

# Route selection in a large river during the homing migration of Chinook salmon (*Oncorhynchus tshawytscha*)

Matthew L. Keefer, Christopher C. Caudill, Christopher A. Peery, and Theodore C. Bjornn

**Abstract:** Upstream-migrating adult salmon must make a series of correct navigation and route-selection decisions to successfully locate natal streams. In this field study, we examined factors influencing migration route selections early in the migration of 4361 radio-tagged adult Chinook salmon (*Oncorhynchus tshawytscha*) as they moved upstream past dams in the large (~1 km wide) Columbia River. Substantial behavioral differences were observed among 11 conspecific populations, despite largely concurrent migrations. At dams, Chinook salmon generally preferred ladder passage routes adjacent to the shoreline where their natal tributaries entered, and the degree of preference increased as salmon proximity to natal tributaries increased. Columbia River discharge also influenced route choices, explaining some route selection variability. We suggest that salmon detect lateral gradients in orientation cues across the Columbia River channel that are entrained within tributary plumes and that these gradients in cues can persist downstream for tens to hundreds of kilometres. Detection of tributary plumes in large river systems, using olfactory or other navigation cues, may facilitate efficient route selection and optimize energy conservation by long-distance migrants.

**Résumé :** Les saumons adultes en migration vers l'amont doivent prendre une série de décisions précises de navigation et de sélection de parcours afin de réussir à trouver leur cours d'eau d'origine. Notre étude de terrain examine les facteurs qui influencent le choix de la route de migration tôt dans le processus chez 4361 saumons chinook (*Oncorhynchus tshawytscha*) adultes munis d'étiquettes radio alors qu'ils se déplacent vers l'amont à travers des barrages dans la partie large (~1 km de largeur) du Columbia. On observe d'importantes différences dans le comportement des 11 populations conspécifiques, même si les migrations sont en grande partie simultanées. Au niveau des barrages, les saumons quinnat préfèrent généralement les routes avec échelles à poissons situées près de la rive sur laquelle aboutit leur tributaire d'origine et cette préférence est d'autant plus grande que les saumons s'approchent de leurs cours d'eau de naissance. Le débit du Columbia affecte aussi le choix des parcours, ce qui explique une partie de la variation de la sélection des routes de migration. Nous émettons l'hypothèse selon laquelle les saumons sont capables de déceler les gradients latéraux de signaux d'orientation en travers du chenal du Columbia; ces signaux se forment dans les panaches de diffusion des tributaires et peuvent persister vers l'aval sur des distances de dizaines ou de centaines de kilomètres. La détection des panaches formés par les tributaires dans les grands systèmes fluviaux, par l'intermédiaire de signaux de navigation olfactifs ou autres, peut ainsi faciliter la sélection efficace des parcours et optimiser la conservation d'énergie chez les migrants de longue distance.

[Traduit par la Rédaction]

## Introduction

Long-distance migrations have fascinated naturalists for centuries. Especially intriguing are the migrations of those species that return to natal breeding grounds after movements over thousands of kilometres (Dingle 1996), including sea turtles (e.g., *Chelonia mydas*, Åkesson et al. 2003), shorebirds (Battley et al. 2004), albatross (e.g., *Phoebastria* spp., Hyrenbach et al. 2002), and anadromous salmonids (*Oncorhynchus* and *Salmo* spp.; Groot and Margolis 1991; Quinn

et al. 1999). Ocean migrations by salmonids can cover thousands of kilometres over several years, followed by precise freshwater homing migrations of 1500 km or more to inland spawning grounds (Milligan et al. 1985; Waples et al. 2001). These migrants must balance the physiological demands of migration with precise spatial and temporal homing requirements.

In fresh water, return migration by anadromous adult salmonids appears to be driven largely by chemically based olfactory cues (Scholz et al. 1976), particularly in small

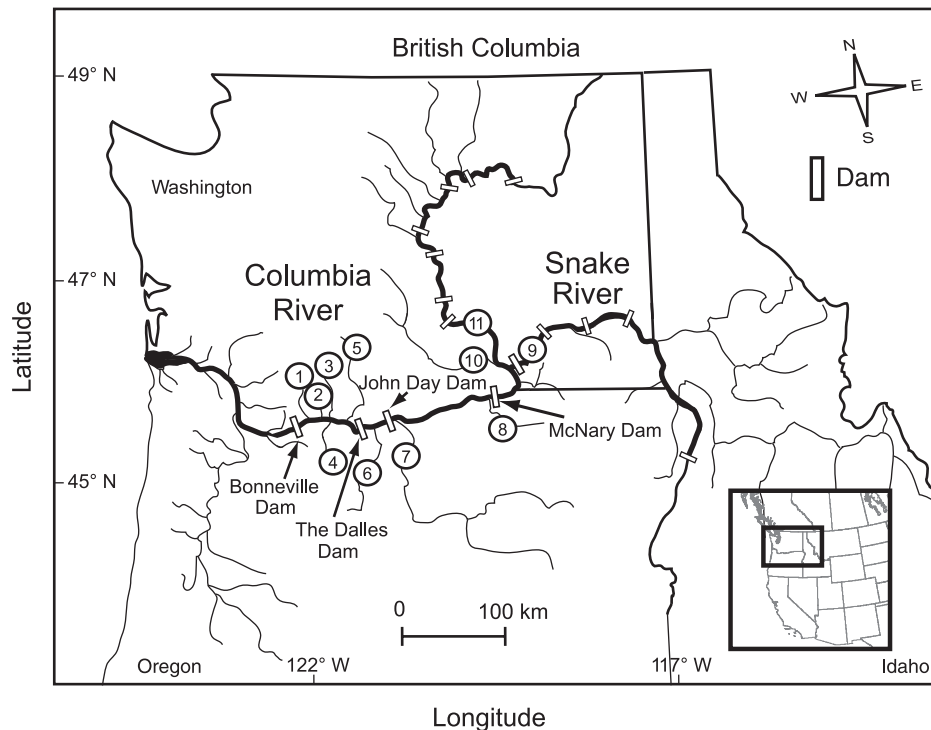
Received 24 August 2005. Accepted 14 March 2006. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 13 July 2006.  
J18860

M.L. Keefer,<sup>1</sup> C.C. Caudill, and T.C. Bjornn.<sup>2</sup> Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844-1141, USA.

C.A. Peery. Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844-1141, USA.

<sup>1</sup>Corresponding author (e-mail: [mkeefe@uidaho.edu](mailto:mkeefe@uidaho.edu)).

**Fig. 1.** Columbia River Basin (Pacific Northwest, USA — inset) accessible to migrating adult Chinook salmon (*Oncorhynchus tshawytscha*), including tributaries where radio-tagged fish were last recorded and four lower river mainstem dams where passage routes were monitored. Tributary rivers: (1) Wind, (2) Little White Salmon, (3) White Salmon, (4) Hood, (5) Klickitat, (6) Deschutes, (7) John Day, (8) Umatilla, (9) Snake, (10) Yakima, and (11) upper Columbia.



ivers and coastal streams. Returning fish use chemosensory memories from site-specific imprinting to natal stream odors as juveniles and memories from additional outmigration sites during the transformation from fresh to marine waters (Dittman and Quinn 1996; McCormick et al. 1998). The reverse sequence of these olfactory signposts (Harden Jones 1968; Quinn et al. 1989) presumably guides adult fish migrating to spawning grounds and facilitates discrimination among alternate routes as fish proceed up river corridors. The chemical and olfactory components of adult orientation and homing have been demonstrated experimentally in the laboratory (e.g., Shoji et al. 2003) and in the field at scales of tens to hundreds of metres (Johnsen and Hasler 1980; Hasler and Scholz 1983). Little is known, however, about how salmonids and other aquatic organisms orient and home in larger-scale natural systems (e.g., tens to hundreds of kilometres; Vickers 2000).

In this study, we examined route selection behaviors by 11 conspecific spring–summer Chinook salmon (*Oncorhynchus tshawytscha*) populations during adult return migration through the very large Columbia River migration corridor. Most study fish were stream-type Chinook salmon, though some summer migrants were ocean- or reservoir-type (Brannon et al. 2004). The river has the second highest mean annual discharge of all US rivers (approximately 244 billion  $\text{m}^3\cdot\text{year}^{-1}$  at the mouth) and historically produced some of the largest salmon and steelhead runs in North America (Chapman 1986). The Columbia main stem has been extensively developed for hydroelectric production, resulting in a series of large run-of-river impoundments. Lower river reservoirs (Fig. 1) average 1–2 km in width and 10–40 m in

depth, with current velocities that vary widely with season and volume (Scheibe and Richmond 2002; US Army Corps of Engineers 2002). Many anadromous migrants, including dozens of reproductively isolated spring–summer Chinook salmon stocks (Myers et al. 1998; Brannon et al. 2004), pass through long sections (e.g., hundreds of kilometres) of this altered migration corridor en route to natal spawning grounds in upstream tributaries. Most returning salmon must pass one to four lower Columbia River dams and reservoirs, and many pass up to five additional dams and reservoirs to reach spawning tributaries. Each of the four lower river dams has two principal passage routes for upstream-migrating fish — one fish ladder near each shoreline — and these routes are readily monitored. This configuration creates a unique opportunity to examine migration behaviors, test hypotheses about salmon route selection, and examine potential orientation mechanisms in a large river.

We used a large radiotelemetry data set developed over multiple years (described in Keefer et al. 2004a) to test two general hypotheses: (1) whether patterns in ladder use among stocks were nonrandom, and if so, (2) whether salmon route selections at dams were consistent with downstream detection of and orientation to natal tributaries. We expected returning adult Chinook salmon would use olfactory or other cues to orient to plumes of natal tributaries, aggregating along the side of the Columbia River downstream from natal river confluences. Such aggregation on the “correct” shoreline would be reflected in stock-specific differences in fish ladder use at dams. If true, salmon returning to south shore tributaries would have a higher probability of using south shore fish ladders, and vice versa. We also expected the

**Table 1.** Mean seasonal discharge ( $\text{m}^3\cdot\text{s}^{-1}$ , April–July) of study tributaries and number of radio-tagged adult Chinook salmon (*Oncorhynchus tshawytscha*) last recorded at each tributary site, 1996–2002.

Tributary (map number)	Mean (range) discharge ( $\text{m}^3\cdot\text{s}^{-1}$ )	No. of Chinook salmon						
		1996	1997	1998	2000	2001	2002	Total
Wind (1)	29 (8–56)	93	53	59	100	25	59	389
Little White Salmon (2)	15 (9–25)	99	24	15	39	10	39	226
White Salmon (3)	37 (22–44)	17	9	2	2	2	2	34
Hood (4)	28 (13–40)	4	10	3			2	19
Klickitat (5)	56 (27–72)	20	28	26	14	3	3	94
Deschutes (6)	168 (126–217)	68	46	74	110	10	30	338
John Day (7)	99 (8–166)	37	7	28	26	7	22	127
Umatilla (8)	15 (14–42)	15	12	9	11	3	16	66
Snake (9)	2488 (811–3832)	122	317	247	210	359	285	1540
Yakima (10)	127 (39–193)	33	19	41	46	88	72	299
Upper Columbia (11)	5371 (2447–7777)	130	224	262	256	156	201	1229
Total		638	749	766	814	663	731	4361

**Note:** Discharge estimates were assembled from daily mean US Geological Survey data; mean = 71 years·site<sup>-1</sup>.

degree of preference would depend on the distance to the tributary confluence and on discharge volume from tributaries and in the main stem, because tributary plumes should remain hydrologically distinct for greater distances downstream for large tributaries and under higher flow conditions (Fischer et al. 1979; Rutherford 1994). Dam operations also potentially influence route selections, both through turbulent mixing and disruption of plumes and through the distribution of attractive flows downstream. Discharge volumes from Columbia River dam fishways are generally constant to maintain suitable hydraulic conditions in the ladders, but both the volume and distribution of river discharge passed through turbines and over spillways varies widely.

Orienting to the natal shoreline prior to reaching natal tributary confluences could have fitness consequences, because such behavior would reduce energetic losses and mortality associated with searching for natal sites, including fallback over dams that occurs when salmon overshoot natal sites (Boggs et al. 2004). Alternatively, a lack of preference for natal shore ladders would suggest individuals use homing mechanisms other than lateral gradients in olfactory cues. For instance, if homing cues are rapidly mixed across the river channel, we expected orientation to tributaries to occur over relatively short spatial scales near the tributary–mainstem confluences, resulting in no ladder bias at downstream dams.

## Materials and methods

### Salmon collection and radio tagging

Adult spring–summer Chinook salmon returning to the Columbia River basin were collected at Bonneville Dam (river kilometre 235) in an adult fish trap adjacent to the north shore fish ladder (Fig. 1). During 6 study years, we collected 5526 spring–summer Chinook salmon, of which 4361 (79%) returned to tributaries upstream from Bonneville Dam or to the upper Columbia Basin (Table 1). Typical fish were ages four or five and had body lengths between 75 and 85 cm. Samples averaged 0.78% of the spring–summer Chinook salmon counted passing Bonneville Dam each year between 1 April and 31 July (US Army Corps of Engineers

2002). Because many Columbia River Basin Chinook salmon populations are listed as threatened or endangered (National Marine Fisheries Service 2000), special collection permits were needed and federal, state, and university animal handling and care protocols were strictly followed.

Salmon were sampled approximately in proportion to daily run counts (as in Keefer et al. 2004b), though we tended to under-sample during count peaks and over-sample during count nadirs. During 1996–1998, salmon were non-selectively collected as they passed through the trap facility during each sampling day. Random sampling was not possible because only fish passing via the north shore ladder could be collected, and no fish were sampled at night. In 2000–2002, we modified our sampling strategy to select for fish with passive integrated transponder (PIT) tags that identified natal sites (Prentice et al. 1990). Use of previously PIT-tagged fish (37% of the 2000–2002 samples) resulted in larger sample sizes for some stocks (see Keefer et al. 2005), but these subsamples represented less than 0.5% of the annual runs and should not affect interpretation of the basic behavioral results presented here, which are based on individual fish route selections.

Protocols for fish trapping, anesthetization (methane sulphate or clove oil), handling, and intragastric insertion of uniquely coded radio transmitters were the same in all years and are described in Keefer et al. (2004c). Salmon recovery from anesthesia occurred in a dark, 2275-L, oxygenated transport tank full of river water. Most fish regained equilibrium within a few minutes, but were held an average of 1.6 h to ensure recuperation. Following recovery, fish were randomly released about 10 km downstream from Bonneville Dam at sites on both sides of the Columbia River in similar percentages (49% from Oregon shore). Total fish mortality was less than 1% during tagging, recovery, and release (Keefer et al. 2004a).

### Stock identification and route monitoring

Chinook salmon were identified as belonging to one of 11 tributary-specific stocks (including the upper Columbia River Basin) based on final recorded fish locations (Table 1).

Identifications were derived primarily from telemetry records at aerial antennas deployed in each major Columbia River tributary and from aerial and underwater antennas at Snake River and upper Columbia River dams (Fig. 1). These data were supplemented with location data collected using mobile antennas attached to boats and trucks and from recoveries of transmitters from hatcheries, tributary spawning ground surveys, and fisheries. Stock identifications should have been accurate given the breadth of our monitoring effort, although some salmon likely strayed into non-natal rivers or were misclassified based on ambiguous telemetry data. During the years 2000–2002 when known-source, PIT-tagged fish were present in the samples, there was 97.8% agreement between stock assignment based on juvenile PIT-tagging location and final telemetry records among PIT-tagged fish. This agreement suggests that bias due to straying was minor. We note that study tributaries included multiple spawning populations, and finer-resolution stock classifications are possible (e.g., Nehlsen et al. 1991).

Fish behavior at the four lower Columbia River dams (Bonneville, The Dalles, John Day, McNary) was monitored with an extensive collection of aerial and underwater antennas in tailraces, fishways, and fish ladders. Radio-tagged salmon could approach dams and enter fishways via many routes, and most fish moved between multiple sites at each dam before selecting and passing a fish ladder (e.g., Keefer et al. 2003). Each dam had two ladders, one immediately adjacent to each shoreline (except the south ladder at Bonneville Dam, which was situated on an island close to the south shoreline). Exits from the tops of these ladders were monitored with highly efficient underwater antenna arrays (mean detection rates >98%). Passage route selections at individual dams were assigned based on the first ladder each fish passed. A small number of passage events (<3%) occurred through navigation locks of dams, and these events were included with the total of the adjacent shoreline. Subsequent passages, which occurred after some salmon fell back over a dam (see Boggs et al. 2004), were excluded, as were passage events that could not be attributed to a specific ladder. The first ladder passage was selected for analyses because all fish were presumably naïve regarding routes (except at Bonneville Dam) and because of the potential for injury during fallback events to affect orientation behavior.

### Statistical analyses

Adult Chinook salmon orient to shorelines during upstream migration (e.g., Hughes 2004). Consequently, we examined the possibility that release site downstream from Bonneville Dam would be associated with ladder use at Bonneville Dam ~10 km upstream. Chi-square tests comparing frequencies of ladder use versus release shore tested whether ladder use deviated significantly from a 50:50 expectation for each stock. For these tests, we combined frequencies across all years, though single-year comparisons yielded similar results (M.L. Keefer, C.C. Caudill, C.A. Peery, and T.C. Bjornn, unpublished data).

We assessed salmon route selections at all four lower Columbia River dams using replicated goodness-of-fit tests (*G* tests; Sokal and Rohlf 1995) that compared salmon passage frequencies between ladders and years for each stock at each dam. We treated year as the replicate and generated ex-

pected frequencies for each year using two null hypotheses. First, we assumed salmon routes would be random at each dam (i.e., ladder use would be 50:50 south shore:north shore). However, counts of salmon at dams indicate clear differences in ladder use among dams within season and among years (see Results; Fig. 2). These differences are likely due to differences in river conditions, dam configuration and operations, and stock composition. Therefore, we also generated expected frequencies using the daily ladder counts for all adult spring–summer Chinook salmon from both ladders at dams during the dates when 90% of the radio-tagged fish from each stock passed each dam in each year. The *G* tests provided tests of both deviations from overall expected proportions for each ladder across all years and simultaneously tested for significant interannual variation in proportions within stock (Sokal and Rohlf 1995). The *G* tests determined whether the radio-tagged sample of each stock differed in ladder use from the overall population that passed each dam during the same period. Such tests were conservative, because each stock was a subpopulation of the total ladder counts during each period, and potential influence of each stock on the expected frequencies should differ based on the relative run size of each stock (i.e., the type II error for relatively large stocks will be greater than that for smaller stocks because large stocks have a greater effect on counts at dams and the expected frequencies).

We also examined the potential for interannual variation in flow to influence ladder use. For each stock at each dam, we regressed the annual proportion of salmon passing via the natal shore ladder against the mean discharge encountered by radio-tagged fish in each year. Discharge and ladder count data were provided by the US Army Corps of Engineers.

## Results

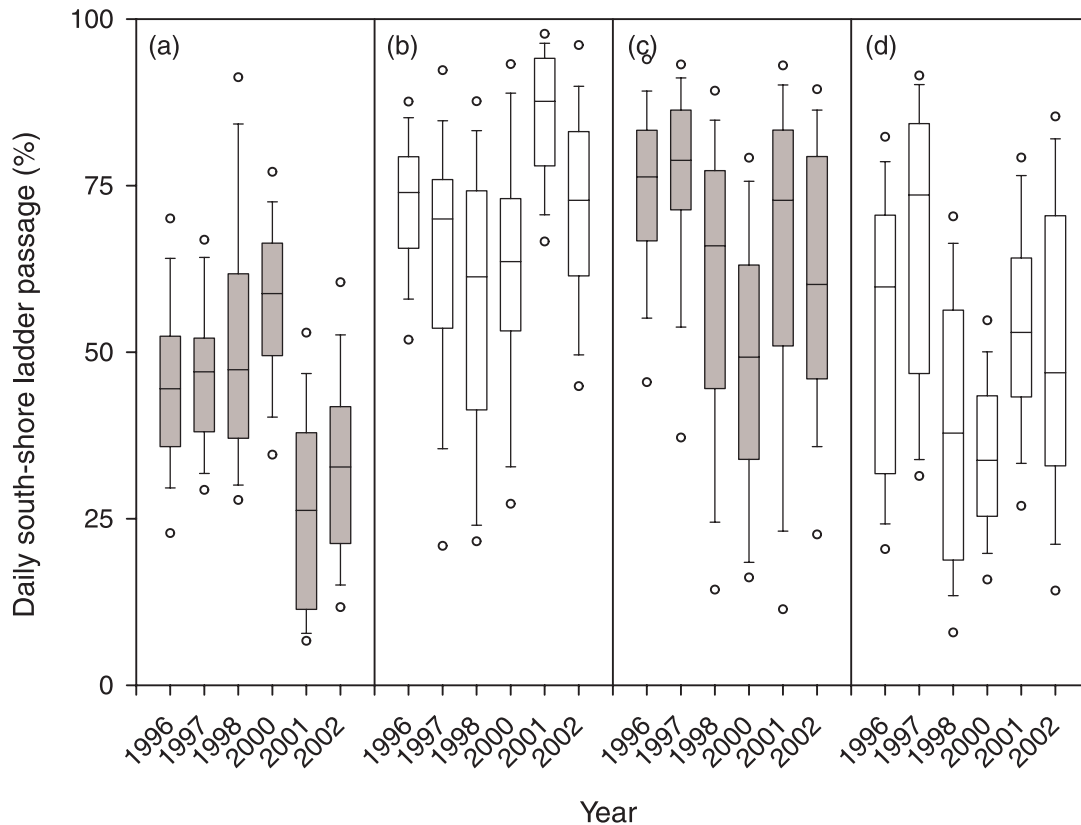
### Effects of release site

Comparisons between the release site (Washington versus Oregon shore) of radio-tagged fish and individual ladder use at Bonneville Dam revealed that many fish crossed the river channel at least one time. Overall, 49.2% ( $n = 2134$ ) individuals passed on the same side as the release site and 50.8% ( $n = 2207$ ) individuals passed on the shore opposite their release site. Within stock, release location was not associated with subsequent ladder passage at Bonneville Dam in 9 of 11 comparisons. The Klickitat River fish were more likely to pass on the same shore as they were released (63.8%;  $P = 0.0058$ ,  $n = 94$ ). Snake River fish were more likely to pass via the Oregon shore ladder (52.0% vs. 48.0%;  $P = 0.0089$ ,  $n = 1530$ ), a pattern resulting primarily from a higher than expected percentage of fish released from the Washington shore passing at the Oregon shore ladder (28.4%).

### Salmon route selection at dams

Daily percentages of all adult spring–summer Chinook salmon counted by the US Army Corps of Engineers passing the four lower Columbia River dams varied widely within years and between years and dams (Fig. 2). Overall, more salmon used ladders near the south shoreline at The Dalles and John Day dams in almost all years and favored ladders near the north shoreline at Bonneville Dam in 2001 and

**Fig. 2.** Daily percentages (box plot showing median, quartile, 5th, 10th, 90th, and 95th percentiles) of all adult spring–summer Chinook salmon (*Oncorhynchus tshawytscha*) counted passing dams that used ladders near the south shoreline at (a) Bonneville, (b) The Dalles, (c) John Day, and (d) McNary dams from April through July during the 6 study years. Data provided by US Army Corps of Engineers (T. Hurd, USACE, P.O. Box 2946, Portland, OR 97208, USA).



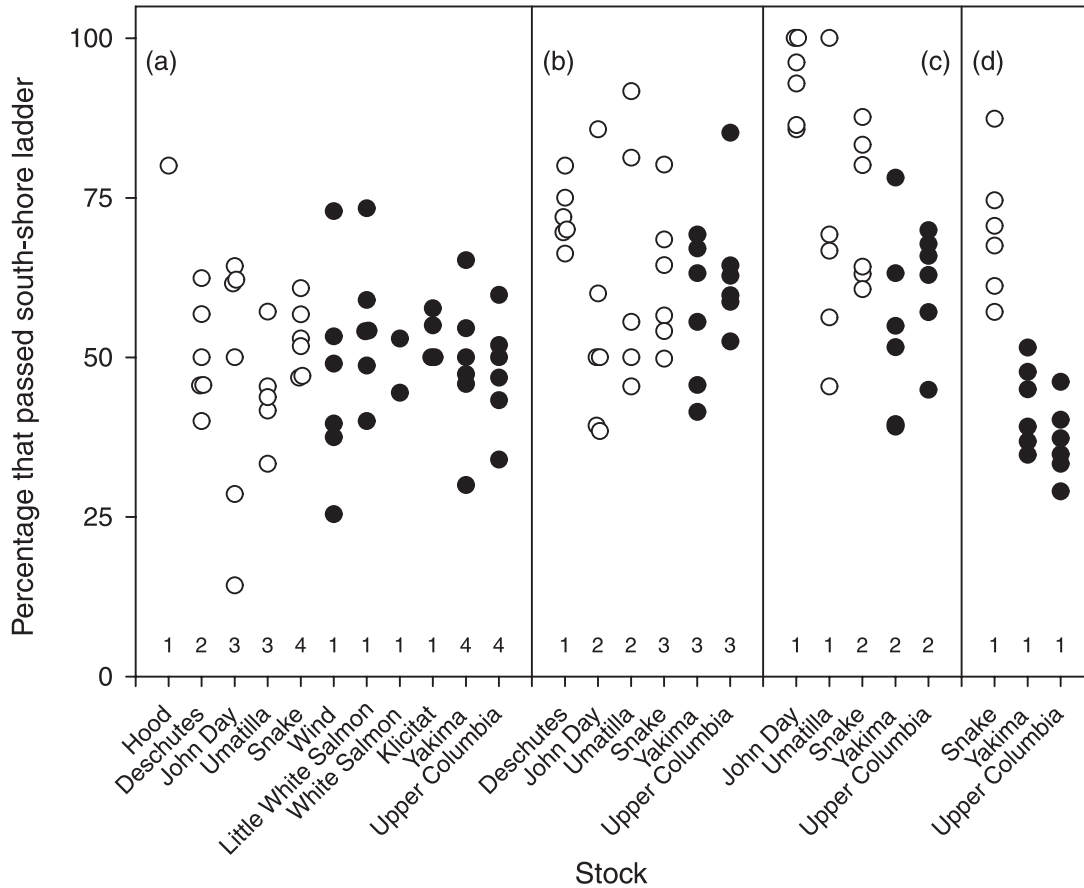
2002. Daily ladder use proportions were most variable at McNary Dam. Stock-specific ladder use by radio-tagged salmon also varied (Fig. 3), with significant ( $G$  tests:  $P < 0.05$ ) between-year differences in 13 of 25 dam  $\times$  stock combinations (Table 2). As expected, tests of the first null hypothesis (expected ladder passage proportions = 50:50) showed that stock-specific ladder use was not random (Table 2). This was especially true at the three upstream dams, where proportions were significantly different from random for 12 of 14 pairs. At Bonneville Dam, just upstream from the release sites, ladder use differed from 50:50 only for Hood River salmon (Table 2, Fig. 3).

Tests of the second null hypothesis (expected ladder passage proportions based on salmon counts at ladders) indicated that many radio-tagged stocks preferentially used dam passage routes adjacent to shorelines where their natal tributaries entered the main river. As with the 50:50 tests, significant departures from expected route selections among stocks were less frequent at Bonneville Dam and progressively more frequent at upstream dams (Table 2). After accounting for between-year differences, salmon stocks selected ladders adjacent to natal shorelines at significantly ( $G$  test  $P < 0.05$ ) higher than expected proportions in 13 of 25 dam  $\times$  stock combinations (Table 2). Four dam  $\times$  stock combinations (Little White Salmon, Yakima, and upper Columbia stocks at Bonneville Dam and upper Columbia stock at The Dalles Dam) passed via a natal shoreline ladder at lower than expected rates ( $P < 0.05$ ).

#### Proximity to confluences and river discharge

Biases in favor of dam passage routes adjacent to natal shorelines increased with the size of the natal tributary and the proximity of dams to each tributary's confluence with the Columbia River. On average, annual ladder biases (observed – expected from null hypothesis 2) were higher for stocks returning to the high-discharge upper Columbia and Snake rivers than for stocks returning to the other nine tributary sites (Fig. 4). Biases averaged +14.4% for the upper Columbia and Snake river stocks at McNary Dam, which is the first dam downstream (52 km) from the upper Columbia – Snake river confluence. Average biases for these two stocks dropped to +6.8% at John Day Dam (two dams and 175 km downstream from the confluence) and were not distinguishable from zero at The Dalles Dam (214 km downstream) and Bonneville Dam (287 km downstream). On average, stocks from the other, smaller tributaries had natal shoreline biases of +6.5% at the dams immediately downstream from their respective confluences and +6.4% two dams downstream. Biases were negative three and four dams downstream (Fig. 4). Exceptions among the stocks from smaller tributaries included the John Day River stock at John Day Dam (confluence 4 km upstream from the dam, bias = +29.2%), the Yakima River at McNary Dam (70 km, +16.0%), and the Deschutes River at The Dalles Dam (20 km, +10.0%) (Fig. 3). These patterns suggest that salmon were more likely to aggregate near the Columbia River shoreline of the natal tributary confluence during migration

**Fig. 3.** Annual percentages of radio-tagged Chinook salmon (*Oncorhynchus tshawytscha*) stocks recorded passing south shore fish ladders at (a) Bonneville, (b) The Dalles, (c) John Day, and (d) McNary dams after release downstream from Bonneville Dam. Open circles (○) are for stocks from south shore tributaries; solid circles (●) are for stocks from north shore tributaries. Numbers above stocks show the number of dams downstream from natal tributary confluences (i.e., Bonneville Dam is one dam downstream from the Hood River in panel a). Stock years with  $n < 5$  were excluded.



as they neared the confluence and that aggregation began at greater distances downstream when natal rivers were large.

Interannual differences in ladder use for some, but not all, stocks were associated with mean annual discharge during the period each stock passed, which ranged from about 3000 to 14 000 m<sup>3</sup>·s<sup>-1</sup>. At McNary Dam, for example, annual use of the south shore ladder by Snake River salmon was positively correlated with mean encountered discharge ( $r = 0.930$ ,  $P = 0.007$ ,  $df = 4$ ), as was use of the north shore ladder by upper Columbia River salmon ( $r = 0.775$ ,  $P = 0.070$ ,  $df = 4$ ) (Fig. 5). Similar correlations were observed at John Day Dam for John Day River ( $r = 0.880$ ,  $P = 0.021$ ,  $df = 4$ ), Umatilla River ( $r = 0.907$ ,  $P = 0.013$ ,  $df = 4$ ), and Snake River ( $r = 0.792$ ,  $P = 0.006$ ,  $df = 4$ ) stocks. No correlations were significant ( $P > 0.10$ ) for any stocks at Bonneville or The Dalles dams, for Yakima River salmon at John Day and McNary dams, or for upper Columbia River salmon at John Day Dam.

**Discussion**

In many cases, the radio-tagged Chinook salmon in this study demonstrated nonrandom ladder use that differed among stocks in a fashion consistent with orientation to upstream natal tributaries. Specifically, many stocks returning to tributaries along the south shore of the Columbia River

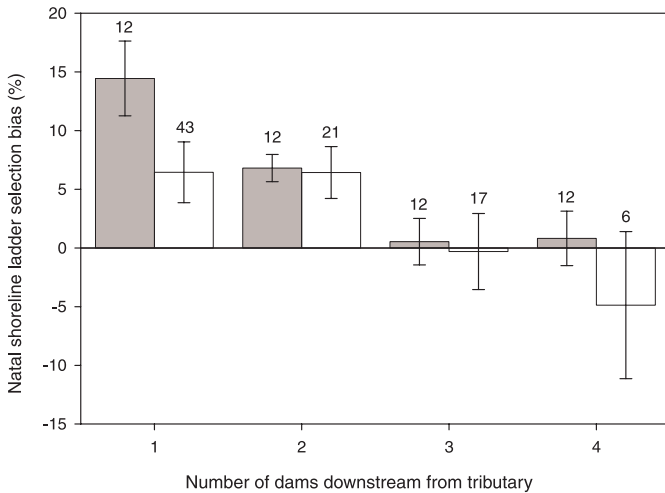
tended to show a south shore ladder bias and vice versa. The degree of route segregation among populations increased as individual stocks neared natal tributaries, was highest when tributaries were either large (i.e., Snake River) or in close proximity to a downstream dam (i.e., John Day River), and was in some cases related to discharge. Early initiation of migration routes that reflected aggregation on natal shorelines was most prevalent for Snake River salmon, some of which exhibited orientation to the “correct” shoreline hundreds of kilometres downstream from the Snake River confluence. The observed preferences may have underestimated the onset of route selection and magnitude of ladder biases because all fish were randomly (relative to their origin) released on either the north or south shore of the Columbia River after tagging, effectively resetting any aggregation to natal shorelines that had occurred downstream of Bonneville Dam prior to tagging. The largely nonsignificant results at Bonneville Dam may reflect this release site protocol, the relative complexity of the tailrace and fishways at Bonneville Dam, or for stocks returning to tributaries of Bonneville reservoir, the relatively small size of these tributaries. Ladder use in other stocks did not display these patterns, perhaps because of small natal tributary size, long distance to the actual spawning grounds, or inadequate sample size. While inferring process from pattern can be prob-

**Table 2.** Results of *G* tests comparing ladder use frequencies at dams by radio-tagged Chinook salmon (*Oncorhynchus tshawytscha*) stocks.

Dam	Stock	<i>n</i>	Year effects (df = 5)		Route effects (df = 1)		Counts at ladders <sup>a</sup>			Obs %
			<i>G</i> (h)	<i>P</i>	<i>G</i> (p)	<i>P</i>	<i>G</i> (p)	<i>P</i>	Exp %	
Bonneville	Wind	387	31.4	<0.0001	0.6	0.4463	0.1	0.7642	47.3	48.1
	Little White Salmon	225	4.0	0.5566	2.0	0.1615	10.1	0.0015	44.1	54.7
	White Salmon	34	5.7	0.3386	0.0	0.9999	0.7	0.3994	42.8	50.0
	Hood <sup>b</sup>	19	2.5	0.4735	4.4	0.0351	7.4	0.0064	42.8	73.7
	Klickitat	94	1.3	0.9318	0.2	0.6801	1.2	0.2774	46.5	52.1
	Deschutes	337	8.9	0.1135	1.3	0.2524	1.7	0.1910	49.6	53.1
	John Day	127	9.4	0.0927	1.8	0.1821	3.9	0.0472	47.1	55.9
	Umatilla	65	1.6	0.9049	0.8	0.3833	0.1	0.8065	46.2	44.6
	Snake	1530	16.2	0.0064	2.4	0.1253	44.1	<0.0001	43.5	52.0
	Yakima	298	11.6	0.0404	0.1	0.7290	8.0	0.0047	40.9	49.0
The Dalles	Upper Columbia	1225	30.2	<0.0001	0.5	0.4751	15.7	<0.0001	43.4	49.0
	Deschutes	327	1.8	0.8748	59.2	<0.0001	30.7	<0.0001	56.1	70.9
	John Day	119	7.9	0.1641	0.0	0.9203	0.6	0.4274	53.2	49.6
	Umatilla	63	9.9	0.0781	7.1	0.0075	5.8	0.0160	51.7	66.7
	Snake	1507	83.2	<0.0001	111.3	<0.0001	6.3	0.0121	60.4	63.5
	Yakima	292	12.1	0.0336	6.1	0.0138	1.9	0.1681	61.1	57.2
	Upper Columbia	1212	52.3	<0.0001	73.0	<0.0001	4.4	0.0364	59.3	62.2
	John Day	127	8.0	0.1562	121.9	<0.0001	61.7	<0.0001	65.7	94.5
	Umatilla	64	13.9	0.0161	6.4	0.0117	0.0	0.8875	64.9	65.6
	Snake	1506	82.7	<0.0001	286.3	<0.0001	39.5	<0.0001	63.8	71.4
McNary	Yakima	293	18.8	0.0021	0.0	0.8625	9.3	<0.0001	59.4	50.5
	Upper Columbia	1183	38.7	<0.0001	51.1	<0.0001	17.3	<0.0001	66.1	60.4
	Snake	1519	89.8	<0.0001	231.2	<0.0001	98.4	<0.0001	56.9	69.3
	Yakima	298	4.5	0.4866	6.5	0.0107	20.5	<0.0001	55.7	42.6
	Upper Columbia	1225	15.1	0.0102	91.7	<0.0001	108.4	<0.0001	51.2	36.4

**Note:** Tests of year effects examined whether ladder use varied between years within stock. Route effect tests compared observed ladder use frequencies with frequencies based on random 50:50 passage (null hypothesis 1) and frequencies based on total counts at ladders (null hypothesis 2), including expected (Exp %) and observed (Obs %) percentages of salmon using south shore ladders.  
<sup>a</sup>Expected percentages are based on total adult Chinook salmon counted at ladders during the date range when 90% of each radio-tagged stock passed each year.  
<sup>b</sup>Year effects df = 3.

**Fig. 4.** Mean annual Chinook salmon (*Oncorhynchus tshawytscha*) ladder selection biases (observed percentage – expected percentage,  $\pm 1$  standard error) for stocks returning to the high discharge Snake and Columbia rivers (shaded bars) and all other stocks (open bars). Positive biases indicate greater than expected passage through the ladder on the same shore as the natal tributary. Expected values were generated from the total number of salmon passing each ladder during the same period. Number of stock years are noted above each bar.

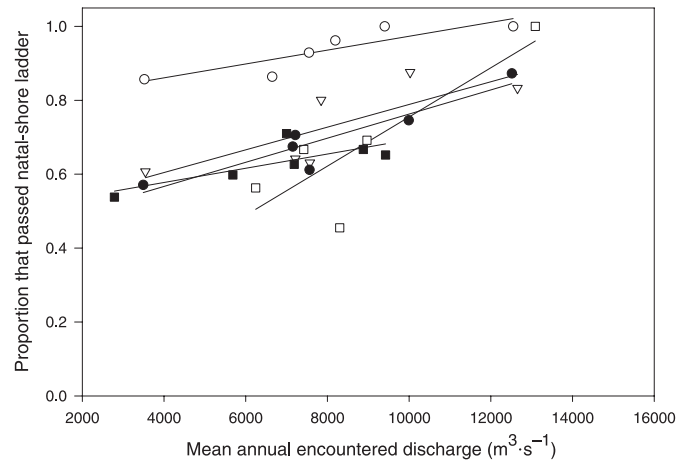


lematic, below we use these data to speculate on potential processes affecting ladder choice by returning adults.

The physical and chemical environment of the lower Columbia River provides several potentially influential orientation cues to upstream migrants. Perhaps the most conspicuous cue is the presence of tributary plumes, which create lateral gradients in physical and chemical properties downstream from confluences. In the Columbia River, plumes from the large Snake River are often visible 175 km downstream at John Day Dam, despite the mixing that occurs at McNary Dam (Chapman et al. 1997; Scheibe and Richmond 2002). Plumes from smaller Columbia River tributaries can also be conspicuous, particularly during the seasonal snowmelt events that coincide with spring–summer Chinook salmon migrations. Measurement of plume characteristics in the Columbia River was beyond the scope of this study, but their general properties are well established (Fischer et al. 1979; Rutherford 1994). In large, low-gradient systems, complete mixing below confluences may not occur until up to several hundred river widths downstream (Rutherford 1994), and sediment, dissolved gas, and temperature plumes can remain hydrologically distinct over hundreds of kilometres (Fischer et al. 1979; Scheibe and Richmond 2002). We frequently observed salmon switching river banks after being released below Bonneville Dam (see also Johnson 2003), suggesting the potential for individuals to sample for any lateral gradients in orientation cues created by tributary plumes and to aggregate on the shoreline with the strongest cues.

A variety of orientation cues within plumes may have influenced ladder choice by adult salmon. Among these, olfactory cues probably had the strongest effect. The use of olfaction during homing by salmon has been experimentally established in fresh water using both occlusion (reviewed in Hasler and Scholz 1983) and chemical imprinting techniques

**Fig. 5.** Annual proportions of Chinook salmon (*Oncorhynchus tshawytscha*) stocks that selected natal shore ladder routes at dams in relation to mean river discharge each stock encountered at each dam during each run year. Plot includes only those stocks with significant ( $P < 0.10$ ) correlations: John Day River stock at John Day Dam (○); Umatilla River stock at John Day Dam (□); Snake River stock at John Day Dam (▽); Snake River stock at McNary Dam (●); and upper Columbia River stock at McNary Dam (■).



(Nevitt et al. 1994; Dittman et al. 1996). Adult salmon recognize home stream odors as well as odors encountered during juvenile outmigration during a sequential imprinting process (Harden Jones 1968; Quinn et al. 1989). Interruptions to imprinting, such as displacement or transportation of juveniles, have resulted in reduced homing for both Pacific (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*) (Jonsson et al. 1994; Chapman et al. 1997; McCormick et al. 1998). The downstream distances that adult salmon can detect odors encountered during imprinting likely depend upon dilution levels, the duration and quality of imprinting, discharge volume, stratification, or prevailing winds or currents (reviewed in Leggett 1977). Our radiotelemetry results suggest that lateral gradients in odors or other cues significantly influenced Columbia River Chinook salmon behavior at distances that range from less than 10 km downstream of confluences for stocks returning to smaller, low-discharge tributaries to several hundred kilometres for those returning to high-discharge sites, such as the Snake River.

Salmon and many other aquatic organisms also orient to other physical and chemical gradients (Vogel 1996; Vickers 2000), such as temperature (Berman and Quinn 1991; Friedland et al. 2001), turbidity, salinity, and flow (Døving et al. 1985; Carton and Montgomery 2003). During the spring–summer Chinook salmon migration, the Columbia River is warmer than most tributaries draining the Cascade Range in western Oregon and Washington and is typically cooler than the Snake River (Quinn et al. 1997), resulting in lateral and vertical thermal gradients. The telemetry data could not be used to assess the relative importance of chemical versus nonchemical physical cues, though it is likely that they differ between spatial and temporal scales and that both attraction and aversion (i.e., avoidance of warm water) may influence fish behaviors.



While the literature suggests olfaction is the dominant freshwater homing mechanism in salmon, particularly as fish near natal sites, additional reference systems may be important. Sun and celestial compass, geomagnetic (Montgomery and Walker 2001; Boles and Lohmann 2003), and (or) geographical landmark (route reversal) tactics (Odling-Smee and Braithwaite 2003) have been reported for a variety of fishes and other aquatic animals (reviewed in Leggett 1977). However, if adult salmon were primarily using fixed mechanisms to orient, we would expect consistent north or south shore route use regardless of distance from natal tributary or environmental conditions — a pattern not clearly supported by these data. In addition, many salmon overshoot natal tributaries by tens to hundreds of kilometres before returning downstream (Boggs et al. 2004), suggesting many adults pass natal tributaries on the wrong shore — an unlikely behavior if precise sun or compass orientation mechanisms were dominant.

The observed ladder bias by Snake River salmon as far downstream as John Day Dam and possibly as far as Bonneville Dam, compared with little evidence for ladder bias in small-tributary stocks except over short distances, was also consistent with orientation to lateral gradients because large tributaries should create longer plumes. However, irrespective of stock and natal destination, there was a strong tendency for selection of specific ladders, and these underlying preferences were related to variability in Columbia River discharge and resulting flows from dam powerhouses and spillways. As discharge increased, both within and among years, salmon were more likely to use the south shore ladder at John Day and McNary dams; salmon preferred the south shore ladder at The Dalles Dam, but increasingly used the north shore ladder as discharge increased and more water was released over the spillway near the north shore. Salmon also favored the north shore ladder at Bonneville Dam in later years, when more river water was directed through the north powerhouse (D. Clugston, US Army Corps of Engineers, Box 2946, Portland, OR 97208, USA, personal communication). This suggests that rheotaxis was a key orientation component during migration, with fish favoring flow pathways at dams with greater attraction volume and (or) velocity. This behavior could either reduce or reinforce the use of natal shoreline routes at dams, depending on the destination of individual fish and the relative attractiveness of flow near the individual's natal shoreline. For example, the preference for south shore ladders by Snake River salmon at John Day and McNary dams may have been related to both the presence of olfactory homing cues within the Snake River plume and the distribution of attractive flows at these dams. Managers seeking to improve fish passage efficiency should consider strategies that promote the retention of plume structures and limit operations that result in cross-channel mixing.

Overall these results suggest that strong swimmers like salmon almost certainly integrate rheotactic and olfactory strategies during homing migration. Odor-conditioned rheotaxis, or the reliance on flow as an orienting stimulus in combination with odor detection (Weissburg 2000), is generally consistent with our results and more specifically with the migration control model developed by Johnsen (1982) and modified by Quinn (2005). The control model hypothe-

sizes that salmonids use rheotaxis and odor recognition to navigate through river networks, using positive (straight upstream) rheotaxis in the presence of familiar or home stream odors, lateral searching or upstream zigzagging along tributary plume boundaries when cues are mixed, or downstream retreat when odors are absent (Johnsen 1982; Quinn 2005). These behaviors may balance the costs and benefits of efficient homing with the energetic constraints imposed by moving through a complex flow environment. Such trade-offs to maximize energetically efficient movement appear to be used by many other genera in diverse aquatic habitats (Zimmer-Faust et al. 1995; Baker et al. 2002). In addition, conditioned rheotaxis may explain the widespread tendency of salmon to follow nearshore routes in large river systems (e.g., Daum and Osborne 1998; Hinch et al. 2002), including the Columbia River (Johnson 2003; Reischel and Bjornn 2003), though hydrodynamic factors also appear to play a strong role (Hughes 2004).

A potential cost of conditioned rheotaxis is that fish that infrequently sample cues along both shorelines may be more likely to miss natal confluences, and this effect may be amplified in reservoir environments. Such overshooting can result in fallback at upstream dams (Boggs et al. 2004) as fish return downstream in search of natal sites. Downstream movements have important implications in regulated rivers, as fallback at dams reduces both effective migration speeds (Keefer et al. 2004a) and survival (Keefer et al. 2005).

Predictable salmon orientation to tributary plumes or to specific shorelines or fishways also has important implications for harvest management, particularly in large rivers with multiple stocks. For example, mixed-stock fisheries near the south shore of the Columbia River downstream from John Day Dam may disproportionately harvest John Day River salmon or even Snake River salmon. Given the evidence for long-distance orientation, shoreline-specific fishing regulations, particularly near confluences, could reduce impacts on stocks of conservation concern in mixed-stock fisheries.

In summary, the observed behaviors suggest that salmon homing in large rivers use a hierarchy of orientation mechanisms. The relative importance of orientation to lateral gradients created by tributary plumes appears to be related to tributary size and proximity, river discharge, and dam operations that affect the distribution of flow. Salmon route selection patterns reported here were consistent with predictions of the classic salmon-homing studies (e.g., Johnsen and Hasler 1980; Hasler and Scholz 1983), where returning adults used olfaction to orient to experimentally manipulated odor plumes in small streams. Whereas the experimental studies described homing strategies on the scale of hundreds of metres, the current results indicate similar phenomena may occur over tens to hundreds of kilometres, a much broader scale than has been described for most other aquatic taxa. We note that this study occurred in an environment transformed by hydroelectric development and that behaviors may be different in unregulated rivers. Tributary plumes may persist for longer distances in reservoirs than in free-flowing rivers, because deeper water columns and slower water velocities in reservoirs can lower vertical and horizontal mixing rates. Such changes may facilitate fish navigation. In contrast, dams produce turbulent mixing and alter flow path-

ways, providing potentially confusing migration cues; therefore, the net effect of dams relative to historical conditions remains unknown. Although the study system is highly altered, these salmon route-selection results offer compelling examples of fish orientation in a large and complex riverine environment and suggest the potential for fish orientation to large-scale plumes in lacustrine, estuarine, coastal shelf, and pelagic waters.

## Acknowledgements

Many people provided time and assistance during the course of this study. We thank R. Ringe, K. Tolotti, M. Jepson, S. Lee, T. Reischel, C. Boggs, G. Naughton, W. Daigle, P. Keniry, M. Heinrich, M. Morasch, T. Dick, D. Joosten, C. Nauman, C. Williams, and A. Snider, who helped with field operations and collection and processing of telemetry data at the University of Idaho. T. Quinn, B. Burke, D. Burkepile, J. Parker, and two anonymous reviewers provided valuable critical reviews. L. Stuehrenberg, A. Matter, S. McCarthy, and T. Bohn (NOAA–Fisheries) helped with data management, and personnel at the Grant, Chelan, and Douglas County Public Utility Districts cooperated with telemetry data collection. The US Army Corps of Engineers provided funding for this study; we thank D. Clugston, R. Dach, T. Hurd, M. Langeslay, T. Mackey, M. Shutters, and K. Zelch for their assistance.

## References

- Åkesson, S., Broderick, A.C., Glen, F., Godley, B.J., Luschi, P., Papi, F., and Rays, G.C. 2003. Navigation by green turtles: which strategy do displaced adults use to find Ascension Island? *Oikos*, **103**: 363–372.
- Baker, C.F., Montgomery, J.C., and Dennis, T.E. 2002. The sensory basis of olfactory search behavior in banded kokopu (*Galaxias fasciatus*). *J. Comp. Physiol. A*, **188**: 553–560. doi:10.1007/s00359-002-0329-3.
- Battley, P.F., Piersma, T., Rogers, D.I., Dekinga, A., Spaans, B., and Van Gils, J.A. 2004. Do body condition and plumage during fueling predict northwards departure dates of Great Knots *Calidris tenuirostris* from north-west Australia? *Ibis*, **146**: 46–60.
- Berman, C.H., and Quinn, T.P. 1991. Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *J. Fish. Biol.* **39**: 301–312.
- Boggs, C.T., Keefer, M.L., Peery, C.A., Bjornn, T.C., and Stuehrenberg, L.C. 2004. Fallback, reascension and adjusted fishway escapement estimates for adult Chinook salmon and steelhead at Columbia and Snake River dams. *Trans. Am. Fish. Soc.* **133**: 932–949.
- Boles, L.C., and Lohmann, K.J. 2003. True navigation and magnetic maps in spiny lobsters. *Nature (London)*, **421**: 60–63. doi:10.1038/nature01226.
- Brannon, E.L., Powell, M.S., Quinn, T.P., and Talbot, A. 2004. Population structure of Columbia River basin Chinook salmon and steelhead trout. *Rev. Fish. Sci.* **12**: 99–232. doi:10.1080/10641260490280313.
- Carton, A.G., and Montgomery, J.C. 2003. Evidence of a rheotactic component in the odour search of freshwater eels. *J. Fish. Biol.* **62**: 501–516. doi:10.1046/j.0022-1112.2003.00015.x.
- Chapman, D. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. *Trans. Am. Fish. Soc.* **115**: 662–670.
- Chapman, D., Carlson, C., Weitkamp, D., Matthews, G., Stevenson, J., and Miller, M. 1997. Homing in sockeye and chinook salmon transported around part of the smolt migration route in the Columbia River. *N. Am. J. Fish. Manag.* **17**: 101–113.
- Daum, D.W., and Osborne, B.M. 1998. Use of fixed-location, split-beam sonar to describe temporal and spatial patterns of adult fall chum salmon migration in the Chandalar River, Alaska. *N. Am. J. Fish. Manag.* **18**: 477–486.
- Dingle, H. 1996. *Migration — biology of life on the move*. Oxford University Press, Oxford, UK.
- Dittman, A.H., and Quinn, T.P. 1996. Homing in Pacific salmon: mechanisms and ecological basis. *J. Exp. Biol.* **199**: 83–91.
- Dittman, A.H., Quinn, T.P., and Nevitt, G.A. 1996. Timing of imprinting to natural and artificial odors by coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **53**: 434–442.
- Døving, K.B., Westerberg, H., and Johnsen, P.B. 1985. Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. *Can. J. Fish. Aquat. Sci.* **42**: 1658–1667.
- Fischer, H.B., List, E.J., Koh, R.C.Y., Imberger, J., and Brooks, N.H. 1979. *Mixing in inland and coastal waters*. Academic Press, New York.
- Friedland, K.D., Walker, R.V., Davis, N.D., Myers, K.W., Boehlert, G.W., Urawa, S., and Ueno, Y. 2001. Open-ocean orientation and return migration routes of chum salmon based on temperature data from data storage tags. *Mar. Ecol. Prog. Ser.* **216**: 235–252.
- Groot, C., and Margolis, L. 1991. *Pacific salmon life histories*. University of British Columbia Press, Vancouver, B.C.
- Harden Jones, F.R. 1968. *Fish migration*. St. Martin's Press, New York.
- Hasler, A.D., and Scholz, A.T. 1983. *Olfactory imprinting and homing in salmon*. Springer-Verlag, Berlin, Germany.
- Hinch, S.G., Standen, E.M., Healey, M.C., and Farrell, A.P. 2002. Swimming patterns and behaviour of upriver-migrating adult pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG telemetry in the Fraser River, British Columbia, Canada. *Hydrobiologia*, **483**: 147–160.
- Hughes, N.F. 2004. The wave-drag hypothesis: an explanation for size-based lateral segregation during the upstream migration of salmonids. *Can. J. Fish. Aquat. Sci.* **61**(1): 103–109.
- Hyrenbach, K.D., Fernandez, P., and Anderson, D.J. 2002. Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Mar. Ecol. Prog. Ser.* **233**: 283–301.
- Johnsen, P.B. 1982. A behavioral control model for homesteam selection in migratory salmonids. *In* Proceeding of the Salmon and Trout Migratory Behavior Symposium, 3–5 June 1981, Seattle, Wash. Edited by E.L. Brannon and E.O. Salo. University of Washington School of Fisheries, Seattle, Wash. pp. 266–273.
- Johnsen, P.B., and Hasler, A.D. 1980. The use of chemical cues in the upstream migration of coho salmon, *Oncorhynchus kisutch* Walbaum. *J. Fish. Biol.* **17**: 67–73.
- Johnson, E.L. 2003. Migration depths of adult spring and summer chinook salmon in the lower Snake River and Columbia River in relation to dissolved gas supersaturation. M.S. thesis, University of Idaho, Moscow, Idaho.
- Jonsson, N., Hansen, L.P., and Jonsson, B. 1994. Juvenile experience influences timing of adult river ascent in Atlantic salmon. *Anim. Behav.* **48**: 740–742.
- Keefer, M.L., Bjornn, T.C., Peery, C.A., Tolotti, K.R., Ringe, R.R., Keniry, P.J., and Stuehrenberg, L.C. 2003. Adult spring and summer Chinook salmon passage through fishways and transition pools at Bonneville, McNary, Ice Harbor, and Lower Granite dams in 1996. Idaho Cooperative Fish and Wildlife Research

- Unit, US Army Corps of Engineers, Portland, Oreg. Tech. Rep. 2003-5.
- Keefer, M.L., Peery, C.A., Bjornn, T.C., Jepson, M.A., and Stuehrenberg, L.C. 2004a. Hydrosystem, dam, and reservoir passage rates of adult chinook salmon and steelhead in the Columbia and Snake rivers. *Trans. Am. Fish. Soc.* **133**: 1413–1439.
- Keefer, M.L., Peery, C.A., Jepson, M.A., Tolotti, K.R., and Stuehrenberg, L.C. 2004b. Stock-specific migration timing of adult spring–summer chinook salmon in the Columbia River basin. *N. Am. J. Fish. Manag.* **24**: 1145–1162.
- Keefer, M.L., Peery, C.A., Ringe, R.R., and Bjornn, T.C. 2004c. Regurgitation rates of intragastric radio transmitters by adult Chinook salmon and steelhead during upstream migration in the Columbia and Snake rivers. *N. Am. J. Fish. Manag.* **24**: 47–54.
- Keefer, M.L., Peery, C.A., Daigle, W.R., Jepson, M.A., Lee, S.R., Boggs, C.T., Tolotti, K.R., and Burke, B.J. 2005. Escapement, harvest, and unknown loss of radiotagged adult salmonids in the Columbia River – Snake River hydrosystem. *Can. J. Fish. Aquat. Sci.* **62**: 930–949.
- Leggett, W.C. 1977. The ecology of fish migrations. *Annu. Rev. Ecol. Syst.* **8**: 285–308.
- McCormick, S.D., Hansen, L.P., Quinn, T.P., and Saunders, R.L. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1): 77–92.
- Milligan, P.A., Rublee, W.O., Cornett, D.D., and Johnston, R.A.C. 1985. The distribution and abundance of chinook salmon (*Oncorhynchus tshawytscha*) in the upper Yukon River basin as determined by a radio-tagging and spaghetti tagging program: 1982–1983. *Can. Tech. Rep. Fish. Aquat. Sci.* **1352**: 1–161.
- Montgomery, J.C., and Walker, M.M. 2001. Orientation and navigation in elasmobranchs: which way forward? *Environ. Biol. Fishes.* **60**: 109–116.
- Myers, J.M., Kope, R.G., Bryant, G.J., Teel, D., Lierheimer, L.J., Wainwright, T.C., Grant, W.S., Waknitz, F.W., Neely, K., Lindley, S.T., and Waples, R.S. 1998. Status review of chinook salmon from Washington, Idaho, Oregon, and California. NOAA–Fisheries, Washington, D.C.
- National Marine Fisheries Service. 2000. Endangered Species Act — Section 7 consultation. Biological opinion. Reinitiation of consultation on operation of the Federal Columbia River Power System, including the juvenile fish transportation program, and 19 Bureau of Reclamation projects in the Columbia Basin. National Marine Fisheries Service, Northwest Region, Seattle, Wash.
- Nehlsen, W., Williams, J.E., and Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho and Washington. *Fisheries*, **16**: 4–21.
- Nevitt, G.A., Dittman, A.H., Quinn, T.P., and Moody, W.J. 1994. Evidence for a peripheral olfactory memory in imprinted salmon. *Proc. Natl. Acad. Sci. U.S.A.* **91**: 4288–4292.
- Odling-Smee, L., and Braithwaite, V.A. 2003. The role of learning in fish orientation. *Fish Fish.* **4**: 235–246.
- Prentice, E.F., Flagg, T.A., and McCutcheon, C.S. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *Am. Fish. Soc. Symp.* **7**: 317–322.
- Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Wash.
- Quinn, T.P., Brannon, E.L., and Dittman, A.H. 1989. Spatial aspects of imprinting and homing in coho salmon, *Oncorhynchus kisutch*. *Fish. Bull.* **87**: 769–774.
- Quinn, T.P., Hodgson, S., and Peven, C. 1997. Temperature, flow, and the migration of adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Can. J. Fish. Aquat. Sci.* **54**: 1349–1360.
- Quinn, T.P., Volk, E.C., and Hendry, A.P. 1999. Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). *Can. J. Zool.* **77**: 766–775.
- Reischel, T.S., and Bjornn, T.C. 2003. Influence of fishway placement on fallback of adult salmon at the Bonneville Dam on the Columbia River. *N. Am. J. Fish. Manag.* **23**: 1215–1224.
- Rutherford, J.C. 1994. River mixing. John Wiley and Sons, Chichester, England.
- Scheibe, T.D., and Richmond, M.C. 2002. Fish individual-based numerical simulator (FINS): a particle-based model of juvenile salmonid movement and dissolved gas exposure history in the Columbia River basin. *Ecol. Model.* **147**: 233–252.
- Scholz, A.T., Horrall, R.M., Cooper, J.C., and Hasler, A.D. 1976. Imprinting to chemical cues: the basis for home stream selection in salmon. *Science (Washington, D.C.)*, **192**: 1247–1249.
- Shoji, T., Yamamoto, Y., Nishikawa, D., Kurihara, D., and Ueda, H. 2003. Amino acids in stream water are essential for salmon homing migration. *Fish. Physiol. Biochem.* **28**: 249–251.
- Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. Freeman, San Francisco, Calif.
- US Army Corps of Engineers. 2002. Annual fish passage report. US Army Corps of Engineers, Portland, Oreg., and Walla Walla, Wash.
- Vickers, N.J. 2000. Mechanisms of animal navigation in odor plumes. *Biol. Bull.* **198**: 203–212.
- Vogel, S. 1996. Life in moving fluids: the physical biology of flow. 2nd ed. Princeton University Press, Princeton, N.J.
- Waples, R.S., Gustafson, R.G., Weitkamp, L.A., Myers, J.M., Johnson, O.W., Busby, P.J., Hard, J.J., Bryant, G.J., Waknitz, F.W., Neely, K., Teel, D., Grant, W.S., Winans, G.A., Phelps, S., Marshall, A., and Baker, B.M. 2001. Characterizing diversity in salmon from the Pacific Northwest. *J. Fish. Biol.* **59**: 1–41.
- Weissburg, M.J. 2000. The fluid dynamical context of chemosensory behavior. *Biol. Bull.* **198**: 188–202.
- Zimmer-Faust, R.K., Finelli, C.M., Pentcheff, N.D., and Wethey, D.S. 1995. Odor plumes and animal navigation in turbulent water flow: a field study. *Biol. Bull.* **188**: 111–116.