Technical Report 2006-2

IDAHO COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT

NON-DIRECT HOMING BY ADULT SPRING–SUMMER CHINOOK SALMON: TRIBUTARY OVERSHOOT, OVERSHOOT FALLBACK, AND TEMPORARY NON-NATAL TRIBUTARY USE IN THE COLUMBIA RIVER BASIN

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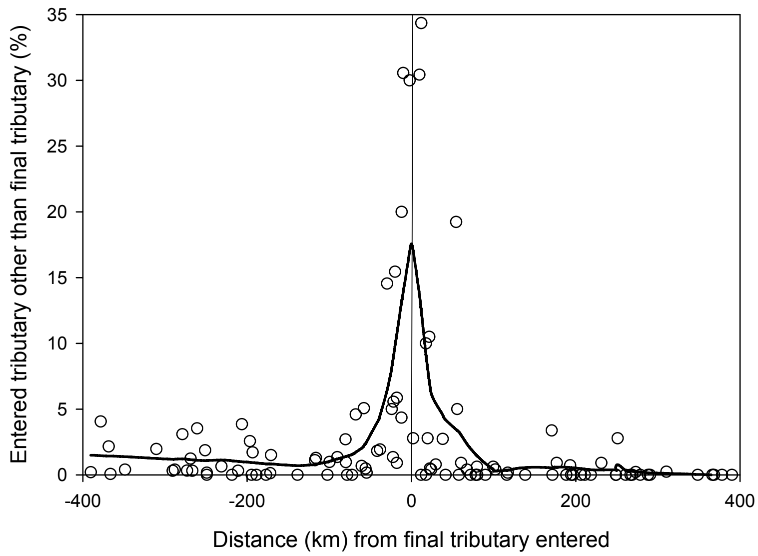

for

U.S. Army Corps of Engineers
Portland and Walla Walla Districts
Portland, Oregon and Walla Walla, Washington

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Preface

Managers of Columbia River basin salmonids *Oncorhynchus* spp. are interested in the circumstances of adult migrants that fail to pass dams, as well as why some fish fall back over dams. Some failed passage attempts and fallback events can be linked to dam operations, but others are probably the result of orientation and homing behaviors unrelated to dams, including overshoot of natal tributaries. In this report, we present summary information on overshoot behavior of radio-tagged adult spring–summer Chinook salmon from 1996-2003. We also examined relationships between overshoot, temporary straying, and a suite of fish characteristics (e.g. sex, origin, migration timing).

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

Acknowledgements

Many people provided time and assistance during the course of this study. We especially acknowledge T. Bjornn and L. Stuehrenberg. R. Ringe, K. Tolotti, M. Jepson, S. Lee, T. Clabough, G. Naughton, W. Daigle, M. Heinrich, D. Queampts, M. Morasch, T. Dick, M. Faulkender, D. Joosten, C. Nauman, and C. Williams helped with field operations and collection and processing of telemetry data at the University of Idaho. A. Matter, S. McCarthy, K. Frick, and T. Bohn, NOAA-Fisheries, helped with data management. We also thank the many collaborating agency staff who PIT-tagged juvenile fish and allowed radio-tagging of these groups. The U.S. Army Corps of Engineers provided funding for this study; we thank D. Clugston, M. Shutters, R. Dach, M. Langeslay, and T. Mackey, for their assistance.

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Abstract

Homing movements of adult salmon and steelhead in the Columbia River system is a poorly understood aspect of migration, yet has important ecological and management implications. In this study, three migration behaviors—overshoot of natal tributaries, fallback at dams upstream from natal tributaries, and temporary non-natal tributary use—were evaluated for more than 5200 radio-tagged spring–summer Chinook salmon *Oncorhynchus tshawytscha*. Over seven years, from 1% to almost 80% of eleven Columbia River study stocks initially overshot natal tributaries and were recorded at upstream Columbia or Snake River dams (*mean* = 29%). Smaller proportions of each stock were recorded falling back at upstream dams (*range* = 0–49%, *mean* = 17%). The contribution of overshoot fallback to total fallback by salmon that returned to tributaries was approximately 20% at The Dalles, John Day, and Ice Harbor dams and was about 40% at McNary Dam. Proportions that temporarily entered non-natal tributaries ranged from 8% to 42% (*mean* = 22%) of each stock. Overshoot, overshoot fallback, and temporary tributary use behaviors were greatest when spawning tributaries and/or dams were in close geographic proximity. For example, 39% of Klickitat River salmon fell back at The Dalles Dam, 49% of Umatilla River salmon fell back at McNary Dam, and salmon from Bonneville pool tributaries were most likely to temporarily use nearby tributaries. In multivariate models, hatchery origin, fish sex, migration timing, and fallback at both upstream and downstream dams were also associated with non-direct homing behaviors. Overshoot and temporary tributary use events were complex and inter-related, likely reflecting a combination of active searching for olfactory cues from natal tributaries, behavioral thermoregulation, and geographic proximity among sites.

Introduction

This radiotelemetry study was undertaken to address concerns of the U.S. Army Corps of Engineers (USACE) and Bonneville Power Administration (BPA), state and federal fishery managers, and native American tribes regarding upstream passage success of Columbia River adult salmon and steelhead (*Oncorhynchus* spp.). Adult passage concerns were raised in section 603 of the Northwest Power Planning Council's 1987 Columbia River Basin Fish and Wildlife Program, and described in the Biological Opinions issued in 1995, 1998, and 2000 for operation of the Federal Columbia River Power System (Hydrosystem). These agencies and opinions recommended studies to ensure that adult salmonid passage past dams and reservoirs was as efficient as possible.

Beginning in 1995, adult study plans were developed for the Hydrosystem in consultation with USACE and biologists and managers from other federal, state, and tribal agencies. The resulting project has addressed a wide range of adult passage questions over multiple years, including fish passage and survival rates (Keefer *et al*. 2004c; Keefer *et al*. 2005a; Naughton *et al*. 2005; Caudill et al. *in review*), fallback at dams (Reischel and Bjornn 2003; Boggs *et al*. 2004), homing and straying (Keefer *et al*. 2005b), effects of dissolved gas and temperature (Peery *et al*. 2003; Johnson *et al*. 2005), and others (see www.cnr.uidaho.edu/ferl for a complete list of reports). Deployment of an extensive radiotelemetry monitoring array—at dams, in reservoirs, and in tributaries—has allowed us to reconstruct detailed migration histories for thousands of adult migrants. These histories have made it possible to examine multiple inter-relationships between migration behaviors, environmental conditions, and fish fates.

In this report, we summarize several homing behaviors with implications for management: overshoot of natal tributaries within main stem Columbia River reservoirs, overshoot fallback at Columbia and Snake River dams, and temporary use of non-natal tributaries. These behaviors illustrate that many salmon do not directly home in the Columbia River system, although homing precision is widely accepted as a fundamental life history characteristic of *Oncorhynchus* species. Salmon homing to natal river systems, and even to specific spawning sites (Quinn *et al*. 1999; Bentzen *et al*. 2001), is thought to reflect adaptation to local conditions and has resulted in the establishment of substantial variation among populations within species (Quinn *et al*., 2000; Beacham *et al*. 2002; Hendry *et al*. 2002). Such homing accuracy is largely attributed to olfactory imprinting on chemical cues present in home waters and during outmigration by juveniles and subsequent recognition of odors as returning adults (Hasler & Scholz 1983; Quinn *et al*. 1989).

To successfully home, salmon must make a series of correct orientation decisions at river confluences and/or dams or other obstacles. When confronted with orientation choices, homing salmon make a variety of searching, proving, temporary straying, and exploratory movements, some of which have been described qualitatively (Ricker 1972; Burger *et al*. 1995; Griffith *et al*. 1999). Most homing studies have identified start and endpoints of migration such as marking juveniles and recapturing adults at spawning grounds and hatcheries. This emphasis has provided relatively few details about the process of homing, however, and is a simplification of homing behaviors. Here, we used the multi-year Columbia River radiotelemetry study to examine route selection decisions by adult Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) at the confluences of major spawning tributaries and within the main stem Columbia River. Over seven years, more than 5200 adult Chinook salmon from 11 tributary basins were monitored. We assessed fine-scale salmon movements among main stem and tributary sites, as well as permanent straying for a sub-sample (21%) of the salmon whose natal streams were known *a priori* from PIT-tags implanted in outmigrating juveniles (also see Keefer *et al*. 2005b). The 11 study stocks migrated in the lower Columbia River during the same season, but returned to sites throughout the basin. This wide spatial distribution of tributary streams made it possible to assess how geographic proximity was related to overshoot, overshoot fallback, and temporary tributary use by salmon. At the individual-fish scale, we developed statistical models describing the relationships between the likelihood of overshoot, overshoot fallback, and temporary tributary use and a suite of fish characteristics, fish behaviors, and migration conditions.

Methods

Study area. – The Columbia River and its principal tributary, the Snake River, drain approximately 673,000 km^2 of the northwestern United States and southeastern British Columbia, Canada (46º N, 124º W; Figure 1). Much of the Columbia River main stem is impounded by a series of fourteen hydroelectric dams, starting with Bonneville Dam at river kilometer (rkm) 235 and ending at Mica Dam (rkm 1539) in Canada. Major spawning tributaries for spring–summer Chinook salmon enter the Columbia River from the river mouth to Chief Joseph Dam (rkm 877). The Snake River enters the Columbia River at rkm 521 and is impounded by 16 mainstem dams (to approximately rkm 1900 from the Columbia River mouth). Most Snake River salmon must pass eight dams, four on the lower Columbia River and four on the lower Snake River, before reaching spawning areas. Anadromous fish passage is currently blocked at Hells Canyon Dam on the Snake River (rkm 919 from the Columbia River mouth). Salmon stocks described in this report returned to all major spawning tributaries upstream from the Bonneville Dam collection site. The studied behaviors occurred in the ~ 400-km reach between Bonneville Dam and Priest Rapids Dam (rkm 639) or Ice Harbor Dam (rkm 538) (Figure 1).

Fish collection and monitoring. – Spring–summer Chinook salmon enter the Columbia River estuary from late winter through mid-summer on their upstream migration. In most years, the earliest migrants arrive at Bonneville Dam in March, but the majority of the annual run enters the study reach between early April and late July. Spawning typically occurs in tributaries from August through October, but varies considerably among populations and life history types. Juveniles of the spring component and some summer-run fish spend a year or more rearing in freshwater before outmigrating (stream-type Chinook salmon, Healey 1991), and spawn mostly in cold, high-elevation streams (Myers *et al*. 1998). Another group of summer-run fish, primarily those in the upper Columbia basin, move rapidly to the ocean following emergence (ocean-type). Adults of this group tend to select lower elevation spawning sites as adults and spawns later in the autumn (Brannon *et al*. 2004). Adult migration timing through the main stem Columbia River overlaps considerably for the two life history types, however, and they are often combined for management and research objectives.

Fish from all major spring and summer Chinook salmon populations upstream from Bonneville Dam were collected, in approximate proportion to the stock composition and timing of each annual run (see Keefer *et al*. 2004b and Appendix A). Salmon were trapped at the Bonneville Dam adult fish facility on the north shore of the river, from early

April through mid- to late July in seven of eight years (1996-2003, excluding 1999). Trapping procedures, fish anesthetization, gastric insertion of radio transmitters, and fish recovery are described in Keefer *et al*. 2004a. A total of 6710 Chinook salmon were radio-tagged and randomly assigned to release sites on both sides of the river about 10 km downstream from Bonneville Dam. Of these, 3741 (56%) were last recorded in Columbia River tributaries between Bonneville and Priest Rapids dams, and another 1528 (23%) were last recorded in tributaries or the main stem Columbia River upstream from continuous monitoring sites at Priest Rapids Dam (Table 1). Stock designations were assigned based on final fish distribution among the major drainages, resulting in 11 study stocks. More precise stock separation is possible within these major drainages (e.g. Nehlsen *et al*. 1991; Keefer *et al*. 2004b), but these operational groupings allowed standardized monitoring of movements among the major drainages given the existing telemetry array.

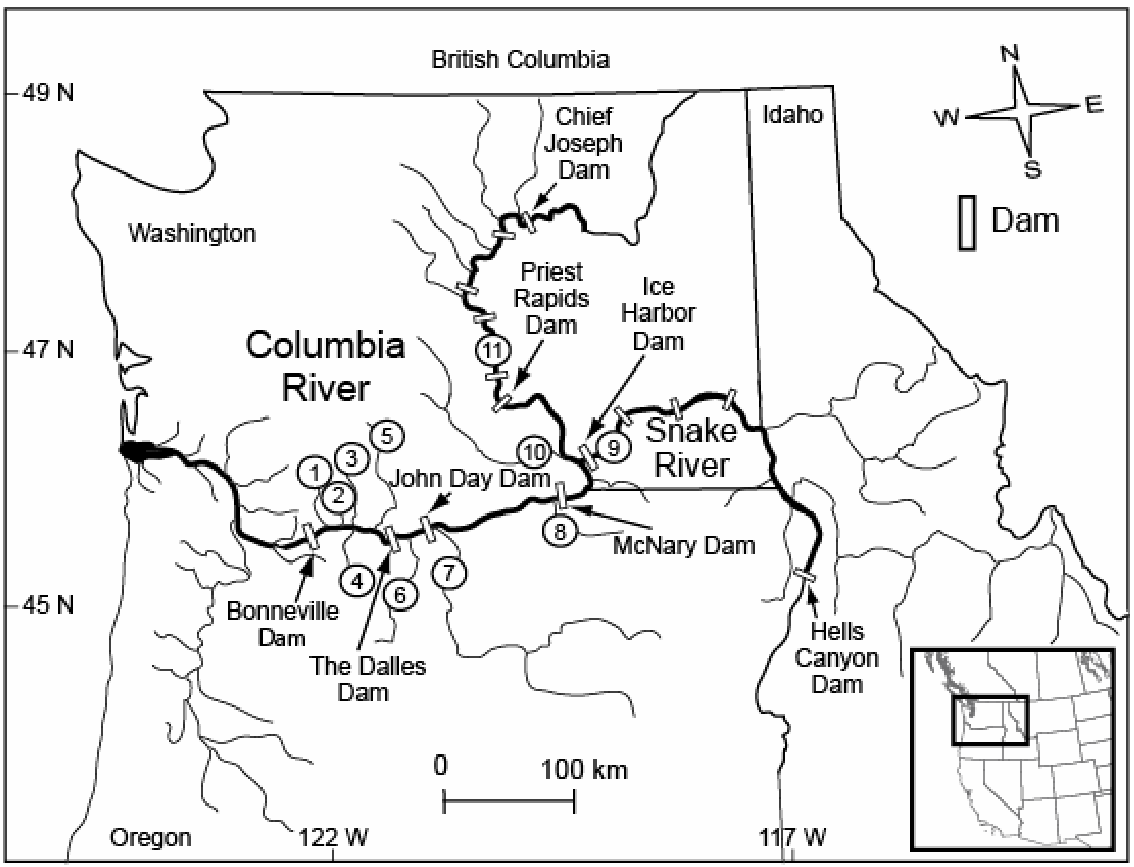

Figure 1. Columbia River system showing natal basins of the 11 studied spring–summer Chinook salmon populations, the collection site (Bonneville Dam), and main stem dams and tributaries where overshoot and temporary straying behaviors were monitored. Study basins: 1) Wind, 2) Little White Salmon, 3) White Salmon, 4) Hood, 5) Klickitat, 6) Deschutes, 7) John Day, 8) Umatilla, 9) Snake, 10) Yakima, and 11) upper Columbia rivers.

Starting in 2000, each annual sample included some salmon that had received passive integrated transponder (PIT) tags as juveniles (Prentice *et al*. 1990). PIT tags identified natal streams or rivers, and these “known-origin” sub-samples were useful for validating stock assignments and fish behaviors, including permanent and temporary inter-basin straying and natal-river overshoot. Unless stated otherwise, salmon were classified by final location, and known-origin data were used only for *post hoc* evaluations and permanent straying summaries. Overall, 1081 of the 5269 study fish (21%) had been PIT tagged as juveniles. Agreement between stock assignment based on PIT-tagging location and final telemetry records was >97%. PIT-tagged samples were not random with respect to stock, reflecting juvenile monitoring priorities that favored upper basin fish. Six drainages had PIT-tagged salmon: the Snake (*n* = 518), upper Columbia (341), Yakima (147), Wind (52), John Day (19), and Umatilla (4) rivers. Selection for PIT-tagged fish likely increased sample sizes for some of these stocks in later years, but were unlikely to seriously bias our estimates of fish behaviors. In general, upstream passage proportions were very similar among radio-tagged salmon and all spring–summer Chinook salmon counted passing fish ladders (Appendix A). For example, the proportions of radio-tagged fish that passed Ice Harbor Dam differed from proportions based on counts at ladders by an average of 2.9%. Differences averaged 5.1% at McNary Dam and 7.1% at Priest Rapids Dam, These relatively small sample biases were not consistently in one direction, suggesting the overall sample was a relatively good surrogate for the runs at large.

Fish movements in the main stem Columbia River and into tributaries were monitored with fixed radiotelemetry sites consisting of one or more antennas and data-storage receivers (Lotek Wireless Inc., Newmarket, Ontario, Canada)[1]. Aerial Yagi antennas were placed in tributaries near confluences with the Columbia River, but far enough upstream so that radio-tagged salmon passing in the Columbia River would not be detected. Extensive arrays of aerial and underwater antennas were also deployed to monitor salmon at all lower Columbia and lower Snake River dams (arrays described in Boggs *et al*. 2004, Keefer *et al*. 2005a, and Naughton *et al*. 2005), as well as at all fish ladder passage routes at Priest Rapids Dam.

Statistical analyses. – Describing the movements of adult salmon with respect to homing is difficult because accurate terms are context-dependent. For instance, all upstream migration movements could be termed “homing,” even if they result in eventual migration failure or return to non-natal sites. Chinook salmon migration movements in this study were operationally classified into four basic behaviors. “Direct homing” was where salmon moved up the Columbia River main stem and then entered and remained in a single tributary (presumably the natal site). Three alternatives to direct homing were identified: 1) overshoot of final tributary sites in the main stem Columbia River or Snake River, 2) temporary use of a tributary other than the final tributary, and 3) permanent inter-basin straying as determined from known-origin fish.

Overshoot within the main stem was defined by detection of a fish at one or more Columbia River or Snake River dams upstream from a fish’s final tributary. The definition of overshoot was restricted to main stem sites to differentiate the behavior from temporary use of other tributaries and because detection rates at dams were > 99%. A portion of the overshoot fish passed dams upstream from final locations and subsequently fell back at one or more dams in order to return. This sub-category of overshoot is referred to as overshoot fallback. Temporary tributary use was defined as salmon detection in one or more tributaries other than their final tributary. For between-

[1] Note – Use of trade names does not constitute endorsement by the USGS or US Army Corps of Engineers

stock comparisons, overshoot and temporary tributary use were expressed as binary responses (*i.e.* individual salmon either did or did not overshoot). Proportions that temporarily entered multiple alternative tributaries or that overshot more than one dam were also described. Identification of permanent straying was only possible for the known-origin salmon, and stray estimates were calculated for these groups only. Given non-random collection of known-origin salmon, straying summaries for basins receiving strays were necessarily qualitative.

The likelihood of overshoot, overshoot fallback, and temporary tributary use by individual salmon was examined using logistic regression. Predictor variables included fish characteristics (stock, estimated sex, length, presence of fin clips), migration environment (year, release date, spring versus summer run timing, Columbia River discharge on date of tagging), and fish behaviors. Predictor behaviors for overshoot and overshoot fallback models included whether individuals had fallen back (Boggs *et al*., 2004) over a downstream dam prior to overshoot, and a categorical temporary tributary use variable (no temporary tributary use, 1 alternate tributary entered, >1 alternate tributaries entered). Predictor behaviors for temporary tributary use models included fallback at up- and downstream dams, and a categorical overshoot variable (no overshoot, overshot 1 dam upstream, overshot > 1 dam upstream). Columbia River discharge on the release date was a good relative measure of river conditions each fish encountered, as most spring–summer Chinook salmon move through the study area quickly (Keefer *et al*. 2004c). Release date was a good surrogate measure of Columbia River water temperature, as these are highly correlated during the studied migrations (Keefer *et al*. 2004c; Naughton *et al*. 2005). The use of fin clips as an independent variable was to help differentiate hatchery fish from wild fish, although fin-clipping was not a universal hatchery protocol. Although the personnel tagging fish were all experienced with salmon sex identification, the accuracy of sex estimates was not evaluated introducing some uncertainty for this variable. We also evaluated several interaction terms, based on previous research indicating that salmon fallback and/or straying vary by year (Boggs *et al*. 2004), among hatchery and wild fish (Quinn 1993), and by sex (Hard & Heard 1999). Interaction terms including stock were also examined, but models with these terms resulted in quasi or complete separation of data (Hosmer & Lemeshow 2000) and were therefore discarded.

We used information-theoretic techniques to identify the model(s) that provided the best description of the data (Burnham & Anderson 2002). The candidate model sets were developed using several *a priori* subsets of the predictor variables (*i.e.* all fish characteristics, migration environment, or fish behaviors) as well as the two most parsimonious subsets identified using backward stepwise regression (Hosmer & Lemeshow 2000). Models were evaluated using Akaike's Information Criterion (AIC). The AIC model selection procedure is effective for observational data because it allows simultaneous comparisons between multiple similar models, balances precision and bias, and is parsimonious (Burnham & Anderson 2002). Models were ranked by AIC (lower values indicate a better fit) and evaluated with respect to ΔAIC (the change in AIC relative to the 'best' model) and Akaike weights (w_i), which measure the weight of evidence for each model considered (Buckland *et al*. 1997; Burnham & Anderson 2002).

Results

Overshoot of tributaries. – Main stem overshoot percentages ranged from more than 70% for radio-tagged Chinook salmon from the Klickitat and Umatilla rivers to less than 1% for Snake River and Yakima River stocks (Table 1). Salmon that overshot were recorded as far as four dams upstream (>250 km) from their final tributary confluence, although the majority (77%) were detected only at the nearest upstream dam (*mean* = 56 km; median = 43 km). These fish did not necessarily pass the upstream dam. Notably, about 10% of the salmon that overshot final sites had entered and exited their final tributary prior to the overshoot-and-return behavior.

Main stem overshoot percentages were strongly related to the proximity between tributary mouths and upstream dams (Figure 2). Percentages were highest when final tributaries were near dams and declined exponentially as the distance between confluences and upstream dams increased ($r^2 = 0.77$, $P < 0.001$). A similar exponential decline was found when individuals overshooting final tributaries by more than one dam were excluded.

Table 1. Number of radio-tagged Chinook salmon last recorded in each tributary, and the percentages (%) that overshot their final sites, as determined by detection at upstream dams, 1996-2003. Dams are located at river kilometer (rkm) 308 (The Dalles Dam), 346 (John Day Dam), 470 (McNary Dam), 538 (Ice Harbor Dam), and 639 (Priest Rapids Dam) from the Columbia River mouth. Single-dam overshoot proportions in bold text. Dashes indicate tributary is downstream of dam.

			Proportion detected at upstream dams (%)				
Final tributary	rkm	*n*	The Dalles	John Day	McNary	Ice Harbor[1]	Priest Rapids
Wind	249	486	**6.2**	1.0	0.4	0.2	
Little White Salmon	261	253	**14.2**	1.6			
White Salmon	271	36	**38.9**	8.3	2.8	2.8	
Hood	273	20	**55.0**	10.0	5.0		
Klickitat	290	110	**70.9**	20.0	7.3	0.9	
Deschutes	328	414	-	**14.5**	3.1	0.7	0.2
John Day	351	148	-	-	**8.8**	3.4	
Umatilla	467	78	-	-	**79.5**	19.2	
Snake	522	1872	-	-	-	-	**0.2**
Yakima	539	324	-	-	-	-	**0.6**
Upper Columbia[2]	639	1528	-	-	-	-	-

[1] on the Snake River
[2] overshoot not assessed

Among the candidate sets of multiple logistic regression models for overshoot behavior, backwards stepwise regression identified the two models with the lowest AIC values, while the global model (all variables included) had the lowest AIC score among models we identified *a priori* (Table 2). The two models identified by stepwise regression were identical except for the inclusion of sex as a predictor in model 7. AIC and Akaike weights (w_i) suggested a higher level of support for model 7 (Table 2), though there was considerable support for model 6 as well (ΔAIC = 2.7). In Model 7, among-stock differences accounted for the most variability ($\chi^2_9 = 367.3$, $P < 0.0001$) (Table 3), a pattern that was probably attributable to the differences in distance between tributaries and dams (Figure 2). Main stem overshoot was also significantly ($P < 0.0001$) associated with later migration, temporary use of alternate tributaries, prior fallback at a downstream dam, and the presence of fin clips (hatchery fish were more likely to overshoot) (Table 3). Males were more likely to overshoot than females. Two interaction terms were also selected in model 7 (downstream fallback×fin-clip and temporary tributary use×sex).

***Overshoot fallback**.* – Upon reaching a dam upstream from their spawning tributary, many fish retreated downstream rather than passing through the fishways, while others passed fishways and subsequently fell back over dams. Overshoot fallback percentages were consistently 2–3 times lower than the basic overshoot percentages reported in Table 1, which did not necessarily include an upstream dam passage. Patterns were very similar otherwise (Table 4). As with the more basic overshoot behavior, overshoot fallback was highest for those stocks whose tributary confluences were close to dams. Overshoot fallback was highest for Umatilla River salmon at McNary Dam (49%) and Klickitat River salmon at The Dalles Dam (39%). Rates were also > 10% for White Salmon and Hood River fish at The Dalles Dam, Klickitat River fish at John Day Dam, and Umatilla River fish at Ice Harbor Dam. Regression results of overshoot fallback and distance to upstream dams were qualitatively similar to those in Figure 2.

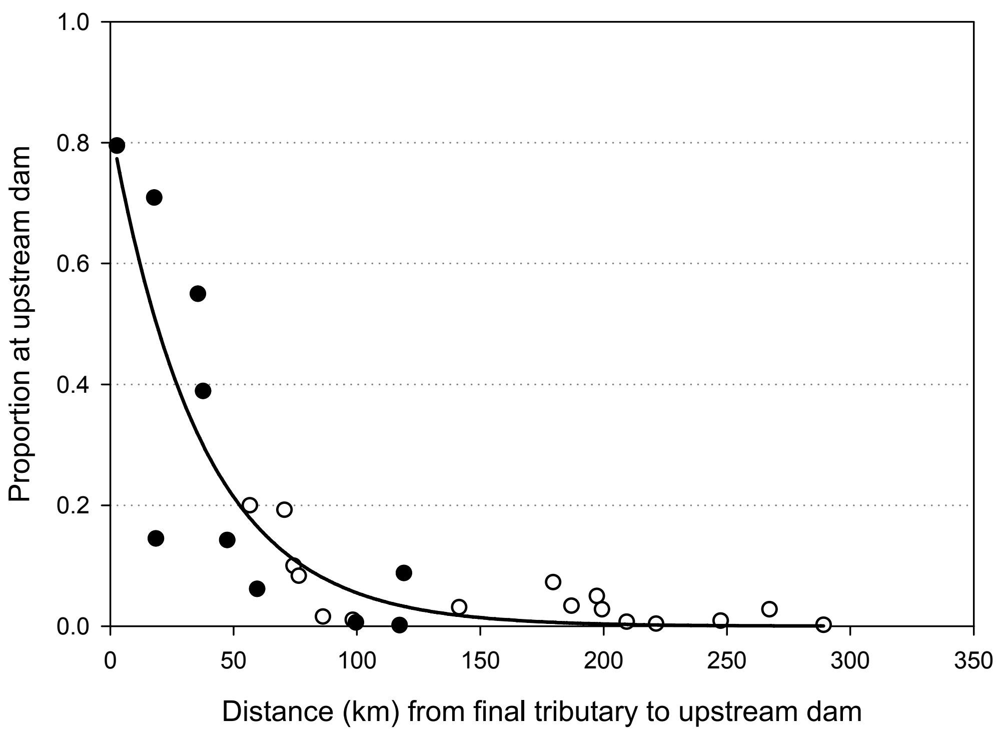

Figure 2. Relationship between overshoot behavior and distance from final tributary location for radio-tagged Chinook salmon. Overshoot events occurred when individuals were observed one or more dams upstream of their final tributary location. Symbols are overshoot percentages at the nearest upstream dam (●) and at dams further upstream (○). Curve (▬) is the exponential decay regression line that best fits the combined data ($r^2 = 0.77$; $y = (0.83 * e^{-0.027*x})$). Tributary-dam combinations with $n = 0$ were excluded.

Table 2. Candidate multiple logistic regression models testing for relationships between main stem overshoot (0,1) by individual Chinook salmon and predictor variables, 1996-2003. Models 1-5 were selected *a priori* and models 6 and 7 were the 'best' subsets identified using stepwise regression. Number of parameters (*K*) included the intercept and each explanatory variable. Models with a lower ΔAIC and a higher Akaike weight (w_i) have greater support. Salmon from the upper Columbia River basin were excluded because their overshoot behavior could not be assessed.

	Candidate models						
			A priori			'Best' subsets	
Variables	1	2	3	4	5[1]	6	7
Fish characteristics							
Stock	x	x	x	x	x	x	x
Sex	x	x	x	x	x		x
Length	x	x	x	x	x		
Fin-clip	x	x	x	x	x	x	x
River environment							
Year		x		x	x		
Date		x		x	x		
Run-type (spring, summer)		x		x	x	x	x
Flow		x		x	x		
Fish behaviors							
Downstream fallback			x	x	x	x	x
Temporary tributary use (0,1,>1)			x	x	x	x	x
Interaction terms							
Year×Downstream fallback					x		
Fin-clip×Downstream fallback					x	x	x
Sex×Downstream fallback					x		
Fin-clip×Temporary tributary use					x		
Sex×Temporary tributary use					x		x
K (df)	5 (12)	9 (21)	7 (15)	11 (24)	16 (36)	7 (15)	9 (18)
AIC	1224.9	1186.1	1173.3	1142.6	1138.6	1133.8	1131.1
ΔAIC	93.8	55.0	42.2	11.5	7.5	2.7	0.0
w_i	0.000	0.000	0.000	0.002	0.018	0.202	0.778

[1] Global model

Results of the multiple logistic regression model comparison for overshoot fallback were generally similar to those for main stem overshoot. Backwards stepwise regression identified the two models with the lowest AIC values, and the global model (all variables included) had the lowest AIC score among models we identified *a priori* (Table 5). The two models identified by stepwise regression were identical except for the inclusion of release date as a predictor in model 6. AIC and Akaike weights (w_i)

suggested a higher level of support for model 7 (Table 5), though support for model 6 was comparable (ΔAIC = 0.3). In Model 7, among-stock differences accounted for the most variability (χ^2_8 = 168.8, $P < 0.0001$) (Table 6), a pattern that was probably attributable to the differences in distance between tributaries and dams (Figure 2). (Note that the Snake River stock was excluded from this analysis because no Snake River fish fell back at Priest Rapids Dam.) Main stem overshoot was also significantly ($P < 0.01$) associated with temporary use of alternate tributaries, prior fallback at a downstream dam, the presence of fin clips, and later migration (Table 6).

Table 3. Results of the multiple logistic regression Model 7 (in Table 2) for predicting the probability of main stem overshoot by individual Chinook salmon, 1996-2003.

Parameter	*df*	Wald chi-square	*P*
Stock	9	367.3	<0.0001
Run-type	1	40.9	<0.0001
Temporary tributary use	2	19.5	<0.0001
Downstream fallback	1	19.0	<0.0001
Fin-clip	1	17.7	<0.0001
Downstream fallback×Fin-clip	1	9.1	0.0025
Sex	1	7.7	0.0055
Temporary tributary use×Sex	2	5.9	0.0516

Table 4. Number of radio-tagged Chinook salmon last recorded in each tributary, and the percentages (%) that were recorded falling back at upstream dams, 1996-2003. Dams are located at river kilometer (rkm) 308 (The Dalles Dam), 346 (John Day Dam), 470 (McNary Dam), 538 (Ice Harbor Dam), and 639 (Priest Rapids Dam) from the Columbia River mouth. Single-dam overshoot fallback proportions in bold text. Dashes indicate tributary is downstream of dam.

			Proportion that fell back at upstream dams (%)				
Final tributary	rkm	*n*	The Dalles	John Day	McNary	Ice Harbor[1]	Priest Rapids
Wind	249	486	**2.5**	0.6	0.2	0.2	
Little White Salmon	261	253	**3.6**	0.4			
White Salmon	271	36	**13.9**	2.8	2.8		
Hood	273	20	**30.0**	5.0			
Klickitat	290	110	**39.1**	11.8	4.5		
Deschutes	328	414	-	**7.5**	2.7	0.5	
John Day	351	148	-	-	**5.4**	1.4	
Umatilla	467	78	-	-	**48.7**	11.5	
Snake	522	1872	-	-	-	-	
Yakima	539	324	-	-	-	**0.9**	
Upper Columbia[2]	639	1528	-	-	-	-	-

[1] on the Snake River
[2] overshoot not assessed

Table 5. Candidate multiple logistic regression models testing for relationships between overshoot fallback (0,1) by individual Chinook salmon and predictor variables, 1996-2003. Models 1-5 were selected *a priori* and models 6 and 7 were the 'best' subsets identified using stepwise regression. Number of parameters (*K*) included the intercept and each explanatory variable. Models with a lower ΔAIC and a higher Akaike weight (w_i) have greater support. Salmon from the upper Columbia River and Snake River basin were excluded because their overshoot behavior could not be assessed (upper Columbia) or no overshoot fallback was recorded (Snake River).

	Candidate models						
	A priori					'Best' subsets	
Variables	1	2	3	4	5[1]	6	7
Fish characteristics							
Stock	x	x	x	x	x	x	x
Sex	x	x	x	x	x		
Length	x	x	x	x	x		
Fin-clip	x	x	x	x	x	x	x
River environment							
Year		x		x	x		
Date		x		x	x	x	
Run-type (spring, summer)		x		x	x	x	x
Flow		x		x	x	x	x
Fish behaviors							
Downstream fallback			x	x	x	x	x
Temporary tributary use (0,1,>1)			x	x	x	x	x
Interaction terms							
Year×Downstream fallback					x		
Fin-clip×Downstream fallback					x	x	x
Sex×Downstream fallback					x		
Fin-clip×Temporary tributary use					x		
Sex×Temporary tributary use					x		
K (df)	5 (11)	9 (20)	7 (14)	11 (23)	16 (35)	9 (16)	8 (15)
AIC	795.5	791.3	729.2	731.9	746.2	715.5	715.2
ΔAIC	80.3	76.1	14.0	16.7	31.0	0.3	0.0
w_i	0.000	0.000	0.000	0.000	0.000	0.462	0.537

[1] Global model

Table 6. Results of the multiple logistic regression Model 7 (in Table 5) for predicting the probability of overshoot fallback by individual Chinook salmon, 1996-2003.

Parameter	*df*	Wald chi-square	*P*
Stock	8	168.8	<0.0001
Temporary tributary use	2	43.8	<0.0001
Downstream fallback	1	12.7	0.0004
Fin-clip	1	7.4	0.0064
Run-type	1	7.3	0.0067
Downstream fallback×Fin-clip	1	5.7	0.0168
Flow	1	4.4	0.0358

Contribution of overshoot fallback to total fallback. – Between 21 and 22% of all fish that fell back at The Dalles, John Day, and Ice Harbor dams were considered overshoot fallbacks as were 40% of fallback fish at McNary Dam (Table 7). Fallback percentages differed between years, consistent with the effects of total river discharge and spill at dams (see Boggs *et al*. 2004). The contribution of overshoot fish also varied between years and dams, in response to river environment but also to run composition differences and the proximity of downstream tributaries to individual dams. In 1996, for example, relatively large percentages of salmon returned to lower river tributaries and smaller percentages returned to the Snake and upper Columbia. Upper river stocks had larger runs in later years, and this was amplified slightly in our samples by selection for known-origin fish. Later years also were also characterized by lower total flow and spill, and therefore lower fallback rates at all projects. In any case, overshoot fallback tended to make up smaller proportions of total fallback in the later years, particularly at The Dalles and John Day dams (Table 7).

Snake River fish, the most abundant stock in the study, contributed most to fallback estimates at the three lower Columbia River dams (38-56%) and Ice Harbor Dam (79%) (Figure 3). Upper Columbia River fish made up 8-18% of the fallback fish at the three lower Columbia River dams. Other stocks that contributed more than 10% at individual dams included: Klickitat River fish at The Dalles Dam (12%), Deschutes River fish at John Day Dam (14%), and Umatilla River fish at McNary Dam (24%) (Figure 3). These patterns indicate that total fallback was related to the composition of runs at a broad scale, while individual stocks contributed overshoot fallback at the nearest dams. Given reasonably proportional tagging (Appendix A), estimates in Figure 3 and Table 7 should represent general fallback composition at the study dams.

Temporary tributary use. – Overall, 14.1% of the radio-tagged salmon temporarily used at least one tributary other than their final tributary, and 2.3% used two or more alternate sites. Stocks from the Bonneville-The Dalles reach and the Umatilla River had the highest temporary use percentages, ranging from 23 to 42%. The remaining stocks (Deschutes, John Day, Snake, Yakima, upper Columbia) all had temporary use percentages between 8 and 11%.

As with overshoot behavior, temporary use percentages were strongly related to distance between sites (Figure 4). The greatest concentration of temporary tributary use occurred between Bonneville and The Dalles dams, where five tributaries enter the Columbia River in a 42-km reach (Figure 1). Of ten stock-tributary use combinations where percentages were ≥ 10%, nine were for pairs within this reach, including four where percentages were ≥ 30% (Table 8). Salmon temporarily entered tributaries both up- and downstream from final locations, but almost all temporary use percentages were < 5% when distances between sites exceeded 50 km in either direction (Figure 4).

Salmon from the three upriver populations (Snake, Yakima, upper Columbia) were relatively unlikely to temporarily enter lower Columbia River tributaries. On average, 0.7% to 1.3% of the salmon from these stocks entered individual lower river tributaries, with the exception that 3.1% to 4.1% of each stock entered the Little White Salmon River. In addition, 5.9% of Yakima River fish were recorded in the Snake River.

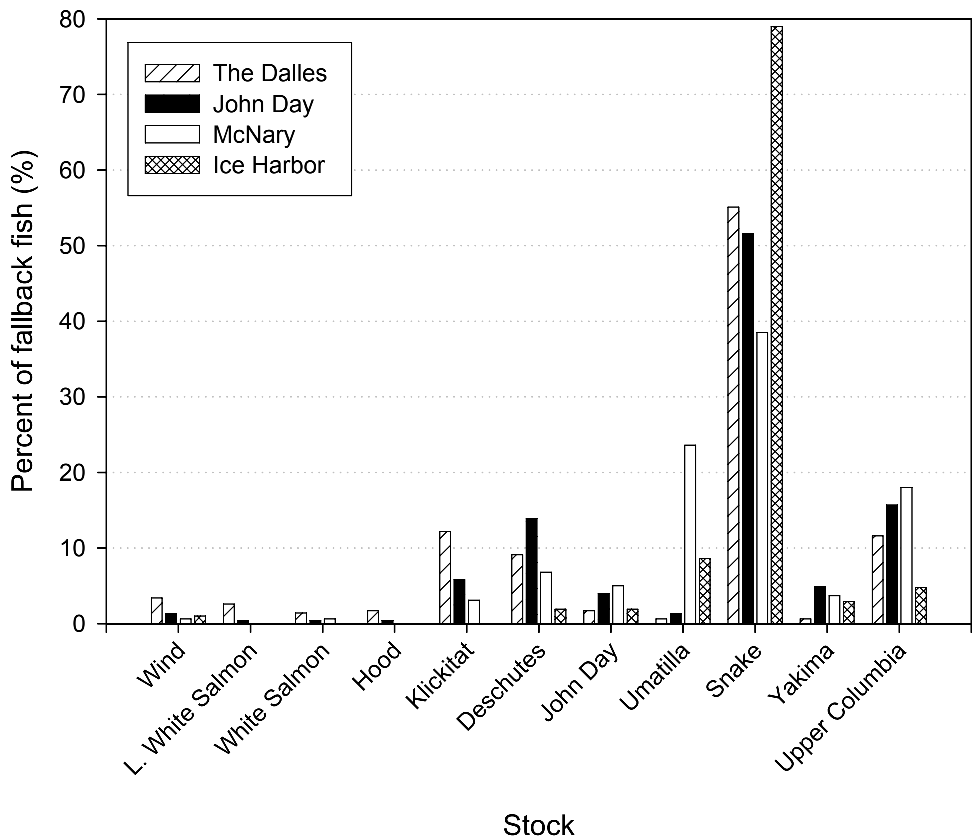

Figure 3. Contributions (%) by individual stocks to fallback at The Dalles, John Day, McNary, and Ice Harbor dams, 1996-2003. (Note: only includes fish that returned to major tributaries.)

Salmon from the three upriver populations (Snake, Yakima, upper Columbia) were relatively unlikely to temporarily enter lower Columbia River tributaries. On average, 0.7% to 1.3% of the salmon from these stocks entered individual lower river tributaries, with the exception that 3.1% to 4.1% of each stock entered the Little White Salmon River. In addition, 5.9% of Yakima River fish were recorded in the Snake River.

Similar to the regression analyses for overshoot behaviors, stepwise multiple logistic regression selected the models with the lowest AIC values (Table 9). These models differed only in the inclusion of sex as a predictor and again there was considerable support for both (ΔAIC = 1.2). In Model 7, the model with the lowest AIC, among-stock differences were most strongly associated with temporary tributary use ($\chi^2_{10} = 319.3$, $P < 0.0001$) (Table 10), again likely reflecting the effects of distance. Four of the remaining terms in Model 7 were associated with salmon movements in the Columbia River (*e.g.* main stem overshoot or fallback at dams). The inclusion of year and flow variables in Model 7 also may have reflected increasing fallback behavior at all dams in high-flow years. Hatchery effects were indicated by the selection of both the fin-clip term and the interaction prior-downstream-fallback×fin-clip; fish with fin clips were more likely to temporarily use tributaries. Run-type (spring versus summer) and tag date terms were also selected, reflecting greater temporary tributary use by later migrants (Table 10).

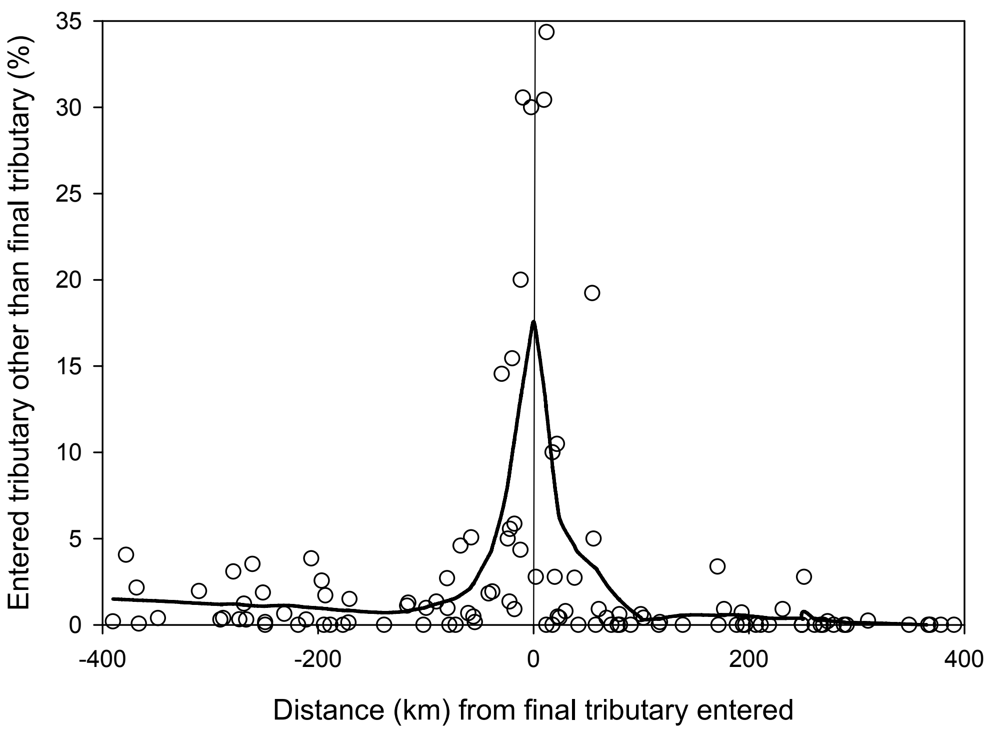

Figure 4. Percentages (○) of spring–summer Chinook salmon stocks that entered tributaries other than the final tributary entered, by distance between tributary mouths, 1996-2003. All stock-tributary combinations included (*n* = 110). Curve (▬) is loess-smoothed relationship between distance and proportions.

Table 7. Annual fallback percentages for all fish recorded passing The Dalles, John Day, McNary, and Ice Harbor dams, including the proportions of overshoot and non-overshoot fallback fish. (Note: These estimates are for fish that successfully returned to major tributaries. See Boggs *et al*. 2004 and *in review* for fallback estimates that include both successful and unsuccessful migrants.)

Dam	Year	Passed dam (*n*)	Fell back (*n*)	Fell back (%)	Contribution Overshoot (%)	Contribution Non-Overshoot (%)
The Dalles	1996	424	52	12.3	34.6	65.4
	1997	645	84	13.0	23.8	76.2
	1998	677	61	9.0	23.0	77.0
	2000	669	62	9.3	16.1	83.9
	2001	628	30	4.8	13.3	86.7
	2002	627	24	3.8	4.2	95.8
	2003	768	39	5.1	15.4	84.6
	Total	4438	352	7.9	21.3	78.7
John Day	1996	344	32	9.3	21.9	78.1
	1997	596	52	8.7	30.8	68.2
	1998	601	53	8.8	26.4	73.6
	2000	556	28	5.0	25.0	75.0
	2001	616	14	2.3	21.4	78.6
	2002	598	23	3.8	8.7	91.3
	2003	689	21	3.0	4.8	95.2
	Total	4000	223	5.6	22.4	77.6
McNary	1996	297	21	7.1	42.9	57.1
	1997	571	34	6.0	67.6	32.4
	1998	563	44	7.8	70.5	29.5
	2000	521	21	4.0	57.1	42.9
	2001	605	7	1.2	71.4	28.6
	2002	567	19	3.4	42.1	57.9
	2003	662	15	2.3	46.7	53.3
	Total	3786	161	4.3	39.8	60.2
Ice Harbor	1996	123	9	7.3	22.2	77.8
	1997	316	27	8.5	18.5	81.5
	1998	251	15	6.0	26.7	73.3
	2000	216	22	10.2	27.3	72.7
	2001	360	4	1.1	25.0	75.0
	2002	286	11	3.8	9.1	90.9
	2003	327	17	5.2	17.6	82.4
	Total	1879	105	5.6	21.0	79.0

Table 8. Number of radio-tagged Chinook salmon last recorded in each tributary, and the percentages (%) that were recorded in alternate tributaries, 1996-2003.

			Proportion (%) recorded in tributary										
Final tributary	rkm	*n*	Wind	L. White Salmon	White Salmon	Hood	Klickitat	Deschutes	John Day	Umatilla	Snake	Yakima	Upper Columbia
Wind	249	486		34.4	10.5	0.4		0.6	0.4		0.2		
Little White Salmon	261	253	4.4		30.4		0.8	0.4					
White Salmon	271	36	5.6	30.6		2.8	2.8				2.8		
Hood	273	20	5.0	20.0	30.0		10.0	5.0					
Klickitat	290	110	1.8	14.6	15.5	0.9		2.7	0.9		0.9		
Deschutes	328	414	1.0	4.6	5.1	0.5	1.9		0.5		0.7		0.2
John Day	351	148		1.4	2.7		0.7	1.4			3.4		
Umatilla	467	78		3.9	2.6				1.3		19.2		
Snake	522	1872	0.3	3.5	1.9	0.2	0.6	1.7	1.5	0.2			0.2
Yakima	539	324	0.3	3.1	1.2	0.3		0.3			5.9		0.6
Upper Columbia	639	1528	0.2	4.1	2.2	0.1	0.4	2.0	0.4	0.1	1.1	1.0	

Table 9. Candidate multiple logistic regression models testing for relationships between temporary tributary use (0,1) by individual Chinook salmon and predictor variables, 1996-2003. Models 1-5 were selected *a priori* and models 6 and 7 were the 'best' subsets identified using stepwise regression. Number of parameters (*K*) included the intercept and each explanatory variable. Models with a lower ΔAIC and a higher Akaike weight (w_i) have more support.

	Candidate models						
			A priori			'Best' subsets	
Variables	1	2	3	4	5[1]	6	7
Fish characteristics							
Stock	x	x	x	x	x	x	x
Sex	x	x	x	x	x	x	
Length	x	x	x	x	x		
Fin-clip	x	x	x	x	x	x	x
River environment							
Year		x		x	x	x	x
Date		x		x	x	x	x
Run-type (spring, summer)		x		x	x	x	x
Flow		x		x	x	x	x
Fish behaviors							
Downstream fallback			x	x	x	x	x
Upstream fallback			x	x	x	x	x
Main stem overshoot (0,1,>1)			x	x	x	x	x
Interaction terms							
Downstream fallback×Year					x		
Upstream fallback×Year					x		
Downstream fallback×Fin-clip					x	x	x
Upstream fallback×Fin-clip					x		
Main stem overshoot×Fin-clip					x		
Downstream fallback×Sex					x		
Upstream fallback×Sex					x		
Main stem overshoot×Sex					x		
K (df)	5 (13)	9 (22)	8 (17)	12 (26)	20 (46)	12 (26)	11 (25)
AIC	3916.3	3882.5	3750.8	3725.3	3736.3	3718.3	3717.2
ΔAIC	199.1	165.3	33.6	8.1	19.1	1.1	0.0
w_i	0.000	0.000	0.000	0.011	0.000	0.362	0.627

[1] Global model

Table 10. Results of multiple logistic regression Model 7 (in Table 8) for predicting the probability of temporary straying by individual Chinook salmon, 1996-2003.

Parameter	*df*	Wald chi-square	*P*
Stock	10	319.3	<0.0001
Downstream fallback	1	96.7	<0.0001
Year	6	22.8	0.0009
Date	1	17.9	<0.0001
Run-type	1	16.7	<0.0001
Main stem overshoot	2	15.7	0.0004
Fin-clip	1	14.0	0.0002
Downstream fallback×Fin-clip	1	8.4	0.0038
Flow	1	5.5	0.0185
Upstream fallback	1	5.5	0.0194

Behaviors of known-origin fish. – A total of 2.5% (27/1081) of the known-origin Chinook salmon were considered permanent strays into non-natal basins. About a quarter of these (7/27) were harvested in non-natal basins, and whether these individuals would have eventually homed to natal tributaries is unknown. The three upriver stocks made up more than 93% of the known-origin sample, and these groups had permanent straying rates of 2.7% (Snake River), 2.3% (upper Columbia River), and 0.7% (Yakima River). Permanent stray percentages were 5.8% for 52 Wind River salmon. No straying was observed in the small sample of known-source John Day River salmon (N = 19). Given the small samples, permanent stray estimates for the two lower Columbia River stocks should be interpreted cautiously.

Most permanent strays entered lower Columbia River tributaries, with the largest numbers last recorded in the Deschutes (8/27, 30%), Little White Salmon (26%), and Klickitat (15%) rivers. One to two fish (4-8% of all strays) entered the Wind, White Salmon, John Day, Umatilla, Snake, and upper Columbia drainages. Qualitatively, these strays represent only minor contributions to most receiving populations. Potential exceptions included those drainages that have relatively small spawning populations, such as the White Salmon and Klickitat rivers. Almost 60% (16/27) of the permanent strays were recorded at one or more dams upstream from the tributary where they were last recorded and were considered ‘overshoot’ fish. A smaller percentage (26%, 7/27) was recorded in at least one tributary other than the stray site.

Temporary tributary use behaviors by same-stock pairs of known- and unknown-origin salmon were generally similar, though exact comparisons were not possible because permanent straying could not be assessed for unknown-origin fish. For example, temporary tributary use percentages were approximately 7.8% for known-origin Snake River salmon and 8.1% for Snake River salmon identified solely by final location during the four years (2000-2003) with known-origin samples. Temporary use was approximately 10.6% and 9.0% for the upper Columbia River known- and unknown-origin groups, respectively. Differences among other pairs were based on smaller sample sizes and were somewhat larger for Yakima, Wind, and John Day River fish: in all three cases, 3-9% more known-origin fish temporarily entered tributaries than fish identified solely by final location.

Same-stock comparisons of main stem overshoot differed by < 0.7% for all stocks except for the John Day River pair (0.0% overshoot for 19 known-origin fish versus 10.9% for the comparison group). Similarly, overshoot fallback percentages from 2000-2003 were slightly lower for known-origin fish from the Wind River (0.0% for 52 known-source fish versus 1.8% for 225 unknown-origin fish last recorded in the Wind River) and from the John Day River (0.0% for 19 known-origin fish versus 7.5% for 53 unknown-origin fish). These differences suggest that overshoot fallback estimates may be inflated for these stocks and others (i.e. Deschutes, Little White Salmon, and Klickitat rivers) receiving permanent strays from upriver sites. This bias will vary based on the number of strays entering a tributary and the size of the receiving population, but should be small overall given relatively low permanent straying rates. Of the 27 permanent strays detected, 16 (59%) had apparent main stem overshoot behavior and 6 (22%) had overshoot fallbacks.

Discussion

Many adult Chinook salmon in this study made non-direct homing movements while *en route* to natal spawning sites throughout the Columbia River basin. The findings suggest that direct, point-to-point homing may be less common than is typically reported for adult salmonids. Instead, initial passage of natal tributaries and temporary non-natal tributary use by the study stocks demonstrate that the homing process in the Columbia River system can be quite complex. The results suggest that extensive searching behaviors may be necessary for some populations to detect and respond to appropriate olfactory and environmental cues from natal sites. Understanding these behaviors is important for differentiating temporary tributary use and permanent straying, managing fisheries that target specific stocks, and interpreting salmon movements near dams and river confluences. The results also provide some insights regarding fish that fail to pass dams and those that fall back downstream over dams, two important management concerns in the Columbia River. Geographic proximity of tributary confluences and dams, salmon orientation tactics, river environment, and impoundment all appeared to affect the observed salmon migration behaviors and these mechanisms are discussed below.

The geographic arrangement and spacing between sites explained much of the variability in non-direct homing behaviors. Radio-tagged salmon were far more likely to temporarily enter rivers near their eventual spawning sites than to enter more distant tributaries. Similarly, the vast majority of salmon that overshot presumed natal sites were detected only at the closest upstream Columbia River dam. Regional differences in spatial habitat spacing may therefore explain the observed patterns better than other factors such as genetically-based differences in behavior or specific fish characteristics.

Other studies documenting these types of non-direct homing movements are few, in part because their study requires continuous monitoring of many individual fish and at multiple sites throughout migration. One good example, however, is a telemetry study of several populations of Kasilof River sockeye salmon (*O. nerka*) (Burger *et al*. 1995). In that study, 16% of tributary-spawning and 21% of lake-spawning salmon entered nearby streams prior to final spawning sites. These percentages were comparable to the overall rate of temporary tributary use (14%), and were within the range of stock-specific rates (8 to 42%) in our study. Most sockeye salmon in the Burger *et al*. sockeye research confined temporary straying movements to the lower reaches of nearby tributaries, and typical stays were brief (< 5 d). Although we did not thoroughly examine temporary tributary use times for this summary, most Chinook salmon used alternate tributaries for less than 2 d. Similar patterns were observed in several homing studies described in Ricker (1972).

One might expect the factors influencing temporary tributary use to be closely related to those affecting permanent straying, and that appears to be the case with geographic proximity. For example, Quinn and Fresh (1984) reported that more than 95% of permanent spring Chinook salmon strays from the Cowlitz River (a Columbia River tributary downstream from Bonneville Dam) entered tributaries within 30 km of the Cowlitz, while only one fish (0.2%) overshot as far as Priest Rapids Dam (550 km upstream). Autumn (fall) Chinook salmon from lower Columbia River hatcheries also predominantly strayed into nearby rivers, with less than 2% overshooting as far as Bonneville Dam (Quinn *et al*. 1991). Alaskan Chinook salmon strays mostly entered rivers within 25 km of their home site (Hard & Heard 1999), and Vancouver Island coho salmon (*O. kisutch*) strayed just 16 km on average (Labelle 1992). Straying distances were somewhat greater in studies of New Zealand and British Columbia Chinook salmon (Unwin & Quinn 1993; Candy & Beacham 2000), Oregon steelhead (*O. mykiss*) (Schroeder *et al*. 2001), and Norwegian Atlantic salmon (*Salmo salar* L.) (Jonsson *et al*. 2003), but most fish in these cases also strayed into nearby sites.

The strong link between geographic location and non-direct homing suggests that salmon may use fixed orientation mechanisms (*e.g.*, sun or compass orientation, Friedland *et al*. 2001) or geographic ‘odometer’ cues to return to approximate natal locations. As fish approach natal sites, use of fixed mechanisms is likely diminished as fish rely more on olfactory cues (Dittman & Quinn 1996). The combination of these orientation strategies could explain the limited detection of study salmon at distant sites, and the extensive non-direct movements in the Bonneville reservoir reach, where several tributaries enter in close proximity. Salmon in this reach may need to actively search for home sites because the mix of chemical cues are confusing or diluted within the large (1-2 km wide) main stem Columbia River.

Many adult salmon use near-shore migration routes (*e.g*., Daum & Osborne 1998; Reischel & Bjornn 2003), and appear to orient to natal tributary plumes for considerable distances downstream from natal tributary mouths (Keefer et al. *in press*). Shoreline and plume orientation may result in some fish “missing the turn” or overshooting if they migrate on the opposite shore when passing the natal tributary confluence. Such behavior may be exacerbated in impounded rivers, particularly if salmon must locate olfactory cues from tributaries with small discharge relative to main stem reservoir volume, as in the Bonneville reservoir. Inundation of tributary mouths may also have contributed to the behaviors as these reaches likely provide migrants a confusing mix of reservoir and tributary cues. Alternatively, fish returning to closely-spaced tributary rivers may have substantial genetic overlap, particularly in the Columbia River where many stocks have shared hatchery lineages. Some tributary sampling by stocks from neighboring Bonneville reservoir tributaries, for example, may simply reflect this overlapping genetic and hatchery history.

Social, reproductive, or environmental cues in either natal or non-natal rivers may also affect non-direct homing behaviors. For example, the recorded movements may reflect basic sampling activities related to olfactory imprinting (Ricker 1972; Griffith *et al*. 1999), where salmon move upstream verifying the presence or absence of cues imprinted on during juvenile outmigration. When familiar or desirable cues are not present, the fish retreat downstream and test other routes. Similarly, migrants may temporarily enter non-natal sites if favorable conspecific cues are present or if use of the non-natal site provides energetic or other benefits such as thermoregulation (Berman & Quinn 1991). Increased temporary straying by spring–summer Chinook salmon that encountered warmer water temperatures supports a behavioural thermoregulation hypothesis, particularly as similar patterns have been observed for Columbia basin steelhead (High *et al*., 2006; Keefer *et al*., 2004a) and autumn (fall) Chinook salmon (Goniea *et al*., 2006). In each case, migrants widely used cooler non-natal tributaries during periods when the main stem Columbia River was warm. In the same vein, fish may similarly avoid natal tributaries when temperature or discharge is unfavorable (*e.g.*, Major & Mighell 1967; Hallock 1970; Hodgson & Quinn 2002; Hyatt *et al*. 2003), if fish maturation is incomplete, or if conspecifics are absent.

The multivariate analyses of individual salmon behavior identified stock, hatchery origin, fallback at dams, migration timing, and fish sex as influential predictors of overshoot and/or temporary tributary use. We note that two of these variables had a fair amount of associated uncertainty: sex and origin. Sex was identified only from visual cues, which are imprecise, particularly early in the migration. Similarly, many hatchery fish were not fin-clipped. These two sources of error each potentially mask true underlying differences related to sex or origin. Less likely is that sex or origin classification errors created false differences. In any case, these predictors were secondary in all models. By far, stock had the most explanatory power, revealing considerable variation among populations in the probability of overshooting, overshoot fallback, and temporary tributary use. Less precise homing for hatchery fish may have been the result of rearing and release protocols or genetic factors (*i.e.* hatchery use of non-native brood stocks) (Quinn 1993; Candy & Beacham 2000). The strong relationships between fallback at dams, overshoot, and temporary straying were probably multifaceted. Fallback salmon migrate more slowly (Keefer *et al*. 2004c) and are less likely to complete migration (Keefer *et al*. 2005a), suggesting disorientation or reduced fitness. Increased fallback and orientation problems have also been associated with salmon transported as juveniles (Chapman *et al*. 1997; Keefer *et al*. *in review*) and with hatchery fish (Keefer *et al*. 2006). More directly, fallback at dams may simply reflect active searching for natal sites (Boggs *et al*. 2004).

It is unclear why later migrants were more likely to overshoot and stray temporarily. Perhaps early downstream juvenile migration by summer-run Chinook salmon (Brannon *et al*. 2004) reduces imprinting opportunities for these stocks and leads to less precise homing by adults. Alternately, later migrants encountered warmer water temperatures in all years and therefore may have been more likely to temporarily seek thermal refugia, as described above. The increased likelihood of non-direct homing for males is also unclear, but may reflect male searching strategies that seek to maximize mating opportunities (Hard & Heard 1999; Morbey 2000).

Almost 80% of the salmon in this study were of unknown origin and stock assignment for these fish was uncertain. Several possible misinterpretations of the data were therefore possible. First, unknown-source salmon identified as directly homing may have been permanent strays from other sites. Second, some overshoot behavior may have been migration failure by upriver stocks that instead permanently strayed into lower tributaries. Third, fish identified as temporary tributary users may have entered the correct site initially, only to exit and permanently stray elsewhere. Fourth, temporary tributary users may have been permanent strays that never entered their natal tributary. It was impossible to quantify these stock identification errors, particularly for basins with no known-origin salmon. Nonetheless, consistency among behaviors by known- and unknown-origin fish of the same stocks and the low rate (<3%) of permanent straying by known-origin salmon suggest stock misclassification was at most a minor problem. Had all salmon origins been known, estimates of non-direct homing and permanent straying would likely have increased rather then decreased. Greater resolution of this uncertainty will require additional PIT-tagging of juvenile salmon and follow-up monitoring of returning adults from lower river populations. The current PIT-tag monitoring system within the Hydrosystem, however, can identify only a portion of overshoot behaviors because not all dams are monitored. For example, from 2002-2005, 551 John Day River Chinook salmon were detected at Bonneville Dam and 10% (n = 55) of these were recorded at PIT-tag readers in the McNary Dam and 3% were detected at Lower Granite Dam (data from PTAGIS). These estimates should be considered minimums, because fewer than 551 fish likely survived from Bonneville Dam to John Day Dam. In these same years, 493 Umatilla River salmon were recorded at Bonneville Dam, of which 49% were recorded overshooting at McNary Dam and 4% were recorded at Lower Granite Dam. Again, these estimates should be considered minimums.

These results have important implications for managing adult fish in the Columbia River basin. In general, non-direct homing movements suggest an increased probability of capture in in-river fisheries. More specifically, salmon fisheries target specific stocks in many large river systems by restricting harvest to limited geographic areas, often delineated by river confluences. Such fisheries may inadvertently take otherwise protected fish that overshoot or use non-natal tributaries. This harvest may be of consequence for stocks at risk of extinction such as Hood River and upper Columbia River spring Chinook salmon, or for populations where recovery efforts take precedence over harvest, such as Snake River and John Day River stocks (Nehlsen *et al*. 1991; Myers *et al*. 1998). Non-direct homing may also be an important consideration at hatcheries and fish weirs, particularly when they are near one or more river confluences. These facilities could cull non-target fish, prevent homing by temporary strays, and have the potential to artificially inflate escapement and permanent straying estimates (Griffith *et al*. 1999). We note that all the described behaviors occurred upstream from Bonneville Dam; it is likely, however, that some salmon also use tributaries between the estuary and Bonneville Dam, and some fish from lower tributaries almost certainly overshoot and fall back at Bonneville Dam.

Understanding non-direct homing behaviors is also important for managers of the Columbia River Hydrosystem. High main stem overshoot rates by some stocks indicate that many migrants use fishways and fish ladders at hydroelectric dams upstream from natal sites. Quantifying these behaviors accounts for some apparent unsuccessful passage at dams and also explains why some fish fall back downstream over dams. We estimate that about 20% of fallback fish at The Dalles, John Day, and Ice Harbor dams and almost 40% of 'successful' fallback fish at McNary Dam fell back as a result of overshooting. There was considerable annual variability in these estimates, and some concern regarding the assignment of origin. Nonetheless, the results do suggest that a substantial portion of adult fallback by spring–summer Chinook salmon is related to overshoot of natal tributaries. We emphasize that these results are for successful fish—those that reached potential spawning tributaries. The proportions of overshoot fish among those that fall back and are either harvested or are unaccounted for remain unknown. This adds considerable uncertainty to the contribution of overshoot to total fallback, as approximately 25% of spring–summer Chinook salmon that fall back at lower Columbia River dams do not reach spawning tributaries (Boggs *et al*. 2004).

Finally, given that many Chinook salmon do overshoot natal sites, it may be important for dams in the Columbia River to offer benign downstream passage routes for adult fish. Such routes may be especially important for those stocks whose natal rivers are relatively close to upstream dams, such as those from the Klickitat, Deschutes and Umatilla rivers.

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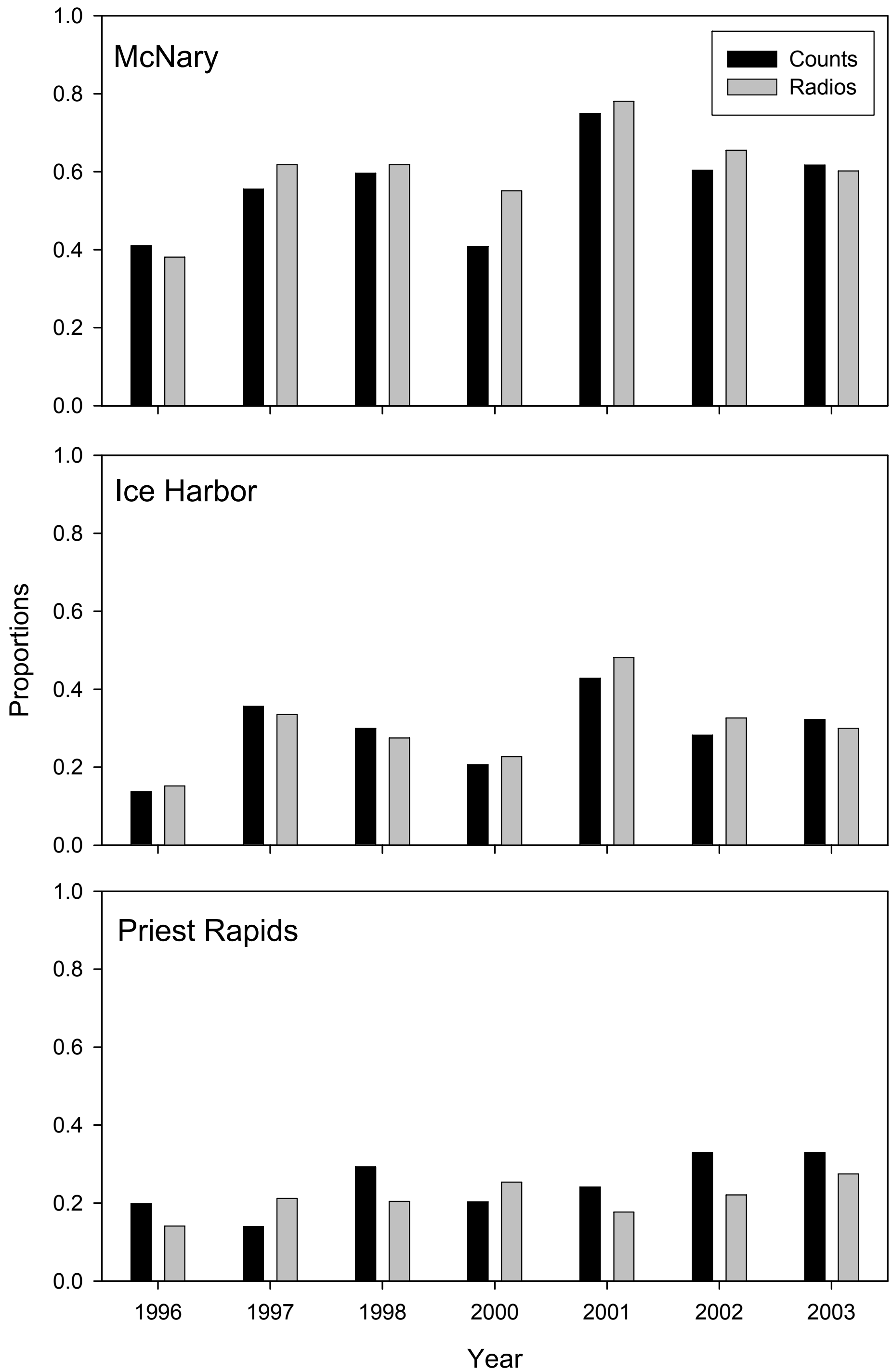

Appendix A. Comparison of fish counted or recorded (radio-tagged samples) passing Bonneville Dam that were subsequently counted or recorded at McNary, Ice Harbor, and Priest Rapids Dams. Counts were for all adult spring–summer Chinook salmon, as reported in USACE annual Fish Passage Reports.