Technical Report 2006-7

IDAHO COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT

EFFECTS OF TRANSPORT DURING JUVENILE MIGRATION ON BEHAVIOR AND FATE OF RETURNING ADULT CHINOOK SALMON AND STEELHEAD IN THE COLUMBIA-SNAKE HYDROSYSTEM, 2000-2003

Report for study code ADS-00-4

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for
U.S. Army Corps of Engineers
Portland and Walla Walla Districts
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Preface

Studies of adult salmon and steelhead *Oncorhynchus* spp. migrations past dams, through reservoirs, and into tributaries have been ongoing since the early 1990's. Adult spring–summer Chinook salmon (*O. tshawytscha)* and steelhead (*O. mykiss*) were first tagged with transmitters at Ice Harbor Dam in 1991 and 1992 and at John Day Dam in 1993. The focus of adult salmonid passage studies shifted to include the lower Columbia River dams and tributaries starting in 1996. From 1996 to 2003 we radio-tagged various combinations of spring–summer Chinook salmon, fall Chinook salmon, steelhead, and/or sockeye salmon (*O. nerka*) at Bonneville Dam and monitored them as they migrated upstream. Portions of each sample in 2000-2003 were fish of known origin, identified by juvenile PIT tags, and included a sub-sample of Snake River fish PIT-tagged as juveniles at Lower Granite Dam. In this report we present summary information on the relationships between juvenile transportation history (barged versus in-river migration) and adult migration behaviors (homing, straying, fallback) by Snake River spring–summer Chinook salmon and steelhead.

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

Abstract

We used radiotelemetry to examine the effects of juvenile transportation on adult fate and migration behaviors of 1,184 Snake River spring–summer Chinook salmon and steelhead. All study fish were collected and tagged with passive integrated transponder (PIT) tags as juveniles at Lower Granite Dam on the Snake River from 1998-2002 and returned as adults during 2000-2003. Approximately 60% of the adults radio-tagged in this study were transported in barges as juveniles from Snake River dams to release sites downstream from Bonneville Dam on the Columbia River. Juveniles that were not transported migrated downstream in-river.

Adult homing was significantly lower and unaccounted loss and permanent straying into non-natal basins was higher for both spring–summer Chinook salmon and steelhead that were barged as juveniles. On average, adult fish barged as juveniles homed to Lower Granite Dam at rates about 10% lower than fish that had migrated in-river. Homing to Lower Granite Dam differed between juvenile release years for both species, reflecting differences in treatments and river environment during both juvenile and adult migrations. The presence of fin clips (certain hatchery origin) was not significantly associated with Chinook salmon homing, while unclipped steelhead returned to Lower Granite Dam at significantly lower rates than fin-clipped fish. Straying rates in both species were higher among groups barged as juveniles. When compared to in-river migrants, barged Chinook salmon were 1.9 times more likely and barged steelhead were 1.3 times more likely to fall back at dams as adults. Among fish that fell back, a significantly greater proportion of barged fish also experienced multiple fallback events than in-river migrants.

Decreased homing, increased fallback, and increased straying rates by transported fish were inter-related and linked to hatchery origin in some cases. The results were consistent between species and years, strongly suggesting that juvenile transport impaired adult orientation of both hatchery and wild fish during return migration. Streams-of-origin and hatcheries-of-origin were unknown for most fish and differences among sub-basin stocks may have influenced results. However, there were clear associations between adult behavior and transport history, despite the potential presence of underlying sub-basin variation. Future studies are needed to isolate the effects migration timing, of origin, and of in-stream residence times upstream from Lower Granite Dam from those of transport history for Snake River salmon and steelhead. Overall, the results suggest that the benefits of barging juveniles may be reduced due to negative effects on returning adults. These effects are typically difficult to quantify and may include both adult losses and significant changes to population genetic structure caused by increased straying of barged fish.

Introduction

Efforts to increase juvenile survival and adult returns of Snake River salmon and steelhead have included mass juvenile transportation through the hydrosystem (Raymond 1979; Rieman et al. 1991; Ward 1997). This involves collection of juveniles at dam bypass facilities, separation, loading on barges and transportation in constantly replenished river water to release locations downstream from Bonneville Dam. Reported unintended consequences of juvenile transportation for adult fish may include reduced homing, increased straying into non-natal tributaries, and delay, disorientation, and fallback behavior at dams (Ebel 1980; Mundy et al. 1994; Bugert et al. 1997; Chapman et al. 1997).

Relationships between juvenile transport and subsequent adult behaviors are a concern for managers because, (1) straying by hatchery fish to spawning sites of wild salmonids may compromise genetic integrity and recovery efforts for wild listed stocks (Chilcote 1998; Weber and Fausch 2003), (2) adult fallback at dams biases fishway counts used for escapement estimates and harvest quotas (Dauble and Mueller 2000; Boggs et al. 2004), and (3) slowed adult migration at dams and fallback can be associated with high energetic costs, pre-spawn mortality, and prolonged exposure to fisheries (Brown et al. 2002; Keefer et al. 2005; Naughton et al. 2005).

From 2000 to 2003, our radio-tagged samples included 457 spring–summer Chinook salmon and 727 steelhead that were collected and PIT-tagged as juveniles at Lower Granite Dam by the National Marine Fisheries Service (NOAA-Fisheries). Sixty percent of the radio-tagged adult Chinook salmon and 62% of the steelhead were transported as juveniles. The remaining fish outmigrated to the ocean by swimming through bypasses or over dams (in-river migrants). For this report, we compared adult fallback behavior, homing and straying rates, and mainstem harvest rates of barged fish to those of the in-river control groups, and evaluated how adult behavior and fate were related to transportation history.

Methods

Fish Sampling**.** – All juvenile spring–summer Chinook salmon and steelhead were collected from 1998-2002 in the juvenile collection/transportation facility at Lower Granite Dam, and PIT-tagged as part of a NMFS project (Table 1, Figure 1). After PIT tagging, juveniles were either released back into the river downstream from Lower Granite Dam or placed on transportation barges. Some of the PIT-tagged fish released in-river at Lower Granite Dam were subsequently collected at Little Goose or Lower Monumental dams and barged downstream. All barged fish were transported through the Snake/Columbia hydrosystem to release sites downstream from Bonneville Dam (Figure 1).

Adults were collected opportunistically at the Adult Fish Facility (AFF) at Bonneville Dam from 2000-2003. An automated PIT-tag detection system (McCutcheon et al. 1994) in the AFF identified the fish that had been PIT-tagged at Lower Granite Dam, and those fish were diverted for radio tagging when possible. Chinook salmon were tagged throughout the spring–summer run (April-July) and steelhead were tagged from June-October. Tagged fish were released either 9.5 km downstream from Bonneville Dam (both sides of the river) or in the Bonneville Dam forebay (limited samples in 2001 and 2002 only, as part of an evaluation of fish ladder exit locations). Proportions of barged and in-river fish released in the forebay did not differ for Chinook salmon in either year or for steelhead in 2001. However, significantly more (19%) barged than in-river steelhead (11%; $\chi^2 = 4.0$, $P = 0.047$, Appendix

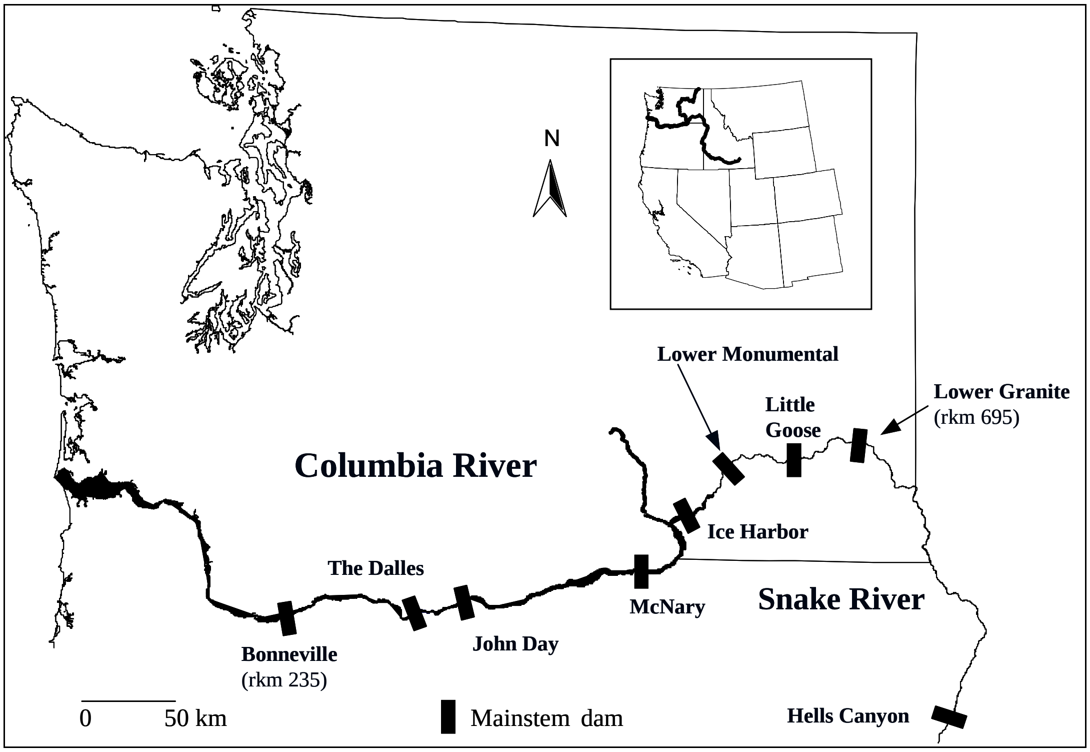

Figure 1. Map of the Columbia/Snake hydrosystem. Juvenile Chinook salmon and steelhead were all collected at Lower Granite Dam. Transported fish were barged from either Lower Granite, Little Goose or Lower Monumental dams. Retuning adults were collected and radio-tagged at Bonneville Dam.

Table A-1) were released in the forebay in 2002. Adult release location may have affected adult behaviors, and so this term was included in models to evaluate transportation effects.

Forty-five percent of radio-tagged Chinook salmon and 20% of steelhead had fin clips, indicating hatchery origin. We considered fish lacking fin clips to be of wild origin because fin-clipping is a standard protocol at all Snake River hatcheries; we note, however, that this sample may have included a small number of unclipped hatchery fish. Overall, 51% of barged Chinook salmon were hatchery fish versus 35% for in-river salmon ($\chi^2 = 11.4$, $P < 0.001$, $n = 457$). Conversely, 15% of barged steelhead were hatchery versus 28% of in-river steelhead ($\chi^2 = 19.8$, $P < 0.001$, $n = 727$). These proportions differed between treatments in 3 of 5 species-year combinations, with barged hatchery Chinook salmon and barged wild steelhead being the two most common groups of radio-tagged adults (Appendix Table A-2). These proportions were similar among years within species, except for the 1999 steelhead outmigration, which was dominated by hatchery fish. These differences were due to year-to-year changes in hatchery and/or barging protocols beyond our control. Because hatchery rearing may have affected adult behaviors, this term was included in models.

Adult Monitoring. – Adult passage and fallback behaviors at all dams in the lower Columbia and Snake rivers were monitored using aerial and underwater antennas in tailraces and fishways. Major tributaries were monitored with fixed aerial antennas near tributary mouths and with mobile-tracking units attached to trucks and boats (details in Bjornn et al. 2000, Boggs et al 2004, and Keefer et al. 2004b). At Lower Granite Dam (the treatment homing site), radio-tagged fish could be detected with both radio antenna arrays in the fishway and tailrace and by PIT-tag detectors at the dam (Harmon 2003). PIT-tag detectors increased the likelihood of identifying fish that had regurgitated radio transmitters, thereby reducing errors in fate designations (Keefer et al. 2004a, 2005).

Analysis**.** – Four fish fates were identified: return to Lower Granite Dam (homed), reported fisheries harvest downstream from Lower Granite Dam (fishery), permanent straying into tributaries downstream from Lower Granite Dam (stray), or last recorded in the hydrosystem with unknown fate. Fish with unknown fate (unaccounted) were presumed mortalities, although other fates were possible (*e.g.* unreported harvest). Fish that strayed into non-natal tributaries included those recaptured at hatcheries or weirs and those last detected by fixed or mobile telemetry units in a tributary. All harvested fish, including those harvested in downstream tributaries, were excluded from most analyses because treatment effects on fish fate could not be assessed. Exclusion of fish harvested in non-natal tributaries may have resulted in the underestimation of total straying. Across years, 11.2% of Chinook salmon and 11.0% of steelhead were reported harvested in fisheries. Harvest rates did not differ for barged and in-river migrants (Chinook salmon: χ^2 = 1.0, P = 0.310, n = 457: steelhead: χ^2 = 2.0, P = 0.153, n = 727. Harvest also did not differ by treatment for individual juvenile collection or adult return years for either species ($P \geq 0.13$).

During the 2001 outmigration year, all juveniles were barged, resulting in no control group. These fish were excluded from multinomial analyses of transportation effects, but were included in tables for reference. Patterns in the adult migration of the 2001 outmigration cohort were qualitatively compared to the other outmigration cohorts.

To isolate effects of juvenile transportation from potentially confounding differences in timing of juvenile or adult migrations, we first tested for differences in mean out-migration and return migration date between barged and in-river groups using the general linear model (GLM) date = transport + origin + transport*origin + error.

To test for transportation effects on fish fate (*i.e.* home, stray, unaccounted) and fallback behavior, we used a series of binary and multinomial models (Allison 1999). These models tested for associations between categorical response variables with two or more classes (fate) and one or more categorical predictor variables (transportation, origin, year, etc). Empty cells occurred when no fish strayed or fell back within a given year, and consequently, some interactions could not be tested. When interaction terms were non-significant ($P \geq 0.13$ in all cases) they were excluded to increase statistical power and the reduced model results were reported. Predictor variables included transportation treatment (barged, in-river), juvenile release year, adult release site (downstream, forebay), and/or hatchery origin (wild, hatchery). Juvenile release year and return year were highly correlated among fish within species because most fish returned at the same age, and we included juvenile release year rather than return year because this variable statistically controls for differences in juvenile collection location and river environment during outmigration (the treatment) among years. We note that because of differences among years in juvenile collection and adult release locations, inter-annual differences in results will reflect both inter-annual variability related to environmental conditions and any variability caused by differences between collection and release sites.

Results

With all years combined, 60% of Chinook salmon and 62% of steelhead were barged as juveniles (Table 1). Nearly all (> 97%) barged Chinook salmon and 81% of barged steelhead were transported from Lower Granite Dam in 1998, 1999, 2001 and 2002. In 2000, most barged fish (> 97% of Chinook salmon and >93% of steelhead) were transported from Little Goose Dam. Adult fates of fish barged from Little Goose and Lower Monumental dams were statistically indistinguishable from those barged from Lower Granite Dam (Appendix Table A-3), so all barged samples were combined.

Table 1. Numbers of radio-tagged adult Chinook salmon and steelhead released near Bonneville Dam, 2000-2003[1]. All fish had been collected and PIT-tagged at Lower Granite Dam during juvenile outmigration; juvenile fish either migrated in-river or were barged from Lower Granite, Little Goose or Lower Monumental dams to release sites downstream from Bonneville Dam.

Year of:			Juvenile transport location			
Adult return	Outmigration	In-river	L. Granite	L. Goose	L. Mon.	Total
Chinook salmon						
2000	1998	8	15			15
2001	1998	6	5			5
	1999	91	162	1	4	167
2002	1999	13	19			19
	2000	34		24	1	25
2003	2000	33		18		18
	2001[1]		23			23
	Total	185	224	43	5	272
Steelhead						
2001	1999	40	64	1	4	69
	2000	88		96	5	101
2002	1999	1	1			1
	2000	128		140	10	150
	2001[1]		71			71
2003	2000				1	1
	2001[1]		20	1	1	22
	2002	17	7	25	6	38
	Total	274	163	263	27	453

[1] 2001 outmigration data not used in statistical tests of transportation treatment effects

The mean timing of juvenile collection differed between treatment and origin groups and among years in complex ways (Figure 2, Appendix Table A-4). Among Chinook salmon, juvenile hatchery fish were collected 4-11 d later than wild fish in 1998 and 1999. After controlling for the origin differences, barged salmon were collected 2-9 d later than in-river migrants, a difference that was significant in 1999 only (Appendix Table A-4). In contrast, only wild Chinook salmon were PIT-tagged in 2000, and barged fish were collected 4 d earlier than in-river migrants (Figure 2). Juvenile hatchery steelhead were collected 3-13 d later than in-river migrants in 1999 and 2000, and barged steelhead were collected 7-13 d later than in-river fish in 1999 (Figure 2, Appendix Table A-4).

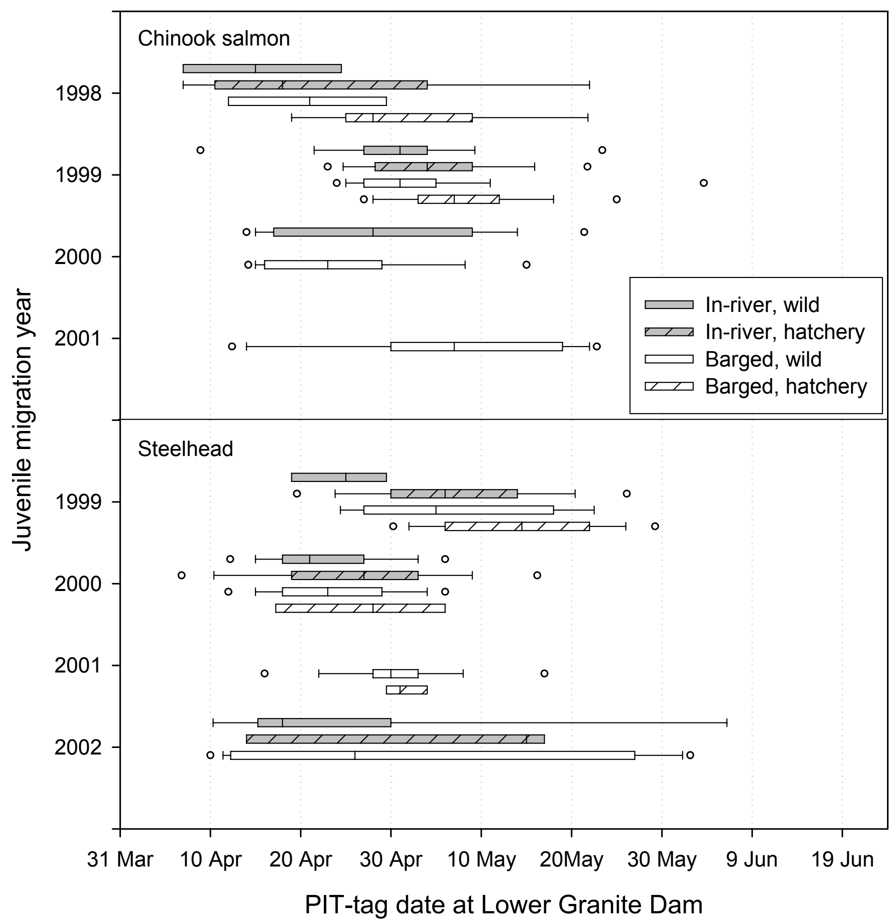

Figure 2. Juvenile collection date distributions at Lower Granite Dam, stratified by outmigration year, transportation treatment, and origin (hatchery, wild). Box plots include 5, 10, 25, 50, 75, 90, and 95 percentiles.

The timing of adult return also exhibited clear effects of origin in both species. Hatchery Chinook salmon returned to Bonneville Dam 12-16 d earlier than wild salmon in 2001 and 2002 (Figure 3, Appendix Table A-5). In contrast, hatchery steelhead returned 13-34 d later than wild fish in 2001 and 2003, a pattern that may reflect the relatively large hatchery contribution among late-migrating (B-group) adult steelhead. No significant effect of transport treatment on adult tagging date was observed in either species in any year (Figure 3, Appendix Table A-5).

Chinook Salmon Fate. – Qualitatively, juvenile transportation history was associated with fate in Chinook salmon, with the barged group homing less and straying more (Table 2). However, treatment effects could not be assessed across all years and fates simultaneously (home, stray, unaccounted) because straying by Chinook salmon was not observed in all years. Therefore, we first tested whether there were treatment effects on fate (home versus unaccounted), stratified by outmigration year, origin (hatchery, wild) and adult release location and then separately tested for straying effects (home versus stray) for those years where straying was observed. Salmon that out-migrated in 2001 were excluded because all juveniles were barged.

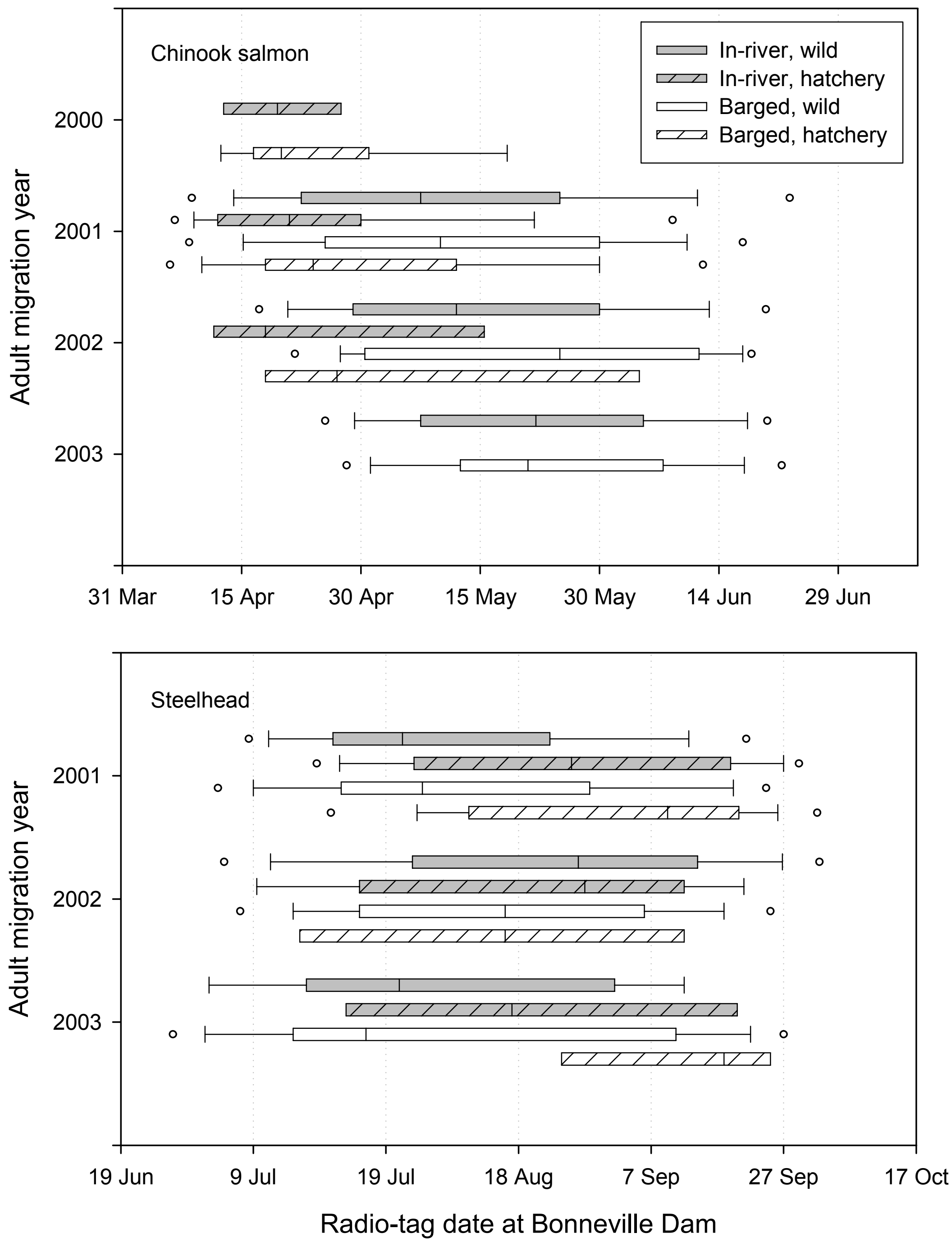

Figure 3. Adult collection date distributions at Bonneville Dam, stratified by adult return year, transportation treatment, and origin (hatchery, wild). Box plots include 5, 10, 25, 50, 75, 90, and 95 percentiles.

Table 2. Number and percent of radio-tagged adult Chinook salmon that homed, permanently strayed, or were unaccounted for during upstream migration, by juvenile transportation history, adult return year, juvenile outmigration year, and rearing history. All harvested fish were excluded.

				Percent (%)		
Group by:	Year	Treatment	*n*	Homed	Strayed	Unaccounted
All fish	All	In-river	161	92.6	0.6	6.8
		Barged	245	82.5	3.3	14.3
Outmigration	1998	In-river	14	85.7	0	14.3
		Barged	19	63.2	0	36.8
	1999	In-river	85	94.1	0	5.9
		Barged	163	82.2	4.9	12.9
	2000	In-river	62	91.9	1.6	6.5
		Barged	40	92.5	0	7.5
	2001	In-river	-	-	-	-
		Barged	23	82.6	0	17.4
Adult return	2000	In-river	8	75.0	0	25.0
		Barged	14	64.3	0	35.7
	2001	In-river	81	93.8	0	6.2
		Barged	151	83.4	4.6	11.9
	2002	In-river	42	95.2	2.4	2.4
		Barged	40	82.5	2.5	15.0
	2003	In-river	30	90.0	0	10.0
		Barged	40	85.0	0	15.0
Hatchery	All	In-river	53	90.6	0	9.4
		Barged	117	80.3	6.0	13.7
Wild	All	In-river	108	93.5	0.9	5.6
		Barged	128	84.4	0.8	14.8

A significantly lower percentage of the Chinook salmon barged as juveniles (1998-2000) homed to Lower Granite Dam than Chinook salmon that had migrated in-river as juveniles ($\chi^2 = 4.7$, $P = 0.031$, $df = 1$; Table 2). Barged Chinook salmon were 1.51 (95% CI odds ratios: 1.04-2.19) times more likely than in-river migrants to be unaccounted for as adults. Chinook salmon fates (home, unaccounted) differed significantly among outmigration years ($\chi^2 = 8.0$, $P = 0.018$, $df = 2$), but were not significantly related to origin ($\chi^2 = 0.1$, $P = 0.724$, $df = 1$) or adult release location ($\chi^2 = 2.3$, $P = 0.127$, $df = 1$). The pattern of lower homing and higher rates of unknown fate for barged Chinook salmon was consistent for all adult return years, adult release sites, for hatchery and wild fish, and for all but the 2000 outmigration year (Table 2).

In comparisons between Chinook salmon adults that homed versus strayed, there was a strong association between straying and barging (Table 2). Overall, 8 of 9 strays were barged as juveniles. Eight of the strays out-migrated in 1999, and all had been barged ($\chi^2 = 6.8$, $P = 0.009$, $df = 1$). Notably, 7 of the 8 strays from the 1999 outmigration were hatchery fish, resulting in a significant origin effect ($\chi^2 = 13.7$, $P < 0.001$, $df = 1$). A single wild, in-river juvenile migrant strayed in 2000, resulting in a significant origin*barge interaction ($\chi^2 = 12.4$, $P < 0.001$, $df = 1$).

Steelhead Fate. – Barged steelhead also had lower homing, higher unaccounted loss, and higher straying than in-river migrants (Table 3). During the juvenile release years when both transportation treatments were performed (1999, 2000, 2002), barged steelhead were 1.39 (95% CI: 1.05-1.85) times more likely to be unaccounted for than to home compared to in-river migrants (χ^2 = 5.3, P = 0.022, df = 1). Steelhead fates (home, unaccounted) differed significantly among outmigration years (χ^2 = 9.2, P = 0.010, df = 2), but proportions did not differ by adult release location (χ^2 = 0.1, P = 0.777, df = 1). Unlike Chinook salmon, steelhead fates were significantly related to origin (χ^2 = 6.8, P = 0.009, df = 1), with higher proportions of wild steelhead being unaccounted.

The probability of straying compared to homing was related to both barging and origin. Across juvenile release years with both transportation treatments, steelhead stray rates were: 2.0% (n = 153 wild, in-river fish), 7.3% (220 wild, barged fish), 7.6% (66 hatchery, in-river fish), and 10.2% (49 hatchery, barged fish). Origin (χ^2 = 4.8, P < 0.029, df = 1) and transport (χ^2 = 5.2, P = 0.023, df = 1) effects were significant in this model.

All juvenile steelhead collected in 2001 were barged, and this group was excluded from the analyses above. Qualitatively, adult fates of the 2001 outmigration population were similar to those observed for other years. In fact, the 2001 group had among the highest point estimates of straying and unaccounted rates, and one of the lowest homing rates among all steelhead year-treatment combinations. In all categories, steelhead exhibited consistent patterns of lower homing and higher rates of unaccounted fate for barged fish (Table 3).

Table 3. Number and percent of radio-tagged adult steelhead that homed, permanently strayed, or were unaccounted for during upstream migration, by juvenile transportation history, adult return year, juvenile outmigration year, and rearing history. All harvested fish were excluded.

				Percent (%)		
Group by:	Year	Treatment	*n*	Homed	Strayed	Unaccounted
All fish	All	In-river	238	88.7	3.4	8.0
		Barged	409	75.6	6.9	17.6
Outmigration	1999	In-river	36	83.3	8.3	8.3
		Barged	61	75.4	4.9	19.7
	2000	In-river	186	89.3	2.7	8.1
		Barged	226	78.8	7.5	13.7
	2001	In-river				
		Barged	87	70.1	8.1	21.8
	2002	In-river	16	93.8		6.3
		Barged	35	68.6	2.9	28.6
Adult return	2001	In-river	112	89.3	5.4	5.4
		Barged	154	72.7	8.4	18.8
	2002	In-river	110	87.3	1.8	10.9
		Barged	201	79.1	7.0	13.9
	2003	In-river	16	93.8		6.3
		Barged	54	70.4	1.9	27.8
Hatchery	All	In-river	70	87.1	7.1	5.7
		Barged	59	79.7	8.5	11.9
Wild	All	In-river	168	89.3	1.8	8.9
		Barged	350	74.9	6.6	18.6

Adult Fallback. – Chinook salmon and steelhead barged as juveniles were more likely to fall back at dams—and fell back at higher frequencies (total number of fallback events/number of fish that fell back)—than in-river migrants (Table 4). Barged Chinook salmon from the juvenile release years with both transport treatments (1998-2000) were 1.90 times (95% CI: 1.33-2.70) more likely to fall back than in-river migrants ($\chi^2 = 12.6$, $P < 0.001$, $df = 1$), and this effect was independent of origin ($\chi^2 = 0.6$, $P = 0.456$, $df = 1$).

Table 4. Percent (n) of radio-tagged adult Chinook salmon and steelhead that fell back at one or more dams during upstream migration, and fallback frequency (total number of fallback events divided by number of fish that fell back), by juvenile transportation history, adult return year, juvenile outmigration year, and rearing history. Harvested fish excluded.

		Percent (n) that fell back				Fallback frequency	
Group by:	Year	In-River	Barged	χ^2	*P*	In-River	Barged
			Chinook salmon				
All fish	All	7.5 (161)	19.2 (245)	10.8	0.001	1.1 (12)	2.7 (47)
Adult return	2000	25.0 (8)	50.0 (14)	1.3	0.251	1.0 (2)	3.1 (7)
	2001	2.5 (81)	15.2 (151)	8.9	0.003	1.0 (2)	3.1 (23)
	2002	14.3 (42)	25.0 (40)	1.5	0.221	1.0 (6)	2.5 (10)
	2003	6.7 (30)	17.5 (40)	1.8	0.180	1.5 (2)	1.1 (7)
Outmigration	1998	21.4 (14)	36.8 (19)	0.9	0.341	1.0 (3)	3.1 (7)
	1999	1.2 (85)	17.2 (163)	13.9	<0.001	1.0 (1)	3.2 (28)
	2000	12.9 (62)	20.0 (40)	0.9	0.336	1.1 (8)	1.4 (8)
	2001		17.4 (23)				1.0 (4)
Hatchery	All	3.8 (53)	18.0 (117)	6.3	0.012	1.0 (2)	3.8 (21)
Wild	All	9.3 (108)	20.3 (128)	5.5	0.019	1.1 (10)	1.8 (26)
			Steelhead				
All fish	All	10.5 (238)	18.1 (409)	6.7	0.010	1.2 (25)	2.1 (74)
Adult return	2001	8.9 (112)	18.8 (154)	5.1	0.024	1.2 (10)	2.1 (29)
	2002	12.7 (110)	13.4 (201)	0.0	0.860	1.1 (14)	1.6 (27)
	2003	6.3 (16)	33.3 (54)	4.6	0.032	1.0 (1)	2.8 (18)
Outmigration	1999	11.1 (36)	14.8 (61)	0.3	0.661	1.0 (4)	1.7 (9)
	2000	10.8 (186)	15.5 (226)	2.0	0.160	1.2 (20)	1.9 (35)
	2001		20.7 (87)				2.3 (18)
	2002	6.3 (16)	34.3 (35)	4.5	0.033	1.0 (1)	2.8 (12)
Hatchery	All	14.3 (70)	13.6 (59)	0.0	0.906	1.1 (10)	2.3 (8)
Wild	All	8.9 (168)	18.9 (350)	8.5	0.004	1.2 (15)	2.1 (66)

Juvenile release year was also significantly associated with the proportion of Chinook salmon that fell back ($\chi^2 = 9.9$, $P = 0.007$, $df = 2$), possibly reflecting differences in juvenile or adult migration environment among years. Adult release site could not be included in the model because no forebay-released salmon (*n* = 78) fell back. Steelhead barged as juveniles in release years with both treatments (1999, 2000, 2002) were 1.34 times (95% CI: 1.03-1.74) more likely to fall back than in-river steelhead ($\chi^2 = 4.7$, $P = 0.031$, $df = 1$); adult release site, juvenile release year, and origin were not significant ($P \geq 0.16$) for steelhead.

Barged fish were approximately twice as likely to fall back multiple times (Table 4). For years with both treatments, 92.6% of in-river Chinook salmon did not fall back, 6.8% fell back once, and 0.6% fell back two or more times. By comparison, proportions for barged Chinook salmon were 80.6% none, 7.7% once, and 11.7% two or more times ($\chi^2 = 17.9$, $P < 0.001$, $df = 2$). Results were similar for steelhead: 89.5% of in-river fish (82.6% of barged fish) did not fall back, 6.8% (9.3%) fell back once, and 1.7% (8.1%) fell back at least twice ($\chi^2 = 11.2$, $P = 0.004$, $df = 2$). Among those fish that did fall back, mean fallback frequencies were 1.08 for in-river compared to 2.84 for barged Chinook salmon, and were 1.20 for in-river compared to 2.02 for barged steelhead. Results for fish from the 2001 outmigration were comparable to those recorded for barged fish in other years (Table 4).

With all years combined, 91% of Chinook salmon fallbacks and 76% of steelhead fallbacks were recorded at the four lower Columbia River dams (Bonneville, The Dalles, John Day, and McNary Dams). Proportionately more barged fish than in-river fish fell back at lower Columbia River dams: 94% of fallbacks by barged Chinook salmon were at lower river dams versus 73% by in-river salmon (χ^2 test, $P = 0.008$), and 84% of barged steelhead fallbacks were at lower river dams versus 33% for in-river steelhead ($P < 0.001$).

Fallback and Fate. – Given significant transportation effects on both adult fate and fallback behavior, we expected strong associations between fallback and fate. Indeed, fallback was the most influential variable in multinomial tests of Chinook salmon fate (home, unaccounted) that included a binary fallback term along with transport, juvenile release year (1998-2000) and origin. Chinook salmon that fell back were 1.70 (95% CI odds ratios: 1.15-2.52) times more likely to be unaccounted than salmon that did not fall back ($\chi^2 = 7.0$, $P < 0.001$, $df = 1$) (Table 5). Juvenile release year was also significantly associated with fate, ($\chi^2 = 6.0$, $P = 0.050$, $df = 2$), but origin and barging were not ($P \geq 0.10$). Among steelhead (1999, 2000, 2002 juvenile release years), fallback fish were 1.90 (95% CI odds ratios: 1.41-2.57) times more likely to be unaccounted than non-fallback fish ($\chi^2 = 17.7$, $P < 0.001$, $df = 1$). Origin ($\chi^2 = 6.7$, $P = 0.010$, $df = 1$), juvenile release year ($\chi^2 = 7.4$, $P = 0.025$, $df = 2$), and transport ($\chi^2 = 4.0$, $P = 0.045$, $df = 1$) were also significantly associated with fate for steelhead.

Straying did not occur for all fallback×transport×origin categories (Table 5), but the aggregated data (including the 2001 outmigration) indicated that fallback fish were more likely than non-fallback fish to stray (Chinook salmon: $\chi^2 = 25.5$, $P < 0.001$, $df = 1$; steelhead: $\chi^2 = 8.1$, $P = 0.005$, $df = 1$). The highest stray rates were for fish that both fell back and were barged as juveniles (Table 5).

Discussion

In this study, spring–summer Chinook salmon and steelhead that were barged downstream as juveniles exhibited reduced adult homing to Lower Granite Dam, increased adult straying, and higher rates of adult fallback at Columbia and Snake River dams compared to non-barged fish. Further, we observed higher straying and lower homing rates for fish that fell back over one or more dams. Overall, annual reductions in adult hydrosystem escapement that were associated with juvenile transport averaged about 10% for both species. The transportation effects we observed were consistent between years and between various fish groupings. Statistical results were similar for inclusive models (across years and with additional variables such as release site, hatchery/wild origin included) and for more simple comparisons (*e.g.* for hatchery or wild fish only, and for individual juvenile release and adult return years).

Table 5. Percent of radio-tagged Chinook salmon and steelhead that homed, permanently strayed, or were unaccounted for during upstream migration, by adult fallback behavior, juvenile transport treatment, and origin. All years were combined and all harvested fish were excluded.

				Percent (%)		
Fallback	Treatment	Origin	*n*	Homed	Strayed	Unaccounted
Chinook salmon						
Fallback	In-river	Wild	9	77.8		22.2
		Hatchery	3	33.3	33.3	33.3
	Barged	Wild	26	69.2	3.8	26.9
		Hatchery	21	57.1	19.0	23.8
No Fallback	In-river	Wild	98	95.9		4.1
		Hatchery	51	92.2		7.8
	Barged	Wild	102	88.2		11.8
		Hatchery	96	85.4	3.1	11.5
Steelhead						
Fallback	In-river	Wild	15	80.0		20.0
		Hatchery	10	100.0		
	Barged	Wild	66	48.5	13.6	37.9
		Hatchery	8	75.0	12.5	12.5
No Fallback	In-river	Wild	153	90.2	2.0	7.8
		Hatchery	60	85.0	8.3	6.7
	Barged	Wild	284	81.0	4.9	14.1
		Hatchery	51	80.4	7.8	11.8

There were slight differences in some years in the timing of juvenile collection between transportation treatment groups due to logistical constraints and sampling error. These differences had the potential to compromise tests of treatment effects if differences in the timing of juvenile migration had strong effects on adult behavior and fate (*i.e.* the tests would be compromised if juvenile timing and barging treatments were strongly correlated and the observed differences were caused by timing rather than transportation effects). The differences in timing between transportation groups were small compared to the timing differences related to origin, which was not strongly related to adult fate or behavior. Additionally, the timing differences were inconsistent among years in contrast to the transportation effects on adult fate. Overall these patterns suggest it was unlikely that differences in the timing of juvenile collection produced the observed associations between transportation treatments and adult fate and behaviors. We also note that radio-tagged fish were anesthetized and handled, which may have influenced homing, though presumably both transported and in-river migrants would be similarly affected.

We emphasize that our estimates of treatment effects may reflect minimum estimates of differences in fitness between transport and in-river groups given that Lower Granite Dam is well downstream from many spawning sites. Our analyses examined only the Hydrosystem portion of the Columbia-Snake basin, and all fish that passed Lower Granite Dam were considered successful. *This definition of success was conservative as we did not assess homing to natal tributaries, pre-spawn mortality, or reproductive success after fish reached spawning grounds.* The results also apply most directly to juveniles collected and PIT-tagged at Lower Granite Dam. Impacts may vary for juveniles PIT-tagged at other sites, or for fish collected and transported but not PIT-tagged.

Collectively, the reduced homing and increased fallback results suggest that juvenile transportation from the Snake River in some way impairs orientation and/or homing abilities among returning adults. One possible explanation for these effects is that transportation interrupts the sequence of juvenile imprinting that occurs during outmigration (Quinn et al. 1989; Quinn 1993; Pascual et al. 1995). Imprinting by salmonids is tied to seasonal (*e.g.* photoperiod), river environment (*e.g.* water temperature), and maturation state (Hansen and Jonssen 1991; Unwin and Quinn 1993). Imprinting occurs both in home streams and during the parr-smolt transformation that typically coincides with outmigration (Hasler and Scholz 1983; Dittman and Quinn 1996). During this transformation, juveniles experience physiological and hormonal changes associated with elevated sensitivity to olfactory imprinting (Nevitt et al. 1994; Lema and Nevitt 2004), suggesting that individuals imprint on a series of cues as they move down the river corridor. The collection and downstream movement of juveniles on barges may disrupt the normal sequence or timing of imprinting cues required for successful adult homing. Additional imprinting disruptions may occur within hatcheries (Nevitt et al. 1994; Dittman and Quinn 1996) or as a result of asynchrony between physiological development and arrival timing of transported smolts in the Columbia River estuary.

Previous studies support the hypothesis that juvenile transportation interrupts sequential imprinting of Pacific salmonids. For example, experiments by Chapman et al. (1997) showed that sockeye and spring–summer Chinook salmon smolts trucked or trucked and barged around portions of the Columbia River behaved like the barged fish in this study: as adults, transported fish fell back over Bonneville Dam at higher rates than control groups and had slower upstream migration rates, reduced homing, and higher straying. Transport solely by truck had more negative effects for adults than combined trucking and barging. Chapman et al. (1997) attributed this to greater imprinting gaps because trucked fish left the river corridor, while barged fish were exposed to pumped river water during transport. In the Snake River, fall Chinook salmon barged past two dams strayed to Columbia River sites at rates 20 times higher (5.9%) than salmon released at their origin hatchery (0.3%) (Bugert et al. 1997). Juvenile coho salmon (*O. kisutch*) trucked relatively short distances in Oregon coastal watersheds (Johnson et al. 1990) and in the lower Columbia River (Solazzi et al. 1991) strayed at rates that were orders of magnitude higher than control groups released at rearing hatcheries.

Mass juvenile transportation of Snake River populations has been a central mitigation strategy in recent decades, with 8 to 15 million yearling Chinook salmon and steelhead barged or trucked from the basin in each year since 1988 (Ward et al. 1997; Fish Passage Center 2003). On average, more than 60% of Snake River spring–summer Chinook salmon and about 80% of steelhead escapement is hatchery derived. Assuming annual transport of four million juvenile Chinook salmon (Ward et al. 1997), adult return rates of 0.5 to 2% (Sandford and Smith 2002; Berggren 2003), 3.3% straying rate, and ~11% harvest rate for transported Chinook salmon from this study (Table 2), approximately 600 to 2,300 barged Snake River salmon may stray into other Columbia River tributaries annually, of which at least 400 to 1,400 (60%) would likely be hatchery fish. From 2,000 to 8,000 transported steelhead might be expected to stray each year (6.5 million transported, 0.5-2% adult return, 6.9% stray rate, 11% harvest rate), 80% of which would be hatchery derived. Clearly these estimates are imprecise, and these rates will vary inter-annually. However, the estimates illustrate the potential negative indirect effects of barging on stock structure.

In particular, the indirect effect of transport-related straying could have a negative impact on recovery of wild listed ESUs. Some intra-basin straying is a normal feature of salmonid metapopulation structure (Cooper and Mangel 1999), but the large number of straying Snake River hatchery fish may be more harmful than beneficial to recovery. More than 90% of Chinook salmon and steelhead strays in this study entered lower Columbia River tributaries, including several rivers (John Day, Klickitat, Wind, White Salmon) where wild populations are at moderate to high risk of extinction (Nehlsen et al. 1991). Proliferation of out-of-basin hatchery salmon and steelhead in lower Columbia tributaries could undermine recovery of listed wild fish (Levin et al. 2001), reduce natural productivity (Chilcote 2003), or have other poorly understood ecological consequences (Weber and Fausch 2003).

In addition to identification of individual fish fates, radio-tagging adult salmon and steelhead of known Snake River origin allowed the quantification and improved interpretation of fallback behavior at dams. In studies where adult destinations are unknown, differentiation between searching-based fallback and fallback based on dam operation or river environment can be difficult (Boggs et al. 2004), particularly when fish do not ultimately enter tributaries (*e.g.* harvest or mortality). The increased fallback for barged Snake River fish, particularly the higher rates of multiple fallbacks, clearly implicate juvenile experience as an important factor in some adult fallback behavior. This finding should help reduce uncertainty about mechanisms affecting fallback, at least for these important Snake River stocks. The significantly reduced escapement observed for adult fallback fish over many years (Keefer et al. 2005) may also be partially attributable to juvenile transport, a linkage that we had not previously identified.

The combination of PIT tag and radiotelemetry data in this study allowed for detailed reconstruction of both juvenile out-migration history and adult return migration for individual fish. Integration of the two methods provides greater insight into the behavioral ecology of migrating salmonids than either method could independently. We suggest that future projects investigating relationships between juvenile histories (*e.g.* transport, hatchery practices) and adult behavior uniquely tag large numbers of juvenile fish to assure adequate adult samples. Systematic sampling of juveniles from hatchery and wild stocks throughout outmigration periods (Mundy et al. 1994) and representative sampling of returning adults from those stocks will also be important in future experiments. Explicit consideration of stock effects would be particularly useful given the potentially large between-stock differences (*i.e.* in adult timing and juvenile rearing, acclimation, survival, residence times, and travel distances to the hydrosystem) (Berggren et al. 2003; Keefer et al. 2004b; Zabel and Achord 2004). To better understand effects of juvenile transportation on listed Columbia basin salmonids, managers should consider additional studies of Snake River stocks (including fall Chinook salmon) and attempt to quantify the full fitness consequences of barging by assessing reproductive success between treatment groups on spawning grounds in one or more index stocks. Finally, these studies were conducted during return years following “good” ocean conditions, and there is the potential that these effects could vary in cohorts returning in poor physiological condition after residence in “poor” ocean conditions.

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Appendix: Supplemental data (5 Tables)

Table A-1. Adult release locations (downstream from Bonneville, Bonneville forebay), by juvenile transport treatment and adult return year.

		Adult release site *n* (%)			
Year	Treatment	Downstream	Forebay	χ^2	*P*
Chinook Salmon					
2000	In-river	8			
	Barged	15			
2001	In-river	70 (72)	27 (28)		
	Barged	117 (68)	55 (32)	0.5	0.479
2002	In-river	40 (85)	7 (15)		
	Barged	42 (95)	2 (5)	2.7	0.098
2003	In-river	33			
	Barged	41			
Steelhead					
2001	In-river	90 (70)	38 (30)		
	Barged	114 (67)	56 (33)	0.4	0.550
2002	In-river	115 (89)	14 (11)		
	Barged	180 (81)	42 (19)	4.0	0.047
2003	In-river	17			
	Barged	61			

Table A-2. Fish origin (wild, hatchery), by juvenile transport treatment and juvenile release year.

		Origin *n* (%)			
Year	Treatment	Wild	Hatchery	χ^2	*P*[1]
Chinook Salmon					
1998	In-river	5 (36)	9 (64)		
	Barged	5 (25)	15 (75)	0.5	0.500
1999	In-river	48 (46)	56 (54)		
	Barged	62 (33)	124 (67)	4.7	0.031
2000	In-river	67			
	Barged	43			
2001	In-river				
	Barged		23		
Steelhead					
1999	In-river	4 (10)	37 (90)		
	Barged	16 (23)	54 (77)	3.0	0.083
2000	In-river	183 (85)	33 (15)		
	Barged	246 (98)	6 (2)	25.3	< 0.001
2001	In-river				
	Barged	89 (96)	4 (4)		
2002	In-river	10 (59)	7 (41)		
	Barged	36 (95)	2 (5)	11.1	0.001

[1] Small sample sizes (<5) in some cells limits power of tests

Table A-3. Fates of adult Chinook salmon and steelhead barged as juveniles from Lower Granite, Little Goose, and Lower Monumental dams. All harvested fish excluded.

Barge site	Homed	Adult fate Strayed	Unaccounted	χ^2	*P*[1]
Chinook salmon					
L. Granite	160 (80)	8 (4)	32 (16)		
L. Goose	37 (93)	0 (0)	3 (7)		
L. Monumental	5 (100)	0 (0)	0 (0)	5.0	0.284
Steelhead					
L. Granite	108 (73)	11 (7)	29 (20)		
L. Goose	180 (77)	16 (7)	39 (17)		
L. Monumental	21 (81)	1 (4)	4 (15)	1.2	0.875

[1] Small sample sizes (<5) in some cells limits power of tests

Table A-4. Results of general linear model (GLM) testing for relationships between juvenile collection dates and transportation treatment, origin, and treatment×origin variables.

	Year	Source	Type III SS	Model *df*	Error *df*	*F*	*P*
Chinook salmon	1998	Transport	355.6	3	30	2.4	0.136
		Origin	564.9			3.7	0.063
		Transport×Origin	26.8			0.1	0.677
	1999	Transport	392.2	3	286	4.7	0.030
		Origin	1100.5			13.3	< 0.001
		Transport×Origin	1.9			0.0	0.881
	2000[1]	Transport	464.4	1	108	3.7	0.056
Steelhead	1999	Transport	1068.5	3	107	10.3	0.002
		Origin	116.7			10.8	0.001
		Transport×Origin	94.4			0.9	0.342
	2000	Transport	10.2	3	464	0.2	0.682
		Origin	256.5			4.2	0.040
		Transport×Origin	4.8			0.1	0.779
	2001[2]	Origin	2.4	1	91	0.0	0.835
	2002	Transport	18.8	3	51	0.0	0.835
		Origin	3.3			0.0	0.931
		Transport×Origin	213.0			0.5	0.486

[1] wild fish only
[2] barged fish only

Table A-5. Results of general linear model (GLM) testing for relationships between adult collection dates and transportation treatment, origin, and treatment×origin variables.

	Year	Source	Type III SS	Model *df*	Error *df*	*F*	*P*
Chinook salmon	2000[1]	Transport	85.1	2	20	0.7	0.400
		Origin	2031.0			17.7	< 0.001
	2001	Transport	1086.0	3	265	2.8	0.094
		Origin	11535.8			30.1	< 0.001
		Transport×Origin	221.0			0.6	0.449
	2002	Transport	512.7	3	87	1.1	0.296
		Origin	2529.6			5.5	0.022
		Transport×Origin	3.5			0.0	0.931
	2003[2]	Transport	20.6	1	72	0.1	0.790
Steelhead	2001	Transport	1349.7	3	294	2.3	0.133
		Origin	29714.5			50.0	< 0.001
		Transport×Origin	452.5			0.8	0.383
	2002	Transport	482.3	3	347	0.7	0.408
		Origin	12.8			0.0	0.893
		Transport×Origin	4.6			0.0	0.936
	2003	Transport	1594.9	3	74	1.8	0.183
		Origin	4772.9			5.4	0.023
		Transport×Origin	921.7			1.1	0.310

[1] only 2 wild fish
[2] wild fish only