperature up to 18.3C. Artificial seawater was mixed, filtered, and added to the sump reservoir of the system to infuse salt water into the tanks without handling or disturbing the fish. A desired salinity of 30 ppt was usually achieved within one hour. Unchallenged, control fish were maintained in fresh water.

At the end of a 24-h challenge, fish were sacrificed to obtain blood plasma. Fish were immobilized in their tanks with 30 mg/L MS-222, weighed, measured, rinsed in fresh water, and their tails blotted dry. Blood was collected from the caudal artery in ammonium heparinized Natelson tubes, centrifuged, and the plasma immediately frozen in liquid nitrogen. Plasma was collected from individual fish in 1992 and 1993, but in 1994 and 1995, blood was pooled from three fish at a time to obtain enough plasma from small premigrant fish collected early in the season. Blood plasma Na^+ was analyzed by flame photometry, and values $\leq$ 165 mmol/L were used to characterize a fall chinook salmon smolt (Clarke and Shelbourn 1985).

Gill filaments were collected for determination of gill ATPase activity of seawater challenged and control fish, and of run-at-large migrants marked at McNary Dam. Gill ATPase activity was analyzed according to the method of Zaugg (1982) in 1992, and using a microassay (Schrock et al. 1994) from 1993 to 1995. Gill ATPase activity of challenged and unchallenged fish were compared using two-sample *t*-tests (SAS 1994) in 1994 and 1995.

Salinity Preference.-The salinity preference of subyearling fall chinook salmon was measured to further define physiological development of premigrants and active migrants. Tests were

conducted concurrently with seawater challenges using subyearling chinook salmon collected in the Hanford Reach of the Columbia River and at McNary Dam in 1995. Salinity preference was evaluated in a two-choice tank (Figure 1A) modified from Baggerman (1960). Each tank was 95 cm long, 50 cm wide, and 65 cm high, and was divided into two equal-sized compartments. A freshwater bridge (15 cm deep) over the center divider allowed fish to pass between the two sides of the tank. Testing was done using a pair of tanks: one saline gradient tank and one freshwater control tank. The tank and compartment that received salt water was randomly determined for each test. Six replicate tests were run per week using new fish in each test. Ten fish were placed in each tank, five in each compartment, and were acclimated for 1 h in fresh water. After acclimation, one compartment was infused with 20 ppt salt water until the outflow and inflow salinities were equal. At this point, the inflow was stopped and behavior in each tank was video taped for 2 h.

Video tapes of fish behavior were analyzed by making counts of fish locations in four arbitrary divisions of the tank (Figure 1B). Observations were made every 3 min throughout the test for a total of 50 observations, and the number of fish observed was summed for each location. Chi-square analysis was performed to compare the distribution of fish on the salt and freshwater sides of each tank to a random distribution for each test (Zar 1984).

Adult Returns

Adult contribution data was obtained from the Regional Mark Information System database maintained by the Pacific States Marine Fisheries Commission, Portland, Oregon. This database contains both observed and estimated numbers of CWT adult salmon recovered in various fisheries and terminal sampling points. Estimated recoveries are expansions of observed numbers to account for different sampling efforts. The full complement of adult recoveries are available for fish marked in 1991 and 1992, but are incomplete for 1993 and 1994. Recoveries for fish marked in 1993 include fish up to four years in age, and recoveries for fish marked in 1994 include fish up to three years in age.

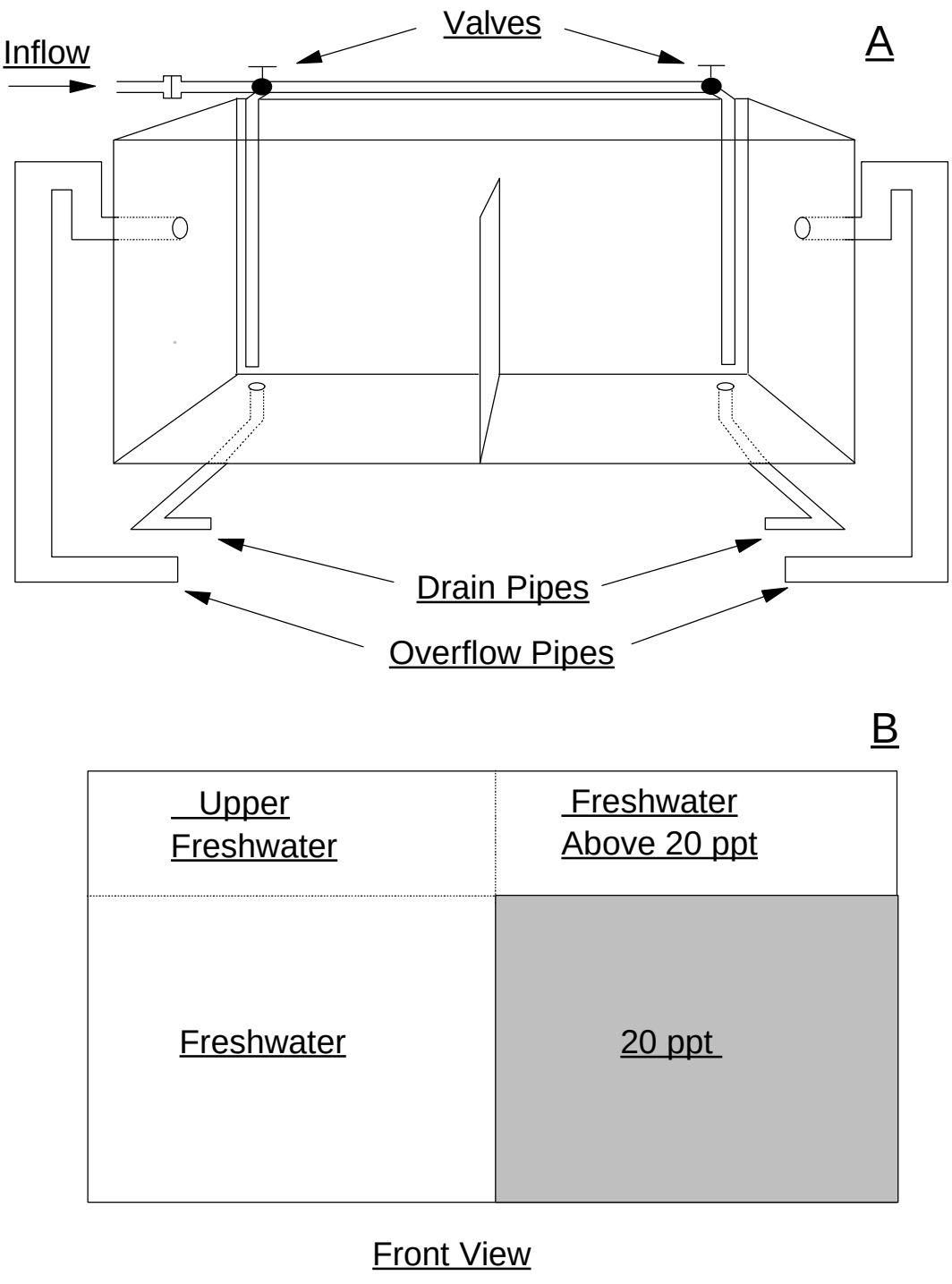

FIGURE 1.-Schematic of the tanks used to test the salinity preference of subyearling fall chinook salmon in 1995 (A). Arbitrary divisions of the salinity preference tanks used for video analysis (B).

Results

Marking, release, and recovery

The number of subyearling fall chinook salmon marked at McNary Dam from 1991 to 1994 ranged from 94,838 to 130,019. An additional 35,654 fish received only CWTs in 1994 to increase the sample size for evaluating adult contribution. A total of 35 CWT groups were released from 1991 to 1994 to estimate travel times. These CWT groups comprised 130 brand groups with a range of 329-7,461 fish per brand group. Delayed mortality of marked fish was low averaging 0.7% for the 4-year period. The composition of the run-at-large subyearling population passing McNary Dam was 73% wild and 27% hatchery fish in 1991 and 1992, and 58% wild and 42% hatchery fish in 1993. Run composition could not be calculated for 1994.

Unexpanded recoveries of individual CWT groups at John Day Dam ranged from 29 to 224 fish, and detections ranged from 1.3% to 16.5% of the number of fish released. Detections of fish marked in the early, middle, and late portions of the outmigration were lowest at John Day Dam in 1992, but otherwise varied between the other years and showed no consistent pattern (Table 1).

Travel time

Travel times of subyearling fall chinook salmon CWT groups through John Day Reservoir from 1991 to 1993 showed a consistent annual pattern of increasing then decreasing over time (Figure 2). Travel times ranged from 6-30 d during 1991-1993, and mean travel times of marked fish were 9.2 d during the early segment, 20.7 d during the middle segment, and 14.2 d during the late segment of the outmigration (Table 2). Mean travel time of the early mark group was significantly different from those of the middle and late groups, which were not significantly different from each other (ANOVA; $P = 0.0007$).

Travel times in 1994 (range 8-23 d) were different compared to those observed in previous years with the fastest travel times occurring for fish in the middle group, and the slowest for a CWT group released early in the season. When data from 1994 were included with the 1991-1993 data set, ANOVA showed the overall mean travel time for the early group increased by 2.1 d, the middle group mean decreased by 2.5 d, and the late group mean was reduced slightly by 0.3 d. The mean travel time for the early group was significantly different from that of the middle group,

TABLE 1.-Number of subyearling fall chinook salmon marked and released at McNary Dam, the percentage subsequently detected, and travel time (d) to John Day Dam from 1991 to 1994. One air-lift pump operated at John Day Dam in 1991 and 1994, and two pumps operated in 1992 and 1993. Passage index and percent detected are adjusted for sampling effort to make years comparable.

Year		Number released	Passage index	Percent detected	Travel time
1991	Early	34,841	1,384	4.0	6
1991	Middle	35,206	2,525	7.2	20
1991	Late	34,103	1,930	5.7	11
1992	Early	35,095	639	1.8	15
1992	Middle	35,052	612	1.7	21
1992	Late	35,103	1,329	3.8	15
1993	Early	35,944	3,138	8.7	8
1993	Middle	35,555	1,362	3.8	25
1993	Late	35,578	1,652	4.6	16
1994	Early	35,848	1,931	5.4	16
1994	Middle	35,935	5,147	14.3	11
1994	Late	23,055	1,558	6.8	15

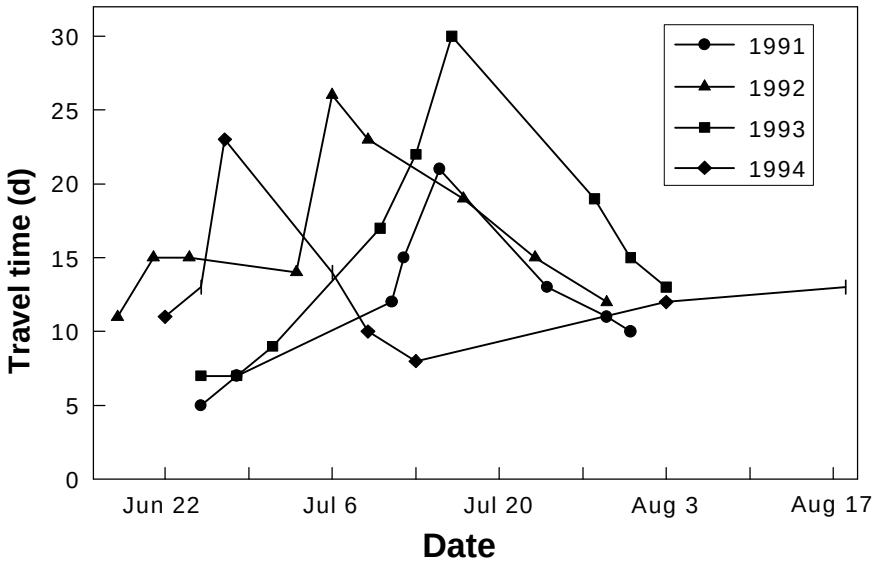

FIGURE 2.-Travel times of marked subyearling fall chinook salmon from McNary Dam to John Day Dam, 1991-1994.

TABLE 2.-Analysis of variance of subyearling fall chinook salmon mark-group travel times from 1991 to 1993 and 1991 to 1994. Means were compared using the Student-Newman-Kuels (SNK) test, and those with the same letter are not significantly different at =0.05.

Group	Mean travel time (d)	N	SNK grouping	F	P
		1991-1993			
Early	9.2	6	A		
Middle	20.7	9	B	10.48	0.0007
Late	14.2	9	B		
		1991-1994			
Early	11.3	9	A		
Middle	18.2	12	B	4.20	0.0251
Late	13.9	11	AB		

but not from that of the late group (ANOVA; $P = 0.0251$). The mean travel times for the middle and late groups were also not significantly different (Table 2).

Stepwise multiple regression of subyearling fall chinook salmon travel time on all independent variables resulted in a model that included reciprocal of minimum flow and mean fork length. These were the only two variables included in the model. Reciprocal of minimum flow and fork length together explained 50% of the variation ($R^2 = 0.50$) in subyearling chinook salmon travel time from McNary to John Day Dam (Table 3). The variance inflation factor for these two variables (1.43) suggested some collinearity existed, but was low enough not to be troublesome (Kleinbaum et al. 1987). Standardized regression coefficients showed that reciprocal of minimum flow (0.833) was more important in explaining subyearling chinook salmon travel time than fork length (-0.590).

Bivariate regression analyses showed significant, but weak, relations between travel time and all flow variables, except maximum flow. There were no significant relations between travel time and day of release, temperature at John Day Dam, mean fork length, or mean gill ATPase activity. The highest bivariate coefficient of determination was obtained by regressing travel time on the reciprocal of minimum flow ($R^2 = 0.26$).

Seawater challenges

Mortality of subyearling fall chinook salmon in seawater challenges was related to fish size and migratory status. Premigrants from nearshore areas of the Hanford Reach showed a decrease in mortality (Figure 3) as mean fork length increased (Figure 4). Once active subyearling migrants began passing McNary Dam usually at sizes > 100 mm mortality was low in seawater challenges. Active migrants challenged in 1992 and 1993 experienced mortality < 2.3%, whereas fish challenged in 1994 and 1995 had mortality rates typically < 10%. The highest mortality rates experienced by active migrants (18%) occurred in a challenge conducted on August 5, 1994. This challenge was preceded by a large fish kill at McNary Dam on July 17, 1994 brought about by thermal stress (Wagner 1995).

Osmoregulatory competence, as measured by plasma Na^+ levels, of subyearling fall chinook salmon developed seasonally as fish size increased. Mean plasma Na^+ remains low (< 165 mmol/L) when juvenile salmon with osmoregulatory competence enter seawater,

TABLE 3.-Multiple regression model for factors affecting subyearling fall chinook travel time from McNary Dam to John Day Dam, 1991-1994.

Variable	Parameter estimate	Standard error	Standardized coefficient	P[a]	Partial R^2	R^2	MSE
Intercept	22.307	4.382	0.000	0.0001		0.50	1.312
Minimum flow^{-1}	1.221	0.229	0.833	0.0001	0.26		
Fork length	-2.968	0.787	-0.590	0.0007	0.24		

[a] Probability that the parameter estimate is not different than zero.

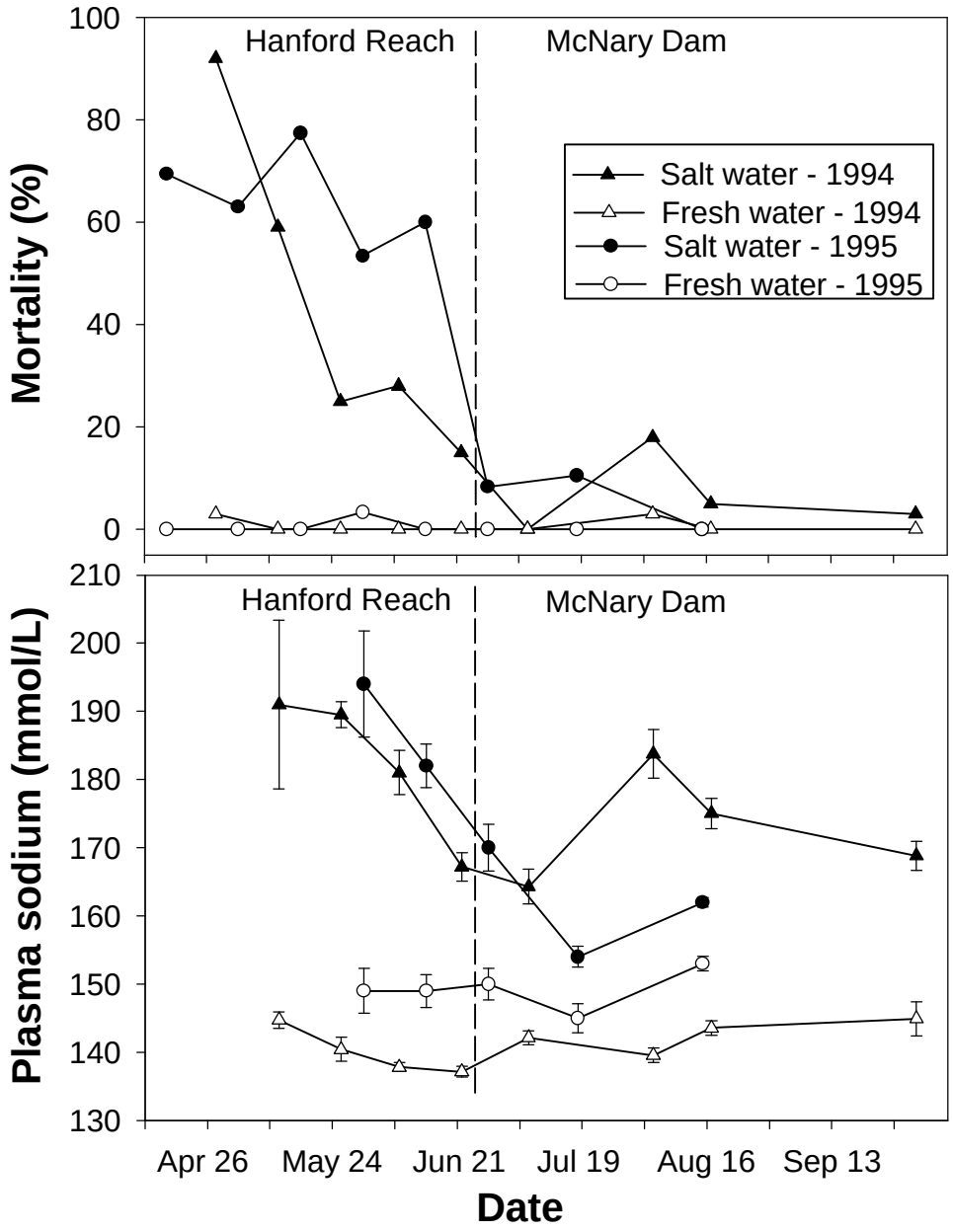

FIGURE 3.-Mortality and plasma Na^+ levels, with standard error bars, of subyearling fall chinook salmon used in seawater challenges in 1994 and 1995. The dashed vertical line delineates fish collected in the Hanford Reach and at McNary Dam.

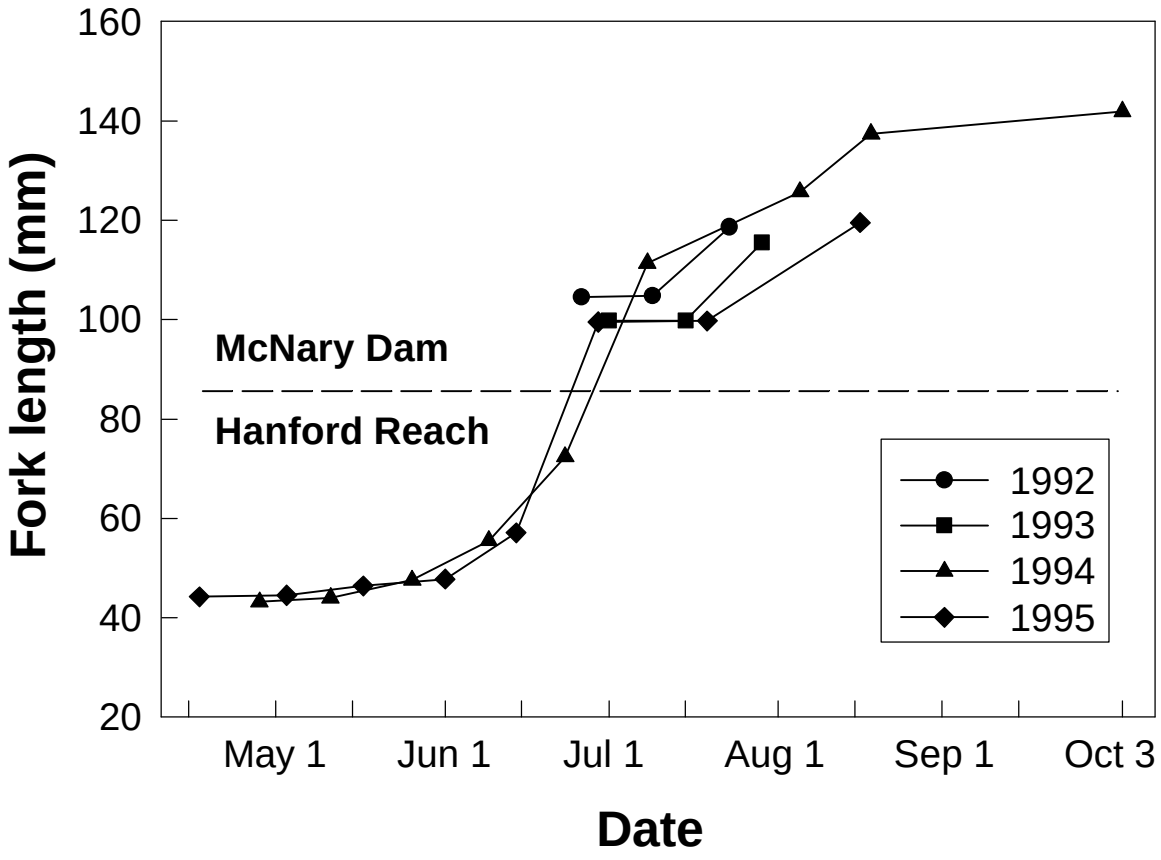

FIGURE 4.-Fork lengths of subyearling fall chinook salmon used in seawater challenges, 1992-1995. The dashed horizontal line delineates fish collected in the Hanford Reach and at McNary Dam.

but increases markedly with an influx of seawater ions among fish unable to osmoregulate in seawater. Mean plasma Na^+ values for subyearlings challenged in 1992 ranged from 150 to 155 mmol/L while values ranged from 153 to 157 mmol/L in 1993 below the critical value (< 165 mmol/L) for successful seawater entry given by Clarke and Shelbourn (1985). Plasma Na^+ values of premigrants in 1994 decreased to 167 mmol/L in the last premigrant challenge in late June when fish were 72 mm (Figure 3). In 1995, plasma Na^+ levels of premigrants dropped to 185 mmol/L by mid June, however, fish were only 58 mm in length at that time. Subyearling chinook salmon were generally able to reduce their plasma Na^+ levels below 165 mmol/L once they became active migrants. Exceptions to this were observed for fish challenged in August and October in 1994 (Figure 3).

Gill ATPase activity in 1994 and 1995 showed a distinct seasonal pattern of increasing during nearshore rearing, peaking in late June or early July, then decreasing during the rest of the outmigration (Figure 5). Gill ATPase activity of fish in seawater challenges were generally significantly higher than mean gill ATPase activities of freshwater control fish only during late May and in June in 1994 and 1995 when gill ATPase activities were rapidly increasing (Figure 5).

Salinity preference

Subyearling fall chinook salmon showed the greatest preference for saltwater from late June to mid July in 1995, although preference for saltwater remained high through August (Table 4). The freshwater side of the tank was generally used less than the saltwater side, especially during mid July when no fish showed a preference for fresh water.

Video analysis allowed us to define fish behavior in salinity preference tests. Fish observed on the saltwater side of the gradient tank primarily used the freshwater layer above the salt water, which accounted for only 25% of the available volume. Fish in this layer usually held position slightly above the salt and freshwater interface. Exceptions to this occurred in mid July and late August when half of the fish in the gradient tank were found in the saltwater layer. Control fish generally used each side of the tank equally throughout the season, and percent use of the different layers was proportional to the available volume of each layer.

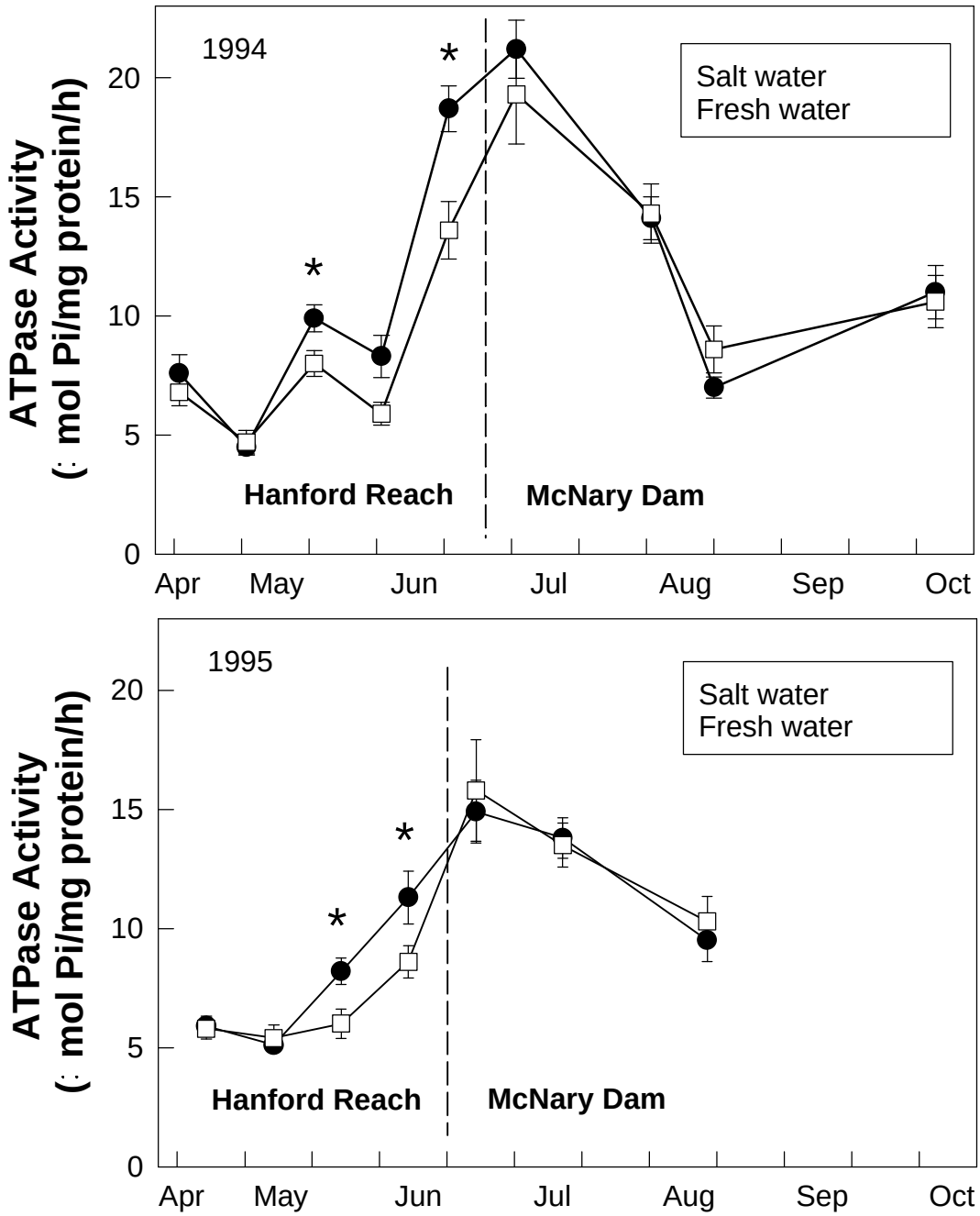

FIGURE 5.-ATPase activities, with standard error bars, of subyearling fall chinook salmon used in seawater challenges in 1994 and 1995. The dashed vertical line delineates fish collected in the Hanford Reach and at McNary Dam.

TABLE 4.-The number of salinity preference tests in which subyearling fall chinook salmon showed a preference for the saltwater side of the gradient tank, freshwater side of the gradient tank, or displayed no preference in 1995. Preferences were determined by Chi-square analyses and are summarized by week of testing.

	Preference		
Week	Salt water	Fresh water	None
May 10	1	0	3
May 23	3	2	1
June 6	3	2	1
June 20	5	1	0
July 12	5	0	1
August 1	4	1	0
August 21	4	1	1
Total	25	7	7

Adult Returns

The only full complements of adult recoveries to date were from fish marked in 1991 and 1992. Subyearling fall chinook salmon marked during the early portion of the outmigration in 1991 contributed nearly twice as many adults as fish marked during the middle and late portions (Table 5). Fish marked during the middle portion of the outmigration contributed the most adults in 1992, but 1992 returns were the lowest of the four years of marking. The return of fish from the 1993 marking shows an increasing trend from fish marked from early to late in the juvenile outmigration. Recoveries of fish from 1994 show that the early group has contributed the most adults followed by the middle and late groups.

Discussion

The relation between subyearling fall chinook salmon travel time and flow was weakly supported by our results. Reciprocal of minimum flow and fork length accounted for only half of the variation observed in travel times from McNary to John Day dams. Our results were similar to those of Giorgi et al. (1997) who showed that migration rates of PIT-tagged subyearling chinook salmon between Rock Island and McNary dams were best explained by fish length and mean flow (R^2 = 0.63). However, the authors also concluded that there was no evidence that subyearling chinook salmon responded to changes in river discharges over the ranges they observed (1,500-5,000 m^3/s). Berggren and Filardo (1993) found that flow was the most important variable in explaining subyearling chinook salmon travel time from McNary to John Day dams. In each study, including our results reported here, the flow variable explained 23-28% of the variation in travel rates in bivariate regressions. Although flow is important to subyearling fall chinook salmon travel rates, it is not the sole determinant of migratory behavior.

One of the reasons our multivariate analysis may not have explained a larger portion of the variation in subyearling fall chinook salmon travel time is that travel times showed a distinct nonlinear pattern from 1991 to 1993. Fish marked for the early group usually had the shortest travel times to John Day Dam followed by the late group and then the middle group. This pattern may have made it difficult to define relations between variables that increase or decrease linearly over time, such as flow, temperature, and day of release. This may be an artifact of the stock differences of fish comprising the three marked groups. Freeze-branded subyearling fall chinook salmon released

TABLE 5.-Adult recoveries of subyearling fall chinook salmon marked and released at McNary Dam from 1991 to 1994. Estimated recoveries are expansions of observed recoveries based on sampling effort. Asterisks indicate incomplete returns.

Group	Median release date	Number released	Number observed	Number estimated	Percent estimated recovery
Early	Jun 27, 1991	35,955	140	295	0.82
Middle	Jul 12, 1991	35,970	52	153	0.43
Late	Jul 30, 1991	36,055	44	172	0.48
Early	Jun 20, 1992	35,854	4	10	0.028
Middle	Jul 6, 1992	35,835	12	48	0.13
Late	Jul 23, 1992	35,805	5	10	0.028
Early	Jun 28, 1993	36,150	38	56	0.15*
Middle	Jul 13, 1993	35,734	32	84	0.24*
Late	Aug 1, 1993	35,788	43	113	0.32*
Early	Jun 25, 1994	49,648	74	116	0.23*
Middle	Jul 11, 1994	49,741	42	80	0.16*
Late	Aug 10, 1994	32,705	23	42	0.13*

from Priest Rapids Hatchery usually arrived at McNary Dam before the majority of the wild population from the Hanford Reach, and were probably the primary constituent of the early mark group (Wagner 1992; Wagner and Hillson 1993; Wagner 1994). An exception to this was in 1992 when both hatchery and wild subyearlings began passing McNary Dam at about the same time. The middle and late groups were probably composed predominantly of wild fish from the Hanford Reach. The late mark group may have traveled faster than the middle group because this group always contained the largest fish that were marked in any given year. Fish size may also have influenced the different travel time pattern observed in 1994. Fish marked during the middle segment of the outmigration the fastest group were larger in 1994 than in the other years for this segment. However, it is difficult to say whether the slight size difference was biologically significant.

Our final multivariate regression model predicting travel time included reciprocal of minimum flow and fork length, but did not include other variables that may be biologically important to subyearling fall chinook salmon migration such as temperature. Water temperatures can exceed 21°C at McNary Dam (USACOE 1992) placing fish at greater risk to disease and thermal stress. This was evident by the massive temperature-related mortality of subyearling fall chinook salmon at McNary Dam in 1994 (Wagner 1995). High water temperatures have also been shown to reduce gill ATPase activity in juvenile coho salmon *O. kisutch* (Zaugg and McClain 1976), juvenile steelhead *O. mykiss* (Zaugg 1981), and juvenile Atlantic salmon *Salmo salar* (Duston et al. 1991), and may have the same effect on fall chinook salmon. Gill ATPase activity was usually declining during the latter half of the summer as water temperature increased to 20°C or higher. High water temperatures may affect primarily later migrants by reducing in-river survival and placing fish at a physiological disadvantage when they reach the estuary.

Gill ATPase activity was included in our analyses as a measure of smoltification, which had been lacking in previous studies, and has been linked to migratory behavior in juvenile salmonids. Zaugg (1989) showed that more completely smolted subyearling fall chinook salmon migrated in faster, off-shore water and at higher rates in the lower Columbia River. Muir et al. (1994) found that juvenile spring chinook salmon with the highest gill ATPase activity at release at Dworshak National Fish Hatchery had the fastest downstream movement and were recovered in greater numbers at Lower Granite Dam on the Snake River. In contrast, elevated gill ATPase activities are not always

necessary for rapid seaward migration in juvenile spring and fall chinook salmon (Ewing et al. 1980). We found that gill ATPase activity was not important in explaining variation in subyearling travel time in bivariate or multivariate regression analyses. Also of interest is that the slowest travel times observed in the middle-mark groups were often associated with some of the highest gill ATPase activities. As a result, gill ATPase activity may not be a good predictor of juvenile fall chinook salmon travel time, but remains an important indicator of physiological development.

The development of osmoregulatory competence in subyearling chinook salmon is partly a function of fish size (Hoar 1976) and growth rate (Wagner et al. 1969). Premigrants rearing in the Hanford Reach grow rapidly and their increase in gill ATPase activity with size is concurrent with their osmoregulatory development. Kreeger (1995) found that two coastal populations of juvenile chinook salmon from the Trask and Rogue rivers, Oregon, demonstrated 100% survival in seawater challenges at 7-8 cm fork length, and could efficiently regulate their plasma Na^+ in seawater at a weight of 5-7 g. Similarly, Clarke and Shelbourn (1985) reported that subyearling chinook salmon did not obtain optimum sodium ion regulation in seawater until they reached a weight of 5-6 g. These sizes correspond to a 75-85 mm fish in the Hanford Reach. Fish larger than about 70 mm were not abundant in nearshore areas of the Hanford Reach and probably had moved off shore to begin migrating seaward. Subyearling fall chinook salmon did not demonstrate complete osmoregulatory competence until they became active migrants and were collected at McNary Dam. It appears that development of seawater tolerance and increasing gill ATPase activity may accompany the initiation of migration in subyearling fall chinook salmon.

Subyearling fall chinook salmon had the greatest preference for saline water in late June and early July when fish were beginning their seaward migration, although preference remained high through August. Gill ATPase activities were also peaking in late June and early July and may have influenced preference for saline water. The fact that fish were often observed above the saline layer in preference tests even though it represented a fraction of the available space may be the result of the short duration of the tests and fish needing more time to adapt to the 20 ppt saline layer. Fish were exposed to a low salinity directly above the salt-freshwater interface as their swimming mixed the water to a small degree. In the estuary, fish are exposed to smaller salinity gradients than what was represented in these tests, which may facilitate transition to sea water. McInerney (1963) proposed that salinity preference may be used to guide fish migrating through the estuary to the ocean. Whether

salinity preference is a cue for seaward migration in freshwater subyearling chinook salmon is unknown. However, salinity preference did increase when fish were actively smolting and beginning their seaward migration, and may therefore serve as an indicator of migratory disposition (Baggerman 1960).

The importance of flow to the migration rates and survival of subyearling fall chinook salmon remains the subject of debate. River flow remains of interest because it is one of the few variables that can be manipulated by fishery managers to benefit seaward migrating salmon. The highest in-river survival of subyearling fall chinook salmon should be realized by fish that reach an appropriate stage of physiological development early enough to migrate under the most favorable environmental conditions.

Both physiological and environmental criteria may be used to define a period of migratory opportunity for subyearling fall chinook salmon. Our data suggested that fish were most physiologically prepared for successful migration from mid June to early July, a time of rapid growth and smolting as evidenced by rising gill ATPase activities, development of osmoregulatory competence, and development of a preference for seawater. Mid June to early July was the time when fish reach a suitable size to initiate migration. Connor et al. (1993) identified a minimum migration size of 85 mm for subyearling Snake River fall chinook salmon. This minimum size may also apply to the Hanford Reach as it was difficult to capture rearing subyearling chinook salmon over 70 mm in beach seines, and active migrants at McNary Dam were generally 90 to 100 mm by late June.

The environmental conditions that would afford the best migratory opportunity would be defined by high flows and low water temperatures. The Columbia River hydrograph decreases throughout the summer and water temperatures rise to over 20°C by August in a typical year (USACOE 1993) creating poor migratory conditions. Smith et al. (1997) and Muir et al. (1998) showed that hatchery subyearling fall chinook salmon released early and that migrated under higher flows in the Snake River survived better than fish that were released later and migrated under lower flows. Similarly, wild fall chinook salmon PIT tagged in the Hells Canyon Reach of the Snake River from 1991 to 1995 had higher detection rates at Lower Granite Dam, a relative measure of survival, when flows were high and temperatures were low (William Connor, U.S. Fish and Wildlife Service, personal communication).

If environmental and physiological factors do partially control successful migration and survival, then it should be

evident in adult returns. In the early 1980s, fish that migrated early in the summer contributed more adults than later migrants (Giorgi et al. 1990). During that study, flows declined from early to late summer while temperatures increased throughout the season (Giorgi et al. 1994). Physiological development was not measured in that study. Our adult return information from 1991 and 1994 also indicated that early migrants may gain a survival advantage from favorable environmental conditions and rapid smoltification. Flows were highest for these groups, temperatures were coolest, and gill ATPase activities were increasing. On the contrary, the return of one to four year old fish from marking in 1993 show that late-marked migrants have contributed more adults than fish marked early and in the middle of the outmigration. This does not support our hypothesis, but is consistent with the results obtained by Giorgi et al. (1990) who found year to year variability in adult recoveries.

The consequence of migratory opportunity should ultimately manifest itself at the population level. If late migrants are the product of late spawning adults, then the loss of a portion of this population segment from poor survival will eventually reduce the genetic fitness of the entire population or else select for an earlier life history timing (Reisenbichler 1997). This may apply to the Hanford Reach population, which produced many of the late migrants that we marked. Given the strength of this population, it is likely that any loss of genetic variability from late spawners may be offset by the conservation of traits passed on by early spawning fish. If, however, the entire population is placed at a survival disadvantage, then population decline will result. This may be true for Snake River fall chinook salmon, which are currently listed as .threatened. under the Endangered Species Act (NMFS 1992). Hydropower development has delayed the early life history of these fish and summer outmigration occurs later than their Columbia River counterparts. Median dates of passage of wild PIT-tagged Snake River fall chinook salmon past McNary Dam ranged from August 8-13 from 1995-1997 (William Connor, U.S. Fish and Wildlife Service, personal communication). This is the same time frame and in some years later in which we marked our late migrants for this study. It may be possible that the late migration timing of the Snake River fall chinook population may have partially contributed to its decline.

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LIST OF APPENDICES

Appendix 1. Allozyme loci

List of enzymes, Enzyme Commission (EC) numbers (IUBMBNC 1992), allozyme locus designations, relative mobilities of allelic variants, tissue screening, and electrophoresis buffers included in the analysis of Snake River juvenile chinook salmon.

Enzyme (EC number)	Locus	Relative mobilities of variant alleles
Aspartate aminotransferase (2.6.1.1)	sAAT-1,2*	85,105,91
	sAAT-3*	90,113,71
	sAAT-4*	130,63
	mAAT-1*	-77,-104
	mAAT-2*	-125,-90
Adenosine deaminase (3.5.4.4)	ADA-1*	83,69
	ADA-2*	105
Aconitate hydratase (4.2.1.3)	sAH*	86,112,108,69
	mAH-1*	65,130
	mAH-2*	83
	mAH-3*	126,74
	mAH-4*	119,112,136
Formaldehyde dehydrogenase (1.2.1.1)	FDHG*	143,131,65,28
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	GAPDH-2*	22
	GAPDH-3*	123
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	G3PDH-3*	112,90
	G3PDH-4*	114
Glucose-6-phosphate isomerase (5.3.1.9)	GPI-B1*	-65
	GPI-B2*	60,135,24
	GPI-A*	105,93,85
	GPIr*	null/null phenotype
Glutathione reductase (1.6.4.2)	GR*	85,110,89,117,71
l-Iditol 2-dehydrogenase (1.1.1.14)	IDDH-1*	-50
	IDDH-2*	61
Isocitrate dehydrogenase (NADP+) (1.1.1.42)	mIDHP-1*	147,30
	mIDHP-2*	154,50
	sIDHP-1*	74,142,94,129,126
	sIDHP-2*	127,50,83,66
l-Lactate dehydrogenase (1.1.1.27)	LDH-B1*	60
	LDH-B2*	112,134,71
	LDH-C*	90,84
Malate dehydrogenase (1.1.1.37)	sMDH-A1,2*	120,27,-45,160
	sMDH-B1,2*	121,70,83,126
	mMDH-1*	
	mMDH-2*	200,180,-55
	mMDH-3*	190
Malic enzyme (NADP+) (1.1.1.40)	sMEP-1*	92,105,86
	sMEP-2*	78/78 phenotype
Mannose-6-phosphate isomerase (5.3.1.8)	MPI*	109,95,113,103
Dipeptidase (3.4.13.18)	PEPA*	90,86,81

Appendix 1. Allozyme loci -extended

Tissues[a]	Buffers[b]
M,H	2,3
E	1,2
L	2,4
M,H	2,3
M,H	2,3
M,H	1
M,H	1
L	2,4
H	2
H	2
M,H	2
M,H	2
E,H	1
H	2a
H	2a
H	2
M,H	2
M	1
M	1
M	1
M	1
M,E,H	2,3
L	4
L	4
M,H	2
M,H	2
M,E,H,L	2,3
M,E,H,L	2,3
E	1,2
E,L	1,2
E	1,2
M,H,L	2
M,H	2
H	2
M,H	2
M,H	2
M,H	3
M,H	3
M,E,H	1
M,E	1

Appendix 1.-continued

Enzyme (EC number)	Locus	Relative mobilities of variant alleles
Tripeptide aminopeptidase (3.4.11.4)	PEPB-1*	130,-350,45
	PEPB-2*	
Proline dipeptidase (3.4.13.9)	PEPD-2*	107,83
Leucyl-l-tyrosine peptidase (3.4.-.-)	PEP-LT*	110,120,88
Phosphogluconate dehydrogenase (1.1.1.44)	PGDH*	90,85,95
Phosphoglycerate kinase (2.7.2.3)	PGK-2*	90,74,95
Phosphoglucomutase (5.4.2.2)	PGM-1*	210,165,50
	PGM-2*	166,136,63
Superoxide dismutase (1.15.1.1)	sSOD-1*	-260,580,1260,-175
	sSOD-2*	120
	mSOD*	142,70
Triose-phosphate isomerase (5.3.1.1)	TPI-1*	-155
	TPI-2*	-400
	TPI-3*	104,106,96
	TPI-4*	104,75,102

[a] M = muscle, H = heart, E = eye, L = liver

[b] 1 = TG, tris-glycine pH 8.5 (Holmes and Masters 1970); 2 = CAME, citrate amine pH 6.8 (Clayton and Tretiak 1972) modified with 1mM EDTA, 2a includes addition of NAD to electrode tray buffer; 3 = TC-4, tris-citrate pH 5.95 (Schaal and Anderson 1974); 4 = RW, tris-citric acid gel buffer pH 8.2 and lithium hydroxide-boric acid electrode buffer pH 8.0 (Ridgway et al. 1970).

Appendix 1.-continued -extended

Tissues[a]	Buffers[b]
M,H	1,3
H	1
M,H	2,3
M	1,3
M,E	2
M,E	2
M,H	1
M,H	1
M,H,L	1,3,4
H	3
M,H	1,3
M,E	1
M,E	1
M,E	1
M,E	1

Appendix 2: Allele Frequencies

Allele frequencies at 28 loci for juvenile Snake River chinook salmon estimated to be fall race in four years, and for three years' samples combined. The following 12 loci, which often show variant alleles in other chinook salmon populations, had a frequency of 1.000 for the *a (100) allele in all estimated fall race samples: sAAT-1,2*[a], AAT-3*, ADA-2*, mAH-3*, sMDH-A1,2*[a], PEPD-2*, PGDH*, PGM-1*, PGM-2*, and mSOD*. The number of fish successfully scored per locus is denoted by N.

Locus, allele code (mobility)[b]	Snake River juvenile fall race samples, Sample year (Brood year)				
	91 (90)	93 (92)	94 (93)	95 (94)	93-95 (92-94)
sAAT-4*					
N	142	50	110	110	270
*a (100)	0.993	1.000	0.959	0.986	0.978
*b (63)	0.007	0.000	0.041	0.014	0.022
mAAT-1*					
N	142	59	114	111	284
*a (-100)	0.975	0.975	0.965	0.968	0.968
*b (-77)	0.025	0.000	0.026	0.023	0.019
*c (-104)	0.000	0.025	0.009	0.009	0.012
mAAT-2*					
N	104	52	95	109	256
*a (-100)	0.716	0.644	0.721	0.794	0.736
*c (-90)	0.284	0.356	0.279	0.206	0.264
ADA-1*					
N	143	59	114	111	284
*a (100)	1.000	0.983	1.000	1.000	0.996
*b (83)	0.000	0.017	0.000	0.000	0.004
sAH*					
N	143	58	112	111	281
*a (100)	0.892	0.914	0.835	0.869	0.865
*b (86)	0.101	0.086	0.152	0.131	0.130
*d (108)	0.007	0.000	0.013	0.000	0.005
mAH-4*					
N	142	50	103	109	262
*a (100)	0.912	0.830	0.913	0.881	0.884
*b (119)	0.088	0.170	0.087	0.119	0.116

Appendix 2.-continued

Locus, allele code (mobility)[b]	Snake River juvenile fall race samples Sample year (Brood year)				
	91 (90)	93 (92)	94 (93)	95 (94)	93-95 (92-94)
FDHG*					
N	143	59	115	111	285
*a (100)	0.983	0.992	0.996	0.982	0.989
*b (143)	0.017	0.008	0.004	0.018	0.011
GPI-B2*					
N	129	35	87	100	222
*a (100)	0.973	1.000	0.983	0.975	0.982
*b (60)	0.027	0.000	0.017	0.025	0.018
GPI-A*					
N	138	53	100	106	259
*a (100)	0.996	1.000	1.000	1.000	1.000
*b (105)	0.004	0.000	0.000	0.000	0.000
GPIr*[c]					
N	133	42	82	105	229
*a (100)	0.992	1.000	0.963	0.943	0.961
*b (null)	0.008	0.000	0.037	0.057	0.039
GR*					
N	143	59	115	111	285
*a (100)	0.997	0.975	0.965	0.995	0.979
*b (85)	0.003	0.025	0.035	0.005	0.021
mIDHP-2*					
N	143	59	115	111	285
*a (100)	0.983	1.000	0.974	0.982	0.982
*b (154)	0.017	0.000	0.026	0.018	0.018
sIDHP-1*					
N	143	57	113	111	281
*a (100)	1.000	0.991	0.996	1.000	0.996
*c (74)	0.000	0.000	0.004	0.000	0.002
*l (126)	0.000	0.009	0.000	0.000	0.002

Appendix 2.-continued

Locus, allele code (mobility)[b]	Snake River juvenile fall race samples, Sample year (Brood year)				
	91 (90)	93 (92)	94 (93)	95 (94)	93-95 (92-94)
sIDHP-2*					
N	143	57	114	111	282
*a (100)	0.930	0.912	0.803	0.914	0.869
*b (127)	0.063	0.079	0.167	0.086	0.117
*g (83)	0.007	0.009	0.031	0.000	0.014
LDH-B2*					
N	143	59	115	111	285
*a (100)	1.000	1.000	0.996	1.000	0.998
*d (71)	0.000	0.000	0.004	0.000	0.002
LDH-C*					
N	143	59	113	111	283
*a (100)	1.000	0.975	0.996	0.986	0.988
*b (90)	0.000	0.025	0.004	0.014	0.012
sMDH-B1,2*[a]					
N	143	59	115	111	285
*a (100)	0.976	0.954	0.983	0.977	0.975
*b (121)	0.010	0.017	0.015	0.007	0.012
*c (70)	0.014	0.025	0.002	0.016	0.012
*e (126)	0.000	0.004	0.000	0.000	0.001
mMDH-2*					
N	142	59	113	111	283
*a (100)	0.975	0.958	0.991	0.950	0.968
*b (200)	0.021	0.042	0.009	0.032	0.025
*d (-55)	0.004	0.000	0.000	0.018	0.007
sMEP-1*					
N	143	58	111	110	279
*a (100)	0.734	0.819	0.811	0.755	0.791
*b (92)	0.266	0.181	0.189	0.245	0.209
MPI*					
N	143	59	115	111	285
*a (100)	0.654	0.780	0.700	0.640	0.693
*b (109)	0.346	0.220	0.300	0.360	0.307

Appendix 2.-continued

Locus, allele code (mobility)[b]	Snake River juvenile fall race samples, Sample year (Brood year)				
	91 (90)	93 (92)	94 (93)	95 (94)	93-95 (92-94)
PEPA*					
N	143	59	115	111	285
*a (100)	0.979	0.966	1.000	0.959	0.977
*b (90)	0.021	0.034	0.000	0.041	0.023
PEPB-1*					
N	143	59	115	111	285
*a (100)	0.853	0.847	0.743	0.806	0.789
*b (130)	0.147	0.144	0.252	0.180	0.202
*c (-350)	0.000	0.008	0.004	0.014	0.009
PEP-LT*					
N	140	57	98	106	261
*a (100)	0.829	0.860	0.883	0.882	0.877
*b (110)	0.171	0.140	0.117	0.118	0.123
PGK-2*					
N	143	59	113	111	283
*a (100)	0.566	0.585	0.602	0.577	0.588
*b (90)	0.434	0.415	0.398	0.423	0.412
sSOD-1*					
N	143	59	115	111	285
*a (100)	0.629	0.754	0.570	0.595	0.618
*b (-260)	0.367	0.246	0.430	0.405	0.382
*e (-175)	0.003	0.000	0.000	0.000	0.000
sSOD-2*					
N	115	37	20	108	165
*a (100)	0.883	0.905	0.850	0.861	0.870
*b (120)	0.117	0.095	0.150	0.139	0.130
TPI-4					
N	143	59	115	111	285
*a (100)	0.997	0.992	0.961	1.000	0.982
*b (104)	0.003	0.008	0.039	0.000	0.018

[a] These isolocus pairs represent two loci whose common alleles have the same electrophoretic mobility, and in which variant alleles can not be assigned to either locus. Frequencies are for

Appendix 2.-continued

both loci combined (4 alleles per isolocus).
[b] Allele codes (*a, *b, etc.) and relative mobilities follow standards accepted by participants in the Coast-Wide Genetic Stock Identification Consortium for Chinook Salmon.
[c] Genotypic frequencies for the phenotypes 100/100 and null/null are presented. Heterozygous phenotypes are not scorable.