

## Migration Timing, Growth, and Estimated Parr-to-Smolt Survival Rates of Wild Snake River Spring–Summer Chinook Salmon from the Salmon River Basin, Idaho, to the Lower Snake River

STEPHEN ACHORD,\* RICHARD W. ZABEL, AND BENJAMIN P. SANDFORD

National Oceanic and Atmospheric Administration, National Marine Fisheries Service,  
Northwest Fisheries Science Center, Fish Ecology Division,  
2725 Montlake Boulevard East, Seattle, Washington 98112-2097, USA

**Abstract.**—Survival, growth, and juvenile migration timing are key life history traits for at-risk salmon populations. To estimate these traits in threatened wild Snake River spring–summer Chinook salmon *Oncorhynchus tshawytscha*, we tagged fish as parr in 3–17 natal streams per year from 1991 to 2003. We injected passive integrated transponder tags into parr collected from streams within the Salmon River basin in Idaho. Each spring, after the previous summer’s tagging, fish were detected as smolts in the juvenile fish bypass systems of lower Snake River dams. Estimated parr-to-smolt survival to Lower Granite Dam (excluding migration year 1992) ranged from 3% to 48% for individual populations and from 8% to 25% (yearly average = 16%) for all streams combined. From 1998 to 2004, estimated parr-to-smolt survival declined from 25% to 8%, in part because of parr density-dependent effects. Overall annual average growth rates from tagging to detection at Little Goose Dam ranged from 39.7 to 43.3 mm during 2001–2004, and significant differences in growth were observed among sites and years. Growth of individuals was positively related to elapsed time between tagging and recapture and negatively related to fork length at tagging. Annual migration timing distributions for fish populations from the different streams varied highly within and between years. Timing of the 10th to 90th percentile passing Lower Granite Dam ranged from 20 to 45 d for the combined wild populations (average = 38 d). Median passage date was negatively related to autumn temperature, spring temperature, and March river flow, and was positively related to elevation of the tagging site. Baseline data generated by this project provide a foundation for understanding the biocomplexity of these populations, which is critical to effective recovery efforts for these threatened wild fish stocks.

In fish populations, age-specific survival and growth rates are key elements of population fitness (Gross 1987; Roff 1992). For migratory species, such as Pacific salmon *Oncorhynchus* spp., timing of the juvenile migration is often strongly related to subsequent survival (Randall et al. 1987; Zabel and Williams 2002) and thus is also a key component of fitness. Because of local adaptation (believed common in salmon populations; Ricker 1972; Taylor 1991) and variability in spawning and rearing habitats, these key life history traits typically vary among populations that comprise a species. Hilborn et al. (2003) concluded that this complexity in life history traits among Bristol Bay populations of sockeye salmon *O. nerka* fostered their continued existence under varying climatic conditions. Thus, understanding variability in life history traits among closely related salmon populations is useful not only for predicting the future viability of a population (Cole 1954) but also for developing effective recovery strategies for threatened populations.

The Snake River basin extends from Yellowstone

National Park in Wyoming and drains most of Idaho, a large portion of eastern Oregon, and southeastern Washington State. Salmon are excluded from the Snake River and tributaries upstream of Hells Canyon Dam. Presently, its major tributary, the Salmon River within central Idaho, produces the majority of spring–summer Chinook salmon. The lower part of the Snake River passes through southeastern Washington State and enters the Columbia River 522 km from the Pacific Ocean. Snake River spring–summer Chinook salmon *O. tshawytscha* spawn in late summer in small tributaries in Idaho and Oregon, where juveniles spend their initial rearing period (Matthews and Waples 1991). These fish are considered to be stream-type Chinook salmon (Gilbert 1912). Most stream-type juveniles migrate from their natal streams in late summer and fall to overwinter in larger rivers (Healey 1991) and initiate seaward migration during the following spring as smolts (Hoar 1976; Folmar and Dickhoff 1980). They subsequently spend 1–3 years in the Pacific Ocean, where the majority of their growth occurs before returning to spawn as adults.

Snake River spring–summer Chinook salmon were once part of the largest runs of Chinook salmon in the world (Netboy 1980) and produced an estimated 39–

\* Corresponding author: steve.achord@noaa.gov

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45% of all spring and summer Chinook salmon adults returning to the Columbia River (Matthews and Waples 1991). By the last decade of the 20th century, these populations had experienced a drastic decline due to dams, over-exploitation, habitat degradation, and misuse of fish hatcheries (NRC 1996). In 1991, Snake River spring–summer Chinook salmon were identified as an evolutionarily significant unit (ESU) based on its reproductive isolation and importance as an evolutionary component of the species (Matthews and Waples 1991; Waples 1991). In 1992, this ESU was listed as threatened in response to petitions under the U.S. Endangered Species Act (NMFS 1992).

This decline and listing prompted the need for more detailed monitoring of survival and migration behavior of wild juvenile spring–summer Chinook salmon. Although monitoring wild Snake River populations of Chinook salmon began in the early 1960s (Raymond 1979), information was only gathered on batch-marked fish after smolts began their downstream migration. With the development and application of passive integrated transponder (PIT) tag technology in the late 1980s (Prentice et al. 1990a, 1990b, 1990c), the ability existed to uniquely mark parr in their rearing habitats and record their subsequent movements throughout the lifetime of the fish (Achord et al. 1996). This allowed monitoring of survival, growth, and juvenile migration timing during the parr-to-smolt stage of cohorts from different habitats and populations.

We report research conducted since the early 1990s to characterize variability among years and streams in smolt migration arrival timing and parr-to-smolt survival for 16 wild populations of Chinook salmon in the Salmon River basin to Lower Granite Dam on the Snake River. We also relate these data to environmental factors for the purpose of explaining variability among years and streams. Finally, we report parr-to-smolt growth rates of these fish from 2001 to 2004. These data provide a foundation for understanding the biocomplexity of these populations, which is critical to effective recovery efforts.

### Study Area

Fish were collected and tagged in Idaho streams within the 36,000-km<sup>2</sup> Salmon River basin, which extends throughout most of central Idaho (Figure 1). The Salmon River headwaters begin at an elevation of 2,759 m, and the river flows 663 km to its confluence with the Snake River (303 km above the mouth) at an elevation of 270 m. Human population density in this region is low, and timber harvesting, mining and agriculture (predominately livestock grazing) are the dominant land use practices. The U.S. Forest Service and the Bureau of Land Management manage 89% of

the Salmon River basin; 27% of the basin is designated and managed as wilderness area. Collection areas in study streams ranged in elevation from 1,158 m in lower Big Creek to 2,017 m in Cape Horn Creek. Distances of the study streams to Lower Granite Dam (river kilometer [rkm] 173 on the Snake River) range from 429 km for the Secesh River to 756 km for Valley Creek. Lower Granite Dam is 695 km from the Pacific Ocean.

Fish were tagged in three streams in the South Fork Salmon River drainage: Lake Creek, Secesh River, and South Fork Salmon River. Nine streams were sampled in the Middle Fork Salmon River: Bear Valley, Camas, Cape Horn, Elk, Loon, lower Big–Rush, Marsh, Sulfur, and upper Big creeks. Five tributary streams were sampled off the main-stem Salmon River: Valley Creek, Herd Creek, East Fork Salmon River, Chamberlain Creek, and West Fork Chamberlain Creek. We collected and PIT-tagged wild spring–summer Chinook salmon parr during July and August of 1991–2003. During this period, we tagged fish in as few as 3 streams and as many as 17 streams each year; collection and tagging were dependent upon permits, area closures due to forest fires, and availability of sufficient parr densities (Table A.1).

In general, fish collections began in late July in streams of the upper Middle Fork Salmon River and continued for streams in the eastern part of the basin. Sampling in streams of the South Fork Salmon River was completed in late August. Minimum fish size for tagging and the timing of parr movement out of natal rearing areas were the major considerations that dictated stream order. The average crew size was nine people per stream, and frequently we worked in two streams simultaneously. This allowed us to complete up to 17 streams in a 5–6-week period.

### Methods

*Collection, PIT tagging, and release.*—Fish were collected and tagged from various established reaches of each stream. Two collection methods were used: electrofishing and seining. Seining was the preferred method due to the lower mortality caused by this collection method.

Where seining was possible, we positioned one seine securely across the lower end of a run or pool and placed a second seine across the stream, approximately 10 m upstream. The second seine was moved downstream, gently crowding fish toward the lower seine. Captured fish were maintained in ambient water by allowing the center of the seine to remain submerged. Fish were transferred in a water-tight sanctuary dip net (Matthews et al. 1986) to a 20-L

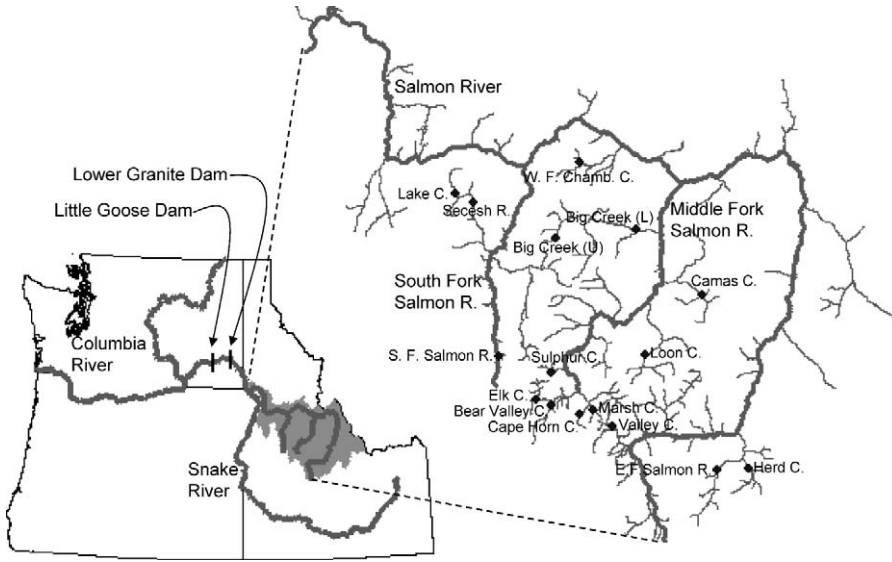


FIGURE 1.—Map of the Salmon River basin, Idaho, and Lower Granite and Little Goose dams on the Snake River, Washington. Locations where wild spring–summer Chinook salmon parr were tagged with passive integrated transponder tags are indicated.

bucket and were portaged to live-cages for subsequent tagging.

In many streams, low parr densities or difficult terrain prevented successful seining. Such streams were fished using Smith-Root model 12 electrofishers. Stunned fish were collected from the river with standard dip nets and placed in 20-L buckets for portaging to the live-cages. To minimize collection stress, we terminated all activity when water temperatures reached 16°C or when any other signs suggested an adverse effect on fish.

In 1991, we used an automatic tag injector with a push-rod system, which injected tags into the body cavity by means of air pressure (Prentice et al. 1990c). Thereafter, fish were tagged using individual modified syringes and hypodermic needles (Prentice et al. 1990c). To minimize disease transmission, tags and all associated equipment were disinfected for a minimum of 10 min with 70% ethanol. Beginning in 2000, we supplied medical-grade oxygen to the 20-L fish-transfer containers and to all pans and buckets during tagging operations. In 2001, oxygen use was expanded to collection buckets during electrofishing and seining.

Tagging was conducted at portable stations that were designed and constructed specifically for use beside streams (Prentice et al. 1990c; Achord et al. 1996). Detailed tagging procedures have been described elsewhere (Achord et al. 1996). When both fork length (FL; mm) and mass (g) were obtained on PIT-tagged

fish, we calculated the Fulton condition factor (CF; Ricker 1975; Anderson and Gutreuter 1983), defined as

$$CF = (\text{mass}/FL^3) \times 10^5.$$

After tagging, fish were allowed to recover in freshwater, transferred back to a live-cage in the stream, and held for a minimum of 0.5 h before being released, usually less than 100 m from the collection area. Approximately 8–12% of the fish were held in live-cages for 24 h to evaluate tag loss and delayed mortality.

*Monitoring at Little Goose Dam.*—Beginning in 2001, we used automated diversion gates in the juvenile fish bypass system at Little Goose Dam (Snake River rkm 113) to separate fish based on PIT tag code (Downing et al. 2001). Fish from our study streams were diverted to a holding tank for reexamination. Up to 100 wild fish from each study stream were collected using this separation-by-code system (Marsh et al. 1999; Downing et al. 2001). Recaptured fish were handled using water-to-water transfer and other best handling practices described by Matthews et al. (1997). Fish were anesthetized, scanned for PIT tags, measured, weighed, and allowed to recover before their return to the bypass system for release below the dam. We calculated the annual mean FL, mass, and CF for fish from each stream separately and compared the values to those at tagging.

*Survival and migration timing estimates at Lower Granite Dam.*—To estimate the number of tagged fish

from each stream that passed Lower Granite Dam each day during each migration year, we used the method of Schaefer (1951), as modified and detailed by Sandford and Smith (2002). For each day of the migration season, we estimated numbers of all wild Chinook salmon that were PIT-tagged above Lower Granite Dam and that passed the dam detected and undetected. We thus developed a series of daily detection estimates as follows. (1) Fish detected on a given day at Little Goose Dam that had previously been detected at Lower Granite Dam were tabulated according to their detection (passage) day at Lower Granite Dam. (2) Fish detected on the same day at Little Goose Dam that had not previously been detected at Lower Granite Dam were assigned an estimated nondetection passage day, assuming that the temporal distribution of undetected fish at Lower Granite Dam was proportionate to that of detected fish. (3) We repeated this process for all days of detection at Little Goose Dam. (4) We then summed all detected and undetected fish for a given day at Lower Granite Dam. (5) We estimated the day's detection probability by calculating the proportion of detected fish relative to the total (detected plus undetected fish) after adjusting for fish transported at Lower Granite Dam. We modified the method slightly for estimates in the tails of the passage distribution where the above process was not applicable (e.g., for days when no detections occurred at Little Goose Dam). Because too few fish from any one stream were detected daily, we pooled all PIT-tagged fish to make daily estimates of detection probability. Thus, by necessity, we assumed equal detection probabilities for fish from all streams passing on the same day. We summed the daily estimates of fish passage for each stream over the migration season and divided by the numbers of PIT-tagged parr released the previous summer, resulting in survival estimates for each stream.

Standard errors for individual stream survival estimates and annual totals were calculated using bootstrap methods (Efron and Tibshirani 1993). A bootstrap resample of the entire set of detection histories for all released fish and associated detection date information at Lower Granite Dam, Little Goose Dam, or both, were obtained. The Schaefer method was employed for each bootstrapped data set to produce a bootstrap set of daily detections at Lower Granite Dam. The observed daily detections at Lower Granite Dam for each stream were expanded by the bootstrap set of probabilities, resulting in bootstrap passage estimates; after dividing by the release numbers, we obtained bootstrap survival estimates for each stream. This process was repeated 1,000 times, resulting in 1,000 bootstrap survival estimates for each stream. The standard error for each stream's survival estimate (or

the original data set) was the standard deviation of these values. We used the process of bootstrapping the whole data set and a subsequent estimation process to capture the pertinent components of variability.

*Statistical analyses.*—We assessed variability between years and streams using analysis of variance (ANOVA) for estimated parr-to-smolt survival, growth, and various migration distribution statistics (i.e., 10th, 50th, and 90th percentiles, and the width of the 10th to 90th passage percentile). Year and stream were considered random factors. Because we did not have data from all streams in all years, these tests could provide only approximate comparisons between treatments. We compared means using Fisher's least significant difference procedure (Peterson 1985), and visually examined residuals to assess normality. Although we report timing and survival estimates for 1996 and 1997, we omitted those years from the ANOVA because fish from only three streams were tagged in each of the previous years.

We also related median passage date at Lower Granite Dam to a variety of factors in an attempt to explain variability among years or streams. To do this, we used general linear models that included either site (if the predictor variable varied by year) or year (if the predictor variable varied by site) as factors. Thus, for environmental factors, which varied yearly, we used the following model:

$$T_{s,y} = \beta_0 + \beta_s + \sum_{i=1}^n \beta_i \cdot X_{i,y} + \varepsilon_{s,y},$$

where  $T_{s,y}$  is the median passage date by site ( $s$ ) and year ( $y$ ),  $\beta_0$  is the regression constant coefficient,  $\beta_s$  is the coefficient for stream for variable  $i$ ,  $X_{i,y}$  is the value of predictor variable  $i$  in year  $y$ ,  $n$  is the number of predictor variables, and the error term  $\varepsilon$  is normally distributed. Similarly, if we were examining the influence of a predictor variable that varied across sites, we used the following model:

$$T_{s,y} = \beta_0 + \beta_y + \sum_{i=1}^n \beta_i \cdot X_{i,s} + \varepsilon_{s,y}.$$

We began by including all candidate predictor variables and used stepwise regression methods to remove terms that were not significant ( $P > 0.05$ ). For stream effects, we examined elevation (m) of the tagging site and distance (rkm) of the tagging site from Lower Granite Dam. For year effects, we tested mean monthly flow ( $\text{m}^3/\text{s}$ ) in the Salmon River measured at Whitebird, Idaho (the lowermost gauge station in the Salmon River basin), during the migration season (March–June) and seasonal average temperature ( $^{\circ}\text{C}$ ) from three sites in the Salmon River basin (seasons

defined as January–March, April–June, July–September, and October–December). We did not include tagging date as a predictor variable, as the fish were tagged in a relatively short time of a few weeks several months before (including winter) the smolt migration season. In addition, minimum fish size for tagging dictated stream tagging order, and the order was similar each year. Tagging date as a predictor variable was further confounded with stream site, elevation, and distance from the dam, all of which would probably affect survival and migration timing more so than would tagging date.

## Results

### *Fish Collection, Tagging, and Release*

Of 147,131 wild spring–summer Chinook salmon parr collected in Idaho streams from 1991 to 2003, 117,727 were PIT-tagged and released to their natal streams, along with nontagged live fish (Table A.1). Overall average yearly mortality associated with all parr collection and tagging activities was 1.5% (range = 0.5–2.6%). About 90% of this mortality rate (1.4%) was associated with collection activities (most from electrofishing), and the remainder was associated with tagging. Tag loss was almost nonexistent: only one lost tag was observed over 13 years.

In 5 of the 13 years from 1991 to 2003, there were from one to five streams where we collected comparable fish numbers by both seining and electrofishing. Subsequent detection rates at dams in the subsequent years for these groups indicated no long-term delayed mortality effect between fish captured by electrofishing (677 of 8,179, or 8.3%) and those captured by seining (638 of 7,918, or 8.1%).

The addition of medical grade oxygen during collection activities in 2000 and 2001 appeared to reduce the already low average yearly collection mortality from 1.6% for 1991–1999 to 0.9% for 2000–2003. The addition of oxygen did not reduce the already very low mortality associated with tagging (0.1–0.3%).

### *Estimated Parr-to-Smolt Survival to Lower Granite Dam*

Excluding migration year 1992, overall average yearly parr-to-smolt survival estimated for the combined wild populations from Idaho was 16% and ranged from 8% to 25%. Yearly standard errors were generally less than 1%, except during 1996–1998, when Chinook salmon parr were PIT-tagged in only a few streams (Table A.1). Survival varied significantly among years ( $P < 0.001$ ) and streams ( $P < 0.001$ ) and was highest for fish migrating in 1998 and 2001 (>20%) and lowest for those migrating in 2004 (8%);

survival in other years ranged from 9% to 18% (Figure 2). Average survival for Chinook salmon that were PIT-tagged in lower Big–Rush creeks was much higher than in Loon Creek (35% versus 23%), which in turn was higher than the other 14 streams. Survival in these 14 streams ranged from 12% in the South Fork Salmon River to 19% in Marsh, Herd, and Camas creeks (Figure 2). Estimated survival of individual populations over these years was variable, ranging from 3% for South Fork Salmon River fish in 2003 to 48% for Elk Creek fish in 1998 (Table A.1).

### *Migration Timing at Lower Granite Dam*

Migration timing exhibited highly significant ( $P < 0.001$ ) variability by stream and year in all statistics examined (10th percentile, median, 90th percentile, and range of the 10th to 90th percentile passage dates). For example, the average median passage date for fish from lower Big–Rush creeks was over 3 weeks earlier than for fish from upper Big Creek, and similar differences were observed when comparing median passage date in 1997 with that in 1991. The variability in range from the 10th to 90th percentile passage date was also notable; the mean difference varied from 1 to 2 months (a twofold increase) when comparing lower Big–Rush creeks to Lake Creek and when comparing 2001 to 1997 (Table A.1; Figure 3).

Variability among years in median passage date at Lower Granite Dam was related to autumn temperature, spring temperature, and March flow (Table 1). The model predicted that an incremental increase in mean seasonal temperature of 0.325°C in autumn or 0.287°C in spring or an incremental increase in mean March flow of 17.7 m<sup>3</sup>/s would result in a 1-d decrease in median passage date. Variability in median passage date among streams was related to elevation (Table 1); the model predicted that a 122-m decrease in elevation would decrease median arrival date by 1 d.

### *Parr-to-Smolt Growth Rates as Measured at Little Goose Dam*

We recaptured 420, 483, 426, and 974 wild smolts at Little Goose Dam in 2001, 2002, 2003, and 2004, respectively. Significant differences in growth between marking and recapture existed among sites ( $P < 0.001$ ) and years (Table 2;  $P < 0.001$ ). Recaptured fish had grown an average of 43.3 mm in 2001, 39.7 mm in 2002, 42.4 mm in 2003, and 41.3 mm in 2004 (Figure 4).

When we analyzed variability in growth among individuals while accounting for year and site effects, we found that the highly significant factors were FL at tagging and the elapsed time between tagging and recapture at Little Goose Dam (Table 2). As elapsed

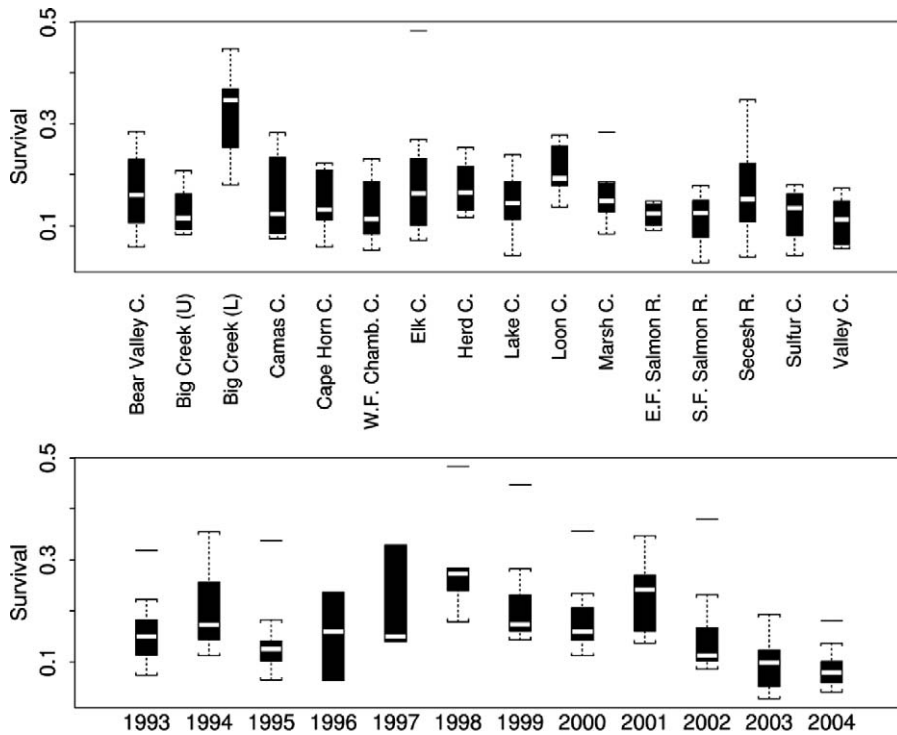


FIGURE 2.—Box plots (Cleveland 1993) of estimated parr-to-smolt survival to Lower Granite Dam (Snake River) for wild spring–summer Chinook salmon tagged in the Salmon River basin, Idaho, by tagging site (upper panel) and migration year (lower panel). Medians (unshaded portions of bars), upper and lower quartiles (dark areas within bars), upper and lower adjacent values (capped vertical lines), and outliers (isolated horizontal lines) are presented.

time increased by 5.3 d, growth increased by 1 mm; as FL at tagging decreased by 1.44 mm, growth increased by 1 mm. These relationships led to smaller fish arriving at the dam later in the season. After accounting for year and site, a linear model predicted that an incremental decrease of 1.92 mm in fish FL at tagging led to an increase of 1 d in arrival at the dam.

### Discussion

Populations of wild Snake River spring–summer Chinook salmon clearly exhibited variability in parr-to-smolt survival, migration timing, and growth rate, both among years and among streams of origin. Understanding how variability in these traits relates to key drivers of survival can potentially yield important information on the life history variability of this threatened ESU. Recent studies have provided insight into survival variability in this ESU. For example, parr-to-smolt survival among streams has been negatively associated with both degraded habitat (Paulsen and Fisher 2001) and the presence of exotic brook trout *Salvelinus fontinalis* in natal rearing areas (Levin et al. 2002).

Beginning in the 1997 tagging year, parr-to-smolt survival consistently decreased (except for tagging year 2000), and tagging year 2003 yielded the lowest parr-to-smolt survival on record. This may indicate density-dependent processes at work as numbers of wild adult spawners in the basin increased. Achord et al. (2003) observed that juvenile survival among years was negatively associated with parr densities in streams.

Unexpectedly, variability in juvenile survival among years or streams has not been related to mean FL at tagging (Zabel and Achord 2004). However, the relative size of juveniles within a population does have a strong influence on survival; the largest parr survive to the smolt stage at nearly twice the rate of smaller parr (Zabel and Achord 2004). Also, survival was not related to CF measured either among or within populations (Zabel and Achord 2004).

Patterns in migration timing of wild Snake River spring–summer Chinook salmon have received much less attention than those of survival trends in general, although migration timing is related to smolt-to-adult survival (Zabel and Williams 2002; Williams et al. 2005). For example, smolts arriving early at Lower

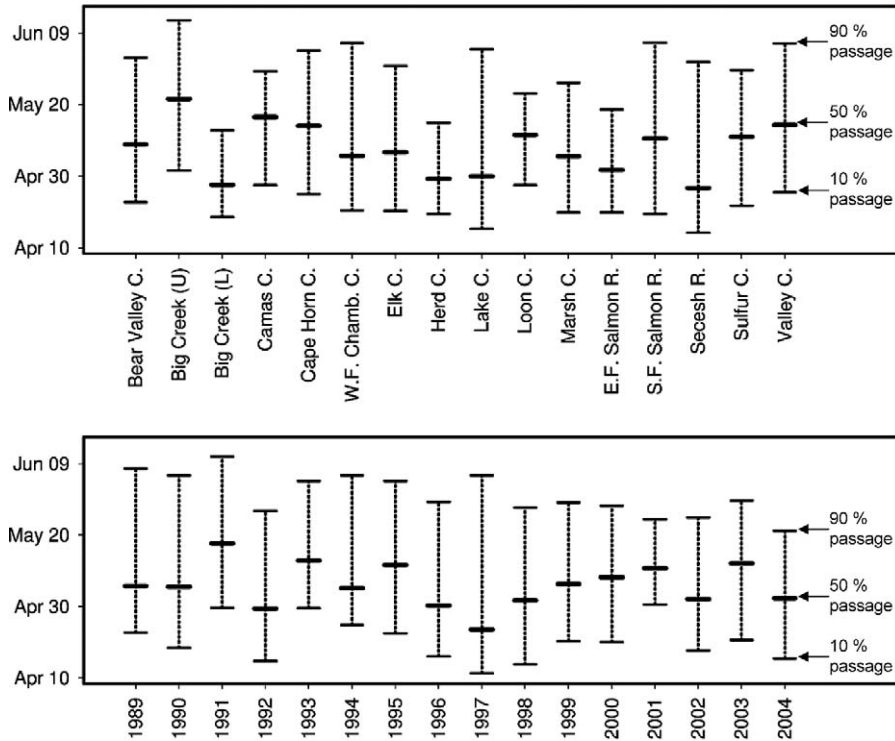


FIGURE 3.—Mean passage timing of wild spring–summer Chinook salmon smolts at Lower Granite Dam (Snake River) by tagging site (averaged across years; upper panel) within the Salmon River basin, Idaho, and by migration year (averaged across sites; lower panel). Passage timing for individual and combined populations in 1989–1992 were based on unadjusted detections at the dam (see Achord et al. 1996); adjustments for estimated survival and passage timing were not made in those years.

Granite Dam survive to adulthood at higher rates than those arriving later. Zabel and Williams (2002) estimated that based on migration year 1995, a 1-week delay in migration to this dam would decrease smolt-to-adult survival by 16.5%. Further, larger smolts consistently return as adults at greater rates than smaller ones (Zabel and Williams 2002; Williams et al. 2005).

Timing of migration is heritable (Randall et al. 1987;

Taylor 1990, 1991), and evidence exists that for some species of Pacific salmon, distinct populations have synchronous out-migration timing (Beacham and Murray 1987; Brannon 1987). Pearcy (1992) suggested that populations may adapt their migration timing to exploit optimal conditions during ocean entry, either in terms of feeding opportunities or predator avoidance, resulting in synchronous migration timing among populations. Our data and supporting studies suggest that migration timing of these fish is determined by a balance between migrating as early as possible in the

TABLE 1.—Results for general linear modeling of year and site effects on median arrival date of spring–summer Chinook salmon at Lower Granite Dam (Snake River) versus a variety of environmental factors.

Factor	Coefficient	SE	df	P(F)
<b>Year effect models</b>				
Site			15	<0.001
Autumn temperature	-3.09	0.597	1	<0.001
Spring temperature	-3.48	0.506	1	<0.001
March flow	-0.00160	0.000418	1	<0.001
<b>Site effect models</b>				
Year			15	<0.001
Elevation	0.00819	0.00346	1	0.019

TABLE 2.—Results of general linear modeling of spring–summer Chinook salmon growth versus year, site, length at tagging in the Salmon River basin, and elapsed time between tagging at recapture at Little Goose Dam on the Snake River.

Factor	Coefficient	SE	df	P(F)
Year			3	<0.001
Site			13	<0.001
Elapsed time	0.189	0.0117	1	<0.001
Length at tagging	-0.692	0.0239	1	<0.001

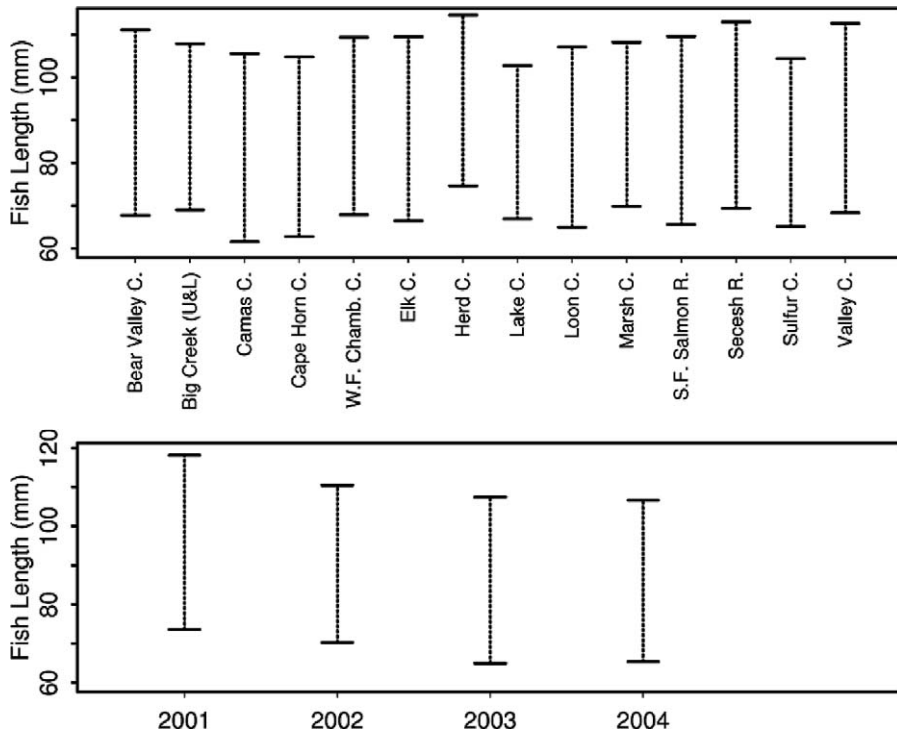


FIGURE 4.—Mean lengths (FL; mm) of wild spring–summer Chinook salmon at the time of release in the Salmon River basin (bottom bars within plots) and at recapture at Little Goose Dam on the Snake River (top bars within plots) by tagging site (averaged across years; upper panel) and migration year (averaged across sites; lower panel). Vertical dashed lines represent mean growth between release and recapture.

spring and attaining adequate size to maximize survival through adulthood.

The strong variability we observed in run timing among populations does not support the hypothesis that run timing of these populations has evolved to exploit some optimal time period. In fact, fish populations that rear in lower elevations (with warmer thermal regimes) migrate earlier than those in higher elevations. This would support the hypothesis that growth and developmental time strongly influence migration timing; the finding that large fish migrate earlier also supports this hypothesis. Finally, the positive relationship between smolt-to-adult survival and earlier migration time–greater fish size indicates a selective force maintaining this trade-off.

Understanding the complicated trade-off present during rearing stages is difficult because wild Snake River spring–summer Chinook salmon exhibit a variety of behaviors in the period between summer tagging as parr and arrival at Lower Granite Dam as smolts. Juveniles typically undergo a summer to fall migration from natal rearing areas to large rivers downstream, where they overwinter (Edmundson et al. 1968; Bjornn

1971; Raymond 1979); however, some juveniles burrow into the substrate during winter in natal rearing areas. Factors such as stream discharge, temperature, turbidity, and habitat availability affect the magnitude of these migrations (Bjornn 1971). In spring, smoltification and downstream migration of Chinook salmon occurs in response to increased photoperiod and water temperature (Ewing et al. 1979; Muir et al. 1994). During migration from the Salmon River to Lower Granite Dam, travel time is related to river flow and to a lesser extent, fish size (Zabel 2002), which may be related to developmental level. Further study of the relationships between migration timing and these factors is needed.

We are currently undertaking detailed studies of the effect of climate and potential climate change on parr-to-smolt survival and migratory behavior. As these studies expand with additional use of environmental water quality monitors, instream PIT tag monitors, and traps in study streams, we can more accurately monitor fry, parr, and smolt movements out of rearing areas and examine the relationships between these movements and environmental conditions within the streams.



These parameters mapped over time, along with weather and climate data, may provide tools for a development of models to predict movement and survival in different wild fish stocks. Such tools will be crucial to recovery planning for threatened or endangered species of Pacific salmon.

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### References

- Achord, S., G. M. Matthews, O. W. Johnson, and D. M. Marsh. 1996. Use of passive integrated transponder (PIT) tags to monitor migration timing of Snake River Chinook salmon smolts. *North American Journal of Fisheries Management* 16:302–313.
- Achord, S., P. S. Levin, and R. W. Zabel. 2003. Density-dependent mortality in Pacific salmon: the ghost of impacts past? *Ecology Letters* 6:335–342.
- Anderson, R. O., and S. Gutreuter. 1983. Length, weight and associated structural indices. Pages 283–300 in L. A. Nielsen and D. L. Johnson, editors. *Fisheries techniques*. American Fisheries Society, Bethesda, Maryland.
- Beacham, T. D., and C. B. Murray. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 44:244–261.
- Bjornn, T. C. 1971. Trout and salmon movements in two Idaho streams related to temperature, food, stream flow, cover, and population density. *Transactions of the American Fisheries Society* 100:423–502.
- Brannon, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing. Pages 120–124 in H. D. Smith, L. Margolis, and C. C. Wood, editors. *Sockeye salmon (Oncorhynchus nerka) population biology and future management*. Canadian Special Publication of Fisheries and Aquatic Sciences 96.
- Cleveland, W. S. 1993. *Visualizing data*. Hobart Press, Summit, New Jersey.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29:103–137.
- Downing, S. L., E. F. Prentice, R. W. Frazier, J. E. Simonson, and E. P. Nunnallee. 2001. Technology developed for diverting passive integrated transponder (PIT) tagged fish at hydroelectric dams in the Columbia River Basin. *Aquacultural Engineering* 25:149–164.
- Edmundson, E., F. E. Everest, and D. W. Chapman. 1968. Permanence of station in juvenile Chinook salmon and steelhead trout. *Journal of the Fisheries Research Board of Canada* 25:1453–1464.
- Efron, B., and R. J. Tibshirani. 1993. *An introduction to the bootstrap*. Chapman and Hall, New York.
- Ewing, R. D., S. L. Johnson, H. J. Pribble, and J. A. Lichatowich. 1979. Temperature and photoperiod effects on gill (Na+K)-ATPase activity in Chinook salmon (*Oncorhynchus tshawytscha*). *Journal of the Fisheries Research Board of Canada* 36:1347–1353.
- Folmar, L. C., and W. W. Dickhoff. 1980. The parr-smolt transformation (smoltification) and seawater adaptation in salmonids: a review of selected literature. *Aquaculture* 21:1–37.
- Gilbert, C. H. 1912. Age at maturity of Pacific coast salmon of the genus *Oncorhynchus*. *U.S. Bureau of Fisheries Bulletin* 32:57–70.
- Gross, M. R. 1987. Evolution of diadromy in fishes. Pages 14–25 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. *Common strategies of anadromous and catadromous fishes*. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Healey, M. C. 1991. The life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311–393 in C. Groot and L. Margolis, editors. *Life history of Pacific salmon*. University of British Columbia Press, Vancouver.
- Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the USA* 100(11):6564–6568.
- Hoar, W. S. 1976. Smolt transformation: evolution, behavior, and physiology. *Journal of the Fisheries Research Board of Canada* 33:1234–1252.
- Levin, P. S., S. Achord, B. E. Feist, and R. W. Zabel. 2002. Non-indigenous brook trout and the demise of Pacific salmon: a forgotten threat? *Proceedings of the Royal Society of London B Biological Sciences* 269:1663–1670.
- Marsh, D. M., G. M. Matthews, S. Achord, T. E. Ruehle, and B. P. Sandford. 1999. Diversion of salmonid smolts tagged with passive integrated transponders from an untagged population passing through a juvenile collection system. *North American Journal of Fisheries Management* 19:1142–1146.
- Matthews, G. M., D. L. Park, S. Achord, and T. E. Ruehle. 1986. Static seawater challenge test to measure relative stress levels in spring Chinook salmon smolts. *Transactions of the American Fisheries Society* 115:236–244.
- Matthews, G. M., N. N. Paasch, S. Achord, K. W. McIntyre, and J. R. Harmon. 1997. A technique to minimize the adverse effects associated with handling and marking salmonid smolts. *Progressive Fish-Culturist* 59:307–309.
- Matthews, G. M., and R. S. Waples. 1991. Status review for Snake River spring and summer Chinook salmon. NOAA Technical Memorandum NMFS F/NWC-200.
- Muir, W. D., W. S. Zaugg, A. E. Giorgi, and S. McCutcheon. 1994. Accelerating smolt development and downstream movement in yearling Chinook salmon with advanced photoperiod and increased temperature. *Aquaculture* 123(3–4):387–399.

- Netboy, A. 1980. Columbia River salmon and steelhead trout: their fight for survival. University of Washington Press, Seattle.
- NMFS (National Marine Fisheries Service). 1992. Endangered and threatened species; threatened status for Snake River spring/summer Chinook salmon, threatened status for Snake River fall Chinook salmon. Federal Register 57:78(22 April 1992):14653–14662.
- NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.
- Paulsen, C. M., and T. R. Fisher. 2001. Statistical relationship between parr-to-smolt survival of Snake River spring-summer Chinook salmon and indices of land use. Transactions of the American Fisheries Society 130:347–358.
- Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. University of Washington, Washington Sea Grant Program, Seattle.
- Peterson, R. G. 1985. Design and analysis of experiments. Marcel Dekker, New York.
- Prentice, E., T. Flagg, C. S. McCutcheon, and D. F. Brastow. 1990a. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. Pages 323–334 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Prentice, E., T. Flagg, C. S. McCutcheon, D. F. Brastow, and D. C. Cross. 1990b. Equipment, methods, and an automated data-entry station for PIT tagging. Pages 335–340 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Prentice, E. F., T. A. Flagg, and C. S. McCutcheon. 1990c. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pages 317–322 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Randall, R. G., M. C. Healey, and J. B. Dempson. 1987. Variability in length of freshwater residence of salmon, trout, and char. Pages 27–41 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966 to 1975. Transactions of the American Fisheries Society 108:505–529.
- Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 19–160 in R. C. Simon and P. A. Larkin, editors. The stock concept of Pacific salmon. H. R. MacMillan lectures in fisheries, University of British Columbia, Vancouver.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Canadian Bulletin of Fisheries and Aquatic Sciences 191.
- Roff, D. 1992. The evolution of life histories; theory and analysis. Chapman and Hall, New York.
- Sandford, B. P., and S. G. Smith. 2002. Estimation of smolt-to-adult return percentages for Snake River basin anadromous salmonids, 1990–1997. Journal of Agricultural Biological and Environmental Statistics 7:243–263.
- Schaefer, M. B. 1951. Estimation of the size of animal populations by marking experiments. U.S. Fish and Wildlife Service Fishery Bulletin 52:191–203.
- Taylor, E. B. 1990. Phenotypic correlates of life-history variations in juvenile Chinook salmon, *Oncorhynchus tshawytscha*. Journal of Animal Ecology 59:455–468.
- Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185–207.
- Waples, R. S. 1991. Pacific salmon *Oncorhynchus* spp. and the definition of “species” under the Endangered Species Act. Marine Fisheries Review 53:11–22.
- Williams, J. G., S. Achord, R. W. Zabel, and B. J. Sandford. 2005. Effects of the federal Columbia River power system on salmon populations. NOAA Technical Memorandum NMFS-NWFSC-63.
- Zabel, R. W. 2002. Using “travel-time” data to characterize the behavior of migrating animals. American Naturalist 159:372–387.
- Zabel, R. W., and S. Achord. 2004. Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology 85:795–806.
- Zabel, R. W., and J. G. Williams. 2002. Selective mortality in Chinook salmon: what is the role of human disturbance? Ecological Applications 12:173–183.

**Appendix: Tagging, Survival, and Migration Timing Details**

TABLE A.1.—Tagging details, parr-to-smolt survival estimates ( $\pm$ SE), and passage timing at Lower Granite Dam during the year after tagging for populations of wild spring–summer Chinook salmon from the Salmon River basin, Idaho.

Tagging year	Tagging details				Parr-to-smolt survival (SE)	Percentile passage dates		
	Number released	Mean fork length (mm)	Mean mass (g)	CF		10th	50th	90th
<b>Bear Valley Creek</b>								
1991 <sup>a</sup>	1,042	68	4.3	1.29		15 Apr	2 May	24 May
1992	1,014	74	4.6	1.12	14.3 (2.0)	29 Apr	16 May	22 Jun
1993	856	63	3.7	1.41	26.5 (3.2)	22 Apr	6 May	29 May
1994	1,455	63	3.5	1.47	10.7 (1.2)	28 Apr	18 May	12 Jun
1997	427	75	5.9	1.36	28.6 (3.7)	25 Apr	6 May	23 May
1998	820	65	3.6	1.27	16.0 (2.6)	23 Apr	3 May	7 Jun
1999	837	62	3.3	1.36	15.9 (2.5)	18 Apr	7 May	2 Jun
2000	581	73	4.7	1.18	23.1 (2.0)	8 May	16 May	28 May
2001	1,495	66	3.9	1.34	16.7 (2.5)	16 Apr	4 May	31 May
2002	1,022	62	3.3	1.33	9.8 (1.5)	14 Apr	5 May	28 May
2003	1,494	61	3.0	1.27	5.8 (1.0)	15 Apr	7 May	28 May
<b>Elk Creek</b>								
1991 <sup>a</sup>	462	70	5.1	1.41		11 Apr	30 Apr	28 May
1992	628	78	5.7	1.21	14.0 (2.6)	2 May	16 May	11 Jun
1993	998	64	4.5	1.42	18.8 (2.4)	23 Apr	4 May	21 May
1994	1,512	67	4.1	1.33	10.1 (1.2)	18 Apr	11 May	5 Jun
1997	246	77	6.3	1.35	48.4 (6.1)	7 Apr	2 May	15 May
1998	700	68	3.9	1.25	23.1 (3.6)	21 Apr	3 May	27 May
1999	660	65	3.6	1.28	18.6 (2.8)	15 Apr	28 Apr	19 May
2000	44	78	5.7	1.19	27.3 (7.7)	30 Apr	11 May	27 May
2001	1,519	68	4.1	1.26	10.3 (1.9)	16 Apr	29 Apr	2 Jun
2002	975	62	3.6	1.47	7.1 (1.3)	20 Apr	6 May	29 May
2003	1,520	63	3.3	1.30	7.7 (1.0)	18 Apr	8 May	4 Jul
<b>Marsh Creek</b>								
1991 <sup>a</sup>	981	66	3.9	1.38		17 Apr	7 May	2 Jun
1992	1,000	71	5.1	1.37	17.9 (2.4)	29 Apr	15 May	27 May
1993	944	69	4.6	1.44	18.6 (2.4)	23 Apr	4 May	18 May
1994	1,575	69	4.0	1.28	13.8 (1.4)	17 Apr	9 May	24 May
1998	769	70	4.2	1.23	28.3 (3.7)	21 Apr	1 May	25 May
1999	554	66	4.0	1.36	12.5 (2.8)	21 Apr	28 Apr	27 May
2001	1,056	72	4.8	1.27	16.0 (2.5)	18 Apr	4 May	23 May
2002	997	66	4.5	1.44	13.0 (2.4)	14 Apr	5 May	29 May
2003	1,535	65	3.7	1.28	8.4 (1.0)	16 Apr	28 Apr	10 May
<b>Cape Horn Creek</b>								
1991 <sup>a</sup>	209	63	3.6	1.48		12 Apr	28 Apr	30 May
1992	205	67	4.1	1.25	22.4 (5.7)	8 May	19 May	26 Jun
1994	1,442	62	2.6	1.18	12.2 (1.3)	29 Apr	14 May	19 Jun
1998	270	61	2.8	1.26	20.7 (5.3)	29 Apr	22 May	29 May
1999	423	61	3.0	1.30	14.2 (4.8)	1 May	24 May	1 Jun
2002	562	59	2.9	1.39	11.2 (1.6)	21 Apr	17 May	1 Jun
2003	671	61	3.4	1.36	5.8 (1.0)	15 Apr	4 May	24 May
<b>Sulfur Creek</b>								
1991 <sup>a</sup>	210	67	4.1	1.37		16 Apr	3 May	23 May
1992	712	71	4.3	1.20	8.0 (1.7)	28 Apr	16 May	12 Jun
1994	728	62	3.0	1.20	16.1 (2.1)	2 May	23 May	9 Jun
1998	443	63	3.2	1.30	16.3 (3.9)	24 Apr	19 May	27 May
1999	838	60	3.3	1.37	18.1 (2.5)	15 Apr	7 May	24 May
2002	560	64			10.9 (1.0)	2 May	25 May	8 Jun
2003	1,048	63	3.1	1.32	4.1 (1.0)	10 Apr	25 Apr	11 May
<b>Valley Creek</b>								
1991 <sup>a</sup>	969	70	4.8	1.36		15 Apr	30 Apr	27 May
1992	1,026	74	5.7	1.37	7.3 (1.6)	30 Apr	16 May	2 Jun
1993	848	67	4.2	1.30	14.4 (2.8)	24 Apr	4 May	3 Jun
1994	1,551	64	3.7	1.37	6.4 (0.9)	4 May	2 Jun	8 Jul
1998	1,001	69	4.2	1.27	17.4 (2.5)	24 Apr	13 May	12 Jun
1999	1,009	64	3.6	1.36	14.9 (2.1)	20 Apr	12 May	29 May
2000	1,004	72	5.2	1.34	16.0 (1.3)	10 May	19 May	1 Jun
2001	1,497	70	4.7	1.33	11.3 (1.9)	24 Apr	20 May	3 Jun
2002	2,266	62	3.4	1.43	5.7 (0.8)	14 Apr	17 May	28 May
2003	2,498	63	3.5	1.32	5.5 (1.0)	25 Apr	11 May	26 May

TABLE A.1.—Continued.

Tagging year	Tagging details				Parr-to-smolt survival (SE)	Percentile passage dates		
	Number released	Mean fork length (mm)	Mean mass (g)	CF		10th	50th	90th
<b>East Fork Salmon River</b>								
1991 <sup>a</sup>	669	76	5.9	1.35		13 Apr	21 Apr	16 May
1992	843	76	5.9	1.31	9.1 (1.6)	25 Apr	6 May	18 May
1993	883	72	5.3	1.37	11.2 (1.9)	22 Apr	28 Apr	17 May
1994	986	74	5.4	1.34	13.7 (1.6)	14 Apr	28 Apr	10 May
1999	674	65	4.1	1.43	14.8 (2.5)	21 Apr	7 May	25 May
<b>Herd Creek</b>								
1991 <sup>a</sup>	307	72	5.1	1.30		14 Apr	20 April	10 May
1992	224	79	6.4	1.32	13.8 (3.8)	26 Apr	30 April	18 May
1993 <sup>b</sup>	119	74	5.6	1.36	19.3 (5.4)			
1994	534	74			13.9 (2.2)	18 Apr	3 May	14 May
1998	959	71	4.7	1.34	21.9 (3.0)	20 Apr	29 Apr	10 May
1999	315	70	5.1	1.41	21.3 (4.2)	16 Apr	25 Apr	18 May
2000	311	82	7.9	1.40	25.4 (2.8)	30 Apr	4 May	14 May
2001 <sup>a,b</sup>	24							
2002	799	76	6.2	1.35	12.3 (1.4)	16 Apr	3 May	26 May
2003	968	67	4.1	1.31	11.5 (2.0)	16 Apr	30 Apr	10 May
<b>Camas Creek</b>								
1992	1,012	68	4.2	1.25	14.5 (2.1)	3 May	16 May	27 May
1993	215	64			28.4 (7.7)	30 Apr	15 May	26 May
1994	1,528	61	3.2	1.28	8.4 (1.1)	27 Apr	12 May	5 Jun
1999	763	61	3.3	1.43	23.5 (4.0)	26 Apr	25 May	2 Jun
2002	976	61	3.0	1.32	7.5 (1.7)	2 May	24 May	30 May
2003	1,005	62	3.3	1.38	10.0 (1.0)	18 Apr	8 May	24 May
<b>Loon Creek</b>								
1992	261	70	4.7	1.36	18.0 (3.9)	5 May	12 May	17 May
1993	396	64	3.6	1.38	25.8 (4.8)	29 Apr	10 May	24 May
1994	964	65	3.5	1.41	18.3 (1.9)	23 Apr	11 May	28 May
1998	1,029	67	3.9	1.32	27.8 (3.3)	30 Apr	18 May	27 May
1999	719	63	3.7	1.45	19.6 (3.3)	22 Apr	8 May	24 May
2002	830	65	3.9	1.45	19.3 (2.5)	30 Apr	17 May	28 May
2003	860	64	3.7	1.37	13.7 (2.0)	23 Apr	5 May	15 May
<b>Upper Big Creek</b>								
1991 <sup>a</sup>	998	70	4.2	1.24		22 Apr	8 May	3 Jun
1992	451	71	4.5	1.22	8.2 (2.7)	8 May	18 May	26 May
1993	535	64		1.43	11.4 (2.7)	3 May	19 May	19 Jul
1994	755	62	3.4	1.38	14.2 (2.0)	5 May	23 May	9 Jun
1998	960	67	4.2	1.33	16.2 (2.6)	28 Apr	14 May	3 Jun
1999	701	65	3.9	1.39	20.7 (3.6)	30 Apr	27 May	14 Jun
2002	1,004	61	3.4	1.51	10.3 (2.2)	6 May	25 May	1 Jun
2003	1,504	62	3.4	1.39	9.3 (1.0)	18 Apr	12 May	5 Jun
<b>Lower Big Creek and Rush Creek</b>								
1992	307	80			31.8 (4.0)	24 Apr	29 Apr	13 May
1993	196	70	4.3	1.29	35.7 (6.0)	23 Apr	29 Apr	11 May
1994	742	75	5.3	1.22	33.8 (2.9)	19 Apr	1 May	14 May
1998	494	81	6.3	1.29	44.7 (6.0)	19 Apr	28 Apr	23 May
1999	389	74	5.7	1.36	35.5 (5.1)	19 Apr	30 Apr	13 May
2001	423	76	5.2	1.24	38.1 (6.9)	15 Apr	25 Apr	7 May
2002	720	68	4.3	1.29	19.0 (1.3)	14 Apr	26 Apr	18 May
2003	951	72	4.4	1.16	18.0 (3.0)	15 Apr	23 Apr	4 May
<b>West Fork Chamberlain and Chamberlain creeks</b>								
1991 <sup>a</sup>	1,395	65	3.4	1.14		15 Apr	26 Apr	3 Jun
1992 <sup>c</sup>	498	72			18.7 (2.9)	28 Apr	15 May	23 Jun
1993	572	67			11.5 (2.4)	24 Apr	1 May	5 Jul
1994	1,157	66	3.3	1.03	10.5 (2.4)	16 Apr	9 May	20 Jun
2001 <sup>c</sup>	510	67	3.7	1.16	23.1 (4.9)	26 Apr	4 May	20 May
2002	795	63		1.06	5.2 (2.1)	23 Apr	20 May	26 May
2003	996	62	3.1	1.28	8.2 (2.0)	11 Apr	24 Apr	10 May
<b>South Fork Salmon River</b>								
1991 <sup>a</sup>	1,027	64	3.5	1.30		14 Apr	29 Apr	27 May
1992	998	68	4.0	1.25	15.5 (2.4)	29 Apr	16 May	2 Jun

TABLE A.1.—Continued.

Tagging year	Tagging details				Parr-to-smolt survival (SE)	Percentile passage dates		
	Number released	Mean fork length (mm)	Mean mass (g)	CF		10th	50th	90th
1993	803	59	2.9	1.37	14.9 (2.8)	27 Apr	15 May	28 Jun
1994	1,571	59	2.6	1.27	10.1 (1.1)	20 Apr	10 May	10 Jun
1995	700	61	3.1	1.37	6.3 (1.6)	19 Apr	15 May	9 Jun
1996	700	64	3.6	1.37	15.0 (3.1)	13 Apr	28 Apr	12 Jun
1997	1,007	64	3.3	1.27	17.9 (2.0)	25 Apr	12 May	15 Jun
1998	998	63	3.5	1.37	14.3 (2.4)	31 Mar	4 May	1 Jun
1999	1,010	62	3.3	1.40	11.2 (2.0)	20 Apr	18 May	31 May
2000	1,010	65	3.7	1.32	13.7 (1.2)	29 Apr	14 May	1 Jun
2001	1,534	63	3.5	1.35	8.5 (1.8)	15 Apr	3 May	24 May
2002	1,035	60	2.9	1.33	2.8 (1.2)	19 Apr	16 May	3 Jun
2003	1,490	62	3.2	1.21	6.9 (1.0)	16 Apr	10 May	02 June
<b>Secesh River</b>								
1991 <sup>a</sup>	1,012	64	3.6	1.33		13 Apr	29 Apr	4 Jun
1992	327	68	3.8	1.14	17.1 (3.4)	26 Apr	16 May	16 Jun
1993	422	60	2.8	1.27	16.1 (3.1)	22 Apr	26 Apr	11 Jul
1994	1,549	63	3.2	1.28	11.6 (1.2)	14 Apr	1 May	24 May
1995	571	65	4.0	1.34	15.9 (3.6)	14 Apr	25 Apr	29 May
1996	260	70	5.1	1.44	33.1 (6.4)	10 Apr	18 Apr	4 May
1997	588	63	3.1	1.20	27.4 (3.3)	8 Apr	24 Apr	28 May
1998	936	65	3.4	1.24	14.5 (2.5)	3 Apr	23 Apr	25 May
1999	907	65	4.0	1.39	12.8 (2.1)	13 Apr	23 Apr	4 Jun
2000	586	72	5.1	1.34	34.8 (2.3)	16 Apr	28 Apr	13 May
2001	1,489	63	3.2	1.24	10.1 (1.9)	13 Apr	21 Apr	17 May
2002	1,040	61	3.0	1.28	3.8 (0.8)	18 Apr	30 Apr	1 Jun
2003	1,142	62	3.0	1.25	4.3 (1.0)	4 Apr	27 Apr	28 May
<b>Lake Creek</b>								
1992	255	72			18.8 (3.9)	23 Apr	9May	22 Jun
1993	252	62	3.1	1.24	15.1 (4.0)	21 Apr	28 Apr	19 May
1994	405	63			13.1 (2.7)	17 Apr	10 May	10 Jun
1995	135	64	4.0	1.48	23.7 (8.4)	15 Apr	21 Apr	19 May
1996	400	71	5.0	1.40	14.0 (3.6)	11 Apr	25 Apr	2 Jul
1997	418	63	3.5	1.36	23.9 (3.3)	4 Apr	25 Apr	26 May
1998	545	67	3.8	1.27	14.5 (3.3)	20 Apr	26 Apr	27 May
1999	603	65	3.9	1.44	15.3 (3.3)	13 Apr	4 May	4 Jun
2001	695	64	3.7	1.35	11.4 (3.5)	16 Apr	29 Apr	3 Jun
2002	709	62	3.5	1.37	4.1 (1.7)	6 Apr	6 May	4 Jun
2003	664	61	3.2	1.30	6.8 (2.0)	14 Apr	25 Apr	28 May

<sup>a</sup> No survival estimates were made for this year.

<sup>b</sup> Insufficient numbers were detected to estimate timing.

<sup>c</sup> Fish were tagged in only West Fork Chamberlain Creek for this year.