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Combined Effects of Barge Transportation, River Environment, and Rearing Location on Straying and Migration of Adult Snake River Fall-Run Chinook Salmon

Morgan H. Bond*[1]

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA

Peter A. H. Westley

College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 905 North Koyukuk Drive, Fairbanks, Alaska 99775, USA

Andrew H. Dittman

National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Environmental and Fisheries Sciences Division, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Dean Holecek

U.S. Army Corps of Engineers, 201 North Third Street, Walla Walla, Washington 99362, USA

Tiffani Marsh

National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Fish Ecology Division, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

Thomas P. Quinn

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA

Abstract

Homing and straying in salmon have been extensively studied, yet it has proven difficult to disentangle the biotic and abiotic factors that influence straying. In the Columbia River basin, some juvenile salmon are collected at dams and transported downstream to increase survival during seaward migration, and as returning adults they experience a range of environmental conditions as they ascend the river. We examined 8 years of PIT tag detection data for hatchery-reared, fall-run Chinook Salmon *Oncorhynchus tshawytscha* released in the Snake River to evaluate the combined effects of juvenile barging, rearing and release locations, and environmental conditions on adult migration speed and straying below and above the Columbia River–Snake River confluence. Straying to the upper Columbia River was 10–19 times more likely among adults that were barged as juveniles from Snake River dams than among adults that were in-river migrants or that were transported from McNary Dam (below the confluence) as juveniles. Similarly, barging from Snake River dams and warmer Columbia River temperatures increased the likelihood of straying into streams below the confluence. Furthermore, adult upstream migration was slower among

*Corresponding author: morgan.bond@noaa.gov
[1]Present address: National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Fish Ecology Division, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA.

juveniles that were reared at two mid-Columbia River hatcheries and juveniles that were barged, indicating possible navigational impairment. However, rearing location, release distance, and release age had relatively minimal effects on straying. Collectively, our results indicate that (1) adult migration and homing are affected by a complex combination of processes that take place during smolt out-migration and the adult return migration, and (2) enhancement efforts can inadvertently add to the challenge. The straying of barged fish demonstrates the potential for increasing adult returns to the Snake River by changing the barging process so that it more adequately supports the proper imprinting of juveniles.

Homing, defined as the ability and tendency to return to the natal site, is central to the population dynamics, evolution, and conservation of migratory animals (Dingle 1996). Homing has been documented in many kinds of fish (Quinn and Dittman 1992), such as sharks (Feldheim et al. 2002), tunas (Rooker et al. 2014), and Atlantic Cod *Gadus morhua* (Svedang et al. 2007), but it has been most closely studied in salmonids, which possess highly developed homing abilities (Hasler and Scholz 1983; Quinn 1993; Hendry et al. 2004). However, a variable but typically small fraction of salmon that survive to maturity will stray—entering and in many cases breeding in nonnatal sites—and this natural phenomenon is as important to salmon ecology as homing (Quinn 1993; Dittman et al. 1996; Keefer and Caudill 2014). Natural colonization of previously unoccupied habitat only occurs when individuals reproduce outside of their natal stream. Therefore, straying is a mechanism that promotes recovery of disturbed populations and colonization of newly available habitat (Leider 1989; Milner et al. 2008; Anderson et al. 2015). However, strays are numerically lost to their natal population and may exhibit reduced reproductive success, as selection has shaped their physiology and behavior for natal waters (Hendry et al. 2004). Furthermore, straying may lead to maladaptive gene flow into recipient populations and can mask patterns in the productivity of those populations (Chilcote 2003; Brenner et al. 2012). Finally, stray hatchery-produced fish that breed with wild fish of a different lineage may compromise conservation objectives and confound escapement estimates by masking a lack of local natural production (Naish et al. 2008).

During homeward migration in lotic habitats, adult salmon largely rely on identifying odors upon which they had imprinted sequentially during their juvenile seaward migration some years before (Dittman and Quinn 1996). Straying may result from a number of processes; prominent among them are (1) failure to imprint at the juvenile stage, and (2) environmental stimuli that cause returning adults to temporarily enter or remain in nonnatal rivers. Disruption of the normal sequential imprinting process along the juvenile migration pathway (e.g., due to transportation of the juveniles from the rearing site to a different site for release) can elevate straying rates (Quinn 1993). Such "off-site releases" occur in many regions (e.g., Candy and Beacham 2000), but an additional form of disruption occurs in the Columbia River system, where many juvenile salmon are released into Snake River tributaries to migrate downstream until some of the fish are collected and transported through the extensive hydropower system by barge and (to a lesser extent) by truck.

The U.S. Army Corps of Engineers has transported smolts collected at dam passage facilities on the Snake and Columbia rivers since the 1970s (Ebel et al. 1973; Ebel 1980). Juvenile salmon are collected at one of four dams (Lower Granite, Little Goose, Lower Monumental, and McNary), are transported primarily by barge down the river via navigational locks at the dams, and are released below Bonneville Dam, a trip that takes approximately 40 h and extends 470 river kilometers (rkm) from Lower Granite Dam (Figure 1). Transport of juveniles largely alleviates the immediate negative effects of dam passage and in-river migration through high-mortality zones, and survival from collection to release is high (in-river survival, ~60%; Muir et al. 2001; survival of barged fish, ~98%; McMichael et al. 2011). However, effects of transport that are not expressed until later (i.e., through the increased postrelease mortality of juveniles or increased straying of adults) are more difficult to quantify than dam passage mortality but are potentially no less important (Chapman et al. 1997; Muir et al. 2006; Keefer et al. 2008; Holsman et al. 2012).

Increased straying by transported salmon has been observed, yet the mechanisms leading to impaired homing are not clear (Quinn 1993; Keefer and Caudill 2014). Fish that are transported via truck have limited exposure to the changing olfactory environment experienced by free-swimming fish during migration, and truck-transported fish may thus display high rates of straying (California Department of Fish and Game 2001; Lasko et al. 2014). Barged fish experience the river via water exchanges during transport, although exchange rates may be insufficient for proper imprinting. Furthermore, fish in barges move downstream much faster than migrating fish, and barges are restricted to the main navigation channel, so the fish might not have the time or opportunity to detect and learn the appropriate tributary odors. Finally, barged fish do not experience natural migration and therefore do not receive many of the associated environmental cues (e.g., novel water exposure and flow) that stimulate thyroid hormone signaling, which is involved in successful olfactory imprinting (Dittman and Quinn 1996).

Although some evidence indicates that hatchery-reared fish stray more than naturally produced smolts, straying rates vary markedly among fish of the same species and run that have
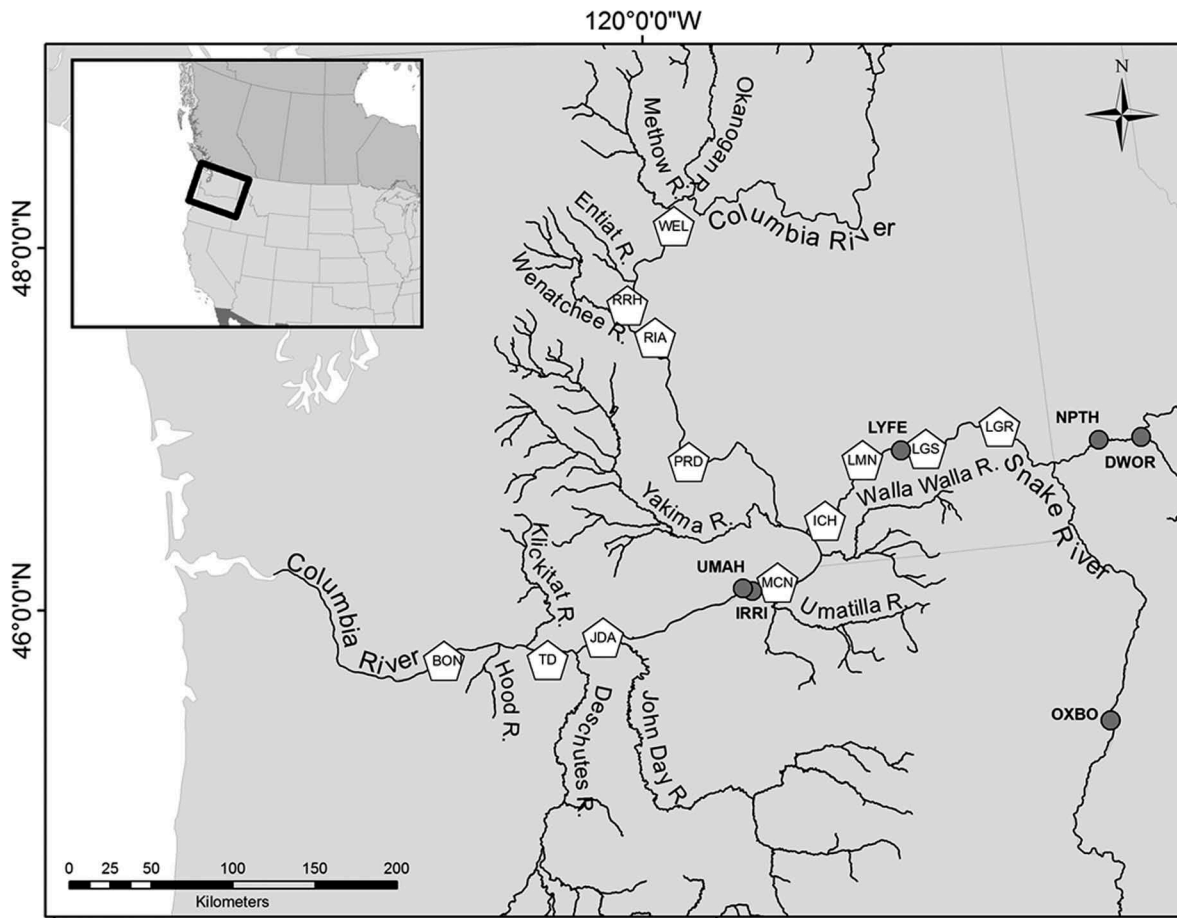
FIGURE 1. Map of the Columbia River basin (Washington–Oregon–Idaho), depicting the locations of main-stem Columbia River and Snake River dams where detections of PIT-tagged Snake River fall-run Chinook Salmon were made (open pentagons; BON = Bonneville; TD = The Dalles; JDA = John Day; MCN = McNary; PRD = Priest Rapids; RIA = Rock Island; RRH = Rocky Reach; WEL = Wells; ICH = Ice Harbor; LMN = Lower Monumental; LGS = Little Goose; LGR = Lower Granite). Juveniles were transported from MCN, LMN, LGS, and LGR. Hatcheries are identified by gray circles (UMAH = Umatilla Hatchery; IRRI = Irrigon Hatchery; LYFE = Lyons Ferry Hatchery; NPTH = Nez Perce Tribal Hatchery; OXBO = Oxbow Hatchery; DWOR = Dworshak National Fish Hatchery). Only tributary rivers where strays were detected are displayed and labeled.

been reared at different hatcheries, indicating that homing is affected by aspects of the rearing and release process, the local watershed environment, or population-specific attributes (Quinn et al. 1991; Pascual and Quinn 1994; Westley et al. 2013). However, many evaluations of the effect of transport on straying in the Columbia River basin have used smolts of unknown origin that were collected and tagged at main-stem dams (Keefer et al. 2008; Ruzycki and Carmichael 2010). Therefore, the transport collection process may overrepresent or underrepresent some populations that are predisposed to stray at higher rates due to differences in arrival timing or movement behavior as fish approach dams. Ideally, in-river migrants and transported individuals of known rearing origin should be used in evaluations of straying rates (Keefer et al. 2005).

Environmental conditions that are experienced by returning adult salmon can also influence straying. Several studies have demonstrated the influence of river temperature on straying (Goniea et al. 2006; Westley et al. 2015). When main-stem temperatures are high, individuals may seek thermal refuges in tributaries or may slow their migrations (Goniea et al. 2006). Although elevated river temperatures may have a larger influence on temporary straying, wherein individuals ultimately return to their home stream, the increased migration time for temporary strays may increase their susceptibility to disease, fishing mortality, or other sources of prespawn mortality (Keefer and Caudill 2014). Such fish would be lost to the source population whether or not they successfully spawn in nonnatal habitats.

The broad purpose of this study was to evaluate straying of Snake River fall-run Chinook Salmon *Oncorhynchus tshawytscha* by investigating the combined effects of juvenile barging and environmental factors (at the juvenile and adult stages) on adult straying. Specifically, we sought to evaluate

how juvenile rearing and migration history and the biotic and environmental factors experienced by adults affect two broad-scale categories of straying. Although many of these factors have been tested individually in other studies (for a comprehensive review, see Keefer and Caudill 2014), the large number of tagged fall Chinook Salmon in the Snake River allows for the simultaneous testing of all covariates. We evaluated migration detections of tagged fish to determine the relative effects of the following factors on straying: initial rearing location (hatchery), distance from the rearing location to the release location (release distance, rkm), the age at release (yearling or subyearling), the juvenile migration mode (migrating in-river or being barged from one of several dams), and the water temperature and total flow at several locations during adult upstream migration. We used various combinations of these covariates to test specific hypotheses about two broad categories of straying: (1) adults entering nonnatal tributaries of the lower and mid-Columbia River prior to reaching the Columbia River–Snake River confluence (lower-river straying), and (2) adults ascending the Columbia River and associated tributaries upstream of the Columbia River–Snake River confluence (upper-river straying). For each straying category, we evaluated the relative strength of anthropogenic (barging, rearing site, and release distance), biotic (age at release and upstream migration timing), and environmental (temperature and flow) factors in terms of their influences on the straying and migration time of adult fall-run Chinook Salmon.

METHODS

Chinook Salmon movement data.—Since the late 1980s, hatcheries in the Snake River basin have been tagging fall-run Chinook Salmon with PIT tags prior to release, primarily to evaluate the smolt-to-adult return rate. Each individual carries a PIT tag with a unique identification code, which allows for automated detection at dams and stream sites throughout the life of the fish (Prentice et al. 1990a, 1990b; Zydlewski et al. 2006). During downstream migration, some individuals use juvenile bypass systems at dams, where the detection of PIT tags is virtually assured (Axel et al. 2005). Most of the bypassed fish are subsequently transported, and the others continue as in-river migrants. However, previously PIT-tagged fish that enter the bypass system are primarily sorted to continue as in-river migrants unless managers designate them a priori for transportation. In addition to information on the routes taken by seaward-migrating smolts, automated PIT tag detectors at several dams and some tributaries allow for monitoring of the migratory pathways taken by tagged adult salmon during their spawning migration.

Data from more than 3.8 million fall Chinook Salmon juveniles reared at six hatcheries (Dworshak National Fish Hatchery, Umatilla Hatchery, Lyons Ferry Hatchery, Nez Perce Tribal Hatchery, Irrigon Hatchery, and Oxbow Hatchery) and released from Snake River basin tributaries during spring 2002 through fall 2011 were retrieved from the Columbia River basin PIT Tag Information System (PTAGIS; www.ptagis.org), which is operated by the Pacific States Marine Fisheries Commission (PSMFC). Of those 3.8 million fish, almost 2 million individuals were detected at least once as juveniles or adults by PIT tag detectors in streams and at dam passage facilities. All of the release sites and all but two of the rearing sites were located within the Snake River basin. The exceptions were Irrigon Hatchery and Umatilla Hatchery, which rear fish along the main-stem Columbia River (near McNary Dam) and release them upstream in the Snake River basin. We matched tagging data with detection data that were collected at dam passage facilities and instream sites throughout the Columbia River basin to assess migration timing, straying, and the environmental conditions experienced by each migrant.

Most fish that were tagged as juveniles were never detected as adults, presumably because of natural mortality or fishery harvest, but the records provided abundant information on surviving Chinook Salmon that migrated to sea and back again. However, some complexities in Chinook Salmon life history had to be considered when interpreting the records. First, some males mature as parr without leaving freshwater and spawn during the year of their release (Beckman and Larsen 2005). All precocious parr that were recorded on adult detectors during the year of release were excluded from this study. An additional migratory variant—individuals that overwinter in main-stem reservoirs before continuing downstream during the spring after release (Connor et al. 2005)—was included because these fish are difficult to separate from individuals with more prevalent life histories. Inclusion of those fish may have resulted in overestimation of the number of years spent at sea by some fish. All individuals that were observed in freshwater after July 1 of the year following their release were assumed to be upstream-migrating anadromous adults and were retained for analysis. We also determined which fish had been transported in barges by matching the route conducted through the juvenile bypass systems for each individual. The final PIT tag detectors at each dam where transport occurs (Lower Granite, Lower Monumental, Little Goose, and McNary dams) were used to determine whether fish were transported downstream or were returned to the river. For each fish that was transported, we determined the mode of transport (barge or truck) by comparing the transport dates to the dates of barge and truck operations, as obtained from the Columbia River Data Access in Real Time (DART) database (Columbia Basin Research, University of Washington, Seattle; www.cbr.washington.edu/dart/query/transport_daily). Virtually all (99.995%) of the transported fish had been barged; therefore, our analysis was restricted to 4,782 barged fish, and we excluded the 17 individuals that were transported by truck.

Designation of strays.—The PIT tag detection history for each adult was used to classify that individual into one of four categories related to its return to the natal (i.e., Snake River) basin: (1) homing, (2) straying and then homing (temporary stray), (3) straying as the final disposition (permanent stray), and (4) unknown. The PIT tag detection systems in the Snake River basin have (with few exceptions) been installed in smaller tributaries due to technological constraints on detection range and because their primary purpose has been to assess juvenile emigration survival of steelhead *O. mykiss* and spring Chinook Salmon. Therefore, we could not assess straying at a finer spatial scale than their return to the Snake River basin, and fish were classified as having returned home if their final detection was in the Snake River system. Temporary strays were defined as fish that were detected in a nonnatal tributary of the Columbia River or in the main-stem Columbia River above the Snake River confluence but then eventually ascended the Snake River. Permanent strays were defined as fish whose final detection was in a nonnatal tributary or in the Columbia River upstream of the Snake River confluence. Classification as a permanent stray does not necessarily indicate a fish's intent to spawn in nonnatal waters. An individual that would have eventually returned to natal waters (temporary stray) may have been captured in a fishery, entered a hatchery, or suffered another form of prespawn mortality in nonnatal waters. Fish were classified as having an unknown fate if (1) they were detected in the adult fishway at Bonneville Dam, The Dalles Dam, or McNary Dam but were not observed again, and (2) their disposition beyond the lower Columbia River could not be determined. Finally, we separated all strays (both temporary and permanent) into two different regions. Lower-river strays included individuals that entered nonnatal tributaries of the lower and mid-Columbia River prior to reaching the Columbia River–Snake River confluence, whereas upper-river strays ascended the Columbia River and associated tributaries above the confluence.

Covariates describing fish experience.—In addition to considering whether or not the fish had been transported as juveniles, we also considered the potential influences of other covariates on the straying behavior of each fish: (1) the rearing hatchery and (2) absolute distance (rkm) from the rearing hatchery to the initial release site or acclimation site above Lower Granite Dam. In some instances, only the region or reach of release rather than the specific release site was recorded in the database; in those cases, the midpoint of the region was assigned as the release distance. Release distance ranged from 0 rkm (i.e., release at the hatchery site) to 476 km from the rearing location. In addition, because fish length at tagging was not available for approximately 20% of the fish, we assigned fish to either yearling (~1 year after emergence) or subyearling (~3 months after emergence) release groups based on their release date. Yearlings were released during the first 4

months of their second year, whereas subyearlings were released after April of their first year. Therefore, in our analysis, all individuals that were released prior to day 115 (i.e., day of the year) were classified as yearlings, and those released on or after day 115 were classified as subyearlings.

Environmental covariates.—We compiled daily adult fall Chinook Salmon index counts, water temperatures, and flow records at Bonneville, Priest Rapids, and Ice Harbor dams from Columbia River DART (www.cbr.washington.edu/dart). To model lower-river straying, the temperature and flow conditions experienced during river ascent at Bonneville Dam were assigned to each detected adult on the date that the individual passed the dam. To model upper-river straying, we estimated the conditions at Priest Rapids Dam (Columbia River) and Ice Harbor Dam (Snake River) that were experienced by each adult at the Snake River–Columbia River confluence (i.e., where fish receive exposure to the waters of both rivers; see Figure 1). We assigned the daily conditions at each dam (temperature and total flow [calculated as powerhouse discharge plus spill]) to each adult 1 d after it passed McNary Dam, when we estimated it would reach the confluence. Fish that were not detected at McNary Dam were assigned the daily conditions that would be experienced by a migrant with the median travel rate arriving at the confluence (Bonneville Dam to McNary Dam: 5.58 d; Bonneville Dam to Ice Harbor Dam: 7.14 d). Therefore, temperature, flow, and the number of Chinook Salmon counted at Ice Harbor and Priest Rapids dams were assigned to each individual 7 d after detection at Bonneville Dam to approximate the conditions that were experienced by fish approaching the Columbia River–Snake River confluence.

Statistical analyses.—Fish ladders at Bonneville Dam provide the first opportunity to detect returning adult Snake River Chinook Salmon entering the Columbia River system. Migrating individuals with impaired homing capabilities may take longer to travel between Bonneville Dam and the Snake River, thus increasing their susceptibility to various sources of mortality. Therefore, for each hatchery, we used Fisher's exact test to compare the proportions of the total number of both juvenile migrant types (in-river and barged) detected at Bonneville Dam that were not subsequently detected upstream.

To evaluate the effects of juvenile and adult covariates on straying, we constructed a series of alternative logistic regression models to determine which juvenile fish experiences and environmental covariates influenced lower-river and upper-river straying. For both types of straying, the predictors included migration mode (in-river migration or the dam of collection for barged fish), hatchery, release distance from the hatchery, release age (yearling or subyearling), and ocean age (1–3). In addition, for lower-river straying, we included water temperature, flow, and the number of conspecifics at Bonneville Dam on the day of upstream passage (for a complete list of parameters and data sources, see Table A.1). For upper-river straying, we included temperature, flow, and the

number of conspecifics at Ice Harbor and Priest Rapids dams on the estimated day of arrival at the Columbia River–Snake River confluence. In modeling both types of straying, we included adult return year as a random effect. We used Akaike's information criterion (AIC) to compare several alternative hypotheses for explaining both types of straying behavior separately: (1) an intercept-only model, (2) a full model with all predictor terms and no interactions, (3) a model that included environmental parameters only (temperature and flow), (4) a model with fish experience parameters only (number of conspecifics, migration mode, return year, and hatchery), (5) a model with migration mode only; and (6) a model that included transport, return year, and hatchery. We used the 95% confidence interval (CI) of the odds ratio for each predictor to determine the predictors' relative importance to the model (Bland and Altman 2000). Parameters with odds ratio 95% CIs that were entirely greater than 1.0 were correlated with increased straying, whereas intervals that were entirely less than 1.0 were associated with lower rates of straying. We report estimates for parameters with 95% CIs spanning 1.0 if they were included in the final averaged model, but we placed no weight on their estimates in the evaluation results. All logistic regressions were performed with the lme4 package in R version 2.13.0 (R Core Team 2011).

In addition to our assessment of straying, we evaluated a subtler form of migration impairment: delayed migration for fish that ultimately homed to the Snake River as adults. For the 15,586 adult fish that homed and were detected at both Bonneville Dam and Lower Granite Dam, we calculated travel rate as the number of days between the last detection at Bonneville Dam and the first detection at Lower Granite Dam. We then evaluated a set of covariates that were related to juvenile experience and environmental factors as predictors of travel rate. We used AIC to evaluate a set of alternative linear models with sets of predictors similar to those used in the straying analysis, but we additionally included return date (date of first detection at Bonneville Dam). Return year was included as a random effect. Because the distribution of observed travel times was extremely right-skewed, we used quantile regression to model the 50th percentile (median travel time), 10th percentile (fastest migrations), and 90th percentile (slowest migrations) separately. Quantile regressions were performed with the lqmm package in R.

RESULTS

Lower Columbia River Straying

Overall, 24,533 PIT-tagged adult Chinook Salmon from juvenile release locations in the Snake River were detected as ascending the Columbia River past Bonneville Dam. Of those, 18,463 fish had sufficient detections to permit determination of their migration history. We detected a total of 370 strays (152 permanent and 218 temporary) at six rivers below the Columbia River–Snake River confluence, although the

TABLE 1. Odds ratios from the top logistic regression model explaining temporary and permanent straying (both types combined) into the lower Columbia River by adult Snake River fall Chinook Salmon. Bold italic values indicate 95% confidence intervals that did not contain 1.0 (i.e., a significant effect was indicated; CL = confidence limit).

Parameter	Odds ratio	95% CLs Upper	95% CLs Lower
Run-of-the-river migrants	Base		
Barged from Lower Granite Dam	*3.10*	*2.15*	*4.47*
Barged from Little Goose Dam	*2.15*	*1.48*	*3.12*
Barged from Lower Monumental Dam	*1.85*	*1.08*	*3.15*
Barged from McNary Dam	0.69	0.16	2.91
Release distance	1.00	0.99	1.00
Rearing at Dworshak National Fish Hatchery	Base		
Rearing at Irrigon Hatchery	0.94	0.39	2.28
Rearing at Lyons Ferry Hatchery	1.25	0.84	1.86
Rearing at Nez Perce Tribal Hatchery	1.40	0.93	2.11
Rearing at Oxbow Hatchery	1.63	0.81	3.28
Rearing at Umatilla Hatchery	1.96	0.71	5.43
Release age	1.02	0.65	1.62
Bonneville Dam temperature	*2.20*	*1.58*	*3.05*
Bonneville Dam flow	1.00	0.99	1.01

vast majority were detected in the Deschutes River (139 permanent and 191 temporary). Examination of AIC values indicated that the full model was the best-performing model from our candidate set (Table A.2) in terms of explaining overall lower-river straying. Four parameter estimates had odds ratios with 95% CIs entirely exceeding 1.0, indicating that they were associated with increased straying (Table 1). Straying increased with increasing temperature at Bonneville Dam on the day of upstream passage (odds ratio = 2.20 per °C). The three Snake River dams from which fish were barged as juveniles had significant effects on lower-river straying (odds ratio = 1.85–3.10), but there was no effect of barging from McNary Dam on the Columbia River. Although included in the best model, there was no significant effect of hatchery, release age, or release distance on lower-river straying (Table 1). Thus, increases in river temperature and barging at Snake River dams were strongly associated with increases in lower-river straying.

Upper Columbia River Straying

We detected a total of 215 strays (196 permanent and 19 temporary) at five rivers and three dams above the Columbia River–Snake River confluence. Based on AIC values, the model that included barging location, release distance, and hatchery was the best model from our candidate set

TABLE 2. Odds ratios derived from parameter estimates for the best-fitting logistic regression model used to explain temporary and permanent straying (both types combined) into the upper Columbia River by adult Snake River fall Chinook Salmon. Bold italic values indicate 95% confidence intervals that did not contain 1.0 (i.e., a significant effect was indicated; CL = confidence limit).

Parameter	Odds ratio	95% CLs Upper	Lower
Run-of-the-river migrants	Base		
Barged from Lower Granite Dam	*15.34*	*10.53*	*22.33*
Barged from Little Goose Dam	*10.35*	*7.04*	*15.21*
Barged from Lower Monumental Dam	*19.36*	*12.82*	*29.24*
Barged from McNary Dam	1.99	0.27	14.52
Release distance	1.31	0.85	2.01
Rearing at Dworshak National Fish Hatchery	Base		
Rearing at Irrigon Hatchery	0.51	0.15	1.75
Rearing at Lyons Ferry Hatchery	*0.53*	*0.31*	*0.92*
Rearing at Nez Perce Tribal Hatchery	*2.71*	*1.66*	*4.43*
Rearing at Oxbow Hatchery	*2.17*	*1.14*	*4.13*
Rearing at Umatilla Hatchery	1.16	0.32	4.20

(Table A.3) for explaining overall straying. Therefore, environmental factors were not included in the final model. Five parameters had estimated odds ratios associated with increased straying, but juvenile barging from the three Snake River dams had much greater effects (odds ratio = 10.35–19.36) than any other factor (Table 2). In contrast, fish that

were barged from McNary Dam below the Columbia River–Snake River confluence were no more likely than in-river migrants to exhibit upper-river straying. Additionally, rearing at the Nez Perce Tribal Hatchery (odds ratio = 2.71) and Oxbow Hatchery (odds ratio = 2.17) was associated with increased upper-river straying. Fish that were reared at Lyons Ferry Hatchery (odds ratio = 0.53) were less likely to stray. All other predictors had odds ratio 95% CIs that encompassed 1.0 (Table 2), thereby indicating no significant effect.

Travel Success and Travel Time from Bonneville Dam to Lower Granite Dam

The percentage of fish that ascended Bonneville Dam but were not subsequently detected was higher for the barged group (29.7%) than for the in-river group (22.7%), although the rate of loss varied among fish from different hatcheries (Table 3). Travel time from Bonneville Dam to Lower Granite Dam ranged from 7.7 to 88.1 d (59.8–5.2 km/d), and the median travel time for all fish was 12.1 d (38.0 km/d).

For fish that were observed at both Bonneville Dam and Lower Granite Dam, the full model (i.e., including temperature and flow at Bonneville Dam; and migration mode, hatchery, release distance, and river arrival day) best explained the differences in travel time (Table A.4). However, a comparison of parameter estimates among models for the groups with 10th-, 50th- (median), and 90th-percentile travel times indicated a change in the importance of some factors from the slowest to the fastest migration times (Table 4). For example, barging had no significant effect on travel time for the 10th-percentile group (fish with the fastest migration) but was associated with increased travel times for the 50th- and 90th-percentile groups. Fish from Irrigon Hatchery and

TABLE 3. Numbers of PIT-tagged adult Snake River fall Chinook Salmon that passed Bonneville Dam (Columbia River) during the study period (2006–2013), categorized by juvenile migration mode and rearing hatchery. Total lost (percent lost) indicates the number (percentage) of adults that were not detected again after passing Bonneville Dam. Proportions were compared between migration modes for each hatchery by using Fisher's exact test (**P < 0.001, ***P < 0.0001). Median (50th percentile) and 90th-percentile travel times indicate the median and 90th-percentile number of days from the last detection at Bonneville Dam to the first detection at Lower Granite Dam for adults that were detected at both locations.

Migration mode	Hatchery	Total past Bonneville Dam	Total lost	Percent lost	Median travel time (d)	90th-percentile travel time (d)
In-river migrant	Dworshak	6,607	1,408	21.3	12.1	18.3
	Irrigon	626	139	22.2	12.1	18.4
	Lyons Ferry	9,753	2,358	24.2	12.2	18.6
	Nez Perce Tribal	852	186	21.8	12.3	16.8
	Oxbow	588	117	19.9	11.8	13.9
	Umatilla	1,527	319	20.9	11.6	15.6
Barged	Dworshak	1,282	327	25.5**	12.9	21.8
	Irrigon	172	60	34.9**	12.8	21.8
	Lyons Ferry	2,172	659	30.3***	12.8	22.6
	Nez Perce Tribal	241	94	39.0***	13.7	18.1
	Oxbow	161	43	26.7	12.2	21.4
	Umatilla	552	178	32.2***	12.0	19.1

TABLE 4. Parameter estimates for the best-fitting quantile regression model explaining variation in travel time between Bonneville Dam and Lower Granite Dam for adult Snake River fall Chinook Salmon with 10th-percentile, median (50th percentile), and 90th-percentile travel times. The year of adult return was included as a random effect. Bold italic values indicate parameters that were significant ($P < 0.05$).

Parameter	10th percentile (fastest migration)			Median migration			90th percentile (slowest migration)		
	Estimate	±95% CI	P	Estimate	±95% CI	P	Estimate	±95% CI	P
Intercept	*22.71*	*15.25*	*<0.01*	*24.06*	*17.47*	*0.01*	*33.29*	*23.15*	*0.01*
Temperature	−0.34	0.45	0.14	−0.29	0.51	0.27	*−0.86*	*0.71*	*0.02*
Flow	−0.06	0.26	0.63	*0.52*	*0.48*	*0.03*	*1.51*	*0.47*	*<0.001*
Run-of-the-river migrants	Base								
Barged juveniles	0.14	0.18	0.15	*0.57*	*0.22*	*<0.001*	*4.06*	*0.78*	*<0.001*
Rearing at Dworshak National Fish Hatchery	Base								
Rearing at Irrigon Hatchery	*0.58*	*0.60*	*0.06*	*1.14*	*0.73*	*<0.01*	*3.14*	*1.45*	*<0.001*
Rearing at Lyons Ferry Hatchery	0.18	0.21	0.10	0.41	0.44	0.07	*1.54*	*0.73*	*<0.001*
Rearing at Nez Perce Tribal Hatchery	−0.20	0.38	0.30	−0.28	0.63	0.38	−0.81	1.51	0.28
Rearing at Oxbow Hatchery	−0.74	1.46	0.32	−1.01	2.76	0.47	−1.44	2.94	0.33
Rearing at Umatilla Hatchery	*0.56*	*0.47*	*0.02*	*0.91*	*0.78*	*0.02*	*3.25*	*1.73*	*<0.001*
Release distance	*−0.24*	*0.16*	*0.00*	*−0.48*	*0.21*	*<0.001*	*−1.54*	*0.60*	*<0.001*
River arrival day	−0.05	0.06	0.12	−0.05	0.07	0.19	−0.07	0.09	0.11

Umatilla Hatchery were slower in all percentiles, and migration time decreased with increasing release distance among all percentiles. Total flow at Bonneville Dam was not correlated with travel time for the 10th-percentile group but was associated with slower migration for the 50th- and 90th-percentile groups.

DISCUSSION

Lower Columbia River Straying

Straying of upstream-migrating adult Chinook Salmon into lower Columbia River tributaries was greater during higher river temperatures for both migration groups (barged and in-river migrants). Such temporary lower-river straying suggested that many fish used tributaries for thermal refuge or rest during their upstream migration. Other studies of Columbia River salmon and steelhead have demonstrated the temporary use of thermal refuges when water temperatures are high during river ascent (Goniea et al. 2006; Keefer et al. 2009). However, the limitations of PIT tag detection data prevented us from distinguishing Chinook Salmon that spawned in lower-river tributaries from those that temporarily occupied those streams to avoid thermally stressful conditions but succumbed to fishing mortality or other sources of mortality while waiting for more favorable conditions. However, the observed high incidence of temporary straying agrees with extensive previous research on temporary straying in both steelhead (High et al. 2006; Keefer et al. 2009) and fall Chinook Salmon (Goniea et al. 2006), indicating that

temporary straying in the lower river may be driven largely by fish seeking temporary thermal refuge.

Although nearly half of the Chinook Salmon that were detected in lower Columbia River tributaries ultimately homed to the Snake River, the fate of the remaining fish could not be determined from PIT tag detections. The vast majority of lower-river strays (89%) were detected at the Deschutes River mouth, less than 500 m upstream from its confluence with the Columbia River. With the exception of the detection system at the mouth (rkm 0) of the Hood River, the other rivers had detectors located farther upstream than that in the Deschutes River (Klickitat River: rkm 4; Umatilla River: rkm 5; Walla Walla River: rkm 15; John Day River: rkm 17). These rivers, along with others where strays were not detected, may attract temporary strays in reaches downstream of the detection areas covered by PIT tag antennas. Furthermore, our estimates of straying are minimum values, as substantial straying could have occurred in streams without detectors or in streams with poor detector efficiency. Previous studies have demonstrated straying and spawning in the John Day River by Snake River-origin steelhead and spring Chinook Salmon, primarily by barged individuals, suggesting extensive permanent straying in some streams below the Snake River confluence (Ruzycki and Carmichael 2010). However, we identified only two temporary strays and one permanent stray that entered the John Day River, demonstrating little use of that habitat by Snake River fall-run Chinook Salmon, possibly because the John Day River has no natural population of fall Chinook Salmon and because access above

Tumwater Falls is poor during the late summer and fall. Other studies of hatchery-reared Chinook Salmon have also demonstrated that warm main-stem and tributary temperatures increase straying (Westley et al. 2015), although Goniea et al. (2006) reported that relatively few fall Chinook Salmon entered lower and mid-Columbia River tributaries. Goniea et al. (2006) hypothesized that the short time window between entry into the Columbia River and spawning may promote rapid passage through the lower river despite thermally stressful conditions.

Unlike the John Day River, which attracts steelhead and spring Chinook Salmon (Ruzycki and Carmichael 2010), fall Chinook Salmon primarily stray to the Deschutes River (Naughton et al. 2009). During August, the lower Deschutes River is, on average, 1.5°C colder than the John Day River (U.S. Department of Agriculture, NorWeST stream temperature data; www.sciencebase.gov/gisviewer/NorWeST/; August mean temperature, 1993–2011), making it more attractive for late-summer-migrating fish like fall Chinook Salmon. Therefore, as temperature and hydrologic conditions in Columbia River basin streams continue to change (Isaak et al. 2012), the relative attractiveness of both natal and nonnatal streams may also fluctuate, altering the source–sink dynamics of salmon throughout the basin.

Upper Columbia River Straying

Upper-river straying was distinct from lower-river straying in several key ways. First, substantial lower-river straying was displayed by both barged and in-river fish, whereas upper-river straying was dominated by fish that were barged from the three Snake River dams. Second, much of the lower-river straying was temporary, and many lower-river strays ultimately homed to the Snake River; in contrast, nearly all straying to upper-river sites met our definition of permanent straying. Therefore, movement up the Columbia River beyond the confluence with the Snake River was consistent with either (1) an inability to recognize the Snake River as home, or (2) rejection of the Snake River in favor of the Columbia River, primarily by fish that had been barged through the confluence as juveniles. Although the Columbia River is generally cooler than the Snake River, we found no temperature-related effects on straying. However, there may be some attraction to the Hanford Reach, the largest fall Chinook Salmon spawning area in the main-stem Columbia River, located just upstream of the confluence with the Snake River (Harnish et al. 2014). Hence, there is a trade-off: collection and transport of Chinook Salmon from Snake River dams increase smolt survival but also increase the straying of adults and their loss to the adult populations in the Snake River. Recent gains in the in-river survival of juveniles have weakened the benefits of barging (McCann et al. 2015), but there is some potential for increasing adult returns to the Snake River with changes to the barging process that more adequately support the proper imprinting of juveniles.

The distance between the hatchery of origin and the release site (i.e., release distance) was not correlated with upper-river or lower-river straying. Although previous work detected higher rates of straying in groups that were transported farther (Solazzi et al. 1991; Marsh et al. 2012), the coarse spatial scale of our evaluation was such that fish only had to return to the Snake River to be classified as having successfully homed. In addition, previous studies have largely transported fish downstream prior to release, whereas the juvenile Chinook Salmon included in our study were often moved upstream to an acclimation site prior to their release into the river. Thus, substantial fine-scale straying after Snake River entry may have occurred but without being detected.

We observed greater straying by fish reared at the Nez Perce Tribal Hatchery and Oxbow Hatchery than at other hatcheries, whereas the straying rate was lower for Lyons Ferry Hatchery-origin fish. Although fish that were reared at the Nez Perce Tribal Hatchery and Oxbow Hatchery originate farther upstream than those at many of the other hatcheries, the factors that caused differences in broadscale straying among fish from the various hatcheries were unclear. Snake River fall-run Chinook Salmon are managed as a major population group (Snake River) in a single evolutionarily significant unit. As such, hatchery production and rearing are spread throughout the basin, yet nearly all broodstock adults are collected at Lower Granite Dam, and there is no effort to maintain separate breeding lines based on origin. Therefore, the primary effects of rearing and release locations on straying rate as observed in our analyses were more likely to have been environmental than genetic. However, the overwhelming effect of transport and the relatively weak effect of hatchery implicate barging rather than hatcheries as the primary factor that impairs homing and natal site fidelity. Fall Chinook Salmon are moved throughout the basin at several different life stages; a more detailed analysis of spawning site, hatchery, and release site—all of which may vary for an individual fish—as well as specific hatchery practices (e.g., size at release) in relation to homing fidelity may lead to a more comprehensive understanding of how hatchery practices influence straying.

In addition to the implications of our study for the conservation of Columbia River basin salmonids, our results also provide insights into the complicated imprinting and homing process. The propensity of fish that were barged from McNary Dam to home successfully to the Snake River indicates that fish experiencing the Columbia River–Snake River confluence during natural migrations can imprint successfully despite subsequent barging. Fish that are barged from McNary Dam make no further confluence transits during the transportation process, suggesting that salmon are able to overcome other gaps in their olfactory experience if key river intersections are experienced appropriately. Recent studies to identify methods for improving homing fidelity in barged salmon suggest that pausing to expose fish to novel waters at key tributary junctions may improve imprinting (Dittman et al. 2014).

Travel Time between Bonneville Dam and Lower Granite Dam

Adult Chinook Salmon migrated upstream between Bonneville Dam and Lower Granite Dam (461 km) more slowly if they had been barged as juveniles than if they had migrated in the river. In addition, fish that were exposed to higher Columbia River water temperatures as adults migrated more slowly than fish that experienced cooler water. Other studies have shown that high temperatures delay or block migration (Major and Mighell 1967; Strange 2010) and that salmon temporarily enter cooler tributaries to avoid thermally stressful main-stem water, thereby slowing the overall travel rate (Goniea et al. 2006). Consequently, the barging of juveniles, combined with warm river temperatures during adult migration, may lead to lower adult survival via increased exposure to fishing mortality or natural mortality agents in the lower Columbia River. Additionally, barged fish may have higher rates of fallback at main-stem dams, which contribute to slower travel rates (Keefer et al. 2008).

We observed longer travel times by Chinook Salmon from Irrigon Hatchery and Lyons Ferry Hatchery in the median travel time group, whereas travel times by fish from the Nez Perce Tribal Hatchery were shorter. Lyons Ferry, Irrigon, and Umatilla hatcheries receive embryos for rearing from Lyons Ferry and are situated downstream of Lower Granite Dam. However, rearing at Umatilla Hatchery had no significant effect on travel time. In some cases, the geography of the hatchery may slow the migration if fish must pass their rearing location to reach their release location (Figure 1). In contrast, the Nez Perce Tribal Hatchery and Dworshak National Fish Hatchery are located on the Clearwater River and well upstream of Lower Granite Dam, thus creating a more straightforward sequence of waypoints for adults that are retracing their juvenile migration. Our analysis of travel rates included only those Chinook Salmon that eventually homed to the Snake River, whereas individuals with the most impaired homing abilities may not reach the Snake River at all.

Mean travel time from Bonneville Dam to Lower Granite Dam was 12.1 d (37.9 km/d), similar to travel times through the same reach for spring–summer Chinook Salmon (Marsh et al. 2012). However, some adults migrated considerably faster: the shortest travel time detected was 7.7 d for a yearling migrant ocean age-2 fish. Assuming an average FL of 74.6 cm for a Chinook Salmon of this age from Lyons Ferry (1993–2008 return years; queried from the Regional Mark Processing Center; RMPC.org), the individual with the shortest travel time averaged 0.93 body lengths/s or 59.7 km/d while passing six main-stem dams. This rate is similar to the maximum travel rates observed in Chinook Salmon migrating through free-flowing river sections of the Columbia River basin (Keefer et al. 2004), and the Yukon River (Eiler et al. 2015).

Population-Level Effects of Straying

The absolute rates of straying in this study are minimum values and likely are far less accurate than the rates estimated by use of alternative approaches, such as coded wire tagging (Quinn et al. 1989; Westley et al. 2013) or parentage-based tagging (PBT; Steele et al. 2013). Coded wire tags are far more numerous than PIT tags and are monitored at every hatchery in the Columbia River basin, providing good estimates of permanent straying. Similarly, PBT ensures that essentially all hatchery fish are tagged genetically, and estimates of straying are limited only by sample collection. However, despite the limitations of in-stream PIT tag reader coverage or operational efficiency, PIT tags currently constitute the only technology that allows for the separate identification of barged and run-of-the-river juvenile migrants. Therefore, it is not practical to calculate absolute straying rates, which are undoubtedly biased low compared to other studies of fall-run Chinook Salmon, wherein the reported rates are greater than 30% (Keefer and Caudill 2014). However, we can use the regression coefficients to compare barged and in-river-migrant groups in terms of their relative rates of straying to the upper river, where most straying is permanent. Over the years of our study, barged fall Chinook Salmon comprised 16% of the adult returns; on average, 19% of the fish migrating past McNary Dam (the uppermost dam prior to the confluence of the Columbia and Snake rivers; Figure 1) ascend the Snake River, while the remainder continue up the Columbia River (Columbia River DART; www.cbr.washington.edu/dart/query/adult_annual_sum). The coefficients of our logistic regression indicated that (1) straying adults that migrated in-river as juveniles contributed at least 1,385 fish (0.05%) to the 2.4 million Chinook Salmon migrating in the upper Columbia River during 2004–2015, and (2) straying adults that were barged as juveniles contributed 22,105 fish (0.9%) to the group of upper-river migrants. Therefore, although the numbers of additional strays noted here are minimum values due to limitations in PIT tag detection, the contribution of strays from fish barged as juveniles was vastly greater than the contribution from the in-river migrant group. That said, for overall straying rates to make a substantial contribution to the upper river, they would have to be much higher than what has been detected with the current PIT tag array infrastructure, and strays are only likely to be problematic to local populations if they form a large proportion of the adults in specific spawning reaches.

Although it is difficult to assess the overall effects of barging on Snake River fall-run Chinook Salmon, estimates of smolt-to-adult survival for barged and in-river-migrating smolts have indicated a higher return of barged fish in only a few study years, and most estimates have demonstrated no substantial benefit of barging over in-river migration (McCann et al. 2015). Therefore, from the perspective of the donor population (i.e., Snake River fall Chinook Salmon), higher rates of adult straying likely offset some of the survival benefits obtained from juvenile transportation. The larger management issue with regard to straying may be the relative

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rates at which strays enter streams containing small local recipient populations (Keefer and Caudill 2014). Spawning areas that tend to receive relatively large numbers of strays may become swamped by a nonlocal stock, although this issue is muted in the upper river where there is little natural production of fall-run Chinook Salmon outside of the main-stem Hanford Reach region. Additionally, the strays in our study were only strays in the coarsest context: they missed the Snake River–Columbia River confluence. The effects of barging on additional straying of fish that successfully home to the Snake River remain unknown and undetectable with our study design and given the current number of instream PIT tag detection systems in the basin. As additional instream PIT tag arrays become operational, future studies should focus on where strays may challenge local stocks and how straying to those areas can be mitigated (Pascual and Quinn 1994).

The higher incidence of straying by Chinook Salmon that were transported as juveniles from dams upstream of the Snake River–Columbia River confluence indicated that for many of those adults, homing to the Snake River was compromised despite their exposure to Snake River water and confluence water during barge transport as juveniles. On the other hand, individuals that migrated naturally through the confluence and were then transported rarely strayed into the upper Columbia River. From these patterns, we infer that migration though the confluence was important in allowing the fish to form a navigational waypoint for the return migration to the Snake River. These results suggest that river confluences are critical points for imprinting and that water exposure in the barges, as currently operated, may not replicate the odor exposure experienced by salmon migrating volitionally through the Snake and Columbia rivers. Juvenile salmon make complex movements as they migrate downstream, experiencing different habitats and tributary waters along a cross section of the river (e.g., Harnish et al. 2012; Li et al. 2015), whereas barged salmon only experience water that is pumped from the navigation channel, which is typically near the middle of the river. Alternatively, juvenile salmon that are placed in barges may not be physiologically prepared to imprint even if they receive the appropriate water exposure for the proper duration (Clarke et al. 2016). Furthermore, telemetry studies have indicated that Snake River Chinook Salmon pause at the confluence of major rivers during their downstream migration (Hockersmith et al. 1999), perhaps facilitating the learning of these key olfactory waypoints, whereas barged fish are transported downstream at a relatively fast and constant rate.

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REFERENCES

Anderson, J. H., P. L. Faulds, K. D. Burton, M. E. Koehler, W. I. Atlas, and T. P. Quinn. 2015. Dispersal and productivity of Chinook (*Oncorhynchus tshawytscha*) and Coho (*Oncorhynchus kisutch*) salmon colonizing newly accessible habitat. Canadian Journal of Fisheries and Aquatic Sciences 72:454–465.

Axel, G. A., E. F. Prentice, and B. P. Sandford. 2005. PIT-tag detection system for large-diameter juvenile fish bypass pipes at Columbia River basin hydroelectric dams. North American Journal of Fisheries Management 25:646–651.

Beckman, B. R., and D. A. Larsen. 2005. Upstream migration of minijack (age-2) Chinook Salmon in the Columbia River: behavior, abundance, distribution, and origin. Transactions of the American Fisheries Society 134:1520–1541.

Bland, J. M., and D. G. Altman. 2000. Statistics notes: the odds ratio. British Medical Journal 320:1468.

Brenner, R. E., S. D. Moffitt, and W. S. Grant. 2012. Straying of hatchery salmon in Prince William Sound, Alaska. Environmental Biology of Fishes 94:179–195.

California Department of Fish and Game. 2001. Final report on anadromous salmonid fish hatcheries in California. California Department of Fish and Game, Fisheries Branch, Sacramento.

Candy, J. R., and T. D. Beacham. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged Chinook Salmon (*Oncorhynchus tshawytscha*) populations. Fisheries Research 47:41–56.

Chapman, D., C. Carlson, D. Weitkamp, G. Matthews, J. Stevenson, and M. Miller. 1997. Homing in Sockeye and Chinook salmon transported around part of their smolt migration route in the Columbia River. North American Journal of Fisheries Management 17:101–113.

Chilcote, M. W. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 60:1057–1067.

Clarke, L. R., W. A. Cameron, and R. W. Carmichael. 2016. No evidence of increased survival or decreased straying from acclimating subyearling fall Chinook Salmon to release locations in the Umatilla River of Oregon. North American Journal of Fisheries Management 36:161–166.

Connor, W. P., J. G. Sneva, K. F. Tiffan, R. K. Steinhorst, and D. Ross. 2005. Two alternative juvenile life history types for fall Chinook Salmon in the Snake River basin. Transactions of the American Fisheries Society 134:291–304.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, New York.

Dittman, A. H., D. May, P. D. Hoppe, T. M. Marsh, and W. D. Muir. 2014. Evaluation of imprinting methods to improve the homing fidelity of barged juvenile salmonids. Annual Report of Research for the U.S. Army Corps of Engineers, Walla Walla, Washington.

Dittman, A. H., and T. P. Quinn. 1996. Homing in Pacific salmon: mechanisms and ecological basis. Journal of Experimental Biology 199:83–91.

Dittman, A. H., T. P. Quinn, and G. A. Nevitt. 1996. Timing of imprinting to natural and artificial odors by Coho Salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 53:434–442.

Ebel, W. J. 1980. Transportation of Chinook Salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, smolts in the Columbia River and effects on adult returns. U.S. National Marine Fisheries Service Fishery Bulletin 78:491–505.

Ebel, W. J., D. L. Park, and R. C. Johnsen. 1973. Effects of transportation on survival and homing of Snake River Chinook Salmon and steelhead trout. U.S. National Marine Fisheries Service Fishery Bulletin 71:549–563.

Eiler, J. H., A. N. Evans, and C. B. Schreck. 2015. Migratory patterns of wild Chinook Salmon *Oncorhynchus tshawytscha* returning to a large, free-flowing river basin. PLoS (Public Library of Science) One [online serial] 10(4):e0123127.

Feldheim, K. A., S. H. Gruber, and M. V. Ashley. 2002. The breeding biology of Lemon Sharks at a tropical nursery lagoon. Proceedings of the Royal Society B 269:1655–1661.

Goniea, T. M., M. L. Keefer, T. C. Bjornn, C. A. Peery. D. H. Bennett, and L. C. Stuehrenberg. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook Salmon in response to high Columbia River water temperatures. Transactions of the American Fisheries Society 135:408–419.

Harnish, R. A., G. E. Johnson, G. A. McMichael, M. S. Hughes, and B. D. Ebberts. 2012. Effect of migration pathway on travel time and survival of acoustic-tagged juvenile salmonids in the Columbia River estuary. Transactions of the American Fisheries Society 141:507–519.

Harnish, R. A., R. Sharma, G. A. McMichael, R. B. Langshaw, and T. N. Pearsons. 2014. Effect of hydroelectric dam operations on the freshwater productivity of a Columbia River fall Chinook Salmon population. Canadian Journal of Fisheries and Aquatic Sciences 71:602–615.

Hasler, A. D., and A. T. Scholz. 1983. Olfactory imprinting and homing in salmon. Springer-Verlag, Berlin.

Hendry, A. P., T. Bohlin, B. Jonsson, and O. K. Berg. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. Pages 92–126 *in* A. P. Hendry and S. C. Stearns, editors. Evolution illuminated: salmon and their relatives. Oxford University Press, Oxford, UK.

High, B., C. A. Peery, and D. H. Bennett. 2006. Temporary staging of Columbia River summer steelhead in coolwater areas and its effect on migration rates. Transactions of the American Fisheries Society 135:519–528.

Hockersmith, E. E., S. G. Smith, W. D. Muir, B. P. Sandford, J. G. Williams, and J. R. Skalski. 1999. Survival estimates for the passage of juvenile salmonids through Snake River dams and reservoirs, 1997. Annual Report to the Bonneville Power Administration, Project 93-29, Portland, Oregon.

Holsman, K. K., M. D. Scheuerell, E. Buhle, and R. Emmett. 2012. Interacting effects of translocation, artificial propagation, and environmental conditions on the marine survival of Chinook Salmon from the Columbia River, Washington, USA. Conservation Biology 26:912–922.

Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980 to 2009 and implications for salmonid fishes. Climatic Change 113:499–524.

Keefer, M. L., and C. C. Caudill. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Reviews in Fish Biology and Fisheries 24:333–368.

Keefer, M. L., C. C. Caudill, C. A. Peery, and S. R. Lee. 2008. Transporting juvenile salmonids around dams impairs adult migration. Ecological Applications 18:1888–1900.

Keefer, M. L., C. A. Peery, J. Firehammer, and M. L. Moser. 2005. Straying rates of known-origin adult Chinook Salmon and steelhead within the Columbia River basin, 2000–2003. University of Idaho, Moscow.

Keefer, M. L., C. A. Peery, and B. High. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. Canadian Journal of Fisheries and Aquatic Sciences 66:1734–1747.

Keefer, M. L., C. A. Peery, M. A. Jepson, and L. C. Stuehrenberg. 2004. Upstream migration rates of radio-tagged adult Chinook Salmon in riverine habitats of the Columbia River basin. Journal of Fish Biology 65:1126–1141.

Lasko, G. R., R. G. Titus, J. R. Ferreira, and R. M. Coleman. 2014. Straying of late-fall run Chinook Salmon from the Coleman National Fish Hatchery into the lower American River, California. California Fish and Game 100:665–682.

Leider, S. A. 1989. Increased straying by adult steelhead trout, *Salmo gairdneri*, following the 1980 eruption of Mount St. Helens. Environmental Biology of Fishes 24:219–229.

Li, X., Z. D. Deng, J. J. Martinez, T. Fu, P. Scott Titzler, J. S. Hughes, M. A. Weiland, R. S. Brown, B. A. Trumbo, M. L. Ahmann, and J. F. Renholds. 2015. Three-dimensional tracking of juvenile salmon at a mid-reach location between two dams. Fisheries Research 167:216–224.

Major, R. L., and J. L. Mighell. 1967. Influence of Rocky Reach Dam and temperature of the Okanogan River on upstream migration of Sockeye Salmon. U.S. National Marine Fisheries Service Fishery Bulletin 66:131–147.

Marsh, D. M., W. D. Muir, B. P. Sandford, S. G. Smith, and D. Elliott. 2012. Alternative barging strategies to improve survival of salmonids transported from Lower Granite Dam: final report from the 2006–2008 spring/summer Chinook Salmon and steelhead juvenile migrations. National Marine Fisheries Service and U.S. Geological Survey, Seattle.

McCann, J., B. Chockley, E. Cooper, H. Schaller, S. Haeseker, R. Lessard, C. Petrosky, E. Tinus, E. Van Dyke, R. Ehlke, and M. DeHart. 2015. Comparative survival study of PIT-tagged spring/summer/fall Chinook, summer steelhead, and sockeye. Annual Report to the Bonneville Power Administration, Project 1996-02-00, Portland, Oregon.

McMichael, G. A., J. R. Skalski, and K. A. Deters. 2011. Survival of juvenile Chinook Salmon during barge transport. North American Journal of Fisheries Management 31:1187–1196.

Milner, A. M., A. L. Robertson, K. A. Monaghan, A. J. Veal, and E. A. Flory. 2008. Colonization and development of an Alaskan stream community over 28 years. Frontiers in Ecology and the Environment 6:413–419.

Muir, W. D., D. M. Marsh, B. P. Sandford, S. G. Smith, and J. G. Williams. 2006. Post-hydropower system delayed mortality of transported Snake River stream-type Chinook Salmon: unraveling the mystery. Transactions of the American Fisheries Society 135:1523–1534.

Muir, W. D., S. G. Smith, J. G. Williams, E. E. Hockersmith, and J. R. Skalski. 2001. Survival estimates for migrant yearling Chinook Salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers, 1993–1998. North American Journal of Fisheries Management 21:269–282.

Naish, K. A., J. E. Taylor III, P. S. Levin, T. P. Quinn, J. R. Winton, D. Huppert, and R. Hilborn. 2008. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. Advances in Marine Biology 53:61–194.

Naughton, G. P., M. A. Jepson, C. A. Peery, C. V. Brun, and J. C. Graham. 2009. Effects of temporary tributary use on escapement estimates of adult fall Chinook Salmon in the Deschutes River, Oregon. North American Journal of Fisheries Management 29:1511–1518.

Pascual, M. A., and T. P. Quinn. 1994. Geographical patterns of straying of fall Chinook Salmon, *Oncorhynchus tshawytscha* (Walbaum), from Columbia River (USA) hatcheries. Aquaculture and Fishery Management 25(Supplement 2):14–30.

Prentice, E. F., T. A. Flagg, and C. S. McCutcheon. 1990a. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pages 317–322 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, and D. F. Brastow. 1990b. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. Pages 323–334 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Quinn, T. P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fisheries Research 18:29–44.

Quinn, T. P., E. L. Brannon, and A. H. Dittman. 1989. Spatial aspects of imprinting and homing in Coho Salmon, Oncorhynchus kisutch. U.S. National Marine Fisheries Service Fishery Bulletin 87:769–774.

Quinn, T. P., and A. H. Dittman. 1992. Homing in fishes. Pages 145–211 in F. Papi, editor. Animal homing. Chapman Hall, London.

Quinn, T. P., R. S. Nemeth, and D. O. McIsaac. 1991. Homing and straying patterns of fall Chinook Salmon in the lower Columbia River. Transactions of the American Fisheries Society 120:150–156.

R Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: https://www.R-project.org/. (November 2016).

Rooker, J. R., H. Arrizabalaga, I. Fraile, D. H. Secor, D. L. Dettman, N. Abid, P. Addis, S. Deguara, F. S. Karakulak, A. Kimoto, O. Sakai, D. Macias, and M. N. Santos. 2014. Crossing the line: migratory and homing behaviors of Atlantic Bluefin Tuna. Marine Ecology Progress Series 504:265–276.

Ruzycki, J. R., and R. W. Carmichael. 2010. Preliminary summary of out-of-basin steelhead strays in the John Day River basin. Oregon Department of Fish and Wildlife, La Grande.

Solazzi, M. F., T. E. Nickelson, and S. L. Johnson. 1991. Survival, contribution, and return of hatchery Coho Salmon (Oncorhynchus kisutch) released into fresh-water, estuarine, and marine environments. Canadian Journal of Fisheries and Aquatic Sciences 48:248–253.

Steele, C. A., E. C. Anderson, M. W. Ackerman, M. A. Hess, N. R. Campbell, S. R. Narum, and M. R. Campbell. 2013. A validation of parentage-based tagging using hatchery steelhead in the Snake River basin. Canadian Journal of Fisheries and Aquatic Sciences 70:1046–1054.

Strange, J. S. 2010. Upper thermal limits to migration in adult Chinook Salmon: evidence from the Klamath River basin. Transactions of the American Fisheries Society 139:1091–1108.

Svedang, H., D. Righton, and P. Jonsson. 2007. Migratory behaviour of Atlantic Cod Gadus morhua: natal homing is the prime stock-separating mechanism. Marine Ecology Progress Series 345:1–12.

Westley, P. A. H., A. H. Dittman, E. J. Ward, and T. P. Quinn. 2015. Signals of climate, conspecific density, and watershed features in patterns of homing and dispersal by Pacific salmon. Ecology 96:2823–2833.

Westley, P. A. H., T. P. Quinn, and A. H. Dittman. 2013. Rates of straying by hatchery-produced Pacific salmon (Oncorhynchus spp.) and steelhead (Oncorhynchus mykiss) differ among species, life history types, and populations. Canadian Journal of Fisheries and Aquatic Sciences 70:735–746.

Zydlewski, G. B., G. Horton, T. Dubreuil, B. Letcher, S. Casey, and J. Zydlewski. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. Fisheries 31:492–502.

Appendix: Additional Data

TABLE A.1. Covariates that were used to explain variation in Chinook Salmon upstream travel time and straying rates, presented with data sources (PTAGIS = PIT Tag Information System; DART = Columbia River Data Access in Real Time; PNNL = Pacific Northwest National Laboratory).

Covariate	Abbreviation	Model coding and notes	Source
Day of the year of Bonneville Dam fish ladder ascent	River Arrival Day	Continuous	PitPro
Migration mode	Trans Dam	Factor; in-river migration or barging from Lower Granite, Lower Monumental, Little Goose, or McNary Dam	PitPro
Release distance: river kilometer from rearing site to release site	Rel Dist	Continuous	Google Earth
Rearing hatchery	Rear Site	Factor; Dworshak National Fish Hatchery, Irrigon Hatchery, Lyons Ferry Hatchery, Nez Perce Tribal Hatchery, Oxbow Hatchery, or Umatilla Hatchery	PTAGIS
Age at release	Rel Age	Factor; subyearling or yearling	Calculated
Bonneville Dam fish ladder temperature	Temp	Continuous; temperature on the day of ascent at the Bonneville Dam fish ladder	DART
Bonneville Dam fish ladder flow	Flow	Continuous; discharge plus spill during ascent at the Bonneville Dam fish ladder	DART
Flow at Ice Harbor Dam	Ice Flow	Continuous; discharge plus spill 1 d after McNary Dam ascent	DART
Temperature at Ice Harbor Dam	Ice Temp	Continuous; temperature 1 d after McNary Dam ascent	DART
Flow at Priest Rapids Dam	Priest Flow	Continuous; discharge plus spill 1 d after McNary Dam ascent	DART
Temperature at Priest Rapids Dam	Priest Temp	Continuous; temperature 1 d after McNary Dam ascent	DART, PNNL

TABLE A.2. Candidate logistic regression models explaining the straying rate of Snake River-origin fall Chinook Salmon to the lower Columbia River, compared based on Akaike's information criterion corrected for small sample sizes (AIC_c; K = number of parameters estimated in the model; ΔAIC_c = difference in AIC_c between the given model and the best-performing model [shown in bold italics]; w_i = AIC_c weight for the given model; LL = log likelihood). In all models, the adult return year was included as a random effect. Covariate abbreviations are defined in Table A.1.

Model	K	AIC_c	ΔAIC_c	w_i	LL
Trans Dam + Rel Dist + Rear Site + Rel Age + Temp + Flow	*17*	*2,541.7*	*0.0*	*1.0*	*−1,244.4*
Trans Dam	6	2,566.9	25.2	0.0	−1,277.4
Temp	3	2,571.0	29.2	0.0	−1,282.5
Trans Dam + Rel Dist + Rear Site + Rel Age	13	2,571.6	29.9	0.0	−1,272.8
Temp + Flow	4	2,572.1	30.4	0.0	−1,282.1
Null	1	2,620.3	78.6	0.0	−1,309.1

TABLE A.3. Candidate logistic regression models explaining the straying rate of Snake River-origin fall Chinook Salmon to the upper Columbia River, compared based on Akaike's information criterion corrected for small sample sizes (AIC_c; K = number of parameters estimated in the model; ΔAIC_c = difference in AIC_c between the given model and the best-performing model [shown in bold italics]; w_i = AIC_c weight for the given model; LL = log likelihood). In all models, adult return year was included as a random effect. Covariate abbreviations are defined in Table A.1.

Model	K	AIC_c	ΔAIC_c	w_i	LL
Trans Dam + Rear Site + Rel Dist	*11*	*1,884.7*	*0.0*	*0.6*	*−931.1*
Trans Dam + Rel Dist + Rear Site + Rel Age + Ice Flow + Priest Flow + Ice Temp	16	1,885.6	0.8	0.4	−922.8
Trans Dam	6	1,930.2	45.5	0.0	−959.1
Rear Site	7	2,218.0	333.2	0.0	−1,102.0
Rel Dist	3	2,251.7	366.9	0.0	−1,122.8
Rel Age	3	2,257.9	373.1	0.0	−1,125.9
Ice Flow + Priest Flow + Ice Temp	5	2,273.4	388.7	0.0	−1,131.7
Null	1	2,296.0	411.3	0.0	−1,147.0

TABLE A.4. Candidate regression models explaining variation in median travel time of adult Chinook Salmon between Bonneville Dam and Lower Granite Dam, compared based on Akaike's information criterion (AIC; K = number of parameters estimated in the model; ΔAIC = difference in AIC between the given model and the best-performing model [shown in bold italics]; w_i = AIC weight for the given model; LL = log likelihood). In all models, adult return year was included as a random effect. Covariate abbreviations are defined in Table A.1.

Model	K	AIC	ΔAIC	w_i	LL
Temp + Flow + Trans Dam + Rear Site + Rel Dist + River Arrival Day	*11*	*83,358*	*0.00*	*1*	*−41,666*
Temp + Flow	3	83,596	237.34	0	−41,793
River Arrival Day	2	83,636	277.86	0	−41,814
Trans Dam + Rear Site + Rel Dist	8	83,958	599.97	0	−41,969
Trans Dam	2	84,019	660.32	0	−42,005
Rear Site	6	84,061	702.42	0	−42,022
Null	1	84,066	707.39	0	−42,030