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Stock-Specific Migration Timing of Adult Spring–Summer Chinook Salmon in the Columbia River Basin

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Abstract.—An understanding of the migration timing patterns of Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* is important for managing complex mixed-stock fisheries and preserving genetic and life history diversity. We examined adult return timing for 3,317 radio-tagged fish from 38 stocks of Columbia River basin spring–summer Chinook salmon *O. tshawytscha* over 5 years. Stock composition varied widely within and between years depending on the strength of influential populations. Most individual stocks migrated at similar times each year relative to overall runs, supporting the hypotheses that run timing is predictable, is at least partially due to genetic adaptation, and can be used to differentiate between some conspecific populations. Arrival timing of both aggregated radio-tagged stocks and annual runs was strongly correlated with river discharge; stocks arrived earlier at Bonneville Dam and at upstream dams in years with low discharge. Migration timing analyses identified many between-stock and between-year differences in anadromous salmonid return behavior and should aid managers interested in protection and recovery of evolutionarily significant populations.

The Columbia River drains more than 673,000 km^2 in seven U.S. states and British Columbia, and was historically one of the most productive rivers for anadromous salmon *Oncorhynchus* spp. and steelhead *O. mykiss* in the world (Chapman 1986; Nemeth and Kiefer 1999). Major declines in wild Columbia River basin salmonids have been attributed to habitat degradation and loss, excessive harvest, hatchery propagation, water diversion, and development and operation of main-stem hydroelectric dams (Raymond 1988; National Research Council 1996). Twelve Columbia River basin salmon and steelhead runs are currently protected under the U.S. Endangered Species Act (ESA); three of these runs are listed as endangered (NMFS 2000). Spring–summer Chinook salmon *O. tshawytscha* listed as threatened include the Snake River evolutionarily significant unit (ESU), the lower Columbia River ESU, and the upper Willamette River ESU; the upper Columbia River spring Chinook salmon ESU is endangered.

Columbia River basin ESUs cover large geographic areas, and each ESU contains a hierarchy of Chinook salmon subpopulations whose boundaries and conservation status were delineated by the National Marine Fisheries Service (NMFS) (Myers et al. 1998). Each ESU includes distinct populations (or metapopulations) that are reproductively isolated from conspecific populations and that represent an important evolutionary component of the species (Waples 1991). As defined, reproductive isolation between ESUs need not be absolute, but should be strong enough that genetic differences occur at evolutionary time scales. Metapopulations at the ESU level include many populations linked by genetic exchange within shorter ecological time scales (Cooper and Mangel 1999), and each population can include multiple locally adapted stocks within a watershed (Nehlsen et al. 1991; Emlen 1995). Within this population framework, differentiation between and protection of intraspecific groups are critical for maintaining genetic diversity and for recovery of both small-scale assemblages (i.e., local stocks) and broader ESU-level populations (National Research Council 1996; Policansky and Magnuson 1998).

Management of Columbia River basin spring–summer Chinook salmon ESUs and their hierarchy of subpopulations and stocks is particularly com-

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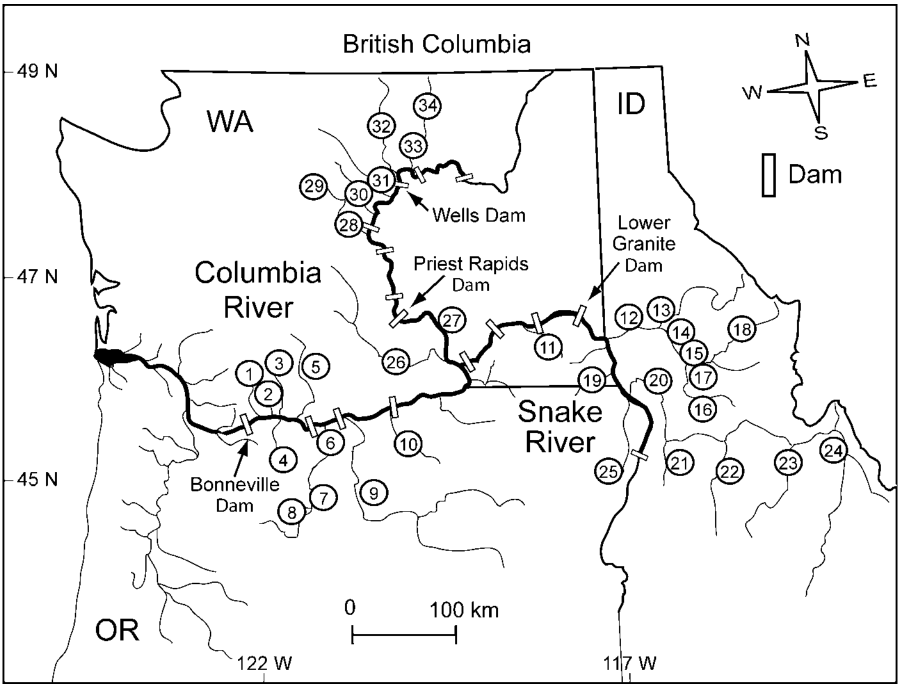

FIGURE 1.—Map of the Columbia River drainage illustrating the distribution of spatially separated spring–summer Chinook salmon stocks identified by returning radio-tagged adult fish, 1996–2001. Stocks 1–10 are from the lower Columbia River basin, stocks 11–25 are from the Snake River basin, and stocks 26–34 are from the upper Columbia River basin. See Table 2 for specifics.

plex. The run includes a large number of commercially and socially important populations, and both juvenile seaward and adult return migrations pass through multiple state, federal, international, and tribal jurisdictions. Spatial and temporal overlap is extensive during adult return migration, and fish from many stocks and multiple year-classes pass through lower Columbia River commercial, sport, and tribal fisheries at similar times.

Migration timing is an adaptive and heritable behavior (Smoker et al. 1998; Stewart et al. 2002), and can therefore be used to help manage Columbia River basin stocks of concern. Timing statistics have been used to differentiate between Alaskan Chinook salmon stocks (Burger et al. 1985; Wuttig and Evenson 2001), to reconstruct sockeye salmon *O. nerka* runs (Starr and Hilborn 1988), and to evaluate abundance, escapement, and harvest of pink salmon *O. gorbuscha*, sockeye salmon, and Chinook salmon (McDonald 1981; Mundy 1982; Merritt and Roberson 1986; Jensen and Mathisen 1987; Pahlke and Bernard 1996; Smoker et al. 1998).

For this study, we analyzed migration timing of Columbia River basin spring–summer Chinook salmon adults during 5 years from 1996 to 2001. Fish were captured and radio-tagged at Bonneville Dam, the downstream-most hydroelectric project in the Columbia River, and were monitored as they migrated upstream past dams and into tributaries or hatcheries throughout the basin. Unique transmitter frequencies and a comprehensive monitoring program allowed construction of detailed migration histories for each fish. Our objectives were to identify discrete, spatially separated stocks and to calculate and compare migration timing statistics at several locations for those stocks both within and between years. We also evaluated stock composition patterns within each migration year and examined relationships between individual and aggregate stock timing and Columbia River and Snake River discharge.

Methods

Fish trapping and tagging.—Adult spring–summer Chinook salmon were trapped at Bonneville Dam (river kilometer 235) in the adult fish facility (AFF) adjacent to the Washington shore fish ladder as they migrated upstream in the Columbia River (Figure 1). Spring-run Chinook salmon are those

TABLE 1.—Number of adult spring-summer Chinook salmon tagged with radio transmitters at Bonneville Dam and the number recorded as returning to major tributaries, hatcheries, adult traps, or weirs or to Wells Dam, 1996–2001.

Category	1996	1997	1998	2000	2001	Total
Number radio-tagged	853	1,014	957	1,132	1,117	5,073
Number returning	505	662	635	711	804	3,317
Percent returning	59.2	65.3	66.4	62.8	71.2	65.4

that pass Bonneville Dam during April and May, while summer-run fish pass the dam in June and July (USACE 2001). On each day in which fish tagging was conducted, a weir was lowered into the ladder to divert fish into the AFF via a short secondary ladder. Once inside the facility, fish entered a large tank and were either diverted into anesthetic tanks for tagging or returned via a chute to the main ladder.

In the five study years, counts of adult spring–summer Chinook salmon at Bonneville Dam ranged from about 59,800 to 467,600 fish (USACE 2001). Radio transmitters were placed in a total of 5,073 salmon (0.24–1.61% of the count each year), and 3,317 (65%) of the tagged fish returned to tributaries or hatcheries (Table 1). The remainder were reported harvested in main-stem Columbia River or Snake River fisheries or had unknown fates in the main stem. We unselectively tagged near-random samples in 1996, 1997, and 1998. Fish were tagged as they were trapped, but samples were not truly random because only fish passing via the Washington shore ladder were sampled, the proportion sampled each day varied, no fish were sampled at night, and we did not tag small jack (precocious adult, by size) salmon. The length of daily trapping periods depended on the number of fish that received transmitters and the number moving up the ladder. In 2000 and 2001, we followed the same tagging protocols as in earlier years, but also selected fish with passive integrated transponder (PIT) tags that identified where fish were tagged as juveniles. We used an automated PIT-tag detection system (McCutcheon et al. 1994) to identify PIT-tagged fish before they were diverted into the anesthetic tank. In 2000, 94% of the salmon tagged with transmitters were unselectively sampled and 6% had PIT tags, for a total sample similar to those in 1996–1998; in 2001, 70% had PIT tags, and 30% were unselectively tagged. Selection for PIT-tagged fish in 2001 increased sample sizes for the tributaries and hatcheries where fish were PIT-tagged as juveniles, but should not have affected timing analyses, as fish were tagged as they arrived throughout the run.

We attempted to radio-tag the fish in proportion to their abundance based on long-term averages of runs at Bonneville Dam (Figure 2). However, run timing varied each year, causing some deviations that could not be compensated for by in-season adjustments to the tagging schedule. We tagged fish throughout each run, and as a result tended to under-sample during migration peaks and over-sample during passage nadirs. The largest departures from representative sampling occurred in July 1996 and late July in 1997 and 1998, when no fish were tagged. These omissions primarily affected sample sizes for upper Columbia River summer Chinook salmon stocks and should not have substantially compromised interpretation of results. During 1996–1998, fish were tagged for approximately 10 d, followed by 4 d with no tagging. Tagging took place on almost all days in 2000 and 2001.

A concentration of 100 mg of tricaine methanesulfonate (MS-222)/L (Wedemeyer 1970) or 22 mg of clove oil/L (Peake 1998) was used to anesthetize fish. Once anesthetized, fish were moved to a tagging tank, where we recorded fork length, estimated sex, and examined fish for injuries, scars, fin clips, and other marks. A transmitter (Lotek Wireless, Inc., Newmarket, Ontario) was coated with glycerin and inserted into the stomach through the esophagus (Mellas and Haynes 1985). We primarily used 7-V radio transmitters that transmitted a unique, digitally coded signal every 5 s on a set frequency. We also used combination radio/data-storage transmitters (RDST tags) in 2000 and combination acoustic/radio transmitters (CART tags) in 2001. All transmitters were cylindrical and were equipped with 43–47-cm antennas. Seven-volt tags weighed 29 g in air (8.3 $\times$ 1.6 cm), RDST tags were 34 g (9.0 $\times$ 2.0 cm), and CART tags were 28 g (6.0 $\times$ 1.6 cm). Lithium batteries powered the transmitters, and all had a rated operating life that exceeded migration time. After tagging, fish were moved to a 2,275-L oxygenated recovery and transport tank, where they were held until their release (usually after 0.5–3 h) through a trap door. All fish radio-tagged from 1996 to 1998 were released about 9.5 km downstream from Bonneville Dam at sites on both sides

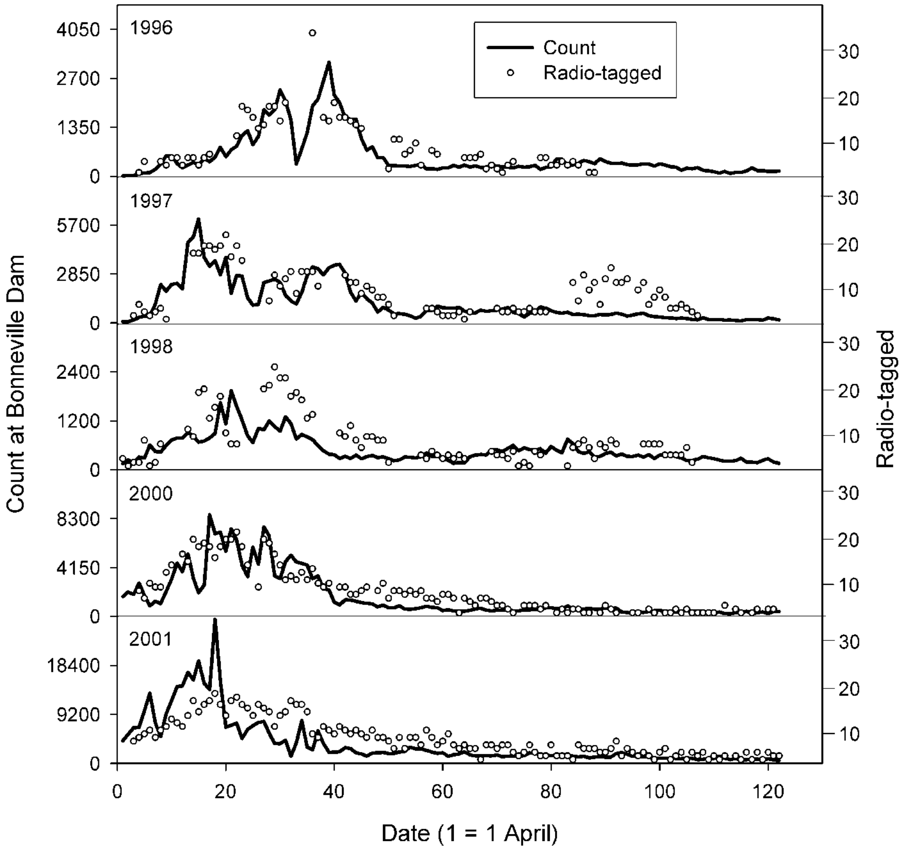

FIGURE 2.—Counts of adult spring–summer Chinook salmon passing Bonneville Dam from April to July 1996–2001 and the numbers trapped and radio-tagged at the dam each year.

of the river. In 2000 and 2001, 86% and 73% were released at the downstream sites, and the rest of the fish were released in the Bonneville Dam forebay for a separate evaluation.

Monitoring and final distribution of fish.—The study area included the Columbia River and its major tributaries upstream from Bonneville Dam, including the Snake River and its tributaries (Figure 1). We assessed the final distribution of radio-tagged fish with fixed radiotelemetry receivers, by mobile radio-tracking from trucks and boats in areas not covered by fixed telemetry receivers, and from the return of transmitters from fisheries, hatcheries, and adult traps and weirs.

Radio-tagged fish were monitored at the four lowest Columbia River dams (Bonneville, The Dalles, John Day, and McNary) and at Priest Rapids Dam on the upper Columbia River in all years. Monitoring also took place at the four lower Snake River dams in all years except 1996, when only Ice Harbor and Lower Granite dams were monitored. Shoreline-mounted aerial antennas were used in all major Columbia River tributaries between Bonneville and Priest Rapids dams in all years, except the Umatilla River in 1996. Major Snake River tributaries and tributaries to the Salmon and Clearwater rivers were similarly monitored in all years except 1996, when only the Clearwater River was monitored (Figure 1). To locate fish with transmitters between and upstream of fixed receivers, we conducted systematic mobile tracking surveys throughout the basin by truck along the main-stem Columbia and Snake rivers and in all tributaries with road access. Surveys were conducted at approximately 2–4-week intervals, and final comprehensive surveys were made after fall spawning periods. Receiver efficiency and antenna arrays during the 1996 migration, as well as data processing methods, are described in Bjornn et al. (2000); similar data from other years are available.

Concurrent cooperative telemetry projects by the Grant County, Chelan County, and Douglas

County (Washington) public utility districts (PUDs) provided data from some upper Columbia River locations for fish we radio-tagged at Bonneville Dam. The most upstream Columbia River location with near-continuous monitoring was at Wells Dam; telemetry receivers were used in some upper Columbia River tributaries, but were not maintained by us (Figure 1). Additional data from upper Columbia River tributaries came from periodic mobile tracking, spawning ground surveys conducted by ourselves and other fisheries agencies, and transmitters returned to us after fish were recaptured in fisheries and at hatcheries.

Stock identification and analyses.—Fish were identified as belonging to individual stocks either by the geographic location of their final telemetry record in a tributary or from transmitter returns from hatcheries, traps, or counting weirs in tributaries. The personnel at all basin hatcheries, traps, and weirs cooperated with transmitter returns. Fish that were reported as harvested in tributary fisheries were assumed to have originated from those tributaries because adult fidelity to natal sites is high and out-of-basin straying rates are low (Matthews and Waples 1991). Fish last recorded or harvested in the main-stem Columbia or Snake rivers were excluded from all timing analyses.

Fish returning to each major tributary were treated as unique stocks, except when stocks could be further separated based on returns to specific hatcheries or secondary tributaries within a watershed. For example, salmon that returned to the Deschutes River were separated into three distinct stocks: the Warm Springs Hatchery stock, the Pelton Dam Trap stock (associated with Round Butte Hatchery), and the group last recorded in the main-stem Deschutes River. Main-stem tributary stocks likely included a mixture of subbasin stocks, although some main-stem tributary spawning occurs. The only stock we designated that did not return to a tributary or hatchery included fish last recorded at Wells Dam on the upper Columbia River, above which monitoring was limited. The Wells Dam group likely included Methow and Okanogan river stocks and Wells Hatchery fish, which are out-planted into those systems.

Descriptive migration timing statistics calculated for each stock included the mean, median, quartile, 5th and 95th percentiles, coefficient of variation, skewness, and kurtosis (Wuttig and Evenson 2001) of the dates that stocks were tagged at Bonneville Dam. Similar statistics were calculated for stock passage dates at Priest Rapids Dam (the uppermost dam monitored each year passed by upper Columbia River fish) and Lower Granite Dam (the uppermost dam passed by Snake River fish). Timing statistics were calculated for individual years and for all 5 years combined. In this paper, we summarize statistics only for those stocks represented by more than 10 radio-tagged fish. No calculations were made for four stocks—Rock Creek, Walla Walla River, Selway River (tributary of the Clearwater River in the Snake River basin), and Chelan River—all of which were represented by fewer than 10 tagged fish for all 5 years combined. Bootstrapping with replacement was used to evaluate the accuracy of medians (Dixon 1993). Stock timing distributions were compared by use of nonparametric Kruskal–Wallis one-way analysis of variance (ANOVA) tests for all stocks represented by more than 10 fish. To characterize the relative uniqueness of timing distributions, we calculated mean pairwise distances between stocks by use of Tukey's tests with error rates adjusted for multiple comparisons (SYSTAT 2002).

Mean daily discharge data and daily counts of adult spring–summer Chinook salmon at dams on the Columbia and Snake rivers were obtained from the U.S. Army Corps of Engineers (USACE)[3] and the Grant County PUD (compiled by the University of Washington at http://www.cqs.washington.edu/dart/dart.html). Relationships between mean seasonal river discharge (April–July) and migration timing medians were evaluated by use of linear regression for both radio-tagged salmon (1996–2001) and for all adult salmon counted by USACE or the Grant County PUD at Bonneville, Lower Granite, and Priest Rapids dams (1975–2001). The latter data series was included to provide a long-term context for the telemetry data, starting with the year hydrosystem construction was finished. Radio-tagged fish from multiple similar stocks were aggregated in discharge–timing analyses to increase sample sizes.

Results

Migration Composition and Timing

We identified 38 spatially separated spring–summer Chinook salmon stocks from 3,317 radio-tagged fish that returned to tributaries, hatcheries, traps, weirs, or Wells Dam during the five study years (Table 2). For all years combined, stocks

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[3] The U.S. Army Corps of Engineers does not warrant the accuracy, reliability, or suitability of its data for any particular purpose (http://www.npr75.nwd.usace.army.mil/welcome.html).

TABLE 2.—Final known distribution of Chinook salmon radio-tagged at Bonneville Dam that volitionally returned to tributaries, hatcheries, adult traps, or weirs or to Wells Dam, 1996–2001, with the percentage that returned to each major subbasin each year. Stock numbers correspond to those in Figure 1.

Stock number	Tributary or hatchery	1996	1997	1998	2000	2001	Total
	Lower Columbia River[a]						
	Rock Creek		3				3
1	Wind River	94	53	59	101	41	348
2	Little White Salmon River	99	24	15	42	14	194
3	White Salmon River	17	9	2	2	2	32
4	Hood River	4	10	3			17
5	Klickitat River	19	28	26	19	5	97
6	Deschutes River	42	23	49	64	9	187
7	Warm Springs Hatchery	17	11	11	51	2	92
8	Pelton Dam Trap	9	12	14	6	5	46
9	John Day River	37	7	28	30	10	112
10	Umatilla River	15	12	9	12	4	52
	Walla Walla River				1		1
	Subbasin total	353	192	216	328	92	
	Subbasin percent	70	29	34	46	11	
	Snake River						
11	Tucannon River	4	6	4	2	1	17
12	Clearwater River[b]	6	17	7	14	31	75
13	North Fork Clearwater River		7	11	13	3	34
14	Dworshak Hatchery	10	24	14	10	8	66
15	Lolo Creek		2	4	3	3	12
16	South Fork Clearwater River	5	12	10	14	31	72
17	Clear Creek	1	8	2	1	4	16
18	Lochsa River	2	15	16	18	25	76
	Selway River		3	5		1	9
19	Grande Ronde River	1	2	18	13	21	55
20	Salmon River[b]	3	9	6	4	54	76
21	Little Salmon River	11	88	39	41	66	245
22	South Fork Salmon River	10	39	39	57	134	279
23	Middle Fork Salmon River	1	15	19	8	23	66
24	Upper Salmon River basin	4	10	15	18	26	73
25	Imnaha River	6	10	13	10	42	81
	Subbasin total	64	267	222	226	473	
	Subbasin percent	13	40	35	32	59	
	Upper Columbia River[c]						
26	Yakima River	33	19	41	59	121	273
27	Ringold Hatchery	7	8	40	1		56
28	Wenatchee River[b]	6	65	32	22	16	141
29	Icicle River	15	21	18	21	15	90
30	Entiat River	1	3	5	11		20
	Chelan River		1			1	2
31	Wells Dam	21	37	51	32	46	187
32	Methow River	1	17	4	5	15	42
33	Okanogan River[b]	4	17	2	2	18	43
34	Similkameen River		15	4	4	7	30
	Subbasin total	88	203	197	157	239	
	Subbasin percent	17	31	31	22	30	

[a] Between Bonneville Dam and the Snake River confluence.
[b] Last recorded at main-stem tributary sites.
[c] Upstream from the Snake River confluence.

were represented by an average of 87 radio-tagged fish (median = 66; SD = 85). Four stocks had more than 200 tagged fish and another five stocks had more than 100 tagged fish. Stock sample sizes in individual years averaged 16–24 fish (median = 7–15; SD = 16–31).

Fish distribution among major subbasins varied widely from 1996 to 2000, the 4 years when radio-tagged samples were the most random. Return proportions in those years were 29–70% for lower Columbia River stocks (between Bonneville Dam and the Snake River confluence), 13–40% for Snake River stocks, and 17–31% for upper Columbia River stocks (upstream from the Snake

River confluence) (Table 2). The less-random sample in 2001 was comprised mainly of upriver fish: 59% of radio-tagged fish returned to the Snake River, and 30% returned to the upper Columbia River. For comparison, about 40% of the total 2001 run counted at Bonneville Dam eventually entered the Snake River, and 22% passed Priest Rapids Dam.

Stock composition among radio-tagged salmon changed throughout each run, and several influential stocks strongly affected annual distributions among the three major subbasins. In general, lower Columbia River stocks declined in proportion over the tagging period, whereas Snake River stocks increased in proportion until June and then precipitously declined (Figure 3). Upper Columbia River stock proportions were low during April and May, but stocks from this subbasin predominated during June and July (Figure 3). Between years, lower Columbia River and Snake River stocks were variable in contribution: lower Columbia River stocks comprised up to 80% of the spring run in 1996, when Wind, Little White Salmon, and Deschutes river stocks dominated the migration. About 40% of the spring run in 1997 and 1998 were from lower Columbia River stocks. Snake River stocks made up less than 30% of the tagged fish throughout 1996, compared to more than 45% of the 1997 sample from April to early June. In 1997, 1998, and 2000, combinations of Little Salmon, Wind, and Deschutes river stocks contributed most to the early run, followed by Yakima River fish in all years and Ringold Hatchery fish in 1998. South Fork Salmon River fish from the Snake River basin were the most abundant stock in early June of 1997, 1998, and 2000.

For all 5 years combined, median migration dates at Bonneville Dam for the 34 individual stocks with more than 10 fish fell into three clusters (Figure 4). The first and largest cluster included mainly spring Chinook salmon stocks from all three subbasins; median passage dates at Bonneville Dam fell between 20 April and 6 May. The second cluster included upper Salmon, Klickitat, Imnaha, and South Fork Salmon river stocks, and median passage dates occurred between 22 and 29 May; each of these lower Columbia River and Snake River stocks had a mixture of spring- and summer-run fish, based on Bonneville Dam passage dates. The third cluster consisted of five upper Columbia River summer Chinook salmon stocks whose median passage dates at Bonneville Dam were between 26 June and 3 July.

Median stock passage dates at Bonneville Dam

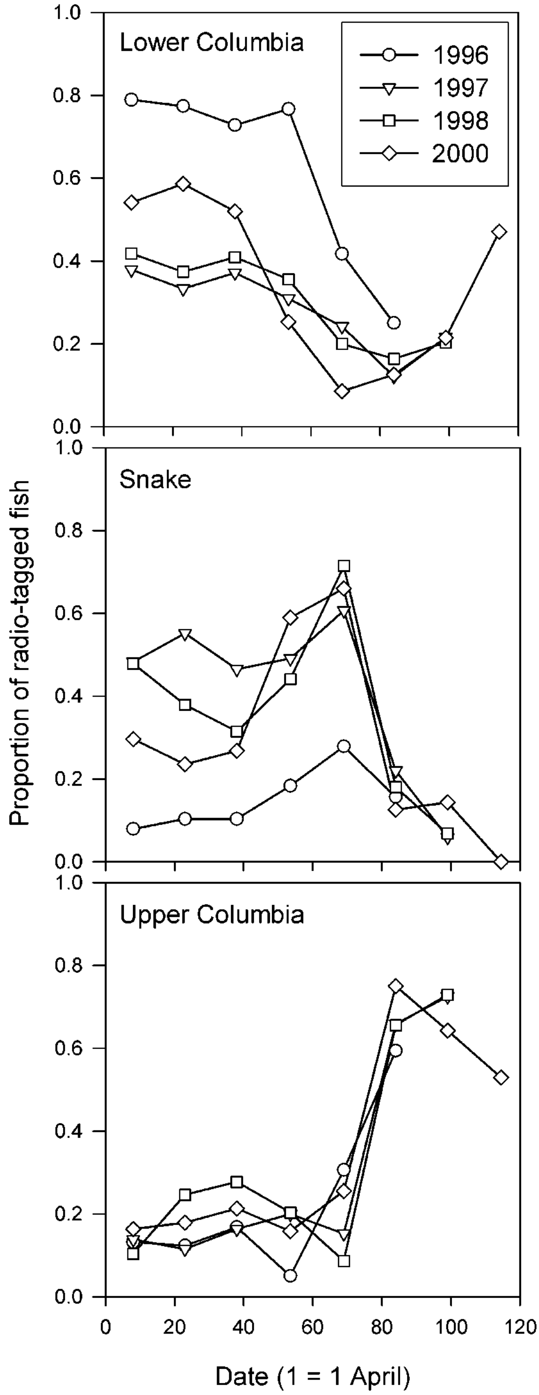

FIGURE 3.—Semimonthly proportions of radio-tagged spring–summer Chinook salmon that returned to lower Columbia River, Snake River, or upper Columbia River subbasins in 1996, 1997, 1998, and 2000.

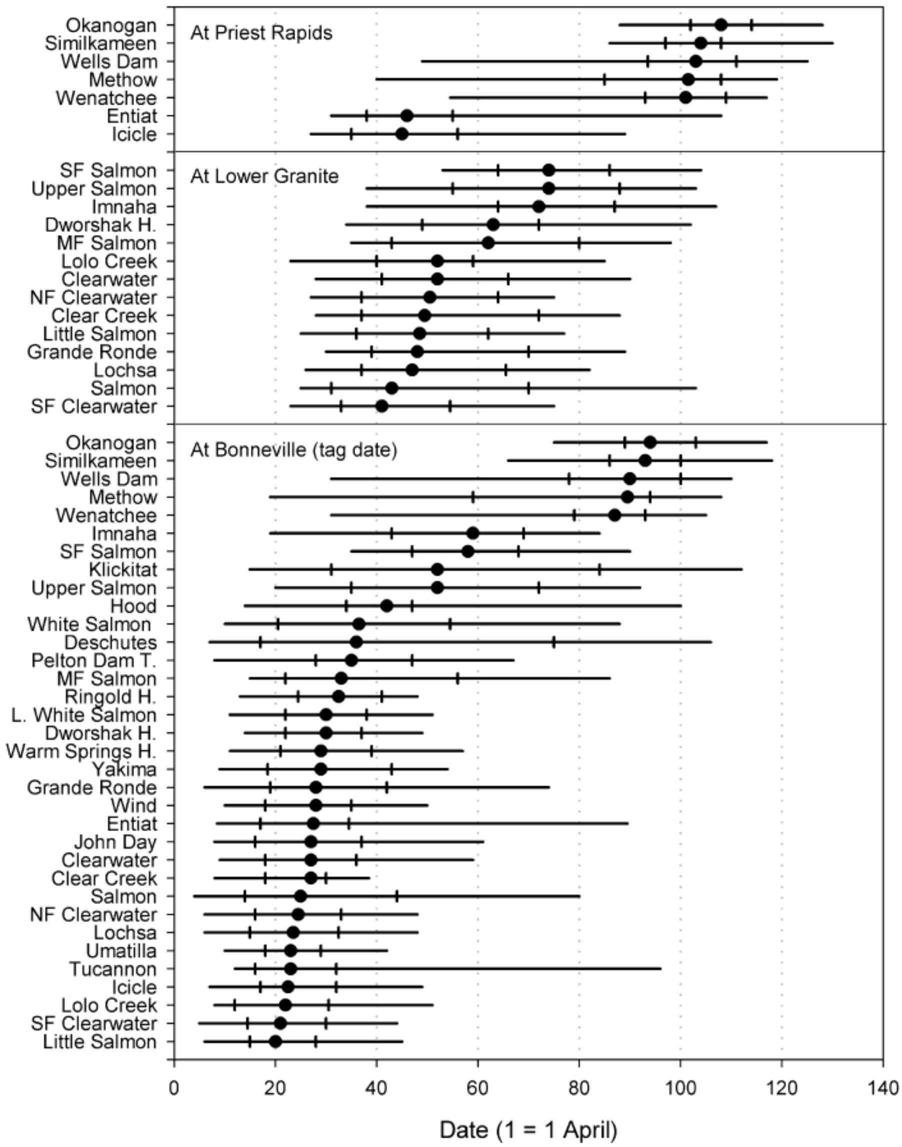

FIGURE 4.—Spring–summer Chinook salmon stock timing distributions at Bonneville, Lower Granite, and Priest Rapids dams, 1996–2001, including median, quartile, 5th percentile, and 95th percentile dates (SF = south fork; MF = middle fork; NF = north fork; H = hatchery; T = trap).

were similar to medians generated from 1,000 bootstrapped subsamples of the data. For 29 of 34 stocks, the 90% confidence intervals around bootstrapped estimates of median dates were within 6 d of the medians listed in Table 3, indicating that medians were reasonably accurate. Confidence intervals around bootstrapped medians were wider for Klickitat, upper Salmon, Middle Fork Salmon, Entiat, and White Salmon river stocks, which each included a mixture of spring- and summer-run fish.

Snake River stocks passed Lower Granite Dam more or less in a continuum, South Fork Clearwater (median = 11 May) and main-stem Salmon River (13 May) stocks passing earliest and upper Salmon River (13 June) and South Fork Salmon River (13 June) stocks passing latest (Figure 4). Upper Columbia River stocks passed Priest Rapids Dam in two nearly exclusive groups, with bimodal passage distributions in each year: Entiat and Icicle river spring Chinook salmon stocks had median

TABLE 3.—Migration timing statistics, including mean and median dates, interquartile range, coefficient of variation (CV), skewness (γ_1), and kurtosis (γ_2), for Columbia River basin Chinook salmon stocks at the time of radio-tagging at Bonneville Dam for all years combined, 1996–2001. In a normal distribution, both γ_1 and γ_2 are zero. Negative γ_1 indicates skewness to the left; positive γ_1 indicates skewness to the right. Negative γ_2 indicates a flat distribution with thin tails; positive γ_2 shows a high-peaked distribution and/or fatter tails. Sample sizes are provided in Table 2.

Tributary or hatchery	Median date	Mean date	Interquartile range (d)	CV	Skewness (γ_1)	Kurtosis (γ_2)
Lower Columbia River						
Wind River	Apr 28	Apr 27	17	0.44	0.72	1.49
Little White Salmon River	Apr 30	Apr 30	16	0.42	1.19	5.23
White Salmon River	May 6	May 9	34	0.63	1.03	0.89
Hood River	May 12	May 16	13	0.55	0.95	0.52
Klickitat River	May 22	May 27	53	0.54	0.37	−0.97
Deschutes River[a]	May 6	May 15	58	0.73	0.74	−0.68
Warm Springs Hatchery	Apr 29	Apr 30	25	0.50	0.51	0.21
Pelton Dam Trap	May 5	May 7	19	0.51	0.45	0.36
John Day River	Apr 27	Apr 29	21	0.56	1.23	2.27
Umatilla River	Apr 23	Apr 24	11	0.37	0.45	−0.42
Snake River						
Tucannon River	Apr 23	Apr 29	16	0.70	2.42	7.01
Clearwater River[a]	Apr 27	Apr 29	18	0.58	1.92	6.42
North Fork Clearwater River	Apr 24	Apr 26	17	0.60	1.68	5.12
Dworshak Hatchery	Apr 30	Apr 30	15	0.37	0.40	−0.23
Lolo Creek	Apr 22	Apr 22	19	0.56	0.83	0.43
South Fork Clearwater River	Apr 21	Apr 22	16	0.52	0.38	−0.49
Clear Creek	Apr 27	Apr 24	12	0.43	−0.17	−0.68
Lochsa River	Apr 23	Apr 24	18	0.51	0.57	0.13
Grande Ronde River	Apr 28	May 2	23	0.61	1.03	0.64
Salmon River[a]	Apr 25	May 1	30	0.73	1.01	0.39
Little Salmon River	Apr 20	Apr 22	13	0.51	0.80	0.47
South Fork Salmon River	May 28	May 28	21	0.26	0.26	0.01
Middle Fork Salmon River	May 3	May 11	34	0.55	0.70	−0.40
Upper Salmon River basin	May 22	May 23	37	0.42	0.09	−0.86
Imnaha River	May 29	May 25	26	0.37	−0.49	0.22
Upper Columbia River						
Yakima River	Apr 29	May 1	18	0.46	0.97	2.22
Ringold Hatchery	May 2	May 2	17	0.38	0.87	3.25
Wenatchee River[a]	Jun 26	Jun 21	14	0.25	−1.90	3.95
Icicle River	Apr 22	Apr 26	15	0.59	1.89	5.84
Entiat River	Apr 27	May 3	18	0.77	1.51	1.26
Wells Dam	Jun 29	Jun 23	22	0.28	−1.33	1.25
Methow River	Jun 28	Jun 15	35	0.39	−0.95	−0.42
Okanogan River[a]	Jul 3	Jul 5	14	0.11	−0.05	0.31
Similkameen River	Jul 2	Jun 30	14	0.14	−0.43	1.64

[a] Last recorded at main-stem tributary sites.

dates in mid-May, and five mainly summer-run Chinook salmon stocks had median passage dates between 10 and 17 July. The Methow and Wenatchee rivers support both spring- and summer-run stocks, but because subbasin monitoring was restricted, spring-run Methow River stocks and some spring-run Wenatchee River fish could not be separated from summer-run fish based on final location alone. Based on timing distributions, however, spring-run Methow and Wenatchee river stocks passed Priest Rapids Dam at similar times as spring-run Entiat and Icicle river stocks.

For all years combined, interquartile ranges for most stocks at Bonneville Dam were about 20 d (mean = 22 d, median = 18 d; Table 3). Mean and median interquartile ranges were about 28 d at Lower Granite Dam and 15 d at Priest Rapids Dam (Table 4). Annual interquartile ranges for each stock at Bonneville, Lower Granite, and Priest Rapids dams were similar to, or slightly narrower than, the multi-year values.

About 80% (27/34) of stock passage date distributions at Bonneville Dam were skewed to the right for all years combined (Table 3), and 62% (62/100) of distributions were right-skewed for in-

TABLE 4.—Migration timing statistics, including mean and median dates, interquartile range, coefficient of variation (CV), skewness (γ_1), and kurtosis (γ_2), for Snake River Chinook salmon stocks recorded as passing Lower Granite Dam and for upper Columbia River stocks recorded as passing Priest Rapids Dam, 1996–2001.

Tributary or hatchery	Median date	Mean date	Interquartile range (d)	CV	Skewness (γ_1)	Kurtosis (γ_2)
Snake River stocks at Lower Granite Dam						
Clearwater River	May 22	May 26	25	0.36	0.75	0.41
North Fork Clearwater River	May 21	May 21	27	0.35	0.82	1.38
Dworshak Hatchery	Jun 2	Jun 1	23	0.30	0.67	0.84
Lolo Creek	May 22	May 21	19	0.36	0.43	−0.01
South Fork Clearwater River	May 11	May 15	22	0.35	0.61	−0.42
Clear Creek	May 20	May 25	35	0.39	0.29	−1.34
Lochsa River	May 17	May 22	29	0.40	1.49	4.67
Grande Ronde River	May 18	May 24	31	0.37	0.61	−0.50
Salmon River	May 13	May 22	39	0.48	0.76	−0.41
Little Salmon River	May 19	May 19	26	0.34	0.24	−0.68
South Fork Salmon River	Jun 13	Jun 15	22	0.21	0.26	−0.22
Middle Fork Salmon River	Jun 1	Jun 2	37	0.36	0.52	−0.39
Upper Salmon River basin	Jun 13	Jun 10	33	0.31	−0.11	−0.63
Imnaha River	Jun 11	Jun 13	23	0.26	−0.19	−0.07
Upper Columbia River stocks at Priest Rapids Dam						
Wenatchee River	Jul 10	Jul 7	16	0.19	−1.59	4.42
Icicle River	May 15	May 20	21	0.40	1.55	3.01
Entiat River	May 16	May 24	17	0.45	1.42	0.81
Wells Dam	Jul 12	Jul 8	18	0.21	−1.29	1.77
Methow River	Jul 11	Jun 30	23	0.31	−0.99	−0.14
Okanogan River	Jul 17	Jul 18	12	0.10	−0.03	−0.14
Similkameen River	Jul 13	Jul 9	11	0.11	0.30	2.67

dividual stock-years with at least 10 fish. Stocks with left-skewed distributions were predominately summer-run stocks that included a few spring-run fish (e.g., Imnaha, Wenatchee, Methow, and Okanogan rivers, and Wells Dam). Kurtosis values indicated that most (74%, 25/34) timing distributions at Bonneville Dam had high peaks or broad distributions with flat tails (leptokurtosis) for all years combined (Table 3), as did about half of all individual stock-years (48%, 48/100). High-peaked distributions were observed for Little White Salmon and Icicle river stocks; Tucannon, main-stem Clearwater, and North Fork Clearwater river stocks had relatively fat-tailed distributions. Stocks with flatter or bimodal distributions (platykurtosis) included the Klickitat, main-stem Deschutes, and upper Salmon river stocks, all of which had mixtures of spring- and summer-run fish.

Between-stock migration timing distributions were significantly different at Bonneville, Lower Granite, and Priest Rapids dams for all years combined and for all individual years ($P \leq 0.004$; Kruskal–Wallis one-way ANOVA). Upper Columbia River stocks with large summer-run components had the most statistically distinct timing distributions at Bonneville Dam, followed by stocks with mixtures of spring- and summer-run fish (Tukey's pairwise comparison tests). The earliest spring migrants (Little Salmon and South Fork Clearwater rivers) also had relatively large pairwise distances at Bonneville Dam; the least distinct stocks were hatchery or hatchery-influenced spring Chinook salmon groups, including the Warm Springs Hatchery, Ringold Hatchery, Grande Ronde River, Little White Salmon River, and Dworshak Hatchery stocks. At Lower Granite Dam, pairwise distances were greatest for late-migrating South Fork Salmon, Imnaha, and upper Salmon river stocks, followed by early-migrating South Fork Clearwater River fish. Pairwise distances at Priest Rapids Dam were greatest for Icicle and Entiat river stocks, which passed significantly earlier than Wenatchee River, Okanogan River, Similkameen River, Methow River, and Wells Dam stocks.

Stock timing sequences within individual years were similar to sequences constructed for all years combined, though same-stock timing varied widely between years at some sites (Figure 5). A total of 21 stocks at Bonneville Dam, 10 stocks at Lower Granite Dam, and 3 stocks at Priest Rapids Dam had 10 or more tagged fish in each of three or more years (Table 2). Significant between-year timing differences ($P < 0.005$, Kruskal–Wallis one-way

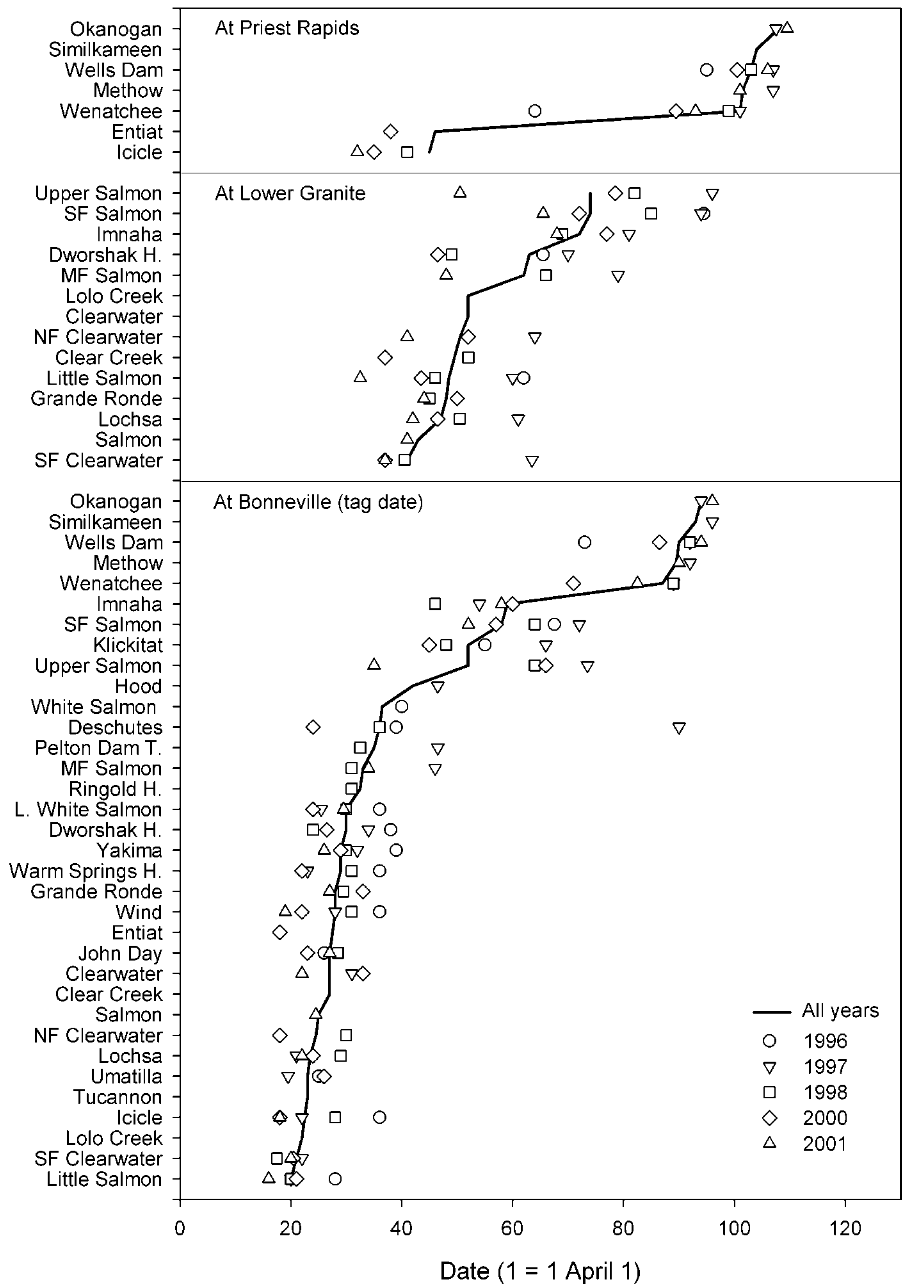

FIGURE 5.—Annual median dates during which radio-tagged spring–summer Chinook salmon stocks were tagged at Bonneville Dam or were recorded as passing Lower Granite or Priest Rapids dams, 1996–2001 (SF = south fork; MF = middle fork; NF = north fork; H = hatchery; T = trap).

ANOVA) were found for 57% (12/21) of the stocks at Bonneville Dam, 80% (8/10) of those at Lower Granite Dam, and 100% (3/3) of those at Priest Rapids Dam. The difference between minimum and maximum median passage dates ranged from 19 to 28 d for stocks with significant between-year differences and from 10 to 11 d for nonsignificant pairs at all three dams (Figure 5).

Effects of River Discharge

Columbia River discharge during the five study years varied widely and included one of the low-

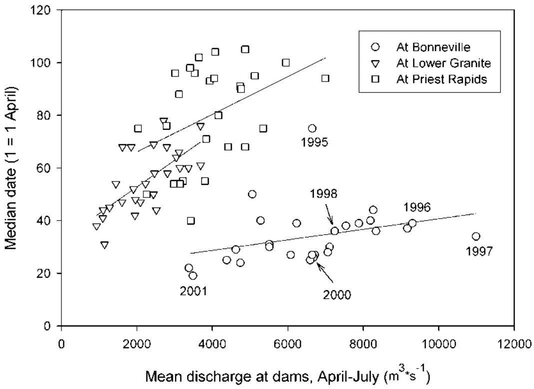

FIGURE 6.—Linear regressions of mean April–July river discharge and median passage dates for all fish counted as passing the fishways at Bonneville, Lower Granite, and Priest Rapids dams from 1975 to 2001.

est-discharge years on record (2001), two relatively high-discharge years (1996, 1997), and two near-average years (1998, 2000). Peak discharge occurred in late May or early June during 1996–1998, in late April during 2000, and in mid-May during 2001. Between-year differences in Snake River discharge at Ice Harbor Dam and in upper Columbia River discharge at Priest Rapids Dam were proportionately similar to those for the lower Columbia River.

Median annual passage dates for all adult spring–summer Chinook salmon counted as passing fishways at Bonneville, Lower Granite, and Priest Rapids dams were positively correlated with mean April–July discharge at those dams from 1975 to 2001 (Figure 6). Half the spring–summer Chinook salmon run passed Bonneville Dam by as early as 19 April in low-discharge years; median dates occurred during early to mid-May in high-discharge years (median date = 19.3 + [0.002·discharge]; $P = 0.012$; $r^2 = 0.23$; linear regression, one outlier excluded). Median passage dates were more variable and regression slopes were steeper at the upstream dams. Medians at Lower Granite Dam ranged from early May in low-discharge years to mid-June in high-discharge years (median date = 32.6 + [0.010·discharge]; $P < 0.001$; $r^2 = 0.46$). Medians at Priest Rapids Dam ranged from 10 May in low-discharge years to 14 July in high-discharge years (median date = 51.9 + [0.007·discharge]; $P = 0.031$; $r^2 = 0.17$). As was the case during 1975–2001, median passage dates for all fish counted at Bonneville, Lower Granite, and Priest Rapids dams during the five study years were positively correlated with mean April–July discharge at those dams ($0.09 < P < 0.12$; $0.60 < r^2 < 0.68$).

Timing distributions of most radio-tagged stocks were also positively correlated with river discharge. Median dates at Bonneville Dam were 13–19 d earlier in low-discharge 2001 than in high-discharge 1996 or 1997 for all lower Columbia River stocks ($r^2 = 0.71$; $P = 0.071$) and for late-migrating Snake River stocks ($r^2 = 0.98$; $P = 0.001$) (Table 5). Early and late Snake River stocks and early upper Columbia River stocks passed Lower Granite or Priest Rapids dams significantly earlier as annual discharge decreased ($0.007 < P < 0.047$; $0.78 < r^2 < 0.94$); median passage dates were 24–28 d earlier at both dams in 2001 than in the high-discharge years, 1996 and 1997. Timing of late-migrating upper Columbia River stocks

TABLE 5.—Results from linear regressions (β = slope, *a* = intercept) of mean April–July Columbia River or Snake River discharge and median passage dates (day of year, where 1 = 1 April) of radio-tagged spring–summer Chinook salmon at Bonneville, Lower Granite, and Priest Rapids dams from 1996 to 2001. Stocks are aggregated based on similar timing and geographic distribution.

Dam	Stocks[a]	r^2	P	β	a
Bonneville	All lower Columbia River	0.71	0.071	0.002	15.7
	Early Snake River	0.11	0.580	0.001	20.4
	Late Snake River	0.98	0.001	0.003	42.0
	Early upper Columbia River	0.37	0.278	0.001	20.1
	Late upper Columbia River	0.03	0.792	−0.000	89.5
Lower Granite	Early Snake River	0.78	0.047	0.010	26.1
	Late Snake River	0.94	0.007	0.012	50.8
Priest Rapids	Early upper Columbia River	0.89	0.016	0.005	21.4
	Late upper Columbia River	0.00	0.922	−0.000	101.0

[a] Early Snake River stocks consist of all Clearwater, Tucannon, Grande Ronde, Little Salmon, and Middle Fork Salmon River stocks; late Snake River stocks consist of Imnaha, South Fork Salmon, and upper Salmon River stocks. Early upper Columbia River stocks consist of Ringgold hatchery and Yakima, Icicle, and Entiat River stocks; late upper Columbia River stocks consist of Wells Dam and Wenatchee, Methow, Okanogan, and Similkameen River stocks.

was not correlated with discharge at Bonneville or Priest Rapids dams, perhaps because most fish migrated after annual peak discharge.

Discussion

Results from this study indicated that return migration timing of individual Columbia River spring–summer Chinook salmon populations is influenced by both river discharge and heritable genetic traits. The influence of river environment was evident in the positive correlations between run timing and river discharge from our telemetry data, as well as in the 1975–2001 count data. A genetic influence on migration timing was evident from the similarity between annual stock arrival sequences: the earliest spring stocks tended to be from the Clearwater River and Salmon River basins each year, and summer-run stocks from upper Columbia River watersheds were typically the latest migrants.

Run-timing differences among salmonids are, at least partially, adaptations to predictable thermal and flow regimes in migration corridors and spawning streams (Healey 1991; Quinn et al. 2002). Many stocks, including stocks of Chinook salmon (Burger et al. 1985), sockeye salmon (Gilhousen 1990), and pink salmon (Smoker et al. 1998), time migrations to arrive at home streams just prior to optimal environmental and biological spawning conditions. Other stocks time their migrations to avoid difficult passage environments. Examples of such stocks include some sockeye salmon (Hodgson and Quinn 2002) and steelhead (Robards and Quinn 2002) that migrate well before spawning periods to avoid high water temperatures in migration corridors, and Atlantic salmon *Salmo salar* that time migration to avoid low flows (Hansen and Jonsson 1991).

Most Columbia River basin spring Chinook salmon and many Snake River summer Chinook salmon stocks spawn in high-elevation headwater tributaries characterized by low water temperatures (Matthews and Waples 1991). Use of these tributaries requires longer egg incubation and therefore early spawning dates, an adaptation also observed among Fraser River sockeye salmon stocks (Brannon 1987). Upper Columbia River summer Chinook salmon stocks spawn in larger and warmer low-elevation rivers, a life history strategy more similar to that of fall Chinook salmon, and one that selects for later migration and arrival at spawning grounds (Matthews and Waples 1991). Most Columbia River basin spring–summer Chinook salmon stocks migrate prior to peak main-stem warming but often during peak annual discharge, which suggests that arrival at spawning grounds during optimal times is a stronger selective pressure than avoidance of the difficult passage associated with high discharge.

Annual discharge differences, however, did explain much of the between-year variation in run timing in this study. River discharge most strongly affected run timing at Lower Granite Dam on the Snake River, probably due to differences in migration speed during different discharge regimes. For example, radio-tagged spring Chinook salmon migrated through the 460-km reach between Bonneville Dam and Lower Granite Dam 2.4 times faster in the low-discharge year 2001 (median = 33 km/d) than in high-discharge year 1997 (14 km/d) (Keefer et al. 2004); median passage dates at Lower Granite Dam were 1 May in 2001 versus 31 May in 1997. In a similar study, sockeye salmon migration rates were also negatively correlated with river discharge in Alaska's Copper River (Merritt and Roberson 1986), and stock arrival at upstream locations was later in high-discharge years. The Columbia River is impounded, and therefore fish behaviors are not strictly comparable to those in free-flowing rivers. However, run-of-river management of main-stem Columbia River reservoirs does approximate the seasonal discharge patterns of free-flowing systems, although the magnitude of maximum and minimum discharge events has been altered; discharge variability within and between years remains high, and adult salmon clearly responded to annual and seasonal differences.

Progressive shifts in seasonal water temperature and discharge patterns due to Columbia River hydrosystem development and management have the potential to influence the migration timing of Chinook salmon stocks. Sockeye salmon and American shad *Alosa sapidissima* have migrated progressively earlier in the Columbia River as main-stem water temperatures have increased and discharges have decreased (Quinn and Adams 1996), whereas steelhead have shown complex responses to the changing river environment, including extensive holding behavior (Robards and Quinn 2002). American shad have altered migration such that they now migrate in similar or cooler water temperatures than in the mid-20th century, while sockeye salmon have responded less rapidly and now migrate during warmer temperatures than previously, suggesting a greater genetic influence on timing for sockeye salmon (Quinn and Adams 1996). We suspect that Chinook salmon, which are obligatory migrants like sockeye salmon, may also have less flexibility in their migration timing response to environmental change. If so, some Columbia River Chinook salmon stocks are likely exposed to higher temperatures than those under which they evolved, and temperature-related stress and elevated metabolic demands may lead to higher incidence of prespawn mortality.

Spring–summer stocks historically used most of the suitable tributary spawning habitat upstream from Bonneville Dam, particularly in the Snake River basin (West Coast Chinook Salmon Biological Review Team 1997). The Columbia River is near the middle of the Chinook salmon latitudinal range, and numerous local stocks have evolved in the basin's vast array of habitat types. The historic diversity of life history types and local adaptations probably buffered the basin's runs from short-term ecological or environmental changes and local catastrophic events (Winans 1989). However, dams constructed without fish passage facilities resulted in major genetic losses among Chinook salmon returning to the upper Columbia, Snake, and Clearwater rivers and to tributaries draining the Cascade Range (National Research Council 1996). Excessive harvest near the turn of the 20th century and summertime water withdrawals from spawning tributaries decimated summer-run stocks—historically the strongest, but now the weakest of the Columbia River life history groups (Chapman 1986). It is unknown how much genetic variation was lost by Columbia River basin Chinook salmon, but elimination, weakening, and dilution of many stocks has resulted in decreased productivity and fitness of the basin's metapopulations (MacLean and Evans 1981; Adkison 1995).

The 38 stocks we identified from the radiotelemetry and recapture data do not fully reflect current spring–summer Chinook salmon stock diversity in the Columbia River basin. For example, telemetry monitoring favored identification of Snake River stocks, which were combined into a single ESU by NMFS (2000), at finer scales than in the lower or upper Columbia River subbasins. The Wind, Klickitat, John Day, Yakima, Methow, and Okanogan rivers and other rivers all have more than one discrete spawning aggregation of spring- and/or summer-run fish, but we grouped fish from those drainages into single stocks and therefore underrepresented diversity. Finer-scale monitoring would be necessary to capture more of the conspecific stock diversity within subwatersheds.

In terms of migration timing, hatchery or hatchery-influenced stocks, including Dworshak Hatchery, North Fork Clearwater River, Warm Springs Hatchery, Ringold Hatchery, Little White Salmon River, and Grande Ronde River stocks, were among the least distinct radio-tagged stocks in terms of their migration patterns. Of these, all except the Warm Springs Hatchery fish (Deschutes River) share overlapping hatchery lineages. Each has included Carson Hatchery stock (a composite from lower Columbia River hatcheries), Rapid River stock (an upper Snake River composite, reared in Idaho's Little Salmon River basin), and/or Lookingglass Hatchery stock (a mixed-origin group that includes Carson Hatchery stock, reared in the Grande Ronde River basin) (Matthews and Waples 1991; West Coast Chinook Salmon Biological Review Team 1997). Local adaptation is less likely to occur or persist for such out-of-basin transfers or hatchery composites (Ricker 1972; MacLean and Evans 1981), because the introduced stocks typically have low survival to maturity and are unlikely to optimize habitat use, migration times, or spawning times. The shared genetic heritage for these stocks may partly explain the high migration timing synchrony for populations with wide geographic distribution and dramatically different migration requirements. Broodstock selection at hatcheries can also affect stock timing, especially when strategies cull fish from early- or late-returning portions of a run; altered migration timing has been observed for several Columbia River hatchery steelhead stocks (Busby et al. 1996), and similar shifts have likely occurred with Chinook salmon.

Supplementation with out-of-basin stocks also has a tendency to dilute or suppress small native populations (National Research Council 1996). Nehlsen et al. (1991) identified 214 native, naturally spawning Pacific salmon stocks, of which nearly half were at high risk of extinction. High-risk wild spring–summer Chinook salmon stocks in the Columbia River basin upstream from Bonneville Dam included Salmon River summer Chinook salmon, as well as Hood River, Tucannon River, Asotin Creek, and Salmon River spring Chinook salmon. Medium-risk stocks included Grande Ronde, Imnaha, and Methow river stocks; John Day River and Okanogan River spring Chinook salmon were stocks of concern (Nehlsen et al. 1991). Within the medium-risk group, the Imnaha River (spring–summer) and South Fork Salmon River (summer) stocks had among the most unique return migration timing distributions at Bonneville Dam and are primarily locally-derived stocks (Matthews and Waples 1991). Radio-tagged

Imnaha River and South Fork Salmon River fish migrated more or less concurrently through the lower Columbia River after the large group of spring-run stocks and prior to the upper Columbia River summer-run stocks. Unique timing for these salmon may allow for unique management strategies.

Other stocks that could benefit from timing-based management include the Little Salmon River spring Chinook salmon, which were among the earliest migrants to pass Bonneville Dam each year, and upper Salmon River summer Chinook salmon, which passed Bonneville Dam early relative to the upper Columbia River summer stocks. Management based on run timing alone would be more difficult for other stocks identified by Nehlsen et al. (1991). Hood River, Tucannon River, Methow River, and Okanogan River spring Chinook salmon stocks migrated through the lower Columbia River during the highly mixed spring run. Fewer than 20 fish were radio-tagged from each of these stocks during the 5 years of the study, making differentiation from other spring-run groups difficult with this method. Timing distributions for the more numerous John Day River and Salmon River (e.g., main-stem, middle-fork, and upper-river stocks) spring Chinook salmon were also difficult to separate from the aggregated spring run.

In an early review of Columbia River fisheries, Galbreath (1966) concluded that individual Chinook salmon stocks could not be identified or afforded additional protection based on migration timing alone. Our results partially support that finding, because stock intermingling occurred throughout each migration, and no stocks passed dams in complete temporal isolation. However, many stocks and groups of stocks were readily differentiated from each other and from the run-at-large each year, and those differences followed predictable patterns.

Our samples of radio-tagged Chinook salmon showed that both the composition and timing of Columbia River basin spring–summer Chinook salmon runs can vary widely. As such, stock-specific management strategies based on run timing should be conservative. Errors in stock identification, run composition, or timing predictions could substantially affect escapement of specific groups (Starr and Hilborn 1988), particularly when fisheries are nonterminal and consist of mixed stocks, as in the lower Columbia River. Overharvest of weaker or smaller stocks in mixed-stock fisheries has resulted in complete elimination of some salmonid populations, such as wild coho salmon *O. kisutch* in the lower Columbia River (Policansky and Magnuson 1998), and depression of many other populations, including many North American Atlantic salmon runs (Saunders 1981), Fraser River sockeye salmon (Collie et al. 1990), and British Columbia chum salmon *O. keta* (Beacham et al. 1987).

In this study, 4–10% of radio-tagged Chinook salmon were reported as being harvested in main-stem fisheries each year, and 24–35% were last recorded in the main-stem Columbia or Snake rivers and could not be assigned to specific stocks. In all years, main-stem harvest rates were higher in spring—when fisheries were open—than in summer. Main-stem fisheries occur primarily in lower Columbia River reservoirs, and therefore the harvested fish could have been from most spring-run stocks. Proportionately more fish with unknown fates at main-stem sites were also last detected in lower Columbia River reservoirs in spring. The latter may have died, been harvested but not reported, or entered tributaries undetected; a small number may have spawned at main-stem sites. Transmitter loss was estimated to be 3% (Keefer et al. 2004b), a rate similar to recent reports for adult sockeye salmon (Ramstad and Woody 2003). Other tag effects should be minimal: Matter and Sandford (2003) reported that radio-tag insertion and handling of the Chinook salmon in this study had no significant biological effect on upstream migration behavior.

The stock-specific migration timing and stock composition summaries presented here, combined with harvest location data, could be used for stock-of-origin estimates for harvested fish and for unassigned fish with unknown fates. Origin estimation for harvested fish, whether based on behavioral data like run timing or genetic sampling (e.g., Beacham et al. 1987; Shaklee et al. 1999), should be a component of any restoration plan for Columbia River basin runs, as should efforts to characterize the vulnerability of selected stocks or groups of stocks to harvest or other management activities.

In conclusion, radiotelemetry programs can greatly facilitate migration reconstruction for anadromous salmonid runs. Depending on the resolution of monitoring efforts, behavioral data can be collected across the range of population hierarchies, from individual spawning aggregations and stocks to ESU-level metapopulations. Individually identifiable fish can help clarify stock composition and behavior in highly complex mixed-stock runs. Effective management of threatened and endangered native Columbia River salmonids should include the quantification of migration timing and continued emphasis on understanding the dynamics of multiple subpopulations and unique, locally adapted stocks.

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References

Adkison, M. D. 1995. Population differentiation in Pacific salmon: Local adaptation, genetic drift, or the environment? Canadian Journal of Fisheries and Aquatic Sciences 52:2762–2777.

Beacham, T. D., A. P. Gould, R. E. Withler, C. B. Murray, and L. W. Barner. 1987. Biochemical genetic survey and stock identification of chum salmon (*Oncorhynchus keta*) in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44:1702–1713.

Bjornn, T. C., M. L. Keefer, C. A. Peery, K. R. Tolotti, R. R. Ringe, and P. J. Keniry. 2000. Migration of adult spring and summer Chinook salmon past Columbia and Snake River dams, through reservoirs, and distribution into tributaries, 1996. Idaho Cooperative Fish and Wildlife Research Unit, Technical Report 2000-5, University of Idaho, Moscow.

Brannon, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing. Canadian Special Publication of Fisheries and Aquatic Sciences 96:120–124.

Burger, C. V., R. L. Wilmot, and D. B. Wangaard. 1985. Comparison of spawning areas and times for two runs of Chinook salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 42:693–700.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27.

Chapman, D. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. Transactions of the American Fisheries Society 115: 662–670.

Collie, J. S., R. M. Peterman, and C. J. Walters. 1990. Experimental harvest policies for a mixed-stock fishery: Fraser River sockeye salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 47:145–155.

Cooper, A. B., and M. Mangel. 1999. The dangers of ignoring metapopulation structure for the conservation of salmonids. Fisheries Bulletin 97:213–226.

Dixon, P. M. 1993. The bootstrap and the jackknife: describing the precision of ecological indices. Pates 290–318 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York.

Emlen, J. 1995. Population viability of the Snake River Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 52:1442–1448.

Galbreath, J. L. 1966. Timing of tributary races of Chinook salmon through the lower Columbia River based on analysis of tag recoveries. Oregon Fish Commission Research Briefs 12(1):58–80.

Gilhousen, P. 1990. Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. International Pacific Salmon Fisheries Commission Bulletin 26.

Hansen, L. P., and B. Jonsson. 1991. Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 38:251–258.

Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311–393 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Hodgson, S., and T. P. Quinn. 2002. The timing of adult sockeye salmon migration into freshwater: adaptations by populations to prevailing thermal regimes. Canadian Journal of Zoology 80:542–555.

Jensen, K. A., and O. A. Mathisen. 1987. Migratory structure of the Kvichak River sockeye salmon (*Oncorhynchus nerka*) escapement, 1983. Canadian Special Publication of Fisheries and Aquatic Sciences 96:101–109.

Keefer, M. L., C. A. Peery, T. C. Bjornn, and L. C. Stuehrenberg. 2004a. Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and steelhead in the Columbia and Snake rivers. Transactions of the American Fisheries Society 133: 1413–1439.

Keefer, M. L., C. A. Peery, R. R. Ringe, and T. C. Bjornn. 2004b. Regurgitation rates of intragastric radio transmitters by adult Chinook salmon and steelhead during upstream migration in the Columbia and Snake rivers. North American Journal of Fisheries Management 24:47–54.

MacLean, J. A., and D. O. Evans. 1981. The stock concept, discreteness of fish stocks, and fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 38:1889–1898.

Matter, A. L., and B. P. Sandford. 2003. A comparison of migration rates of radio- and PIT-tagged adult Snake River Chinook salmon through the Columbia River hydropower system. North American Journal of Fisheries Management 23:967–973.

Matthews, G. M., and R. S. Waples. 1991. Status review for Snake River spring and summer Chinook salmon. NOAA Tech Memorandum NMFS F/NWC-200.

McCutcheon, C. S., E. F. Prentice, and D. L. Park. 1994. Passive monitoring of migrating adult steelhead with PIT tags. North American Journal of Fisheries Management 14:220–223.

McDonald, J. 1981. The stock concept and its application to British Columbia salmon fisheries. Canadian Journal of Fisheries and Aquatic Sciences 38:1657–1664.

Mellas, E. J., and J. M. Haynes. 1985. Swimming performance and behavior of rainbow trout (*Salmo gairdneri*) and white perch (*Morone americana*): effects of attaching telemetry transmitters. Canadian Journal of Fisheries and Aquatic Sciences 42:488–493.

Merritt, M. F., and K. Roberson. 1986. Migratory timing of upper Copper River sockeye salmon stocks and its implications for the regulation of the commercial fishery. North American Journal of Fisheries Management 6:216–225.

Mundy, P. R. 1982. Computation of migratory timing statistics for adult Chinook salmon in the Yukon River, Alaska, and their relevance to fisheries management. North American Journal of Fisheries Management 4:459–470.

Myers, J. M., R. G. Kope, G. J. Bryant, D. Teel, L. J. Lierheimer, T. C. Wainwright, W. S. Grant, F. W. Waknitz, K. Neely, S. T. Lindley, and R. S. Waples. 1998. Status review of Chinook salmon from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-35.

NMFS (National Marine Fisheries Service). 2000. Federal Columbia River Power System biological opinion: reinitiation of consultation on operation of the federal Columbia River Power System and Juvenile Transportation Program and 19 Bureau of Reclamation projects in the Columbia basin. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Region, Seattle.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington D.C.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Nemeth, D. J., and R. B. Kiefer. 1999. Snake River spring and summer Chinook salmon: the choice for recovery. Fisheries 24(10):16–22.

Pahlke, K. A., and D. R. Bernard. 1996. Abundance of the Chinook salmon escapement into the Taku River, 1989–1990. Alaska Fisheries Research Bulletin 3(1):9–20.

Peake, S. 1998. Sodium bicarbonate and clove oil as potential anesthetics for nonsalmonid fishes. North American Journal of Fisheries Management 18: 919–924.

Policansky, D., and J. J. Magnuson. 1998. Genetics, metapopulations, and ecosystem management of fisheries. Ecological Applications 8(1)(Supplement):119–123.

Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77(4):1151–1162.

Quinn, T. P., J. A. Peterson, V. F. Gallucci, W. K. Hershberger, and E. L. Brannon. 2002. Artificial selection and environmental change: countervailing factors affecting the timing of spawning by coho and Chinook salmon. Transactions of the American Fisheries Society 131:591–598.

Ramstad, K. M., and C. A. Woody. 2003. Radio tag retention and tag-related mortality among adult sockeye salmon. North American Journal of Fisheries Management 23:978–982.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook salmon and steeelhead in the Columbia River basin. North American Journal of Fisheries Management 8:1–24.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 27–160 *in* R. C. Simon and P. A. Larkin, editors. The stock concept in Pacific salmon. University of British Columbia Press, Vancouver.

Robards, M. D., and T. P. Quinn. 2002. The migratory timing of adult summer-run steelhead in the Columbia River over six decades of environmental change. Transactions of the American Fisheries Society 131: 523–536.

Saunders, R. L. 1981. Atlantic salmon (*Salmo salar*) stocks and management implications in the Canadian Atlantic provinces and New England, USA. Canadian Journal of Fisheries and Aquatic Sciences 38:1612–1625.

Shaklee, J. B., T. D. Beacham, L. Seeb, and B. A. White. 1999. Managing fisheries using genetic data: case studies from four species of Pacific salmon. Fisheries Research 43:45–78.

Smoker, W. W., A. J. Gharrett, and M. S. Stekoll. 1998. Genetic variation of return date in a population of pink salmon: a consequence of fluctuating environment and dispersive selection? Alaska Fisheries Research Bulletin 5(1):46–54.

Starr, P., and R. Hilborn. 1988. Reconstruction of harvest rates and stock contribution in gauntlet salmon fisheries: application to British Columbia and Washington sockeye (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 45:2216–2229.

Stewart, D. C., G. W. Smith, and A. F. Youngson. 2002. Tributary-specific variation in timing of return of Atlantic salmon (*Salmon salar*) to fresh water has

a genetic component. Canadian Journal of Fisheries and Aquatic Sciences 59:276–281.
SYSTAT. 2002. SYSTAT 10 for Windows. SYSTAT Software, Richmond, California.
USACE (U.S. Army Corps of Engineers). 2001. Annual fish passage report. U.S. Army Engineer Districts, Portland, Oregon, and Walla Walla, Washington.
Waples, R. S. 1991. Definition of ''species'' under the Endangered Species Act: application to Pacific salmon. NOAA Technical Memorandum NMFS F/NWC-194.
Wedemeyer, G. 1970. Stress of anesthesia with MS-222 and Benzocaine in rainbow trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 27:909–914.
West Coast Chinook Salmon Biological Review Team. 1997. Review of the status of Chinook salmon (*Oncorhynchus tshawytscha*) from Washington, Oregon, California, and Idaho under the U.S. Endangered Species Act. NOAA Technical Memorandum NMFS-NWFSC-35.
Winans, G. A. 1989. Genetic variability in Chinook salmon stocks from the Columbia River basin. North American Journal of Fisheries Management 9:47–52.
Wuttig, K. G., and M. J. Evenson. 2001. In-river abundance, spawning distribution, and migratory timing of Copper River Chinook salmon in 2000. Alaska Department of Fish and Game, Fishery Data Series 01-22, Anchorage, Alaska.