North American Journal of Fisheries Management 22:703–712, 2002
American Fisheries Society 2002

Juvenile Life History of Wild Fall Chinook Salmon in the Snake and Clearwater Rivers

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Abstract.—Dam construction in the 1950s and 1960s blocked passage to the historical spawning area of Snake River fall chinook salmon *Oncorhynchus tshawytscha*. We obtained water temperature data and collected juvenile fall chinook salmon in three present-day spawning areas from 1992 to 2000 to investigate the relation between water temperature and juvenile life history events. We used historical water temperatures and the literature to depict juvenile life history in the historical spawning area. Water temperatures in the three present-day spawning areas differed significantly from winter to spring, when eggs were incubating ($P \leq 0.0001$), as well as during spring, when juveniles were rearing and starting seaward migration ($P \leq 0.0001$). When water temperatures were warmer, the timing of most life stages was generally earlier. The life stages included fry emergence ($r^2 = 0.85$, $N = 14$, $P < 0.0001$), growth to parr size ($r^2 = 0.94$, $N = 15$, $P < 0.0001$), and smolt emigration ($r^2 = 0.93$, $N = 14$, $P < 0.0001$). The percentage of parr that overwintered in freshwater and migrated seaward the next spring increased when spring water temperatures decreased ($r^2 = 0.40$, $N = 12$, $P = 0.02$). As the historical spawning area was warmer than present-day spawning areas, fall chinook salmon juvenile life history progressed on an earlier time schedule. We conclude that dam construction changed juvenile fall chinook salmon life history in the Snake River basin by shifting production to areas with relatively cool water temperatures and comparatively lower growth opportunity.

Construction of dams altered the freshwater habitat of anadromous salmonids in North America (e.g., Moffitt et al. 1982; Wunderlich et al. 1994; Kondolf et al. 1996; Dauble and Watson 1997; Dauble and Geist 2000). Dam construction can effect population declines, especially if historical spawning and rearing habitats are eliminated or migration corridors are impounded. This was the case with the Snake River stock of fall chinook salmon *Oncorhynchus tshawytscha* listed as threatened under the Endangered Species Act in 1992 (NMFS 1992).

Prior to 1963, the primary area for Snake River fall chinook salmon production was in a 49-km reach of river between Swan Falls Dam and Marsing, Idaho (Groves and Chandler 1999), which we refer to as the Marsing reach of the Snake River (Figure 1). Fall chinook salmon were extirpated from the Marsing reach following construction of Brownlee, Oxbow, and Hells Canyon dams. Lower Granite, Little Goose, Lower Monumental, and Ice Harbor dams impounded the lower 224 km of the Snake River by 1975. This left a continuous 173-km reach of riverine habitat between Hells Canyon Dam and the upper end of Lower Granite Reservoir for fall chinook salmon production. Spawners also had access to the lower reaches of the Imnaha, Salmon, Grande Ronde, and Clearwater rivers (Figure 1), but the historical evidence that these rivers supported the Snake River stock of fall chinook salmon is not conclusive.

From 1991 to 1999, annual redd searches were conducted in the Snake, Imnaha, Salmon, and Grande Ronde rivers and in the Clearwater River basin (Idaho Power Company, Nez Perce Tribe, and U. S. Fish and Wildlife Service, unpublished data). A grand total of 1,867 fall chinook salmon redds was counted with an inter-annual range of 54–579. Timing of redd construction ranged from October to early December with a peak in early to mid November. Approximately 58% of the redds was counted in the Snake River, 27% in the lower Clearwater River, and 15% in the other areas combined.

Offspring of fall chinook salmon spawners make up the majority of wild fry and parr that inhabit

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Received February 6, 2001; accepted October 31, 2001

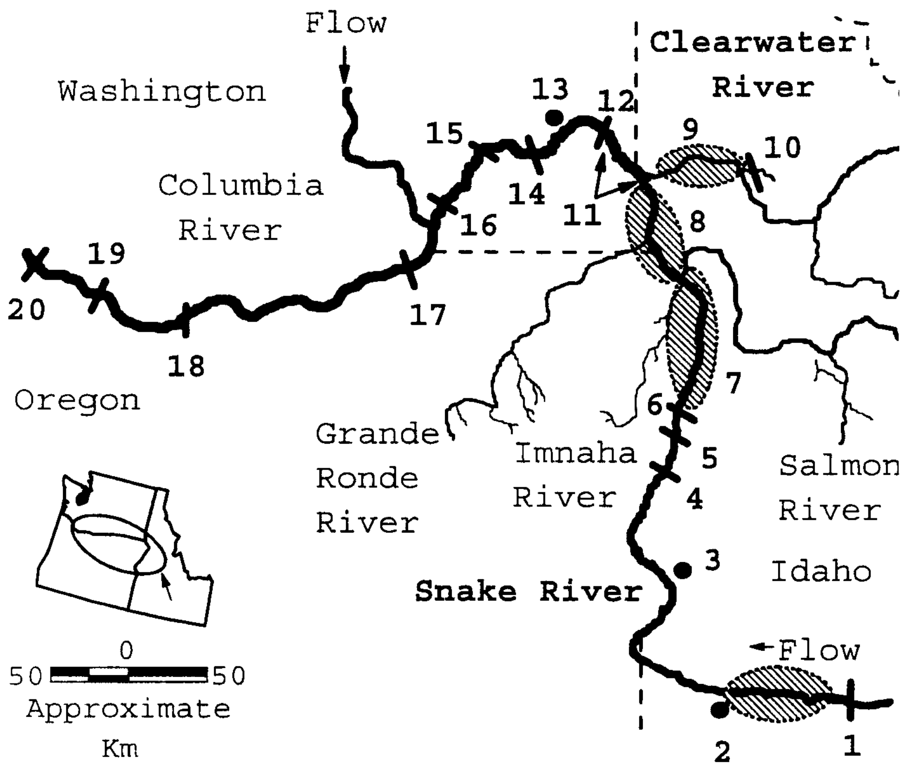

FIGURE 1.—Locations of the upper and lower reaches of the Snake River and the lower Clearwater River, the sites where adult fall chinook salmon spawn and their offspring were captured with a beach seine (the three northernmost crosshatched ellipses), the historical spawning area between Swan Falls Dam and Marsing, Idaho (the southernmost crosshatched ellipse), and other landmarks. The locations are as follows: 1 = Swan Falls Dam; 2 = Marsing, Idaho; 3 = dipper trap (Krcma and Raleigh 1970); 4 = Brownlee Dam; 5 = Oxbow Dam; 6 = Hells Canyon Dam; 7 = upper reach of the Snake River; 8 = lower reach of the Snake River; 9 = lower Clearwater River; 10 = Dworshak Dam; 11 = Lower Granite Reservoir; 12 = Lower Granite Dam (PIT tag monitoring); 13 = fyke net collection site (Mains and Smith 1964); 14 = Little Goose Dam (PIT tag monitoring); 15 = Lower Monumental Dam (PIT tag monitoring); 16 = Ice Harbor Dam; 17 = McNary Dam (PIT tag monitoring); 18 = John Day Dam (PIT tag monitoring); 19 = The Dalles Dam; 20 = Bonneville Dam (PIT tag monitoring).

the shorelines of the Snake and lower Clearwater rivers. From 1995 to 1997, genetic samples showed that 100% of the wild chinook salmon in the Snake River upstream of the Salmon River confluence (hereafter, the upper reach; Figure 1) were subyearling fall chinook salmon (Marshall et al. 2000; W. P. Connor, unpublished data). From 1993 to 1998, roughly 76% of the wild subyearling chinook salmon in the Snake River between the Salmon River confluence and the upper end of Lower Granite Reservoir (hereafter, the lower reach; Figure 1) was progeny of fall chinook salmon spawners (Connor et al. 2001a). The remaining 24% was offspring of spring and summer chinook salmon that spawn in low-order streams in the Snake River basin. These wild subyearling spring and summer chinook salmon dispersed long distances from natal streams into the Snake River where they reared and migrated seaward a little earlier than fall chinook salmon (Connor et al. 2001a, 2001b). Small amounts of data also suggest the presence of early rearing and seaward migrating subyearling spring chinook salmon in the lower Clearwater River (Connor, unpublished data). For simplicity, we refer to the wild subyearling chinook that inhabit present-day spawning areas as fall chinook salmon.

In this paper, we describe and compare the water temperature regimes of the upper and lower reaches of the Snake River and the lower Clearwater River. We describe and compare life history of juvenile fall chinook salmon in these three spawning areas. We test the relation between water temperature and juvenile life history events. We use historical water temperature data, growth opportunity theory (Metcalfe and Thorpe 1990; Taylor 1990), and past studies to depict juvenile fall chinook salmon life history in the Marsing reach of the Snake before dam construction.

Methods

Water temperature and life history data were aggregated by brood year. For example, mean water temperature from winter 1991 to spring 1992 was reported as water temperature in brood year 1991. Young fall chinook salmon collected in spring of 1995, which were spawned in 1994, are identified as being from brood year 1994.

Water temperature data.—Data for brood years 1991–1998 were collected using hourly recording thermographs or standard U. S. Geological Survey temperature monitoring equipment. Thermograph locations in the Snake River varied by year and flow level, but included stations at river kilometers (rkms) 383, 369, 346, 325, and 303 in the upper reach of the Snake River and rkms 290, 287, 274, 265, and 251 in the lower reach of the Snake River. Data were collected at rkm 35 (brood years 1992–1994) and rkm 19 (brood years 1991 and 1995–1998) in the lower Clearwater River. Data for the Marsing reach of the Snake River were collected at Swan Falls Dam for brood years 1960–1969 with a continuously recording thermograph.

Daily mean water temperatures were calculated from thermograph output. Data for two or more thermographs in the Snake River were averaged within a reach to provide one daily mean water temperature value. Missing daily mean values were predicted by using ordinary least-squares regression (r^2 = 0.93–0.99). For example, missing daily mean values were predicted for October 15–22, 1968, based on a regression model fit using observed day of year (e.g., January 1 = 1) and daily mean water temperatures collected 2 weeks before October 15 and 2 weeks after October 22.

We calculated two water temperature indices from the daily mean water temperature data to compare spawning areas and for regression analyses. Winter–spring (December 21 to June 20) water temperatures were used to index conditions during egg incubation and fry emergence. Mean spring (March 20 to June 20) water temperatures were used to index conditions during shoreline rearing and the onset of seaward migration.

Life history.—We sampled the upper reach of the Snake River during brood years 1994–1999, the lower reach of the Snake River during brood years 1991–1999, and the lower Clearwater River during brood years 1992–1994. We captured juvenile fall chinook salmon by using a beach seine (Connor et al. 1998). Sampling typically started in April, soon after fry began emerging from the gravel, and was conducted 1 d/week at permanent stations within each spawning area. Once a majority of fish were at least 60 mm fork length, we sampled additional stations in each spawning area for three consecutive weeks. We discontinued all sampling in June or July when the majority of fish had moved into Lower Granite Reservoir or to points further downstream.

We used the capture dates of fish under 46 mm fork length to describe fry emergence timing. We used the capture dates for fish over 45 mm fork length to describe the timing when fish achieved parr size. All capture dates were adjusted to Sunday's date the week of sampling to account for differences in day of sampling among the three spawning areas (e.g., a Sunday capture date was assigned to fry and parr collected on the following Tuesday).

We inserted passive integrated transponder (PIT) tags (Prentice et al. 1990a) into parr 60 mm or longer (fork length; Connor et al. 1998). Tagged parr were released at the collection site after a 15-min recovery period. Juvenile bypass systems of dams equipped with PIT tag monitors (Matthews et al. 1977; Prentice et al. 1990b; Figure 1) detected some of the tagged fish as smolts as they passed downstream. Operation schedules for the fish bypass systems varied by dam and year. Most of the detections were from the systems of Lower Granite, Little Goose, and Lower Monumental dams (operated from early April to early November) and the McNary Dam (operated from early April to early December).

We used the detection data collected at Lower Granite Dam, which is the first dam encountered en route to the Pacific Ocean, to represent smolt emigration timing. We used the detection data collected at all dams equipped with PIT tag monitoring equipment to determine the annual percentage of tagged fish that overwintered in freshwater and migrated seaward the next spring. We calculated this percentage as follows: number of fish released in year t that were last detected in year $t + 1$, divided by the total number of fish released in year t that were detected in years t and $t + 1$, multiplied by 100.

Statistical analyses.—We calculated grand mean winter–spring and spring water temperatures. For example, grand mean winter–spring water temperature was calculated as the mean of all the mean

TABLE 1.—Seasonal mean water temperatures (°C) for the upper and lower reaches of the Snake River and the lower Clearwater River during fall chinook salmon brood years 1991 to 1998. All three grand means (°C ± SE) within each seasonal period were significantly (α = 0.05) different.

	Winter–spring			Spring		
Brood year	Upper reach, Snake River	Lower reach, Snake River	Lower Clearwater River	Upper reach, Snake River	Lower reach, Snake River	Lower Clearwater River
1991	8.9	9.0	7.9	12.7	12.9	11.1
1992	7.6	7.1	5.7	11.8	11.0	8.6
1993	8.0	7.8	6.3	12.0	11.8	9.2
1994	8.2	7.6	5.7	11.8	10.9	8.2
1995	8.7		6.1	12.7		8.2
1996	8.7	7.9	6.8	12.4	11.2	8.9
1997	8.3	8.1	7.3	12.0	11.5	9.9
1998	8.5	7.5	6.3	12.3	10.6	8.2
Grand means	8.4 ± 0.2	7.9 ± 0.2	6.5 ± 0.3	12.2 ± 0.1	11.4 ± 0.3	9.0 ± 0.4

annual winter–spring water temperatures. We compared grand mean water temperatures by seasonal period among the three spawning areas using analysis of variance (ANOVA; α = 0.05) and a randomized block design (year = blocks and spawning areas = treatment). Tukey pair-wise comparisons (α = 0.05) were made to test for significant differences between grand means of two spawning areas.

We were unable to sample all three spawning areas every year, so we did not statistically test for differences in life history. We generally compared life history based on the grand mean dates of fry emergence, growth to parr size, smolt emigration, and the grand mean percentage of fish that overwintered in freshwater and emigrated seaward the next spring.

We used ordinary least-squares regression (α = 0.05) to test the relation between water temperature and life stage timing and the percentage of fish that overwintered in freshwater and migrated seaward the next spring. We tested four null hypotheses: (1) fry emergence timing is not related to winter–spring water temperature; (2) timing of growth to parr size is not related to spring water temperature; (3) smolt emigration timing is not related to spring water temperature; and (4) the percentage of fish that overwinter in freshwater and emigrate seaward the next spring is not related to spring water temperature.

Results

Water Temperature Brood Years 1991–1998

Winter–spring water temperatures (Table 1) among the upper and lower reaches of the Snake River and the lower Clearwater River differed significantly ($P \leq 0.0001$), as did spring temperatures ($P \leq 0.0001$). In both seasonal periods the upper reach of the Snake River was the warmest, followed by the lower reach of the Snake River and then the lower Clearwater River.

Life History

Fry emerged earliest in the upper reach of the Snake River, followed by the lower reach of the

TABLE 2.—Wild fall chinook salmon fry (<45 mm fork length) emergence timing (calendar date medians and ranges adjusted to Sunday's date for each week) and sample sizes (N) for the upper and lower reaches of the Snake River and lower Clearwater River, brood years 1991 to 1999. Grand means are reported as day of year ± SE.

	Upper reach, Snake River		Lower reach, Snake River		Lower Clearwater River	
Brood year	Median (range)	N	Median (range)	N	Median (range)	N
1991			Apr 26 (Mar 29–May 24)	355		
1992			May 16 (Apr 4–Jun 20)	199	Jun 27 (Jun 27–Jul 4)	18
1993			May 15 (Apr 3–Jun 5)	440	Jun 5 (Apr 24–Jun 26)	54
1994	Apr 23 (Apr 2–May 21)	117	Apr 30 (Apr 2–Jun 4)	257	Jun 18 (Apr 2–Jul 2)	90
1995	Apr 28 (Apr 14–May 5)	14	May 5 (Apr 14–Jun 23)	268		
1996		1	May 4 (Apr 20–Jun 29)	114		
1997	Apr 19 (Apr 12–May 10)	101	Apr 26 (Apr 12–Jun 14)	322		
1998	May 2 (Apr 4–May 23)	97	May 2 (Apr 4–Jun 27)	278		
1999	Apr 9 (Apr 2–May 14)	683	Apr 9 (Apr 2–Jun 4)	415		
Grand means	113 ± 4		122 ± 4		168 ± 6	

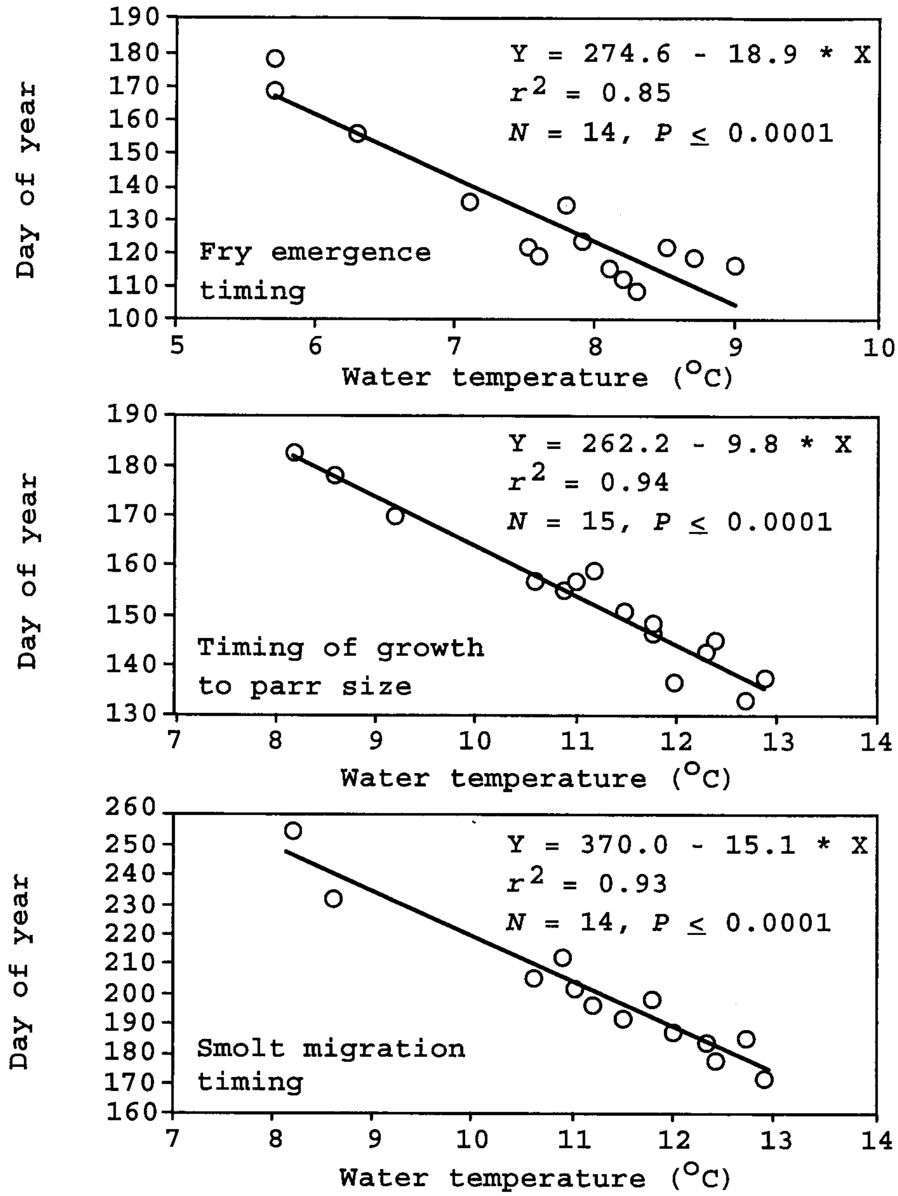

FIGURE 2.—The relations between life history events (Y) and water temperature (X) for wild fall chinook salmon in the upper and lower reaches of the Snake River and the lower Clearwater River. The timing of fry emergence is a function of winter–spring water temperature, that of growth to the parr stage and smolt migration a function of spring water temperature. Data for the regressions are given in Tables 1–4.

Snake River and then the lower Clearwater River (Table 2). Fry generally emerged earlier when mean winter–spring water temperature was warmer than when it was cooler ($P < 0.0001$; Figure 2.

Parr size was achieved earliest in the upper reach of the Snake River and latest the lower Clearwater River (Table 3). Growth to parr size was generally earlier when the mean spring water temperatures were warmer rather than cooler ($P \leq 0.0001$; Figure 2).

We PIT-tagged a grand total of 13,605 parr, of which a grand total of 2,663 smolts were subsequently detected as they passed Lower Granite Dam. Smolt emigration timing was earliest for fish tagged in the upstream reach of the Snake River and latest for fish tagged in the Lower Clearwater

TABLE 3.—Timing of wild fall chinook salmon growth to parr size (>45 mm fork length) as the median and range of calendar date (adjusted to Sunday's date for each week) and sample size (N) for the upper and lower reaches of the Snake River and lower Clearwater River, brood years 1991 to 1999. Grand means are reported as day of year ± SE.

	Upper reach, Snake River		Lower reach, Snake River		Lower Clearwater River	
Brood year	Median (range)	N	Median (range)	N	Median (range)	N
1991			May 17 (Mar 29–Jun 7)	1,765		
1992			Jun 6 (Apr 11–Jul 18)	2,215	Jun 27 (Jun 27–Jul 18)	533
1993			May 29 (Apr 3–Jul 10)	4,346	Jun 19 (Apr 10–Jul 10)	967
1994	May 28 (Apr 9–Jun 18)	985	Jun 4 (Apr 2–Jul 2)	1,408	Jul 2 (May 7–Jul 23)	695
1995	May 12 (Apr 14–Jun 16)	118	May 26 (Apr 14–Jul 14)	756		
1996	May 25 (Apr 20–Jun 15)	119	Jun 8 (Apr 20–Jul 13)	938		
1997	May 17 (Apr 12–Jul 5)	1,078	May 31 (Apr 12–Jul 5)	2,512		
1998	May 23 (Apr 11–Jun 27)	1,493	Jun 6 (Apr 4–Jul 11)	1,647		
1999	Apr 23 (Apr 2–Jun 11)	1,064	May 14 (Apr 2–Jun 25)	1,578		
Grand means	137 ± 5		150 ± 3		177 ± 4	

River (Table 4). Smolts generally began emigration earlier when mean spring water temperatures were warmer rather than cooler ($P \leq 0.0001$; Figure 2).

A grand total of 3,528 of the PIT tagged parr were detected as smolts as they passed dams in the lower Snake and Columbia rivers. The percentage of fish that overwintered in freshwater and emigrated the next spring generally increased as spring water temperature decreased ($P = 0.02$; Figure 3) and was lowest for the upper reach of the Snake River and highest for the lower Clearwater River (Table 5).

Water Temperature Brood Years 1960–1969

On average, winter–spring water temperature for brood years 1960–1969 were 1–3°C warmer in the Marsing reach of the Snake River than in the three contemporary spawning areas during brood years 1991–1998 (Tables 1, 6). Mean spring water temperatures were also an average of 2–4°C warmer in the Marsing reach of the Snake River than in the three contemporary spawning areas.

Discussion

Life history of juvenile fall chinook salmon in the upper and lower reaches of the Snake River and the lower Clearwater River progressed on three separate but overlapping time schedules. We did not collect data to establish causal linkages between this finding and every factor that can affect life history variation in juvenile anadromous salmonids. Differences in the temperature regimes, however, offer the most plausible explanation for the life history variation we observed.

Emergence timing differed among fry of the contemporary spawning areas largely because the rate of egg development is positively correlated with water temperature and because water temperature varied among spawning areas. Timing of growth to parr size, which was a crude measure

TABLE 4.—Smolt migration timing (medians and ranges of calendar dates) at Lower Granite Dam and sample size (N) for wild fall chinook salmon that were initially captured, tagged with passive integrated transponders, and released in the upper and lower reaches of the Snake River and lower Clearwater River, brood years 1991 to 1999. Grand means are reported as day of year ± SE.

	Upper reach, Snake River		Lower reach, Snake River		Lower Clearwater River	
Brood year	Median (range)	N	Median (range)	N	Median (range)	N
1991			Jun 20 (May 4–Jul 21)	39		
1992			Jul 21 (May 31–Oct 25)	234	Aug 20 (Jul 14–Oct 5)	19
1993			Jul 17 (May 23–Nov 1)	193		1
1994	Jul 18 (Jun 4–Oct 24)	203	Aug 1 (Jun 2–Oct 26)	238	Sep 12 (Jul 2– Oct 30)	30
1995	Jul 4 (May 20–Jul 25)	19	Jul 22 (May 17–Oct 31)	126		
1996	Jun 27 (Jun 4–Aug 13)	22	Jul 16 (Jun 14–Oct 13)	97		
1997	Jul 7 (May 19–Aug 21)	173	Jul 11 (May 29–Oct 19)	380		
1998	Jul 3 (Jun 2–Aug 28)	319	Jul 25 (Jun 1–Aug 30)	241		
1999	Jun 27 (May 6–Jul 18)	72	Jul 2 (May 18–Oct 28)	257		
Grand means	186 ± 3		196 ± 4		244 ± 12	

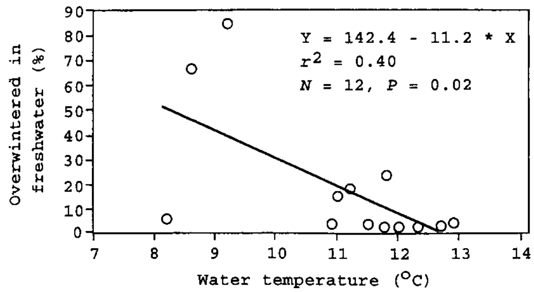

FIGURE 3.—The relation between spring water temperature (X) and the percentage of wild fall chinook salmon tagged with passive integrated transponders that overwintered in freshwater and emigrated seaward the next spring (Y) based on detection data collected at dams in the Snake and Columbia rivers. Data for the regression are given in Tables 1 and 5.

of growth in fork length, varied among fish in the contemporary spawning areas, partly because of fry emergence timing. The differences in water temperature among spawning areas also help explain variability in timing of growth to parr size because growth of young fall chinook salmon increases as water temperature increases within a range of 10.0–18.3°C, provided that food is not limiting (Banks et al. 1971).

Water temperature also played a role in smolt migration timing. We suggest that there are two probable causes for this finding. Curet (1994) reported that juvenile fall chinook salmon remained along the shoreline of Lower Granite Reservoir later into the year when the water was cool and that dispersal from the shoreline occurred when water temperature exceeded 18.0°C. Researchers have also suggested that fast-growing chinook salmon progress from the parr to smolt stages earlier in life than do those that grow more slowly (Beckman and Dickhoff 1998; Connor et al. 2001b). Differences in timing of offshore movement and smoltification caused by water temperature differences among spawning areas would help explain the variability we observed in smolt migration timing.

Others have attributed variability in anadromous salmonid life history to water temperature variation. Metcalfe and Thorpe (1990) developed a growth opportunity index based on mean air temperature (used as a surrogate for water temperature) and photoperiod that explained 82% of the observed variability in age at smolting for wild Atlantic salmon *Salmo salar*. Juvenile Atlantic salmon that reared in warmer stream reaches migrated seaward earlier than those from cooler stream reaches. Taylor (1990) analyzed data from 160 chinook salmon populations from California to Alaska and showed that areas with low growth opportunity tended to produce juveniles that emigrated seaward as yearlings.

The results in our study are consistent with those of Metcalfe and Thorpe (1990) and Taylor (1990). The warmest contemporary spawning area, the upper reach of the Snake River, mainly fostered an "ocean-type" early life history (Healey 1991). Young fall chinook salmon emerged in spring, reared for 2–3 months and then emigrated seaward. The lower Clearwater River, which is the coolest of the contemporary spawning areas, sometimes produced juvenile chinook salmon with a "stream-type" early life history (Healey 1991). Fry emergence was in late spring and early summer. Many subyearling fall chinook salmon began seaward movement in summer and fall, overwintered in reservoirs, and then resumed emigration in spring.

TABLE 5.—The percentage of wild fall chinook salmon tagged with passive integrated transponders in the upper and lower reaches of the Snake River and the lower Clearwater River that overwintered in freshwater and migrated seaward the next spring (based on signal detection data collected at dams in the Snake and Columbia rivers) for brood years 1991 to 1999 and the total number of final detections (N). Grand means are reported ± SE.

	Upper reach, Snake River		Lower reach, Snake River		Lower Clearwater River	
Brood year	Percent	N	Percent	N	Percent	N
1991			4.4	68		
1992			15.7	351	67.1	70
1993			24.6	334	84.6	26
1994	0.9	328	3.8	364	6.3	48
1995	3.3	30	4.7	169		
1996	0.0	45	18.5	173		
1997	1.9	324	3.9	693		
1998						
1999	4.3	139	13.9	366		
Grand means	2.1 ± 0.8		11.2 ± 2.9		52.7 ± 23.7	

TABLE 6.—Seasonal means and the grand means ± SE for water temperatures in the Snake River as measured at Swan Falls Dam during brood years 1960 to 1969.

Mean temperatures (°C) by brood year										Grand mean
1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	
					Winter–spring					
9.5	10.2	9.0	9.7	8.5	9.1	9.7	9.9	10.0	10.2	9.6 ± 0.2
					Spring					
14.2	14.4	13.5	13.8	12.7	12.9	14.2	13.7	13.9	14.8	13.8 ± 0.2

Growth opportunity can be used as a basis for depicting juvenile fall chinook salmon life history in the Marsing reach of the Snake River. Historical redd surveys suggest that fall chinook salmon spawned at about the same time (if not earlier) as spawners in the contemporary areas (Idaho Department of Fish and Game, unpublished data). Therefore, the relatively warm Marsing reach of the Snake River would have fostered an ocean-type life history that progressed earlier than observed in contemporary spawning areas during the 1990s. Studies by Krcma and Raleigh (1970) and Mains and Smith (1964) support this depiction, especially when compared with the lower reach of the Snake River and the lower Clearwater River.

Krcma and Raleigh (1970) used a "migrant dipper" trap in 1962 and 1963 to capture offspring of adult fall chinook salmon that spawned in the Marsing reach of the Snake River in 1961 and 1962. The trap was located just upstream of Brownlee Reservoir (Figure 1), and it was operated daily from April through June. No fry were captured after mid-April in 1962, or after mid-May in 1963 (Krcma and Raleigh 1970). We captured fry in the lower reach of the Snake River from late May to early June, and in the lower Clearwater River from late June to early July. Approximately 98% of the juvenile fall chinook salmon population of the historical spawning area reached parr size and started emigrating by the end of May in both 1962 and 1963 (Krcma and Raleigh 1970). During the 1990s, an average of approximately 50% of the fish in the lower reach of the Snake River and lower Clearwater River had not grown to parr size or started to emigrate by the end of May.

Mains and Smith (1964) sampled juvenile anadromous salmonids in 1954 and 1955 using adjacent fyke nets that spanned the unimpounded Snake River at rkm 132 between the present locations of Lower Granite and Little Goose dams (Figure 1). Aging and genetic sampling were not conducted, but catch presumably included subyearling offspring of spring, summer, and fall chinook salmon that spawned throughout the Snake River basin in 1953 and 1954. Based on daily catch data, passage of the entire chinook salmon smolt run was complete by the end of June well before flow descended to base levels (Mains and Smith 1964). In the 1990s, by the end of June an average of less than 50% of the smolts from the three contempoary fall chinook salmon spawning areas had passed Lower Granite Dam at rkm 173.

Management Implications

We conclude that dam construction changed juvenile fall chinook salmon life history in the Snake River basin by shifting production to areas with relatively cooler water temperatures and comparatively lower growth opportunity. Consequently, smolt emigrations do not begin until late spring and summer. Smolt passage in the lower Snake River reservoirs occurs after spring runoff has ended, when summer water temperatures reach critical levels (Connor et al. 1998). Some young fall chinook salmon that survive in reservoirs over summer fail to reach the sea until they are yearlings.

The efficacy of the proposed Snake River fall chinook salmon recovery plan (NMFS 1995) relies in part on mitigation for dam-caused life history changes. Summer flow augmentation (Connor et al. 1998) and smolt transportation (Ward et al. 1997) are implemented annually to offset delays in seaward migration. Fishery managers need to know whether summer flow augmentation increases downstream migration rate and survival of smolts in Lower Granite Reservoir and whether transportation of smolts from Lower Granite Dam increases smolt-to-adult return rates. Research is also needed to determine if egg incubation and growth could be accelerated by selective releases of upstream reservoir water.

Acknowledgments

Employees of the U. S. Fish and Wildlife Service, Idaho Fishery Resource Office; Nez Perce

Tribe; Idaho Power Company; and U. S. Geological Survey collected the data used in our study. Personnel of the Pacific States Marine Fisheries Commission maintained the PIT tag database. We express special thanks to B. Arnsberg, C. Eaton, P. Groves, A. Garcia, D. Marvin, R. Nelle, M. Pishl, D. Rondorf, J. Sneva, D. Steele, C. Stein, and K. Tiffan. Early drafts of the manuscript were reviewed by D. Bennett, P. Bigelow, J. Congleton, R. Graves, and K. Steinhorst. The editor, an associate editor, and two anonymous reviewers improved the manuscript. Initial funding was provided by the U. S. Fish and Wildlife Service Lower Snake River Compensation plan, and continued funding was provided by the rate payers of the Bonneville Power Administration through Contract Number DE-AI79-91BP21708 administered by D. Docherty, M. Galloway, and M. Beeman.

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