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18 October 2004

To: Marvin Shutters and David Clugston, USACE
From: Matt Keefer, Chris Peery and Jon Firehammer (University of Idaho), and Mary Moser (NOAA-Fisheries)

Re: Summary of straying rates for known-origin adult Chinook salmon and steelhead in the Columbia/Snake hydrosystem; Letter Report.

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. 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, 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 which fish 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 letter 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 mainstem water temperatures or other stimuli. Factors that appear to affect straying—including water temperature, fallback and juvenile transportation—are discussed.

Methods: 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. 2004 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.

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. For example, the latter could identify fish that lost radio transmitters during migration.

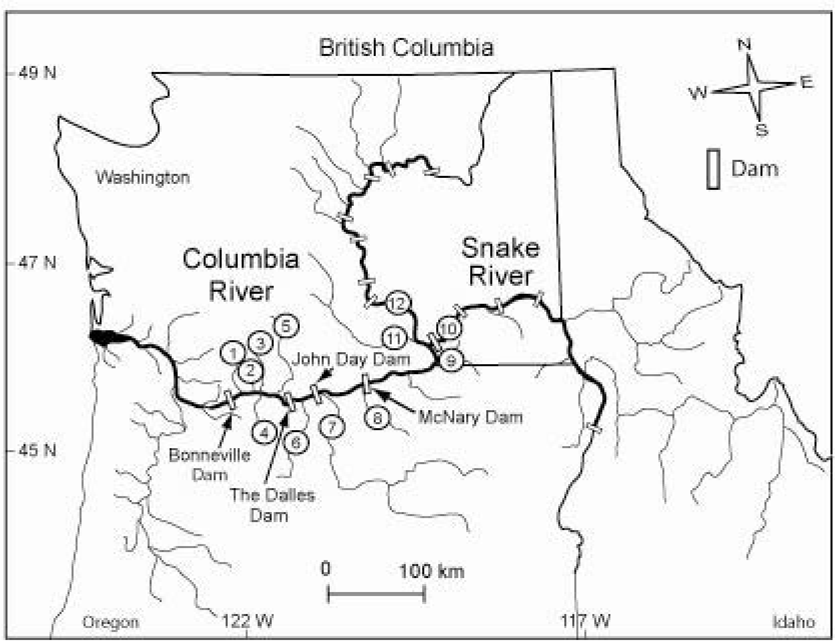

Figure 1. Columbia River basin, including major tributary basins where radio-tagged fish were last recorded. Tributary basins: 1) Wind, 2) Little White Salmon, 3) White Salmon, 4) Hood, 5) Klickitat, 6) Deschutes, 7) John Day, 8) Umatilla, 9) Walla Walla, 10) Snake, 11) Yakima, and 12) upper Columbia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

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 mainstem 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 mainstem fisheries (N_{MH}) were censored (Equations 3). We ran several iterations of Equation 3 to better define the sensitivity of the basic estimates to mainstem 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 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 mainstem harvest censored: $(N_S) / (N_R - N_{MH})$

Equation 4, basic stray rate with mainstem harvest censored and tributary harvest excluded: $(N_S - N_H) / (N_R - N_{MH})$

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 were almost significant 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.

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 ($P \leq 0.051$) (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.

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

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).

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)

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.

Fall Chinook salmon: Relatively few juvenile fall Chinook salmon have been PIT-tagged in the Columbia River. 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 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.

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).

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)

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 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)
<u>All Snake R.</u>	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)
<u>All upper Columbia R.</u>	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)	

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 mainstem fisheries: Censoring of mainstem-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 mainstem 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 mainstem 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 mainstem Columbia River.

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

Discussion: We used complete migration histories for more than 3,000 radio-tagged adult salmon and steelhead of known origin to estimate intra-basin adult straying rates in 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. Juvenile transportation from the Snake River increased the likelihood of straying for spring–summer Chinook salmon and steelhead, although tests of significance had varying results. Steelhead of hatchery origin (with fin clips), and early steelhead migrants (radio tagged before 15 August) were also more likely to stray than their counterparts.

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 mainstem water temperatures are high (Goniea 2002; High 2002; Keefer et al. 2002). 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). We also observed increased adult fallback for transported fish (Boggs et al. 2004), a behavior also reported in other Columbia River transportation studies. Among the radio-tagged fish, straying spring–summer Chinook salmon and steelhead were more likely to have fallen back than non-strays, significantly so for salmon. The observed increased straying by hatchery steelhead may be related to rearing, release timing, fallback, or other factors.

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).

Treatment of strays can affect interpretation of escapement estimates (Dauble and Mueller 2000). For example, if escapement was defined as return to potential spawning areas, then most strays in this study would be considered successful migrants. If success was defined solely by return to natal sites, all strays would be considered unsuccessful. Such calculations affect escapement estimates for both receiving basins (possible escapement inflation) and donor basins (reduced escapement). In our escapement estimates for these groups (see Keefer et al. *in review*), we defined escapement as return to tributary sites, regardless of straying behavior. We also noted 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.

Applying the basic stray rates reported here in future years without radiotelemetry studies would be most appropriate for the known-source groups studied. The rates could be applied, for example, to counts of Snake River or upper Columbia stocks detected at Bonneville Dam PIT-tag interrogators. In the absence of telemetry and associated reward programs, identifying mainstem-harvested fish will be difficult. Harvest within tributaries where straying occurred, which varied considerably between runs and stocks, will also be difficult to measure. As a result, calculation of harvest-adjusted stray rates (equations 2-4) will be less precise. Fortunately, censoring of mainstem-harvested fish in this study resulted in relatively small increases in stray estimates, suggesting the range of stray rates reported here may be broadly applicable to estimating future stray rates. Managers will need to consider techniques to estimate harvest rates if differentiation of stray types or rate adjustments are necessary.

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