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STRAYING RATES OF KNOWN-ORIGIN ADULT CHINOOK SALMON AND STEELHEAD WITHIN THE COLUMBIA RIVER BASIN, 2000-2003

by

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Preface

Studies of inter-basin straying by adult salmon and steelhead *Oncorhynchus* spp. in the Columbia River basin) began in the year 2000, when radio-tagged samples first included known-origin fish. Portions of each sample collected at Bonneville Dam in 2000-2003 were fish of known origin, identified by juvenile PIT tags, mostly representing stocks from the Snake River, Yakima River and upper Columbia River basin. In this report we present summary information on permanent adult straying rates, and examine the relationships between straying, hatchery origin, juvenile transportation history (barged versus in-river migration), adult migration behaviors, and river environment.

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

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Table of Contents

Preface ii
Abstract iv
Introduction 1
Methods 1
  Fish sampling and monitoring 1
  Stray rate calculations 2
  Modeling of steelhead straying 3
Results 5
  Spring–summer Chinook salmon 5
  Fall Chinook salmon 6
  Steelhead 7
  Effects of censoring fish harvested in main stem fisheries 10
  Steelhead modeling results 10
Discussion 14
References 16

Abstract

As part of a large-scale radiotelemetry study of Columbia River adult salmon and steelhead (*Oncorhynchus* spp.), we investigated permanent inter-basin straying by several important known-origin stocks. From 2000 to 2003 we radio-tagged 1,588 spring–summer Chinook salmon, 166 fall Chinook salmon, and 1,414 steelhead at Bonneville Dam that had been PIT-tagged as juveniles in tributaries, at hatcheries or at Snake or Columbia River dams. The largest samples were from the Snake River basin, including about 49% of spring–summer Chinook salmon, 73% of fall Chinook salmon, and 64% of steelhead. Between 16 and 33% of the samples were from the Columbia River basin upstream from Priest Rapids Dam, and 14% of the spring–summer Chinook were from the Yakima River.

Overall, 2.2% of spring–summer Chinook salmon, 4.2% of fall Chinook salmon, and 6.8% of steelhead strayed into non-natal tributaries. Rates varied somewhat between years, but most inter-annual differences were not statistically significant. Among spring–summer Chinook salmon, fish from the Wind River basin strayed at the highest rate (9.7%), while stray rates for Yakima, Snake, and upper Columbia stocks were between 0.4 and 2.1%. Steelhead from upper Columbia and Snake River sites strayed at comparable rates (5.6 and 7.0%), but Snake River fish tended to stray into Oregon-shore tributaries and upper Columbia fish mostly strayed into Washington-shore tributaries. Strays mostly entered cold-water tributaries, particularly the Little White Salmon, Deschutes and White Salmon rivers. Many strays from the Snake River also entered the John Day River.

Fish of certain hatchery origin (with fin clips) and those that were transported as juveniles were consistently more likely to stray. Adult fallback at dams was also strongly associated with increased straying, particularly among fish that fell back multiple times. Early-migrating steelhead were more likely to stray than later migrants, likely reflecting differential exposure to high water temperatures in the lower Columbia River. Results should be useful for managers responsible for monitoring inter-basin straying, measuring adult salmon and steelhead escapement, and aiding recovery of listed Columbia River populations.

Introduction

Documentation of adult salmon and steelhead straying rates is necessary to reliably evaluate 2000 Biological Opinion survival goals for ESA-listed populations in the Columbia River basin (National Marine Fisheries Service [NMFS] 2000). Although some level of straying occurs in most anadromous salmonid populations, the combination of hydroelectric development, juvenile transportation, proliferation of hatchery stocks, and depressed wild populations has elevated the potential for negative impacts of straying to occur in the Columbia River system. Upriver stocks (e.g., Snake River) that stray to non-natal tributaries are considered escapement losses from natal streams and can artificially inflate escapement estimates in non-natal populations. Straying can also result in harvest of federally-listed stocks in non-natal tributaries, where they may not have the same protections, and possible swamping of small wild populations by out-of-basin hatchery stocks (e.g., Snake River hatchery steelhead that stray into the John Day River). Such out-of-basin spawning by hatchery fish can directly harm local wild populations (Waples 1991; Chilcote 2003).

In our 1996 and 1997 radiotelemetry studies, we evaluated temporary (fish eventually homed correctly) straying and found that 64-70% of steelhead and 12-16% of spring/summer Chinook salmon that passed Lower Granite Dam entered lower Columbia River tributaries during their upstream migration (Bjornn et al. 2000; Keefer et al. 2002). Similar high temporary straying rates were also recorded for radio-tagged steelhead and fall Chinook salmon in more recent study years (Goniea 2002; High 2002). Prior to the 2000 study year, we could not identify fish that permanently strayed because all radio-tagged fish were of unknown-origin.

To assess permanent straying, where adult fish entered and remained in non-natal basins, we radio-tagged known-source adult spring–summer and fall Chinook salmon and steelhead during 2000-2003 migration years. Fish origins were identified from PIT tags implanted when the fish were juveniles. Most of these PIT-tagged fish were from the Snake, upper Columbia, Yakima and Wind river basins. This report presents straying estimates for adult steelhead and spring–summer and fall Chinook salmon runs, including comparisons between years and between stocks within runs. We also describe out-of-basin harvest rates, a component of straying that may include fish that were straying only temporarily as a response to warm main stem water temperatures or other stimuli. Factors that appear to affect straying—including water temperature, adult fallback at dams, hatchery origin and juvenile transportation—are examined using a variety of statistical methods.

Methods

Fish sampling and monitoring. – Adults were collected opportunistically at the Adult Fish Facility (AFF) at Bonneville Dam (Figure 1). An automated PIT-tag detection system (McCutcheon et al. 1994) in the AFF identified PIT-tagged fish available for use in these studies. When identified, these fish were diverted for radio tagging (see Keefer et al. 2004a for fish collection and tagging details). Chinook salmon were tagged throughout the spring–summer (April-July) and fall (August-October) runs and steelhead were tagged from June-October. All fish were released either ~10 km downstream from Bonneville Dam (both sides of the river) or in the Bonneville Dam forebay.

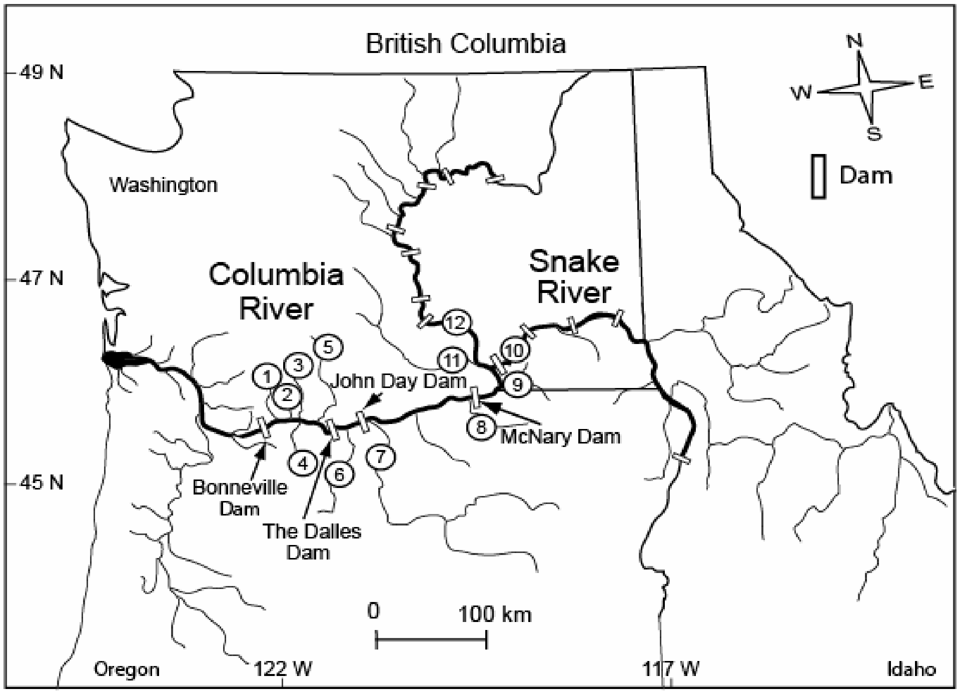

Figure 1. Columbia River basin, including major tributary basins where radio-tagged fish were last recorded. Tributary basins: 1) Wind, 2) Little White Salmon, 3) White Salmon, 4) Hood, 5) Klickitat, 6) Deschutes, 7) John Day, 8) Umatilla, 9) Walla Walla, 10) Snake, 11) Yakima, and 12) upper Columbia (includes Hanford Reach).

Fish fates were identified from the combination of telemetry records at dams and in tributaries, PIT-tag interrogation records at dams, and recapture data from fisheries, hatcheries and weirs. Permanent straying status was designated for those fish with final records (telemetry or recapture) in river basins outside their natal basins, as identified by juvenile PIT-tag location. Because monitoring of small tributaries was limited, we only considered straying at the large-river scale. For example, we generally did not examine straying within or between Snake River tributaries, but instead considered the Snake River basin as a whole. Errors in identifying straying fish should have been relatively small given broad telemetry coverage and data provided by PIT-tag interrogators at dams. The latter, for example, could identify fish that lost radio transmitters during migration.

Stray rate calculations. – Basic stray rates were calculated by dividing the number of permanently straying fish (N_S) by the number of radio-tagged fish released from that population (N_R) (Equation 1). These rates included fish harvested in non-natal basins, although some may have been temporary strays had harvest not occurred. We calculated a second stray rate that treated fish harvested in non-natal rivers (N_H) as non-strays, providing estimates that should be considered minimums (Equation 2). Combined, these two estimates provide the potential range of the proportions of fish that strayed, with the full samples at Bonneville Dam as the denominator baseline. We note, however, that values may be underestimates because some fish were harvested in main stem fisheries and did not have the opportunity to stray. This bias should decrease as fish progress upstream past the tributaries where most straying occurred. To address this question, we calculated some additional stray rates where fish harvested in main stem fisheries (N_{MH}) were censored (Equations 3). We ran several iterations of Equation 3 to better define the sensitivity of the basic estimates to main stem harvest effects (e.g., only harvest in the Bonneville pool censored, harvest in the Bonneville and The Dalles pools censored, etc.). We present Equation 3 results primarily to put the basic stray estimates in context. Equation 4 modifies Equation 3 by treating strays harvested in tributaries (N_H) as non-strays.

Equation 1, basic stray rate: N_S / N_R

Equation 2, basic stray rate with tributary harvest excluded: $(N_S - N_H) / N_R$

Equation 3, basic stray rate with main stem harvest censored: $(N_S) / (N_R - N_{MH})$

Equation 4, basic stray rate with main stem harvest censored

and tributary harvest excluded: $(N_S - N_H) / (N_R - N_{MH})$

Modeling of steelhead straying. – Logistic regression models were constructed to identify influential variables that increased the probability of straying. Predictive models were only developed for radio-tagged steelhead due to the low number of strays recorded during the spring–summer and fall chinook salmon migrations. Only steelhead data from 2001 and 2002 were used in the analysis because of the low number of fish with known fates from the 2000 migration; the 2003 data was used to test the models. Finally, only Snake and Upper Columbia River steelhead were included in models due to small sample sizes for fish from the Yakima, Umatilla, Walla Walla, and Wind river basins. The known-source sample in 2003 was more limited than in 2001 and 2002, and only the Snake River group had a sufficient sample size to use for model testing.

Fish that homed and those that strayed were considered the two response categories in the logistic regression models. Because fish harvested in non-natal tributaries (harvested strays) may have been ambiguously classified as permanent strays, separate models were developed in which the stray category omitted this group of fish. Fish that were harvested in the lower Columbia River main stem or were unaccounted for were excluded because their straying could not be assessed.

Twelve categorical and continuous variables that described the rearing and migratory history of juvenile and adult fish were evaluated as covariates in the modeling analysis. Categorical variables included year, sex (based on visual estimate at time of tagging), stock (Snake or upper Columbia River), presence of fin clips, transport history, and fallback. The transport history variable discriminated Snake River fish that were barged from Lower Granite, Little Goose, or Lower Monumental dams from fish that were not transported. Two adult fallback variables were included, one that discriminated between fish that fell back one time from those that did not fallback (fallback-1), and a second that discriminated fish that fell back more than once from those that did not fallback (fallback-2).

The five continuous variables used in the regression models included date of radio-tagging, average daily temperature and flow recorded at Bonneville Dam on day of tagging, fish length, and the number of elapsed days between juvenile PIT-tag and adult radio-tag events. Single-day measures of temperature and flow can not capture the environmental conditions experienced by individual steelhead during their protracted migration times through the lower Columbia (Keefer et al. 2004b), but temperature and flow at time of tagging should be broadly representative of the average regimes encountered by steelhead as they moved through the lower river. The number of elapsed days between outmigration and return to freshwater was used as an index of the length of time fish spent at sea. We hypothesized that fish that spent a longer time at sea may undergo 'memory decay' and would be more likely to stray that those that returned at an earlier age, as has been reported in other salmonid straying studies (Quinn et al. 1991; Jonsson et al. 2003).

Model selection analysis, using the information-theoretic approach, was used to estimate the logistic regression model that best approximated the observed straying data (Burnham and Anderson 1998). This approach is preferred for analyzing observational data or for data that have not been collected under an experiment designed to test a priori hypotheses. The best model was selected from a set of likely candidate models that included a full model with all twelve predictor variables and additional models each of which included a different subset of the twelve variables. The relative plausibility of each model in approximating the data was assessed using Akaike's Information Criterion (AIC). The model with the smallest AIC value was considered to be the best model; models that under-fit (not enough estimated parameters to approximate the data) or over-fit (the inclusion of unnecessary estimated parameters) the observed data had higher AIC values. The validity of the selected model was also assessed using the goodness-of-fit test developed by Hosmer and Lemeshow (1989).

Confidence in the 'best' model was assessed by evaluating the relative likelihood of other candidate models as plausible best models. A model was considered to have substantial support as the best and included in the 'confidence set' of approximating models if its AIC value was not more than 2 units greater than the best model's AIC (i.e. $\Delta AIC_i \leq 2$; Burnham and Anderson 1998). A model's ΔAIC was also used to calculate its Akaike weight (w_i) according to the following equation:

$$w_i = \exp(-0.5*\Delta AIC_i)/\sum (\exp(-0.5*\Delta AIC_i))$$

Akaike weight provided a relative measurement of the suitability of the best model relative to others in the 'confidence set' (Burnham and Anderson 1998). For example, a model with a w_i of 0.5 would be considered five times more likely to be the best model than a model with a w_i of 0.1 (i.e. 0.5/0.1). The Akaike weights were also used to quantify the relative importance of model covariates in explaining straying. A predictor variable's importance was evaluated by summing up the w_i's over the subset of models that included that variable. A variable's relative importance may range from 0 (i.e. variable was not included in any models) to 1 (i.e. variable was included in every model).

To further assess the predictor variables' influence on straying, odds ratios were calculated for those covariates chosen for inclusion in the best approximating model. Odds ratios were calculated as the exponential of a variable's estimated parameter value in the regression, and were interpreted as an increase (decrease) in straying probability when comparing fish with different values for that variable. In the case of a categorical variable, the odds ratio compared the relative stray probabilities for the two classifications of the variable. For example, a parameter estimate of 0.69 for the barged variable would yield an odds ratio of 2 ($e^{0.69}$) and indicate that a barged fish was twice as likely to stray as a non-barged fish. For a continuous variable, the odds ratio measured the change in the stray probability for a one-unit difference in the variable. For example, a parameter estimate of 0.40 for the variable tag date would yield an odds ratio of 1.5 ($e^{0.40}$) and indicate that a fish tagged on any given day would be 1.5 times as likely to stray than a fish tagged the previous day. This interpretation was extended to assess changes in probability for a difference in a continuous variable greater than one unit. Using the parameter estimate from the previous example, a fish tagged on any given day would be 270 times as likely to stray than a fish tagged two weeks earlier (i.e. odds ratio = $e^{(0.40*14\text{ d})}$).

Results

Spring–summer Chinook salmon. – We radio-tagged a total of 1,588 known-source adult spring–summer Chinook salmon from 2000-2003 (Table 1). The basic stray rate with all years and stocks combined was 2.2%. A total of 35 salmon strayed, of which 12 were harvested in non-natal tributaries. Treatment of the latter group as non-strays resulted in a minimum stray rate of 1.4% (Table 1). With all stocks combined, annual basic stray rates ranged from 1.6% in 2001 to 4.5% in 2000 (Table 2). In paired tests, differences between years neared significance in two cases (2000 vs. 2001, $P = 0.085$; 2001 vs. 2003, $P = 0.075$; χ^2 tests). Stray rates were similar for fin-clipped ($n = 927$) and unclipped ($n = 661$) salmon.

Table 1. Numbers and proportions of known-source spring–summer[1] Chinook salmon groups that were last recorded straying into non-natal tributaries, 2000-2003. Basic stray rate includes fish harvested in non-natal tributaries. Tributary harvest excluded stray rate treats fish harvested in non-natal tributaries as non-strays and is therefore a conservative estimate. Table only includes stocks or aggregates with ≥10 fish, except Umatilla River stock, which had straying fish.

Stock	n	Basic stray rate % (n)	Tributary harvest excluded stray rate % (n)
All spring–summer Chinook	1,588	2.2% (35)	1.4% (23)
All Snake R.	776	2.1% (16)	1.3% (10)
Known Snake R. transport	303	3.3% (10)	2.6% (8)
Lower Granite Dam	239	4.2% (10)	3.3% (8)
Little Goose Dam	49	0.0% (0)	0.0% (0)
Lower Monumental Dam	15	0.0% (0)	0.0% (0)
No known Snake R. transport	473	1.3% (6)	0.4% (2)
Lower Granite Dam	186	2.2% (4)	0.5% (1)
Clearwater R.	22	0.0% (0)	0.0% (0)
Grande Ronde R.	40	0.0% (0)	0.0% (0)
Salmon R.	106	0.9% (1)	0.0% (0)
Imnaha R.	38	2.6% (1)	2.6% (1)
All upper Columbia R.	460	1.7% (8)	1.7% (8)
All Wells Hatchery	82	6.1% (5)	6.1% (5)
Near Wells release	25	8.0% (2)	8.0% (2)
Near Wanapum release	20	5.0% (1)	5.0% (1)
Near Priest Rapids release	31	6.5% (2)	6.5% (2)
All East Bank Hatchery	133	1.1% (1)	1.1% (1)
Near Wells release	25	0.0% (0)	0.0% (0)
Near Rocky Reach release	46	0.0% (0)	0.0% (0)
Near Rock Island release	62	1.6% (1)	1.6% (1)
Rocky Reach Dam	94	1.1% (1)	1.1% (1)
Rock Island Dam	123	0.8% (1)	0.8% (1)
Icicle R.	15	0.0% (0)	0.0% (0)
Yakima R.	227	0.4% (1)	0.4% (1)
Umatilla R.	*7*	*14.3% (1)*	*14.3% (1)*
John Day R.	24	0.0% (0)	0.0% (0)
Carson Hatchery	93	9.7% (9)	1.4% (3)

[1] some upper Columbia stocks are considered summer–fall Chinook salmon

Table 2. Basic annual stray rates for selected spring–summer Chinook salmon stocks, 2000-2003.

	Percent (*n*) that strayed			
	2000	2001	2002	2003
All spring–summer Chinook	4.5% (67)	1.6% (768)	2.2% (447)	3.3% (306)
All Snake R.	3.6% (28)	2.1% (473)	1.1% (185)	3.3% (90)
Known Snake R. transport	6.7% (15)	4.1% (195)	2.0% (49)	0.0% (44)
Known Snake R. not transported	0.0% (13)	0.7% (278)	0.7% (136)	6.5% (46)
Salmon R.	0.0% (1)	1.3% (75)	0.0% (28)	0.0% (2)
All upper Columbia R.	5.3% (38)	0.7% (142)	0.0% (99)	2.8% (181)
All Wells Hatchery	16.7% (6)	5.0% (20)	0.0% (4)	5.6% (54)
All East Bank Hatchery	3.2% (31)	0.0% (102)		
Rocky Reach Dam			0.0% (34)	1.6% (61)
Rock Island Dam		0.0% (9)	0.0% (50)	1.5% (65)
Yakima R.		0.0% (120)	1.0% (97)	0.0%(10)
Carson Hatchery	0.0% (1)	3.4% (29)	12.5% (48)	13.3% (15)

Stray rates for aggregated stocks from the major basins were 2.1% for 776 Snake River fish, 1.7% for 460 upper Columbia River fish, 0.4% for 227 Yakima River fish and 9.7% for 93 Carson Hatchery (Wind River) fish (Table 1). The stray rate for the upper Columbia River group was significantly higher in 2000 than in 2001 or 2002 ($P \le 0.051$) (Table 2); annual rates did not differ ($P > 0.05$) for Snake River, Yakima River, or Carson Hatchery stocks, though sample sizes for the latter two stocks were small in some years.

With all years combined spring–summer Chinook salmon that had been transported from the Snake River strayed at higher rates (3.3%) than non-transported salmon (1.3%) ($P = 0.052$, Table 1). Within individual years, transported fish were significantly more likely to stray only in 2001 (4.1% versus 0.7% for non-transported fish; $P = 0.012$) (Table 2).

Spring–summer Chinook salmon were most likely to stray into the Little White Salmon (31% of all strays) and Deschutes rivers (26%) (Table 3). Salmon also strayed into the Sandy, Wind, White Salmon, Klickitat, John Day, Umatilla, Snake, and upper Columbia rivers. Seven of the nine (78%) Carson Hatchery strays were last recorded in the Little White Salmon River (Table 3).

Fall Chinook salmon. – Relatively few juvenile fall Chinook salmon have been PIT-tagged in the Columbia River basin. We radio-tagged a total of 166 known-source adult fall Chinook salmon from 2000-2003 (Table 4). The basic stray rate with all years and stocks combined was 4.2%. A total of 7 salmon strayed, none of which were harvested in non-natal tributaries. More than 70% of the known-source fall Chinook salmon originated in the Snake River basin, and the aggregated stray rate for that group was 3.3%. None of the 26 fish from the upper Columbia basin strayed, and 2 of 12 (16.7%) from the Yakima River strayed (Table 4). Annual sample sizes of straying fish were too small to provide meaningful between-year comparisons.

Only 16 Snake River fall Chinook salmon were known transported as juveniles (Table 4). Three transported fish strayed (18.8%), a significantly higher rate than for non-transported fish (1.0%, $n = 105$; $P < 0.001$). Fall Chinook salmon tended to stray into the Hanford Reach or to the upper Columbia River upstream from Priest Rapids Dam. The two strays from the Yakima River and three from the Snake River were all last recorded in or upstream from the

Hanford Reach. The Umatilla River stray entered the Yakima River. The final stray, a non-transported Snake basin fish from the Tucannon River, was last recorded upstream from Lower Granite Dam.

Table 3. Stray locations for spring–summer Chinook salmon, based on juvenile PIT tag sites.

	Juvenile PIT tag site for spring–summer Chinook salmon						
Stray location	All fish	All Snake River fish	Snake River transport	Snake River not transported	Upper Columbia River	Yakima/ Umatilla River	Carson Hatchery
Sandy R.	1						1
Wind R.	2	2	2				
L. Wh. Sal. R.	11	3	1	2	1		7
Wh. Salmon R.	3				2		1
Klickitat R.	4	2	1	1	2		
Deschutes R.	9	5	3	2	3	1[1]	
John Day R.	2	2	2				
Umatilla R.	1	1		1			
Snake R.	1					1[2]	
Upper Col. R.	1	1	1				
Total	**35**	**16**	**10**	**6**	**8**	**1**	**9**

[1] stray from Yakima R.
[2] stray from Umatilla R.

Table 4. Numbers and proportions of known-source fall[1] Chinook salmon groups that were last recorded straying into non-natal tributaries, 2000-2003. Basic stray rate includes fish harvested in non-natal tributaries. Table only includes stocks or aggregates with ≥10 fish, except Umatilla River stock, which had straying fish.

Stock	n	Total stray rate % (n)
All fall Chinook	166	4.2% (7)
All Snake R.	121	3.3% (4)
Known Snake R. transport	16	18.8% (3)
Lower Granite Dam	10	10.0% (1)
Known Snake R. not transported	105	1.0% (1)
All Lyons Ferry Hatchery	82	0.0% (0)
Snake R. release	29	0.0% (0)
Clearwater R. release	50	0.0% (0)
Snake R. above L. Granite	10	0.0% (0)
All upper Columbia R.	26	0.0% (0)
Yakima R.	12	16.7% (2)
Umatilla R.	*5*	*20.0% (1)*

[1] based on adult run timing at Bonneville Dam; some may have been summer-run fish

Steelhead. – We radio-tagged a total of 1,414 known-source adult steelhead from 2000-2003 (Table 5). The basic straying rate with all years and stocks combined was 6.8%. A total of 96 steelhead strayed, of which 30 were harvested in non-natal tributaries. Treatment of the latter group as non-strays resulted in a minimum stray rate of 4.7% (Table 5). With all stocks combined, annual stray rates ranged from 6.1% in 2002 to 9.1% in 2000 (Table 6). Annual rates did not differ ($P > 0.05$) in paired χ^2 tests.

Table 5. Numbers and proportions of known-source steelhead groups that were last recorded straying into non-natal tributaries, 2000-2002. Basic stray rate includes fish harvested in non-natal tributaries. Tributary harvest excluded stray rate treats fish harvested in non-natal tributaries as non-strays and is therefore a conservative estimate. Table only includes stocks or aggregates with ≥10 fish, except the Dayton Pond (Walla Walla River) and Wind River stocks, which had straying fish.

Stock	n	Total stray rate % (n)	Tributary Harvest excluded stray rate % (n)
All steelhead	1,414	6.8% (96)	4.7% (66)
All Snake R.	905	5.6% (51)	4.6% (42)
Known Snake R. transport	464	6.9% (32)	5.8% (27)
Lower Granite Dam	166	7.8% (13)	5.4% (9)
Little Goose Dam	265	6.4% (17)	6.0% (16)
Lower Monumental Dam	33	6.1% (2)	6.1% (2)
No known Snake R. transport	441	4.3% (19)	3.4% (15)
Lower Granite Dam	275	4.0% (11)	2.9% (8)
Clearwater R.	61	1.6% (1)	1.6% (1)
Grande Ronde R.	23	4.3% (1)	4.3% (1)
Salmon R.	31	3.2% (1)	3.2% (1)
Imnaha R.	28	10.7% (3)	10.7% (3)
All upper Columbia R.	469	7.0% (33)	3.0% (14)
Rock Island Dam	76	7.9% (6)	5.3% (4)
Rocky Reach Dam	64	18.8% (12)	9.4% (6)
All Wells Hatchery	329	4.6% (15)	1.2% (4)
Wells Dam tailrace release	162	5.6% (9)	1.9% (3)
Wells pool release	147	3.4% (5)	0.7% (1)
Okanogan R. release	20	5.0% (1)	0.0% (0)
Wind R.	*4*	*25.0% (1)*	*25.0% (1)*
Walla Walla R. (Dayton Pond)	*4*	*100.0% (4)*	*50.0% (2)*
Umatilla R.	22	22.7% (5)	22.7% (5)
Yakima R.	10	20.0% (2)	20.0% (2)

Table 6. Basic annual stray rates for selected steelhead stocks, 2000-2003.

	Percent (*n*) that strayed			
	2000	2001	2002	2003
All steelhead	9.1% (11)	7.3% (698)	6.1% (587)	6.8% (118)
All Snake R.	0.0% (9)	6.7% (359)	5.1% (435)	4.9% (102)
Known Snake R. transport	0.0% (1)	8.6% (174)	6.2% (227)	4.7% (64)
No known Snake R. transport	0.0% (8)	4.9% (185)	3.8% (208)	5.3% (38)
All upper Columbia R.	50.0% (2)	6.4% (326)	7.9% (140)	0.0% (1)
All Wells Hatchery	50.0% (2)	2.0% (197)	8.4% (131)	
Rocky Reach Dam		18.3% (60)	0.0% (2)	0.0% (1)
Rock Island Dam		8.7% (69)	0.0% (7)	

Stray rates for aggregated stocks from the major basins were 5.6% for 905 Snake River fish, 7.0% for 469 upper Columbia River fish, and were greater than 20% each for the small samples from the Wind, Walla Walla, Umatilla, and Yakima rivers (Table 5). No significant (*P* > 0.05) between-year stray rate differences were found for the Snake or upper Columbia River stocks (Table 6). Stray rates also did not differ between Snake and upper Columbia stocks in the two years with adequate sample sizes for both stocks (2001 and 2002).

With all years combined steelhead that had been transported from the Snake River strayed at higher rates (6.9%) than non-transported steelhead (4.3%), but the difference was not significant (*P* = 0.091, Table 5). In 2001 and 2002, transported fish were more than 1.6 times as likely to stray, but differences were not significant (*P* > 0.05) (Table 6). Steelhead with fin clips were significantly (*P* < 0.001) more likely to stray than were fish with no fin clips (8.4% versus 3.5%).

Steelhead were most likely to stray into the Little White Salmon (23% of all strays) and Deschutes rivers (21%), and many also entered the John Day (17%) and White Salmon (15%) rivers (Table 7). Snake River fish mostly entered the John Day (31%) and Deschutes (24%) rivers. Upper Columbia steelhead mostly entered the Little White Salmon (42%) and White Salmon (27%) rivers (Table 7). Differences in straying locations between Snake and upper Columbia steelhead may have been related to shoreline preferences: Snake River fish entered south-shore tributaries and upper Columbia fish entered north-shore tributaries. Transported and non-transported Snake River fish also had somewhat different straying patterns: proportionately more transported fish entered the John Day River and more non-transported fish entered the Little White Salmon River. Steelhead strays from the Umatilla and Walla Walla rivers mostly entered the Snake River.

Table 7. Stray locations for steelhead, based on juvenile PIT tag sites.

Stray location	All fish	All Snake River fish	Snake River Trans.	Snake River no Trans.	Wind River	Upper Columbia River	Umatilla River	Walla Walla River	Yakima River
Eagle Cr.	2	1		1		1			
Herman Cr.	5	2	1	1	1	2			
Wind R.	4	4	2	2					
L. W. Sal. R.	22	7	2	5		14			1
W. Sal. R.	14	2	2			9	1	1	1
Klickitat R.	2	2	1	1					
Deschutes R.	20	12	7	5		6	2		
John Day R.	16	16	13	3					
Snake R.	6					1	2	3	
Tucannon R.	2	2	2						
Salmon R.	1	2		1[1]					
Hanford Rch.	1	1	1						
Upper Col. R.	1	1	1						
Total	**96**	**51**	**32**	**19**	**1**	**33**	**5**	**4**	**2**

[1] 1 steelhead PIT-tagged in the Tucannon River was last detected in the Salmon River, Idaho

There was a strong tendency for early-migrating steelhead to stray at higher rates than later migrants (Table 8). With all stocks combined, fish tagged prior to 15 August (the approximate mid-point of our steelhead tagging effort) strayed at significantly (*P* < 0.05) higher rates than those tagged after 15 August (Table 8). This significant pattern also occurred in 2001 and 2002, but not in 2003. Considered separately, Snake and upper Columbia River stocks also followed the pattern of higher straying by early migrants, but differences were significant (*P* < 0.05) only for Snake River fish (2001 and all years combined).

Table 8. Proportions of steelhead tagged before and after 15 August that strayed into non-natal tributaries. *P* values based on χ^2 tests of proportions.

	Stray percent (*n*)		
	Tag date ≤ 15 Aug	Tag date > 15 Aug	*P*
All steelhead	9.3% (776)	3.7% (627)	0.000
Year 2001	10.0% (402)	3.7% (296)	0.002
Year 2002	8.4% (299)	3.8% (288)	0.022
Year 2003	9.3% (75)	2.3% (43)	0.145
All Snake R.	8.0% (448)	3.3% (457)	0.002
Year 2001	9.8% (183)	3.4% (176)	0.015
Year 2002	6.9% (202)	3.4% (233)	0.097
Year 2003	6.7% (60)	2.4% (42)	0.324
All Upper Columbia R.	8.1% (298)	4.7% (171)	0.163
Year 2001	7.7% (208)	4.2% (118)	0.222
Year 2002	9.1% (88)	4.2% (52)	0.480
Year 2003	0.0% (1)		
All Umatilla R.	22.2% (18)	25.0% (4)	

Effects of censoring fish harvested in main stem fisheries. – Censoring of main stem-harvested salmon and steelhead had relatively limited impact on straying estimates (Table 9). Basic stray rates were higher by 0.1 to 0.4 (5 to 7% of the non-censored estimates) for the three runs when fish harvested downstream from The Dalles Dam were censored. When all fish harvested in the lower Columbia River main stem were censored (downstream from McNary Dam) basic stray rates were higher by 0.2 to 0.8 (9 to 17% of the non-censored estimates) (Table 9). Censoring of main stem harvest had similar effects (not shown) on the stray rate estimates adjusted for tributary harvest (e.g., using equation 4).

Table 9. Basic stray rates for known-source spring–summer and fall Chinook salmon and steelhead as adjusted by censoring fish that were harvested in the lower main stem Columbia River.

	Basic stray rates		
	Sp-Su Chinook	Fall Chinook	Steelhead
No censoring	2.2%	4.2%	6.8%
Censored = main stem harvest downstream from The Dalles	2.3%	4.5%	7.2%
Censored = main stem harvest downstream from John Day	2.4%	4.7%	7.4%
Censored = main stem harvest downstream from McNary	2.4%	4.9%	7.6%

Steelhead modeling results. – A total of 987 steelhead were used in logistic regression analyses to model the probability of straying: 909 fish were considered to home, 53 fish were recorded as strays, and 25 fish were recorded as harvested strays. When including harvested strays in the stray response category, the logistic regression model which best approximated the steelhead data included fallback, fin clips, transport history, tag date, and sex as influential covariates (Table 10). As indicated by the positive parameter estimates, fish that fell back more than once were more likely to stray than fish that did not fall back, fin-clipped fish were more likely to stray than non-clipped fish, barged fish were more likely to stray than non-barged fish, and males were more likely to stray than females. The negative parameter estimate for tagging date implied that the probability of straying decreased as tagging date advanced throughout the migrations. The fallback variable that discriminated fish that fell back one time from fish that did not fall back was not significant in the selected model (Table 1; p=0.984). However, statistical texts recommend keeping all variables created from a classification category (e.g. fallback) in the structure of the model if any were considered significant.

Table 10. Parameter estimates for predictor variables included in the logistic regression model that best approximated the probability of straying for radio-tagged Snake and Upper Columbia River steelhead, 2001-2002. Positive (negative) parameter estimates indicated higher (lower) probabilities of straying for the first classification in each of the categorical variables. Response categories for the logistic model were home and stray (including harvested strays).

Predictor variable	Categorical variable differentiation	Parameter Estimate	Standard error	p-value
Fallback-1	1 vs 0[a]	-0.01	0.422	0.984
Fallback-2	≥ 2 vs 0[b]	1.39	0.454	0.002
Fin clips	Clipped vs Not clipped	1.06	0.308	0.001
Transport	Barged vs Not barged	0.75	0.312	0.017
Radio-tag date	Not applicable	-0.01	0.005	0.029
Sex	Male vs Female	0.41	0.248	0.101

[1] Differentiated fish that fellback once from those that did not fallback

[2] Differentiated fish that fellback at least twice from those that did not fallback

The relative influence of the predictor variables on the probability of straying was better described by the odds ratio estimates (Table 11). Fish that fell back at least twice at dams were 4 times more likely to stray than fish that did not fall back; clipped fish were 2.8 times more likely to stray than non-clipped fish; fish that were barged were twice as likely to stray as fish that were not barged; and males were 1.5 times more likely to stray than females. As expected from its insignificant parameter estimate, fish that fell back once during their migration were just as likely to stray as fish that did not fall back (fallback-2 odds ratio estimate = 0.99). The odds ratio estimate for tag date indicated that each increase in tag date by one day decreased the probability of straying by a factor of 0.99. In a longer time context, a steelhead tagged on any given day was 0.74 times more likely to stray than a fish tagged 30 d earlier (i.e. odds ratio = $e^{(-0.01*30)}$).

Table 11. Odds ratio estimates for predictor variables that were included in the logistic regression model that best approximated the probability of straying for radio-tagged Snake and Upper Columbia River steelhead, 2001-2002 (see Table 1 for interpretation of categorical variables). Response categories for the logistic model were home and stray (including harvested strays).

Predictor variable	Odds ratio estimate	95% Confidence limit Lower limit	Upper limit
Fallback-1	0.99	0.434	2.265
Fallback-2	4.01	1.649	9.762
Fin clips	2.87	1.570	5.256
Transport	2.11	1.146	3.890
Radio-tag date	0.99	0.980	0.999
Sex	1.50	0.924	2.444

The selected model was not convincingly best as nine other models were considered to have substantial support as best (Table 12). The lack of confidence in the selected best model was also apparent when Akaike weights were used to assess relative model strength (Table 12). The selected model (model 1; w_i = 0.168) was not more than 1.5 times as likely to be the best as any of the next three models under consideration (models 2-4; w_i = 0.145-0.116), and not more than 3 times as likely to be the best as the remaining six models under consideration (models 5-10; w_i = 0.085-0.062). However, most of the models in the 'confidence set' included each of the five covariates that were included in the selected best model (Table 12). Fallback events, fin clips, transport history, and tag date were included in all ten models, and sex was included in seven models. By comparison, temperature, fish length, ocean residence and discharge were not influential.

Table 12. The list of logistic regression models that received support as best approximating the straying data (i.e ΔAIC ≤ 2) for radio-tagged Snake and Upper Columbia River steelhead, 2001-2002. The first model was selected as the best approximating model with an AIC value of 532.69 (Full model AIC = 542.04). Listed for each model is its Akaike weight, w_i (see text for calculation), which provided a measurement of its weight of evidence as the best model. Response categories for the modeling analysis were home and stray (including harvested strays).

Model	Predictor variables included in the model	ΔAIC	w_i
1	fallback, clips, transport, tag date, sex	0	0.168
2	fallback, clips, transport, tag date, sex, temperature	0.30	0.145
3	fallback, clips, transport, tag date, sex, temperature, length	0.55	0.128
4	fallback, clips, transport, tag date	0.74	0.116
5	fallback, clips, transport, tag date, sex, length	1.37	0.085
6	fallback, clips, transport, tag date, temperature	1.40	0.084
7	fallback, clips, transport, tag date, sex, temperature, ocean residence	1.60	0.076
8	fallback, clips, transport, tag date, sex, ocean residence	1.79	0.069
9	fallback, clips, transport, tag date, temperature, length	1.80	0.068
10	fallback, clips, transport, tag date, sex, flow	2.00	0.062

The selected best model was limited in its potential to differentiate individuals that strayed from those that homed based on model-generated straying probabilities. As expected, the percentage of fish assigned a low probability of straying (0.00 to 0.05) was greater for homed fish (29%) than for strays (10%), and the percentage of fish assigned a high probability of straying (0.1 to 0.5) was greater for strays (47%) than for homed fish (22%). However, considerable overlap in straying probability existed between the two groups. Forty-nine percent of homed fish and 42% of strays were assigned straying probabilities between 0.05 and 0.10 (Figure 2).

Modeling results were not substantially altered when harvested strays were omitted from the stray response category, although some differences existed. Similar to the first modeling analysis, fallback events, fin clips, transportation history, and tag date were included as influential covariates in the selected best model. Sex was omitted as a covariate. Odds ratios for the four selected covariates did not considerably change when harvested strays were excluded. Fish that fell back at least twice at dams were 5 times more likely to stray than fish that did not fall back, clipped fish were 1.9 times more likely to stray than non-clipped fish, fish that were barged were 2.3 times as likely to stray than fish that were not barged, and an increase in tag date by one day decreased the probability of straying by a factor of 0.99. As with the initial analysis, there was uncertainty in the selected best model as eight other models received support as best. The selected model (w_i = 0.165) was not more than 1.5 times as likely to be the best as any of the next three models under consideration (w_i = 0.111-0.159), and not more than 2.5 times as likely to be the best as the remaining five models under consideration (w_i = 0.070-0.098). Notably, the four covariates included in the best model (fallback, fin clips, transport, tag date) were also found in at least seven of the other eight models. Indices of relative importance for these variables ranged from 0.90 to 1.00.

Seventy-two radio-tagged Snake River steelhead from the 2003 migration were used to validate the predictive capabilities of the selected best model developed from the first modeling analysis. Of the 72 fish, 67 were recorded as homed and 5 were strays (including harvested strays) (Figure 2). The expected number of strays, calculated as the summation of the model-generated stray probabilities for all 72 fish, was 6. Although the expected and observed stray rates were similar (6.9 versus 8.3%), the model was limited in its ability to accurately assign individual steelhead into either homing or stray categories. Fish that homed were assigned similar model-generated stray probabilities as fish that had strayed. Fifty-two percent of homed fish and 60% of strays were assigned straying probabilities between 0.05 and 0.10, and the highest straying probabilities were assigned to four fish that had homed.

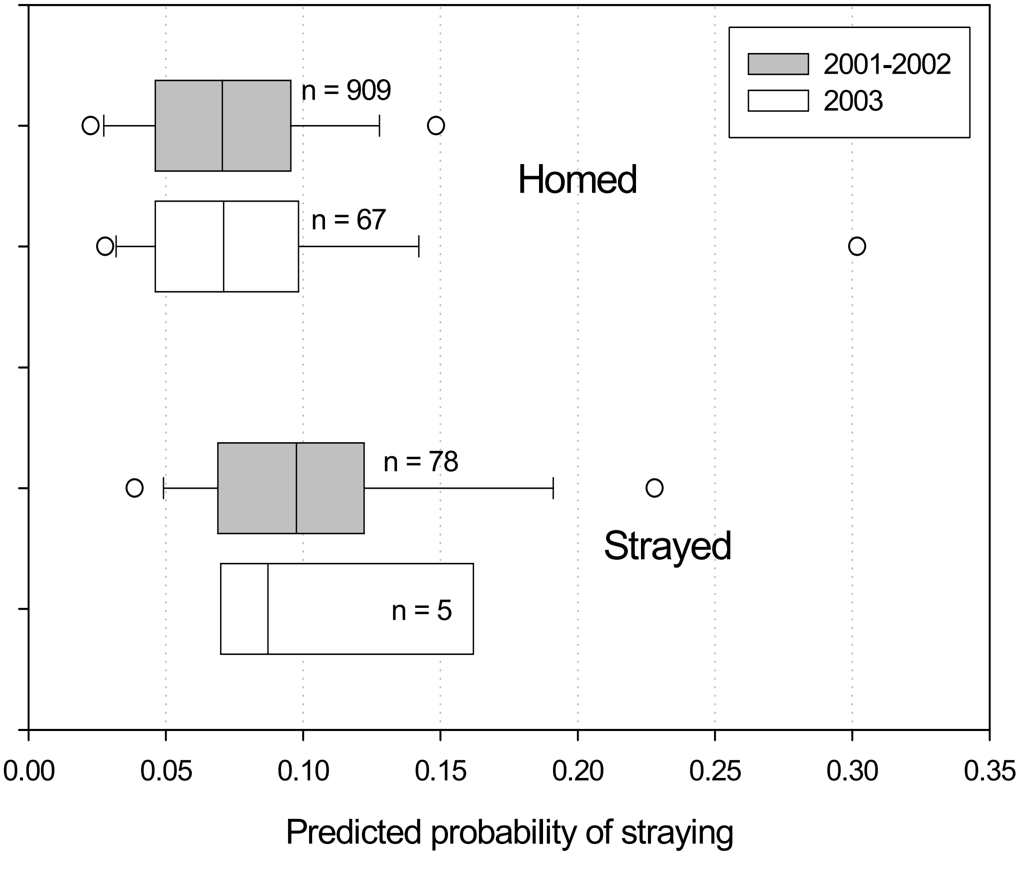

Figure 2. Distribution (median, quartile, 5th, 10th, 90th and 95th percentiles) of steelhead straying probabilities generated from the best selected logistic regression model (see Table 10). Data from 2001-2002 were used in model formulation, and 2003 data were used to test the model.

Discussion

We used complete migration histories for more than 3,000 radio-tagged adult salmon and steelhead of known origin to estimate inter-basin adult straying rates within the Columbia River basin. Basic, unadjusted stray rates were 2.2% for spring–summer Chinook salmon, 4.2% for fall Chinook salmon and 6.8% for steelhead when all years and stocks were combined. Straying fish mostly entered lower Columbia River tributaries, especially the Little White Salmon, Deschutes, John Day, and White Salmon rivers. Straying into these systems may be partially the result of fish (especially fall Chinook salmon and steelhead) seeking cool water refugia when main stem water temperatures are high (Goniea 2002; High 2002; Keefer et al. 2002).

While intra-basin straying is an essential feature of salmonid metapopulations (Cooper and Mangel 1999), the relatively large number of straying Snake and upper Columbia River fish may be harmful. Many hatchery fish from these upriver populations strayed into tributaries where wild populations are at risk of extinction, including the John Day, Wind, and Klickitat rivers (Nehlsen et al. 1991). Other researchers have documented strays from upriver populations in lower tributary spawning areas (e.g., Chilcote 1998) where they compete with native stocks. Interactions between strays, particularly hatchery strays, and native populations could undermine recovery of listed wild fish (Levin et al. 2001), reduce productivity, or have other poorly understood ecological consequences (Chilcote 2003; Weber and Fausch 2003).

Our analyses indicated that juvenile transportation increased the likelihood of straying by Snake River spring-summer Chinook salmon, and both transportation and artificial rearing increased the likelihood of straying for steelhead. The apparent influence of juvenile transportation on increased straying is likely related to interruptions in sequential imprinting during outmigration (Quinn et al. 1989). Transportation has been linked to higher straying rates among Columbia River sockeye and fall Chinook salmon (Mundy et al. 1994; Bugert et al. 1997; Chapman et al. 1997) and by coho salmon in the lower Columbia River (Solazzi et al. 1991) and coastal rivers in Oregon (Johnson et al. 1990). The observed increased straying by hatchery steelhead may be related to rearing, release timing, fallback, or a combination of these and other factors.

Repeated fallback behavior increased the probability of straying by four to five times, and was the variable most strongly associated with straying probability. Straying spring–summer Chinook salmon and steelhead were more likely to have fallen back than non-strays, significantly so for salmon. In more detailed investigations of adult fallback behavior, we have noted significantly increased fallback rates by fish that were transported as juveniles (Boggs et al. 2005; Keefer et al. *unpublished analysis*), a response also identified by other Columbia River basin researchers (Bugert et al. 1997; Chapman et al. 1997). The current results indicate that barged fish, hatchery fish, and fish that fell back several times during their migration were more likely to stray, suggesting potential cumulative or interactive effects. It was difficult, however, to determine which of these variables (e.g. transportation, fallback, hatchery origin) were causative factors. Fallback, for example, may have been at least partially a symptom of increased straying behavior, hatchery origin, or transportation. Larger sample sizes would be required to separate the effects on straying of these inter-related factors.

The steelhead modeling analysis also indicated that early-migrating fish were more likely to stray than later migrants. This suggests that fish with different run timings, or different life-history strategies, may have different stray probabilities. Early steelhead are typically exposed to high main stem river temperatures (e.g. > 20º C) for longer time periods than late migrants, and are much more likely to stray temporarily into cooler lower Columbia River tributaries (High 2002; Keefer et al. 2002). This behavior almost certainly influences permanent straying rates. Although temperature at the time of radio tagging was not identified as one of the primary factors influencing permanent straying in the modeling analysis, this metric was likely a poor proxy for the cumulative thermal effects experienced by steelhead, particularly given their often protracted migration times in the lower river (Keefer et al. 2004b).

Although fallback, artificial propagation, barging, and early run timing were influential factors that increased the probability of steelhead straying, the modeling analysis revealed limitations in the predictive capabilities of these variables. The model did provide a relatively accurate prediction of the proportion of steelhead that strayed in the 2003 sample, but there was insufficient evidence for a decisively best model for predicting steelhead straying. In addition, the selected model poorly discriminated between individual fish that had homed and those that had strayed. The model's inability to differentiate between the two groups of fish was not entirely unexpected as the probability of straying was likely low for any fish, regardless of its rearing or migratory history.

The degree of salmon and steelhead straying can affect interpretation of escapement estimates, one of the critical management issues in the Columbia River basin (Dauble and Mueller 2000). For example, if escapement is defined as return to potential spawning areas, then most strays in this study would be considered successful migrants. If success is defined solely by return to natal sites, all strays would be considered unsuccessful. Such calculations affect escapement estimates for both basins receiving strays (possible escapement inflation) and donor basins (reduced escapement). In our escapement summaries for the radio-tagged fish in this study (Keefer et al. *in press*), we defined escapement as return to tributary sites, regardless of straying behavior. We noted, however, that escapement estimates for the known-source groups should be revised downward by approximately the straying proportions if return to natal sites was the measure of success.

The results presented here are based on very extensive radiotelemetry coverage. Caution should be taken when applying the basic stray rates reported here to years without radiotelemetry studies, and any future application would be most appropriate for the known-source groups we studied. The rates could potentially be used, for example, to estimate likely stray rates from counts of Snake River or upper Columbia stocks detected at Bonneville Dam PIT-tag interrogators. A complicating factor will be identification of main stem-harvested fish, which will be difficult in the absence of telemetry and associated reward programs. Harvest within tributaries where straying occurred, which varied considerably between runs and stocks, will also be difficult to measure. As a result, future estimation of harvest-adjusted stray rates (equations 2-4) will be less precise. Fortunately, censoring of main stem-harvested fish in this study resulted in relatively small increases in stray estimates, suggesting that the range of stray rates reported here may be relatively robust. We note, however, that stray rate estimation may be sensitive to larger fluctuations in the percentage of fish harvested in each year, and this should be considered in future analyses. Managers will also need to carefully consider techniques to estimate harvest rates if differentiation of stray types or rate adjustments are necessary.

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