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ADULT SALMON AND STEELHEAD PASSAGE TIMES THROUGH HYDROSYSTEM AND RIVERINE ENVIRONMENTS OF THE COLUMBIA RIVER BASIN, 1996-2002

by

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Preface

Studies of adult salmon and steelhead *Oncorhynchus* spp. migrations past dams, through reservoirs, and into tributaries began in 1990 with planning, purchase, and installation of radio telemetry equipment for studies at the Snake River dams. Adult spring–summer Chinook salmon (*O. tshawytscha)* and steelhead (*O. mykiss*) were outfitted with transmitters at Ice Harbor Dam in 1991 and 1992, and at John Day Dam in 1993; reports of those studies are available (Bjornn et al. 1992; 1994; 1995; 1998a). The focus of adult salmonid passage studies shifted to include the lower Columbia River dams and tributaries starting in 1996. From 1996 to 2002 we radio-tagged various combinations of spring–summer Chinook salmon, fall Chinook salmon, steelhead and/or sockeye salmon at Bonneville Dam and monitored them as they migrated upstream. In this report we present summary information on adult Chinook salmon and steelhead passage times and rates at dams, through reservoirs and through longer hydrosystem reaches. Summaries of spring–summer Chinook salmon passage times in unimpounded reaches and tributaries are also included for comparative purposes. For all groups, we examine within- and between-year variation in passage time behaviors, and evaluate how broad-scale river environment affected this variability.

Acknowledgements

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Abstract

We assessed upstream migration rates of more than 12,000 radio-tagged adult spring–summer and fall Chinook salmon (*Oncorhynchus tshawytscha)* and steelhead (*O. mykiss*) past Columbia and Snake river dams, reservoirs and longer hydrosystem reaches that included multiple dams and reservoirs. Passage rates were also calculated for 1,800 spring–summer Chinook salmon as they passed through 12 unimpounded reaches and tributaries. Most radio-tagged fish from all runs passed mainstem Columbia and Snake River dams in less than two days. Migration behavior in reservoirs and through multiple dam/reservoir reaches varied substantially within and between years and between species. Within years, spring–summer Chinook salmon migrated more rapidly as water temperature and date of migration increased; between years, spring–summer Chinook salmon migrated quickly in low-discharge years and slowly in high-discharge years. Steelhead migrations slowed dramatically when summer water temperatures peaked within each year then increased as rivers cooled in fall. Mean summer temperatures explained more between-year variation in steelhead passage rates than did differences in discharge. Fall Chinook salmon also slowed migration through the mainstem Columbia River during warm water periods. Protracted passage times within the hydrosystem were most likely for fish from all runs that fell back over and reascended dams, and for steelhead that sought thermal refugia by straying temporarily into coldwater tributaries. In tributaries and unimpounded reaches, migration date explained the most variance in spring–summer Chinook salmon migration rates while river discharge, migration year and migration reach were secondary. Both within and between years, spring–summer Chinook salmon migrated more rapidly as migration date increased and more slowly when discharge was high.

Introduction

Development of the Columbia River hydrosystem has significantly altered migration conditions for anadromous salmonids, with potential negative consequences on the ability of fish to reach spawning areas and successfully reproduce. Interior salmon and steelhead populations may be especially vulnerable to changes to migration corridors because of long distances these fish must migrate to reach spawning habitat. Most anadromous adult salmonids *Oncorhynchus* spp. migrating upstream in the Columbia River and its major tributary, the Snake River, migrate in an environment altered by mainstem hydropower dams. From Bonneville (river kilometer [rkm] 235) to Chief Joseph dams (rkm 877) on the Columbia River are nine hydroelectric projects and approximately 550 km of impoundments. Fish that migrate to spawning areas in the Snake River must pass eight dams and impoundments from Bonneville Dam to the upstream extent of Lower Granite Reservoir near Asotin, WA (rkm 755). Construction and management of the Columbia–Snake hydropower system have been implicated, along with habitat degradation, hatchery management, and other issues, in basin-wide declines of wild anadromous salmonids (Raymond 1988; National Research Council 1996). Twelve Columbia basin stocks are currently listed under the Endangered Species Act (ESA), three as endangered (National Marine Fisheries Service 2000).

Management concerns for adult migrants in the Columbia River basin include delays and reduced reproductive fitness associated with dam and reservoir passage (Dauble and Mueller 1993; Geist et al. 2000). Mandated protection of listed stocks prompted comprehensive evaluations of fish passage facilities and issues affecting upstream migration, and as a result, numerous operational changes have been made within the federal hydrosystem. Many improvements have focused on facilitating passage by identifying and reducing migration 'delay' at dams and as a result, adult migration research has largely addressed passage time objectives. Radiotelemetry has been a preferred research method for this research, as both fine-scale behaviors (e.g., in dam fishways) and behaviors over long distances (e.g., past multiple dams) can be effectively addressed with individually radio-tagged fish.

Large-scale radio tagging of adult salmonids in the Columbia basin began in the early 1990's (Bjornn et al. 1998a, 2002), when several thousand adult spring–summer Chinook salmon and steelhead (*O. mykiss*) were radio tagged from 1991 to 1994 to study passage through the lower Snake River. Concurrently, Blankenship and Mendel (1994) studied radio-tagged adult fall Chinook salmon passage through the lower Snake River, and Stuehrenberg et al. (1995) studied adult Chinook salmon behavior at selected upper-Columbia River dams. These studies and earlier work by many other researchers (reviewed by Bjornn and Peery 1992) identified passage problems and established baseline information on adult migration through portions of the basin.

Advances in radiotelemetry have facilitated increasingly large-scale monitoring of individual adult fish. In 1996, we began radio-tagging adult salmonids at Bonneville

Dam, the most downstream Columbia River site where large numbers of adult fish can be collected. Over six years (1996, 1997, 1998, 2000, 2001, and 2002) we tagged and released more than 15,000 adult salmon and steelhead near the dam and monitored them as they migrated upstream through the hydrosystem and into major tributaries. This comprehensive, multi-year research effort had many objectives, including monitoring fine-scale movements at dams (Peery et al. 1998; Keefer et al. 2003a, 2003b), measuring fallback rates and routes at dams (Bjornn et al. 2000a, 2000b, 2000c; Reischel and Bjornn 2003; Boggs et al. 2004), documenting distribution to tributaries and hatcheries, harvest and survival rates (Bjornn et al. 2000d; Keefer et al. 2002b). [Reports are available online at: http://www.cnr.uidaho.edu/uiferl/reports.]

Our objectives for this report were 1) to summarize Chinook salmon and steelhead passage at individual Columbia and Snake River dams and reservoirs, and through longer hydrosystem reaches that included multiple dams and reservoirs (1996-2001) and 2) to summarize spring–summer Chinook salmon passage rates in unimpounded reaches and tributaries (1997-2002). We provide here separate summaries of adult passage through each migration environment, with evaluations of how migration timing, river discharge, and water temperature were related to migration behaviors.

Methods

Fish trapping and tagging

Adult salmon and steelhead were trapped in the Bonneville Dam adult fish facility (AFF) adjacent to the Washington-shore ladder as they migrated upstream. In six years, radio transmitters were placed in 15,822 fish: 6,290 spring–summer Chinook salmon, and 4,208 fall Chinook salmon, and 5,324 steelhead (Table 1). Spring Chinook salmon were tagged in all years in April and May, summer Chinook salmon in June through mid- to late July, and fall Chinook salmon from early August (2000-2002) or September (1998) through October. Steelhead were tagged from early to mid-June through October (1996, 1997, 2000, 2001, 2002). We used dates established by the U.S. Army Corps of Engineers (USACE) to separate between spring, summer, and fall-run Chinook salmon at Bonneville Dam (USACE 2002). For our purposes, radio-tagged fish kept their run designation regardless of date of passage at upstream sites. Spring and summer Chinook salmon were combined for some analyses, which is common in basin research. Most processing of 2002 data was incomplete at the time of this writing, and only tributary passage rate data are included here.

Each day fish were tagged, a weir was lowered in the Washington-shore ladder to divert fish into the AFF via a short section of ladder. Adult fish entered the lab into a large tank and were either diverted into anesthetic tanks for tagging or returned via a chute to the main ladder. We did not tag smaller jack (precocious) salmon or steelhead with fork length < 50 cm. We tagged with transmitters near-random

Table 1. Number of adult salmon and steelhead tagged with radio transmitters at Bonneville Dam from 1996 to 2002 that were released[1] downstream from the dam or into the dam forebay.

	1996	1997	1998	2000	2001	2002	**Total**
All fish released downstream from Bonneville Dam							
Spring/Summer Chinook	853	1,014	957	973	829	900	5,526
Fall Chinook			1,032	745	561	756	3,094
Steelhead	765	975		843	804	945	4,332
All fish released into Bonneville Dam forebay							
Spring/Summer Chinook				159	288	317	764
Fall Chinook				373	431	310	1,114
Steelhead				317	347	328	992
Total	1,618	1,989	1,989	3,410	3,260	3,556	15,822

[1] 25 fish (0.16%) were not released with transmitters, for various reasons

samples of adult fish in 1996, 1997 and 1998. Samples were not truly random because only fish passing via the Washington-shore ladder were sampled, the proportion sampled each day varied and no fish were sampled at night; some small steelhead were excluded when we had deployed all of the smaller transmitters on a given tagging day. During fall Chinook salmon runs, we selected for ‘upriver-bright’ fish that spawn mostly in the Hanford Reach, Snake, or Deschutes rivers and against sexually mature ‘Tules’ that return to Bonneville reservoir hatcheries. Differentiation between the two groups was based on coloration, an imperfect but useful measure (Myers et al. 1998). In 2000, 2001 and 2002, 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.

We attempted to tag fish in proportion to their abundance, based on long-term averages of runs at Bonneville Dam. However, run timing varied each year, causing some deviations that could not be wholly compensated for by in-season adjustments to the tagging schedule. We tagged fish throughout each run, and therefore tended to under-sample during migration peaks and over-sample during passage nadirs. The largest departures from representative sampling occurred from gaps in tagging: no summer Chinook salmon were tagged in July 1996 or the second half of July in 1997 and 1998, and high water temperatures precluded tagging fall Chinook salmon in August of 1998. We intentionally radio-tagged more late-migrating (B-group) than early-migrating (A-group) steelhead to increase samples of Snake River fish for analyses at Snake River dams. Radio-tagged samples averaged ~0.75% of spring–summer Chinook salmon, ~0.40% of fall Chinook salmon, and ~0.25% of steelhead counted passing Bonneville Dam each year (USACE 2002).

Anesthesia, intragastric tagging methods and radio transmitter types used were described in Keefer et al. (2004a). After tagging, fish were moved to a 2,275 L oxygenated recovery and transport tank where they were held until released (usually 0.5 to 3 h). All fish radio-tagged from 1996 to 1998 fish were released about 9.5 km downstream from Bonneville Dam at sites on both sides of the river. From 2000-2002, 74 to 86% of spring–summer Chinook salmon, 57 to 71% of fall Chinook salmon and 70 to 74% of steelhead were released at the downstream sites and the rest were released into the Bonneville Dam forebay. Forebay releases were used to evaluate dam operations and specific fish behaviors related to fishway exit sites (Reischel and Bjornn 2003; Boggs et al. 2004). Fish released in the forebay were not used in Bonneville Dam or reservoir passage time analyses, but were included in upstream summaries.

Study area and telemetry monitoring

The study area included four mainstem dams and reservoirs in the lower Columbia River (Bonneville, The Dalles, John Day, McNary), four lower Snake River dams and reservoirs (Ice Harbor, Lower Monumental, Little Goose, Lower Granite), and two upper-Columbia River dams (Priest Rapids, Wanapum) (Figure 1). Monitoring occurred throughout each migration at the four lower Columbia River dams, Ice Harbor, and Lower Granite dams in all years, at Lower Monumental and Little Goose dams in all years except 1996, at Priest Rapids Dam from 1996 to 1998, and at Wanapum Dam in 1997. Twelve unimpounded and/or tributary reaches were also monitored (Figure 2). Data were collected for the Deschutes, Snake, Clearwater and Salmon River reaches in all five years; monitoring also occurred in the Hanford Reach of the Columbia River in 1997 and 1998 and in the Yakima River in 2001 and 2002.

We assessed movements and passage rates of radio-tagged fish with fixed radiotelemetry receivers. Aerial Yagi antennas were placed on shorelines adjacent to tailrace areas at dams (Figure 1) and tributary mouths, and underwater antennas made of coaxial cable were used to monitor ladder exits at dams. Configurations were similar between locations. On average, tailrace receivers operated 91% to > 99% of the time at lower Columbia and Snake River dams. Top-of-ladder receivers operated > 95% of the time (except for one damaged at McNary Dam). Receivers at Priest Rapids and Wanapum dams operated more than 85% of the time. Outages at dams occurred primarily because of power loss, receiver malfunction, vandalism, or full memory banks. Aerial Yagi antennas were also placed near tributary mouths and at the lower end of unimpounded reaches of the Columbia and Snake rivers. Additional aerial antennas were deployed at upstream sites in some tributaries and near Priest Rapids Dam on the Columbia River. Receivers operated more than 95% of the time during the spring–summer Chinook salmon migrations at all sites used for monitoring unimpounded reaches.

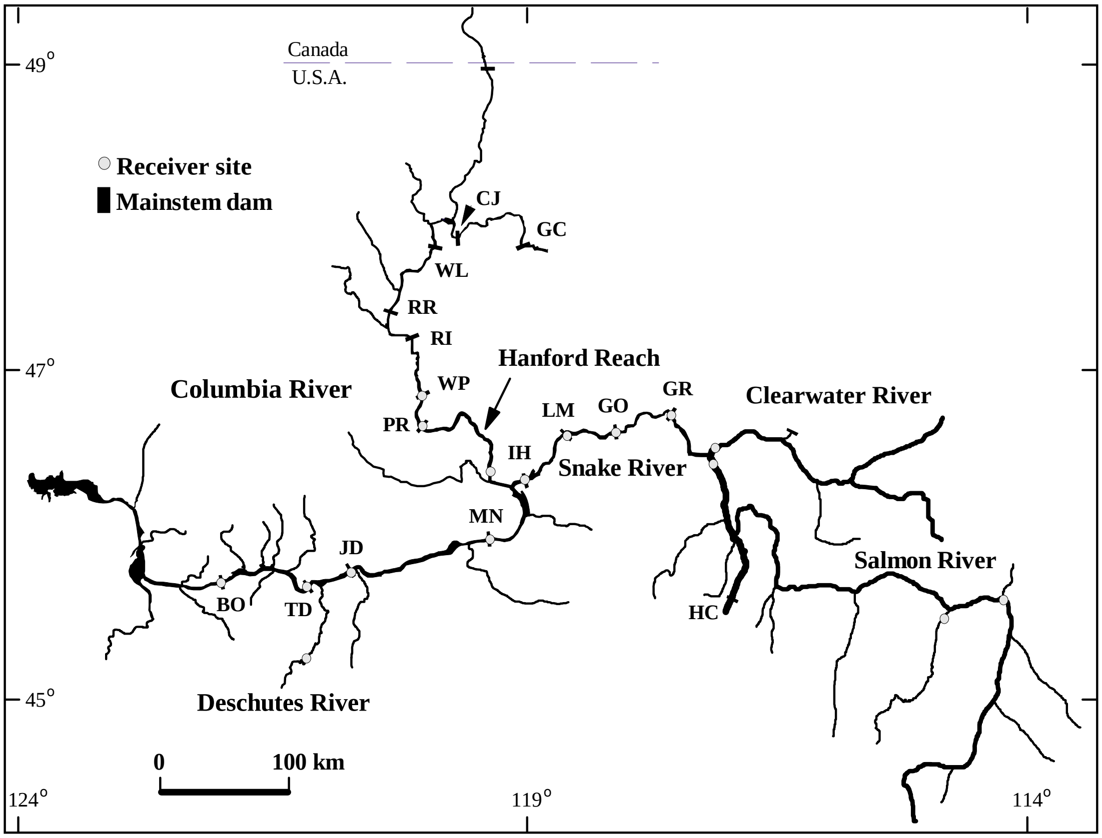

Figure 1. Map of the Columbia River basin showing receiver sites at mainstem dams: BO = Bonneville, TD = The Dalles, JD = John Day, MN = McNary, PR = Priest Rapids, WP = Wanapum, RI = Rock Island, RR = Rocky Reach, WL = Wells, CJ = Chief Joseph, GC = Grand Coulee, IH = Ice Harbor, LM = Lower Monumental, GO = Little Goose, GR = Lower Granite, and HC = Hell's Canyon.

Passage time calculations

All passage times (d) and rates (km•d^{-1}) were calculated from telemetry records at the fixed receivers. Dam passage times were calculated from the first record at a tailrace receiver (0.5 to 3.2 km downstream from dams) to the last record at a top-of-ladder receiver (see Bjornn et al. 2000 and Keefer et al. 2003b for additional details on receiver locations). Dam passage times included time fish spent migrating downstream out of a tailrace, a behavior we believe was related to route searching or a reaction to unfavorable passage conditions at dams. Some fish from all stocks fell back over dams and reascended ladders one or more times; only first passage times are reported here. Reservoir passage rates (km•d^{-1}) were calculated from the last top-of-ladder record at the downstream dam to the first tailrace record at the upstream dam. When fish fell back and reascended the downstream dam before migrating upstream, the reservoir start time began after the last passage at the downstream dam. Reservoir passage rates were calculated in the lower Columbia and Snake rivers, but not in the upper-Columbia River where monitoring was limited.

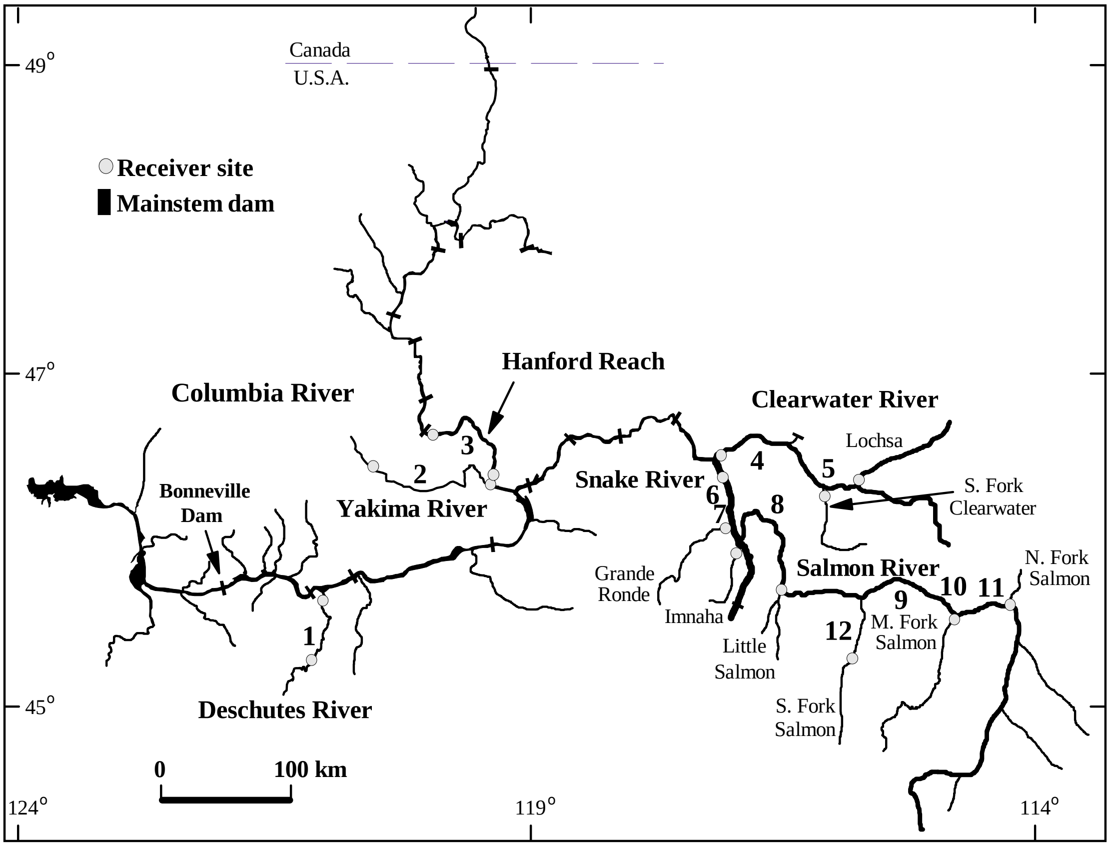

Figure 2. The Columbia River basin, the spring–summer chinook salmon radio tagging site (Bonneville Dam), and the radiotelemetry receivers (open circles) used to monitor fish behavior in the Deschutes, Columbia, Yakima, Snake, Clearwater and Salmon rivers. Reach numbers correspond to Table 2.

Passage times and rates were also calculated for longer hydrosystem reaches that integrated multiple dam and reservoir passages and time fish spent falling back over and reascending dams. Hydrosystem passage times were calculated from the Bonneville tailrace past McNary (4 dams, 3 reservoirs, 238 km), Priest Rapids (5 dams, 4 reservoirs and Hanford Reach, 407 km), and Lower Granite (8 dams, 7 reservoirs, 462 km) dams, and from the Ice Harbor tailrace past Lower Granite Dam (4 dams, 3 reservoirs, 157 km.)

All spring–summer Chinook salmon migration rates in unimpounded reaches and tributaries were calculated from the first record at the up- and downstream receivers bracketing the reach (Table 2). If a fish exited the downstream end of a reach, was detected outside of the reach, and then re-entered and passed through the reach, the last entry was used as the start time; very few salmon displayed this behavior.

With all passage time and rate calculations, we did not differentiate between periods of active upstream migration, diel rhythms, temporary holding, downstream movements related to route searching, or pre-spawn staging. The small number of steelhead that overwintered within study reaches were excluded from passage rate calculations. We noted when behavior by spring-migrating steelhead differed from that of fall-migrating fish. Time steelhead strayed temporarily into downstream tributaries during summer and fall were included in calculations as the behavior was widespread and an integral part of the migration (e.g., more than 50% of tagged fish strayed temporarily, Keefer et al. 2002; High 2002). Distributions of passage times were right-skewed because some fish took several days or weeks to pass each dam or reservoir, and therefore medians and quartiles were used to describe passage times and rates.

Table 2. River reach name, length (km) and mean discharge ($m^3 \bullet s^{-1}$), with location of reach start and end (in river kilometers from the Columbia River mouth).

River reach	Start (rkm)	End (rkm)	Length (km)	Mean[1] *Q* ($m^3 \bullet s^{-1}$)
Deschutes	Deschutes mouth (329)	Sherars Falls (396)	67	170
Yakima	Yakima mouth (546)	Roza Dam (745)	199	80
Columbia	Hanford Reach (553)	Hanford Reach (639)	86	5,520
Clearwater (1)	Clearwater mouth (754)	S.F. Clearwater (868)	114	821
Clearwater (2)	Clearwater mouth (754)	Lochsa R. (904)	150	821
Snake (1)	Snake at Asotin (759)	Grande Ronde (795)	36	1,741
Snake (2)	Snake at Asotin (759)	Imnaha R. (853)	94	1,741
Snake/Salmon[2]	Snake at Asotin (759)	Little Salmon R. (963)	204	721
Salmon (1)	Little Salmon R. (963)	MF Salmon R. (1,144)	181	721
Salmon (2)	Little Salmon R. (963)	NF Salmon R. (1,204)	241	721
Salmon (3)	MF Salmon R. (1,145)	NF Salmon R. (1,204)	59	92
Salmon/SF Sal.	Little Salmon R. (963)	SF Salmon R. (1,095)	132	721

[1] Mean daily discharge during study years from April-July, at closest gage station

[2] The USGS gage at Whitebird, ID (rkm 911) was used for all Salmon River reaches except Salmon 3 for which data from the Salmon, ID gage (rkm 1,242) was used.

Statistical analyses

For this report, we were most interested in summarizing the large volume of passage time data that has been collected, and in examining at a broad scale the influences of migration timing, river discharge and water temperature on fish behavior. Distributions of most migration rates and times were non-normal (Kolmogorov-Smirnov tests), and therefore medians and quartiles are presented in data summaries. Hydrosystem passage times for fish that fell back at one or more dams were compared to times for fish that did not fall back using nonparametric Kruskal-Wallis χ^2 tests of medians.

Individual radio-tagged fish, and fish from different portions of each run, could encounter a wide and complex range of river environmental conditions during their upstream migration. As a result, individual fish passage times and rates were highly variable and were poorly correlated (r^2 mostly < 0.10) with most available environmental variables (e.g., Bjornn et al. 2000d). To reduce this variability in individual passage times within years, we grouped fish with similar passage dates at each location (using semimonthly blocks of 15 or 16 d) and used median times or rates for each block as the dependent variable. Annual (full migration) medians were used in between-year comparisons. Clearly, many other statistical methods could have been used to analyze passage times: some of these methods, including event-time analyses and individual-based models, are currently being explored by our group and will be included in future reports.

Two environmental variables were considered within the hydrosystem reaches: river discharge and water temperature. These were selected because data were of fairly good quality and were available for most of each year at most dams. Other measures, such as river velocity, may have been better predictors of fish behavior, but such data were unavailable. Dissolved gas and spill were highly correlated with discharge at all projects and were excluded for this report. Within years, mean discharge and temperature for each semimonthly block were used as predictors. Mean values over the date range when 90% of radio-tagged fish passed a site, or means over longer periods (e.g., April-July, June-August) were used to evaluate between-year differences. Because exposure to elevated temperatures has been associated with pre-spawn mortality (Gilhousen 1990; McCullough 1999; Macdonald 2000), the number of days when mainstem temperatures exceeded 21ºC (the incipient lethal temperature identified in Coutant 1999 and McCullough et al. 2001) was also used as an independent variable in between-year comparisons.

Migration timing—the semimonthly block when each fish arrived at a dam or reservoir)—was used as a third independent variable. Timing integrates environmental conditions and the maturation changes occurring for adult migrants and can be a good predictor of fish activity (Økland et al. 2001; Hodgson and Quinn 2002). Semimonthly blocks were numbered sequentially, with the earliest arriving fish from each run in Block 1 (e.g., April 1-15 = Block 1 for spring–summer Chinook salmon and August 1-15 = Block 1 for fall Chinook salmon).

The effects of seasonal migration timing, water temperature, and river discharge on within-hydrosystem migration times were examined using weighted linear and quadratic regression models (SAS Institute 2000) during semimonthly blocks within each year. Weighting was by the number of fish/block. Although linear models were adequate for most analyses, environmental variables like temperature during the steelhead and fall Chinook salmon migrations were parabolic, and quadratic regressions were more appropriate. Regression results were considered significant at $P < 0.05$. We were more interested in general patterns than in producing predictive passage models for individual dams or reservoirs. Therefore we report specific regression results for each site but also include qualitative summaries.

Spring–summer Chinook salmon passage in unimpounded reaches and tributaries were analyzed using multiple regression models. River discharge and Julian date at reach entry (continuous variables) along with river reach and year (classification variables) were used as independent variables. No attempt was made to separate the effects of water temperature and date, which were strongly positively correlated during the spring–summer Chinook salmon migration ($r > 0.96$ in all study years) in both the Columbia and Snake rivers. Temperature data were unavailable for tributaries, which are typically cooler but follow the same seasonal warming patterns as the larger rivers. Each fish likely encountered a range of discharge and velocity levels within each reach, but it was not possible to calculate exposure given the length (*mean* = 130 km), variable gradients and complexity (i.e. non-constant discharge due to entry of multiple secondary tributaries) of reaches and uncertainty regarding fish locations while between receiver sites. To simplify analyses, the mean daily discharge on the date fish entered a reach was used as the independent variable. This metric was selected because day-to-day discharge variance at gage sites was relatively low and because it reflected seasonal discharge patterns (i.e. snowmelt runoff).

The multiple regression models used to assess relationships between the independent variables and tributary migration rates included a complete model with all data from all reaches and years, as well as models that examined effects of date, discharge and reach within each year, and the effects of year, date and discharge within each reach. Type III tests (partial sums of squares) were used to describe the proportion of the total variance in migration rates explained by each independent variable, after correcting for all other terms in each model (SAS Institute, 2000) .

We obtained mean daily discharge and water temperature data at dams on the Columbia and lower Snake rivers from the U.S. Army Corps of Engineers and Grant County Public Utility District (compiled by the University of Washington at http://www.cqs.washington.edu/dart/dart.html). Temperature data collection ended in September or October at many dams and so temperature was not used in some steelhead and fall Chinook salmon analyses. Discharge data for the Deschutes (rkm ~331), Yakima (rkm ~589), Snake (rkm ~800), Clearwater (rkm ~764) and Salmon (rkm ~911) rivers came from U.S. Geologic Survey (USGS) gage stations (http://waterdata.usgs.gov/usa/nwis/nwis) (all rkms are approximate distance from Columbia River mouth).

Results

Hydrosystem Passage Rates: Chinook Salmon

Among radio-tagged Chinook salmon, spring Chinook migrated most slowly through the Columbia River hydrosystem and summer Chinook migrated fastest. Median passage rates in the Columbia River were 13 to 33 $km \cdot d^{-1}$ for spring Chinook salmon, 24 to 38 $km \cdot d^{-1}$ for summer Chinook salmon and 24 to 31 $km \cdot d^{-1}$ for fall Chinook salmon (Table 3). The fastest migrants from each run migrated from Bonneville to past McNary Dam (4 dams, 3 reservoirs) in about 6 d, and most migrated through that reach in less than 20 d (Figure 3). Most Chinook salmon migrated from Bonneville to past Priest Rapids Dam (5 dams, 4 reservoirs, and the Hanford Reach) or past Lower Granite Dam (8 dams, 7 reservoirs) in between 15 and

30 d. Chinook salmon typically passed through the lower Snake River at slightly lower rates than through the Columbia River (Table 3).

Table 3. Median (Med.) passage times (d) and rates (km•d^{-1}) and number (n) of radio-tagged fish recorded from the Bonneville (BO) tailrace to pass McNary (MN), Priest Rapids (PR) and Lower Granite (GR) dams and from the Ice Harbor (IH) tailrace past Lower Granite Dam for each year studied, with between-year standard deviations (SD). Steelhead that wintered over within a reach not included where the behavior affected passage times.

	BO-MN (238 km)			BO-PR (407 km)			BO-GR (462 km)			IH-GR (137 km)		
Year	n	Med. time	Med. rate	n	Med time	Med rate	n	Med time	Med rate	n	Med time	Med rate
Spring Chinook												
1996	190	13.0	18	40	20.0	20	62	28.4	16	48	13.0	12
1997	265	18.6	13	39	26.1	16	228	33.4	14	218	12.5	13
1998	271	11.0	22	16	22.1	18	173	21.8	21	186	8.6	18
2000	296	11.2	21	72	17.8	23	144	17.7	26	172	5.3	30
2001	289	8.2	29	14	13.0	31	271	14.1	33	408	4.7	33
Summer Chinook												
1996	84	10.0	24	60	14.2	29	18	19.5	24	12	6.0	26
1997	87	7.4	32	76	13.6	30	40	16.9	27	42	7.2	22
1998	160	7.0	34	14	12.0	34	35	16.8	28	41	6.3	25
2000	189	6.9	34	125	11.8	34	23	14.8	31	37	5.8	27
2001	167	6.7	35	99	12.0	34	48	12.3	38	65	4.7	33
Fall Chinook												
1998	343	8.9	27	8	14.0	29	8	16.5	28	8	5.1	31
2000	239	8.7	27	42	16.6	24	17	18.1	26	19	8.4	19
2001	214	8.0	30	29	16.4	25	24	15.1	31	55	5.5	29
Steelhead												
1996	323	16.1	15	17	22.0	18	231	35.0	13	179	8.1	19
1997	320	31.7	7	22	23.6	17	238	43.0	11	265	7.6	21
2000	386	24.4	10	30	26.0	16	219	43.7	11	320	8.0	20
2001	456	28.1	8	150	32.9	12	259	48.9	9	339	7.4	21

Seasonal Migration Timing -- Hydrosystem passage rates for spring–summer Chinook salmon (runs combined) increased within each year as migration date at Bonneville Dam progressed. Semimonthly median passage rates increased significantly ($P \leq 0.05$) through time in 10 of 15 weighted linear regression models from the Bonneville tailrace past McNary, Priest Rapids, and Lower Granite dams (Appendix 1). On average, rates increased between 2 and 5 km•d^{-1} every two weeks in all years. The pattern of increasing rates over time was less prevalent in the lower Snake River (Ice Harbor-Lower Granite). Passage rates in the Snake increased significantly through time only in 1997 (Appendix 1).

Most radio-tagged fall Chinook salmon returned to lower Columbia River tributaries or the Hanford Reach with relatively few migrating up the Snake or upper-Columbia rivers (Table 3). In 2000, semimonthly median migration rates from Bonneville to McNary dam decreased significantly ($P < 0.005$) from 33 to 19 km•d^{-1}

from August to October (Appendix 1). Semimonthly medians ranged from 18 to 32 km•d^{-1} in 1998 and 2001, with no significant trends through time.

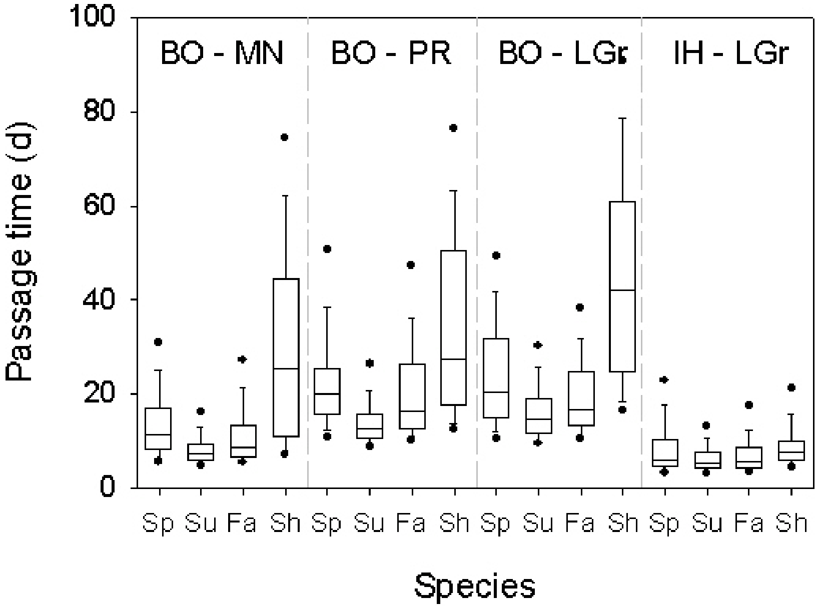

Figure 3. Median, quartile, 5th, 10th, 90th and 95th percentile passage times (d) from the Bonneville tailrace past McNary (MN), Priest Rapids (PR) and Lower Granite (GR) dams, and from the Ice Harbor (IH) tailrace past Lower Granite Dam; all years combined. Sp = spring Chinook, Su = summer Chinook, Fa = fall Chinook, Sh = steelhead.

River Discharge and Temperature – Mean daily Columbia River discharge at Bonneville Dam from April through July—the date range including the annual snowmelt event and passage of almost all spring–summer Chinook salmon—ranged from 51% of the 30-year mean in 2001 to 137% of average in 1997 (1972-2001 *mean* = 6,800 m^3•s^{-1}) (Table 4). Peak discharge at Bonneville Dam occurred in late May or early June in 1996-1998, in late April 2000, and in mid-May 2001 (Figure 4). Between-year differences in Snake River discharge at Ice Harbor Dam were proportionately similar to those for the lower Columbia River. Mainstem water temperatures in the Columbia and Snake rivers ranged from about 6 ºC during early April to 21 to 23 ºC in late August and early September. Mean water temperatures during spring–summer Chinook salmon migrations at Bonneville Dam were coolest in 1996 and 1997 and warmest in 1998 and 2001 (Table 4). August temperature means and maxima tended to be highest in 1998 and 2001.

Within years, river discharge was generally not correlated with spring–summer Chinook salmon migration rates through the three hydrosystem reaches that started at Bonneville Dam (Appendix 1). Thirteen of 15 regression models using semimonthly Columbia River discharge and median passage times were non-

Table 4. Mean April-July discharge ($m^3 \cdot s^{-1}$) and water temperature (° C), and mean and maximum August temperatures at Bonneville (BO) and Ice Harbor (IH) dams, 1996-2001.

	April-July means				August temperatures			
	Discharge ($m^3 \cdot s^{-1}$)		Temperature (ºC)		Mean (ºC)		Maxima (ºC)	
	BO	IH	BO	IH	BO	IH	BO	IH
1996	9,300	3,100	14.0	15.4	20.5	20.4	21.1	22.4
1997	11,000	3,800	14.0	13.6	22.1	20.9	22.8	21.4
1998	7,200	2,800	15.0	14.7	22.1	22.1	23.2	22.9
2000	6,600	2,100	14.8	14.8	20.9	21.6	21.9	22.9
2001	3,500	1,200	14.8	14.9	21.3	21.3	21.9	23.5

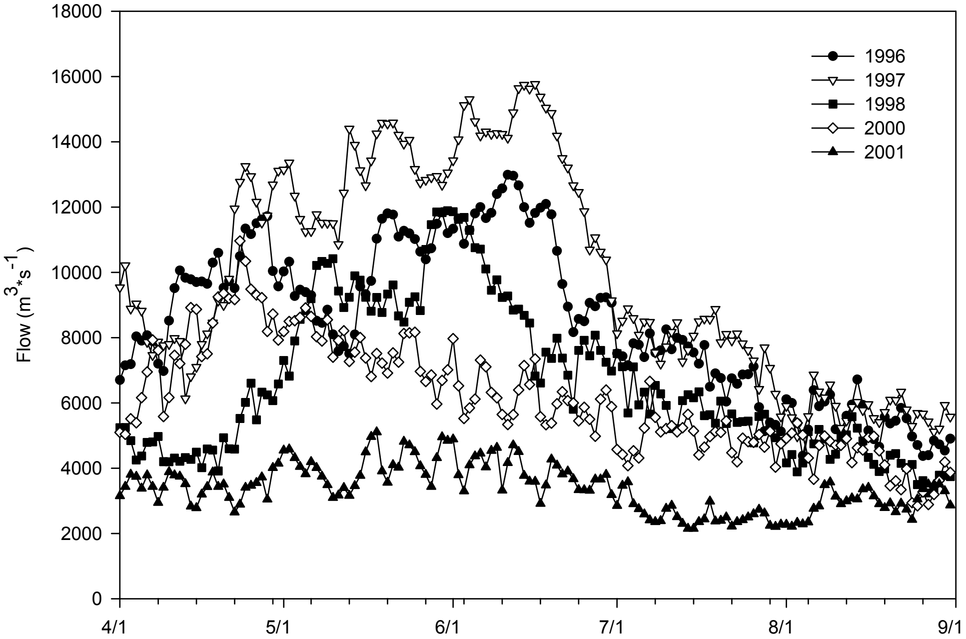

Figure 4. Mean daily discharge ($m^3 \cdot s^{-1}$) at Bonneville Dam, 1996-2001.

significant ($P > 0.05$). The two exceptions were in 2001, when rates increased as discharge increased through the Bonneville-Lower Granite reach, and in 2000 when rates decreased as discharge increased through the Bonneville-McNary reach. Discharge was not correlated with passage spring–summer Chinook salmon rates in the lower Snake River, except in 1998 when rates decreased as discharge increased. Water temperature was strongly positively correlated with migration date (Julian day) during the spring–summer Chinook salmon migrations, and regression results were similar to the models for migration timing (Appendix 1).

Fall Chinook salmon migrations were characterized by low discharge, especially in 2001. Migration rates from Bonneville-McNary decreased significantly as discharge increased in 2001 but not in 2000 (Appendix 1). Fall Chinook salmon migrated significantly faster as temperatures decreased in 2000. The relationship was parabolic in 2001: passage rates were lowest when water temperatures were warmest and again when temperatures were low late in the migration.

Much of the between-year variability in median hydrosystem passage times for spring–summer Chinook salmon was explained by Columbia River discharge. Spring Chinook salmon passed fastest in low-discharge years and slowest in high-discharge years ($0.76 < r^2 < 0.90$; $0.01 < P < 0.053$, weighted linear regression) from Bonneville past McNary, Priest Rapids, and Lower Granite dams (Figure 5). Passage times for the three reaches were approximately twice as long in 1997 (mean April-May discharge = 10,988 $m^3 \cdot s^{-1}$) as in 2001 (mean = 3,483 $m^3 \cdot s^{-1}$). Mean discharge and water temperature were negatively correlated, so migration rates were highest in warm (low-discharge) years. Water temperature-rate models had lower r^2 values than discharge-rate models.

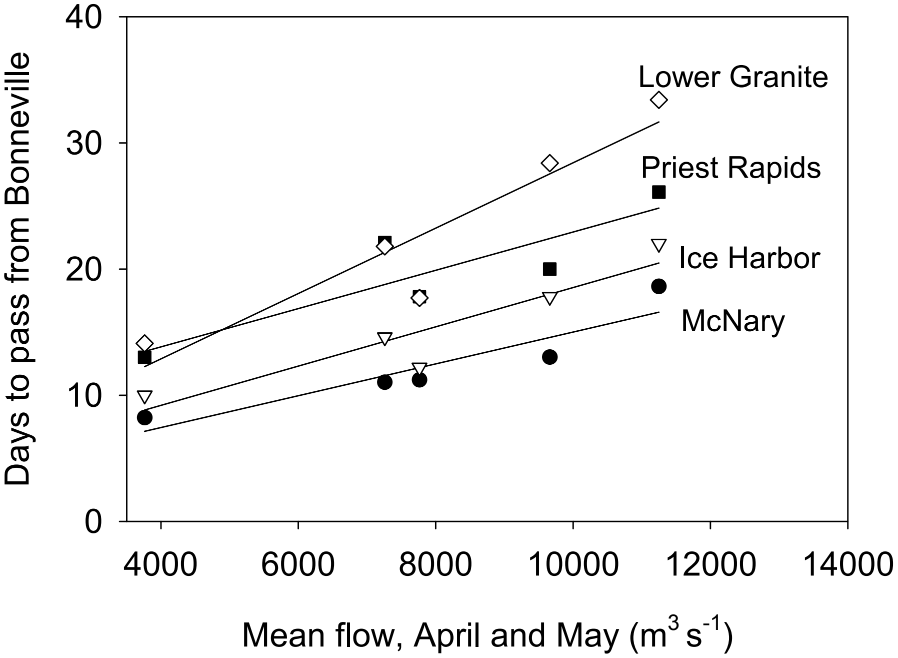

Figure 5. Median annual spring chinook passage times (d) from the Bonneville (BO) tailrace past McNary (MN), Priest Rapids (PR), Ice Harbor (IH), and Lower Granite (GR) dams with mean daily Columbia River discharge from April-May, 1996 to 2001. Linear regressions weighted by the number of fish/year produced r^2 values of 0.86 ($P = 0.023$) for the BO-MN reach, 0.76 ($P = 0.053$) for the BO-PR reach, 0.89 ($P = 0.016$) for the BO-IH reach, and 0.90 ($P = 0.014$) for the BO-GR reach.

Summer Chinook salmon passage was slower in years with high June-July discharge, but models were less significant than for spring fish, at least partially because no summer Chinook salmon were tagged in July 1996. With 1996 data included, no regressions were significant ($P > 0.05$). Without 1996 data, Bonneville-

McNary summer Chinook salmon passage times were strongly correlated with mean June-July discharge ($r^2 = 0.99$; $P = 0.007$). Bonneville-Lower Granite and Bonneville-Priest Rapids models ($r^2 \sim 0.70$; $P \sim 0.08$) were not significant.

Passage rates in the Snake River were negatively correlated with discharge at Ice Harbor Dam for spring (May-June discharge, $r^2 = 0.91$; $P = 0.01$) and summer Chinook salmon (15 June-15 July discharge, $r^2 = 0.95$; $P = 0.005$). Between-year differences in all hydrosystem passage rates were proportionately smaller in summer than in spring, and inclusion of 1996 summer Chinook salmon data did not substantially change results. Fall Chinook salmon hydrosystem passage rates varied little between years (Table 3).

Fallback -- With all years combined, 19% of spring Chinook salmon, 8% of summer Chinook salmon and 3% of fall Chinook salmon fell back over and reascended a dam at least once before passing McNary Dam (Table 5). Median Bonneville-McNary passage times for spring Chinook salmon that fell back before passing McNary Dam were 3 to 9 d longer than for fish that did not fall back each year ($P < 0.001$, Kruskal-Wallis χ^2 tests). Median times were 1 to 3 d longer for summer Chinook salmon that fell back and time differences were significant ($P < 0.02$) in two of five years. Medians were 10 to 15 d longer for fall Chinook salmon that fell back ($P < 0.005$, all years). Higher proportions of each run fell back before passing Lower Granite Dam than before passing McNary Dam (Table 5). Median Bonneville-Lower Granite times for fallback fish were longer by 5 to 14 d (spring Chinook salmon), 0 to 9 d (summer Chinook salmon) and 9 to 26 d (fall Chinook salmon) than for non-fallback fish. Differences were significant ($P < 0.05$) in all five years for spring Chinook salmon, one of two years for fall Chinook salmon (none fell back in 1998), and in no years for summer Chinook salmon.

Hydrosystem Passage Rates: Steelhead

Seasonal Migration Timing – Median steelhead migration rates through multiple dam-reservoir hydrosystem reaches were slower and more variable than for Chinook salmon (Figure 3). Rates in each year tended to be slowest through the Bonneville-McNary reach and fastest through the lower Snake River reach (Table 3). Semimonthly median times for the Bonneville-McNary reach were about 10 d (24 km•d^{-1}) in June and early July, increased rapidly to between 30 and 60 d (4-8 km•d^{-1})in August, then decreased through September until times were near 10 d again in late October. Median Bonneville-Lower Granite passage times were about 25 d (18 km•d^{-1}) for fish arriving in early June, increased in all years to more than 60 d (8 km•d^{-1}) for late June or July arrivals, then steadily decreased until times were near 20 d (23 km•d^{-1}) in late October. Weighted quadratic regression models fit the median passage rate data well for the Bonneville-McNary and Bonneville-Lower Granite reaches in each year (Appendix 1). Patterns were similar for the Bonneville-Priest Rapids reach, but models were non-significant ($P > 0.05$) in the first three years when samples of upper Columbia steelhead were small. Passage times varied least through the lower Snake River reach, where most semimonthly medians were between 8 and 15 d (10 to 20 km•d^{-1}). Steelhead with the longest Ice Harbor-Lower Granite passage times mostly entered the reach in August.

Table 5. Median passage times (d) and number (n) of radio-tagged spring, summer and fall chinook salmon and steelhead recorded passing lower Columbia and Snake River dams for each year studied.

			Median Dam Passage Time in Days (n)					
Year	Bonn.	The Dalles	John Day	McNary	Ice Harbor	Lower Mon.	Little Goose	Lower Granite
Spring Chinook								
1996	1.0 (628)	1.1 (258)	1.1 (227)	1.3 (192)	0.8 (62)			1.6 (55)
1997	1.4 (615)	2.8 (351)	2.1 (354)	0.7 (249)	0.9 (228)	1.1 (245)	1.0 (230)	1.1 (233)
1998	0.9 (601)	1.2 (375)	1.5 (342)	1.1 (255)	1.5 (192)	0.8 (165)	0.8 (128)	1.1 (135)
2000	1.3 (677)	1.1 (413)	1.0 (309)	1.0 (306)	0.6 (204)	0.5 (186)	0.6 (181)	0.7 (155)
2001	1.4 (497)	1.0 (589)	1.0 (509)	0.7 (457)	0.5 (416)	0.5 (294)	0.6 (358)	0.4 (363)
Summer Chinook								
1996	0.7 (122)	0.7 (94)	2.4 (80)	0.6 (102)	0.4 (14)			1.8 (55)
1997	0.7 (286)	0.6 (204)	1.1 (173)	0.5 (71)	0.6 (48)	0.5 (44)	0.5 (33)	1.2 (233)
1998	0.7 (245)	0.7 (155)	1.0 (163)	0.6 (101)	0.6 (43)	0.5 (29)	0.4 (33)	1.3 (135)
2000	0.8 (217)	0.6 (142)	1.3 (184)	0.5 (159)	0.9 (37)	0.7 (30)	0.4 (27)	0.9 (155)
2001	0.7 (205)	0.6 (242)	1.4 (182)	0.7 (141)	0.3 (68)	0.7 (60)	0.5 (47)	0.5 (363)
Fall Chinook								
1998	0.9 (780)	0.7 (216)	1.0 (297)	0.4 (283)	0.3 (25)	0.4 (17)	0.4 (17)	0.6 (7)
2000	0.9 (543)	0.8 (300)	1.3 (260)	0.7 (178)	0.3 (27)	1.0 (14)	0.5 (18)	2.3 (6)
2001	0.7 (474)	0.7 (468)	0.9 (283)	0.6 (272)	0.3 (86)	0.5 (52)	0.6 (43)	0.7 (22)
Steelhead								
1996	0.7 (679)	0.7 (366)	0.8 (393)	0.4 (206)	0.6 (234)			1.1 (151)
1997	0.7 (744)	0.6 (302)	0.7 (473)	0.4 (299)	0.6 (347)	0.4 (266)	0.4 (192)	0.9 (205)
2000	0.8 (748)	0.7 (656)	0.8 (511)	0.4 (369)	0.3 (415)	0.5 (311)	0.4 (266)	0.9 (223)
2001	0.8 (737)	0.7 (820)	0.8 (505)	0.4 (421)	0.3 (399)	0.4 (291)	0.4 (239)	0.8 (207)

River Discharge and Temperature – Within years, semimonthly discharge at Bonneville Dam was poorly correlated with steelhead migration rates from Bonneville-McNary (Appendix 1). Water temperature was a better predictor of Bonneville-McNary migration rates: rates were lowest when temperatures at Bonneville Dam were high in all years. Bonneville-Priest Rapids, Bonneville-Lower Granite, and Ice-Harbor-Lower Granite passage rates were mostly not correlated with either discharge or available temperature data using semimonthly blocks within years (19 of 24 regressions non-significant at $P < 0.05$) (Appendix 1).

Correlating annual steelhead hydrosystem passage rates with annual discharge and temperature data was difficult because migrations were so protracted. Most steelhead migrated during the decreasing hydrograph in all years and discharge differences did not explain much between-year variation. Broad measures of mainstem water temperatures were better predictors of steelhead behavior. Migration rates were lowest in years when mainstem water temperatures were highest and warm water periods were prolonged. Median Bonneville-McNary passage times for steelhead were nearly twice as long in warm years 2001 and 1997 than during cooler 1996 (Table 3). Weighted linear regressions for the four years were significant for both mean summer temperature (r^2 = 0.91; P = 0.048) and total days over 21ºC (r^2 = 0.96; P = 0.022). Median Bonneville-Lower Granite passage time was positively correlated with mean summer temperatures in the Columbia (r^2 = 0.81; P = 0.098) and Snake (r^2 = 0.87; P = 0.067) rivers. Bonneville-Priest Rapids passage times increased with lower- and upper-Columbia water temperatures, but no models were significant (P > 0.05). Median steelhead travel times through the lower Snake River varied by less than 1 d between years (Table 3), and no environmental metrics were significant.

Fallback -- With all years combined, 8% of radio-tagged steelhead fell back at least once before passing McNary Dam and 15% fell back at least once before passing Lower Granite Dam (Table 6). Steelhead that fell back took 12 to 26 d longer to pass through the Bonneville-McNary reach than those that did not fall back ($P \leq 0.053$, all years, Kruskal-Wallis χ^2 tests). Fallback fish took 8 to 16 d longer to pass from Bonneville to Lower Granite Dam, times that were significantly longer ($P \leq 0.02$) than for non-fallback steelhead in two of four years.

Table 6. Percent of radio-tagged fish by species that fell back and reascended at a dam before they passed McNary and Lower Granite dams each year. Sample sizes are the same as in Table 3.

	Percent that Fell Back Before Passing McNary Dam				Percent that Fell Back Before Passing Lower Granite Dam			
	Spring Chinook	Summer Chinook	Fall Chinook	Steelhead	Spring Chinook	Summer Chinook	Fall Chinook	Steelhead
1996	22.6	10.7		9.3	35.5	22.2		12.1
1997	27.5	13.8		7.8	36.4	12.5		14.7
1998	19.6	10.6	1.7		28.3	25.7	0.0	
2000	20.9	8.5	3.8	8.8	35.4	17.4	5.9	16.9
2001	7.6	0.6	3.7	4.8	10.4	2.0	16.7	16.2
Total	19.3	8.1	2.9	7.5	26.6	13.9	10.2	15.0

Dam Passage Times: Chinook Salmon

Most radio-tagged adult Chinook salmon passed each lower Columbia or Snake River dam where they were detected, primarily via fishway ladders but also through navigation locks. Tagged fish passed dams almost exclusively during daylight hours, though a few that ascended ladders during evening exited at night. Most passed dams less than 36 h after passing tailrace receivers (Table 5). When fish from the same run were combined across years, median dam passage times ranged from 0.52 to 1.25 d at lower Columbia River dams (Figure 6) and from 0.48 to 1.03 d at lower Snake River dams (Figure 7). Long passage times were most frequent for all Chinook salmon runs at John Day Dam, where 9 to 14% of each run took more than 5 d to pass (Table 7).

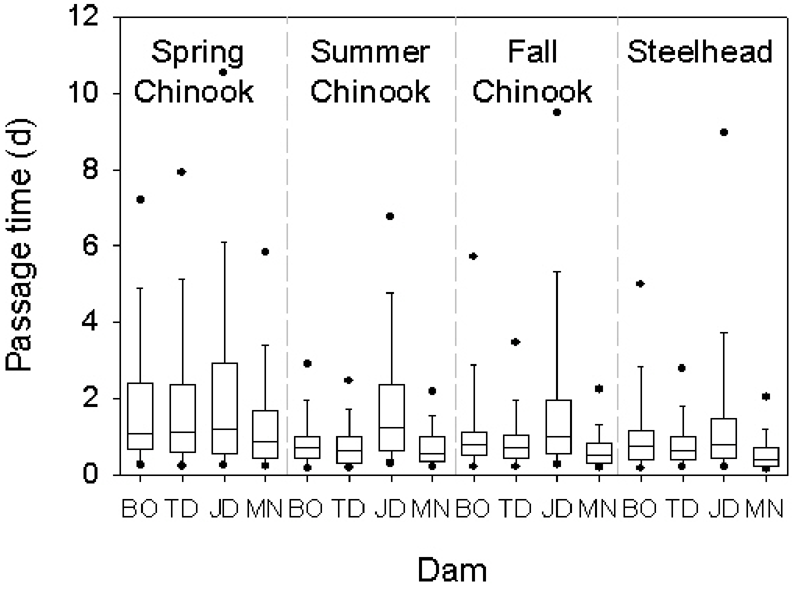

Figure 6. Median, quartile, 5th, 10th, 90th and 95th percentile times for radio-tagged salmon and steelhead to pass (d) Columbia River dams; all years combined. Dam abbreviations: BO = Bonneville, TD = The Dalles, JD = John Day, MN = McNary.

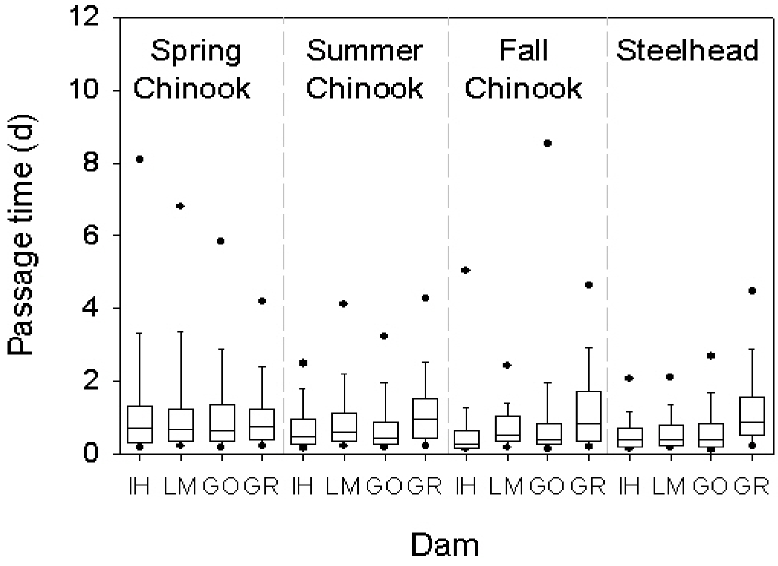

Figure 7. Median, quartile, 5th, 10th, 90th and 95th percentile times for radio-tagged salmon and steelhead to pass (d) Snake River dams; all years combined. Dam abbreviations: IH = Ice Harbor, LM = Lower Monumental, GO = Little Goose, GR = Lower Granite.

Table 7. Percent of radio-tagged fish by species (all years combined) that took more than 5 d to pass dams and reservoirs. (Sample sizes in Tables 6 and 8.)

	Dam passage				Reservoir passage			
	Chinook salmon				Chinook salmon			
	Spring	Summer	Fall	SH	Spring	Summer	Fall	SH
Bonneville	9.7	1.9	5.5	5.0	2.5	0.3	9.5	41.0
The Dalles	10.8	1.3	3.4	1.9	0.3	0.2	7.6	19.9
John Day	13.7	9.1	11.1	8.3	0.6	0.1	0.9	12.3
McNary[1]	6.1	1.9	2.7	1.8	2.0	0.1	5.5	21.1
McNary[2]					1.3	0.5	12.0	14.1
Ice Harbor	7.7	1.4	5.1	2.2	0.4	0.0	0.0	4.9
L. Monumental	7.1	2.5	1.2	1.3	0.0	0.0	5.0	3.7
Little Goose	5.9	5.1	5.1	1.6	0.3	0.7	2.4	5.2
Lower Granite[3]	4.3	4.6	2.9	4.2	2.3	2.1	24.2	25.1
Lower Granite[4]					10.8	45.5	66.7	46.8

[1] McNary to Ice Harbor

[2] McNary to lower Hanford receiver

[3] Lower Granite to Snake River receiver

[4] Lower Granite to Clearwater River receiver

Median passage times at Priest Rapids Dam in 1996, 1997, and part of 1998 were 2.97 d for 81 spring Chinook salmon and 1.40 d for 157 summer Chinook salmon. At Wanapum Dam, medians were 0.67 d for 39 spring Chinook salmon and 0.91 d for 137 summer Chinook salmon in 1997.

***Seasonal Migration Timing* --** Dam passage times for spring–summer Chinook salmon (runs combined) steadily decreased ($P < 0.05$) as migrations progressed in four of five years at Bonneville and The Dalles dams and two of five years at McNary Dam (Appendix 2). No relationship between migration date and passage time was observed at John Day Dam. Patterns were inconsistent and mostly non-significant at Snake River dams (Appendix 2). Fall Chinook salmon passage times at lower Columbia River dams tended to increase slightly as migrations progressed. No patterns in fall Chinook salmon passage times were evident at lower Snake River dams, where sample sizes were small.

***River Discharge and Temperature* –** As through hydrosystem reaches, water temperature and date were positively correlated for spring–summer Chinook salmon at individual dams within each year. Regression results using temperature were similar to those described above using migration timing. In almost all years, river discharge was not correlated with passage times for spring–summer Chinook salmon at either lower Columbia or lower Snake River dams (Appendix 2).

Water temperatures during fall Chinook salmon migrations rose from August to early-September, and then decreased steadily. Most radio-tagged fish passed dams during the cooling phase. No linear or quadratic regression models with semimonthly temperature and median fall Chinook salmon passage times were significant ($P > 0.05$) at Bonneville or McNary dams, the only two dams with temperature data available for the full migrations. Models using discharge at the four lower Columbia River dams were almost all non-significant (Appendix 2).

Differences in discharge and temperature explained some between-year variability in median dam passage times for spring Chinook salmon, with slower passage in years with higher mean discharge, and faster passage in warm years. However, weighted regression models for both temperature and discharge were almost all non-significant ($P > 0.10$) using data from the date ranges when most spring Chinook salmon passed each dam. Likewise, no models were significant for between-year comparisons of summer Chinook salmon dam passage times.

Dam Passage Times: Steelhead

Like Chinook salmon, radio-tagged steelhead passed dams primarily during daylight hours, and most passed each dam where they were detected. Steelhead passed dams faster than Chinook salmon (Figure 6), with median times between 0.4 and 0.8 d at lower Columbia dams and 0.3 and 1.1 d at lower Snake dams (Table 5). In the upper-Columbia, 41 steelhead passed Priest Rapids Dam in 1996 and 1997 (*median* = 0.87 d) and 23 passed Wanapum dam in 1997 (0.49 d). Few steelhead (all years combined) took more than 5 d to pass individual dams, except at John Day Dam (Table 7).

Seasonal Migration Timing – Non-overwintering steelhead passed dams from late May through December. Steelhead passage times were typically fastest in late September and October and for some of the earliest June migrants. Passage was slowest when water temperatures peaked in August and again in November and early December before the onset of overwintering. Regression models using semimonthly blocks were mostly non-significant ($P > 0.05$) at lower Columbia River dams, except passage times decreased through time in 2001 at The Dalles and John Day dams ($P < 0.05$, weighted linear regression) (Appendix 2). In the Snake River, quadratic models were significant ($P < 0.05$) in 2000 and 2001 at Ice Harbor Dam, and in 1997 at Lower Monumental and Little Goose dams: in all cases steelhead passage times were relatively high in late summer and late fall and were lowest in September and early October.

River Discharge and Temperature – Temperature data were unavailable at most dams during the second half of the steelhead migrations each year and analyses were not performed on the partial datasets. Discharge was low through most of each steelhead migration, and regression models were generally not predictive (Appendix 2).

Reservoir Passage Rates: Chinook Salmon

Median migration rates through the eight lower Columbia and lower Snake River reservoirs (all years combined) ranged from 47 to 70 $\text{km}\cdot\text{d}^{-1}$ for spring Chinook salmon (Figures 8 and 9), 61 to 77 $\text{km}\cdot\text{d}^{-1}$ for summer Chinook salmon, and 51 to 65

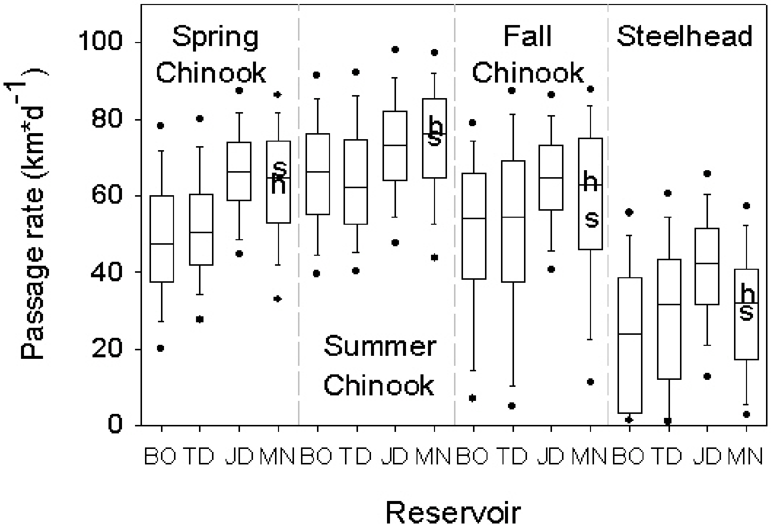

Figure 8. Median, quartile, 5th, 10th, 90th and 95th percentile passage rates (km•d^{-1}) through Columbia River reservoirs; all years combined. Medians rates for the McNary reservoir are designated *s* for fish that entered the Snake River and *h* for those that entered the Hanford Reach of the Columbia River.

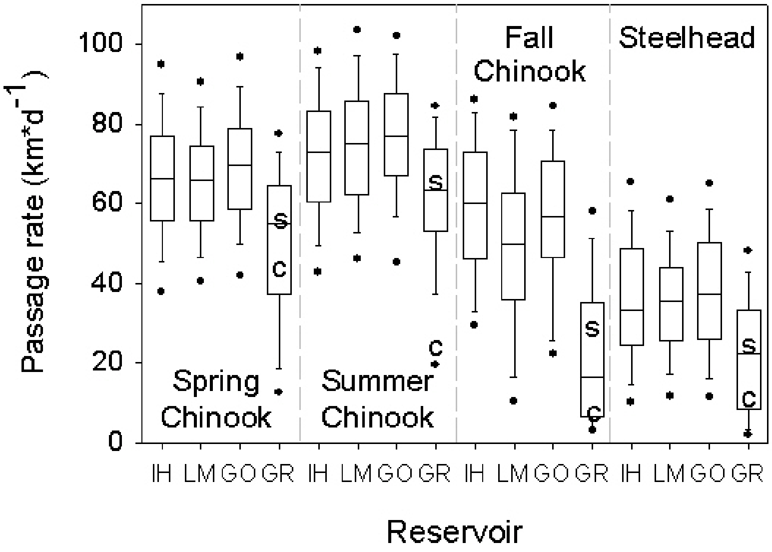

Figure 9. Median, quartile, 5th, 10th, 90th and 95th percentile passage rates (km•d^{-1}) through Snake River reservoirs; all years combined. Medians rates for the Lower Granite reservoir are designated *c* for fish that entered the Clearwater River and *s* for those that continued up the Snake River.

km•d^{-1} for fall Chinook salmon through all but Lower Granite reservoir (Table 8). In the lower Columbia River, spring and summer Chinook salmon consistently migrated more rapidly through John Day and McNary reservoirs than through the Bonneville and The Dalles reservoirs (Table 8). Fall Chinook salmon also migrated fastest through the John Day reservoir. In the McNary reservoir, fall Chinook salmon that returned to the Hanford Reach migrated quickly while those that returned to the Snake River migrated more slowly, at rates similar to those through the Bonneville and The Dalles reservoirs. In the three lower Snake River reservoirs, summer Chinook salmon migrated fastest and spring Chinook salmon migrated slowest. Migration rates were lower through Lower Granite reservoir, especially for fish that returned to the Clearwater River (Table 8). Few spring–summer or fall Chinook salmon took more than 5 d to pass through any reservoirs except Lower Granite reservoir (Table 7).

Seasonal Migration Timing – Reservoir migration rates for spring–summer Chinook salmon increased with reservoir entry date within each year (runs combined) (Appendix 3). Median rates for fish grouped by semimonthly blocks increased significantly ($P < 0.05$) through time in 16 of 20 weighted linear regression models for lower Columbia reservoirs (e.g., Figure 10). Models were not significant ($P > 0.05$) for Bonneville (1998), John Day (1996), and McNary (1996, 1997) reservoirs. Rates increased about 4 km•d^{-1} (*range* 1.5 to 6.0 km•d^{-1}) every two weeks in the significant models. In the three lower Snake River reservoirs, rates increased with entry date in all years, and 5 of 13 weighted linear models were significant ($P < 0.05$), including one year (1998) for the Ice Harbor reservoir and two years (1997, 2000) for the Lower Monumental and Little Goose reservoirs. As through downstream reservoirs, migration rates through the Lower Granite reservoir to the Clearwater and Snake River receivers increased with Lower Granite reservoir entry date in all years, though statistical models were constricted by sample sizes.

Within years, semimonthly migration rates for fall Chinook salmon in the Bonneville and The Dalles reservoirs were relatively constant. In contrast, fall Chinook salmon migration rates through the John Day and McNary-Hanford reservoirs were highest in August and again in early November, with rate nadirs in October.

River Discharge and Temperature – Within years, river discharge was not correlated with spring–summer or fall Chinook salmon reservoir passage rates through lower Columbia River reservoirs, with one exception. The exception was in 2000, when spring–summer Chinook salmon rates decreased significantly as discharge increased through the The Dalles, John Day, and McNary reservoirs (Appendix 3). Spring–summer Chinook salmon migrated through lower Snake River reservoirs more quickly when discharge was low, but only models for passage through the Lower Monumental and Little Goose reservoirs in 1997 and 2000 were significant (Appendix 3). Discharge peaked early in 2000, and most spring–summer Chinook salmon migrated during the decreasing hydrograph. Significant models for discharge may have reflected underlying influences of migration timing and water temperature.

Table 8. Median passage rates (km•d^{-1}) and number (n) of radio-tagged spring, summer and fall chinook salmon and steelhead recorded passing through lower Columbia and Snake River reservoirs for each year studied. IH = Ice Harbor Dam, GR = Lower Granite Dam, HAN = Hanford receiver, SNR = Snake River receiver, CWR = Clearwater River receiver.

Run	Year	Bonneville (70 km)	The Dalles (37 km)	John Day (120 km)	McNary-IH (67 km)	McNary-HAN (83 km)
Spring Chinook	1996	39 (349)	41 (217)	61 (192)	55 (79)	
	1997	38 (405)	43 (375)	63 (330)	57 (191)	56 (35)
	1998	51 (404)	50 (382)	67 (303)	60 (188)	62 (75)
	2000	47 (409)	52 (344)	69 (307)	69 (202)	64 (82)
	2001	66 (436)	62 (526)	70 (450)	74 (439)	60 (112)
Summer Chinook	1996	54 (99)	51 (88)	61 (99)	64 (17)	
	1997	59 (214)	57 (184)	68 (179)	70 (25)	62 (37)
	1998	66 (157)	60 (176)	73 (111)	74 (32)	77 (112)
	2000	69 (106)	63 (210)	77 (153)	78 (37)	77 (154)
	2001	79 (200)	78 (191)	83 (158)	80 (66)	83 (122)
Fall Chinook	1998	47 (246)	49 (392)	64 (278)	49 (32)	66 (278)
	2000	54 (235)	58 (294)	63 (199)	53 (29)	55 (273)
	2001	59 (326)	55 (307)	67 (308)	50 (89)	71 (322)
Steelhead	1996	24 (381)	30 (421)	43 (244)	35 (197)	
	1997	19 (288)	30 (519)	40 (369)	31 (298)	35 (29)
	2000	25 (511)	31 (541)	41 (380)	29 (422)	33 (103)
	2001	30 (600)	38 (552)	46 (457)	31 (375)	49 (209)

		Ice Harbor (51 km)	Lower Mon. (46 km)	Little Goose (59 km)	GR-SNR (64 km)	GR-CWR (59 km)
Spring Chinook	1996	60 (63)			45 (36)	39 (21)
	1997	60 (246)	59 (229)	59 (237)	44 (148)	33 (84)
	1998	62 (158)	59 (129)	64 (141)	51 (120)	30 (65)
	2000	69 (195)	69 (174)	73 (177)	61 (106)	40 (61)
	2001	72 (402)	72 (262)	78 (360)	64 (317)	52 (104)
Summer Chinook	1996	59 (13)			68 (17)	
	1997	72 (45)	77 (31)	75 (42)	60 (38)	16 (4)
	1998	78 (29)	65 (33)	76 (29)	56 (38)	20 (5)
	2000	72 (30)	77 (27)	84 (24)	71 (37)	
	2001	72 (61)	82 (48)	82 (51)	71 (62)	
Fall Chinook	1998	62 (17)	50 (18)	57 (10)	36 (5)	
	2000	67 (15)	48 (17)	50 (7)	24 (12)	8 (7)
	2001	58 (54)	50 (45)	57 (25)	32 (16)	9 (35)
Steelhead	1996	38 (5)			25 (146)	14 (42)
	1997	36 (274)	34 (200)	37 (215)	24 (138)	10 (63)
	2000	32 (322)	36 (279)	36 (245)	24 (203)	17 (109)
	2001	33 (292)	37 (244)	39 (209)	23 (235)	14 (111)

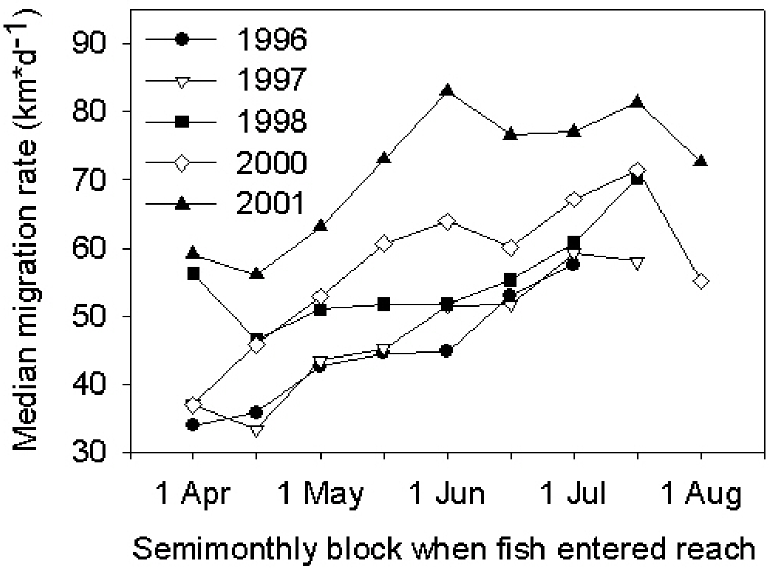

Figure 10. Semimonthly median migration rates (km•d^{-1}) for spring–summer Chinook salmon passing through The Dalles reservoir.

Between-year differences in reservoir migration rates for spring–summer Chinook salmon were strongly related to mean discharge over the date range when 90% of each run entered a reservoir. Fish migrated fastest through the Bonneville, The Dalles, and John Day reservoirs in years with low mean discharge for both spring ($0.66 < r^2 < 0.95$, linear regression) and summer ($0.80 < r^2 < 0.94$) Chinook salmon. Rates also increased as annual seasonal discharge decreased in the McNary reservoir for fish that entered the Snake ($r^2 = 0.83$ spring Chinook salmon, 0.36 summer Chinook salmon; 5 years) or upper-Columbia rivers ($r^2 = 0.64$ spring Chinook salmon, 0.94 summer Chinook salmon; 4 years). Spring Chinook salmon migrated faster ($0.84 < r^2 < 0.97$) through all four Snake River reservoirs in low-discharge years, as did summer Chinook salmon ($0.12 < r^2 < 0.80$). Substituting mean discharge for the full migration period (April-July) produced similar regression coefficients.

Fall Chinook salmon migrated through lower Columbia reservoirs (including McNary-Hanford) faster in 2001 (low discharge) than in 2000 (near-average discharge) in almost all semimonthly pairs, but differences were small.

Reservoir Passage Rates: Steelhead

Steelhead migrated through lower Columbia and lower Snake River reservoirs much more slowly than Chinook salmon, with median rates (all years combined) from 22 to 41 km•d^{-1} (Figures 8 and 9). Compared to Chinook salmon, relatively large proportions (12 to 47%) of steelhead took more than 5 d to pass through lower

Columbia reservoirs and Lower Granite reservoir (Table 7), and 12 to 34% took more than 10 d to pass through the Bonneville, The Dalles, McNary-Ice Harbor, and Lower Granite reservoirs. Telemetry records at fixed receivers in tributaries indicated that many steelhead strayed temporarily into cold water refugia during reservoir passage, particularly during the warmest periods, and the behavior was strongly associated with the long migration times.

***Seasonal Migration Timing* –** Within years, steelhead migration behavior in lower Columbia River reservoirs varied widely with reservoir entry date and availability and use of cool-water tributaries during times of peak mainstem temperatures. In all four years, median rates through the Bonneville reservoir were between 25 and 50 km•d^{-1} in June and early July and dropped to less than 10 km•d^{-1} when mainstem temperatures neared peak levels in late July and August. Rates increased rapidly in September and October (e.g., Figure 11). Quadratic regression models fit the Bonneville reservoir passage data in all years (Appendix 3). A similar, though less pronounced pattern was evident through The Dalles reservoir; only the model for 1996 was significant. Median rates through the John Day reservoir did not follow the parabolic relationship observed downstream. Instead, rates decreased slightly but significantly during fall in 1997 and 2000 (Appendix 3). Only the 1997 model was significant for the McNary reservoir.

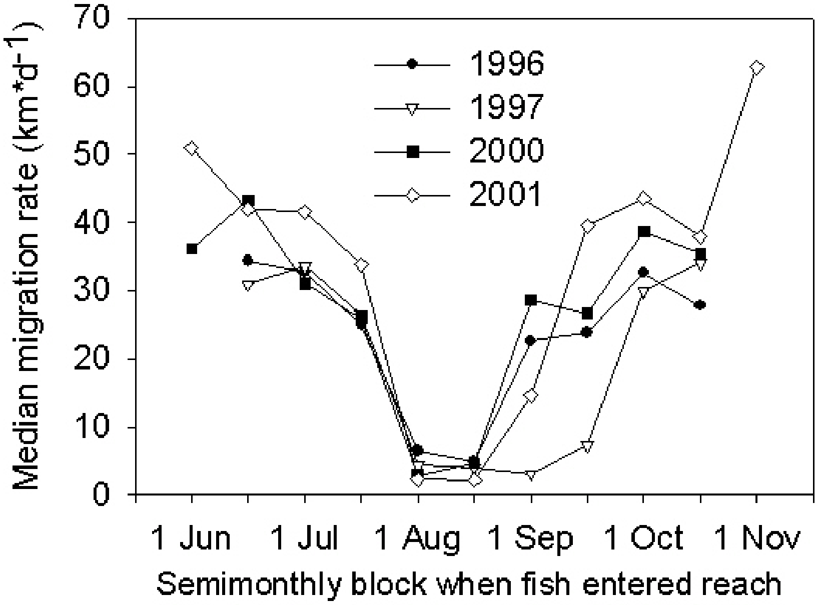

Figure 11. Semimonthly median migration rates (km•d^{-1}) for steelhead passing through Bonneville reservoir.

Most steelhead passed the three lower Snake River reservoirs in September and October. Migration rates were widely variable for the few fish that passed from June to August, and then decreased from September through December. Semimonthly medians decreased significantly from 30 to 45 km•d^{-1} in early September to less than 10 km•d^{-1} in December through the Ice Harbor, Lower Monumental and Little Goose reservoirs in 1997 and 2000 (Appendix 3), but not in 2001. In Lower Granite reservoir, steelhead migrated at rates mostly less than 10 km•d^{-1} from June through early September and then accelerated in September and October: medians were 20 to 33 km•d^{-1} for fish that continued up the Snake River and 10-15 km•d^{-1} for Clearwater River fish. Most steelhead that wintered over in the lower Snake River migrated rapidly (35 to 45 km•d^{-1}) through reservoirs in spring.

***River Discharge and Temperature* –** Within years, steelhead migration rates in Columbia and Snake reservoirs varied widely and were not generally correlated with river discharge (Appendix 3). Migration rates decreased significantly as temperatures increased through the Bonneville reservoir in all four years. Temperature data was incomplete at The Dalles and John Day dams, and no significant models were found for the McNary reservoir (Appendix 3).

Between-year variability in median steelhead migration rates through reservoirs was relatively low (SD < 5 km•d^{-1} through all reservoirs except McNary-Hanford, Table 8). As a result, regression models using seasonal discharge and temperature averages produced some significant ($P < 0.05$) correlations, but models were inconsistent. As annual June-August discharge increased, migration rates increased through some reservoirs and decreased through others. Models using June-August temperature and total days over 21ºC were equally inconsistent. As with intra-annual temperature measures, median annual passage rates may have been inappropriate for analyses given long reservoir residency times for some fish and the wide range of steelhead migration rates in reservoirs within each year.

Tributary Passage Rates: Spring–Summer Chinook salmon

A total of 2,463 migration rates were calculated for 1,801 unique radio-tagged spring–summer Chinook salmon during the five study years (Table 9). Most fish migrated upstream at rates between 10 and 30 km•d^{-1} (medians), with maximum rates of more than 50 km•d^{-1} through the low-gradient Snake River mainstem and Hanford Reach of the Columbia River (Figure 12). The lowest median migration rates, both in individual years and with all years combined, were recorded in the Deschutes and Clearwater rivers; salmon returning to both rivers were also among the earliest migrants each year and passed those reaches when water temperatures were relatively low. The lowest median rate for a single reach/year was recorded in 1997 for fish passing through the Snake River reach (Snake 1) that ended at the Grande Ronde River (*median* = 4.0 km•d^{-1}, $n = 9$); mean Snake River discharge encountered by those fish was *c*. 3,270 m^3•s^{-1}, more than double the mean encountered by fish during 1998-2002 (*mean* = 1,380 m^3•s^{-1}).

Table 9. Number of radio-tagged adult spring–summer chinook salmon used for migration rate calculations in each river reach during 1997-1998 and 2000-2002.

	Number of chinook salmon					
	1997	1998	2000	2001	2002	Total
Deschutes	39	64	99	11	34	247
Yakima				70	65	135
Columbia	151	31				182
Clearwater (1)	13	14	10	31	24	92
Clearwater (2)	22	21	16	24	16	99
Snake (1)	9	20	14	23	27	93
Snake (2)	9	13	11	30	12	75
Snake/Salmon	145	114	113	286	191	849
Salmon (1)	23	32	25	57	53	190
Salmon (2)	7	15	14	22	26	84
Salmon (3)	8	14	14	22	28	86
Salmon/SF Salmon	35	39	56	131	71	332

Within-year variability in migration rates was lowest in the Salmon/SF Salmon reach (C.V. = 19-34) and the three Salmon River reaches (21-41) and was highest in the Snake 1 (40-132), Clearwater 2 (43-70) and Snake 2 (46-89) reaches. Median annual migration rates varied by less than 4 km•d^{-1} through all reaches except the Snake 1 (S.D. = 15.1 km•d^{-1}), Snake/Salmon (6.7 km•d^{-1}) and Salmon 1 (5.1 km•d^{-1}) reaches. Annual median migration rates through the reaches with the greatest between-year differences were negatively correlated with mean encountered discharge. Migration rates in the Snake/Salmon reach decreased approximately 6 km•d^{-1} with every 500 m^3•s^{-1} increase in Salmon River discharge (r^2 = 0.86, P = 0.0237; linear regression, weighted by the number of fish in each year) (Figure 13). Similarly, median annual rates in the Snake 1 reach decreased by about 8 km•d^{-1} with every 500 m^3•s^{-1} increase in mean encountered Snake River flow (r^2 = 0.76, P = 0.0042); no correlation was found for the Salmon 1 reach (P = 0.43).

Migration rates were calculated for two consecutive reaches for most fish returning to the Salmon River basin. Individual fish speed in the Snake/Salmon reach was a good predictor ($0.53 < r^2 < 0.63$, $P < 0.001$, linear regressions) of how fast the same fish traveled through the Salmon 1, Salmon 2 or Salmon/SF Salmon reaches just upstream. Most individual fish traveled through the Snake/Salmon reach more rapidly than through the upstream reaches; however, about 2% of fish in the Salmon/SF Salmon reach and 35% of fish in the Salmon 1 and Salmon 2 reaches migrated faster in the upstream reaches, almost exclusively during the early portion of the migration and prior to peak Salmon River runoff.

The Snake/Salmon reach had the largest sample size (N = 848) among all reaches, with fish arriving at the Snake River receiver from late April through July and encountering a wide range of Snake and Salmon River conditions in each year (Figure 14). Chinook salmon migrated more rapidly through the Snake/Salmon reach as migration date increased each year ($0.61 < r^2 < 0.83$; $P < 0.001$; linear

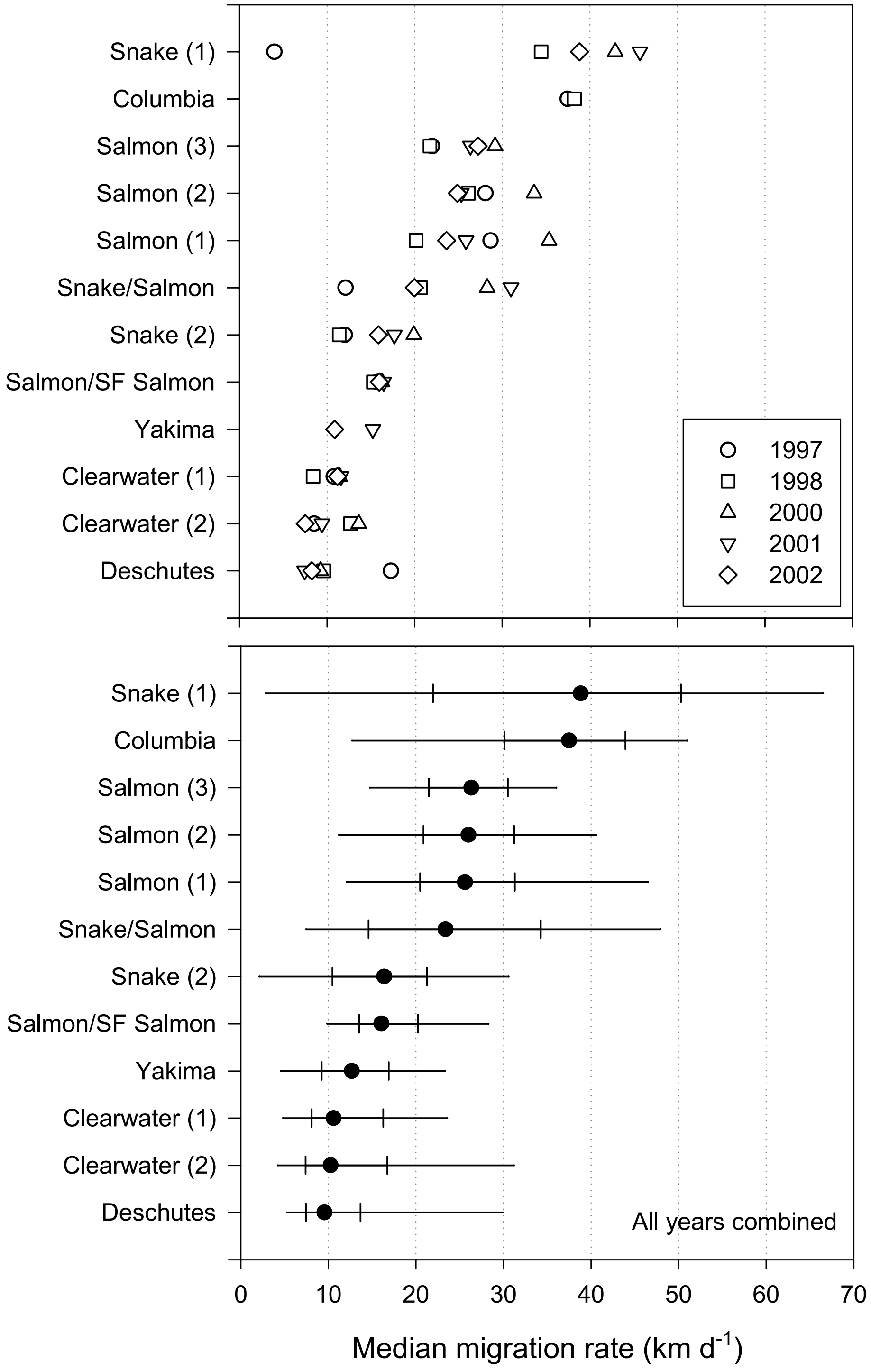

Figure 12. Median annual spring–summer chinook salmon migration rates (km•d^{-1}) recorded each year in the 12 study reaches (top panel) and median, quartile and 5th and 95th percentiles of rates in each reach with all years combined (bottom panel).

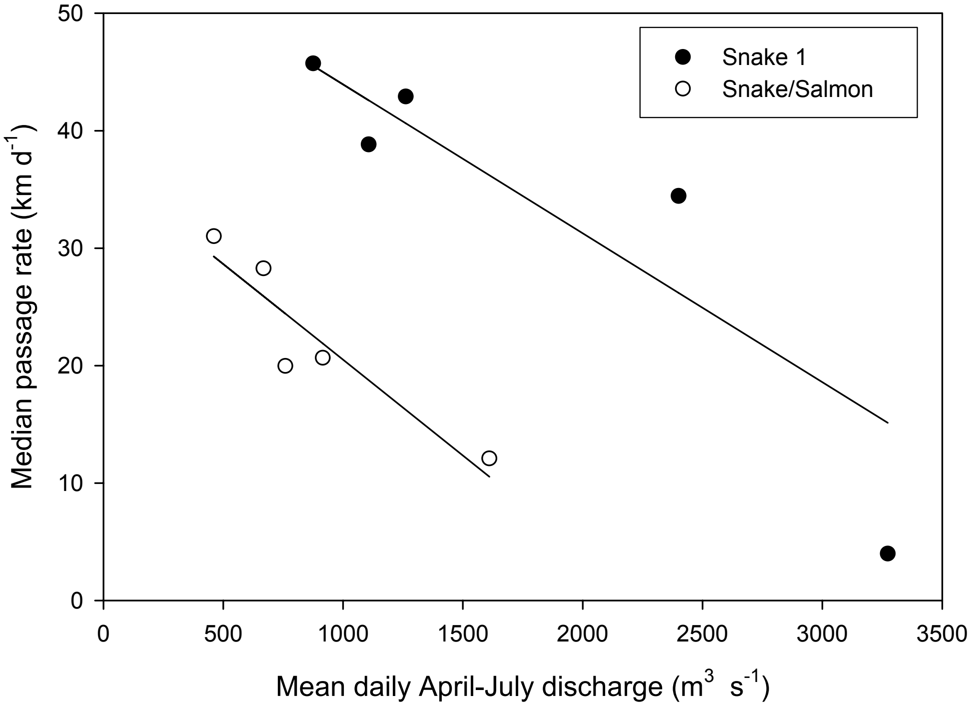

Figure 13. Weighted regressions of annual median spring–summer chinook salmon migration rates (km•d^{-1}) in the Snake 1 (closed circles) and Snake/Salmon (open circles) reaches and mean encountered river discharge in the Snake or lower Salmon rivers, 1997-2002.

regression). Migration rate distributions were near normal for this reach, and so regression results were similar for log-transformed rates ($0.53 < r^2 < 0.86$, $P < 0.001$). Migration rates in the Snake/Salmon reach decreased significantly ($P < 0.05$) within each year as both Salmon and Snake River flows increased, but discharge explained less than 31% of the variability in untransformed migration rates in all years except 1997 ($r^2 = 0.67$, $P < 0.0001$). The stronger relationship between discharge and migration rates in 1997 was likely because more than 95% of radio-tagged salmon entered the reach after peak flows and during the decreasing hydrograph when flow and migration date were strongly negatively correlated ($r^2 = 0.83$ from 15 May to 31 August). A relatively large proportion of tagged fish entered the Snake/Salmon reach prior to peak flows only in 2002 (Figure 14), when 55% entered the reach before 2 June. In that year, early-arriving fish migrated at rates mostly between 15 and 30 km•d^{-1} compared to 7 to 18 km•d^{-1} during the ascending hydrograph.

Multiple Regression Analyses – Date of migration was the strongest predictor ($F = 59.3$, $P < 0.0001$) of log-transformed salmon migration rates when all data from all reaches were combined ($n = 2{,}429$) (Table 10). Migration year and migration reach also explained significant ($P < 0.0001$) portions of the total variability in migration rates, as did several interaction terms; river discharge was non-significant ($P = 0.163$) (Table 10). With all independent variables and single interaction terms

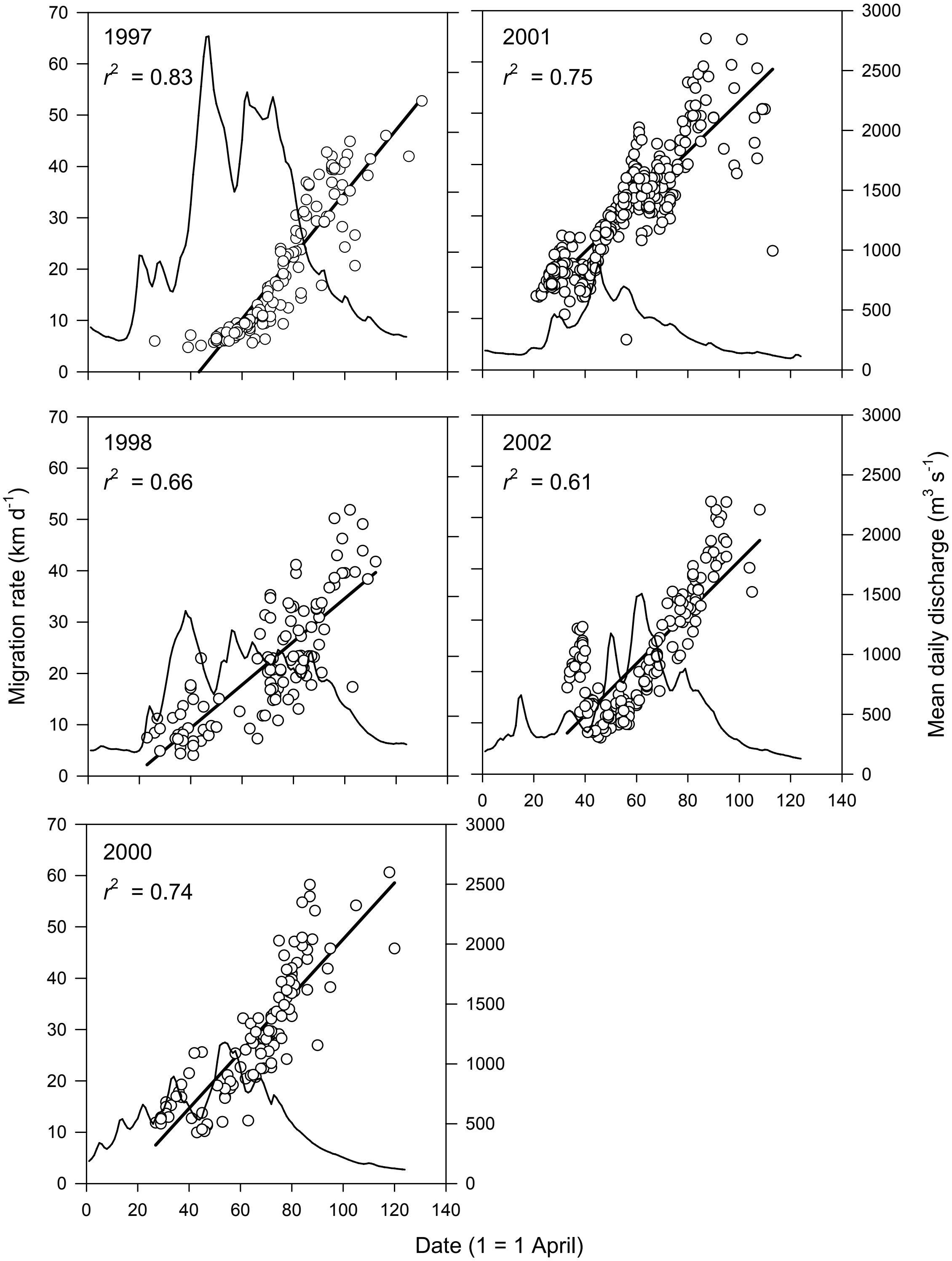

Figure 14. Individual spring–summer chinook salmon migration rates (km•d^{-1}) (open circles) in the Snake/Salmon river reach by the date each fish entered the reach, with mean daily discharge (m^3•s^{-1}) (solid line) in the lower Salmon River.

Table 10. Results of multiple regression analysis of spring–summer chinook salmon migration rates (km•d^{-1}) in all[1] study reaches with all years combined.

Source	*df*	Type III SS	Mean Square	*F*	*P*
Year	4	4.2	1.1	7.6	<0.0001
Reach	11	10.7	1.0	7.0	<0.0001
Date	1	8.2	8.2	59.3	<0.0001
Discharge	1	0.3	0.3	2.0	0.1630
Year*Reach	37	30.6	0.8	5.9	<0.0001
Year*Date	4	2.0	0.5	3.6	0.0060
Year*Discharge	4	8.4	2.1	15.1	<0.0001
Reach*Date	11	30.3	2.8	19.8	<0.0001
Reach*Discharge	11	10.3	0.9	6.8	<0.0001
Date*Discharge	1	1.4	1.4	9.9	0.0017

[1] 2002 flow data unavailable for Deschutes River

included, the overall model r^2 was 0.67. Ratios of the *F* values for the independent variables showed the relative importance of migration date, which explained approximately eight times as much of the migration rate variability as either migration year or reach and about 30 times as much as river discharge.

To address possible bias created by including two migration rates for most Salmon River fish, a second model was run that excluded migration rates for Salmon River fish upstream from the Snake/Salmon reach (model n = 1,737). Results were similar to the initial model (r^2 = 0.68), with migration date explaining the most variability (F = 49.7, P < 0.0001), followed by migration date×migration reach (F = 25.2, P < 0.0001) and migration year×discharge (F = 13.0, P < 0.0001). As with the initial model, discharge alone was non-significant (F = 2.0, P = 0.1589).

Within each year, migration date (1997, 1998), migration date×migration reach (2000) or migration date×discharge (2001, 2002) explained the highest proportions of the variability in salmon migration rates (4.8 < F < 37.9, P < 0.0005), with overall r^2 values between 0.61 and 0.74. Models for individual reaches produced mixed results. Migration date had the highest *F* values (P < 0.0002) for the Snake/Salmon, Salmon 2 and Salmon 3 reaches, migration date×discharge had the highest values (P < 0.042) for the Deschutes, Clearwater 2 and Snake 2 reaches and discharge was highest (P < 0.013) for the Salmon 1, Salmon/SF Salmon and Yakima reaches.

Discussion

***Hydrosystem* --** In the studies described here we used large-scale radiotelemetry monitoring over multiple years to evaluate factors that influence the migration rates of adult anadromous salmonids returning through the Columbia River hydrosystem. Both the Columbia and lower Snake rivers have been transformed by construction and management of the hydrosystem from lotic systems characterized by large annual snowmelt floods and low winter discharge to a series of dams and impoundments with attenuated hydrographs. Diminished peak discharge and higher fall and winter discharge have been accompanied by earlier warming of the lower river, higher peak temperatures, and later fall cooling (Quinn and Adams 1996; Quinn et al. 1997). Consequences of these changes for adult migrants vary widely between species and between years, and are not fully understood. From our analyses of Chinook salmon and steelhead passage times we found significant inter- and intra-annual effects of seasonal migration timing, river discharge, and water temperature on passage behaviors.

Hydrosystem passage by most radio-tagged Chinook salmon in this study included slight to moderate delays at dams followed by periods of rapid upstream swimming through reservoirs. Spring–summer Chinook salmon, whose migrations overlap with peak discharge but precede peak summer water temperatures, passed most rapidly through all environments when discharge was low and temperatures were moderate. Spring Chinook salmon passage through the hydrosystem may be faster now than through the unimpounded Columbia, as reservoir velocities and springtime discharge are lower and slightly warmer than historically. Adult summer Chinook salmon may also benefit from reduced peak discharge, but are likely exposed to warmer mainstem temperatures for longer periods than during pre-dam conditions. Fall Chinook salmon and steelhead migrations occur mostly after peak discharge and during and after peak mainstem warming, and some fish from both runs showed extensive holding and delayed migration during the warmest periods. The majority of the tagged steelhead and many fall Chinook salmon destined for upriver spawning sites temporarily strayed into cooler lower Columbia River tributaries (Goniea 2002; High 2002; Keefer et al. 2002), a behavior that was associated with long passage times for this species.

Efforts were made to radio tag fish from throughout each migration, approximately in proportion to overall runs. As such, results should reasonably reflect upstream migration behaviors for the studied populations. Collection of fish only from the Washington-shore ladder at Bonneville Dam may have imposed a slight but unavoidable bias for stocks returning to Washington-shore tributaries. Bjornn et al. (2000), however, found that fish released at sites on both sides of the river downstream from Bonneville Dam passed both Bonneville fishways in similar proportions, suggesting that the bias was minor. Selection for known-source (PIT-tagged) fish also introduced some bias. Most of the known-source groups were from upriver stocks (Snake, Yakima, upper Columbia) and may have slightly different passage strategies at lower Columbia River dams and reservoirs as compared to lower river stocks. Passage times for these groups were not, however, substantially different from the runs at large and we believe the bias was small.

Interpretation of telemetry data is also predicated upon the assumption that tagged fish behave similarly to untagged fish. Several researchers have reported downstream movement after radio tagging adult salmonids (Bernard et al. 1999; Mäkinen et al. 2000), but overall effects appear to be low, and most fish complete migration (Burger et al. 1985; Thorstad et al. 2000; Jokikoko 2002). We attempted to minimize fish stress during handling and anesthetization, and allowed extended recuperation in a dark tank of oxygenated river water. Pre-release mortality was less than 1% for all runs. After release, passage times were calculated only after fish had acclimated and volitionally resumed upstream migration, which should have reduced any inflation of passage times related to tagging effects.

With the addition of PIT-tag monitoring equipment in ladders at Bonneville and Lower Granite dams it was possible to compare passage times for radio-tagged fish to those for PIT-tagged fish without radios in later years of the study. Results suggest that there were no biologically significant differences between migration rates of radio- and PIT-tagged adult fish without radio transmitters (Matter and Sandford 2003). Using Chinook salmon from this study, Matter and Sandford (2003) found that the median passage time from Bonneville Dam to Lower Granite Dam for radio-tagged fish (14.1 d) was actually less than the median for PIT-tagged fish without transmitters (15.9 d).

As runs progressed upstream, distributions of passage dates for radio-tagged fish were similar to those for all fish counted at each dam. Median tag dates for spring Chinook salmon were within 2 to 4 days of medians for all spring Chinook salmon counted at Bonneville Dam in all years except 2001 (difference = 12 d) when the run was exceptionally large and early. Differences between median tag dates and overall run medians averaged 4.8 d for summer Chinook salmon, 5.7 d for fall Chinook salmon and 9.0 d for steelhead (Keefer et al. 2004b). These differences are small in relation to the duration of each run (approximately two months each for spring and summer Chinook runs, three months for fall Chinook runs, and five or more months for steelhead).

Separating the complex effects of discharge and temperature on fish behaviors in the Columbia basin is challenging, as the two variables can be closely correlated during salmonid migrations, particularly across years (e.g., low-discharge years are typically warmer). Contemporaneous migrants can also encounter widely different in-river conditions depending on migration route (e.g., at dams or through reservoirs), daily operations at dams, and timing of fish movements (e.g., day versus night). In our analyses, discharge was the best between-year predictor of radio-tagged spring and summer Chinook migration rates through reservoirs and hydrosystem reaches, and water temperature was secondary. Within years, migration rates and dam passage times increased with temperature but were correlated with mainstem hydrosystem discharge in only a handful of tests. Stronger flow-related relationships may have been found had we studied river velocity in addition to discharge, although the two tend to be correlated. Slower migration would be expected for fish exposed to high velocity discharge (Bernatchez and Dodson 1987), but collecting data on encountered velocity is difficult, especially in large, complex systems over long distances. Given that much of the Columbia and lower Snake rivers are impounded, encountered velocities (in reservoirs) are likely considerably lower than during pre-hydrosystem times.

Increasing migration speed during warming within years may have been both a function of elevated metabolic activity and increased reproductive motivation as runs progressed and spawning times approached (Gard 1973; Hellawell et al. 1974; Gilhousen 1990; Erkinaro et al. 1999; Økland et al. 2001). It is also possible that fish migrated faster as a mechanism to seek potentially cooler water upstream. Separation of these physiological and reproductive imperatives is confounded by close correlation of date and Columbia River temperature ($r > 0.94$) in all years from April through August or September.

High water temperature during upstream migration has been linked to higher pre-spawning mortality for spring Chinook (Schreck et al. 1994), summer and fall Chinook (Dauble and Mueller 2000), and sockeye salmon (Major and Mighell 1966) within the Columbia River basin, sockeye salmon in the Fraser River, British Columbia (Gilhousen 1990; Macdonald 2000), and for steelhead in several systems (Baigun 2000). Maximum river temperatures in all years of this study were within the range where adult migration may be blocked (McCullough et al. 2001). Exposure to these elevated water temperatures can increase susceptibility to disease and compromise reproductive performance through increased metabolic demands, reduced allocation to gonadal development and reduced egg viability (Berman and Quinn, 1991; Rand and Hinch 1998; Torgersen et al. 1999; Hinch and Rand 2000; Kinnison et al. 2001). In the Columbia basin, use of thermal refugia may ameliorate some costs of high mainstem temperatures, particularly for steelhead that pass through the lower river six to ten months before spawning. Obligate migrants like summer and fall Chinook, however, may be compromised by temperature-related delays and exposure to sub-lethal temperatures through elevated metabolic costs, altered energy allocation, or late arrival at spawning grounds.

Compared to spring–summer Chinook salmon, radio-tagged fall Chinook salmon and steelhead appeared to be more affected by water temperature than discharge. Slowed migration related to high temperatures and associated temporary straying and holding behavior may have physiological costs, including elevated stress and increased likelihood of disease propagation. Concentrations of fall Chinook and steelhead in the cold plumes in and near non-natal tributary mouths may also result in prolonged exposure to mainstem and tributary fisheries for those stocks migrating during the warmest times (Goniea 2002; High 2002).

Just as migration delays related to river environment can be costly, route-finding confusion or impediments like dams or other obstructions may have negative energetic consequences. Geist et al. (2000) used physiological telemetry to evaluate energy expenditure of adult fall Chinook salmon in the Columbia River and estimated that fish taking longer than five days per dam may have insufficient energy reserves to complete spawning. In our study, most radio-tagged fish from each run-year passed dams in less than 36 h. However, more than 30% of spring Chinook took more than 5 d to pass The Dalles and John Day dams in 1997, the year with highest discharge, and 10 to 20% took that long at other dams and in other years (see Table 7). Similar long passage times occurred for 5 to 15% of fall Chinook salmon and steelhead at John Day and Bonneville dams each year. Extended passage times we observed were broadly consistent with those reported by other basin researchers

(Stuehrenberg et al. 1995; Bjornn et al. 2000d and as reviewed in Bjornn and Peery 1992). Extrapolating the results from Geist et al. (2000) to other species is problematic, however, and we use the 5 day cutoff simply for heuristic purposes. Additional research on passage time-survival relationships is needed, and we are currently using the passage time database to examine survival patterns.

We are unaware of any literature that has rigorously evaluated dam-related delay and its affect on survival, although temporary delays for adult migrants have been recorded at dams on many smaller rivers, including steelhead in the Yakima River, Washington (Hockersmith et al. 1995), spring Chinook in the Willamette River, Oregon (Schreck et al. 1994) and Atlantic salmon (*Salmo salar*) in the River Tummel, Scotland (Gowans et al. 1999) and Rhine River, France (Gerlier and Roche 1998). In these studies, some fish took several days or weeks to pass individual projects, but survival to spawning was not typically evaluated in terms of passage behavior.

Interruptions in adult salmon migrations have also been reported for fish in less regulated rivers due to obstructions other than dams, such as falls, rapids, or channel constrictions. For example, migration speeds for Fraser River sockeye salmon were lowest through constricted and high velocity areas (Gilhousen 1990; Hinch et al. 1996; Hinch and Rand 1998), and Atlantic salmon migrations are temporarily blocked at falls in Norway (Jensen et al. 1989). Pre-dam passage rates in the free-flowing mainstem Columbia/Snake are unknown, but can be estimated from rates for fish in unimpounded segments of the Snake River and its tributaries. Using rates recorded from the Snake and Salmon rivers (e.g., Figure 12) we estimate that pre-dam spring Chinook passage times from Bonneville Dam past Lower Granite Dam (460 km) would have been 1.0 to 1.4 times longer than we measured with dams in place during this study. Using the same measure, migration times of summer Chinook would have been shorter without dams at 0.7 to 0.9 times current rates. There are obvious limitations to such estimates, but they do suggest that cumulative hydrosystem delay (or gain) differs substantially between runs and years. Similar comparisons using data from steelhead are less likely to be informative because many steelhead overwinter in the unimpounded reaches upstream from Lower Granite Dam or migrate through those reaches when environmental conditions are quite different than those encountered in the lower hydrosystem (i.e., when water temperatures are low and discharge levels are near annual lows).

‘Delay’ at Columbia and Snake River dams has been a major focus of adult salmonid research. In response, the U.S. Army Corps of Engineers has made many structural improvements to fishways, collection channels, and ladders and implemented operational changes to improve adult passage efficiency and reduce passage times at dams (e.g., Bjornn et al. 1998b; Naughton and Peery 2003). Fallback and reascension at dams, however, remains as one of the more substantial and difficult-to-address sources of adult delay (Dauble and Mueller 1993; 2000). In most years, radio-tagged fish in this study that fell back had significantly longer (up to several weeks longer) hydrosystem passage times than fish that did not fall back. The proportion of each run that fell back and fallback rates were highest in years of high discharge, in part because most fish fall back via spillways and spill volumes are greatest when discharge is high (Reischel and Bjornn 2003; Boggs et al. 2004). From our work in progress (Keefer et al. *in press*) fish that fall back at dams are significantly less likely to escape to spawning tributaries. However, it is unclear whether the fallback itself, the migration delays that result, or some other factors like initial fish condition are the driving factor in this pattern.

Tributaries and Unimpounded Reaches – Results from the study of spring–summer Chinook salmon passage in unimpounded reaches generally supported the conclusions from the hydrosystem portion of these fishes' migration. Migration timing and arrival at spawning sites appeared to be stronger imperatives for spring–summer Chinook salmon than avoidance of difficult migration conditions. The cold, high-elevation sites used for spawning by these Chinook salmon stocks require early egg deposition (August and September) and long incubation periods to ensure fry development and emergence at appropriate times (Groot & Margolis, 1991). These reproductive requirements, along with climate and the great distance between ocean and natal sites may have shaped the somewhat unusual life history strategy of upstream migration during annual peak flows. Fraser River sockeye salmon (*O. nerka*) exhibit a similar migration (Brannon, 1987) as do some large-bodied Atlantic salmon (Trépanier *et al*., 1996). In contrast, most other Pacific salmonids time migration to at least partially avoid peak flow and difficult passage, including steelhead (Robards & Quinn, 2002), fall Chinook salmon (Dauble & Watson, 1997), sockeye salmon (Hodgson & Quinn, 2002) and coho salmon (*O. kisutch*).

Given the narrow reproductive window for spring–summer Chinook salmon stocks in the Columbia basin, it is not surprising that migration timing was a better predictor of migration speed than was river discharge. If discharge was the primary mechanism driving migration rates for these stocks across years and river reaches, one would expect large variation in migration rates in response to within- and between-year discharge fluctuations. Instead, discharge was a secondary predictor of salmon migration rates in most analyses, while the pattern of increasing migration rates through time occurred in both relatively small tributaries and large mainstem reaches in all years.

While discharge was secondary to migration timing in most riverine reaches within each year, it did explain some between-year variability in migration rates, with lower median rates recorded in years with higher flow. This was especially true in the Snake and Snake/Salmon reaches. The interaction terms migration date×discharge and year×discharge were also significant in several models, suggesting that both seasonal and annual discharge patterns affected salmon passage in riverine reaches. This differs somewhat from results in the hydrosystem reservoirs, where discharge was strongly negatively correlated with annual median reservoir passage rates but explained relatively little within-year variance. In both hydrosystem and riverine reaches, migration rates increased with increasing date of migration in all years, lending support to the persistent influence of migration timing (and associated seasonal warming) on migration rates for these Chinook salmon stocks.

In both hydrosystem and riverine studies, the use of mean discharges as predictor variables complicates analyses, as they do not reflect the spatial and temporal variability in discharge and velocity encountered by individual migrants, nor the tendency for some species and stocks to seek the most energetically efficient routes (Hinch & Rand, 2000; Crossin *et al*., 2003). More fine-scale measurements of discharge and velocity encountered by individual fish could produce more predictive behaviour models than the ones presented here, but such data are difficult to collect over large spatial scales.

The strong influence of migration timing on upstream spring–summer Chinook salmon riverine migration rates was likely a combination of ecological adaptations to spawning requirements and the physiological effects of water temperature on swimming performance. For example, early in the migration, when migration rates were typically slowest, reproductive development was probably incomplete (Healey, 1991) and metabolic rates were low due to low river temperatures. Increasing temperatures coincided with advancing reproductive maturation and increased metabolic rates, a combination that may explain the faster passage rates recorded later in the migrations, as has been suggested for other salmonids (Gilhousen, 1990; Schreck *et al*., 1994; Erkinaro *et al*., 1999; Økland *et al*., 2001).

Disentangling environmental and physiological stimuli (e.g., the effects of increasing temperature on swimming performance) from genetic and reproductive stimuli is challenging. Evidence supporting genetic control of anadromous salmonid migration timing and arrival at spawning grounds (and by extension migration rates) have been reported for many species including Atlantic (Hansen & Jonsson, 1991), Chinook (Burger *et al*., 1985; Quinn et al., 2002), sockeye (Gilhousen, 1990) and pink salmon (*O. gorbuscha*) (Smoker *et al*., 1998). Strategies for optimal adult arrival range from very early migration and long freshwater residence (*e.g*., some steelhead and Atlantic salmon stocks) to rapid migration by mature fish just prior to spawning (*e.g*., some Columbia River fall Chinook salmon). With either strategy, arrival at the most suitable time can lead to reproductive advantages for individual fish, such as selection of prime spawning sites and safe holding positions, and improved overall population fitness (Hawkins & Smith, 1986; Smoker *et al*., 1998). Alternatively, fish entering the river relatively late within each run face reduced mating opportunities if they reach the spawning grounds after most spawning activity has occurred. These fish may swim more rapidly, irrespective of discharge or temperature to reach spawning grounds before the window of opportunity for spawning closes. The observed seasonal increase in spring–summer Chinook salmon migration rates may incorporate a variety of these mechanisms, though the contribution of each remains unknown.

Riverine migration rates reported in this study for spring–summer Chinook salmon tended to be higher than, or similar to, those reported for Atlantic salmon (Hawkins & Smith, 1986; Mills, 1989; Trépanier *et al*., 1996; Gerlier & Roche, 1998) and were higher than those of Chinook and sockeye salmon in more northern Pacific rivers in Alaska and Canada (Gard, 1973; Hinch *et al*., 1996; Bernard *et al*., 1999).

Rates in the monitored reaches were more similar to those of radio-tagged spring Chinook salmon in the Willamette River, a major Columbia River tributary downstream from Bonneville Dam (Schreck *et al*., 1994). As in this study, early-run Willamette River fish moved upriver more slowly than later migrants, with rates increasing more or less in a continuum through each run. Both freshets and low flows occasionally slowed Willamette River migrants. Migration rates in the Columbia basin may be higher than in other rivers reported in the literature due to lower latitude, long migration distances, warmer temperatures, lower encountered velocities, or because most monitored reaches were well downstream from spawning grounds.

***Conclusion* --** Although researchers have studied hydrosystem impacts for decades, the complex effects of altered environment and hydrosystem operations on adult salmon and steelhead behavior and survival are not fully understood. This report presents summary data of adult Chinook salmon and steelhead migration times and rates in the developed Columbia River hydrosystem and for spring–summer Chinook salmon in relatively unimpacted tributaries. The data from multiple types of passage environments are complimentary and should be useful for evaluating hydrosystem impacts on adult fish.

In general, we found that most radio-tagged fish passed dams relatively efficiently and that rapid migration through lower Columbia and Snake River reservoirs may partially compensate for the relatively slower passage at dams. It is impossible, however, to draw any universal conclusions about adult passage times, given widely divergent life history strategies, migration timing and behavior and the multiple-stock structure in the basin. For example, high water temperatures slow some migrants, especially steelhead and fall Chinook salmon that pass through the lower river between July and September. Steelhead, in particular, may spend up to several months holding or temporarily straying into cool lower river tributaries. In contrast, warmer temperatures were correlated with faster upstream passage for adult spring–summer Chinook salmon, which migrate mostly before peak annual temperatures. Using rough estimates, it appears that spring Chinook salmon may migrate through the hydrosystem at faster rates than through the historic unimpounded Columbia River, while summer Chinook salmon may take longer to pass through the system. It is unclear how fall Chinook salmon and steelhead migrations compare to pre-dam conditions, but from these results, it seems likely that some stocks have slowed migrations, particularly during the warmest periods. Because hydrosystem development and operation have resulted in warmer temperatures and generally reduced flows, it is also possible that the timing of some runs may be advanced relative to historic timing, resulting in longer freshwater residency prior to spawning—at warmer temperatures—with unknown consequences for overall survival.

We recommend that future research more fully examine relationships between migration delays, fallback, temporary straying, and sub-lethal temperature exposure and how these factors affect escapement, spawning success, juvenile recruitment, and population-level dynamics.

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Appendix 1. Regression coefficients and significance levels for weighted regression models where semimonthly migration rates (km•d^{-1}) through hydrosystem reaches were dependent and migration timing (semimonthly block), river discharge, and water temperature were predictors. Results from linear models presented except when quadratic models provided better fit for fall chinook and steelhead (timing and temperature only). All models weighted by the number of fish in each block.

			Timing		Discharge	Temperature	
Reach and run		Blocks	β_1	β_2	β_1	β_1	β_2
Bonneville to McNary							
Sp-Su Chinook	1996	6	2.3†		-0.001	1.6†	
	1997	8	4.2**		0.000	2.6**	
	1998	7	3.2**		-0.000	1.9**	
	2000	8	2.9**		-0.004*	1.9**	
	2001	8	1.4†		0.004	0.9*	
Fall Chinook^1	2000	6	-3.1**		0.006	2.2*	
	2001	5	3.6		-0.017*	119.1**	-3.1**
Steelhead	1996	8	-18.6*	1.4*	0.000	-3.9*	
	1997	8	-13.5*	1.1*	0.000	-2.3*	
	2000	10	-13.0*	1.0*	-0.003	-3.1**	
	2001	10	-21.4**	1.5**	0.003	-4.8**	
Bonneville to Priest Rapids							
Sp-Su Chinook	1996	6	2.8*		-0.000	1.9†	
	1997	8	3.1**		-0.000	1.8**	
	1998	5	3.9*		0.002	2.4†	
	2000	8	2.4*		-0.003†	1.6*	
	2001	8	1.3†		-0.003	0.7	
Steelhead	1996	6	2.8		-0.004	1.2	
	1997	8	-12.9†	1.1†	-0.000	-1.3	
	2000	6	-0.7		-0.000	-1.3	
	2001	9	-17.2**	1.5**	0.002	-2.4†	
Bonneville to Lower Granite							
Sp-Su Chinook	1996	6	2.1*		0.001	1.5*	
	1997	7	3.9**		0.002	2.4**	
	1998	7	1.2		-0.001	0.4	
	2000	6	2.3*		-0.001	1.4*	
	2001	7	2.4†		0.010*	1.3*	
Steelhead	1996	8	-12.2†	1.0*	-0.001	-3.2*	
	1997	8	-3.5*	0.4**	-0.001	-0.8	
	2000	10	-6.1*	0.6**	-0.005†	-2.7**	
	2001	9	-7.0**	0.7**	-0.003	-2.0	
Ice Harbor to Lower Granite^2							
Sp-Su Chinook	1996	5	3.1		-0.005	4.1*	
	1997	7	2.3*		-0.003	1.4*	
	1998	7	1.4		-0.006*	1.4	
	2000	7	-1.1		0.002	-0.7	
	2001	8	0.8		0.001	0.4	
Steelhead	1996	11^2	4.1	-0.3	-0.021	0.4	

1997	9	13.6*	-0.8*	-0.062	17.5†	-0.5†
2000	10	8.2*	-0.4*	-0.297	10.1†	-0.3†
2001	12[2]	4.0	-0.2	-0.532*	15.9†	-0.5†

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[1] 1998 Fall Chinook salmon data excluded because only 3 semimonthly blocks were represented

[2] Temperature data unavailable at Ice Harbor Dam for part of fall 1996 and 2001

$^{\dagger}P \le 0.10$ $^{*}P \le 0.05$ $^{**}P \le 0.005$

Appendix 2. Regression coefficients and significance levels for weighted regression models where semimonthly migration times past dams (d) were dependent and migration timing (semimonthly block), river discharge, and water temperature were predictors. Results from linear models presented except when quadratic models provided better fit for fall chinook and steelhead (timing and temperature only). All models weighted by the number of fish in each block.

			Timing		Discharge	Temperature	
Reach and run		Blocks	β_1	β_2	β_1	β_1	β_2
Bonneville Dam							
Sp-Su Chinook	1996	7	-0.3		-0.000	-0.2	
	1997	8	-0.3*		-0.000	-0.2*	
	1998	7	-0.1*		-0.000	-0.0**	
	2000	9	-0.2**		0.000†	-0.1**	
	2001	8	-0.3*		-0.000	-0.2**	
Fall Chinook	1998	4	0.1		-0.001	-0.1	
	2000	6	0.1†		-0.000	-0.1†	
	2001	6	0.0		-0.000	-0.0	
Steelhead	1996	8	-0.0		0.000	-0.5*	0.0*
	1997	8	-0.0		0.000	0.0	
	2000	9	-0.1†		0.000†	0.0	
	2001	12	-0.0		-0.000	-0.0	
The Dalles Dam[1]							
Sp-Su Chinook	1996	7	-0.3†		-0.000	-0.2	
	1997	8	-0.7**		0.000	-0.4*	
	1998	8	-0.2*		-0.000	-0.1*	
	2000	9	-0.1*		0.000	-0.1*	
	2001	9	-0.1**		0.000	-0.0**	
Fall Chinook	1998	6	0.0		-0.000		
	2000	8	0.0		-0.000†		
	2001	6	0.1		-0.000		
Steelhead	1996	10	0.0		-0.000		
	1997	10	-0.0		0.000		
	2000	11	0.0		0.000		
	2001	13	-0.0*		0.000		
John Day Dam[1]							
Sp-Su Chinook	1996	7	0.2		0.000	0.1	
	1997	8	-0.6		0.000	-0.3	
	1998	8	-0.1		0.000	-0.1†	
	2000	9	0.1		-0.000	0.0	
	2001	9	0.0		-0.000†	-0.0	
Fall Chinook	1998	5	0.1†		-0.001		
	2000	8	0.0		0.003		
	2001	6	-0.9*	0.2*	-0.000		
Steelhead	1996	11	-0.8	0.1	0.000		
	1997	12	-0.6	0.0	-0.000		
	2000	12	-0.0		0.000		
	2001	13	-0.1*		0.000		
McNary Dam							
Sp-Su Chinook	1996	7	-0.3†		-0.000*	-0.2†	
	1997	9	-0.1		-0.000	-0.1	

	1998	8	-0.1*		0.000	-0.1*	
	2000	10	-0.1*		0.000*	-0.1**	
	2001	9	-0.0		-0.000	-0.0	
Fall Chinook	1998	5	0.1		-0.001	-0.0	
	2000	8	0.1		0.000	-0.0	
	2001	6	-0.0		0.000†	0.0	
Steelhead	1996	10	-0.0		0.000†	0.0	
	1997	12	-0.2†	0.0†	-0.000	-0.0	
	2000	12	-0.3†	0.0*	0.000	-0.0	
	2001	12	-0.0		0.000	-0.4*	0.0*
Ice Harbor Dam[2]							
Sp-Su Chinook	1996	7	-0.1		0.001	-0.3	
	1997	7	0.0		0.000	-0.0	
	1998	7	-0.1		0.000	-0.2	
	2000	8	0.0		-0.000	0.0	
	2001	8	-0.0		0.000†	-0.0	
Steelhead	1996	12	-0.1	0.0	0.000		
	1997	11	-0.5†	0.0†	0.000	-0.7*	0.0*
	2000	12	-0.3**	0.0**	0.000†	-0.1†	0.0†
	2001	12	-0.2**	0.0**	0.001*	-0.2	0.0
Lower Monumental Dam[1]							
Sp-Su Chinook	1997	7	-0.1		0.000	-0.1	
	1998	7	-0.1		0.001†	-0.1	
	2000	7	0.1*		-0.000†	0.0*	
	2001	7	0.0		-0.000	0.0	
Steelhead	1997	11	-0.4*	0.0*	-0.000		
	2000	10	-0.5*	0.0*	0.000		
	2001	13	-0.1	0.0†	0.000		
Little Goose Dam[1]							
Sp-Su Chinook	1997	7	0.1		0.000	0.0	
	1998	7	-0.0		0.001	-0.1	
	2000	6	0.1		-0.000	0.0	
	2001	7	-0.0		0.000*	-0.0	
Steelhead	1997	11	-0.8**	0.0**	0.000		
	2000	9	-0.3	0.0	-0.000		
	2001	12	-0.1*		0.001		
Lower Granite Dam[1]							
Sp-Su Chinook	1996	6	0.2		-0.000	0.1	
	1997	8	0.0		0.000	0.0	
	1998	7	0.0		0.000	-0.0	
	2000	6	0.2†		-0.000	0.1	
	2001	7	0.0		-0.000	0.0	
Steelhead	1996	9	0.2		0.001		
	1997	9	-1.1†	0.1†	-0.000		
	2000	9	-1.8*	0.1*	-0.005		
	2001	11	0.0*		-0.000		

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[1] Temperature data unavailable during fall at The Dalles, John Day, L. Monumental, L.Goose, and L. Granite dams

[2] No results presented for fall Chinook salmon at Snake River dams due to small samples

$^{\dagger}P \leq 0.10$ $^{*}P \leq 0.05$ $^{**}P \leq 0.005$

Appendix 3. Regression coefficients and significance levels for weighted regression models where semimonthly migration rates through reservoirs (km•d^{-1}) were dependent and migration timing (semimonthly block), river discharge, and water temperature were predictors. Results from linear models presented except when quadratic models provided better fit for fall chinook and steelhead (timing and temperature only). All models weighted by the number of fish in each block.

			Timing		Discharge	Temperature	
Reach and run		Blocks	β_1	β_2	β_1	β_1	β_2
Bonneville reservoir							
Sp-Su Chinook	1996	7	5.9^{**}		0.000	4.0^{*}	
	1997	8	5.5^{**}		-0.002	3.3^{**}	
	1998	8	1.3		-0.000	0.8	
	2000	9	5.0^{**}		$-0.006^{\dagger}$	3.2^{**}	
	2001	9	3.7^{*}		0.003	2.3^{**}	
Fall Chinook	1998	4	2.0		-0.016	-1.1	
	2000	8	0.4		-0.011	-0.4	
	2001	7	-13.2	1.7	-0.009	-1.9	
Steelhead	1996	9	-23.6^{*}	2.1^{*}	0.001	-5.8^{*}	
	1997	9	-28.6^{*}	2.3^{*}	$0.004^{\dagger}$	-5.5^{**}	
	2000	10	$-18.0^{\dagger}$	1.6^{*}	-0.005	-5.2^{**}	
	2001	11	-31.4^{*}	2.8^{**}	-0.010	-10.0^{**}	
The Dalles reservoir[1]							
Sp-Su Chinook	1996	7	3.7^{**}		-0.000	2.6^{**}	
	1997	8	4.1^{**}		-0.002	2.5^{**}	
	1998	8	2.5^{**}		-0.000	1.5^{**}	
	2000	9	4.0^{**}		-0.005^{**}	2.5^{**}	
	2001	9	4.2^{**}		0.001	2.4^{**}	
Fall Chinook	1998	5	5.8		-0.042		
	2000	8	-3.0		-0.007		
	2001	8	-1.7^{*}		0.007		
Steelhead	1996	10	-12.0^{**}	0.9^{**}	0.002^{*}		
	1997	10	-3.9	0.3	0.001		
	2000	12	-0.5		0.002		
	2001	13	-7.5	0.7	-0.001		
John Day reservoir[1]							
Sp-Su Chinook	1996	6	1.2		0.000	0.7	
	1997	8	2.0^{*}		-0.001	1.2^{*}	
	1998	8	1.5^{*}		-0.000	1.0^{**}	
	2000	9	2.2^{**}		-0.003^{*}	1.3^{**}	
	2001	9	3.2^{*}		-0.001	1.7^{**}	
Fall Chinook	1998	4	-1.6		0.011		
	2000	8	-15.1^{*}	1.4^{*}	0.019^{*}		
	2001	7	-4.2	0.6	0.006		
Steelhead	1996	10	-0.4		0.000		
	1997	10	6.8^{*}	-0.6^{*}	0.001		
	2000	12	$6.5^{\dagger}$	-0.8^{*}	0.006		
	2001	12	-0.6		0.002		
McNary reservoir[2]							
Sp-Su Chinook	1996	6	2.2		-0.002	1.4	
	1997	8	$2.9^{\dagger}$		-0.001	$1.8^{\dagger}$	

	1998	8	3.0^{*}		0.001	2.0^{*}	
	2000	7	4.2^{**}		-0.006^{**}	2.4^{**}	
	2001	7	3.2^{*}		$0.011^{\dagger}$	$1.7^{\dagger}$	
Fall Chinook	1998	5	-4.2		0.045	1.8	
	2000	9	-21.4^{**}	2.3^{**}	$0.019^{\dagger}$	-21.4^{**}	0.7^{**}
	2001	8	-18.1^{*}	1.6	0.033^{*}	-36.0^{*}	1.1^{*}
Steelhead	1996	13	$11.4^{\dagger}$	-0.5	-0.007^{*}		
	1997	12	9.0^{*}	-0.6^{*}	0.000	1.0	
	2000	12	1.5		-0.007	7.8	-0.3
	2001	14	0.2		-0.003	-4.4	0.2
Ice Harbor reservoir[3]							
Sp-Su Chinook	1996	5	2.3		-0.005	5.0	
	1997	7	2.8		-0.005	$1.9^{\dagger}$	
	1998	7	3.1^{*}		-0.003	2.1^{*}	
	2000	7	1.7		-0.005	0.8	
	2001	8	2.7		-0.003	1.5	
Steelhead	1997	11	$11.4^{\dagger}$	-1.0^{*}	0.020^{*}	3.2^{**}	
	2000	11	$6.8^{\dagger}$	-0.5^{*}	0.008	1.2^{*}	
	2001	12	$1.3^{\dagger}$		-0.014	-0.6	
Lower Monumental reservoir[1]							
Sp-Su Chinook	1997	7	4.7^{*}		-0.007^{*}	3.0^{**}	
	1998	7	1.8		-0.000	1.3	
	2000	6	3.0^{*}		-0.011^{*}	$1.8^{\dagger}$	
	2001	7	3.6		0.002	2.0	
Steelhead	1997	11	15.4^{*}	-1.0^{*}	0.004		
	2000	10	11.8^{*}	-0.8^{*}	0.018		
	2001	12	6.6^{*}	$-0.3^{\dagger}$	$-0.022^{\dagger}$		
Little Goose reservoir[1]							
Sp-Su Chinook	1997	7	4.1^{*}		-0.006^{*}	2.4^{*}	
	1998	7	1.8		$-0.005^{\dagger}$	1.4	
	2000	6	5.1^{*}		-0.019^{**}	3.3^{**}	
	2001	7	3.7		0.000	2.0	
Steelhead	1997	11	15.3^{*}	-1.1^{*}	0.018		
	2000	8	-4.7^{**}		$0.064^{\dagger}$		
	2001	12	8.2	-0.5	$-0.043^{\dagger}$		
Lower Granite reservoir[1] (to Snake River receiver)							
Sp-Su Chinook	1996	6	9.5^{**}		$-0.008^{\dagger}$	3.7^{*}	
	1997	8	$6.3^{\dagger}$		-0.005	$3.2^{\dagger}$	
	1998	7	4.3^{*}		-0.003	$2.1^{\dagger}$	
	2000	7	1.2		-0.003	0.6	
	2001	7	$3.1^{\dagger}$		-0.001	1.2	
Steelhead	1996	11	7.9	-0.5	0.004		
	1997	9	0.8		0.000		
	2000	9	29.9^{*}	$-1.5^{\dagger}$	0.045		
	2001	12	3.5^{*}		-0.007		
Lower Granite reservoir[1] (to Clearwater River receiver)							
Sp-Su Chinook	1996	3	18.5		-0.017	10.2	
	1997	7	6.0		-0.004	1.7	
	1998	7	7.0		-0.003	3.4	
	2000	5	12.0^{*}		-0.037	$6.0^{\dagger}$	
	2001	4	$23.2^{\dagger}$		-0.052	13.0	

Steelhead	1996	10	0.7		-0.006
	1997	7	-3.9*	0.3*	-0.006*
	2000	7	0.4		0.002
	2001	11	1.3		0.010

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[1] Temperature data unavailable during fall at The Dalles, John Day, L. Monumental, L.Goose, and L. Granite dams

[2] McNary reservoir to Ice Harbor tailrace for spring-summer Chinook salmon and steelhead and to Hanford reach for fall Chinook salmon

[3] No results presented for fall Chinook salmon at Snake River reservoirs due to small samples

$^{\dagger}P \le 0.10$ $^{*}P \le 0.05$ $^{**}P \le 0.005$