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[Article]

Fallback by Adult Sockeye Salmon at Columbia River Dams

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Abstract.—We implanted radio transmitters into sockeye salmon *Oncorhynchus nerka* in 1997 to determine the (1) fallback percentage and rate at eight Columbia River dams, (2) effect of fallback on adult counts at each dam, (3) relations between spillway discharge and fallback, (4) relations between injuries and fallback, and (5) relations of fallback and survival to spawning tributaries. The rate of fallback, that is, the total number of fallback events at a dam divided by the number of fish known to have passed the dam, ranged from 1.9% to 13.7% at the eight dams. The rate of fallback was highest at Bonneville Dam, the dam with the most complex fishway. Fallback produced overcounts of 2% to 7% at most dams. Fallback was weakly related to spill volume at Bonneville Dam. Significantly more sockeye salmon with head injuries fell back than fish without head injuries. About 40% of the sockeye salmon had injuries from marine mammals, but these injuries were not associated with the rate of fallback. The rate of survival was similar between fish that fell back (68.0%) and fish that did not fall back (67.5%). We suggest that fisheries managers adjust counts for fallback but note that these relationships were obtained under high-discharge conditions. We conclude that fallback biases dam counts and that the relationship between spawning success and fallback should be an area of future research.

The single greatest change to rivers worldwide has been the large-scale construction of dams (Postel and Richter 2003). Many species of migratory fishes currently move upstream over dams and through fish passage facilities (Clay 1995). To complete their life cycles, many of these species must move downstream over these same dams as juveniles (as in Pacific salmon species). Often adults must also pass downstream, such as in iteroparous anadromous species, including steelhead *Oncorhynchus mykiss*, and American shad, *Alosa sapidissima*. However, the semelparous Chinook salmon *O. tshawytscha* have also been observed moving downstream during adult spawning migrations, and such movement by adult salmonids in the Columbia River system has been termed fallback (Boggs et al. 2004a). Other than the data for Chinook salmon and steelhead reported by Boggs et al. (2004a), fallback and its consequences have not been quantified for species occupying impounded systems.

Sockeye salmon *O. nerka* in North America typically enter freshwater in early summer and generally spawn in late summer and early autumn (Burgner 1991). Rivers that sustain sockeye salmon populations in northern latitudes are largely unimpounded, whereas sockeye salmon in the most southern extent of their range encounter hydroelectric dams during their spawning migration. This is the case in the Columbia River where sockeye salmon must pass at least seven main-stem dams and associated river-run reservoirs en route to their natal spawning grounds. A major concern is that dams may hinder migration and subsequently reduce both escapement to spawning grounds and population viability (Quinn et al. 1997; Dauble and Mueller 2000). Dams may also slow hydrosystem migration times, which has been associated in the Columbia River with unsuccessful sockeye salmon migration to spawning tributaries (Naughton et al. 2005). Fallback is one potential negative outcome of dam construction. Fallback is characterized as an exit from a fishway at a dam followed by downstream passage through structures such as spillways, turbine intakes, navigation locks, debris sluiceways, or juvenile fish collection devices. Fallback behavior by Chinook salmon and steelhead has been documented at all Columbia and Snake River dams (Reischel and Bjornn 2003; Boggs et al. 2004a) and has caused extensive migration delays (Keefer et al. 2004a) and decreased escapements to spawning grounds (Boggs et al. 2004b; Keefer et al. 2005). Reischel and Bjornn (2003) also

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examined sockeye salmon behavior at Bonneville Dam on the Columbia River.

Two different mechanisms are thought to induce fallback, and two types of fallback are recognized: disorientation fallback and overshoot fallback. Disorientation fallback occurs within minutes or hours after exiting a fishway and before migrating out of the forebay and is presumably related to poor orientation in the forebay. Overshoot fallback occurs when a fish passes a dam located upstream of its natal tributary and must fallback at the dam to reach this tributary (Boggs et al. 2004). In constrast to disorientation fallback, overshoot fallback includes successful passage upstream of the forebay followed by continued upstream movement or residency for a period of more than 24 h, sometimes weeks. Levels of disorientation and overshoot fallback have been correlated with dam configuration, forebay configuration, flow pathways around the dam, and river flow and temperature (Reischel and Bjornn 2003; Boggs et al. 2004).

Fallback by adult Chinook and sockeye salmon at Bonneville Dam has been attributed to a complex fishway design (Reischel and Bjornn 2003). At Bonneville Dam there are two fishways: The Washington shore fishway exits on the river's north shore, and the Bradford Island fishway exits on Bradford Island. Fallback behavior at Bonneville Dam is observed most frequently at the Bradford Island fishway because fish exit the ladder and follow the shoreline across the forebay into the spillway (Reischel and Bjornn 2003).

Injury as a potential mechanism for fallback has received little attention. Head injury on Chinook salmon and steelhead has been observed in fishways of Columbia River dams since the 1970s (NMFS 1997). Possible causes of head injury include gas supersaturation and high flows in fishways (Elston 1996), as well as fallback (Wagner and Hilsen 1992). Injury can also result with encounters with marine mammals, which are increasing in numbers in the Pacific Northwest (Barlow et al. 1995; Fryer 1998).

Independent of underlying mechanisms, fallback has the potential to affect the management of adult salmon and steelhead stocks in the Columbia River basin by biasing ladder counts at each dam. Fish counts at dams are used to manage harvest levels and estimate interdam survival rates (Dauble and Mueller 2000). Fish that fall back and reascend a fishway may be counted more than once, leading to inflated counts and survival estimates (Boggs et al. 2004a).

We studied sockeye salmon in 1997 to determine the (1) fallback rate at eight Columbia River dams, (2) effect of fallback on adult counts at each dam, (3) relationship between spillway discharge and fallback, (4) influence of injuries on fallback, and (5) influence of fallback on survival to spawning tributaries.

Study Area

The Columbia River study area included four mainstem dams and reservoirs in the lower Columbia River (Bonneville, the Dalles, John Day, and McNary) and five mid-Columbia River dams and reservoirs (Priest Rapids, Wanapum, Rock Island, Rocky Reach, and Wells) and all major tributaries between Bonneville and Chief Joseph dams on the Columbia River (Figure 1). Two fishways at Bonneville through Wanapum dams provide access to upstream migrating anadromous fish species. Rock Island Dam has three fishways and Rocky Reach Dam has one. The University of Idaho Cooperative Fish and Wildlife Research Unit maintained radio receivers and antennas at dams and tributaries between Bonneville and Wanapum dams; concurrent telemetry projects by the Chelan and Douglas County Public Utility Districts (Alexander et

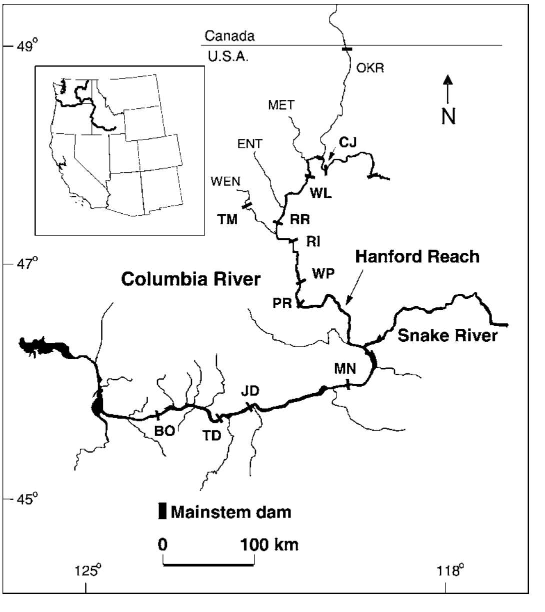

FIGURE 1.—Map of Columbia River study region, including locations of the dams and major tributaries where sockeye salmon fallback at dams was investigated in 1997. Receiver locations at mid-Columbia River and tributary sites were maintained by the public utility districts for Chelan and Douglas counties. Dam abbreviations are as follows: BO = Bonneville, TD = the Dalles, JD = John Day, MN = McNary, PR = Priest Rapids, WP = Wanapum, RI = Rock Island, RR = Rocky Reach, WL = Wells, TM = Tumwater, and CJ = Chief Joseph. Tributary abbreviations are as follows: WEN = Wenatchee River, ENT = Entiat River, MET = Methow River, and OKR = Okanagan River.

al. 1998) provided data from Rock Island, Rocky Reach, Wells, and Chief Joseph dams.

We also monitored main-stem and tributary sites with mobile radio-tracking units, and additional data were collected from hatcheries, fisheries, and spawning-ground surveys. All Columbia River stocks of sockeye salmon tagged at Bonneville Dam could therefore be tracked to spawning tributaries. Currently most sockeye salmon spawn in tributaries of Lakes Wenatchee (Wenatchee River basin) and Osoyoos (Okanogan River basin, Figure 1) in September and October (Mullan 1986; Quinn et al. 1997), located 842 river kilometers (rkm) and 946 rkm from the mouth of the Columbia River, respectively. Together, they compose less than 4% of the historical sockeye salmon nursery habitat in the upper Columbia River basin (Gustafson et al. 1997). The Chelan and Douglas County Public Utility Districts also monitored the Entiat and Methow rivers, which are potential sockeye spawning tributaries.

River conditions during the 1997 study were characterized by high flows. Mean daily Columbia River discharge in June and July was 10,724 m^3/s, nearly double the 10-year average (1987–1996) of 5,635 m^3/s (Columbia River DART 1993). Consequently, discharge over the spillway of dams (spill) was 4,591 m^3/s, often several times higher than the 10-year average of 1,657 m^3/s. Water temperatures in the lower Columbia River ranged from about 13°C in early June to 23°C in late August, levels that were nearly average. Mean summer water temperatures in the mid-Columbia River upstream from the Snake River confluence averaged 3–5°C cooler than in the lower Columbia River. The average Secchi disk visibility at Bonneville Dam during the study period was 2.7 m.

Methods

Radiotagging.—The methods used for trapping, tagging and telemetry monitoring have been described in detail by Reischel and Bjornn (2003), Keefer et al. (2004b), and Naughton et al. (2005). As they migrated upstream, adult sockeye salmon were trapped for intragastric radiotagging (Mellas and Haynes 1985) in the adult fish facility adjacent to the Washington-shore ladder at Bonneville Dam. The fish were radio-tagged with 3-V radio transmitters (Lotek Wireless, Inc., Newmarket, Ontario) that transmitted a unique digitally coded signal every 5 s. Radio tags were cylindrical and weighed 11 g in air (4.3 × 1.4 cm). Once a fish was anesthetized, we recorded its length and estimated its sex. After tagging, fish were moved to a 2,275-L oxygenated, insulated transport tank and held until released (usually 0.5–2 h) at locations 9.5 km downstream from Bonneville Dam on both sides of the river. Between 9 June and 5 August, we radio-tagged 577 sockeye salmon approximately in proportion to daily run counts. We selected fish haphazardly and tagged them in approximate proportion to the number passing the dam each day, but tagging was not truly random because only fish passing through one of the Washington shore ladders were sampled. Further, the proportion sampled each day varied slightly, and we did not sample at night because few sockeye salmon pass dams at night (Quinn and Adams 1996; Naughton et al. 2005).

Radiotracking.—Fixed radiotelemetry sites were the primary means of documenting the fallback of radio-tagged sockeye salmon in 1997. We used SRX receivers (Lotek Wireless, Inc.) with aerial Yagi antennas to monitor tailrace areas at dams and tributary mouths; we also used digital spectrum processors (DSP) with underwater coaxial cable antennas to monitor fishways and ladder exits at dams. On average, receivers operated more than 90% of the time at lower Columbia River dams and more than 80% of the time at Priest Rapids and Wanapum dams. Trucks and boats outfitted with aerial antennas were used to track fish in areas not covered by fixed-site receivers, including reservoirs, accessible tributaries, and the Hanford Reach below Priest Rapids dam. At the Wenatchee River, fixed-site receivers were deployed at the mouth and at Tumwater Dam (53 rkm upstream from the mouth). Mobile tracking upstream from Wells Dam was conducted approximately every 2 weeks from late July to early November, a period much shorter than the typical period between sockeye salmon arrival in the Okanogan River and the initiation of spawning (Hodgson and Quinn 2002).

We used a combination of telemetry records, spawning ground surveys, and radio-tag returns from fisheries to classify fish as successful migrants or as mortalities. Successful migrants included salmon with telemetry records in known spawning tributaries, those found as carcasses in spawning tributary surveys, or those that returned to their hatchery of origin. Mortalities included returns from fisheries and salmon with final telemetry records outside of spawning tributaries, usually between dams. Fish last recorded in tributaries downstream from known spawning habitat (all tributaries downstream from Rock Island Dam) were considered strays that did not survive to spawning areas.

Fallback at dams.—Fallbacks by radio-tagged fish were determined exclusively from telemetry records. We scored a fallback when a fish exited from the top of a fish ladder at a dam (or was conclusively detected at a telemetry site upstream from the dam) and was then recorded at a telemetry site downstream from that dam. Most fallbacks were easily identified because of the large number of monitoring sites. We also used a chi-square test to analyze differences in sockeye salmon fallbacks between the Washington shore and Bradford Island fishways.

Fallback percentage (i.e., the proportion of sockeye salmon that fell back at a dam) was calculated by dividing the number of unique radio-tagged fish that fell back at a dam by the number of unique fish known to have passed the dam. Fallback rate, which included multiple fallback events by individual fish at a dam, was the total number of fallback events at a dam divided by the number of fish known to have passed the dam. Reascension proportion was the proportion of individual fish that fell back at a dam, subsequently reascended the dam where the fallback occurred, and were last located upstream from that dam. We also calculated an overall fallback percentage by dividing the number of individual fish that fell back at least once at a dam by the total number of radio-tagged fish.

Fallback and adult counts.—We evaluated the effect of fallback on adult sockeye salmon counts in four steps. First we calculated adjustment factors to estimated errors in counts at each dam. We calculated adjustment factors (Boggs et al. 2004a) as the number of radio-tagged fish permanently passing the dam divided by the number of passage events by radio-tagged fish using the following formula:

$$AF = (LP_K + NLP_K - FB_{UF} + RA_{UF})/TLP_K;$$

LP_K = the number of unique fish with transmitters known to have passed the dam via the ladders (assumes that unrecorded fish passed dam via ladder)

NLP_K = the number of unique fish with transmitters known to have passed the dam via the navigation lock (only Bonneville and McNary locks monitored)

FB_{UF} = the number of unique fish that fell back at the dam one or more times

RA_{UF} = the number of unique fish that reascended the dam and stayed upstream from the dam regardless of the number of fallbacks

TLP_K = the total number of times fish with transmitters were known to have passed the dam via ladders (includes initial passage and all reascensions)

The second step was to obtain adult count data collected at each dam (hereafter, unadjusted adult count) except Wanapum Dam. Counts were a complete census of the run (Columbia River DART 1993). Third, we calculated an adjusted adult count by multiplying the unadjusted adult count made at a dam by the adjustment factor calculated for the dam. Fourth, we subtracted the adjusted adult count from the unadjusted adult count. The resulting number represented the overcount that we also expressed as a percentage of the adult count.

Sockeye salmon counts for Priest Rapids Dam were provided by Grant County Public Utility District (PUD). Counts for Rock Island and Rocky Reach Dams were provided by the Chelan County Public Utility District.

Relationship between fallback and spillway discharge.—We used logistic regression to test whether spill volume influenced sockeye salmon fallback at individual dams. The hourly percent of flow discharged over the spillway (spill percentage) at the time each fish exited the top of a ladder at each dam was obtained from Columbia River DART (1997) database. Fish that fell back more than 24 h after exiting a fishway were not used in the analysis because the fallback event was probably not related to environmental conditions. Spill percent at the time of exit was used as a predictor because the time of fallback could not be determined precisely and because hourly spill volume and mean daily spill volume were correlated at all dams (Pearson correlation $r > 0.8$) except Rocky Reach ($r = 0.6$). We focused on spill percentage because it is under operational control and because it should reflect the hydrologic conditions in the forebay that presumably provide orientation cues to migrating adults. However, river environmental variables were intercorrelated during the sockeye salmon run in 1997 (Naughton et al. 2005), and consequently, we caution that inferences about the causal effects of spill are tenuous because of the correlations among the suite of potential environmental predictors.

We used McFadden's ρ^2 to assess the logistic regression model as a whole. McFadden's ρ^2 is a transformation of the likelihood ratio statistic intended to mimic an R^2, and similarly, a higher ρ^2 corresponds to more significant results (Steinberg and Colla 1997). Although ρ^2 tends to be much lower than R^2, low values do not necessarily indicate a poor fit (Steinberg and Colla 1997). We assessed the classificatory accuracy of the model using a prediction success table and tested the goodness-of-fit of the logistic regression model to the data using a Hosmer–Lemeshow test (Steinberg and Colla 1997) in Systat v.10. Low P-values indicate a poor fit of the data to the model. We used a Bonferroni correction to control for comparisons at multiple dams (Sokal and Rohlf 1995), considering $P \leq 0.006$ as statistically significant (i.e., overall $P \leq 0.05$) or $P \leq 0.012$ marginally significant (overall $P \leq 0.10$).

Fallback and injury.—During tagging, we examined fish for head and body injuries. Head injuries included cuts and scrapes, hook marks, torn opercula and maxillaries, and gill damage attributed to marine mammals. We recorded bite and scrape wounds attributed to marine mammals as described by Fryer (1998) and used Pearson chi-square tests to examine whether fallback was associated with injuries. Separate tests were conducted for head injuries and for scrapes and bites. The percentage of injured fish for each category that fell back was calculated by dividing the total number of injured fish that fell back by the total number of injured fish. We also tested for potential seasonal effects of marine mammal attacks while controlling for the effects of migration timing via the binary logistic regression model: survived to tributary (yes/no) = marine mammal marks (yes/no) + tag date. The interaction between marine mammal mark and tag date was not significant ($P > 0.1$) and was dropped from the model.

Fallback and survival.—We determined whether a fish survived to reach a known spawning tributary based on telemetry records. Fish designated as survivors were last tracked into known spawning tributaries, were recovered as carcasses during redd surveys, or returned to their hatchery of origin. Fish designated as unsuccessful migrants included those recovered in a fishery or last tracked into areas where sockeye salmon do not spawn (e.g., between dams in the Columbia River). We also used chi-square tests to determine whether survival to a spawning tributary was associated with fallback history (fell back at one or more dams) and fallback frequency. The percentage surviving to a tributary entry was calculated by dividing the number of fish that fell back at an individual dam and survived to enter a tributary by the total number of fish that fell back at the dam.

Results

Tagging and Tracking

The 577 sockeye salmon tagged between 9 June and 5 August represented 1.2% of the 46,645 fish counted passing Bonneville Dam during the tagging period (Columbia River DART 1993). Five fish (0.9%) had adipose or ventral fin clips, and 99.1% were unclipped, presumably wild fish. Fork lengths of the tagged fish ranged from 38 to 63 cm (mean, 49.5 cm). We estimated that 72% of the 577 radio-tagged fish were males and 28% were females, a sex ratio typical in returning sockeye salmon (e.g., Gustafson et al. 1997). We did not tag fish suffering penetration of the coelomic cavity or with injuries that affected swimming performance (<1% of all fish trapped). No sockeye salmon mortalities occurred during tagging or transport and release. Three of the 577 fish regurgitated transmitters and were excluded from the analyses. The number of tagged fish tracked decreased after passage at Bonneville Dam: 492 were observed at the Dalles Dam, decreasing to 240 at Rocky Reach Dam (Table 1).

Fallback at the Dams

In 1997, 26.7% of radio-tagged sockeye salmon that passed a dam fell back at a dam one or more times during their upstream migration in the Columbia River. Fallback percentages ranged from 1.9% at Rock Island Dam to 11.4% at Bonneville Dam (Table 1). Most (82%) sockeye salmon fallbacks occurred within 24 h of fish passage ($N = 156$). Multiple fallbacks by individual fish occurred at Bonneville, the Dalles, John Day, and Rocky Reach dams, as indicated by higher fallback rates than fallback percentages. Fallback percentages were 2–6 times higher at Bonneville Dam than at other dams. Of 77 fallbacks at Bonneville Dam, 75 (97%) occurred after fish exited the Bradford Island fishway near the south shore compared with only 2 fallbacks by fish exiting the Washington Shore ladder. Fallback rates at Bonneville Dam were also higher for fish that passed the Bradford Island fishway (22.4%, 75 fallbacks for 335 unique fishway exits) compared with fish that passed the Washington-shore fishway (1.1%, 2/187; $\chi^2 = 48.1$, df = 3, $P < 0.001$).

The percentage of fallbacks that reascended lower Columbia River dams ranged from 77.8% at McNary Dam to 92.2% at Bonneville Dam. Reascension rates at mid-Columbia River dams ranged from 62.5% at Rock Island Dam to 94.1% at Wanapum Dam. Of the 26 fallbacks that did not reascend, 16 (61.5%) had unknown fates, 6 (23.1%) were considered strays, 1 (3.8%) was harvested in a tribal fishery, and 3 (11.5%) were apparent overshoots that fell back at Rocky Reach Dam and then entered the Wenatchee River.

Fallbacks and Adult Counts

Fallback resulted in overcounts of adult sockeye salmon ranging from about 800 fish (2%) at Rock Island Dam to nearly 2,300 fish (7%) at Rocky Reach Dam (Table 1). Mean adjustment factors for lower Columbia River dams ranged from 0.953 for the Dalles Dam to 1.044 for McNary Dam (Table 1). Adjustment factors indicate the amount bias in dam count estimates. Adjustment factors less than 1 indicate positive bias (undercounts), while those greater than 1 indicate negative bias (overcounts). Adjustment factors for mid-Columbia River dam passage counts were between 0.926 and 0.981. Overcount was the result of high rates of reascension by fish that fell back (Table 1) combined with the tendency for multiple fallbacks at Bonneville ($N = 10$), the Dalles ($N = 1$), and Rocky Reach ($N = 3$) dams.

Count adjustments were most precise for Bonneville

TABLE 1.—Percent of radio-tagged adult sockeye salmon that fell back and adjusted adult counts at Columbia River dams in 1997. Escapement estimates were unavailable for Wanapum Dam in 1997. Abbreviations are as follows: LP_K = the number of unique fish with transmitters known to have passed the dam via the ladders (this assumes that unrecorded fish passed the dam via the ladder); NLP_K = the number of tagged fish known to have passed via the navigation lock; FB_{UF} = the number of unique fish that fell back; R_{UF} = the number of fish that reascended, TLP_K = the total number of times that fish with transmitters were known to have passed the dam via ladders (includes initial passage and all reascensions); and FB_T = total fallback events. Fallback (%) is defined as $FB_{UF}/LP_K + NLP_K$, fallback rate as $FB_T/LP_K + NLP_K$. The adjustment factor, AF, is defined as $(LP_K + NLP_K - FB_{UF} + R_{UF})/TLP_K$.

Dam	LP_K	NLP_K	FB_{UF}	RU_F	TLP_K	FB_T	Fallback (%)	Fallback rate	Reascension (%)	Unadjusted fish counts	AF	Adjusted fish counts	Bias	% Bias
Bonneville	506	57	64	59	577	77	11.4	13.7	92.2	46,872	0.967	45,329	1,543	3.3
The Dalles	492		24	18	510	25	4.9	5.1	75.0	32,450	0.953	30,923	1,527	4.7
John Day	468		17	15	484	18	3.6	3.9	88.2	35,747	0.963	34,418	1,329	3.7
McNary	429	28	9	7	436	9	2.0	2.0	77.8	37,560	1.044	39,197	−1,637	−4.4
Priest Rapids	433		18	14	447	18	4.2	4.2	77.8	45,430	0.960	43,601	1,829	4.0
Wanapum	427		17	16	443	17	4.0	4.0	94.1		0.962		0	
Rock Island	417		8	5	422	8	1.9	1.9	62.5	41,296	0.981	40,513	783	1.9
Rocky Reach	240		17	14	256	17	7.1	7.9	82.4	30,777	0.926	28,493	2,284	7.4

and McNary dams because all passage routes, including the navigation lock, were monitored. About 10% ($N = 57$) of the sockeye that passed Bonneville Dam passed via the navigation lock, while 6% ($N = 28$) passed the McNary Dam lock, resulting in proportional decreases in count biases of 10% at Bonneville Dam and 6% at McNary Dam. Notably, low fallback and relatively high use of the navigation lock resulted in an overall undercount and an adjustment factor greater than 1 at McNary Dam. We found no statistical difference in fallback percentages between Okanogan (26.4%; $N = 208$) and Wenatchee river stocks (27.2%; $N = 176$; chi-square test, $P = 0.854$).

Relation between Fallback and Spillway Discharge

The relation between fallback at individual dams and mean daily spill percent during the run season was significant at Bonneville Dam and marginally significant at John Day Dam, when corrected for multiple comparisons (Table 2). The number of fallbacks at other dams was low (Table 2), resulting in low statistical power. The Hosmer–Lemeshow test suggested the model was a good descriptor of the data at Bonneville Dam ($P = 0.724$), though the relation was weak (McFadden's $\rho^2 = 0.025$). At Bonneville Dam, the fallback probability under extremely high relative spill conditions (percent spill = 75%, observed maximum = 77%) was 0.436 compared with 0.036 under no-spill conditions. Although, the relationships were weak, six of the eight logistic regression models had positive slope coefficients for spill percentage indicating the probability of a fish falling back increased with spill. The classificatory power of the model based on the prediction success table ranged from 79.8% at Bonneville Dam to 97.3% at McNary Dam. However, the models only produced gains of less than 5% over a purely random model because of the relatively low number of fallbacks.

Fallback and Injury

Of the 574 radio-tagged sockeye salmon, a total of 21 (3.6%) had head wounds. A significantly higher percentage of sockeye salmon with head wounds fell back at least once at a dam compared with those without head wounds ($P = 0.001$; Figure 2). Though 40% (229/574) of the radio-tagged sockeye salmon had fresh marine mammal scrapes and bites, rate of fallback was not significantly associated with injuries due to marine mammals (Pearson chi-square test, $P = 0.703$).

Fallback and Survival

Of the 574 sockeye salmon tagged at Bonneville Dam, a total of 388 (67.6%) survived to enter a known spawning tributary. The percentage of sockeye salmon that fell back at individual dams and survived to

TABLE 2.—Results of binary logistic regression tests of the relation between fallback (0 = no, 1 = yes) and mean hourly percent spill at Columbia River dams. The number of fish that fell back is in parentheses. Reported P-values are uncorrected. A Bonferroni correction was used to control for comparisons at multiple dams (Sokal and Rohlf 1995), considering $P < 0.006$ as statistically significant (overall $P \leq 0.05$) or $P < 0.012$ as marginally significant (overall $P \leq 0.10$).

Dam	N	Estimate	SE	t-ratio	P-value
Bonneville	498 (58)	3.316	1.603	3.006	0.003
The Dalles	410 (17)	2.307	3.945	0.585	0.559
John Day	336 (14)	6.734	2.765	2.518	0.012
McNary	142 (2)	24.145	11.407	2.117	0.034
Priest Rapids	163 (8)	−4.256	4.561	−0.933	0.351
Wanapum	380 (16)	−3.219	2.986	−1.078	0.281
Rock Island	366 (8)	4.311	6.243	0.691	0.490
Rocky Reach	205 (15)	4.231	1.887	2.242	0.025

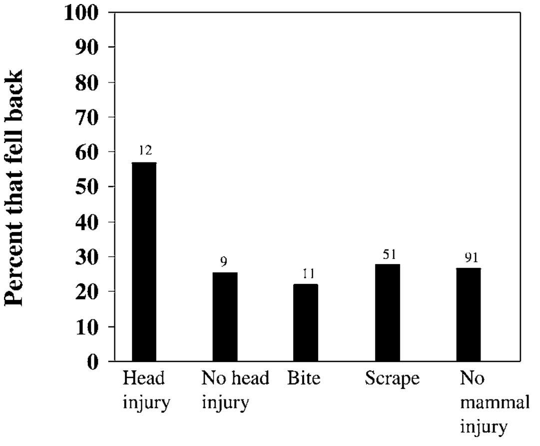

FIGURE 2.—Percentages (actual numbers above bars) of sockeye salmon that fell back at Columbia River dams in 1997, by injury category.

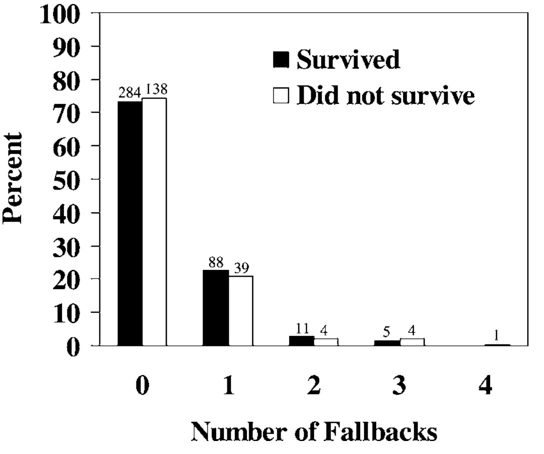

FIGURE 4.—Association between the frequency of fallbacks (0–4) of Columbia River sockeye salmon and subsequent percentages (actual numbers above bars) that survived or did not survive to enter their spawning tributaries in 1997.

spawning tributaries ranged from 37.5% at Rock Island Dam to 94.1% at Wanapum Dam (Figure 3). Survivors were located primarily in the Wenatchee and Okanagon rivers (see Naughton et al. 2005). Only three overshoot fallbacks were recorded for sockeye salmon, all by Wenatchee River fish at Rocky Reach Dam. Rate of survival of sockeye salmon was not dependent on fallback ($P = 0.926$). Similarly, rate of survival was not significantly dependent on fallback frequency ($P = 0.543$; Figure 4).

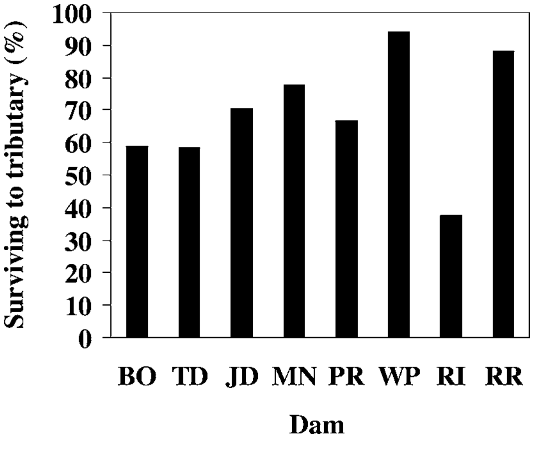

FIGURE 3.—Percentages of sockeye salmon that survived to enter a spawning tributary after falling back at individual dams in 1997. Dam abbreviations are as follows: BO = Bonneville, TD = the Dalles, JD = John Day, MN = McNary, PR = Priest Rapids, WP = Wanapum, RI = Rock Island, and RR = Rocky Reach.

Discussion

More than a quarter of migrating adult sockeye salmon fell back at a Columbia River dam during 1997. Hence, understanding the relations between fallbacks and overall migration behavior, river conditions, dam operations, fish condition, and estimates of run size are important to both a basic understanding of adult migration and effective management of sockeye salmon stocks. Two primary conclusions can be drawn from our study: (1) fallback at dams produced positive biases in fishway counts leading to overestimates in run size; and (2) fallback by adult sockeye salmon did not appear to influence survival to tributaries.

Sockeye salmon fell back at each of the eight dams studied, the highest rate of fallback occurring at Bonneville Dam. Sockeye salmon fallback percentages observed at individual dams (range 2–11%) were generally lower than reported for Chinook salmon and steelhead in the lower Columbia and lower Snake Rivers (Boggs et al. 2004). Fallback percentages at individual lower Columbia River dams ranged from 8% to 15% for spring–summer Chinook salmon and 7% to 11% for steelhead in 1997 (Boggs et al. 2004). Percentages may have been lower for sockeye salmon because they did not exhibit overshoot behavior in the lower river, which lacks any natal tributaries for sockeye salmon. In contrast, Boggs et al. (2004a) found that up to 45% of fall Chinook salmon, 30% of spring–summer Chinook salmon, and 26% of the steelhead that fell back at lower Columbia River dams entered tributaries downstream from these projects. Several factors may have contributed to the lower rates observed in sockeye salmon. The low proportion of overshoot among sockeye salmon fallbacks may be largely related to the restricted distribution of sockeye salmon spawning habitat in the upper reaches of the Columbia River hydrosystem. Nearly all remaining Columbia River sockeye salmon spawn in tributaries of lakes Wenatchee and Osoyoos, which are upstream from Rock Island Dam (Mullan 1986; Fryer 1995). By definition, an overshoot fallback must pass its spawning habitat before returning to a downstream tributary. Therefore, sockeye salmon also had little opportunity to overshoot compared with Chinook salmon and steelhead returning to natal tributaries in the lower and mid-Columbia because there are few dams upstream from the spawning tributaries used by sockeye salmon (Figure 1). Alternatively, if straying rates are higher for Chinook salmon and steelhead than for sockeye salmon, regardless of spatial effects, and if homing has a genetic component, then the difference in straying may be related to the generally higher genetic mixing of Chinook and steelhead stocks during hatchery propagation (McIsaac and Quinn 1988; Pascual et al. 1995). Species-specific differences in imprinting or juvenile experience could also produce differences in homing precision. In particular, large numbers of juvenile salmon and steelhead have been collected annually from the Snake and Columbia rivers during smolt emigration and transported rapidly downstream in barges (e.g., Williams et al. 2001); high adult fallback and stray rates have been reported for transported fish (Bugert et al. 1997; Chapman et al. 1997). Such genetic and imprinting history effects may be complementary rather than mutually exclusive, and consequently would be difficult to distinguish.

The high percentage of fallback by sockeye salmon at the Bonneville Dam Bradford Island exit suggests that conditions encountered around fishway exits or in dam forebays have a greater influence on sockeye salmon fallback than do innate homing behaviors. Detailed telemetry observations of Chinook and sockeye salmon movement following Bradford Island ladder exit, including 110 of the sockeye salmon in this data set, suggest fallback most often occurs because fish follow the island shoreline back downstream into the forebay of the spillway, rather than crossing open water to reach the southern shoreline (Reischel and Bjornn 2003). In contrast, fish ascending the Washington shore ladder are oriented upstream along the shoreline directly after exiting the ladder. The tendency among adult salmon—particularly sockeye salmon—to migrate upstream near shorelines (Burgner 1991) is consistent with the hypothesis that fish orienting downstream along the Bradford Island shoreline toward the spillway were entrained and carried over the spillway with greater frequency during high spill conditions. This pattern was not observed at other dams, suggesting that the configuration of the ladder exits and shorelines at upstream dams result in relatively consistent flow conditions and orientation cues for salmon in the forebays, regardless of spill level.

Fallback caused counts of sockeye salmon to be overestimated by 2% to 7%. Fallback may also affect salmon populations indirectly by upwardly biasing run-size estimates, leading to fisheries quotas that are higher than intended for the true population size. Dauble and Mueller (2000) raised concerns that the use of count data for survival and harvest management could harm listed (U.S. Endangered Species Act) stocks of Chinook salmon and steelhead. In general, count biases we estimated for sockeye salmon in 1997 were lower than for other Columbia and Snake river stocks, reflecting the relatively lower sockeye salmon fallback rates. Estimated correction factors for Chinook salmon and steelhead at lower Columbia and Snake river dams in 1997 produced positive biases ranging from 10% to 19% for spring–summer Chinook and 6% to 14% for steelhead (Boggs et al. 2004a). In this study, count biases for sockeye salmon ranged from −4% to +7%.

Count adjustments were based on the assumption that radio-tagged sockeye salmon were good surrogates for the entire run and were calculated by pooling data for the entire passage period at each dam. Pooling data could bias adjustments by masking temporal variability in both fallback and reascension rates and would be least appropriate for comparisons of temporally separated subbasin stocks within a run because each stock could be exposed to divergent river environments and have differing fallback responses. We believe pooling data for the entire sockeye run was appropriate because we found no temporal segregation of sockeye salmon stocks destined for the Okanogan and Wenatchee river drainages in 1997 (Naughton et al. 2005), and the probability of fallback was relatively constant throughout the migration season. Moreover, there was no statistical difference in fallback percentages between Okanogan and Wenatchee river stocks. Of greater concern, however, is the limitation of estimating a general adjustment factor from a single year, particularly one with unusually high discharge conditions. Because our estimate was derived during a high-flow year, the count adjustment factors presented here may be higher than average if interannual variation in sockeye salmon fallback is positively related to river discharge and spill, as with Chinook salmon and steelhead (Boggs et al. 2004a). Conversely, the adjustment factors we present may be lower than average if fallback increases when water temperatures are high because the Columbia River was cooler than average during the sockeye salmon migration in 1997. In either case, managers should consider applying adjustment factors for escapement and harvest-based decisions because unadjusted dam counts can clearly overestimate run size. Fish managers also need to account for passage in the navigation lock, especially for a strongly shoreline-oriented species such as sockeye salmon. In our study, sockeye salmon that passed Bonneville and McNary dams via the navigation lock comprised 10% and 6%, respectively, of the total number of fish passing these dams. In contrast, Boggs et al. (2004) found that few (<2%) spring–summer Chinook, fall Chinook, and steelhead passed those dams via the locks. Moreover, if adjustment factors are based only on fallback (as with passive integrated transponder tag records from fishways), then the adjustment factor will underestimate the true run size.

Seasonal effects within the run may also play a role in determining the probability of fallback. Peak counts of sockeye salmon at Bonneville Dam in 1997 occurred in mid to late June, concomitant with peaks in river flow and spill. As the sockeye migration progressed upriver, the chance of falling back may have decreased as river flow and spill decreased and because the dams become smaller and less complex. Alternatively, the small number of fallback events at those dams may have prevented detection of significant relations. However, the relation between spill and fallback should be interpreted with caution because spill and other environmental variables (e.g., flow, temperature, and dissolved gas percent) were highly intercorrelated with each other and with date of tagging (e.g., Naughton et al. 2005), making causal inferences problematic. Moreover, the average relationship between spill and fallback may have been obscured because flow and spill during 1997 were nearly double the 10-year average (1987–1996).

Fallback by sockeye salmon was associated with head wounds, whereas fallback was not associated with injury due to marine mammals, even though 40% of the fish we radio-tagged had been injured by marine mammals. Head injuries may have a greater effect on orientation ability than body injuries and, thus, contribute to higher incidence of fallback. It is also possible that injuries from falling back over a dam affected homing ability or disoriented the fish. That 4 of the 10 radio-tagged strays had fallen back over one or more dams before entering a lower Columbia River tributary was suggestive of a relationship between fallback and straying, though this sample is clearly too small to reach a strong conclusion. However, the incidence of head and mammal injuries did not appear to impair survival to spawning tributaries. In fact, fish with marine mammal injuries survived in higher percentages than fish without these injuries, and this effect appeared to be independent of the timing effects on survival because the interaction between marine mammal marks and tag date on migration success was not significant. Whether these injuries contributed to prespawning mortality in sockeye salmon remains unknown and should be considered in future studies.

Rate of survival was similar between sockeye salmon that fell back and sockeye salmon that did not. Perhaps the most important question is whether fallback affects migration and reproductive success, particularly given that Keefer et al. (2005) reported that Chinook salmon and steelhead that fell back over one or more dams were significantly less likely to survive through the hydrosystem than fish that did not fall back. Single or multiple fallback events did not appear to affect survival of sockeye salmon to spawning tributaries in 1997. However, we note that our definition of survival does not account for any prespawn mortality in spawning tributaries. This definition could not identify any delayed effects of fallback that were manifested after individuals reached spawning tributaries and were therefore classified as successful. Timing of arrival at Bonneville Dam, rather than fallback, appeared to have the greatest effect on sockeye survival to known spawning tributaries (Naughton et al. 2005), because the probability of successful migration declined precipitously late in the migration season, coincident with decreasing discharge and the onset of potentially stressful water temperatures (about 20°C; McCullough et al. 2001). In fact, the probability of fallback decreased significantly later in the season (logisitic regression, $P = 0.046$) as mortality increased. We could not evaluate whether fallback costs increased seasonally because only a single late-run fish successfully reached spawning tributaries (Naughton et al. 2005). Nonetheless, we hypothesize that injuries sustained during fallback late in the season under warmer water conditions may be more costly. Consistent with this hypothesis, fallback had less impact on migration success in spring–summer Chinook salmon migrating during cool river conditions compared with fall Chinook salmon and steelhead migrating during warmer water conditions (Keefer et al. 2005).

Adult salmonids can encounter areas of difficult passage during upstream passage in unimpounded rivers as well as at hydroelectric projects. Obstacles such as falls, rapids, and channel constrictions may not effectively differ from dams. For example, migration speeds for Fraser River sockeye salmon are lowest through constricted and high-velocity areas (Gilhousen

1990; Hinch et al. 1996; Rand and Hinch 1998). Whether adult salmonids fallback through such natural constrictions during homing remains unknown. The energetic costs of fallback may actually be greater for natural constrictions requiring burst swimming (i.e., near the maximum capacity of salmon) than for dams with fish ladders. Conversely, the probability of suffering injury or death during fallback at dams is probably higher than for natural constrictions because most adults fallback over spillways with vertical drops of tens of meters. Given that some degree of fallback is probably a natural component of homing in salmon and is required for the completion of adult spawning migration in iteroparous migrants, comparative studies to understand the costs of downstream movement in unimpounded systems are warranted.

We suggest that the findings in this paper have important implications for management and research. Low precision in fish counts has raised concerns that the use of count data for escapement estimates or harvest management could harm stocks listed for protection under the U.S. Endangered Species Act (Dauble and Mueller 2000). Fallback during upstream migration of Pacific salmon may reduce spawning success or lead to increased prespawning mortality due to increased energy expenditure (Geist et al. 2000). Fallback is likely to be a general feature of fish populations in regulated rivers, particularly in species that home to natal sites (as in salmonids), iteroparous anadromous species that require a safe migration corridor to successfully spawn in subsequent years, or as a result of seasonal movements in potadromous species. Consequently, fallback deserves consideration in the monitoring of fish populations, and the design and operation of dams and other flow regulation structures should strive to provide opportunities for benign downstream passage.

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