North American Journal of Fisheries Management 13:48–63, 1993

An Analysis of Variables Influencing the Migration of Juvenile Salmonids in the Columbia River Basin

THOMAS J. BERGGREN AND MARGARET J. FILARDO

Fish Passage Center

2501 Southwest First Avenue, Suite 230, Portland, Oregon 97201-4752, USA

Abstract.—The amount of time that it takes juvenile chinook salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* to migrate (travel time) at different river flows through index reaches in the Snake and Columbia rivers was analyzed with bivariate- and multiple-regression models. Smolt travel time estimates for yearling chinook salmon and steelhead in the Snake River, steelhead in the middle Columbia River, and subyearling chinook salmon in the lower Columbia River were inversely related to average river flows. In the multiple-regression analyses, additional predictor variables that were related either to flow or to smoltification were used. These predictor variables were calculated over the same time period as the travel time estimates. Flow-related variables were referenced at a key hydroelectric site within each index reach, and included average river flow, minimum river flow, and absolute change in river flow. The smoltification-related variables provided indirect indices of smoltification. They included water temperature, date of entry into an index reach, chinook salmon race, and travel time prior to entry into an index reach. The final models included those predictor variables explaining significant variation in smolt travel time. The variables in the final multiple-regression models explained 74% and 39% of the variation in the travel time for yearling chinook salmon within the Snake and middle Columbia river index reaches, respectively; 90% and 62% for steelhead within the Snake and middle Columbia reaches; and 65% for subyearling chinook salmon in the lower Columbia reach. Average river flow made the largest contribution to explaining variation in smolt travel time in the majority of the multiple-regression models. Additional variation in smolt travel time could be explained by including other flow- and smoltification-related variables in the models.

The development of hydroelectric dams on the Snake and Columbia rivers has drastically altered the water flows that juvenile anadromous salmonids encounter as they migrate from fresh water to the ocean. Before construction of the dams, the highest flows had occurred in the spring and early summer, and the migration of juvenile salmonids coincided with those high flows (Park 1969). The development and operation of a basin-wide coordinated hydrosystem, along with water withdrawal for irrigation, changed the historical flow pattern and resulted in regulated flows that are lower in the spring and summer and higher in the fall and winter than they were. Increases in cross-sectional area of the river associated with impoundments further reduced water velocities in spring and summer. Raymond (1968, 1969, 1979) estimated that smolts move through the impoundments from one-half to one-third as fast as they do through free-flowing river stretches of the same length. Smith (1982) postulated that smolts swim upstream at a velocity less than that of the water, and thereby move downstream tail-first more slowly than water. The link between smolt migration speed and water speed pointed to river flow as a key factor in determining how quickly smolts will migrate (travel time) through the reservoirs. Juvenile salmonids must arrive at the estuary within a certain time window while they are still physiologically adapted to make the transition from fresh to salt water (Hoar 1976). If they do not enter seawater as smolts, their salinity tolerance regresses (Hoar 1976) and so does their probability of contributing to adult production. Therefore, mitigation was needed to offset the smolt migration delays caused by the dams and impoundments.

When the Northwest Power Planning Council's Columbia River basin fish and wildlife program, authorized by the Pacific Northwest Power Act (Public Law 96-501), was completed in 1982 (NPPC 1987), it addressed this mitigation need by developing the concept of a water budget. The water budget was a volume of water to be used from April 15 to June 15 to augment river flows and thereby reduce delays in the spring smolt migration caused by the hydrosystem. The purpose of the water budget was to improve smolt survival in spring by reducing the travel time of smolts through the reservoirs. This, it was hoped, would reduce the exposure of smolts to riverine predators and allow smolts to reach the estuary while they were still physiologically able to adapt to seawater. Beginning in 1983, the water budget has been applied annually; flows have increased for part of the spring in the middle Columbia River and for a shorter time during spring in the Snake River. Failures of the water budget to provide adequate mitigation for operation of the hydroelectric system have been documented by the Columbia Basin Fish and Wildlife Authority (1991), and are not further addressed in this paper. Instead, the first objective of our study was to document, with recent smolt migration data, whether or not the increased flows decrease the amount of time needed by smolts to travel through the reservoirs.

At the time the water budget was developed, the summer flows necessary for power generation were expected to be sufficient for the summer smolt migration. Since implementation of the water budget, however, summer flows have been below the historic average, due partly to several years of low natural runoff and partly to the practice of refilling the storage reservoirs following the water budget period. For example, average July flow at The Dalles Dam for the 50-year historic record (1929–1978) was 268,700 ft^3/s, whereas the average July flow over the 8 water budget years, 1983–1990, was 144,600 ft^3/s (range, 204,700 ft^3/s in 1983 to 104,000 ft^3s in 1988). Since the inception of a spring water budget, subyearling chinook salmon *Oncorhynchus tshawytscha* have been migrating through the reservoirs in July and August under even lower summer flow conditions than in earlier years. Earlier studies on the migratory behavior of subyearling chinook salmon from 1981 and 1983 (Miller and Sims 1984; Giorgi et al. 1990) had failed to show a significant relation between river flow and either the rate of movement or residence time of summer migrants in John Day reservoir, in contrast to the inverse relations that had been documented for spring migrants (Sims and Ossiander 1981). More recent migration data for subyearling chinook salmon are available for 1986–1988. Because lower summer flows such as those of 1986–1988 appear to be the more likely flow scenario for the future, there was a need to reevaluate the relation (if any) between summer flow and travel time for subyearling fish. Therefore, the second objective of this study was to determine if the travel time of summer migrants is affected by flow.

In addition to flow, other factors can influence how quickly smolts migrate through the reservoirs to the estuary. Zaugg et al. (1985) documented for hatchery chinook salmon, coho salmon *Oncorhynchus kisutch*, and steelhead *O. mykiss* from the Columbia River basin that a period of river migration increases the level of smoltification (as measured by adenosine triphosphotase [ATPase] activity) above the level resulting if the fish are held in net pens for the same time. In another study with Columbia River steelhead, coho salmon, and yearling chinook salmon, Zaugg (1981) noted that migratory behavior and ability to tolerate seawater appear to develop concurrently and that both activities increase over the migration period. Folmar and Dickhoff (1980) associated smoltification with many morphological, behavioral, and physiological changes that allow salmonids to migrate rapidly and adapt readily to seawater. Hoar (1976, 1988) and Wedemeyer et al. (1980) concluded that day length triggers the onset of smoltification, that water temperature regulates the rate and duration of the process and, once the fish are ready to migrate, that a proximal stimulus such as a sudden increase in river discharge actually provokes the migration. Because the stage of smoltification may influence a smolt's migration rate and environmental factors can influence the rate of smoltification, the third objective of our study was to determine if variation in smolt travel time can be explained by variables in addition to flow.

Methods

Study Areas and Monitoring Procedures

Smolt travel time was estimated along key index reaches within the Columbia River basin (Figure 1) for marked subyearling and yearling chinook salmon and steelhead. The key index reaches for spring-migrating yearling chinook salmon and steelhead were from Lower Granite Dam to McNary Dam (140 miles) in the Snake River and from the mouth of the Methow River to McNary Dam (232 miles) in the middle Columbia River. The key index reach for summer-migrating subyearling chinook salmon was from McNary Dam to John Day Dam (76 miles) in the lower Columbia River. The data used to estimate travel time in these index reaches were from the recapture of marked smolts in the fish-sampling facilities at the hydroelectric projects pertinent to each index reach.

Marked spring-migrating yearling chinook salmon came from Rapid River, Sawtooth, and Dworshak hatcheries in the Snake River drainage and Winthrop Hatchery in the middle Columbia River drainage. Marked summer yearling chinook salmon came from McCall Hatchery in the Snake system. Steelhead came from Dworshak Hatchery in the Snake River drainage and Wells Hatchery in the middle Columbia River drainage. Each of these hatcheries is a major contributor of fish to

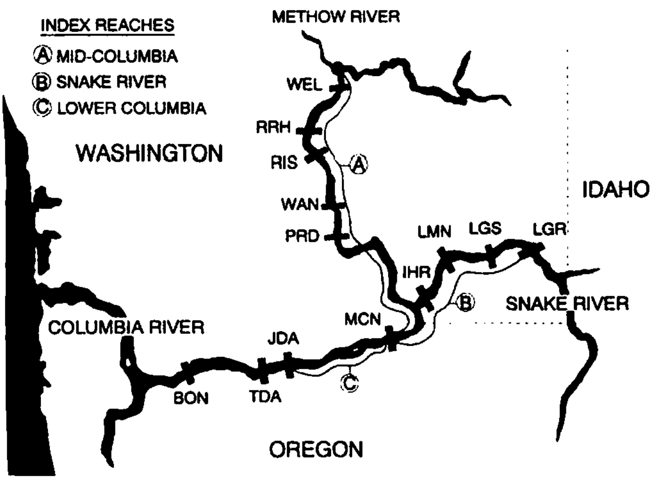

FIGURE 1.—Map of Columbia and Snake river drainages showing the locations of dams and the index reaches used in the travel time analyses. The dams are denoted as follows: LGR = Lower Granite, LGS = Little Goose, LMN = Lower Monumental, IHR = Ice Harbor, MCN = McNary, JDA = John Day, TDA = The Dalles, BON = Bonneville, WEL = Wells, RRH = Rocky Reach, RIS = Rock Island, WAN = Wanapum, and PRD = Priest Rapids.

its respective drainage, and each had a consistent marking program from 1982 or 1983 through 1990. Subyearling chinook salmon were collected at McNary Dam, marked, and released below the dam during two 3-year periods, 1981–1983 and 1986–1988. No marking of subyearling chinook salmon occurred in 1984 and 1985. Each marked subyearling group consisted of an unknown mixture of wild and hatchery stocks of summer and fall chinook salmon. All fish were freeze-branded with silver-tipped brass branding rods cooled in a canister containing liquid nitrogen (Mighell 1969).

The sampling facilities at Lower Granite and McNary dams were similar. At these sites, a proportion of the fish entering the powerhouse were diverted from the turbines by a submersible traveling screen, which directed the fish upward to the gatewell and into a central bypass system (Figure 2). This bypass system was sampled several times per hour and sampled fish were diverted to a holding tank. The sample in the holding tank was counted once every 24 h, and fish were checked for freeze brands. The number of branded fish recovered each day was expanded to a passage index count based on the sampling rate and the proportion of fish estimated to pass the project via the spillway. The proportion of fish passing the project via the spillway was assumed to be equal to the proportion of daily average flow being spilled. A distribution of daily passage indices over time was generated for each marked group.

At John Day Dam, fish were recovered with an airlift sampler (Brege et al. 1990) in one gatewell slot of a turbine unit. In contrast to the continuous collection of fish across all the turbine units at the other dams, this sample came from a single gatewell slot. Hourly collections and brand counts were summed over the 24-h sample period to provide a daily collection as at the other monitoring sites. Daily sample counts were expanded to passage indices by the proportion of daily average river flow going through the sample unit to account for variations in spill and turbine unit loading levels. Again, a distribution of daily passage indices over time was generated for each marked group. Since 1985, fish have been diverted into the gatewell by a submersible traveling screen; however, before that year entry into the gatewell was volitional.

Median Travel Time

Groups of marked smolts with unexpanded mark recoveries of at least 40 were used to estimate median travel time through each index reach (Lower Granite Dam to McNary Dam, Methow River to McNary Dam, and McNary Dam to John Day Dam; Figure 1). The minimum unexpanded sample size of 40 fish was chosen to assure the reliable computation of the travel time estimate. A sample size of 40 recoveries yields a coefficient of variation less than 25% for the relative error associated with recovery of marked fish (deLibero 1986). In addition, the entire data set of all marked groups recovered, regardless of recovery numbers,

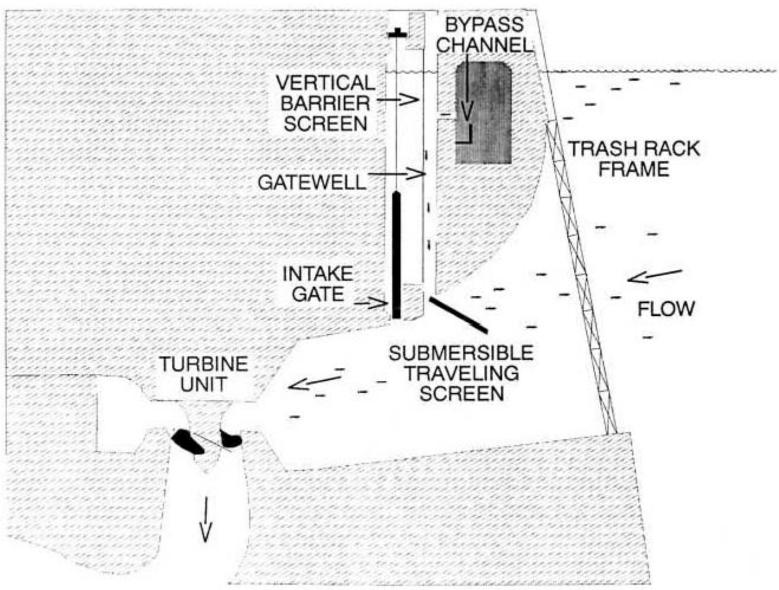

FIGURE 2.—Schematic diagram of the system used to bypass juvenile migrants around turbines and to divert fish to the collection system.

was evaluated for the confidence interval width around the estimated median date of passage. The confidence interval width began to stabilize at 40 unexpanded recoveries.

Most of the brand groups used for this analysis provided unexpanded sample recoveries well in excess of 40 (see Appendix Tables A.1–A.3). The sample size criterion eliminated many of the marked subyearling chinook salmon groups recovered at John Day Dam from 1981 to 1983, when the absence of submersible traveling screens there resulted in very low recoveries of marked fish. Four groups of marked steelhead released from Dworshak Hatchery were eliminated because few marked fish were recovered at McNary Dam as a result of the transportation program at Snake River dams (described later).

The in-river marking of subyearling chinook salmon occurred as part of the transportation study, and could extend over several days until an adequate number of fish were identically marked. Therefore, a criterion of 8 d for the maximum release duration was applied to subyearling chinook salmon releases from McNary Dam to reduce the bias in travel time estimates associated with extended mark–release schedules. Subyearling chinook salmon groups released within the middle 80% of the migration (based on the fish passage timing at McNary Dam for each year) were used in the travel time estimation.

The median travel time for a marked group was estimated as the duration between the group's median date of hatchery release, or dam passage at the upstream end of the index reach, and the median date of dam passage at the downstream end. Median, rather than mean, travel times were computed because passage distributions tended to be skewed. Estimates of median travel time were only as reliable as the estimated dates of median passage at dams, so factors that could affect the distribution of daily passage indices were considered. Two factors to be considered were the transportation program and, of lesser importance, the changes that had occurred in the daily sampling period at recovery sites.

For the Snake River index reach, the distribution of daily passage indices at Lower Granite Dam had to be adjusted to reflect the proportion of the fish that would continue their migration to McNary Dam. Many yearling chinook salmon and most steelhead in the Snake River were collected at Lower Granite and Little Goose dams and transported via barge or truck to release sites in the lower Columbia River. More yearling chinook salmon were transported in years of low flow than in years of high flow, but all steelhead collected were transported regardless of flow. Some chinook salmon were left in the river in all years and some steelhead passed in the spill during high-flow years, and the proportion of fish removed for transportation varied daily in all years. Adjustments for these variables were particularly important for marked summer chinook salmon and steelhead groups that passed Lower Granite and Little Goose dams during periods of transition from a limited to a maximum transportation program. The adjustment factor encompassed the probability of a fish remaining in the river below Lower Granite Dam, conditioned on arriving at Lower Granite Dam, and the probability of that fish remaining in the river below Little Goose Dam, conditioned on arriving at Little Goose Dam. The conditional probabilities were based on deterministic proportions of fish passing with the spill or moving into the powerhouse (passage was assumed proportionally to spill), proportions of fish in the powerhouse going through the turbines or moving through the bypass channel into the collection facility (guidance efficiency research indicated that the traveling screens guided 50% of yearling chinook salmon and 70% of steelhead, on average, into the bypass channel), and the proportion of collected fish actually transported. The daily passage index for each brand group arriving at Lower Granite Dam was multiplied by that day's adjustment factor, and a new distribution of adjusted daily passage indices was obtained for use in subsequent travel time estimation.

The hours defining a 24-h sampling period have differed among monitoring sites and have changed over the years at some sites, so the computation of median travel time had to be standardized. For example, the sampling period had changed from a cycle of noon to noon to one of 0700 to 0700 hours over the years at both Lower Granite and McNary dams. Since each recovery day represented the accumulation of fish collected over the past 24 h, the approach was to interpolate where the median had occurred within that sample period relative to a midnight reference point. This interpolation was made for both release (when applicable) and recovery data. The difference between the two interpolated medians, referenced to midnight, provided the estimate of median travel time in the index reach.

For the middle Columbia River index reach, the date of entry into the Columbia main stem was estimated by allowing a fixed number of days for fish to travel down the Methow River from the hatchery or release site. Marked yearling chinook salmon were assumed to reach the Columbia River at midnight 2 d after release. Marked steelhead also were assumed to reach the main stem at midnight, but on the day of release in 1984–1989 and 1 d after in 1982, 1983, and 1990—differences reflecting changes in release locations over these years.

Sampling occurred 7 d/week in all years at McNary Dam, since 1984 at Lower Granite Dam, and since 1983 at John Day Dam. Prior to this consistent sampling effort, various sampling schedules occurred. In 1982 and 1983, sampling was conducted 6 d/week at Lower Granite Dam. In order to account for noncontinuous sampling, nonsampling days were assigned the average of fish collected on adjacent sampling days for each marked group before estimates of dates of median passage were made. Sampling at John Day Dam was conducted only 5 d/week in 1981 and 1982. Nonsampling days received no average allocation in these cases because few fish were being recovered anyway. Instead, when the computed median date of recovery fell between days of no sampling or between days of sampling with no recoveries at John Day Dam, the date of median recovery was obtained by simple interpolation between those days. Freeze-branded subyearling chinook salmon groups were consistently released below McNary Dam near 2200 hours each year.

To summarize, median travel time through the Snake River index reach was estimated as the difference between the interpolated median date of the adjusted Lower Granite Dam passage distribution and the interpolated median date of McNary Dam passage. Median travel time through the middle Columbia River index reach was estimated as the difference between the adjusted date of entry into the main-stem Columbia River and the interpolated median date of McNary Dam passage. For the lower Columbia River index reach, median travel time was estimated as the difference between the single release dates (1981–1983) or interpolated median release dates (1986–1988) at McNary Dam and the interpolated median date of recovery at John Day Dam.

Predictor Variables

Four variables were considered as surrogates of a marked group's overall smoltification status, or its readiness to migrate. These surrogates were used because no direct measures of the smolts' physiological condition were available for these groups before 1988. The variables considered were river temperature in degrees Fahrenheit (TEMP), prior in-river travel time to Lower Granite Dam in days (TTLGR) for the Snake River migrants, a race indicator variable (RACE) to separate spring and summer chinook salmon in the Snake River, and the day of the year (1–365) that fish entered an index reach (DATE). River temperature stimulates the rate of smoltification (Wedemeyer et al. 1980; Hoar 1988). Yearling chinook salmon and steelhead from the hatcheries used in this analysis have shown substantial increase in ATPase levels during the first 20–30 d of river migration in recent studies (Beeman et al. 1990). Given the different distances hatchery fish travel from release to Lower Granite Dam, 73–465 mi, the TTLGR variable (number of days from release through median recovery date at Lower Granite Dam) was considered an important surrogate for different levels of smoltification among the stocks involved. Date of entry to the index reach (January 1 = day 1) was considered a variable that encompasses the joint effects of all time-related factors (including day length). The RACE variable was 0 for summer chinook salmon and 1 for spring chinook salmon.

Three flow-related variables that might influence smolt migration speed were considered: average flow (FLOW), minimum flow (MINFLOW), and delta-flow (DFLOW). Average flow and minimum flow were considered important variables, given Smith's (1982) findings that smolts tend to orient themselves upstream in the current and to drift downstream at a speed slightly less than that of the water. Delta-flow (maximum minus minimum flow) measured the maximum range of flow encountered by the smolts. To ensure that the conditions experienced by the leading half of a marked group (up to arrival of the median fish) were fully taken into account, average, minimum, and delta-flows, as well as the river temperature, were estimated at a key hydroelectric site in each reach during the time that the first 50% of a group was migrating through that reach. The temperature and flow variables were averages of their daily averages over the estimated median travel times. The key hydroelectric sites chosen to represent conditions in the index reaches were Ice Harbor Dam in the Snake River, Rock Island Dam in the middle Columbia River and John Day Dam in the lower Columbia River.

Bivariate-Regression Analyses

The first two objectives addressed in this paper were whether increased flows decrease smolt travel time through the index reaches, and whether the travel time of subyearling chinook salmon is affected by flow. Bivariate-regression analysis was conducted to address these objectives. The premise was that travel time of fish should follow a similar relation to water passing through a reservoir or series of reservoirs. This would support the findings of Smith (1982) linking smolt travel time to water velocities.

The transit time (in days) of water, or reservoir flow-through time, was estimated by dividing the volume of the reservoir or series of reservoirs by the flow (storage replacement method developed by the U.S. Army Corps of Engineers). Volumes of the reservoirs in each index reach were estimated for capacities designated as full. The flows were referenced at the previously identified sites in each index reach. The Snake River index reach included McNary reservoir, which receives both middle Columbia and Snake river flows. Therefore, the McNary reservoir component of the index reach, a constant adjustment of 140×10^3 ft^3/s (the average spring flow contribution from the middle Columbia River) was added to the flow at Ice Harbor Dam, the lowest dam on the Snake River.

Observed smolt travel time was modeled with a reciprocal flow structure, which is the basis for water transit time through reservoirs. Water transit time is simply a function of flow and the cross-sectional area of the waterway. The similarity of fish travel time to water travel time and what is known about the biology of fish migration suggest that this is the most biologically intuitive model structure.

Multiple-Regression Analyses

The third objective was to determine the importance of other variables for smolt travel time and the relative importance of average flow when other variables were in the model. To address this objective, multiple regression was used on the flow-related and smoltification-related variables.

The goal was to create multiple-regression models having minimal multicollinearity among predictor variables, high R^2 values, and meaningful importance of the variables retained in terms of explaining variation in smolt travel time. All statistical analyses were performed with the SYSTAT statistical package for personal computers (Wilkinson 1990). Visual inspection of bivariate plots and Pearson correlation coefficients provided early indications of the shape and strength of relations between each predictor variable and the dependent variable, and between pairs of predictor variables. In the multiple-regression analysis, a step-flow increased. As a result of the limited range of flows observed in the middle Columbia River, the relation between smolt travel time and flow was not established ($P = 0.95$) for Winthrop Hatchery spring chinook salmon and only marginally established ($P = 0.04$) for Wells Hatchery steelhead (Table 1). The bivariate relations between travel time estimates and average flow are depicted in Figure 3 along with theoretical water transit times for each index reach.

Regression diagnostics indicated the presence of an outlier observation in the bivariate regressions that needed further consideration. This observation was the 1986 yearling chinook salmon group from Dworshak Hatchery. The studentized residual was 4.6, which is within the range that Draper and Smith (1981) defined as an outlier. Because this observation was not a high-leverage point, it did not affect the estimated regression slope or the significance of the regression (Fox 1991). It did, however, substantially increase the variance around the regression. Therefore, this observation was omitted when the bivariate regression model for Snake River yearling chinook salmon was determined (Table 1).

Multiple-Regression Analyses

Snake River index reach.—The predictive model for yearling chinook salmon groups in the Snake River index reach included the reciprocal of average flow ($FLOW^{-1}$), prior travel time to Lower Granite Dam (TTLGR), and delta-flow (DFLOW). The inclusion of the additional variables caused the outlier observation observed in the bivariate analysis to be even more severe (studentized residual, 5.4). The coefficients of the multiple regression did not change significantly with this observation, but the variance about the regression again substantially increased. Therefore, the outlier was excluded, and the resulting model with the remaining 29 observations explained 74% of the variation in smolt travel time (Table 2). The stepwise regression routine selected the variable $FLOW^{-1}$ first ($R^2 = 0.46$), followed by the variables TTLGR ($R^2 = 0.57$) and DFLOW ($R^2 = 0.74$). A 48% reduction in residual error about the

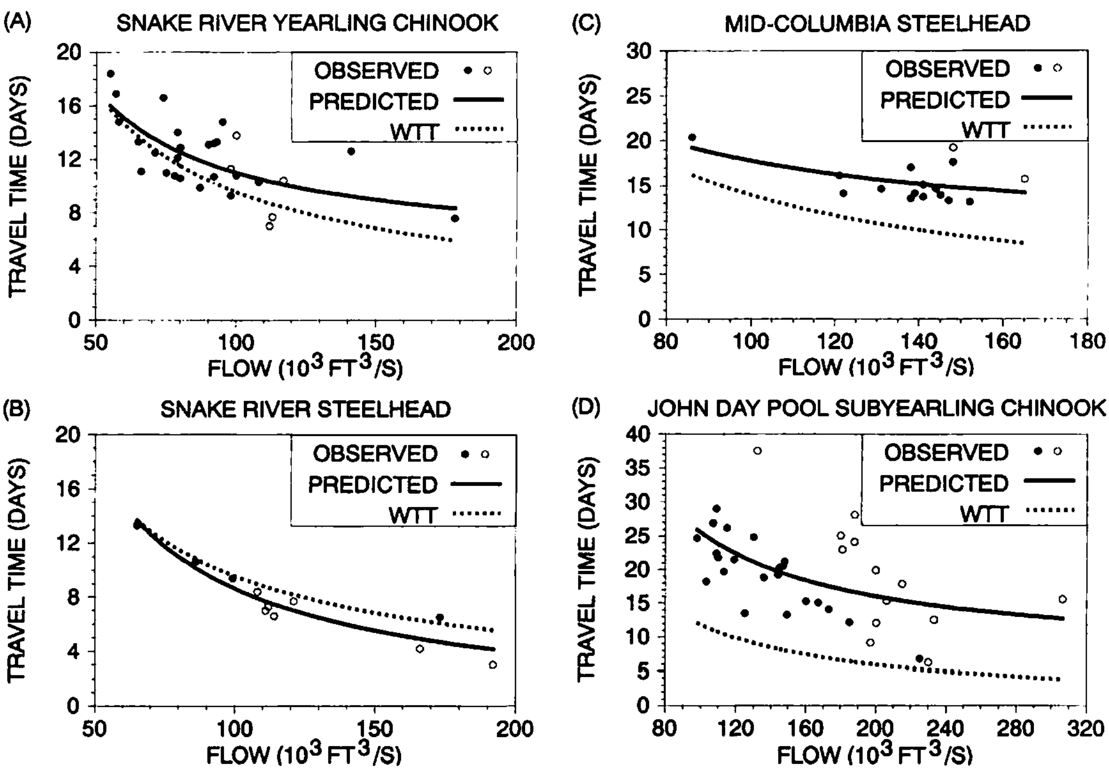

FIGURE 3.—Observed and predicted fish travel time estimates, and estimated water transit time (WTT), versus flow for (**A**) Snake River yearling chinook salmon, (**B**) Snake River steelhead, (**C**) middle Columbia River steelhead, and (**D**) lower Columbia River (John Day pool) subyearling chinook salmon. Open circles (○) denote pre-water budget years 1981–1983; solid circles (●) denote post-water budget years 1984 and beyond.

TABLE 2.—Multiple-regression models for predicting travel time[a] of yearling and subyearling chinook salmon and steelhead in key index reaches of the Columbia River basin.

Group	N	Variable[b]	Coefficient	SE	P[c]	MSE[d]	R^2
		Snake River index reach					
Yearling chinook salmon	29	Constant	6.401	1.541	<0.01	2.13	0.74
		$FLOW^{-1}$	574.072	92.208	<0.01		
		TTLGR	−0.120	0.029	<0.01		
		DFLOW	0.057	0.014	<0.01		
Steelhead	11	Constant	−0.730	0.967	0.47	0.89	0.90
		$FLOW^{-1}$	935.650	103.347	<0.01		
		Middle Columbia River index reach					
Yearling chinook salmon	14	Constant	69.709	16.140	<0.01	5.39	0.39
		DATE	−0.387	0.141	0.02		
Steelhead	16	Constant	42.883	10.108	<0.01	2.05	0.62
		$FLOW^{-1}$	1,040.739	296.388	<0.01		
		TEMP	−0.724	0.209	<0.01		
		Lower Columbia River index reach					
Subyearling chinook salmon	35	Constant	−42.364	9.598	<0.01	16.95	0.65
		$FLOW^{-1}$	3,016.061	445.452	<0.01		
		DFLOW	0.133	0.031	<0.01		
		DATE	0.165	0.042	<0.01		

[a] Median smolt travel time estimate (days) in index reach.
[b] Predictor variables: TTLGR = travel time from hatchery release to Lower Granite Dam (days); $FLOW^{-1}$ = reciprocal of flow (10^3 ft^3/s) averaged over the travel time days; DFLOW = absolute change in daily average flow (10^3 ft^3/s) over travel time days; TEMP = daily river temperature averaged over travel time (°F); DATE = day of entry into the index reach (day 1 = January 1).
[c] Probability (2-tail) that the coefficient is no different from zero; significant when $P \leq 0.05$.
[d] Residual mean-square error.

regression was observed relative to the bivariate model. Because of the high level of independence among the predictor variables (tolerances > 0.94), the beta coefficients were used and showed that $FLOW^{-1}$ explained the highest proportion of the variation in estimated travel time (Table 3). With other variables held fixed, the effect of the TTLGR variable was to shorten travel time in the index reach for yearling chinook salmon groups that migrated a longer time before entering the index reach. The effect of the DFLOW variable was to increase smolt travel time as the difference between minimum and maximum flow increased. This is a function of the curvilinear shape of the relation between average flow and smolt travel time. With the $FLOW^{-1}$ variable in the model, an increasing DFLOW reflected the effect of the time spent migrating at the lower flows.

The bivariate model with $FLOW^{-1}$ for steelhead in the Snake River index reach explained over 90% of the variation in smolt travel time (Table 1). The stepwise multiple-regression routine selected $FLOW^{-1}$ first ($R^2 = 0.90$), and then added TTLGR ($R^2 = 0.97$). However, the positive sign of TTLGR was opposite of what theory would predict and may simply reflect a higher level of smoltification for the later releases in 1982 and 1983. Because $FLOW^{-1}$ alone explained such a high proportion of the variation in smolt travel time, it was retained as the most parsimonious and biologically relevant model (Table 2).

Middle Columbia index reach.—The predictive model for yearling chinook salmon in the middle Columbia River index reach included the day of entry variable DATE. This predictor variable explained 39% of the variation in smolt travel time (Table 2). Smolt travel time decreased for later-migrating groups. The variation in flow experienced by yearling chinook salmon was limited and, therefore, the lack of a significant correlation with $FLOW^{-1}$ was not unexpected. The stepwise regression routine selected the variable DATE first ($R^2 = 0.39$), and then added DFLOW ($R^2 = 0.63$). However, the DFLOW must occur with $FLOW^{-1}$ in the model to retain its biological interpretation. Here, DFLOW may simply reflect that in 1987–1989, flow increased from low levels early in the migration of Winthrop Hatchery spring chinook salmon to levels more similar to the early-May flows of other years. Apparently, the higher flows that occurred later in the migration period, when these hatchery chinook salmon were at a higher smoltification level (Beeman et al. 1990), increased the migration rate and resulted in a shorter

TABLE 3.—Measures of importance of individual predictor variables in the multiple-regression models for smolt travel time.[a]

Group	Variable[b]	Partial coefficient	Tolerance[c]	Beta coefficient[d]
		Snake River index reach		
Yearling chinook salmon	$FLOW^{-1}$	574.072	0.993	0.637
	TTLGR	−0.120	0.942	−0.439
	DFLOW	0.057	0.947	0.418
		Middle Columbia River index reach		
Steelhead	$FLOW^{-1}$	1,040.739	0.983	0.603
	TEMP	−0.724	0.983	−0.595
		Lower Columbia River index reach		
Subyearling chinook salmon	$FLOW^{-1}$	3,016.061	0.738	0.836
	DFLOW	0.133	0.745	0.522
	DATE	0.165	0.988	0.416

[a] Median smolt travel time estimate (days) in index reach.
[b] Predictor variables: TTLGR = travel time from hatchery release to Lower Granite Dam (days); $FLOW^{-1}$ = reciprocal of flow (10^3 ft^3/s) averaged over the travel time days; DFLOW = absolute change in daily average flow (10^3 ft^3/s) over travel time days; TEMP = daily river temperature averaged over travel time (°F); DATE = day of entry into the index reach (day 1 = January 1).
[c] One minus the multiple correlation between a predictor variable and all other predictor variables in the model.
[d] Indicates the relative contribution of each predictor variable in explaining the variation in the dependent variable.

travel time than anticipated, given the low computed average flow. Because the DFLOW variable appears to reflect a more complex flow–smoltification response, which cannot be quantified with available data, the more parsimonious model with only the DATE variable was retained.

The predictive model for steelhead in the middle Columbia River index reach included the reciprocal of average flow ($FLOW^{-1}$) and river temperature (TEMP). These two predictor variables explained 62.3% of the variation in smolt travel time (Table 2). The stepwise regression routine selected DATE first (R^2 = 0.35), then $FLOW^{-1}$ (R^2 = 0.56) and TEMP (R^2 = 0.65). With TEMP in the model, DATE became a nonsignificant contributor (P = 0.36) and was removed in the next step. A 44% reduction in residual error about the regression was observed relative to the bivariate model for these steelhead. Because of the high level of independence between the predictor variables (tolerances > 0.98), the beta coefficients were used and showed that $FLOW^{-1}$ and TEMP explained about equal proportions of the variation in estimated travel time (Table 3). With flow fixed, the effect of increasing river temperatures was to decrease smolt travel time.

Lower Columbia River index reach.—The predictive model for travel time of subyearling chinook salmon through John Day reservoir included the reciprocal of average flow ($FLOW^{-1}$), deltaflow (DFLOW), and day of entry to the reach (DATE). These three variables explained 65% of the variation in smolt travel time (Table 2). The stepwise regression routine selected the reciprocal of minimum flow ($MINFLOW^{-1}$) first (R^2 = 0.35), then DATE (R^2 = 0.52), DFLOW (R^2 = 0.61), and $FLOW^{-1}$ (R^2 = 0.66). With $FLOW^{-1}$ in the model, $MINFLOW^{-1}$ became a nonsignificant contributor (P = 0.58) and was removed in the next step. A 49% reduction in residual error about the regression was observed relative to the bivariate model for subyearlings. A high level of independence occurred between DATE and the other two variables (tolerance = 0.99). A low level of multicollinearity occurred between $FLOW^{-1}$ and DFLOW (tolerance > 0.7), but it was too low to cause any concern about the coefficient estimates (Lewis-Beck 1980). Therefore, the beta coefficients were used and showed that $FLOW^{-1}$ explained the highest proportion of the variation in estimated travel time (Table 3). With the other variables fixed, the effect of DATE was to increase smolt travel time as the summer season progressed. The DATE variable appears to encompass a compounded effect of flow and smoltification. Because flow decreases through the summer migration period each year, the DATE variable includes the effect of this temporal trend. In addition, this variable will encompass smoltification differences in the mixed-stock population. Physiological monitoring of subyearling chinook salmon, begun at McNary Dam in 1990, has shown a lower level of smoltification (as measured by gill ATPase activity) among the later migrants in this mixed population (D. Rondorf, U.S. Fish and Wildlife Service, personal communication).

Discussion

The bivariate- and multiple-regression analyses documented that flows were important during both the spring and summer months when marked groups of salmonid smolts were migrating. With one exception, the relation between smolt travel time and average flow was statistically significant. The marked groups of subyearling and yearling chinook salmon and steelhead, released over 6–9 years during the past decade, showed that the time it takes smolts to migrate through key index reaches in the Columbia River drainage was inversely related to the average flow in the system. The exception was marked groups of yearling chinook salmon migrating in the middle Columbia River index reach, and it may be attributable to the narrow range of higher average flows these groups experienced between 1983 and 1990. When additional variables were considered, average flow was still the most important variable in the model for yearling chinook salmon and steelhead in the Snake River and in the model for subyearling chinook salmon in John Day reservoir. Average flow and temperature (a smoltification-related variable) had about equal importance for steelhead in the middle Columbia River.

Bivariate relations between smolt travel time and average flow and between theoretical water transit time and average flow had similar forms (Figure 3). As stated in the introduction, the link between smolt migration speed and water velocity (Smith 1982) had pointed to river flow as a key factor in determining smolt travel time through reservoirs. The rationale used by the Northwest Power Planning Council (NPPC) when it adopted flow augmentation as a mitigation measure in 1982 for the fish and wildlife program was further substantiated by these analyses.

The NPPC's fish and wildlife program did not provide flow mitigation for summer-migrating subyearling chinook salmon. Studies conducted between 1981 and 1983 had not produced evidence of a relation between average flow and travel time for subyearling migrants (Miller and Sims 1984). Further analysis of these data by Giorgi et al. (1990) again provided no evidence of a significant relation between flow and smolt travel time. In part, the reliability of the travel time estimated used may have been affected by the small sample recoveries. Marked releases of subyearling chinook salmon from McNary Dam between 1986 and 1988 provided additional travel time information (based on samples with higher recovery numbers) under a broader range of flows. With 6 years of data over a broader range of flow and a minimum sample size criterion for all mark groups, both the bivariate- and multiple-regression analyses presented here documented that average flow does have a statistically significant effect on travel time of subyearling chinook salmon during the summer.

The multiple-regression analyses documented the importance of adding a variable to account for the maximum change in flow during migrations. Marked smolts migrate under conditions of changing flow. For yearling chinook salmon in the Snake River and subyearling chinook salmon in the lower Columbia River, increases in delta-flow increased smolt travel time. Because of the curvilinear relation between smolt travel time and average flow, flows below the average have a greater effect on smolt travel time than flows above the average. Therefore, having a large delta-flow about an average level, rather than a relatively constant average flow, would tend to increase smolt travel time. Since yearling chinook salmon migrated during a period of rapidly increasing flows in the spring, and subyearling chinook migrated during a period of rapidly decreasing flows in the summer, the effects of delta-flow were significant. Steelhead tended to migrate closer to the peak of the spring freshet and experienced a longer period when flow fluctuations were lower than those experienced by yearling chinook salmon, so delta-flow was not a significant variable.

The multiple-regression analysis also documented that smoltification, as defined by surrogate variables, played a role in predicting how quickly smolts migrated through the index reaches. Variables including migration time from release at the hatchery to the start of an index reach (at Lower Granite Dam), chinook salmon race, river temperature, and date of entry into the index reach were considered. Other factors that influence smoltification, such as fish size, diet, and disease, were not considered in the modeling because consistent data were not available for all years. The variables used in the analysis were easily obtainable and had a biological link to some stage of smoltification. Travel time to Lower Granite Dam successfully accounted for smoltification differences among the four hatchery stocks of Snake River chinook salmon yearlings that had migrated different distances to the start of the index reach. In-river migration time has been shown to directly increase smoltification (Zaugg et al. 1985). The indicator variable for chinook salmon race was not significant in the model, apparently because potential race differences were already accounted for by the variable of migration time from hatchery to Lower Granite Dam. The summer race of chinook salmon tended to migrate for a longer period of time to the start of the index reach than did the spring race. The day of entry to the index reach captured the effect of the temporal changes (e.g., change in day length; Hoar 1988) on smoltification for middle Columbia River yearling chinook salmon and lower Columbia River subyearling chinook salmon. This variable also included the effect of the decreasing temporal trend in flow that occurs each year for subyearlings. Because day length is so highly correlated ($r > 0.95$) with the day of entry into an index reach, either variable may effectively relate to the level of smoltification attained. Since temperature generally controls the rate of smoltification (Hoar 1988), the presence of river temperature in the middle Columbia River steelhead model may reflect changes in smoltification. Whether day of entry to index reach or river temperature was selected for a particular predictive model may simply have reflected which variable was less correlated with other variables already in the model. Nevertheless, by including a surrogate for smoltification in the models, additional variation in smolt travel time was explained over that possible with flow-related variables alone.

In conclusion, increased flows reduce the travel time of both yearling chinook salmon in the Snake River and steelhead smolts in the middle Columbia and Snake rivers in spring and of subyearling chinook smolts in summer. This means that increased flows can mitigate both the spring and summer outmigration delays that smolts experience as a result of operation of the hydroelectric system in the Columbia River basin. Including variables that account for changes in smoltification during outmigration helps explain additional variation in estimated travel time. Therefore, predicting smolt travel time through key index reaches in the Columbia River basin is best accomplished with multiple-regression models containing both flow-related and smoltification-related variables.

Acknowledgments

Many people have been instrumental in generating the data analyzed in this study, and a special thanks is extended to all these individuals. This includes the hatchery managers and staff who made the fish available for marking, the crews that conducted the marking, and the field crews at each of the monitoring sites who collected the recovery data. We also thank the computer staff of the Fish Passage Center, who compiled and processed the data that went into the anlaysis, created graphics, and prepared the manuscript. We appreciate the time of those individuals who critically reviewed the manuscript and made helpful suggestions for improvements. The Fish Passage Center is funded by the Bonneville Power Administration as directed by the Northwest Power Planning Council's Fish and Wildlife Program.

References

Beeman, J. W., D. W. Rondorf, J. C. Faler, M. E. Free, and P. V. Haner. 1990. Assessment of smolt condition for travel time analysis. Annual report to Bonneville Power Administration, Contract DE-A179-87BP35245, Portland, Oregon.

Brege, D. A., W. E. Farr, and R. C. Johnsen. 1990. An air-lift pump for sampling juvenile salmonids at John Day Dam. North American Journal of Fisheries Management 10:481–483.

Columbia Basin Fish and Wildlife Authority. 1991. The biological and technical justification for the flow proposal of the Columbia Basin Fish and Wildlife Authority. CBFWA, Portland, Oregon.

deLibero, F. 1986. A statistical assessment of the use of the coded wire tag for chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) studies. Doctoral thesis. University of Washington, Seattle.

Draper, N. R., and H. Smith. 1981. Applied regression analysis, 2nd edition. Wiley, New York.

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.

Fox, J. 1991. Regression diagnostics. Sage Publications, Series 7-79, Newbury Park, California.

Giorgi, A. E., D. R. Miller, and B. P. Sanford. 1990. Migrating behavior and adult contribution of summer outmigrating subyearling chinook salmon in John Day reservoir, 1981–1983. Final Report to Bonneville Power Administration, Contract DE-AI79-83BP39645, Portland, Oregon.

Hoar, W. S. 1976. Smolt transformation: evolution, behavior, and physiology. Journal of the Fisheries Research Board of Canada 33:1233–1252.

Hoar, W. S. 1988. The physiology of smolting salmonids. Pages 257–343 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume II, part B. Academic Press, New York.

Lewis-Beck, M. S. 1980. Applied regression, an introduction. Sage Publications, Series 7-22, Newbury Park, California.

Mighell, J. L. 1969. Rapid cold-branding of salmon and trout with liquid nitrogen. Journal of the Fisheries Research Board of Canada 26:2765–2769.

Miller, D. R., and C. W. Sims. 1984. Effects of flow on the migratory behavior and survival of juvenile fall and summer chinook salmon in John Day Reservoir. Annual report to Bonneville Power Administration, Contract DE-AI79-83BP39645, Portland, Oregon.

NPPC (Northwest Power Planning Council). 1987. Columbia River basin fish and wildlife program. NPPC, Portland, Oregon.

Park, D. L. 1969. Seasonal changes in downstream migration of age-group 0 chinook salmon in the upper Columbia River. Transactions of the American Fisheries Society 98:315–317.

Raymond, H. L. 1968. Migration rates of yearling chinook salmon in relation to flows and impoundments in the Columbia and Snake rivers. Transactions of the American Fisheries Society 97:356–359.

Raymond, H. L. 1969. Effect of John Day Reservoir on the migration rate of juvenile chinook salmon in the

Columbia River. Transactions of the American Fisheries Society 98:513–514.

Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvneile chinook salmon and steelhead from the Snake River, 1966 to 1975. Transactions of the American Fisheries Society 108: 505–529.

Sims, C. W., and F. J. Ossiander. 1981. Migrations of juvenile chinook salmon and steelhead in the Snake River, from 1973 to 1979, a research summary. Report to the U.S. Army Corps of Engineers, Contract DACW68-78-C-0038, Portland, Oregon.

Smith, L. S. 1982. Decreased swimming performance as a necessary component of the smolt migration in salmon in the Columbia River. Aquaculture 28:153–161.

Snedecor, G. W., and W. G. Cochran. 1989. Statistical methods, 8th edition. Iowa State University Press, Ames.

Wedemeyer, G. A., R. L. Saunders, and W. C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. U.S. National Marine Fisheries Service, Marine Fisheries Review 42(6):1–14.

Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT, Evanston, Illinois.

Zaugg, W. S. 1981. Relationships between smolt indices and migration in controlled and natural environments. Pages 173–183 *in* E. L. Brannon and E. O. Salo, editors. Salmon and trout migratory behavior symposium. University of Washington, Seattle.

Zaugg, W. S., E. F. Prentice, and F. W. Waknitz. 1985. Importance of river migration to the development of seawater tolerance in Columbia River anadromous salmonids. Aquaculture 51:33–47.

Appendix: Passage Data for Study Reaches

TABLE A.1.—Snake River index reach data. The reach extends from Lower Granite Dam (LGR) to McNary Dam (MCN).

Year	Median release date[a]	Sample number[b] LGR	Sample number[b] MCN	Travel time (d)[c]	Flow (10^3 ft^3/s)[d] Average	Flow (10^3 ft^3/s)[d] Minimum	Flow (10^3 ft^3/s)[d] Delta[e]	Days to LGR[f]	Average river temperature (°F)[d]	Entry day of the year[g]
Dworshak Hatchery spring chinook salmon yearlings										
1983	Apr 1	335	142	13.8	100	41	79	21	53	112
1985	Apr 4	384	378	12.1	79	53	55	23	51	117
1986	Apr 2	479	370	20.8	97	78	42	19	52	111
1987	Apr 2	659	358	12.5	71	42	51	22	55	114
1988	Mar 30	502	555	18.4	55	35	55	21	52	110
1989	Mar 30	1,506	211	13.2	92	57	53	26	53	115
1990	Apr 5	372	254	16.6	74	57	33	24	54	119
McCall Hatchery summer chinook salmon yearlings										
1983	Apr 6	444	289	7.7	113	108	12	29	55	125
1984	Apr 10	196	153	7.6	178	160	37	37	53	137
1985	Apr 3	185	86	13.1	90	59	59	40	54	133
1986	Mar 27	508	170	10.8	100	90	27	37	53	124
1987	Mar 31	98	114	10.6	80	61	32	32	56	122
1989	Mar 21	194	116	9.9	87	56	64	51	55	131
1990	Mar 22	54	91	10.8	78	41	83	61	55	142
Rapid River Hatchery spring chinook salmon yearlings										
1982	Mar 27	159	144	10.4	117	101	25	26	49	112
1983	Mar 22	617	536	11.3	98	41	79	31	53	112
1984	Mar 27	302	262	10.3	108	88	40	31	49	117
1985	Apr 5	593	362	14.0	79	53	55	20	51	115
1986	Apr 5	1,073	295	14.8	95	78	42	15	52	110
1987	Apr 2	194	98	11.0	75	50	44	24	55	116
1988	Mar 23	116	189	16.9	57	35	55	32	53	114
1989	Mar 30	1,407	165	13.3	93	57	53	24	52	113
1990	Mar 24	297	309	13.3	65	53	23	30	54	113
Sawtooth Hatchery spring chinook salmon yearlings										
1983	Mar 29	181	113	7.0	112	98	22	35	54	123
1984	Mar 28	230	156	12.6	141	105	92	39	52	126
1985	Mar 27	216	124	12.9	80	59	49	38	53	124
1986	Mar 17	226	65	9.3	98	85	35	38	52	114
1988	Mar 15	47	88	14.8	58	35	55	42	53	116
1989	Mar 15	304	86	10.7	92	57	53	39	52	113
1990	Mar 17	76	96	11.1	66	53	23	37	54	113
Dworshak Hatchery summer steelhead yearlings										
1982	Apr 19	1,011	268	7.7	121	115	15	8	50	117
1982	Apr 30	512	191	6.6	114	105	21	6	51	126
1982	May 3	508	247	7.3	112	105	17	4	52	127
1982	May 19	613	63	4.2	166	153	43	5	55	144
1983	Apr 20	852	294	8.4	108	96	24	10	54	120
1983	May 3	1,762	301	7.0	111	99	20	5	55	128
1983	May 25	429	140	3.0	192	90	6	5	59	150
1984	May 4	117	67	6.5	173	156	41	10	53	134
1988	May 2	1,000	104	13.3	65	43	39	8	55	130
1989	May 1	714	46	9.4	99	70	51	8	54	129
1989	May 3	623	47	10.6	86	56	64	8	55	131

[a] Release from the hatchery of origin.
[b] Number of marked fish counted at the dam.
[c] Median time to travel the length of the reach.
[d] Measured at Ice Harbor Dam during travel of the leading 50% of the group.
[e] Difference between maximum and minimum flows.
[f] Median time from hatchery release.
[g] Median day of entry into the reach (day 1 = January 1).

TABLE A.2.—Middle Columbia index reach data. The reach extends from the mouth of the Methow River to McNary Dam (MCN). Variables are defined in Table A.1.

Year	Median release date	Sample number, MCN	Travel time (d)	Flow (10^3 ft^3/s)[a]			Average river temperature (°F)[a]	Entry day of the year
				Average	Minimum	Delta		
				Winthrop Hatchery spring chinook salmon yearlings				
1983	Apr 13	480	27.1	159	125	58	48	106
1984	Apr 23	158	23.2	143	101	63	47	116
1985	Apr 16	823	31.1	130	90	68	47	109
1985	Apr 20	457	29.3	133	104	53	48	113
1985	Apr 24	458	28.0	134	104	53	49	117
1986	Apr 21	792	25.8	143	107	63	47	114
1986	Apr 25	546	25.1	140	107	52	48	118
1986	Apr 29	624	22.0	137	107	50	48	122
1987	Apr 20	864	23.2	133	43	134	50	113
1987	Apr 24	658	22.3	145	93	84	51	117
1987	Apr 28	906	22.5	150	108	69	51	121
1988	Apr 19	2,288	24.3	96	55	96	49	112
1989	Apr 18	666	24.7	135	71	97	48	111
1990	Apr 17	425	28.0	143	102	78	48	110
				Wells Hatchery summer steelhead yearlings				
1982	Apr 21	438	19.2	148	114	70	46	113
1983	Apr 23	495	15.7	165	146	38	48	115
1984	Apr 23	454	17.6	148	113	51	46	114
1984	Apr 27	589	13.9	145	113	51	46	118
1985	May 6	611	13.5	138	104	53	49	127
1985	May 10	685	14.6	131	103	54	51	131
1985	May 14	504	14.1	122	90	58	52	135
1986	May 1	645	17.0	138	107	50	48	122
1986	May 5	497	15.1	141	122	35	48	126
1986	May 9	262	14.1	139	114	43	49	130
1987	Apr 23	485	16.1	121	43	119	49	114
1987	Apr 27	449	13.7	141	108	65	50	118
1987	May 1	585	13.1	152	108	66	51	122
1988	Apr 20	559	20.4	86	55	94	48	111
1989	Apr 29	444	14.6	144	102	67	49	120
1990	Apr 26	320	13.3	147	106	74	48	118

[a] Measured at Rock Island Dam.

TABLE A.3.—Lower Columbia index reach data for subyearling summer chinook salmon. The reach extends from McNary Dam to John Day Dam (JDA). Variables are defined in Table A.1.

Year	Median release date	Sample number, JDA	Travel time (d)	Flow (10^3 ft^3/s)[a]			Average river temperature (°F)[a]	Entry day of the year
				Average	Minimum	Delta		
1981	Jun 18	44	15.6	306	221	151	57	170
1981	Jul 10	79	17.9	215	149	116	61	192
1981	Jul 16	65	19.9	200	149	96	63	198
1981	Jul 22	50	12.1	200	162	62	64	204
1981	Jul 29	64	9.2	197	164	78	65	211
1982	Jul 29	44	23.0	181	114	122	66	211
1982	Aug 17	46	37.6	132	91	114	66	230
1983	Jun 16	41	12.6	233	192	91	59	168
1983	Jul 15	42	6.3	230	220	38	63	197
1983	Jul 20	60	15.4	206	171	67	64	202
1983	Jul 23	62	28.1	188	149	90	66	205
1983	Jul 27	41	24.1	188	149	90	66	209
1983	Jul 29	71	25.1	180	130	80	66	211
1986	Jun 15	61	6.8	225	173	77	62	167
1986	Jun 18	104	12.2	185	150	100	63	170
1986	Jun 23	124	21.2	148	88	105	65	175
1986	Jul 13	99	14.1	173	152	55	65	195
1986	Jul 15	123	15.1	167	142	64	66	197
1986	Jul 19	113	15.3	160	141	47	66	201
1986	Jul 21	90	20.5	147	122	66	67	203
1986	Jul 22	110	20.3	145	122	57	67	204
1986	Jul 23	117	19.2	144	122	47	67	205
1986	Jul 30	92	18.8	136	87	73	68	212
1986	Aug 1	46	24.8	130	87	73	69	214
1987	Jun 18	114	26.2	115	86	48	65	170
1987	Jun 23	123	19.7	113	86	46	66	175
1987	Jun 26	84	21.8	110	86	46	66	178
1987	Jul 2	87	26.9	107	78	54	67	185
1987	Jul 9	81	29.0	109	78	56	67	191
1988	Jun 15	104	13.3	149	123	45	62	167
1988	Jun 21	82	13.5	125	85	83	64	173
1988	Jun 23	75	21.5	119	85	79	64	175
1988	Jun 29	69	22.4	109	78	56	65	181
1988	Jul 6	89	24.7	98	77	55	66	188
1988	Jul 13	43	18.2	103	77	55	67	195

[a] Measured at John Day Dam.