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ESCAPEMENT, HARVEST, AND UNACCOUNTED-FOR LOSS OF RADIO-TAGGED ADULT CHINOOK SALMON AND STEELHEAD IN THE COLUMBIA-SNAKE RIVER HYDROSYSTEM, 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; 1998). 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 hydrosystem-wide and reach-specific (dam-to-dam) escapement, harvest, and unaccounted-for loss. We examine within- and between-year variation in escapement, compare escapements for known-source (PIT-tagged) stocks, and evaluate how broad-scale river environment and fallback behavior affected escapement patterns.

This and related reports from this research project can be downloaded from the website: http://www.cnr.uidaho.edu/uiferl/

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Abstract

Accurate estimates of escapement by adult anadromous salmonids are difficult, especially in large, multi-stock river systems. We used radiotelemetry, a fishery reward program, and help from cooperating agencies and hatcheries to calculate escapement, harvest, and unaccounted-for loss rates for 10,498 adult Chinook salmon (*Oncorhynchus tshawytscha*) and 5,324 steelhead (*O. mykiss*) during six migration years in the Columbia River basin. Mean annual escapements to spawning sites, hatcheries, or the upper bounds of the monitored hydrosystem (top of Lower Granite or Priest Rapids dams) were 73.4% (spring–summer Chinook salmon), 61.3% (fall Chinook salmon) and 62.6% (steelhead). Mean reported harvest rates were 8.7% (spring–summer Chinook), 22.0% (fall Chinook) and 15.1% (steelhead) within the mainstem hydrosystem, and 5.9, 3.4 and 5.7%, respectively, in lower hydrosystem tributaries. Harvest-adjusted escapement means for the monitored hydrosystem were 87.5% (spring–summer Chinook), 86.7% (fall Chinook), and 83.4% (steelhead). On average, 12 to 17% of each run had unknown fates within the mainstem hydrosystem.

Escapement, harvest, and loss varied significantly between runs and years, within annual runs, among known-source (PIT-tagged) stocks, and between inter-dam river reaches. Reach escapements tended to be lowest through the Bonneville-The Dalles reach, and increased as fish progressed upstream through the lower Columbia River. Reach escapements were highest in the lower Snake River. Escapement differences among known-source stocks—and between known-source and the randomly-collected unknown-source groups—were statistically significant in some years.

Fallback at dams had a consistently negative impact on escapement. For randomly-collected groups, decreases in harvest-adjusted escapement averaged 6.5% for spring–summer Chinook salmon, 19.5% for fall Chinook salmon, and 13.2% for steelhead that fell back. Fallback impacts on known-source groups were generally similar to the randomly-collected groups, except decreases were higher for Snake River spring–summer Chinook (*mean* = 15.8% decrease). Fallback was associated with negative population-level impacts on escapement ranging from 1 to 4%. Annual spring–summer Chinook salmon escapement was negatively correlated with Columbia River discharge, but not temperature. In contrast, fall Chinook and steelhead escapements were not correlated with either discharge or temperature metrics.

This multi-year quantitative assessment should provide managers a comprehensive review of adult salmonid fates within the federal hydrosystem. The results reduce uncertainty, clarify inter- and intra-annual variability, and can help managers better evaluate fisheries, operate the hydrosystem, identify conservation priorities, and help protect evolutionarily significant populations.

Introduction

The study described here was undertaken because of concerns of the U.S. Army Corps of Engineers (USACE), state, federal, and tribal fish agencies, those expressed in section 603 of the Northwest Power Planning Council (NPPC) 1987 Columbia River Basin Fish and Wildlife Program, and later reflected in the Biological Opinions issued in 1995, 1998, and 2000 for operation of the Federal Columbia River Power System. These agencies and opinions recommended studies to ensure that adult salmon and steelhead passage past dams and through reservoirs was as efficient as possible. Results presented here specifically relate to questions of survival, unaccounted-for loss, fallback, and the effects of river environment as outlined in the 2000 Biological Opinion, Action 107 (National Marine Fisheries Service [NMFS] 2000). Study plans were developed in consultation with USACE personnel, and with biologists in other federal, state, and tribal agencies. Research was conducted by the Idaho Cooperative Fish and Wildlife Research Unit (ICFWRU) and National Marine Fisheries Service (NMFS – NOAA Fisheries). Logistical support, cooperation, and funding came from USACE, Bonneville Power Administration (BPA), and the U.S. Geological Survey.

The Columbia River and its largest tributary—the Snake River—were historically among the most productive anadromous salmonid *Oncorhynchus* spp. river systems in the world (Chapman 1986; Nemeth and Kiefer 1999), with pre-development annual runs estimated at between 10 and 16 million adult fish (Northwest Power Planning Council [NWPPC] 1986). A combination of habitat loss, water diversion, hatchery propagation, excessive harvest, and development of the federal hydrosystem decimated many of the runs (National Research Council 1996; McClure et al. 2003). Numerous Columbia basin stocks are extinct (Nehlsen et al. 1991), and 12 salmon and steelhead *O. mykiss* populations are currently listed as threatened or endangered under the U.S. Endangered Species Act (ESA) (NMFS 2000).

Ensuring adequate adult escapement to natal spawning grounds is critical for managing extant stocks and for re-establishing suppressed or locally extinct populations. Fish counts, performed on returning adult migrants while passing Columbia and Snake River dams, are good relative indicators of annual aggregated run size, but spawning escapement has remained difficult to accurately measure (Dauble and Mueller 1993; 2000). Several factors confound escapement estimates, including counting errors, uncertainties associated with commercial, tribal, sport, and illegal fisheries, problems quantifying inter-dam tributary turnoff, undetected mainstem spawning, temporary or permanent inter-basin straying, and fish fallback and reascension at dams. Given the federal mandate to protect ESA-listed runs, clarification of these and other uncertainties identified in the Biological Opinion on operation of the Federal Columbia River Hydrosystem (NMFS 2000) are among the priorities for agencies involved in the Columbia River salmon and steelhead recovery process (National Research Council 1996; Independent Scientific Advisory Board [ISAB] 2001).

Radiotelemetry has been a useful tool for determining passage timing, spatial distribution and movement patterns, and ultimate fates of large numbers of individually-marked migratory salmonids (Skalski et al. 2001; Wuttig and Evenson 2001; McPherson et al. 2003; Keefer et al. 2004a; 2004b). Mobile and fixed radiotelemetry arrays can passively monitor tagged fish at sites where access is difficult or traditional sampling methods are unrealistic (Eiler 1990; 1995). High transmitter return rates can be achieved through fishery reward programs and cooperative agreements with management agencies (e.g., Bjornn et al. 2000d, 2003; Keefer et al. 2004c). Telemetry methods are particularly effective in river systems where upstream migrants pass through constricted areas like fish ladders at hydroelectric dams (Gerlier and Roche 1998; Gowans et al. 1999) or when fish disperse over wide, but accessible geographic areas (Milligan et al. 1985; Keefer et al. 2002).

To address a wide range of salmon and steelhead migration and passage questions (e.g., Bjornn et al. 2000a-c; Goniea 2002; High 2002; Keefer et al. 2003a; Reischel and Bjornn 2003; Boggs et al. 2004b) we radio-tagged and monitored almost 16,000 adult Chinook salmon and steelhead from 1996 to 2002. All fish were collected at Bonneville Dam, the first hydroelectric project fish encounter after leaving the Pacific Ocean. Our objectives were to examine upstream passage behavior, distribution to tributaries and hatcheries, and escapement through the federal hydrosystem. In this report, we present estimates of dam-to-dam and hydrosystem-wide escapement, along with reach-specific harvest and loss rates for Chinook salmon and steelhead runs and for selected known-source sub-basin populations. We also examine the influence of seasonal river discharge and temperature, and the effects of fallback on annual escapement estimates.

Methods

Fish trapping, tagging, and monitoring

Adult steelhead and spring, summer, and fall Chinook salmon were trapped at Bonneville Dam (river kilometer 235) in the adult fish facility (AFF) adjacent to the Washington-shore fish ladder as they migrated upstream in the Columbia River (Figure 1). Each day fish were tagged, a weir was lowered into the ladder to divert fish into the AFF via a short secondary ladder. Once inside the facility, fish were either diverted into anesthetic tanks for tagging or returned to the main ladder without handling.

During six study years, radio transmitters were placed in a total of 15,822 adult fish: 6,290 spring–summer Chinook salmon (six years), 4,208 fall Chinook salmon (four years) and 5,324 steelhead (five years; Table 1). On average, radio-tagged samples represented 0.78% of spring–summer Chinook salmon, 0.40% of fall Chinook salmon, and 0.26% of steelhead counted passing Bonneville Dam each year (USACE 2002). Fish were tagged throughout each run in approximate proportion to long-term average counts at Bonneville Dam; variability in daily counts and annual run timing precluded precise proportional sampling. Due to high water temperatures, no summer Chinook were tagged in July 1996 and no fall Chinook were tagged in August 1998.

Protocols for fish trapping, handling, intragastric insertion of radio transmitters, and fish recovery were the same in all years and were described in Keefer et al. (2004c). As much as possible, spring–summer Chinook salmon and steelhead were non-selectively tagged as they were trapped from 1996 to 1998. Samples were not truly random because only fish passing via the Washington-shore ladder were sampled, proportions sampled each day varied, and no fish were sampled at night. To accommodate transmitter sizes (see Keefer et al. 2004c for transmitter types and dimensions), we also did not tag jack (precocious adult) salmon or steelhead with fork length < 50 cm. Among fall Chinook salmon, we selected for ‘upriver-bright’ fish—a group that spawns mostly in the Hanford Reach of the Columbia River, the Snake River, or the Deschutes River—and limited

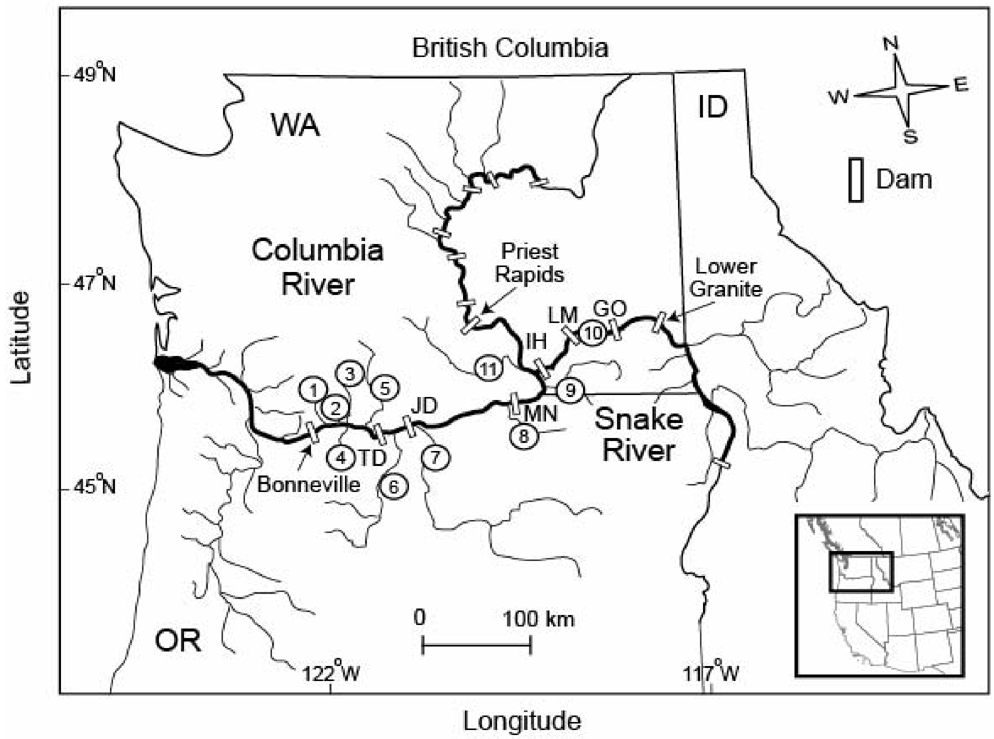

Figure 1. The Columbia and Snake rivers, showing dams monitored with radiotelemetry. For this study, the hydrosystem was bounded by Bonneville, Lower Granite, and Priest Rapids dams. Other monitored dams: The Dalles (TD), John Day (JD), McNary (MN), Ice Harbor (IH), Lower Monumental (LM), and Little Goose (GO). All major Columbia River tributaries upstream from Bonneville Dam were monitored with radio antennas: 1) Wind, 2) Little White Salmon, 3) White Salmon, 4) Hood, 5) Klickitat, 6) Deschutes, 7) John Day, 8) Umatilla, 9) Walla Walla, 10) Snake, and 11) Yakima.

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							
Sp/Su 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							
Sp/Su 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

our collection of sexually mature 'Tule' fall Chinook salmon. Tules return only a short distance upstream to Bonneville reservoir hatcheries (Myers et al. 1998), and during times of high Tule passage we selected against these fish to ensure adequate sample sizes at upstream projects.

In 2000-2002, tagging methods were modified to include use of an automated system (McCutcheon et al. 1994) that identified fish with passive integrated transponder (PIT) tags as they passed through the AFF trap. PIT tags indicated if and where fish were tagged as juveniles (referred to here as "known-source" fish because their natal sites were known), and use of PIT-tagged fish allowed us to make stock-specific harvest, escapement, and unaccounted-for loss estimates. Only approved groups of PIT-tagged fish were available for radio-tagging, and codes for those fish were imported into the automatic detection system in the trap. We attempted to radio tag as many known-source fish as possible within the 2000-2002 tagging schedules. Known-source fish were radio-tagged as they were trapped, and fish without PIT tags made up the remainders of each daily sample. The proportions of 2000, 2001, and 2002 radio-tagged fish that had been PIT-tagged as juveniles were: 6, 70, and 37% (spring–summer Chinook), < 1, 13, and 6% (fall Chinook), and < 1, 61, and 46% (steelhead), respectively (Table 2). To differentiate from known-source groups, unselectively-collected fish without juvenile PIT tags are referred to as 'unknown-source' in this report. Fish PIT-tagged as juveniles at lower Columbia River dams were included in the 'unknown-source' group because their natal sites were unknown. Similarly, very small samples (i.e., $n < 5$/site) of known-source fish from lower Columbia tributaries were included in the 'unknown-source' group. This treatment did not affect results.

Table 2. Number of radio-tagged adult salmon and steelhead of known origin, as identified by PIT tags implanted when fish were juveniles. Groups with samples < 10 were not used in statistical tests and were included in the unknown-source category. See Figure 1 for source locations.

	Downstream releases			Forebay releases		
	2000	2001	2002	2000	2001	2002
<u>Spring–Summer Chinook</u>						
Wind River[1]		17	35		12	14
John Day River			13			2
Snake River	28	348	168		125	19
Yakima River		92	66		28	32
Upper Columbia River[2]	37	105	73		37	26
Other[3]	1	8	1		7	2
<u>Fall Chinook</u>						
Snake River	5	26	36	2	36	3
Other[3]	2	35	16	1	33	4
<u>Steelhead</u>						
Snake River	6	239	370	1	123	66
Upper Columbia River[2]	2	186	84		141	56
Other[3]		11	6		2	5

[1] All fish PIT-tagged at Carson National Fish Hatchery
[2] Upstream from Priest Rapids Dam
[3] Fish in 'other' category were tagged at multiple sites, primarily lower Columbia dams and tributaries, and were included in the unknown-source samples

Several secondary markers were used to help identify fish that lost transmitters during the study period. From 1996 to 1998, each radio-tagged fish had a coded wire tag injected into the dorsal sinus and a unique alphanumeric visible implant (VI) tag inserted into the clear tissue posterior to one eye. VI tags were also used in 2000, and a new PIT tag was inserted into the abdominal cavity of most fish that had not been PIT-tagged as juveniles. In 2001 and 2002, PIT tags (original or newly-inserted) were used exclusively as secondary markers. Based on inspections at Lower Granite Dam, radio transmitter loss averaged 3.0% for spring–summer Chinook salmon, 2.2% for fall Chinook salmon, and 4.0% for steelhead (Keefer et al. 2004c).

After tagging and recovery from anesthesia, all radio-tagged fish in 1996-1998 were released about 9.5 km downstream from Bonneville Dam at sites on both sides of the Columbia 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. 2004b). Downstream release locations were the same in all years, so we primarily present results for fish released at those sites. To reduce bias related to radio tagging, including permanent downstream movement or mortality (e.g., Bernard et al. 1999), downstream-released fish that did not reascend fishways at Bonneville Dam were excluded from analyses. Exclusion of non-reascending fish differed from methods in some previous escapement summaries (e.g., Bjornn et al. 2000d), but we believe this method was warranted to standardize results for comparison between species, years, and known-source groups. Because a similar criterion could not be employed for forebay-released fish, those fish were treated separately and were principally used to validate results from downstream releases when samples were adequate.

Radio-tagged fish were monitored with an extensive array of aerial and underwater antennas at Columbia and Snake River dams and tributaries (Appendix 1). Telemetry coverage generally increased over the course of the study as research objectives evolved and additional Columbia and Snake River monitoring sites were installed. Passage was continuously monitored at the four lower Columbia River dams and at Priest Rapids Dam on the upper Columbia River in all years, and at the four lower Snake River dams in all years except 1996, when only Ice Harbor and Lower Granite dams were monitored. Fixed aerial antennas were installed in all major Columbia River tributaries between Bonneville and Priest Rapids Dams except the Umatilla River in 1996. Additional tributaries downstream from Bonneville Dam had aerial antennas only in 1996 and 1998. Aerial antennas were also in primary and secondary Snake River tributaries upstream from Lower Granite Dam in all years except 1996 (only the Clearwater and Snake rivers were monitored in 1996, at the upper end of Lower Granite reservoir). Data from fixed aerial and underwater antennas were supplemented with data collected while surveying segments of the basin from boats or trucks mounted with receivers and aerial antennas. More complete descriptions of antenna types and locations are included in Keefer et al. (2002).

Fish fate and escapement estimation

Final fish distributions were assessed from the combination of telemetry records from fixed sites, mobile tracking efforts in tributaries and reservoirs, and transmitter returns from hatcheries, fish traps, and spawning ground surveys conducted by cooperating agencies. Transmitters were also returned from commercial, sport, and tribal fisheries through a reward program. Standard reward values printed on all transmitters were US$25 in all years except 1996, when it was US$10. US$100 rewards were offered for return of a sub-sample of 12 to 19% of the transmitters used in 2000-2002. PIT-tag detectors installed in fishways at Lower Granite and other dams provided additional passage data in the later years of the study for fish that may have regurgitated transmitters. This extra monitoring had negligible effect on fate determination for Chinook salmon, but changed fate designations for 1 to 3% of steelhead from 2000 to 2002.

From the above data sources, fates for radio-tagged fish were arranged into six basic categories: fish either 1) passed the upstream extent of the study area for this analysis (Lower Granite or Priest Rapids dams), 2) were reported harvested in a mainstem fishery, 3) entered a tributary (or the Hanford Reach spawning grounds for fall Chinook salmon), 4) were reported harvested in a tributary fishery, 5) entered a hatchery or trap, or 6) had unknown fate (Table 3). Fish that passed Lower Granite or Priest Rapids dams were considered to have escaped the monitored hydrosystem regardless of subsequent downstream movement.

Table 3. Notation used in escapement calculations.

Entered reach *i*	E_i		
Passed[1] reach *i*	P_i		
		Fish was last recorded:	
		within reach *i*	downstream from reach *i*
Mainstem fishery		MF_i	MF_d
Tributary		T_i	T_d
Tributary fishery		TF_i	TF_d
Hatchery/trap		H_i	H_d
Unknown fate		U_i	U_d
Escapement 1	Esc_1	$= (P_i + T_i + T_d + H_i + H_d) \bullet (E_i)^{-1}$	
Escapement 2	Esc_2	$= (P_i + T_i + T_d + H_i + H_d + TF_i + TF_d) \bullet (E_i)^{-1}$	
Escapement 3	Esc_3	$= (P_i + T_i + T_d + H_i + H_d + TF_i + TF_d + MF_i + MF_d) \bullet (E_i)^{-1}$	

[1] Subsequent downstream movement ignored

Fate summaries were used to estimate escapement values for the entire hydrosystem and for specific river segments containing an individual dam and reservoir complex (dam-to-dam reach) for each species and run-year and for subsets of the tagged fish based on release site, release dates, and known-source groups. Individual reaches were bounded by the tops of dam fishways. For example, the Bonneville-The Dalles reach started when fish exited the top of a Bonneville Dam fishway (or were released into the Bonneville Dam forebay) and ended with an exit from the top of a fishway at The Dalles Dam. In this study, the hydrosystem was bounded by the tops of Bonneville Dam, Lower Granite Dam (the most upstream Snake River dam with fish passage), and Priest Rapids Dam (the most upstream Columbia River dam monitored in all years). As a result, passage at Bonneville Dam and through the Lower Granite reservoir was not included in escapement estimates.

Managers use escapement indices for multiple purposes and within different jurisdictions (e.g., for tributary versus mainstem fisheries), so we elected to calculate three estimates with progressively less stringent criteria for defining successful escapement. Escapement 1 (Esc_1) was the most basic and most stringent measure and best matches the traditional definition of the term in which all fish harvested from mainstem or tributary sites (downstream from Lower Granite and Priest Rapids dams) and all fish with unknown fates did not escape (Table 3). Esc_1 was an inappropriate measure for between-group comparisons because stocks originating upstream from Lower Granite or Priest Rapids dams had limited exposure to tributary fisheries downstream from these dams and we did not include harvest upstream from those sites. Escapement 2 (Esc_2) treated fish harvested in hydrosystem tributaries as successful, but mainstem-harvested fish as unsuccessful, and was therefore a measure of total escapement to tributaries or the upper bounds of the monitored hydrosystem. Escapement 3 (Esc_3) treated all harvested fish as successful (i.e., mortality was not associated with hydrosystem operations), and only fish with unknown fates within the hydrosystem were considered unsuccessful. Esc_3 eliminated variability associated with harvest and was therefore the best possible measure of underlying between-year, between-run, and between-stock differences in escapement. Esc_3 also approximated potential escapement through the monitored hydrosystem in the absence of fisheries. In all estimates, fish that passed the upstream end of a reach or the hydrosystem were considered to have escaped, regardless of subsequent downstream movement.

Because there is interest among managers in hydrosystem-wide escapement estimates that include the area at and downstream from Bonneville Dam, we also calculated Esc_3 estimates for known-source groups starting at the time of release downstream from the dam, at time of Bonneville tailrace entry, and at time of Bonneville Dam fishway approach and entry. These estimates compliment the overall escapement summary, but should not necessarily be used as substitutes because our monitoring efforts downstream from the dam were limited; radio transmitter loss and the very limited number of handling mortalities also tended to occur during the time immediately following release, introducing potential bias for estimates for this section of the migration.

We calculated 95% profile likelihood confidence intervals (Lebreton et al. 1992) for each escapement estimate using the mark-recapture software program MARK (White and Burnham 1999). Profile likelihood intervals are asymmetric and appropriate when parameters, like escapement, are bounded by [0,1] (Lebreton et al. 1992). Program MARK was also used to compare escapement estimates (Esc_2 and Esc_3 only – comparison of Esc_1 estimates were potentially misleading given stock distributions) for groups of tagged fish, again focusing on downstream-released fish. Null models that assumed constant escapement within a run-year or across multiple years were compared to models that assumed variable escapement through time. Likelihood ratio tests (LRT) were used to evaluate competing models (White and Burnham 1999) along with χ^2 tests to quantify statistical differences between fish groups (e.g., based on juvenile PIT-tag site, adult release location, or adult release timing). The addition of PIT-tag detectors at Lower Granite and other dams resulted in some changed fish fate designations in later years, so between-year and between-group statistical comparisons of escapement were based on telemetry and recapture data only (PIT data ignored) to reduce bias associated with changes in methodology.

River environment and fallback analyses

Linear regression was used to examine relationships between river environment variables and annual escapement and harvest estimates for the unknown-source groups. Independent variables were annual mean and maximum discharge and temperature collected at Bonneville Dam (http://www.cqs.washington.edu/dart/dart.html) during the date range that each run passed the dam. Run dates for Chinook salmon followed those established by USACE (2002): April-July for spring–summer Chinook salmon and August-October for fall Chinook salmon. Environmental data from June-October were used for steelhead, as the majority of this protracted run passes Bonneville Dam during that period. As with other between-year tests, only telemetry and recapture data were included in escapement estimates (i.e., PIT-tag-only detections at dams were not included). Finer-scale analyses, including individual-fish-based models of escapement, are underway and will be included in future reporting. The scope of the regression analyses presented here was intended to address broader patterns (e.g., inter-annual variability).

Many adult salmon and steelhead pass Columbia River hydrosystem dams and then fall back downstream (Bjornn et al. 2000a-c; Boggs et al. 2004a), sometimes resulting in lower escapement. We therefore compared Esc_3 estimates for fish that either did or did not fall back within both known- and unknown-source groups using Pearson χ^2 tests. The potential cumulative impact of fallback on hydrosystem escapement for each population was calculated by multiplying escapement differences by the proportion of each run (or known-source group) recorded falling back during migration.

Results

Hydrosystem escapement estimates

Unknown-source fish -- Mean hydrosystem Esc_1 estimates for all unknown-source fish released downstream from Bonneville Dam were 0.734 (*SD* = 0.015) for spring–summer Chinook salmon, 0.614 (0.035) for fall Chinook salmon, and 0.626 (0.052) for steelhead (Figure 2). Reported mainstem harvest downstream from Lower Granite and Priest Rapids dams ranged from 5 to 25% of each run, with mean rates of 8.7% (spring–summer Chinook), 22.0% (fall Chinook), and 15.1% (steelhead) (Table 4). Reported harvest in hydrosystem tributaries ranged from 2 to 10% of each run, with means of 5.9% for spring–summer Chinook salmon, 3.4% for fall Chinook salmon, and 5.7% for steelhead. Fish with unknown fates made up 5 to 16% (*mean* = 11.6%) of spring–summer Chinook salmon, 11 to 15% (13.3%) of fall Chinook salmon, and 12 to 23% (16.7%) of steelhead released at the downstream sites.

Means for Esc_2, which treated fish harvested in tributaries as escaped, were 0.792 (*SD* = 0.026) for spring–summer Chinook salmon, 0.647 (0.028) for fall Chinook salmon, and 0.683 (0.041) for steelhead. Means for Esc_3, which treated all fish harvested anywhere downstream from Lower Granite or Priest Rapids dams as successful, were 0.875 (SD = 0.042) for spring–summer Chinook, 0.867 (0.014) for fall Chinook, and 0.834 (0.038) for steelhead. In all within-year comparisons of Esc_2, spring–summer Chinook salmon escaped at higher rates ($0.0000 < P < 0.014$, χ^2 tests) than both fall Chinook salmon and steelhead, and steelhead escaped at higher rates than fall Chinook salmon ($0.022 \leq P \leq 0.051$) (Figure 2). Esc_3 estimates differed significantly in 5 of 12 within-year comparisons: spring–summer Chinook salmon escaped at higher rates than steelhead in

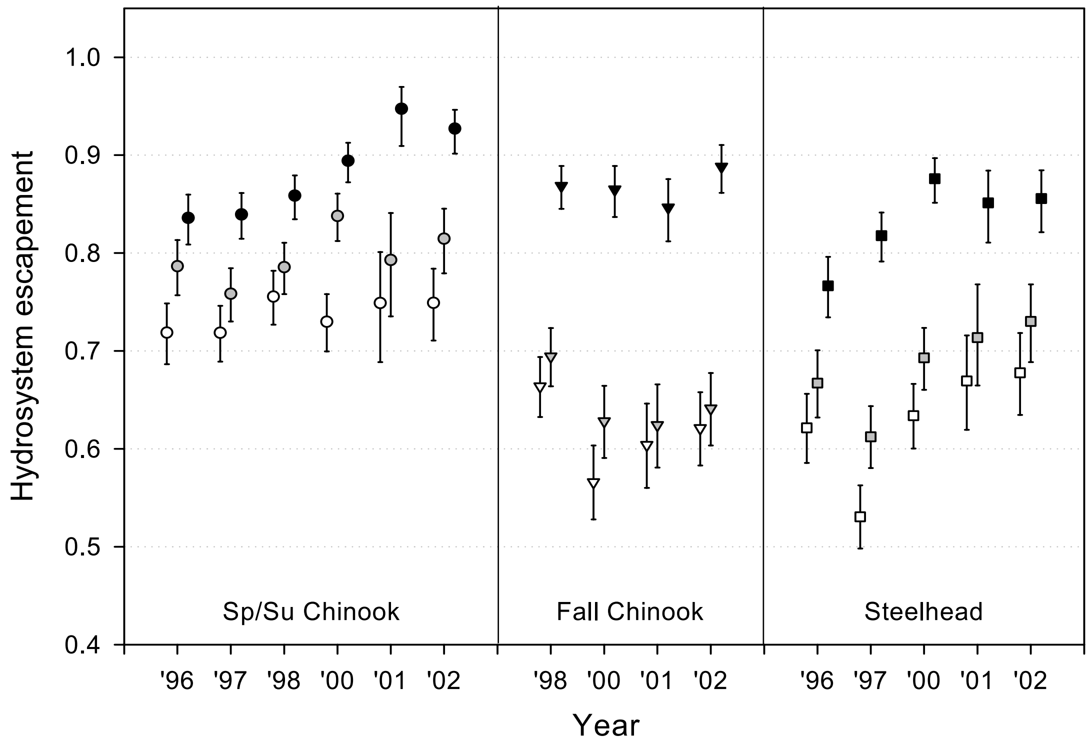

Figure 2. Annual hydrosystem (Bonneville Dam to Lower Granite or Priest Rapids dams) escapement estimates for unknown-source radio-tagged spring–summer and fall Chinook salmon and steelhead released downstream from Bonneville Dam. Open symbols = Esc_1, grey symbols = Esc_2, black symbols = Esc_3. Error bars are 95% profile likelihood confidence intervals.

1996, 2001, and 2002 ($P < 0.001$) and at higher rates than fall Chinook salmon in 2001 ($P = 0.0001$) and 2002 ($P = 0.024$).

Adult escapement was not constant between years for the three runs (Figure 2). Inter-annual variation in Esc_2 estimates was significant for spring–summer Chinook salmon ($\chi^2 = 20.21$, $df = 5$, $P = 0.001$, likelihood ratio test), fall Chinook salmon ($\chi^2 = 10.46$, $df = 3$, $P = 0.015$), and steelhead ($\chi^2 = 16.50$, $df = 4$, $P = 0.002$). Significant inter-annual differences were also found in Esc_3 estimates for spring–summer Chinook salmon ($\chi^2 = 53.84$, $df = 5$, $P < 0.0001$) and steelhead ($\chi^2 = 36.49$, $df = 4$, $P < 0.0001$), but not for fall Chinook salmon ($\chi^2 = 4.37$, $df = 3$, $P = 0.224$).

Within individual run-years (Figure 3), Esc_2 estimates varied significantly over two-week intervals ($P \leq 0.006$, likelihood ratio tests) in four of six spring–summer Chinook salmon runs (1996, 1997, 2000, 2002), all four fall Chinook salmon runs ($P \leq 0.006$), and in two of five steelhead runs (1996, 2002) ($P < 0.011$). Differences in Esc_3 estimates were significant ($P < 0.03$) within two spring–summer Chinook salmon runs (1996, 2002), two fall Chinook salmon runs (2000, 2002), and two steelhead runs (2000, 2002).

Table 4. Number of radio-tagged fish and the percent (*n*) in each fate category, with hydrosystem (top of Bonneville Dam to top of Lower Granite or Priest Rapids dams) escapement estimates for all fish released downstream (ds) from Bonneville Dam or in the Bonneville Dam forebay, for unknown-source (Unknown) stocks and for known-source stocks identified by PIT tags, 1996-2002. Includes corrections from PIT-tag-only detections at dams.

Year	Release	Stock	E_i	P_i	T_{i+d}[1]	H_{i+d}	TF_{i+d}	MF_{i+d}	U_{i+d}	Esc_1	Esc_2	Esc_3
Spring–summer Chinook salmon												
1996	ds	Unknown	810	28 (228)	27 (219)	17 (135)	7 (55)	5 (40)	16 (133)	0.719	0.786	0.836
1997	ds	Unknown	952	52 (499)	10 (95)	9 (90)	4 (38)	8 (77)	16 (153)	0.719	0.758	0.839
1998	ds	Unknown	932	46 (432)	16 (152)	13 (120)	3 (28)	7 (68)	14 (132)	0.755	0.785	0.858
2000	ds	Unknown	888	45 (396)	14 (126)	14 (126)	11 (96)	6 (50)	11 (94)	0.730	0.838	0.894
2001	ds	Unknown	227	59 (135)	10 (22)	6 (13)	4 (10)	15 (35)	5 (12)	0.749	0.793	0.947
2002	ds	Unknown	534	54 (286)	11 (61)	10 (52)	7 (36)	11 (60)	7 (39)	0.747	0.815	0.927
2000	forebay	Unknown	157	53 (83)	15 (23)	10 (15)	5 (8)	5 (8)	13 (20)	0.772	0.823	0.873
2001	forebay	Unknown	124	54 (67)	7 (9)	9 (11)	6 (8)	11 (14)	12 (15)	0.702	0.766	0.879
2002	forebay	Unknown	226	50 (112)	14 (32)	10 (23)	5 (12)	11 (24)	10 (23)	0.739	0.792	0.898
2001	ds	Wind R.	16			31 (5)	44 (7)	6 (1)	19 (3)	0.313	0.750	0.813
2002	ds	Wind R.	35		31 (11)	17 (6)	26 (9)	20 (7)	6 (2)	0.486	0.743	0.943
2001	forebay	Wind R.	12		17 (2)	42 (5)	25 (3)	8 (1)	8 (1)	0.500	0.833	0.917
2002	forebay	Wind R.	13		15 (2)	38 (5)	31 (4)	15 (2)		0.538	0.846	1.000
2002	ds	John Day R.	12		83 (10)		8 (1)		8 (1)	0.833	0.917	0.917
2000	ds	Snake R.	27	78 (21)					22 (6)	0.778	0.778	0.778
2001	ds	Snake R.	338	82 (277)	2 (6)	<1 (1)	1 (2)	11 (36)	5 (16)	0.840	0.846	0.953
2002	ds	Snake R.	165	78 (128)	1 (2)			12 (19)	10 (16)	0.788	0.788	0.903
2001	forebay	Snake R.	124	78 (97)		1 (1)	1 (1)	17 (21)	3 (4)	0.790	0.798	0.968
2002	forebay	Snake R.	19	95 (18)					5 (1)	0.947	0.947	0.947
2001	ds	Yakima R.	92		20 (18)	59 (54)	11 (10)	2 (2)	9 (8)	0.783	0.891	0.913
2002	ds	Yakima R.	65		74 (48)	3 (2)	11 (7)	9 (6)	3 (2)	0.769	0.877	0.969
2001	forebay	Yakima R.	28		14 (4)	71 (20)	11 (3)	4 (1)		0.857	0.964	1.000
2002	forebay	Yakima R.	32		75 (24)	3 (1)	9 (3)	9 (3)	3 (1)	0.781	0.875	0.969
2000	ds	Upper Col.	37	86 (32)	3 (1)			3 (1)	8 (3)	0.892	0.892	0.919
2001	ds	Upper Col.	105	86 (90)	1 (1)			3 (3)	10 (11)	0.867	0.867	0.895
2002	ds	Upper Col.	73	86 (63)				4 (3)	10 (7)	0.863	0.863	0.904
2001	forebay	Upper Col.	35	74 (26)				6 (2)	20 (7)	0.743	0.743	0.800
2002	forebay	Upper Col.	26	85 (21)				4 (1)	12 (4)	0.808	0.808	0.846

Table 4 Cont.

Year	Release	Stock	E_i	P_i	T_{i+d}[1]	H_{i+d}	TF_{i+d}	MF_{i+d}	U_{i+d}	Esc_1	Esc_2	Esc_3
Fall Chinook salmon												
1998	ds	Unknown	913	3 (28)	48 (434)	16 (144)	3 (28)	17 (159)	13 (120)	0.664	0.694	0.869
2000	ds	Unknown	659	11 (73)	39 (258)	6 (42)	6 (41)	24 (156)	14 (89)	0.566	0.628	0.865
2001	ds	Unknown	495	9 (46)	39 (191)	12 (61)	2 (11)	22 (110)	15 (76)	0.602	0.624	0.847
2002	ds	Unknown	644	9 (59)	46 (296)	7 (45)	2 (13)	25 (159)	11 (72)	0.621	0.641	0.888
2000	forebay	Unknown	371	6 (23)	37 (136)	6 (24)	3 (11)	37 (136)	11 (41)	0.493	0.523	0.890
2001	forebay	Unknown	395	10 (40)	38 (149)	11 (44)	2 (7)	22 (88)	17 (67)	0.590	0.608	0.830
2002	forebay	Unknown	307	13 (39)	39 (117)	7 (20)	3 (10)	22 (67)	18 (54)	0.573	0.606	0.824
2001	ds	Snake R.	26	77 (20)	4 (1)			12 (3)	7 (2)	0.808	0.808	0.923
2002	ds	Snake R.	34	59 (20)				24 (8)	18 (6)	0.588	0.588	0.824
2001	forebay	Snake R.	36	72 (26)				3 (1)	25 (9)	0.722	0.722	0.750
Steelhead												
1996	ds	Unknown	724	40 (290)	19 (134)	4 (26)	5 (33)	10 (72)	23 (169)	0.622	0.667	0.767
1997	ds	Unknown	916	37 (342)	12 (110)	4 (34)	8 (75)	21 (188)	18 (167)	0.531	0.612	0.818
2000	ds	Unknown	814	46 (372)	14 (118)	3 (26)	6 (48)	18 (149)	12 (101)	0.634	0.693	0.876
2001	ds	Unknown	363	51 (187)	12 (43)	4 (13)	4 (16)	14 (50)	15 (54)	0.669	0.714	0.851
2002	ds	Unknown	478	49 (234)	17 (82)	2 (8)	5 (25)	13 (60)	14 (69)	0.678	0.730	0.856
2000	forebay	Unknown	315	42 (132)	10 (33)	2 (6)	6 (18)	24 (76)	16 (50)	0.543	0.600	0.841
2001	forebay	Unknown	83	48 (40)	17 (14)	5 (4)	1 (1)	11 (9)	18 (15)	0.700	0.711	0.819
2002	forebay	Unknown	205	53 (108)	12 (25)	1 (2)	7 (15)	10 (20)	17 (35)	0.659	0.732	0.829
2001	ds	Snake R.	234	71 (166)	7 (16)		2 (4)	10 (23)	11 (25)	0.778	0.812	0.893
2002	ds	Snake R.	359	76 (274)	4 (13)		1 (2)	11 (39)	9 (31)	0.799	0.805	0.914
2001	forebay	Snake R.	122	82 (100)	3 (4)		1 (1)	7 (8)	7 (9)	0.852	0.861	0.926
2002	forebay	Snake R.	66	71 (47)	8 (5)			9 (6)	12 (8)	0.788	0.788	0.879
2001	ds	Upper Col.	183	75 (138)	4 (7)		3 (5)	9 (16)	9 (17)	0.792	0.820	0.907
2002	ds	Upper Col.	82	77 (63)	4 (3)		6 (5)	10 (8)	4 (3)	0.805	0.877	0.963
2001	forebay	Upper Col.	141	62 (88)	2 (3)		4 (5)	20 (28)	12 (17)	0.645	0.681	0.879
2002	forebay	Upper Col.	56	66 (37)			5 (3)	20 (11)	9 (5)	0.661	0.714	0.911

[1] Tributary category includes Hanford Reach spawning areas for fall Chinook salmon

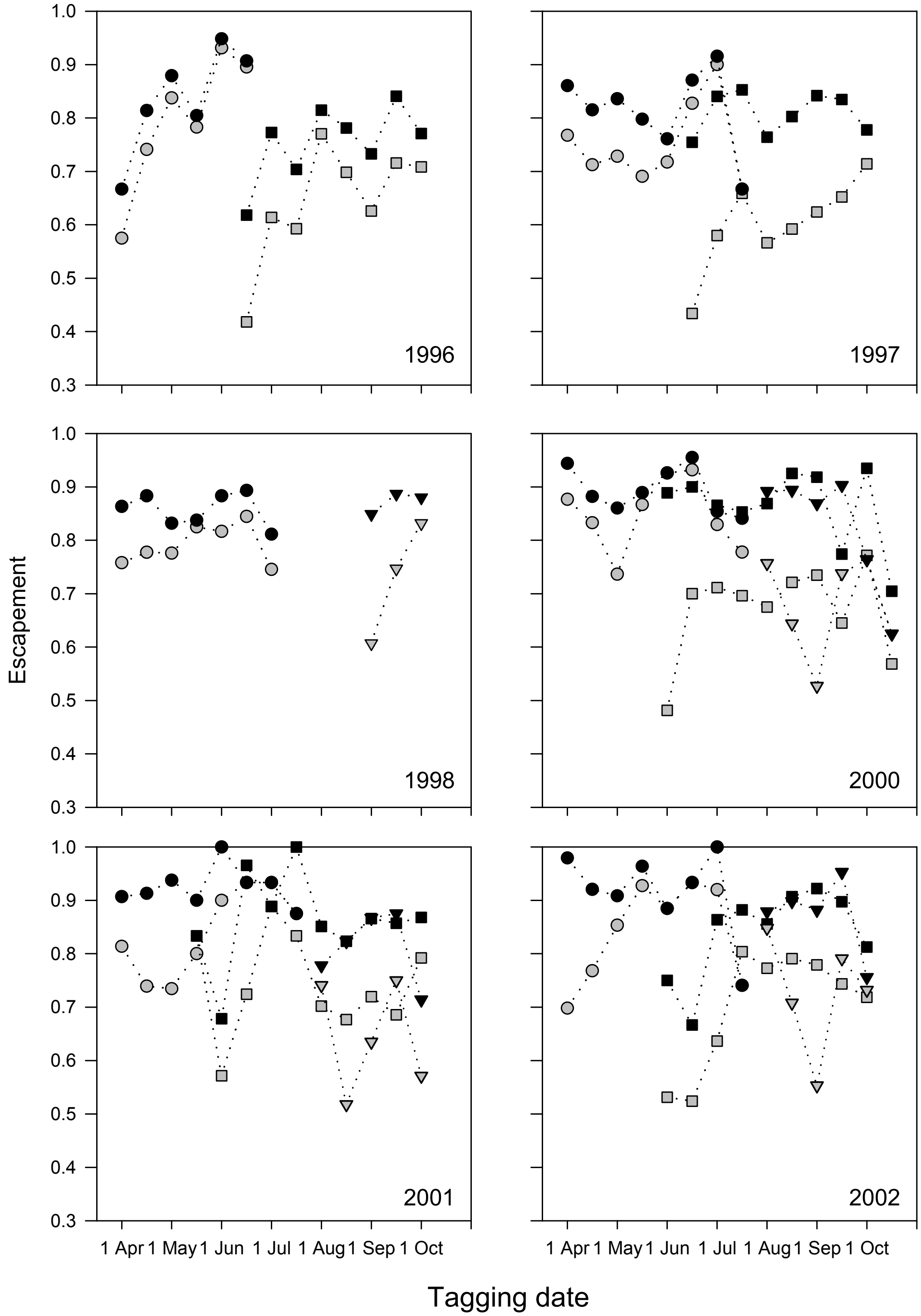

Figure 3. Biweekly hydrosystem Esc_2 (grey symbols) and Esc_3 (black symbols) estimates for radio-tagged spring–summer Chinook salmon (circles), fall Chinook salmon (triangles), and steelhead (squares) released downstream from Bonneville Dam.

Hydrosystem escapement estimates for unknown-source fish released downstream were compared to those for fish released in the forebay in 2000, 2001, and 2002. Of the 27 pairs (3 runs×3 years×3 escapement estimates), 6 (22%) differed significantly ($P \leq 0.05$, χ^2 tests). Forebay-released fish had lower escapement by 6.8 to 10.5% (*mean* = 8.6%) in all six significant pairs, which included spring–summer Chinook salmon in 2001 (Esc_3), fall Chinook salmon in 2000 (Esc_1 and Esc_2) and 2002 (Esc_3), and steelhead in 2000 (Esc_1 and Esc_2) (Table 4). Non-significant pairs differed by < 0.1% to 4.2% (*mean* = 2.3%).

Known-source fish -- Stock-specific hydrosystem escapements were calculated for known-source fish from the Wind, John Day, Yakima, Snake, and upper Columbia rivers (Table 4). Large proportions of downstream-released spring–summer Chinook salmon from the Wind River fish were reported harvested in 2001 and 2002, mostly in the Wind River itself (44 and 26%) but also in the Columbia River mainstem (6 and 20%). Escapement estimates for Wind River fish ranged from 0.313 (Esc_1 in 2001) to 0.943 (Esc_3 in 2002; Figure 4). Less than 1% of Snake River spring–summer Chinook salmon were reported harvested in tributaries downstream from Lower Granite Dam (fish were temporary or permanent strays) and a total of 10.4% (*range* = 0 to 12%) were reported harvested in mainstem fisheries (Table 4). Mean escapements for Snake River spring–summer Chinook salmon were 0.802 (Esc_1), 0.804 (Esc_2), and 0.878 (Esc_3) for the three years (Figure 4). Yakima River spring–summer Chinook salmon were harvested in the Yakima (11% in both 2001 and 2002) and Columbia (2 and 9%) rivers, and escapements ranged from 0.769 (Esc_1) to 0.969 (Esc_3). There was minimal harvest of upper Columbia River spring–summer Chinook salmon, and all escapement estimates were between 0.863 and 0.919. Escapement estimates for forebay-released fish from each of these stocks did not differ ($P \geq 0.09$, χ^2 tests) from those for downstream-released fish.

No downstream-released Snake River fall Chinook salmon were reported recaptured in tributaries downstream from Lower Granite Dam, but 12% (2001) and 24% (2002) were harvested in mainstem fisheries. Escapement estimates were 0.808 (2001) and 0.588 (2002) for both Esc_1 and Esc_2 and were 0.923 (2001) and 0.833 (2002) for Esc_3 (Figure 4). Differences between downstream- and forebay-released fish were not significant ($P > 0.05$).

Nine to 11% of downstream-released Snake River and upper Columbia River steelhead stocks were reported harvested in mainstem fisheries and another 2 to 6% were reported harvested in tributaries downstream from Lower Granite and Priest Rapids dams (fish were temporary or permanent strays). Notably, 20% of forebay-released upper Columbia River steelhead were harvested in mainstem fisheries. Snake River and upper Columbia River steelhead escapements were between 0.778 (Esc_1) and 0.963 (Esc_3) (Figure 4). Forebay-released upper Columbia River steelhead escaped at lower rates ($0.003 < P < 0.056$, Esc_1 and Esc_2) than downstream-released upper Columbia River fish in 2001 and 2002. Escapements did not differ between release sites for Snake River steelhead.

Among-group comparisons – Among spring–summer Chinook salmon, no differences ($P > 0.05$, χ^2 tests) were found in Esc_2 or Esc_3 estimates for the three groups available for comparison in 2000 (unknown-source, Snake, upper Columbia), or the six in 2002 (unknown-source, Wind, John Day, Snake, Yakima, upper Columbia) (Figures 3

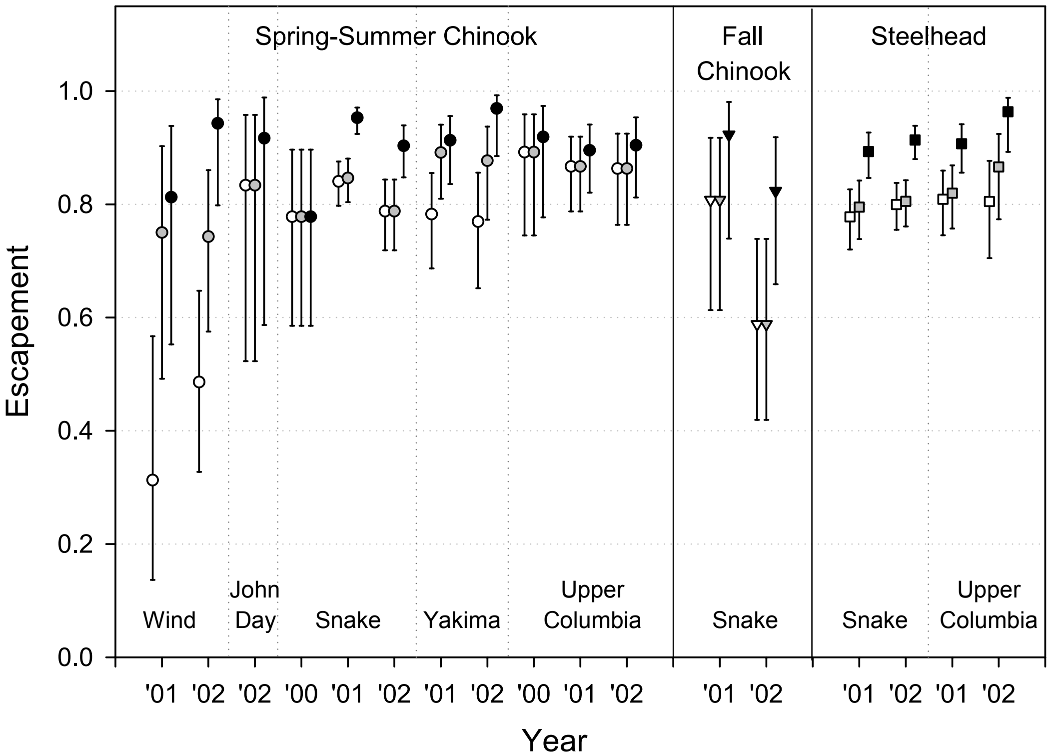

Figure 4. Annual hydrosystem (Bonneville Dam to Lower Granite or Priest Rapids dams) escapement estimates for known-source radio-tagged spring–summer and fall Chinook salmon and steelhead released downstream from Bonneville Dam. Open symbols = Esc_1, grey symbols = Esc_2, black symbols = Esc_3. Error bars are 95% profile likelihood confidence intervals.

and 4). Five groups were compared in 2001 (unknown-source, Wind, Snake, Yakima, upper Columbia): Esc_3 was higher for Snake River fish (0.953) than for upper Columbia River (0.895) and Wind River (0.813) fish ($0.01 < P < 0.04$). Esc_3 was also higher for the unknown-source group (0.947) than for Wind River fish (P = 0.031) in 2001, and Esc_2 was higher for Yakima River fish (0.891) than for the unknown-source group (0.793) (P = 0.038).

No escapement differences ($P > 0.05$) were found between Snake River fall Chinook salmon and unknown-source fall Chinook salmon in 2001 or 2002. Upper Columbia River steelhead escaped at higher rates than Snake River and unknown-source steelhead. Esc_2 estimates were higher ($0.002 < P < 0.045$) for upper Columbia River fish in 2001 and 2002, and Esc_3 estimates were higher ($0.007 < P = 0.034$) in 2002 (Figure 4).

Within individual known-source stocks, no between-year Esc_2 differences were significant ($P > 0.05$) for spring–summer Chinook salmon (Snake, upper Columbia, Yakima, Wind), fall Chinook salmon (Snake) or steelhead (Snake, upper Columbia).

Esc_3 was significantly higher for Snake River spring–summer Chinook salmon in 2001 (0.953) than in 2000 (0.778) (P = 0.002, χ^2 test) and 2002 (0.903, P = 0.032). No other within-stock Esc_3 comparisons differed between years (P > 0.05).

There was less statistically significant within-run-year escapement variance for known-source stocks than for unknown-source groups, in part because sample sizes for each interval were small. Only Snake River spring–summer Chinook salmon in 2001 (Esc_2) and upper Columbia River steelhead in 2001 (Esc_3) showed significant (P < 0.05, likelihood ratio tests) within-run variance. Late-migrating spring–summer Chinook salmon and early-migrating steelhead had lower escapement in those runs.

Treatment of inter-basin strays may have positively biased escapement estimates. Between 1.5 and 2.0% of spring–summer and fall Chinook salmon and about 6% of steelhead from Snake, Yakima, and upper Columbia River stocks were last recorded in lower Columbia River tributaries. Most strays entered tributaries to the Bonneville reservoir or the Deschutes or John Day rivers, and about one-third were harvested and may have been temporary strays only. By our definitions, fish that entered these tributaries were considered escaped (Esc_2 and Esc_3) regardless of ultimate destination. Escapement estimates for known-source groups would be lower by approximately the above percentages if strays were treated as unsuccessful migrants.

Escapement adjusted to include the reach downstream from Bonneville Dam – Among downstream-released known-source groups, hydrosystem Esc_3 estimates that included portions of the reach downstream from Bonneville Dam were lower than or similar to estimates for fish that passed the dam (Table 5). No Esc_3 reductions associated with the area downstream from Bonneville Dam were found for Yakima or upper Columbia spring–summer Chinook salmon, for Wind River spring–summer Chinook salmon in 2002, or for Snake River fall Chinook salmon in 2001. Reductions ranging from less than 0.005 to 0.048 were found for other known-source groups (Table 5). Only John Day River spring–summer Chinook salmon showed in increase in hydrosystem Esc_3 (+0.006 in 2002); the increase was due to inclusion of a fish harvested downstream from the release site.

Reach-specific escapement estimates: Bonneville to McNary

Unknown-source fish -- Escapement estimates through the Bonneville to McNary reach were higher than estimates for the full monitored hydrosystem, but Bonneville-McNary escapement patterns were generally similar to those in Table 4 because most harvest and the majority of tributary turn-off occurred in the lower river. Mean Bonneville-McNary Esc_1 estimates for all unknown-source fish released downstream from Bonneville Dam were 0.776 for spring–summer Chinook salmon, 0.648 for fall Chinook salmon, and 0.730 for steelhead (Table 6). Esc_2 means were 0.851 (spring–summer Chinook), 0.680 (fall Chinook), and 0.777 (steelhead); Esc_3 means were 0.920 (spring–summer Chinook), 0.886 (fall Chinook), and 0.897 (steelhead) (Table 6).

Known-source fish – Escapement estimates for known-source stocks downstream from McNary Dam (Wind and John Day rivers) were the same through the Bonneville-McNary reach and full monitored hydrosystem. As would be expected, stocks originating upstream from McNary Dam (Snake, Yakima, and upper Columbia rivers) had higher escapement estimates through the Bonneville-McNary reach than through the full hydrosystem (Table 6). Esc_3 Bonneville-McNary estimates for these groups were

Table 5. Escapement estimates for known-source groups adjusted to include the area between the downstream release sites and Bonneville Dam, based on increasingly stringent evidence of upstream movement following release.

		———→ Increasingly stringent inclusion criteria ———→									
		All fish Released		Recorded In tailrace		Recorded At dam		Recorded In fishway		From Table 4[1]	
Year	Stock	n	Esc_3	n	Esc_3	n	Esc_3	n	Esc_3	n	Esc_3
Spring–summer Chinook salmon											
2001	Wind	17	*0.765*	17	*0.765*	17	*0.765*	16	*0.813*	16	*0.813*
2002	Wind	35	*0.943*	35	*0.943*	35	*0.943*	35	*0.943*	35	*0.943*
2002	JDR	13	*0.923*	12	*0.917*	12	*0.917*	12	*0.917*	12	*0.917*
2000	SNR	28	*0.750*	28	*0.750*	28	*0.750*	27	*0.778*	27	*0.778*
2001	SNR	347	*0.931*	344	*0.936*	341	*0.944*	339	*0.950*	338	*0.953*
2002	SNR	167	*0.898*	166	*0.898*	166	*0.898*	166	*0.898*	165	*0.903*
2001	Yak	92	*0.913*	92	*0.913*	92	*0.913*	92	*0.913*	92	*0.913*
2002	Yak	65	*0.969*	65	*0.969*	65	*0.969*	65	*0.969*	65	*0.969*
2000	UC	37	*0.919*	37	*0.919*	37	*0.919*	37	*0.919*	37	*0.919*
2001	UC	105	*0.895*	105	*0.895*	105	*0.895*	105	*0.895*	105	*0.895*
2002	UC	73	*0.890*	73	*0.890*	73	*0.890*	73	*0.890*	73	*0.890*
Fall Chinook Salmon											
2001	SNR	26	*0.923*	26	*0.923*	26	*0.923*	26	*0.923*	26	*0.923*
2002	SNR	36	*0.806*	35	*0.800*	34	*0.824*	34	*0.824*	34	*0.824*
Steelhead											
2001	SNR	237	*0.886*	237	*0.886*	236	*0.886*	234	*0.893*	234	*0.893*
2002	SNR	370	*0.889*	366	*0.899*	362	*0.909*	360	*0.911*	359	*0.914*
2001	UC	185	*0.903*	185	*0.903*	183	*0.907*	183	*0.907*	183	*0.907*
2002	UC	84	*0.952*	84	*0.952*	84	*0.952*	83	*0.964*	82	*0.963*

[1] Fish had to pass Bonneville Dam to be included in estimate

higher than the full hydrosystem estimates by 0.0 to 12.0%, reflecting harvest and unaccounted-for loss that occurred upstream from McNary Dam (or downstream from McNary Dam if fish fell back at the dam and did not reascend).

Reach-specific escapement estimates: Ice Harbor to Lower Granite

All fish that passed Ice Harbor Dam were assumed to be of Snake River origin, and so unknown- and known-source fish from all groups were pooled together for escapement calculations for the Ice Harbor to Lower Granite reach. Mean escapement estimates for spring–summer Chinook salmon were 0.977 (Esc_1), 0.977 (Esc_2), and 0.979 (Esc_3) (Table 7). Means for fall Chinook salmon were 0.955 for all three escapement categories, both because samples were small and because there is no fall Chinook salmon harvest in the lower Snake River. Means for steelhead were 0.902 (Esc_1), 0.908 (Esc_2), and 0.938 (Esc_3). Lower escapement for steelhead through this reach, relative to Chinook salmon, were due to fisheries in the lower Snake and Tucannon rivers, possible loss during over wintering, and greater downstream wandering by this species.

Table 6. Number of radio-tagged fish and the percent (*n*) in each fate category, with hydrosystem (top of Bonneville Dam to top of McNary Dam) escapement estimates for all fish released downstream (ds) from Bonneville Dam or in the Bonneville Dam forebay, for unknown-source (Unknown) stocks and for known-source stocks identified by PIT tags, 1996-2002. Includes corrections from PIT-tag-only detections at dams.

Year	Release	Stock	E_i	P_i	T_{i+d}[1]	H_{i+d}	TF_{i+d}	MF_{i+d}	U_{i+d}	Esc_1	Esc_2	Esc_3
Spring–summer Chinook salmon												
1996	ds	Unknown	810	38 (308)	22 (181)	15 (119)	6 (50)	4 (36)	14 (116)	0.751	0.940	0.940
1997	ds	Unknown	952	62 (588)	7 (69)	8 (79)	3 (33)	8 (72)	12 (111)	0.773	0.808	0.883
1998	ds	Unknown	932	62 (576)	12 (116)	7 (67)	2 (23)	5 (46)	11 (104)	0.814	0.839	0.888
2000	ds	Unknown	888	53 (472)	9 (79)	14 (122)	10 (89)	6 (49)	9 (77)	0.760	0.858	0.913
2001	ds	Unknown	227	65 (148)	9 (20)	4 (10)	4 (9)	12 (28)	5 (12)	0.784	0.824	0.947
2002	ds	Unknown	534	60 (323)	8 (41)	9 (48)	7 (36)	11 (58)	5 (28)	0.772	0.839	0.948
2000	forebay	Unknown	157	64 (101)	6 (9)	9 (14)	4 (7)	5 (8)	11 (18)	0.790	0.834	0.885
2001	forebay	Unknown	124	65 (80)	6 (8)	6 (8)	5 (6)	9 (11)	9 (11)	0.774	0.823	0.911
2002	forebay	Unknown	226	57 (128)	11 (24)	9 (20)	5 (11)	10 (23)	9 (20)	0.761	0.710	0.912
2001	ds	Wind R.	16			31 (5)	44 (7)	6 (1)	19 (3)	0.313	0.750	0.813
2002	ds	Wind R.	35		31 (11)	17 (6)	26 (9)	20 (7)	6 (2)	0.486	0.743	0.943
2001	forebay	Wind R.	12		17 (2)	42 (5)	25 (3)	8 (1)	8 (1)	0.500	0.833	0.917
2002	forebay	Wind R.	13		15 (2)	38 (5)	31 (4)	15 (2)		0.538	0.846	1.000
2002	ds	John Day R.	12		83 (10)		8 (1)		8 (1)	0.833	0.917	0.917
2000	ds	Snake R.	27	78 (21)					22 (6)	0.777	0.777	0.777
2001	ds	Snake R.	338	84 (285)	1 (3)	<1 (1)	1 (2)	10 (33)	4 (14)	0.855	0.861	0.959
2002	ds	Snake R.	165	81 (133)	1 (2)			11 (18)	7 (12)	0.818	0.818	0.927
2001	forebay	Snake R.	124	80 (99)		1 (1)	1 (1)	16 (20)	2 (3)	0.807	0.815	0.976
2002	forebay	Snake R.	19	100 (19)						1.000	1.000	1.000
2001	ds	Yakima R.	92	89 (82)				2 (2)	9 (8)	0.891	0.891	0.913
2002	ds	Yakima R.	65	86 (56)	2 (1)			9 (6)	3 (2)	0.877	0.877	0.969
2001	forebay	Yakima R.	28	96 (27)				4 (1)		0.964	0.964	1.000
2002	forebay	Yakima R.	32	88 (28)				9 (3)	3 (1)	0.875	0.875	0.969
2000	ds	Upper Col.	37	86 (32)	3 (1)			3 (1)	8 (3)	0.892	0.892	0.919
2001	ds	Upper Col.	105	91 (96)	1 (1)			3 (3)	5 (5)	0.924	0.924	0.952
2002	ds	Upper Col.	73	92 (67)				4 (3)	4 (3)	0.918	0.918	0.959
2001	forebay	Upper Col.	35	89 (31)				6 (2)	6 (2)	0.886	0.886	0.943
2002	forebay	Upper Col.	26	88 (23)				4 (1)	8 (2)	0.885	0.885	0.923

Table 6 Cont.

Year	Release	Stock	E_i	P_i	T_{i+d} [1]	H_{i+d}	TF_{i+d}	MF_{i+d}	U_{i+d}	Esc_1	Esc_2	Esc_3
Fall Chinook salmon												
1998	ds	Unknown	913	47 (428)	18 (161)	4 (41)	3 (28)	16 (147)	12 (108)	0.690	0.721	0.882
2000	ds	Unknown	659	48 (314)	9 (60)	4 (26)	6 (40)	22 (148)	11 (71)	0.607	0.668	0.892
2001	ds	Unknown	495	47 (234)	13 (63)	4 (21)	2 (10)	21 (102)	13 (65)	0.642	0.663	0.869
2002	ds	Unknown	644	50 (319)	13 (85)	2 (16)	2 (10)	23 (150)	10 (63)	0.654	0.669	0.902
2000	forebay	Unknown	371	38 (142)	10 (37)	4 (15)	3 (11)	36 (132)	9 (34)	0.523	0.523	0.908
2001	forebay	Unknown	395	50 (199)	22 (85)	4 (16)	1 (3)	21 (83)	12 (49)	0.658	0.666	0.876
2002	forebay	Unknown	307	46 (141)	12 (38)	2 (7)	3 (9)	21 (64)	16 (48)	0.606	0.635	0.844
2001	ds	Snake R.	26	81 (21)				12 (3)	7 (2)	0.808	0.808	0.923
2002	ds	Snake R.	34	62 (21)				24 (8)	15 (5)	0.618	0.618	0.853
2001	forebay	Snake R.	36	78 (28)				3 (1)	19 (7)	0.778	0.778	0.806
Steelhead												
1996	ds	Unknown	724	55 (397)	16 (115)	2 (17)	4 (26)	7 (54)	16 (115)	0.731	0.767	0.841
1997	ds	Unknown	916	53 (487)	9 (80)	2 (22)	7 (66)	16 (149)	12 (112)	0.643	0.715	0.878
2000	ds	Unknown	814	58 (476)	12 (100)	2 (18)	5 (40)	15 (120)	7 (60)	0.730	0.779	0.926
2001	ds	Unknown	364	65 (237)	9 (32)	3 (10)	4 (13)	11 (39)	9 (33)	0.767	0.802	0.909
2002	ds	Unknown	478	61 (293)	15 (71)	2 (8)	4 (21)	11 (52)	7 (33)	0.778	0.822	0.931
2000	forebay	Unknown	315	59 (187)	7 (22)	1 (2)	5 (16)	21 (67)	7 (21)	0.670	0.721	0.933
2001	forebay	Unknown	83	61 (51)	13 (11)		1 (1)	13 (11)	11 (9)	0.747	0.759	0.892
2002	forebay	Unknown	205	66 (135)	10 (21)	<1 (1)	6 (13)	7 (14)	10 (21)	0.766	0.829	0.898
2001	ds	Snake R.	234	78 (182)	6 (15)		1 (3)	9 (20)	6 (14)	0.842	0.855	0.940
2002	ds	Snake R.	359	81 (289)	3 (11)		1 (2)	10 (37)	6 (20)	0.836	0.841	0.944
2001	forebay	Snake R.	122	87 (106)	3 (4)		1 (1)	6 (7)	3 (4)	0.902	0.910	0.967
2002	forebay	Snake R.	66	79 (52)	6 (4)			8 (5)	8 (5)	0.849	0.849	0.924
2001	ds	Upper Col.	183	79 (144)	4 (7)		3 (5)	9 (16)	6 (11)	0.825	0.853	0.940
2002	ds	Upper Col.	82	78 (64)	4 (3)		6 (5)	10 (8)	2 (2)	0.817	0.878	0.976
2001	forebay	Upper Col.	141	65 (91)	2 (3)		4 (5)	20 (28)	10 (14)	0.667	0.702	0.901
2002	forebay	Upper Col.	56	71 (40)			5 (3)	18 (10)	5 (3)	0.714	0.768	0.946

[1] Tributary category includes Hanford Reach spawning areas for fall Chinook salmon

Table 7. Number of radio-tagged fish and the percent (*n*) in each fate category, with lower Snake River (top of Ice Harbor Dam to top of Lower Granite Dam) escapement estimates for all fish recorded passing Ice Harbor Dam, independent of Bonneville Dam release site and any PIT-tag origin (almost all fish should be of Snake River origin). Values include corrections from PIT-tag-only detections at dams.

Year	Release	Stock	E_i	P_i	T_{i+d}[1]	H_{i+d}	TF_{i+d}	MF_{i+d}	U_{i+d}	Esc_1	Esc_2	Esc_3
Spring–summer Chinook salmon												
1996	All	All	122	93 (114)	3 (4)	2 (2)			2 (2)	0.984	0.984	0.984
1997	All	All	319	93 (298)	2 (5)	1 (2)	<1 (1)		4 (13)	0.956	0.959	0.959
1998	All	All	256	95 (242)	2 (5)	1 (2)			3 (7)	0.973	0.973	0.973
2000	All	All	249	96 (239)	2 (5)				2 (5)	0.980	0.980	0.980
2001	All	All	504	97 (491)	1 (5)			1 (4)	1 (4)	0.984	0.984	0.992
2002	All	All	381	98 (372)	1 (3)				2 (6)	0.984	0.984	0.984
Fall Chinook salmon												
1998	All	All	29	62 (18)	3 (1)	31 (9)			3 (1)	0.966	0.966	0.966
2000	All	All	33	82 (27)	3 (1)	9 (3)			6 (2)	0.939	0.939	0.939
2001	All	All	93	74 (69)	10 (9)	12 (11)			4 (4)	0.957	0.957	0.957
2002	All	All	73	89 (56)	5 (4)	14 (10)			4 (3)	0.959	0.959	0.959
Steelhead												
1996	All	All	322	84 (272)	2 (8)	2 (8)	1 (4)	2 (6)	7 (24)	0.894	0.907	0.926
1997	All	All	387	82 (317)	2 (7)		<1 (1)	8 (31)	8 (31)	0.837	0.840	0.920
2000	All	All	507	90 (455)	1 (5)	1 (6)	<1 (1)	3 (13)	5 (27)	0.919	0.921	0.947
2001	All	All	516	92 (474)	1 (4)	1 (5)	<1 (2)	1 (6)	5 (25)	0.936	0.940	0.952
2002	All	All	693	92 (636)	1 (4)	<1 (1)	1 (5)	1 (8)	6 (39)	0.925	0.932	0.944

Reach-specific escapement estimates: Dam to Dam

Unknown-source fish -- Individual reach escapements were lowest for all runs between Bonneville and The Dalles dams in the lower Columbia River and were relatively high through all lower Snake River reaches (Figure 5). Mean Esc_1 estimates for downstream-released fish in the Bonneville–The Dalles reach were 0.850 for spring–summer Chinook salmon, 0.837 for fall Chinook salmon, and 0.847 for steelhead. Esc_1 means for spring–summer Chinook salmon were between 0.937 and 0.957 through the other three lower Columbia River reaches and were ≥ 0.991 through the three Snake River reaches. Esc_1 means for fall Chinook salmon and steelhead were between 0.847 and 0.933 through the The Dalles–John Day, John Day–McNary, and McNary–Ice Harbor/Priest Rapids reaches. Esc_1 means in lower Snake River reaches were higher for fall Chinook salmon (0.968 to 1.000) than for steelhead (0.960 to 0.978) (Figure 5).

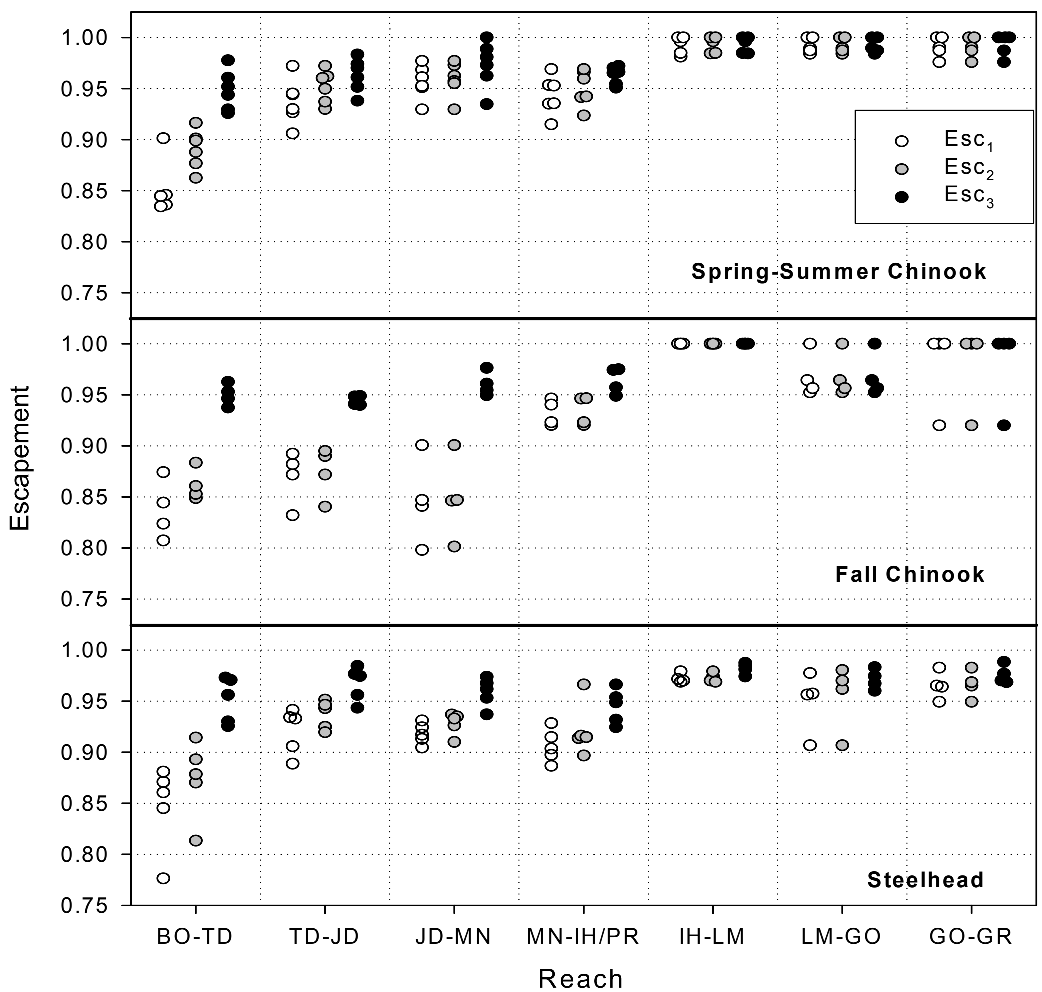

Figure 5. Annual reach-specific escapement estimates for unknown-source radio-tagged spring–summer and fall Chinook salmon and steelhead released downstream from Bonneville Dam. Dam abbreviations: Bonneville (BO), The Dalles (TD), John Day (JD), McNary (MN), Ice Harbor (IH), Lower Monumental (LM), Little Goose (GO), and Lower Granite (GR).

Less than 7% of downstream-released fish that entered each reach were subsequently reported harvested in tributaries [$(TF_i + TF_d)\bullet(E_i^{-1})$] (Figure 6). Most tributary harvest for spring–summer Chinook salmon occurred in the Wind (39% of all tributary harvest), Deschutes (21%), and Little White Salmon (19%) rivers. Tributary harvest of fall Chinook salmon was primarily in the Klickitat River (71%). Most steelhead were harvested in the Deschutes (25%), Klickitat (19%), Little White Salmon (15%), and John Day (13%) rivers. The distribution of tributary harvest resulted in little difference between mean Esc_1 and Esc_2 values in most reaches except Esc_2 means were slightly higher for the Bonneville–The Dalles and The Dalles–John Day reaches (Figure 5).

As many as 15% of downstream-released fish that entered each reach were subsequently harvested in the mainstem Columbia or Snake rivers ([$(MF_i + MF_d)\bullet(E_i^{-1})$]; Figure 6). Mainstem harvest rates were highest for fish entering the Bonneville–The Dalles reach for spring–summer Chinook salmon (*mean* = 5.8%) and steelhead (7.7%) and in the John Day–McNary reach (11.1%) for fall Chinook salmon. Fall Chinook salmon were also harvested at relatively high rates after entering the Bonneville–The Dalles (*mean* = 8.8%) and The Dalles–John Day (7.0%) reaches. Almost no Chinook salmon and relatively few steelhead were harvested in the lower Snake River, but some fish from both species passed one or more Snake River dams, then migrated downstream and were harvested.

On average, 3 to 5% of downstream-released fish from each run had unknown fates [$(U_i + U_d))\bullet(E_i^{-1})$] after entering each lower Columbia River reach and < 1 to 3% had unknown fates after entering Snake River reaches. Resulting Esc_3 estimates for all runs were mostly between 0.930 and 0.980 for lower Columbia River reaches, and were greater than 0.950 for Snake River reaches (Figure 5).

Known-source fish – Mean reach escapements for downstream-released, known-source stocks from upper portions of the basin (Snake, Yakima, and upper Columbia) were typically higher than for the unknown-source, mixed-stock samples, but patterns of escapement were similar (Figure 7). Escapements for known-source, upriver stocks from all runs were lowest through the Bonneville-The Dalles reach, were generally greater than 0.900 through the other three Columbia River reaches and were greater than 0.970 through Snake River reaches for all groups except fall Chinook salmon in 2001 (0.933, n = 15). Reach-specific estimates were not calculated for known-source Chinook salmon from the John Day River (n = 12) or Wind River (this Bonneville pool stock did not fully pass any dam-to-dam reach).

As with unknown-source groups, harvest of known-source fish was concentrated in lower Columbia River reaches. The highest single-reach harvest proportions for spring–summer Chinook salmon were in the Bonneville-The Dalles reach (2002 Snake River = 7.3%; 2001 Yakima = 5.4%; 2002 upper Columbia = 4.1%). The highest proportions for steelhead were in the Bonneville-The Dalles reach (2001 Snake River = 5.6%) or The Dalles-John Day reach (2002 upper Columbia = 5.6%). The highest harvest rates for Snake River fall Chinook salmon were in the John Day-McNary (15.4% in 2002) and Bonneville-The Dalles reaches (7.7% in 2001). Snake River stocks of spring–summer Chinook salmon tended to have lower escapements than upper Columbia River stocks through lower river reaches, reflecting greater harvest effort during the spring run when more Snake River fish migrate. Few differences were seen between steelhead stocks,

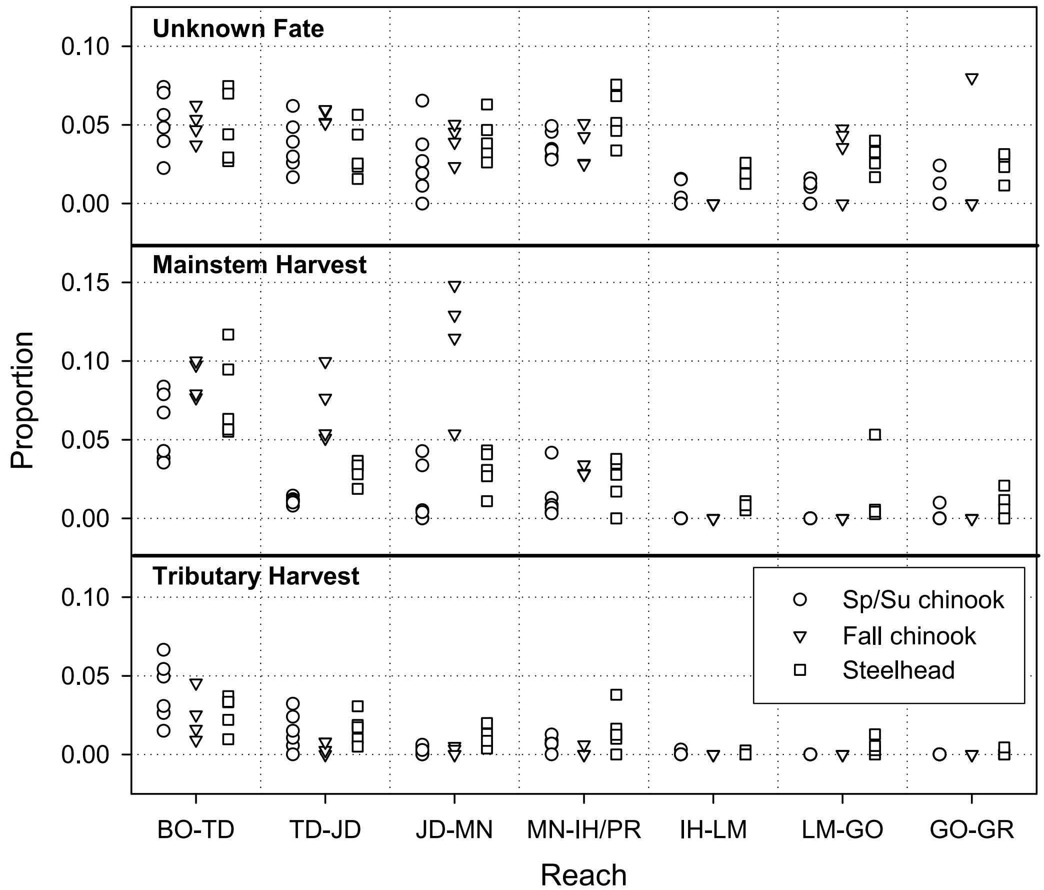

Figure 6. Annual estimates of proportions of radio-tagged spring–summer and fall Chinook salmon and steelhead released downstream from Bonneville Dam that entered hydrosystem reaches and were subsequently harvested in tributary or mainstem fisheries, or had unknown fate (last recorded at a dam or in a reservoir). Dam abbreviations: Bonneville (BO), The Dalles (TD), John Day (JD), McNary (MN), Ice Harbor (IH), Lower Monumental (LM), Little Goose (GO), and Lower Granite (GR).

except Snake River fish were harvested in the Bonneville-The Dalles reach at higher rates than upper Columbia River fish (Figure 7). As with full hydrosystem escapement estimates, lower Columbia River reach estimates for known-source groups would have been slightly lower if strays were treated as unsuccessful. Reach escapement estimates for forebay-released groups were generally similar to those for fish released downstream from Bonneville Dam. The exception was in the Bonneville-The Dalles reach, where escapement estimates tended to be lower for forebay-released fish.

Effects of fallback at dams

Unknown-source fish -- Fallback at monitored hydrosystem dams had a consistent negative effect on fish escapement for fish from all runs and years (Table 8). On average, Esc_3 estimates were lower for fallback fish by 0.065 for spring–summer Chinook salmon, 0.195 for fall Chinook salmon and 0.133 for steelhead. Differences

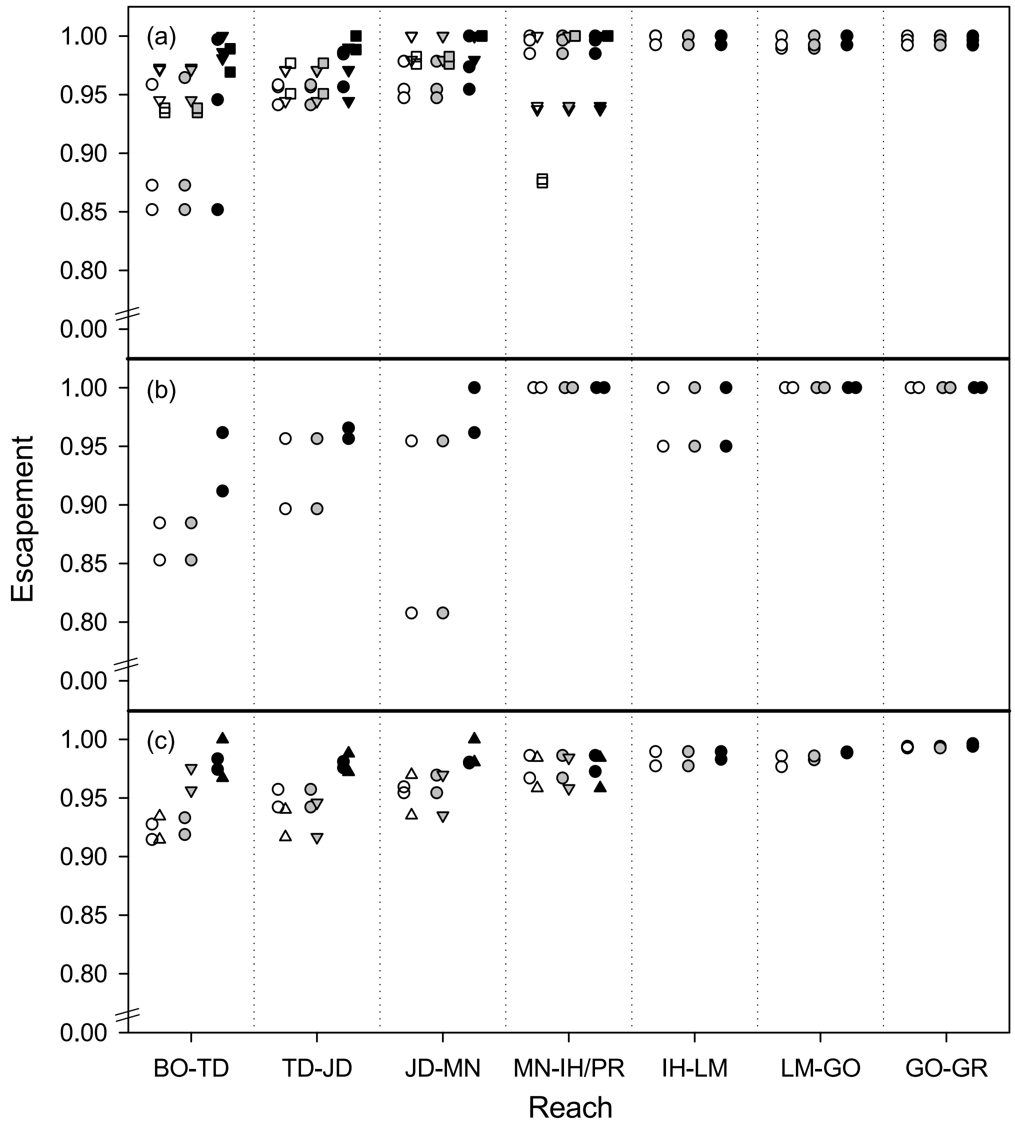

Figure 7. Annual (2000-2002) reach-specific escapement estimates for known-source radio-tagged (a) spring–summer Chinook salmon, (b) fall Chinook salmon, and (c) steelhead released downstream from Bonneville Dam. Circles = Snake River stocks, triangles = upper Columbia River stocks, squares = Yakima River stocks. Dam abbreviations: Bonneville (BO), The Dalles (TD), John Day (JD), McNary (MN), Ice Harbor (IH), Lower Monumental (LM), Little Goose (GO), and Lower Granite (GR). Open symbols = Esc_1, gray symbols = Esc_2, black symbols = Esc_3.

were highly significant ($P < 0.005$, χ^2 tests) in all four fall Chinook salmon runs, four of five steelhead runs, and the 1998 spring–summer Chinook salmon run. Differences were significant at $P < 0.05$ for spring–summer Chinook salmon in 1997 and 2000.

Table 8. Esc_3 estimates (n) for downstream-released unknown-source (Unknown) and known-source fish that either were or were not recorded falling back (FB) over a monitored hydrosystem[1] dam, with differences in Esc_3 estimates for fallback and non-fallback fish (D), proportions recorded falling back at one or more dams (FB%), and the overall Esc_3 reduction (%) associated with fallback. Fallback after hydrosystem passage (top of Lower Granite or Priest Rapids dams) and known-source groups with fewer than 10 fallback fish excluded.

Year	Stock	Esc_3 estimate (n) No fallback	Fallback	Esc_3 Difference (D)	System[1] FB (%)	Esc_3 Reduction (D•FB%)
Spring–summer Chinook salmon						
1996	Unknown	0.847 (632)	0.798 (178)	0.049	22.0	1.08
1997	Unknown	0.858 (683)	0.792 (269)	0.066*	28.3	1.86
1998	Unknown	0.881 (714)	0.784 (218)	0.097**	23.4	2.27
2000	Unknown	0.905 (702)	0.849 (186)	0.055*	20.9	1.15
2001	Unknown	0.931 (202)	0.840 (25)	0.091	11.0	1.00
2002	Unknown	0.931 (452)	0.901 (81)	0.030	15.2	0.46
2000	Snake R.	0.824 (17)	0.700 (10)	0.124	37.0	4.58
2001	Snake R.	0.967 (302)	0.833 (36)	0.134**	10.7	1.42
2002	Snake R.	0.935 (138)	0.720 (25)	0.215**	15.3	3.29
Fall Chinook Salmon						
1998	Unknown	0.881 (805)	0.769 (108)	0.112**	11.8	1.32
2000	Unknown	0.894 (585)	0.635 (74)	0.259**	11.2	2.91
2001	Unknown	0.868 (438)	0.684 (57)	0.183**	11.5	2.11
2002	Unknown	0.914 (567)	0.688 (77)	0.225**	12.0	2.69
Steelhead						
1996	Unknown	0.780 (600)	0.702 (124)	0.078†	17.1	1.34
1997	Unknown	0.866 (700)	0.755 (216)	0.111**	23.6	2.62
2000	Unknown	0.882 (646)	0.774 (168)	0.108**	20.6	2.23
2001	Unknown	0.880 (276)	0.713 (87)	0.168**	24.0	4.02
2002	Unknown	0.872 (382)	0.670 (94)	0.202**	19.7	3.98
2001	Upper Col.	0.906 (170)	0.923 (13)	-0.017	7.1	-0.12
2001	Snake R.	0.909 (186)	0.733 (45)	0.175**	19.5	3.41
2002	Snake R.	0.897 (311)	0.809 (47)	0.089†	13.1	1.16

[1] Bonneville, The Dalles, John Day, McNary, Ice Harbor, Lower Monumental, Little Goose

† $P < 0.10$, * $P < 0.05$, ** $P < 0.005$ Pearson χ^2 tests

Multiplication of the difference in Esc_3 estimates by system-wide fallback proportions indicated overall run escapement reductions ranging from 0.46 to 2.27% (*mean* = 1.30%) for spring–summer Chinook salmon, from 1.32 to 2.91% (2.26%) for fall Chinook salmon, and from 1.34 to 4.02% (2.84%) for steelhead (Table 8).

Known-source fish – Fallback effects for known-source stocks were similar to those for unknown-source samples (Table 8). Only six known-source groups had at least 10 fish that fell back during migration: Snake River spring–summer Chinook salmon in all three years, Snake River steelhead in 2001 and 2002, and upper Columbia River steelhead in 2001. In all cases except 2001 upper Columbia River steelhead, non-fallback fish escaped at higher rates than fallback fish. Esc_3 differences (0.134 to 0.215) were significant (P < 0.005) for Snake River spring–summer Chinook salmon in 2001 and 2002 and Snake River steelhead in 2001 (Table 6).

Effects of river environment

Unknown-source fish – Annual hydrosystem Esc_3 estimates for spring–summer Chinook salmon were significantly and negatively correlated (r^2 > 0.70, P < 0.04) with mean and maximum Columbia River discharge during April-July (Table 9). Maximum discharge was also negatively correlated with mainstem harvest rates of spring–summer Chinook salmon (r^2 = 0.66, P = 0.050), suggesting escapement differences were not due to harvest effects. In contrast, discharge metrics were not correlated with annual hydrosystem Esc_3 estimates or mainstem harvest rates for either fall Chinook salmon or steelhead during their migrations.

Water temperature means and maxima were not correlated with annual Esc_3 estimates for any of the three runs, or with mainstem harvest rates for spring–summer Chinook salmon or steelhead (Table 9). Harvest rates of fall Chinook salmon were significantly higher in cooler years (r^2 > 0.90, P < 0.05) (Table 7), but the regression model was strongly influenced by the low harvest rate in 1998, when no fish were radio-tagged in August.

Small sample sizes precluded making similar types of analyses for known-source fish.

Discussion

This study used thousands of individual adult Chinook salmon and steelhead migration histories to estimate escapement, distribution, harvest, and 'unaccounted for' loss during spawning migrations through the Federal Columbia River hydrosystem. The data provide some of the first comprehensive quantitative summaries of adult escapement and fate in this multi-species, multi-stock system. From the results, we believe five important conclusions can be drawn:

1) Escapement indices for Columbia basin spring–summer and fall Chinook salmon and steelhead varied significantly between species, between and within annual runs, and between some sub-basin populations.

2) High discharge years corresponded with low spring–summer Chinook salmon escapement, but neither discharge nor water temperature were consistently correlated with *annual* fall Chinook salmon or steelhead escapement.

3) Mainstem harvest rates—especially in lower Columbia River reservoirs—differed between runs and may indicate unacceptably high take of some ESA-listed populations (e.g., upper Columbia River steelhead and Snake River fall Chinook salmon).

4) Adult Chinook salmon and steelhead that fell back over dams were significantly more likely to have unknown fates (presumed mortality) and lower hydrosystem escapement.

Table 9. Linear regression results for models of seasonal mean ($_{AVG}$) and maximum ($_{MAX}$) river discharge and temperature, and hydrosystem Esc_3 and mainstem harvest (MF) estimates for unknown-source radio-tagged fish. Environmental variables were for data at Bonneville Dam during the time radio-tagged spring–summer Chinook salmon (April-July), fall Chinook salmon (August-October), and steelhead (June-October) were migrating. Discharge values were log-transformed.

	Years	r^2	*P*	β
Spring–summer Chinook salmon				
$Discharge_{AVG}$ vs. Esc_3	6	0.73	0.030	-0.100
$Discharge_{MAX}$ vs. Esc_3	6	0.71	0.035	-0.102
$Tempearture_{AVG}$ vs. Esc_3	6	0.06	0.631	0.024
$Temperature_{MAX}$ vs. Esc_3	6	0.11	0.517	-0.017
$Discharge_{AVG}$ vs. MF	6	0.57	0.085	-0.075
$Discharge_{MAX}$ vs. MF	6	0.66	0.050	-0.083
$Tempearture_{AVG}$ vs. MF	6	0.01	0.836	0.009
$Temperature_{MAX}$ vs. MF	6	0.19	0.385	-0.019
Fall Chinook salmon				
$Discharge_{AVG}$ vs. Esc_3	4	0.57	0.247	0.089
$Discharge_{MAX}$ vs. Esc_3	4	0.53	0.275	0.061
$Tempearture_{AVG}$ vs. Esc_3	4	0.02	0.869	-0.003
$Temperature_{MAX}$ vs. Esc_3	4	0.12	0.652	-0.007
$Discharge_{AVG}$ vs. MF	4	0.01	0.925	-0.016
$Discharge_{MAX}$ vs. MF	4	0.04	0.801	-0.029
$Tempearture_{AVG}$ vs. MF	4	0.91	0.046	-0.041
$Temperature_{MAX}$ vs. MF	4	0.92	0.042	-0.034
Steelhead				
$Discharge_{AVG}$ vs. Esc_3	5	0.31	0.327	-0.101
$Discharge_{MAX}$ vs. Esc_3	5	0.34	0.303	-0.054
$Tempearture_{AVG}$ vs. Esc_3	5	0.12	0.562	0.048
$Temperature_{MAX}$ vs. Esc_3	5	0.03	0.798	0.009
$Discharge_{AVG}$ vs. MF	5	0.03	0.791	0.030
$Discharge_{MAX}$ vs. MF	5	0.00	0.970	0.002
$Tempearture_{AVG}$ vs. MF	5	0.38	0.269	0.085
$Temperature_{MAX}$ vs. MF	5	0.60	0.127	0.045

5) Reach (dam-to-dam) escapement estimates were lowest in the lower Columbia River and were highest in the lower Snake River.

These findings help clarify patterns of adult fate during upstream migration through the monitored hydrosystem. We wish to emphasize, however, that hydrosystem escapement estimates do not directly translate to spawning escapements. Our treatment of the telemetry data also did not address indirect or delayed effects of migration through the hydrosystem on spawning success. Many fish last detected in hydrosystem tributaries may not have successfully reached spawning sites, and some that reached spawning grounds may have died prior to spawning. Fish recorded passing the upper monitored boundaries of the hydrosystem (Priest Rapids and Lower Granite dams) were considered successful migrants for this summary, but distances from those dams to spawning sites can be considerable (e.g., more than 500 km for some Snake River stocks). Harvest, migration mortality, and pre-spawn mortality continue upstream from the bounds of this study and need to be factored into any spawning escapement estimates. We monitored fish upstream from Lower Granite Dam in all years—though with varying levels of effort—and we intend to summarize fish fate upstream from Lower Granite reservoir in a separate report. Refer to Bjornn et al. (1998, 2003) for Snake River distributions and final fates for Chinook salmon and steelhead radio-tagged at Ice Harbor and John Day dams in previous telemetry projects.

Evaluation of methodology -- Interpretation of the current telemetry data is based on assumptions that tagged fish represent sampled populations, and that tagged fish behave similarly to untagged fish. We made a concerted effort to proportionately and unselectively tag unknown-source fish from throughout each run. However, operational constraints and conflicting research priorities made strictly representative tagging impossible. Run size and timing, the location of the trapping facility (north shore only), and tagging stoppages (no summer Chinook in July 1996 or fall Chinook in August 1998) resulted in departures from representative sampling. We also sampled proportionately more late-migrating steelhead in order to have adequate samples of Snake River fish to address separate research objectives at Snake River dams. Collection of known-source groups was opportunistic and random, and may also have been slightly biased because available fish did not fully capture stock diversity from basins they represented. Known-source fish were principally derived from juvenile salmon and steelhead research projects that included PIT-tagging at Lower Granite and upper Columbia River dams. Fish collected at these facilities should have been reasonably representative of the juveniles passing those dams, but there were gaps in collection (e.g., Berggren et al. 2003) and some stocks were not well represented. Availability of known-source fish from tributaries other than the Snake River was much more limited, and samples of known-source lower Columbia River stocks were especially restricted.

Despite these constraints, we believe radio-tagged samples were good surrogates for the overall runs, and that tagged fish behaved similarly to untagged fish. For example, radio-tagged Chinook salmon had passage times through the hydrosystem (Bonneville Dam to Lower Granite Dam) similar to those of PIT-tagged salmon without radio tags (Matter and Sandford 2003), suggesting that tagging did not significantly affect migration behavior over long distances (~460 km). Run timing distributions of radio-tagged fish were also generally similar to those for all fish counted at dams, both at Bonneville Dam (Keefer et al. 2004b) and at upstream sites. In addition, the vast majority of radio-tagged fish in this study completed migration (Keefer et al. 2004a; 2004b) or could be accounted for in fisheries. This evidence of limited tagging effects is consistent with adult anadromous salmonid telemetry research in other rivers (Burger et al. 1985; Thorstad et al. 2000; Jokikoko 2002).

A final concern in adult telemetry research, downstream movement following tagging (Bernard et al. 1999; Mäkinen et al. 2000), should not have substantively affected our study results. Our focus on downstream-released fish should have ameliorated effects of retrograde movement, as escapement, harvest, and fate estimates were calculated only after fish volitionally resumed upstream migration and passed Bonneville Dam.

Lower escapement by forebay-released fish (*mean* = 3.8% lower than for downstream releases, *n* = 27 pairs) may be a good measure of initial transmitter loss, mortality following tagging, and fish destined for sites downstream from Bonneville Dam. Some censored fish (downstream releases that did not reascend at Bonneville Dam) were harvested in the Columbia River downstream from the dam, entered downstream tributaries (Willamette, Sandy, Cowlitz), and entered the Bonneville Hatchery (fall Chinook salmon). In addition, a number of fish from each run had no telemetry or recapture information following release. Accounting for more of these fish would require substantial monitoring effort—our telemetry coverage in this area was limited to several tributaries in 1996 and 1998 only.

Escapement variability -- The finding of significant escapement variation between species, years, seasons, and stocks was expected. Survival during egg-fry, freshwater rearing, and marine life history stages varies widely among Pacific salmonids (Groot and Margolis 1991; Bradford 1995) as a result of environmental conditions like temperature and discharge, habitat quality, and both density dependent and density independent factors. Similar survival variance was also expected to occur for returning adults given the wide range of seasonal and annual river environments, run size, harvest schemata, and hydrosystem operations encountered during upstream migration. Large annual differences in within-run stock composition and timing (e.g., Keefer et al. 2004b), hatchery contributions, and overall Columbia basin stock diversity (Nehlsen et al. 1991; Waples et al. 2004) also support a predisposition to variable pre-spawn migration success. The inter- and intra-annual escapement variability we observed may have been related to intrinsic stock-specific differences such as vulnerability to fisheries, susceptibility to adverse water temperatures (MacDonald et al. 2000; McCullough 2001; Cooke et al. 2004; Naughton et al. 2005), or underlying genetic characteristics (e.g., Unwin et al. 2003). Initial fish condition upon entering the hydrosystem, including fungal, disease, or parasite loads, frequency and severity of pinniped injuries (Harmon et al. 1994; Fryer 1998), and energetic reserves (Rand and Hinch 1998) may also have influenced observed escapement patterns.

Within-year and among-stock escapement variability strongly suggest that management and operational strategies will not affect all adult migrants equally. Managers should consider timing of runs, stock composition within runs, river environment while stocks of concern are migrating, and dam operations that affect the likelihood of adult fallback when setting escapement goals.

River environment -- The only strong inter-annual escapement effect we identified related to river environment was that spring–summer Chinook salmon escaped at lower rates in high-discharge years. This may reflect general passage difficulty, increased fallback, delay, or orientation problems when flows are high. Losses due directly to bioenergetic exhaustion may also occur (Dodson 1997). Slowed and/or failed migration due to depletion of energy reserves or difficult migration environments have been reported for sockeye (*O. nerka*) and pink (*O. gorbuscha*) salmon (Gilhousen 1990; Standen et al. 2002; Crossin et al. 2003), Atlantic salmon (*Salmo salar*) (Gerlier and Roche 1998; Gowans et al. 1999), and Chinook salmon (Schreck et al. 1994; Geist et al. 2000). In contrast to spring–summer Chinook salmon, inter-annual escapement responses to measured environmental variables were not significant for fall Chinook salmon or steelhead. We suspect, however, that more definitive patterns would emerge with longer data series (steelhead were studied here for five years, and fall Chinook for four years). The significant observed within-year escapement variability for fall Chinook salmon and steelhead (see Figure 3) suggest that environmental factors like temperature may have a large impact for individual fish or groups of fish migrating during the warmest periods. Lower escapement was observed for steelhead migrating early in the season, and many of those fish encountered peak summer temperatures during migration. Such within-year impacts were somewhat masked in this summary because we focused on inter-annual comparisons. Additional (unpublished) individual-based analyses on exposure to high temperatures suggests that steelhead and fall Chinook salmon that have long exposure times to high main stem temperatures escape at lower rates. Naughton et al. (2005) similarly found dramatically reduced escapement for radio-tagged Columbia River sockeye salmon migrating during the warmest period in 1997.

Preliminary analyses using individual fish exposure histories and fates (as opposed to annual escapement estimates) suggest that more significant survival effects related to river environment can be detected with the telemetry database. Research at this individual-fish scale is in progress (also see Goniea 2002 and High 2002). Water temperatures in the Columbia hydrosystem routinely reach levels that can reduce adult survival (McCullough 1999; McCullough et al. 2001), and compromised migrations might be expected given evidence from other studies (Major and Mighell 1967; MacDonald et al. 2000; Baigun 2000; Cooke et al. 2004). Steelhead and fall Chinook salmon, which migrate during peak temperatures in August and September, are the stocks most likely to have negative temperature-related impacts. Late-migrating summer Chinook salmon may also be susceptible to adverse temperature exposure in some years.

Harvest -- Although 12 Columbia basin salmon and steelhead stocks are listed as threatened or endangered (NMFS 2000), mainstem mixed-stock fisheries continue in the Columbia and Snake rivers. Fisheries have been strictly managed in an effort to protect listed populations and reverse continued declines of native runs, with quotas set using predicted run size and run composition criteria, and adjusted within seasons (Lestelle and Gilbertson 1993; ODFW & WDFW 2000). Assessments of impacts on specific stocks, however, remain imprecise. Use of known-source fish in this study provided relatively specific information on the magnitude and distribution of stock-specific harvest upstream from Bonneville Dam. Data from the transmitter reward program suggest harvest rates of 9 to 20% for endangered upper Columbia River steelhead, as high as 17% for threatened Snake River spring–summer Chinook salmon, and as high as 25% for threatened Snake River fall Chinook salmon. Actual harvest of these stocks was likely higher than indicated, because we could only account for voluntarily reported harvest. Illegal and/or unreported harvest did occur, but was difficult to quantify with the telemetry data.

The majority of radio-tagged known-source fish were hatchery derived, but should have been good surrogates for co-migrating wild ESU populations because most harvest of these groups was in the lower hydrosystem in unselective, mixed-stock tribal fisheries. Further restrictions on the timing (e.g., Merritt and Roberson 1986; Hendry et al. 2002), distribution (McPherson et al. 2003), or selectivity of mainstem fisheries may be needed to enhance escapement, productivity, and recovery of the listed populations (Potter et al. 2003). In addition, a large number of known-source fish from the Snake River basin were transported as juveniles, and we did not examine effects of transportation on adult escapement for this report. Unintended consequences of juvenile transportation for adult fish can include reduced homing, increased straying into non-natal tributaries, and delay, disorientation or confusion at dams (Mundy et al. 1994; Bugert et al. 1997; Chapman et al. 1997). Our preliminary analyses using the radio-tagged fish in this study indicate that juvenile transportation may reduce adult survival through indirect effects like increased fallback at dams.

Fallback -- Following harvest, the greatest attributable loss of adult migrants was tied to fallback over dams. Adult fallback can result in longer hydrosystem passage times (Keefer et al. 2004a), longer exposure to harvest, greater energetic expenditures for reascending fish, possible impaired homing, and potential injury or mortality (Dauble and Mueller 1993, 2000; Boggs et al. 2004a). One or a combination of these factors may explain the significantly reduced escapement observed for unknown-source fallback fish (reductions of 3-10% for spring–summer Chinook salmon, 11-26% for fall Chinook salmon, and 8-20% for steelhead). Escapement reductions for Snake River spring–summer Chinook salmon and steelhead were higher than for unknown-source groups, perhaps because these stocks must pass more dams than downstream stocks or because some (e.g., Snake River spring Chinook) migrated through the system when discharge was highest. The larger negative consequences for fall Chinook salmon and steelhead—compared to spring–summer Chinook salmon—may also have been a function of run timing. These migrations coincided with periods of reduced or zero spill at dams in fall when available fallback routes (through generating turbines, ice/trash sluiceways, or juvenile bypass systems) may be less benign than via spillways, the most-used route when spill occurs (Wagner and Hilsen 1992; Boggs et al. 2004a).

The tendency for fallback to increase with Columbia and Snake River discharge (reviewed in Bjornn and Peery 1992), may partially explain the negative discharge-escapement relationship we observed for spring–summer Chinook salmon. Hydrosystem and dam-specific fallback rates were highest in high-discharge years (Bjornn et al. 2000a-c; Boggs et al. 2004a), coincident with the lowest spring–summer Chinook escapement values. Parsing out what portion of the observed lowered escapement was directly due to discharge and/or dam operations like spill, or indirectly to route-searching or overshoot of natal tributaries was beyond the scope of this report. Here we report only hydrosystem-wide effects of fallback; however, the impacts of dam-specific fallback appear to follow similar patterns of lower escapement by fallback fish (unpublished data). Given these results, managers should consider strategies to reduce unwanted fallback, particularly at Bonneville and The Dalles dams, where fallback rates tend to be highest (Boggs et al. 2004a) and the greatest numbers of stocks are affected. Further research is needed to determine whether fallback-related loss can be mediated through structural or operational hydrosystem modifications (e.g., Reischel and Bjornn 2003), and to describe what proportion of the loss can be attributed to initial fish condition, fish origin, juvenile rearing and transportation history, and/or other factors.

Reach-specific patterns -- Partitioning fish fates for individual hydrosystem reaches indicated that greater attrition occurred for both species and all runs in lower portions of the hydrosystem. Dauble and Mueller (2000) also found reduced survival in lower Columbia River reaches relative to lower Snake River reaches. Using estimates of dam passage, harvest, hatchery return, and tributary turnoff, Dauble and Mueller (2000) calculated mean inter-dam conversions (1979-1998) for spring Chinook salmon of 0.885 through lower Columbia and 0.939 through lower Snake River reaches; means were 0.913 and 0.995, respectively, for summer Chinook. The current radiotelemetry results are likely more accurate, particularly in quantifying tributary turnoff and correctly accounting for multiple dam passage events and concomitant count inflation following fallback. Although methodologies of Dauble and Mueller (2000) differed from this telemetry project, results were qualitatively similar, and clearly indicated greater adult loss in the lower river. This pattern may reflect loss associated with unreported or illegal harvest, direct or delayed mortality following contact with fisheries, or more difficult passage environments at lower Columbia River dams or reservoirs. Among passage concerns, high fallback rates at Bonneville and The Dalles dams (Boggs et al. 2004a), long passage times for all runs at John Day Dam (Keefer et al. 2004a), and slow passage and temporary straying by fall Chinook salmon and steelhead (Goniea 2002; High 2002) may have direct escapement consequences.

Unaccounted-for fish -- Distinguishing between mortality and other fates is difficult for non-recovered individuals in many animal survival studies (e.g., Pahlke and Bernard 1996; Francis and Saurola 2002; Heupel and Simpfendorfer 2002; Bjorndal et al. 2003; Gardali et al. 2003). Animals not detected or recovered may have died, emigrated to unsurveyed areas, been removed from the population through unreported or illegal harvest, or survived yet been 'unobservable' for biological or methodological reasons (Lebreton et al. 1992; Kendall and Nichols 2002). Additional possible false negatives for the radio-tagged adult salmonids in this study include undetected mainstem spawning and fish that lost transmitters. Hydrosystem escapement estimates here were principally derived from known survivors and known harvest within the monitored area. These estimates should therefore be accurate, but should be considered minimums given uncertainty regarding the 12 to 17% of each run with unknown fate. Some unknown-fate fish were likely harvested but not reported: had this harvest been identified, Esc_1 and Esc_2 estimates would have been unchanged, while Esc_3 estimates would be higher. Other fish may have spawned at mainstem sites, although only very small aggregations of adults (mostly fall Chinook salmon) have been reported spawning in hydrosystem reservoirs and dam tailraces (Dauble et al. 1999; Groves and Chandler 1999). Proportions of fish with unknown fates as a result of tag loss should also have been small. Mean transmitter regurgitation rates of 2 to 4% were recorded for Snake River fish (Keefer et al. 2004c), but these fish were identified as successful in our escapement estimates, as were fish collected at hatcheries without transmitters or detected only by PIT-tag readers at upper Columbia River dams. A final component—undetected tributary entry or hydrosystem exit—should have been minimal given intensive telemetry coverage at dams, in reservoirs, in hydrosystem tributaries, and upstream from the bounded study area. Detection efficiencies suggest that bias due to missing individual antennas should have been minimal (Naughton et al. 2005).

Conclusion -- These results represent some of the most comprehensive fate, upstream passage, and escapement data ever collected for adult Chinook salmon and steelhead. From the combined telemetry, fishery reward, and PIT-tag databases, it was possible to quantify adult escapement variability, geographically and temporally partition harvest and loss, and contrast escapement patterns between species, runs, and specific stocks. Such summaries should aid managers working to fill gaps in understanding the adult ecology of upstream-migrating salmonids (Dauble and Mueller 1993; 2000; NMFS 2000). Results should also allow managers to target areas where losses are unacceptably high or where stock impacts differ from desired levels.

Given the dramatic and continuing declines in wild Columbia basin salmon and steelhead (Karieva et al. 2000; McClure et al. 2003), we believe additional attention should be afforded returning adults. Small increases in adult escapement within the Columbia River hydrosystem have the potential to directly increase productivity, particularly for wild and listed stocks. Finally, these data will provide a valuable Columbia River basin benchmark for adult fish as management strategies, legal requirements, and environmental conditions continue to evolve.

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Appendix 1. Summary of locations of fixed aerial and underwater antennas at dams, mainstem Columbia and Snake River sites, and tributaries in 2002. Sites included here are representative of monitoring effort in 2000-2002. All sites monitored in 1996-1998 are also included here, although effort was typically less in those years. Exact configurations differed in each study year to accommodate evolving research objectives.

Site	Antennas[1]	River kilometer
Dams[2]		
Bonneville Dam	81	~235
The Dalles Dam	28	~308
John Day Dam	28	~346
McNary Dam	39	~470
Ice Harbor Dam	23	~538
Lower Monumental Dam	24	~589
Little Goose Dam	20	~635
Lower Granite Dam	25	~695
Priest Rapids Dam	3	~639
Other mainstem Columbia and Snake River sites		
Fort Rains	1	235
Bridge of the Gods	1	239
Stevenson boat launch	1	243
Carson Depot Road	1	247
Across from Depot Road	1	247
Hood River Bridge boat launch	1	273
Bingen Marina	1	276
Mayer State Park	1	293
Lone Pine	1	308
Wishram	1	325
Biggs Bridge	1	335
John Day Dam boat launch	2	~345
John Day River boat launch	1	351
Pasture Point boat launch	1	364
Sundale Park	1	382
Roosevelt	1	390
Pine Creek boat launch	1	401
Alder Creek	1	415
Patterson	1	443
Fish Hook Park	1	550
Hanford	2	~553
Walker	1	570
Ayers boat launch	1	604
Willow Creek boat launch	1	659
Asotin	1	762
Heller’s Bar	1	792
Doug’s Bar	1	838
Tributaries[2]		
Herman Creek	1	243

Wind River	2	~249
Little White Salmon River	3	~260
White Salmon River	4	~270
Hood River	1	273
Klickitat River	1	291
Deschutes River	2	~328
Sherars Falls	1	396
Oak Springs	1	405
John Day River	1	356
Rock Creek	1	370
Umatilla River	1	467
Walla Walla River	1	526
Yakima River	1	546
Naches River	1	732
Roza Dam	1	745
Lyons Ferry Hatchery	1	616
Clearwater River	1	753
SF Clearwater River	1	868
Lochsa River	1	904
Selway River	1	906
Grande Ronde River	1	795
Salmon River	1	826
Lower Salmon River	1	963
SF Salmon River	1	1,095
MF Salmon River	1	1,144
Upper Salmon River	1	1,204
Imnaha River	1	853

[1] aerial and underwater combined

[2] additional sites at upper Columbia River dams and tributaries monitored by Public Utility Districts